

DISTURBANCE AND SUCCESSION ON THE KRAKATAU ISLANDS, INDONESIA

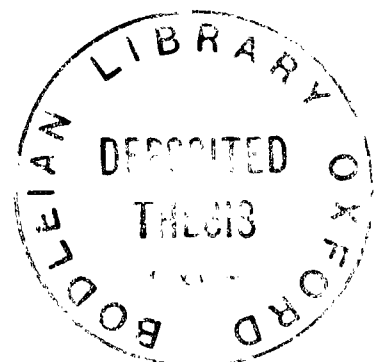
by

SUSANNE F. SCHMITT

**GREEN COLLEGE
AND
SCHOOL OF GEOGRAPHY

UNIVERSITY OF OXFORD**

***THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY AT THE
UNIVERSITY OF OXFORD
TRINITY TERM 1997***



On August 26, 1883 a tiny, unpossessing volcano - that is as volcanoes go - rumbled coughed and smoked somewhat more than had been its habit for the past several month.....

(Krakatoa East of Java, Cinerama Inc.
Presentation cinema brochure, 1968)



TO MY FAMILY AND FRIENDS

DISTURBANCE AND SUCCESSION ON THE KRAKATAU ISLANDS, INDONESIA

Thesis submitted to the University of Oxford for the degree of Doctor of Philosophy,
Trinity Term 1997

Susanne Schmitt, Green College

ABSTRACT

This thesis set out to investigate the influence of disturbance on the succession of the Krakatau islands (Rakata, Sertung, Panjang). The hierarchical model of succession by S. Pickett and colleagues (1987) was adopted as a research framework, and provided the basis for an alternative model of succession on Krakatau that focuses on processes rather than successional pathways.

Investigations were conducted on (i) the meso-scale, and (ii) the patch-scale. (i) quantified the recent disturbance regime, and inter- and intra-island differences in diversity. (ii) compared sapling performance (growth, mortality and recruitment), and species compositional patterning in space and time for saplings and the seed bank with respect to island, gap size and severity of disturbance. Multivariate techniques were used, and amongst other attempts at characterising the light environment, hemispherical photography was employed.

For the first time the effect of a continuous period of volcanic activity (1992-1995) of Anak Krakatau could be directly quantified and compared between Panjang and Sertung (ash-affected) and Rakata (receiving no ash). Increased rates of gap formation in the volcanically active period in comparison to the previous decade were found for *all* islands. This supports the disturbance-driven model of Whittaker and colleagues. However, an extension is required, because, contrary to expectation, Rakata also experienced more disturbance. This increase is argued to be a result of more severe weather conditions, and an increased number of earth tremors, during times of volcanic activity.

The disturbance factors of extreme climatic events (e.g. ENSO events) and human impact are also proposed for inclusion in the alternative model. Drought associated with the 1994 El Niño is of relevance to short-term and potential long-term impact on regeneration dynamics and succession. Attention was drawn to the local human influence of pumice mining on the coastal forests.

Supporting previous findings on the plot- and whole island scales, data from species presence/absence transects established that species richness and beta-diversity on the ash-affected islands was also lower on the meso-scale. Panjang's canopy composition is less uniform, and locally more species-rich than Sertung's.

More evidence of the suggested decline of the mono-dominant species *Neonauclea calycina* and *Timonius compressicaulis* was gathered. The third dominant, *Dysoxylum gaudichaudianum*, is expanding in the lowlands of *all* islands. This is aided by its ability to regenerate in moderate shade, to grow rapidly in gap environments, and its tolerance of ash-fall, drought and herbivory. However, on Rakata, it is not expected to become generally mono-dominant because a considerable number of other potential canopy species are present.

Sapling performance and species composition and its changes were in general strongly affected by ash-fall and drought. These factors tended to override effects of gap size and severity of disturbance. Advance regeneration, and the composition of the local forest type were identified as important factors influencing the composition of the early stages of gap-fill. The local forest type also seemed to contribute most to seed bank composition. As rarer species tended to have clumped distributions, and 'safe sites' for regeneration seemed not to be limiting, dispersal constraints were argued to be the most likely factors slowing diversification, unless further severe volcanic disturbance leads to successional set-back. The latter also strongly limits the predictability of succession on Krakatau.

ACKNOWLEDGEMENTS

Most of all I would like to thank my supervisors Dr Rob Whittaker (School of Geography, University of Oxford) and Dr Bryan Turner (King's College, University of London) for 'giving me the job' and subsequently for advice and guidance throughout the thesis. Particularly Rob Whittaker deserves my special thanks for his patience, and all his hard work in reading numerous drafts with great speed and thoroughness.

I would also like to express my gratitude to the Indonesian Institute of Science (LIPI), Jakarta, for granting me permission to conduct research in Indonesia, and to Puslitbang Biologi and the Herbarium Bogoriense (LIPI), Bogor, to be my sponsors. In particular I would like to thank Dr Soetikno Wirioadmojo, Head of Puslitbang Biologi; Dr Johannes Mogeia, Head of the Herbarium Bogoriense; and Dr Deddi Darnedi, who was then Head of International and Technical Co-operation, LIPI, Bogor; Ms Dewi Soenarijadi, Head of Division of Inter-Institutional Co-operation, LIPI, Jakarta; and Bapak Sanchoyo, LIPI, Jakarta for their time and help in obtaining research permission and visas. I would also like to thank the Directorate of Forestry and Nature Conservation (PHPA) for allowing me to work on the islands. Birdlife International Indonesia Programme provided access to communication and office facilities.

Dr Tukirin Partomihardjo of the Herbarium Bogoriense, who was my official counterpart, deserves my most special thanks. He generously shared his knowledge on the Krakatau islands and its flora, and provided tireless help with fieldwork and general logistics. His beaming smile saved the moment on many occasions. Terima kasih banjak!

There would also be no thesis if it had not been for the many volunteers that helped me collect data during three expeditions to the islands. Fieldwork time was short and precious and pushed me to develop slave-driving tendencies. Many thanks go to Cecilia Luttrell, Claudia Eckardt, Nadja Barsum, Louise Olly, Jamie Probart, Richard Field, David Beale, Edward Pollard, Heidi Abbott, Mercedes Uden, Nike Doggart, Charlotte Woolnough, Sarah Richardson, Lajla White, Boo Conder, Daniella Radice, Nicola Collis, and Cathy Ryan for bearing with me and doing a great job. Raimond Hafkenscheid was of great help during the reconnaissance phase in 1993.

There are also many people I would like to thank here in Oxford. Doug Sheil, Steve Jennings David Burslem (now Department of Plant and Soil Sciences, University of Aberdeen), and Gil Viera (now at INPA, Manaus, Brazil) deserve a special mention for reading drafts of my chapters and providing very helpful advice, encouragement, and friendship. Dr Nick Brown also provided advice, and helped with scanning of hemispherical images. Dr Mario Cortina Borja for life-saving help with statistics and analysis; Dr Steve Stokes for statistics advice, 'excelling' at Excel, and introducing me to the photocopy experience of the decade; Dr Steve Jones for help during the 1993 expedition and comments on chapters.

This research was financed through a NERC studentship (GT4/92/30/L) with extra financial support from two travel grants awarded by the Royal Society South-east Asia Rain Forest Project, and some additional funds from the Krakatau Research Project for the purchase of equipment.

The fact that I had such an enjoyable time at the SoG is due to the friendly and helpful atmosphere provided by all members of staff and post-graduates. Pat Woodward gave support with expedition finance and logistics; Martin Barfoot helped with photographic needs; Marie MacAllister for help, humour and being the 'post-graduate mother'; John Morgan and David Banfield for help with equipment; Mr Pete Hayward and Ms Ailsa Allen for cartographic and Mr Andrew Burke for computer assistance, Sue Bird and Linda Atkinson for making literature search an enjoyable experience; John Marter, Eric Anderson, and Steve Kidsley for being SoG's ever-helpful porters.

A very special mention has to be given to Frank Eckardt, and Paula Goncalves for being good friends and fellow SoG post-graduates, who have provided much moral support, patience, good laughs and fabulous dinner and video sessions. Many thanks also go to Kristina Plenderleith for friendship and moral support.

I also thank Ms Louise Shilton, University of Leeds; Sampurno Bruijnzeel, Free University, Amsterdam; Mr Mark Coode and Dr John Dransfield, from the Herbarium at Kew, Dr Jeremy Holloway; Natural History Museum, London; Professor David Newbery, University of Bern; Prof. Martin Kellman, University of York, Canada; Mr Mal Clarbrough, Dr Stephen Self, Dr Alan Robock, and Dr Colin Risdale;

In Indonesia I also had the pleasure to meet many very friendly and helpful people. I would in particular like to mention my friend Ita and all at the Wisma Ramayana, Laurie Pierce and Jim Jarvie, Like and Bas van Balen, Dono for help with expedition equipment; Adhi and Anto for fantastic expedition food (especially the doughnuts!), and Captain Jakob and his crew of the Harapan for safe boat-journeys, and many more.

Many thanks and love also to my parents, and my sisters for continued support and being there.

Last but not least, my very special thanks go to Paul, not only for his advice and help with logistics during my time in Indonesia, but most of all for his love, moral support and patience, and all the great adventures.

TABLE OF CONTENTS

FRONTISPIECE

ABSTRACT

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GLOSSARY

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW 1

1.1 INTRODUCTION 1

1.2 DISTURBANCE AND GAP ECOLOGY: A REVIEW WITH SPECIAL REFERENCE TO THE KRAKATAU ISLANDS 3

The niche diversification hypothesis 5

The disturbance hypothesis 9

The relevance of the Niche Diversification Hypothesis and the Disturbance Hypothesis to Krakatau 13

1.3 HISTORY OF VEGETATION SUCCESSION AND DESCRIPTION OF PRESENT VEGETATION..... 16

Rakata (1883-1995) 17

Sertung and Panjang (1883-1930) 27

Anak Krakatau (1930-1995) 32

The general colonisation pattern of the Krakatau islands 35

The effect of volcanic disturbance on Sertung and Panjang 36

Forest divergence 39

1.4 THE MAIN SUCCESSION THEORIES AND MODELS AND THEIR RELEVANCE TO THE DEVELOPMENT OF THE KRAKATAU FORESTS 47

1.5 DEVELOPMENT OF THESIS FOCUS..... 54

1.6 AIM AND CENTRAL RESEARCH OBJECTIVES 56

CHAPTER 2: DESCRIPTION OF THE STUDY SITE..... 58

SUMMARY:..... 58

2.1 INTRODUCTION AND GEOGRAPHICAL CONTEXT..... 59

2.2 VOLCANIC HISTORY AND GEOLOGY..... 60

Pre-1883 volcanic activity and island configuration 60

The 1883 eruption..... 60

Anak Krakatau and the post-1883 volcanic activity: 63

2.3 SOILS	67
Soil formation and characteristics	67
Soil mineral content	68
Soil texture and water retention	69
2.4 CLIMATE	70
General climatic conditions	70
Influence of extreme events: the ENSO scenario	74
Lightning and thunderstorms	75
Hydrology and rainfall	76
2.5 GEOMORPHOLOGY AND TOPOGRAPHY	81
Landslides	84
Coastal erosion	85
2.6 HISTORY OF ADMINISTRATION AND EXTENT OF HUMAN IMPACT	87
2.7 CONCLUSIONS:	93

CHAPTER 3: DISTURBANCE AND GAP FORMATION: A MESO-SCALE INVESTIGATION 94

SUMMARY	94
3.1 INTRODUCTION	95
3.2 OBJECTIVES	96
3.3 METHODS	97
Transect disturbance survey	97
Tree mortality	100
Pumice mining	100
3.4 RESULTS	100
Transect disturbance surveys	101
Tree mortality	108
Pumice mining	109
3.5 DISCUSSION	110
3.6 CONCLUSION	114

CHAPTER 4: SAPLING PERFORMANCE 116

SUMMARY	116
4.1 INTRODUCTION	118
4.2 OBJECTIVES	121
4.3 METHODS	122
Small saplings in 4 x 4 m plots	125

Tall saplings.....	126
Light quantification.....	127
Data analysis.....	130
4.4 RESULTS	132
<i>Sapling performance</i>	134
Small sapling height growth in gap plots.....	134
Small sapling height growth in understorey plots	137
Density and small sapling growth in gap plots.....	138
Percentage canopy openness and small sapling height growth in gap plots	138
Mortality and recruitment in gap plots.....	139
Mortality and recruitment in understorey plots	143
Density and small sapling mortality and recruitment dynamics in gap plots	143
Percentage canopy openness and small sapling mortality and recruitment in gap plots.....	144
Tall sapling growth performance in gaps	145
Single species performance: the case of the dominant <i>Dysoxylum gaudichaudianum</i>	150
Mortality and recruitment of tall saplings.....	152
<i>Species compositional changes of the regeneration layer</i>	154
Dynamics and habitat preferences of the small sapling species	154
Species compositional changes in the tall sapling layer	158
4.5 DISCUSSION.....	162
4.6 CONCLUSION.....	165

CHAPTER 5: DIFFERENCES IN INTER- AND INTRA-ISLAND DIVERSITY AND COMPOSITIONAL PATCHINESS

COMPOSITIONAL PATCHINESS	166
SUMMARY	166
5.1 INTRODUCTION	168
5.2 OBJECTIVES.....	171
5.3 METHODS	171
<i>The meso-scale</i>	171
<i>The patch-scale</i>	173
Spatial analyses.....	173
Temporal analyses.....	174
Patch-scale diversity trends	175
5.4 RESULTS	176
<i>The meso-scale</i>	176
<i>The patch-scale</i>	186
Species composition in space	186
Short-term species compositional trends.....	187

Patch-scale diversity trends	193
5.5 DISCUSSION.....	197
<i>The meso-scale</i>	197
<i>The patch scale</i>	201
Spatial analysis of sapling composition.....	201
Short-term species compositional trends.....	202
Patch-scale diversity trends	204
5.6 CONCLUSION.....	206
 CHAPTER 6: SEED BANK CHARACTERISTICS ON THE KRAKATAU ISLANDS	208
SUMMARY.....	208
6.1 INTRODUCTION	210
6.2 OBJECTIVES.....	211
6.3 METHODS	212
6.4 RESULTS	215
Seed bank densities.....	215
Seed bank species composition	218
Seed bank similarity.....	220
6.5 DISCUSSION.....	223
Seed density estimates	223
Seed bank species composition	227
Seed bank composition and succession on Krakatau	232
The case of <i>Macaranga tanarius</i>	233
The current canopy dominants <i>Neonauclea calycina</i> , <i>Timonius compressicaulis</i> , and <i>Dysoxylum</i> <i>gaudichaudianum</i>	235
Some observations on seed-size and seed bank representation.....	239
6.6 CONCLUSIONS.....	240
 CHAPTER 7: CONCLUSIONS, RELEVANCE TO OTHER STUDIES, AND SUGGESTIONS FOR FURTHER RESEARCH	243
7.1 MAIN FINDINGS AND RELEVANCE TO OTHER STUDIES	243
Disturbance, dominance and diversity	243
Regeneration dynamics and pathways	248
The wider picture	252
7.2 RECOMMENDATION FOR FURTHER RESEARCH.....	255
<i>Concluding remarks</i>	260

BIBLIOGRAPHY	262
APPENDIX 1: THE OZALID LIGHT METERING TECHNIQUE AND ITS LIMITATIONS	284
APPENDIX 2: FORMULAE, DATA TABLES AND GRAPHS FOR CHAPTER 4	295
APPENDIX 3: ARTIFICIAL DEFOLIATION EXPERIMENT ON <i>DYSOXYLUM</i> <i>GAUDICHAUDIANUM</i>	307
APPENDIX 4: ADDITIONAL TABLES AND FIGURES FOR CHAPTER 5.....	314
APPENDIX 5: CURRENT BIOLOGICAL STUDIES ON THE KRAKATAU ISLANDS.....	319

LIST OF FIGURES

Fig. 1.1: Map of the Krakatau islands and the Sunda Straits region	2
Fig. 1.2: Gap size and severity and the relative contribution of different pathways of regeneration.	11
Fig. 1.3: Immigration/extinction curves for spermatophyte species on Rakata between 1883-1989.	15
Fig. 1.4: Dispersal-structured model of island colonisation.....	15
Fig. 1.5: The North-western side of Rakata near Zwarte Hoek in June 1886.....	18
Fig. 1.6: South-east side of Rakata in 1919 showing the savanna-like vegetation	23
Fig. 1.7: <i>Neonauclea calycina</i> dominated forest in lowland Rakata today.....	26
Fig. 1.8: Map showing the different lava flows and the vegetation types of Anak Krakatau...	33
Fig. 1.9: Map of approximate areas of damage on Sertung in 1930 and 1953.....	37
Fig. 1.10: Damage from the 1930s eruption to the North-eastern areas of Sertung.	37
Fig. 1.11: <i>Timonius compressicaulis</i> forest on Panjang	40
Fig. 1.12: <i>Dysoxylum gaudichaudianum</i> with a peduncle of nearly ripe fruits.....	41
Fig. 1.13: Principal successional pathways on (A) Rakata and (B) Sertung and Panjang. ...	42
Fig. 1.14: Vegetation maps of (a) Sertung and (b) Panjang.	46
Fig. 1.15: A hierarchical representation of successional processes on Krakatau.	52
Fig. 1.16: A revised hierarchical representation of successional processes on Krakatau	53
Fig. 2.1: The assumed geological history of the Krakatau archipelago	62
Fig. 2.2: Map showing the change in size and shape of Rakata over the last century.....	63
Fig. 2.3: Climate diagram of Panjang from observations by Stehn in 1929.....	73
Fig. 2.4: Map of mean annual rainfall map for the Sunda Strait from 1941-1975 data.....	73
Fig. 2.5: The formation of Anak Krakatau in 1930 showing electrical discharges.....	77
Fig. 2.6: Example of a soil pipe found on Panjang in 1995.	79
Fig. 2.7: Rakata island with the characteristic cloud cap.	80
Fig. 2.8: West side of Rakata with pumice cliffs and hanging gullies.	82
Fig. 2.9: Example of down-cutting of a gully bottom near the South-coast of Rakata.....	83
Fig. 2.10: Treelet partly buried by c.1.3 m thick depositional material.....	84
Fig. 2.11: Change in shape, size, and position of the Sertung spit	86
Fig. 2.12: Pumice digging damage in near-coastal gullies of North-east Panjang.	91

Fig. 3.1: Map showing all transects and the locations of the permanent plots.....	99
Fig. 3.2: Histogram of class 1 (< 2 year) disturbances on Rakata, Panjang and Sertung....	102
Fig. 3.3: Age-class distribution of disturbances for gully transects.....	102
Fig. 3.4: Examples of disturbance encountered during transect surveys	106
Fig. 3.5: Effect of a lightning strike on higher altitude permanent plot R2 on Rakata	107
Fig. 4.1: Map of the islands with all studied gap sites marked.....	122
Fig. 4.2: Sketch map of a typical gap site.	125
Fig. 4.3: Regression analyses of percentage canopy openness values (%C0)	129
Fig. 4.4: Rank order of abundance of gap and understorey small sapling species	156
Fig. 4.5: Sertung forest near S3 gap site during the drought and heavy ash-fall in 1994.....	159
Fig. 4.6: South-east Rakata forest during the 1994 drought and one year after.....	160
Fig. 4.6: Rank abundance plots of tall saplings for S3 and R5	161
Fig. 5.1: Species-area curves from species presence/absence data collected in 20 x 1000 m belt transects on Rakata, Sertung and Panjang.....	177
Fig 5.2: DCA ordination and TWINSpan classification of woody species occurrence in 0.1 ha sections of the 1000 m 'cross-country' transects on Rakata, Sertung and Panjang.....	179
Fig. 5.4: <i>Dysoxylum</i> , <i>Neonauclea</i> , and <i>Timonius</i> occurrence along the Rakata transect in (a) the canopy/lower canopy and (b) the understorey.	181
Fig. 5.5: The total number of occurrences of <i>Dysoxylum</i> , <i>Neonauclea</i> and <i>Timonius</i> in the canopy/lower canopy and the understorey strata along the Rakata transect.	181
Fig. 5.6: <i>Dysoxylum</i> , <i>Neonauclea</i> , and <i>Timonius</i> occurrence along the Panjang transect in (a) the canopy/lower canopy and (b) the understorey..	183
Fig. 5.7: The total number of occurrences of <i>Dysoxylum</i> , <i>Neonauclea</i> , and <i>Timonius</i> in the canopy/lower canopy and the understorey strata along the Panjang transect	183
Fig. 5.8: <i>Dysoxylum</i> , <i>Timonius</i> , and <i>Neonauclea</i> occurrence along the Sertung transect in (a) the canopy/lower canopy and (b) the understorey.	185
Fig. 5.9: The total number of occurrences of <i>Dysoxylum</i> , <i>Neonauclea</i> , and <i>Timonius</i> in the canopy/lower canopy and the understorey strata along the Sertung transect.....	185
Fig. 5.10: DCA ordination and TWINSpan classification of the 1993 sapling abundance data of 4 x 4 m gap and understorey pairs of plots	188
Fig. 5.11: DCA ordination and TWINSpan classification of sapling abundance data of 4 x 4 m gap and understorey pairs of plots in 1993, 1994, and 1995.....	188
Fig. 5.12: Percentage similarity values between gap and understorey pairs of plots for 1993, 1994 and 1995.....	191
Fig. 5.13: Species richness trends between 1993, 1994, and 1995 for (a) all gap plots and (b) all understorey plots.....	194

Fig. 5.14: Simpson index values for 1993, 1994, and 1995 for (a) all gap plots and (b) all understorey plots.....	195
Fig. 6.1: Seed bank germination experiment.....	213
Fig. 6.2: Dendrogram of the cluster analysis of percentage similarity of all gap and understorey seed bank samples.....	221
Fig. 6.3: Smothering by the herbaceous climber <i>Mikania cordata</i> in a gap on Sertung.	228
Fig. 6.4: <i>Neonauclea calycina</i> seedlings on a bare landslide surface on Rakata	237
Fig. A1.1: Ozalid light meter attached to a 1.5 m high bamboo stick.	288
Fig. A1.2: Results of 1994 experimentation with the ozalid light metering technique.	299
Fig. A1.3: Daily total PAR in molm ⁻² during August 1994, in the open, on the Owl Bay beach of Rakata.....	291
Fig. A1.4: Graph showing that ozalid paper reacts mainly to maximum instantaneous radiation rather than cumulative radiation.	294
Fig. A2.1: Hemispherical photographs of <i>Neonauclea</i> forest of inland Rakata in (a) 1993, (b) 1994 and (c) 1995.....	298
Fig. A2.2: Hemispherical photographs of <i>Dysoxylum</i> forest on Sertung in: (a) 1993; (b) in 1994 and; (c) in 1995.	299
Fig. A2.3: Hemispherical photographs of <i>Timonius</i> forest on in: (a) 1993 when picture; (b) in 1994 and; (c) in 1995.	300
Fig. A2.4: Scatter plot for tall saplings (a) dbh and; (b) height growth in each case <i>versus</i> area of sampling..	301
Fig. A3.1: Comparison of height change of <i>Dysoxylum</i> saplings 0, 50, and 75% clipped: (a) 1993-1994, and (b) for 1994-1995.....	310
Fig. A3.2: Distribution of height change of all saplings of the <i>Dysoxylum</i> clipping experiment for the periods 1993-1994 and 1994-1995.....	311

Fig A4.1: Regression analyses of gap species richness and gap size measured as 1993 percentage canopy openness for : (a) 1993; (b) 1994 and; (c) 1995.....	316
Fig. A4.2: Difference in species richness between different size-classes of gaps for: (a) 1993; (b) 1994 and; (c) 1995.	317
Fig. A4.3: Difference in species richness between gaps of light to medium disturbance (sev. 1) and those of severe disturbance (sev. 2) for: (a) 1993; (b) 1994 and; (c) 1995..	317
Fig. A4.4: Difference in Simpson indices between gaps of light to medium disturbance (sev. 1) and those of severe disturbance (sev. 2) for: (a) 1993; (b) 1994 and; (c) 1995..	318

LIST OF TABLES

Table 1.1: Table distinguishing between the <i>Niche Diversification Hypothesis</i> and the <i>Disturbance Hypothesis</i>	3
Table 1.2: Plant collecting surveys on the Krakatau islands.....	30
Table 1.3 A hierarchy of successional causes <i>sensu</i> Pickett <i>et al.</i> (1987).	50
 Table 2.1: Area and altitudes of the Krakatau islands, Rakata, Sertung, Panjang and Anak Krakatau.....	59
Table 2.2: Record of the most severe or notable phases of volcanic activity of Anak Krakatau.	65
Table 2.3: Bulk density values.....	70
Table 2.4: Monthly rainfall on Panjang (1929) and Rakata (1929 and 1930).....	72
Table 2.5: Mean monthly rainfall and temperature data.	72
 Table 3.1: Subjective age-class (range: 1-4) determination of disturbance.....	98
Table 3.2 a: Disturbance survey summary table.....	103
Table 3.2b: Frequency of different types of gap creation.	104
Table 3.3: Mortality of trees in permanent plots in a period without (1989-1992) and with (1992-1995) volcanic activity.....	109
Table 3.4: Mortalities of different dbh-classes of trees from six permanent plots.....	109
 Table 4.1: Summary table listing the physical characteristics of all gap sites.....	123
Table 4.2: GLM of the factors island, gap size, and severity of disturbance with respect to <i>small sapling</i> height growth in <i>gaps</i>	135
Table 4.3: Comparison of small sapling height growth in 4x4 m (a) <i>gap</i> and (b) <i>understorey</i> plots.....	136
Table 4.4: Correlation of small sapling density in gap plots and mean and maximum height growth for 1993-1994, 1994-1995, and 1993-1995.....	138
Table 4.5: Correlation of percentage canopy openness and mean and maximum height growth of small saplings in gap plots.....	139
Table 4.6: Results of the GLM analyses of percent mortality, recruitment, and net recruitment of <i>small saplings</i> in <i>gap</i> plots..	140
Table 4.7a: Comparison of percentage mortality, recruitment, and net recruitment of small saplings in <i>gap</i> plots between Rakata, and the ash-affected islands, between different gaps size-, and disturbance type and severity-classes.).....	142

Table 4.7b: Comparison of percentage mortality, recruitment, and net recruitment of small saplings in 4 x 4 m <i>understorey</i> plots between Rakata, and the ash-affected islands.....	142
Table 4.8: Correlation between small sapling density in gap plots and percentage mortality and recruitment.....	144
Table 4.9: Correlation between percentage canopy openness and percentage mortality, recruitment, and net recruitment of small saplings in 4 x4 m gap plots..	146
Table 4.10: GLM results for <i>tall sapling</i> (a) height and (b) dbh growth modelled with respect to factors island, gap size, and disturbance type and severity.	147
Table 4.11. <i>Tall sapling</i> dbh and height growth: pairwise island comparisons, and between different size-classes with one-tailed Mann-Whitney-U tests.	149
Table 4.11a: Comparison of dbh and height increment of all saplings.	149
Table 4.11b Comparison of dbh and height increment of all saplings excluding <i>Dysoxylum gaudichaudianum</i> ('All - Dg').	149
Table 4.11c: Comparisons of <i>Dysoxylum gaudichaudianum</i> sapling performance.....	150
Table 4.12: GLM analyses of percentage mortality, recruitment and net recruitment of <i>tall saplings</i> in the period 1994-1995.....	153
Table 4.13: Comparison of <i>tall sapling</i> percentage mortality, recruitment, and net recruitment using one-tailed Mann-Whitney-U tests.	153
Table 4.14a: The 10 most abundant <i>small sapling</i> species in 4 x 4 m gap and understorey plots on all islands in 1993, 1994, and 1995..	155
Table 4.14b: Proportions of individuals of the 10 highest ranking species	155
 Table 5.1: Plot- and whole-island-scale species richness for Rakata, Sertung, and Panjang	177
Table 5.2: Summary statistics from the multivariate analyses of the 1000 m transects.....	179
 Table 6.1: (a) Number of seedlings, and (b) number of species germinating from the seed bank samples of gap and understorey plots	216
Table 6.2: Seed densities for all gap and understorey seed bank samples.....	216
Table 6.3: Summary table of the 1993 Krakatau seed bank experiment.....	218
Table 6.4: Sorensen index comparison for seed bank gap and understorey samples, seed bank and gap sapling/seedling similarity.....	222
Table 6.5: Comparison of seed densities, and species richness of seed banks of a selection of published studies	224
Table 6.6: Krakatau seed bank density of <i>Macaranga tanarius</i> and that of two studies in the Palaeotropics.....	236

Table A2.1a: Height growth performance of small saplings in gap plots between 1993-1994, 1994-1995, and 1993-1995.	302
Table A2.1b: Height growth performance of small saplings in understorey plots between 1993-1994, 1994-1995, and 1993-1995.	303
Table A2.2a: Summary table of percentage mortality, recruitment, and net recruitment, and density of saplings in gap plots.	304
Table A2.2b: Summary table of percentage mortality, recruitment, and net recruitment, of saplings in understorey plots.	305
Table A2.3: Tall sapling summary table for dbh and height growth, and percentage mortality, recruitment and net recruitment	306
Table A3.1: Surviving <i>Dysoxylum</i> saplings from clipping treatments of 75, 50 and 0%.	312
Table A4.1: Summary table of gap and understorey species richness and Simpson indices for 1993, 1994, and 1995	316

GLOSSARY

Abbreviations and definitions

andesite	a fine-grained igneous rock of intermediate composition (Challinor, 1964);
AR	advanced regeneration: the seedling and sapling bank that survives gap creation;
cross-country transect	belt transects enumerating species presence/absence in the understorey, lower canopy and canopy strata, with an arbitrarily chosen starting point, following a compass bearing;
%CO	percentage canopy openness
dacite	quartz-andesite
Dbh	diameter at breast height
DCA	Detrended Correspondence Analysis
G	gap plot (4 x 4 m)
gap site	a recently created canopy opening with a pair of 4 x 4 m gap and understorey plots for the enumeration of small saplings; most gap sites also included the enumeration tall sapling regeneration;
GLM	General Linear Model; analysis of variance for unbalanced and nested data sets;
gully transect	transects following the bottom of one or more gullies; they were established for the enumeration of disturbance events;
IDH	Intermediate Disturbance Hypothesis (Connell, 1978)
%M	percentage mortality
MTF	multiple treefall
%net R	percentage net recruitment
LNG	a gap created by lightning
LS	landslide
plot	refers to either a 4 x 4 m gap or understorey plot of a gap site
P	Panjang
P+S	combined set of Panjang and Sertung sapling data
pyroclastic	fragmental rock products (e.g., ash, volcanic bombs, ignimbrite, etc.) ejected by volcanic explosions;
R	Rakata
%R	percentage recruitment
S	Sertung
site	refers to a gap site
small sapling	sapling ≥ 50 cm and ≤ 5 m height
tall sapling	sapling and sub-adult ≥ 1 cm and ≤ 10 cm dbh and ≥ 1.5 m height
TWINSpan	Two Way Indicator Species Analysis
TF	treefall
US	understorey plot (4 x 4 m)

Gap sites and transect abbreviations

R1	Rakata gap site 1
R2	Rakata gap site 2
R2LNG	Rakata gap site 2; gap plot in the lightning part of this large gap
R2G	Rakata gap site 2; gap plot in the treefall part of this large gap
R2root	Rakata gap site 2, seed bank sample taken from the root-zone of one of the fallen trees in this gap
S3	Sertung gap site 3
P4	Panjang gap site 4
R5	Rakata gap site 5
P6	Panjang gap site 6
P7	Panjang gap site 7
P8	Panjang gap site 8
R9	Rakata gap site 9
R10	Rakata gap site 10
R11	Rakata gap site 11
R12	Rakata gap site 12
P13	Panjang gap site 13
S14	Sertung gap site 14
R15	Rakata gap site 15
R16	Rakata gap site 16
P17	Panjang gap site 17
RS 500 m	Rakata 'cross-country' transect for the enumeration of species presence/absence and disturbance located in lowland South Rakata
RSE 1000 m	Rakata 'cross-country' transect for the enumeration of species presence/absence and disturbance located in lowland South-east Rakata
RZH 450 m	Rakata 'cross-country' transect for the enumeration of species presence/absence and disturbance located near Zwarte Hoek (c. 190m a.s.l.) in the North-west of the island;
RSE 1080 m	Rakata 'gully' transect for the enumeration of disturbance located in lowland South-east Rakata
RSE 990 m	Rakata 'gully' transect for the enumeration of disturbance located in lowland South-east Rakata.
RN 780 m	Rakata 'gully' transect for the enumeration of disturbance located in lowland North Rakata; the transect is a composite of two transects from adjacent gullies.
RN 1050 m	Rakata 'gully' transect for the enumeration of disturbance located in lowland North Rakata; the transect is a composite of four short transects in adjacent gullies.
PS 1000 m	Panjang 'cross-country' transect for the enumeration of species presence/absence and disturbance located in the South of Panjang.
PE 600 m	Panjang 'cross-country' transect for the enumeration of species presence/absence and disturbance running East to West in the northern half of Panjang;
PN 710 m	Panjang 'gully transect' for the enumeration of disturbance; located in the North of Panjang;
PN 480 m	Panjang 'gully' transect for the enumeration of disturbance; located in the North of Panjang; the transect is a composite of two short transect in adjacent gullies;
PN 690 m	Panjang 'gully' transect for the enumeration of disturbance; located in the North of Panjang.
S 1000m	Sertung 'cross-country' transect running along the main ridge starting from close to S1 permanent plot .
SNW 1050 m	Sertung 'gully' transect from the North-west coast inland
SW 950 m	Sertung 'gully' transect running from the West coast inland.

Alphabetical species abbreviations and species list:

For authorities see Backer and Bakhuizen (1963-68) and Whittaker *et al.* 1989. For species first recorded after 1983 authorities are given at first mention in the text.

	<i>species name</i>	<i>family</i>
Ae	<i>Artocarpus elasticus</i>	Moraceae
Ac	<i>Allophyllus cobe</i>	Sapindaceae
Aco	<i>Ageratum conyzoides</i>	Compositae
Ah	<i>Ardisia humilis</i>	Myrsinaceae
Aj	<i>Arthropphyllum javanicum</i>	Araliaceae
Al	<i>Antigonon leptopus</i>	Polygonaceae
Am	<i>Antidesma montanum</i>	Euphorbiaceae
A sp	<i>Aglaia species</i>	Meliaceae
Ba	<i>Buchanania arborescens</i>	Anacardiaceae
Bas	<i>Barringtonia asiatica</i>	Lecythidaceae
Bc	<i>Breynia cernua</i>	Euphorbiaceae
Bm	<i>Bridelia monoica</i>	Euphorbiaceae
Bmin	<i>Bridelia minutiflora</i>	Euphorbiaceae
Cba	<i>Cyclea barbata</i>	Menispermaceae
Cf	<i>Capsicum frutescens</i>	Solanaceae
Cd	<i>Clerodendrum disparifolium</i>	Verbenaceae
Ce	<i>Casuarina equisetifolia</i>	Casuarinaceae
Ch	<i>Clidemia hirta</i>	Melastomataceae
Chi	<i>Canarium hirsutum</i>	Burseraceae
Ci	<i>Calophyllum inophyllum</i>	Guttiferae
Cin	<i>Clerodendrum inerme</i>	Verbenaceae
Cp	<i>Crypteronia paniculata</i>	Crypteroniaceae
Cm	<i>Cordia mixa</i>	Boraginaceae
Cs	<i>Cyrtandra sulcata</i>	Gesneriaceae
Ct	<i>Cayratia trifolia</i>	Vitaceae
Cu	<i>Corypha utan</i>	Palmae
Cun	<i>Calamus unifarius</i>	Palmae
Db	<i>Dioscorea bulbifera</i>	Dioscoreaceae
Dg	<i>Dysoxylum gaudichaudianum</i>	Meliaceae
Dr	<i>Digitaria rhopalotricha</i>	Gramineae
Ei	<i>Eleusine indica</i>	Gramineae
Eg	<i>Elaeocarpus glaber</i>	Elaeocarpaceae
El	<i>Elaeagnus latifolia</i>	Elaeagnaceae
Eo	<i>Erythrina orientalis</i>	Leguminosae
Fa	<i>Ficus ampelas</i>	Moraceae
Fc	<i>F. callosa</i>	Moraceae
Ffs	<i>F. fistulosa</i>	Moraceae
Ffv	<i>F. fulva</i>	Moraceae
Fh	<i>F. hispida</i>	Moraceae
Fl	<i>F. lepicarpa</i>	Moraceae
Fm	<i>F. montana</i>	Moraceae
Fp	<i>F. pubinervis</i>	Moraceae
Fr	<i>F. ribes</i>	Moraceae
Fre	<i>F. retusa</i>	Moraceae
Fs	<i>F. septica</i>	Moraceae

continued.....

	species name	family
F sp	<i>Ficus</i> species	Moraceae
Fsum	<i>F. sumatrana</i>	Moraceae
Ft	<i>F. tinctoria</i>	Moraceae
Fv	<i>F. variegata</i>	Moraceae
Gb	<i>Glochidion borneense</i>	Euphorbiaceae
Gg	<i>Gnetum gnemon</i>	Gnetaceae
Gp	<i>Gnaphalium purpureum</i>	Compositae
Gs	<i>Guettardia speciosa</i>	Rubiaceae
G sp	<i>Glochidion</i> species	Euphorbiaceae
Hc	<i>Hedyotis corimbosa</i>	Rubiaceae
Hg	<i>Horsfieldia glabra</i>	Myristicaceae
Ho	<i>Homalanthus populneus</i>	Euphorbiaceae
Hp	<i>Hernandia peltata</i>	Hernandiaceae
Ip	<i>Ipomoea pes-caprae</i>	Convolvulaceae
Lcm	<i>Lantana camara</i>	Verbenaceae
Lc	<i>Leucosyke capitellata</i>	Urticaceae
Ln	<i>Litsea noronhea</i>	Lauraceae
Ls	<i>Leea sambucina</i>	Leeaceae
Ma	<i>Melastoma affine</i>	Melastomataceae
Mag	<i>Messerschmidia argentea</i>	Boraginaceae
Maz	<i>Melia azederach</i>	Meliaceae
Mc	<i>Morinda citrifolia</i>	Rubiaceae
Mco	<i>Mikania cordata</i>	Compositae
Me	<i>Medinilla eximia</i>	Melastomataceae
Ms	<i>Medinilla speciosa</i>	Melastomataceae
Mt	<i>Macaranga tanarius</i>	Euphorbiaceae
Mu	<i>Melochia umbellata</i>	Sterculiaceae
Na	<i>Nervillia aragoana</i>	Orchidaceae
Nb	<i>Nephrolepis bisserata</i>	Pteridophyta
Nc	<i>Neonauclea calycina</i>	Rubiaceae
Nm	<i>Neyraudia madagascariensis</i>	Gramineae
Oi	<i>Oroxylum indicum</i>	Bignoniaceae
Ot	<i>Oncosperma tigillarum</i>	Palmae
Oc	<i>Oplismenus compositus</i>	Gramineae
Pb	<i>Piper blumei</i>	Piperaceae
Pad	<i>Piper aduncum</i>	Piperaceae
Pag	<i>Pipturus argenteus</i>	Urticaceae
Pc	<i>Premna corymbosa</i>	Verbenaceae
Pca	<i>Pityrogramma calomelanos</i>	Pteridaceae
Pd	<i>Planchonella duclitan</i>	Sapotaceae
Pn	<i>Polyscias nodosa</i>	Araliaceae
Pm	<i>Phyllanthus microcarpus</i>	Euphorbiaceae
Pma	<i>Pennisetum macrostachyum</i>	Gramineae
Pp	<i>Peperomia pelusida</i>	Peperomiaceae
Ppa	<i>Pogonatherum paniceum</i>	Gramineae
Ps	<i>Pollia secundiflora</i>	Commelinaceae
Pv	<i>Planchonia valida</i>	Lecythidaceae
Rg	<i>Radermachera glandulosa</i>	Bignoniaceae
Sh	<i>Semecarpus heterophylla</i>	Anacardiaceae
Sn	<i>Saurauia nudiflora</i>	Saurauiaceae
So	<i>Sterculia oblongata</i>	Sterculiaceae
Sp	<i>Syzygium polyanthum</i>	Myrtaceae

continued.....

	species name	family
Spl	<i>Selaginella plana</i>	Selaginellaceae
Ss	<i>Saccharum spontaneum</i>	Gramineae
Ta	<i>Tylophora asthmatica</i>	Asclepidaceae
Tca	<i>Terminalia catappa</i>	Combretaceae
Tcl	<i>Timonius compressicaulis</i>	Rubiaceae
Td	<i>Tarenna dasyphylla</i>	Rubiaceae
Tf	<i>Tarenna fragrens</i>	Rubiaceae
TI	<i>Tetrastigma lanceolarium</i>	Vitaceae
To	<i>Trema orientalis</i>	Ulmaceae
Va	<i>Vernonia arborea</i>	Compositae
Vr	<i>Villebrunea rubescens</i>	Urticaceae
Wb	<i>Widelia biflora</i>	Compositae

note: families of species mentioned in the text are only given here, and abbreviations are generally added even if these do not appear for all species in the text, tables or figures.

CHAPTER 1:

INTRODUCTION AND LITERATURE REVIEW

"There is a growing realisation that disturbance may play as great a role in community dynamics as do biological interactions, such as competition and predation, which have received far more empirical and theoretical attention from ecologists. The interplay between disturbance and these biological processes seems to account for a major portion of the organisation and spatial pattern of natural communities." Sousa (1984), p.383;

"Disturbance and succession are inextricably linked, but we should be careful not to overextend the case by making disturbance the only foundation of vegetation science." Webb et al. (1972), p. 18;

*"On Krakatau, with relatively few canopy tree species (Whittaker & Bush, 1990), it might be expected that this feature [shifting mosaic of species through time] will be less evident. Furthermore, as the forests are undergoing rapid successional change the study of gap-filling may provide a clear test, in different types of forest of whether the dominant species of tree is in the process of changing. In particular it is of interest to determine the extent to which *Dysoxylum gaudichaudianum* may be taking over from *Neonauclea calycina* in some near-coastal regions of Rakata, and the manner in which it is taking over from *Timonius compressicaulis* on Panjang and Sertung."* (Whittaker et al., 1990; p. 12)

1.1 Introduction

These three quotes are intended to set the scene for this study. The first two are general statements stressing the importance of disturbance in community dynamics, but at the same time warning that disturbance alone should not be overstressed. The third quote provides a Krakatau specific outline, and the main questions that are underlying the work in this thesis. This introductory chapter aims to provide an overview of the literature on disturbance and gap ecology, and its importance for regeneration and diversity in tropical rain forests (section 1.2). In so doing I will contrast the equilibrium with the non-equilibrium viewpoints of regeneration and community dynamics. The relevance of these viewpoints with respect to the succession and species diversity of Krakatau forests will be discussed. Section 1.3 describes the history of recolonisation and succession as it is known from the literature, and discusses the influence of the emergence of Anak Krakatau, and its intermittent eruptions on the succession and composition of the Krakatau forests. Since any ecological study on the Krakatau islands is naturally concerned with succession, the

of the Pickett *et al.* (1987) hierarchical model of causes and mechanism of succession, as a research framework for this study is advocated. Using the framework of this model, a hierarchical representation of the succession on Krakatau is given in diagrammatic format. The first diagram emphasises the special significance of volcanic disturbance, in accordance with papers by Whittaker and colleagues in the 1980s/early 1990s (Fig. 1.15; Whittaker *et al.*, 1989; Bush *et al.*, 1992), and the second diagram is a revised model emphasising other external forcing factors in addition to volcanism (Fig. 1.16). The latter already summarises the main findings of this study, and will be frequently referred to throughout the thesis. Section 1.5 briefly describes how the study evolved from a rather different baseline to arrive at the final focus of the thesis, and section 1.6 presents the main aim and research objectives of this study. Detailed objectives are presented in each data chapter (CHAPTERS 3-6).

A detailed description of the study site and its physical characteristics is given in CHAPTER 2, together with the administrative history and human impact on the islands. A map of the island group and the Sunda Straits region is shown below (Fig. 1.1)

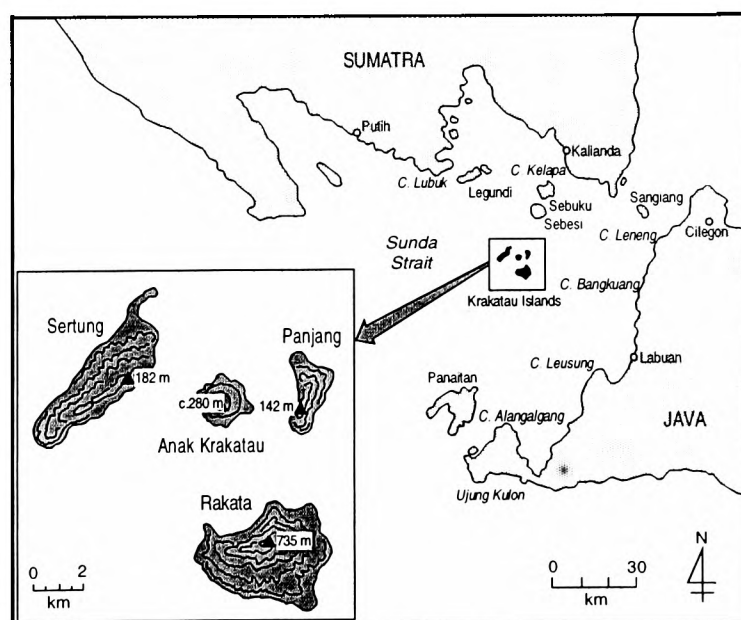


Fig. 1.1: Map of the Krakatau islands and the Sunda Straits region (from Whittaker & Jones, 1994a)

1.2 Disturbance and gap ecology: a review with special reference to the Krakatau islands

In this section the literature on disturbance and gap ecology and the major theories associated with it are reviewed. I pay particular attention to the question of disturbance and diversity in tropical rain forests. First, the increase in attention to, and development of gap ecology are described. Second, the attempt to describe the mechanisms of the maintenance of high species richness and species co-existence is investigated within the two broad headings of equilibrium and non-equilibrium models (Connell, 1978). These are discussed under the 'niche diversification' hypothesis and the 'disturbance' hypothesis respectively. Thirdly, the significance of the two hypotheses for the study of gap ecology and disturbance on the Krakatau islands is assessed.

The importance of ever-changing developmental phases, and of the occurrence of treefall gaps for the regeneration of forests, was first stressed by Aubréville (1938), followed by Watt (1947) and Richards (1952). Their writing encompasses the idea of cyclical forest regeneration. Gaps were identified as sources of environmental heterogeneity (Ricklefs, 1977) which provide regeneration foci, because their creation makes available physical colonisation space and resources, and therefore, reduces competition. Following the recognition of the importance of disturbance to the forest canopy, Whitmore (1978) and Hartshorn (1978) subsequently postulated the theory of gap-phase regeneration dynamics, which stresses the mosaic nature of forests (Whitmore, 1984) with three stages of development: the 'gap', 'building' and 'mature phase' of forests. The coarseness of the mosaic and the proportional distribution of the three phases depends on many factors, such as, for instance, the longevity of the tree species, topography, climate (e.g. frequency of storms; total amount of rainfall), and substrate.

The proliferation of research into the effects of disturbance leading to gap creation in tropical rain forest from the late 1970s onwards, has to be seen in the context of the challenge to the classical ecological paradigm of 'equilibrium theory' (Pickett *et al.*, 1992), and the need to explain the great species richness in tropical rain forest. On the one hand equilibrium theory postulates a stable equilibrium point of ecological systems with the focus on the end points of ecological processes and interactions. On the other hand 'non-equilibrium theory' basically suggests that the process of competitive exclusion is truncated by the occurrence of disturbance (Pickett, 1980). Very importantly this theory concentrates

on processes rather than trying to find endpoints, as, for instance, implied by the idea of a climax community in the Clementian sense. Nevertheless, although patches may be in a number of different states that are changeable through time and space, a compositional equilibrium is still possible on the landscape scale (Pickett *et al.*, 1992; Veblen, 1992). Hence, high species diversity is not, as argued by the equilibrium theory, derived from more and more specialisation allowing coexistence in an equitable environment that has been stable over millions of years (Ashton, 1969). Instead, high species diversity is argued to be explainable by disturbance creating environmental heterogeneity in time and space, whereby the basis for resource partitioning and coexistence of competing species is provided (Ricklefs, 1977).

Two major hypotheses in gap ecology have been advanced to explain the maintenance of high species richness: (i) the niche diversification hypothesis; and (ii) the disturbance hypothesis. They correspond with the equilibrium and the non-equilibrium classification respectively (Table 1.1).

Table 1.1: Table distinguishing between the *Niche Diversification Hypothesis* and the *Disturbance Hypothesis*. Both attempt to explain the generation and maintenance of species diversity in tropical rain forests, and are very relevant to gap ecological studies. Also listed are the paradigms within which the hypotheses are formulated and some examples of references.

<i>hypotheses</i>	<i>paradigm</i>	<i>description</i>	<i>references</i>
Niche Diversification Hypothesis	Equilibrium theory	Gaps may allow the evolution of diversified life-histories, whereby species co-existence may be enhanced due to partitioning by gap size.	Grubb,(1977), Denslow (1980), Brandani <i>et al.</i> (1988), Leibold (1995), Shmida & Wilson, (1985), Smith & Huston (1989);
Disturbance Hypothesis	Non-equilibrium theory	Gaps created by disturbances of different size, and severity and at varying intervals, create heterogeneity and thus prevent competitive exclusion. Intermediate levels of disturbance would allow the persistence of pioneers as well as later successional species resulting in a more diverse forest.	Whitmore (1974, 1984); Intermediate Disturbance Hypothesis (IDH) Connell (1978); Pickett (1980); Hubbell & Foster (1986a,b);

The niche diversification hypothesis

A characteristic feature of tropical rain forests is their great diversity in sympatric species with apparently very similar morphology and ecology. This phenomenon has puzzled researchers for decades, as it seems difficult to comprehend how competitive exclusion could be avoided given that the basic plant resources of water, light, nutrients and carbon dioxide, are so few, and so diffuse.

The niche diversification hypothesis postulates that gaps may allow the evolution of diversified life histories (Viana, 1989), such as, for instance, the evolution of species with specialised regeneration niches (Grubb, 1977). The concept of the regeneration niche seems to have been one of the most influential concepts in gap ecology, as it concentrates on the germination and establishment phase. These phases may be argued to be the most crucial influencing the composition of gap-fill as it is at that point in a plant's life-cycle that the most selective factors apply (Swaine, 1996). The multitude of different regeneration niches needed to enable the coexistence of many rain forest species has been argued to be partially due to partitioning by gap size, which influences microclimatic conditions (Denslow, 1980). Denslow (1980) also stressed temporal and spatial frequencies of gap occurrence as influencing seedling establishment by affecting the probability of a propagule reaching a gap of a particular size. Therefore, the gap size distribution characteristic for a given rain forest should be important for influencing the types and diversity of species present. Furthermore, internal heterogeneity of gaps in terms of nutrient availability and root competition has been argued to lead to special adaptations (Oriens, 1982). In addition Ricklefs (1977) postulated niche specialisation along forest-gap gradients, which he argued had a greater range in soil and microclimatic characteristics from the forest interior to the centre of a gap than such gradients in temperate forests.

Very considerable research-effort has gone into testing for the existence of gap-partitioning and niche diversification. Evidence for the existence of broad regeneration guilds has already existed for a considerable period of time (Richards, 1952; Whitmore, 1974), and has been demonstrated, for example, by a strong correlation of the abundance of heliophilous tree species with frequency of gaps on Barro Colorado Island (Hubbell & Foster, 1986b). The fact that strongly light demanding species are rare in forests that have low frequencies of large gaps (Brown & Whitmore, 1992), and more frequent in forests of

high frequencies of large scale disturbance (Whitmore, 1974) further support the idea of adaptations to gaps of substantially different size, and the influence on the diversity and abundance of, for instance, pioneer species. Yet, there is little evidence for the suggested fine-tuning of regeneration niches (Barton, 1984; Hubbell & Foster, 1986b; Denslow, 1987; Uhl *et al.*, 1988; Brown & Whitmore, 1992; Whitmore & Brown, 1996), with the caveat that it is very difficult to test the theory for several reasons: (i) the difficulty of giving an ecologically meaningful gap definition that allows repeatable measurement of gap size; (ii) the great heterogeneity of the seed and seedling banks which does not allow easy comparison of the growth of seedlings of different species over a wide range of gap sizes; and (iii) comparison of gaps of the same age is difficult unless they are artificially created.

Many gap ecological studies have been undertaken, but comparison of results on species' responses to gaps, forest turnover, and gap characteristics, remains notoriously difficult, because of the lack of a definition of gap size that is objective and biologically meaningful (Pompa *et al.*, 1988). The definition by Brokaw (1982) of a gap as a "hole in the forest extending through all levels down to an average height of 2 m above ground" (p. 159), and "greater than 20 m²" was an attempt to standardise definitions and thereby allow comparison. This definition provides a quantifiable parameter to estimate gap area, that is relatively easy to implement in the field. It has been widely adopted. However, many studies have shown that it is ecologically not a very meaningful measure, since it underestimates gap size. For example, Pompa *et al.* (1988), using the maximum extent of pioneer species as the definition of the gap edge, found that the gap conditions extend well into the understorey. According to their measurements the standard definition can lead to an under-estimation of between 44-515% of the area colonised by pioneers. Most importantly they point out that the gap environment to which pioneer plants respond is a result of many interacting factors of which size is only one. The importance of orientation, slope angle, aspect, nature of gap creation, and height of surrounding canopy has now been widely recognised. Therefore, gaps of the same size may result in very different microclimatic conditions for regeneration (Brown, 1993). In any case, one should see the gap and understorey as forming a continuum of microclimatic conditions, and not a dichotomy. Neither the gap itself, nor the forest understorey are uniform environments. As Lieberman *et al.* (1989) aptly put it "forests are not just Swiss cheese".

Several studies have tried to overcome constraints (ii) and (iii) by, for example, transplanting seedlings and artificially creating gaps, but were, nevertheless, unable to find very species specific regeneration niches. In the case of Brokaw's (1987) study of three pioneer species, a gradient in terms of recruitment, growth and gap-size requirement was found, which might maintain some diversity of gap colonisers. However, substantial overlap in regeneration behaviour still occurred, and the importance of chance in promoting coexistence was stressed. Furthermore, Kennedy and Swaine (1992) drew attention to the fact that the observed abundances of the different species in different sized gaps is a direct reflection of the total number of each species in the forests of Barro Colorado Island.

Pioneer species typically only account for a small fraction of tree species in mature tropical forest (Whitmore, 1984). It is, therefore, important to investigate the degree of difference between the non-pioneer species in order to understand tropical tree regeneration (Brown & Whitmore, 1992; Clark & Clark, 1992; Clark *et al.*, 1993). Brown and Whitmore (1992) conducted a 40-month study of three climax species (*sensu* Swaine & Whitmore, 1988) of contrasting silvicultural characteristics, in lowland dipterocarp forest in Sabah. They suggested that the ability to persist and grow under the closed forest canopy might be more important in determining gap-fill, since they found the most important determinant for initial seedling survival was seedling size at the time of gap creation. Therefore, frequency of disturbance and the duration of the period of release *versus* suppression were suggested to be more important than gap size and radiation levels for the regeneration of climax species, and the maintenance of species diversity in tropical forests (Uhl *et al.*, 1988). However, the importance of longer-term monitoring of regeneration became apparent, when an extension from 40 to 77 months (Whitmore & Brown, 1996) showed that the size advantage of the shade-tolerant *Hopea nervosa* at time of gap creation (bestowed by persistence in the understorey) does not necessarily guarantee eventual gap-fill. In fact, the more light-demanding species *Shorea johorensis* had by 53 months already overtaken *Hopea nervosa*, concurring with the results of recent ecophysiological studies (Press *et al.*, 1996; Whitmore, 1996). These studies found that the more light-demanding species are more flexible in their ability to adjust their architecture, morphology, leaf anatomy and other ecophysiological attributes, in response to increased photosynthetic active radiation (PAR). The Whitmore and Brown (1996) study still found no evidence of fundamental niche differentiation with respect to gap size. However, all species showed increasing rates of growth with increasing gap size, but the rate of change of response differs between species. Thus, the outcome is seen to be the result of a shifting competitive hierarchy

(Keddy, 1989). Brown & Whitmore (1996) pointed out that gap-fill success of the species that responded more slowly may depend on the absence of faster growing competitors.

Some evidence for the postulated importance of internal heterogeneity of gaps (Orians, 1982) for the maintenance of high tree species richness has been found (Barton, 1984; Brandani *et al.*, 1988; Núñez-Farfán & Dirzo, 1988). Thus, different gap zones (root, bole and crown) were found to be more similar to one another, in terms of their species composition, than they are to other zones in the same gap. This non-random pattern was found to establish soon after the formation of the gap, by inter-specific differences in mortality in different gap zones, leading to different species favouring different parts of the gap and in different densities. The latter coincides with Barton's (1984) findings of significantly higher densities of pioneer species in the centre of the gaps than on the edge. Moreover, there is evidence that root-zones and areas of soil disturbance with exposure of mineral soil, have a greater diversity of seedlings than other zones in gaps (Núñez-Farfán & Dirzo, 1988; Kennedy & Swaine, 1992). Nevertheless, considerable overlap among species was still found, although Núñez-Farfán and Dirzo (1988) established that different hierarchical organisation of both zone specific and overlap species occurred due to different size, density and herbivory damage incurred. Thus, to observe possible changes in the species composition at later life-cycle stages also requires longer-term monitoring of the different zones.

It has generally been suggested that monitoring of only the small seedling and sapling stage in gaps is insufficient for a comprehensive understanding of tree regeneration in tropical rain forest (Welden *et al.*, 1991; Clark & Clark, 1992; Clark *et al.*, 1993). Clark *et al.* (1993) argue that it "will require simultaneous measurement of environmental variables and forest structure for all size classes from seed to adult, as well as repeated measurements on the same individuals over a period of at least several years" (p.405). Funding shortages and other practical problems, often make such extended periods of study very difficult. The exceptions are the small numbers of 50 ha permanent plots established in tropical forests around the world (see Condit *et al.*, 1996). Clark *et al.* (1993), however, also point out that our abilities to deal simultaneously with the complexities of more factors (e.g. inter-specific differences in phenology, density dependence or independence, seed dispersal, morphology, allocation patterns and physiology) than, for instance, light and forest structure are still very limited. Therefore, on the one hand one could accept that most rain forest trees are generalist species with broad ecological amplitudes, within a few major life history

guilds (Hubbell, 1979; Hubbell & Foster, 1986a; Lieberman *et al.*, 1995). Yet, on the other hand, such a great array of different factors have been shown to affect tree regeneration patterns that one could still favour the niche diversification hypothesis (this is if it is extended beyond the regeneration niche). Therefore, Clark *et al.* (1993) suggest that an answer to the question of what causes high tree species diversity is likely to lie in “comparative studies integrating ecological and physiological approaches” (p.405).

The disturbance hypothesis

In the disturbance hypothesis, similar to Ricklefs' (1977) proposal, gaps are seen as sources of environmental variability. The difference however is that instead of leading to the evolution of specialised regeneration niches in an equilibrium sense, gaps are argued to prevent the competitive exclusion of ecologically similar species in time and space (Viana, 1989) in a non-equilibrium sense. In this context, intermediate levels of disturbance, in terms of frequency and size, are hypothesised to promote the highest species richness (Connell, 1978). In the intermediate disturbance hypothesis (IDH) only the frequency and size of disturbance, with disturbance being defined as “a discrete displacement or damaging of one or more individuals that directly or indirectly creates an opportunity for new individuals to become established” (Sousa, 1984; p.356) was considered. However, an array of factors may constitute the disturbance regime of a forest (Bazzaz, 1984, 1991; Sousa, 1984). These are the spatial distribution (as also stressed by Denslow, 1980), the return interval (time interval between disturbances), the turnover rate (mean time required to disturb the entire area in question) the predictability, the total area disturbed, and the magnitude of the disturbance (Pickett & White, 1985). The latter is defined by the severity (e.g. basal area removed) and intensity (e.g. the wind speed of a hurricane) of the disturbance, and synergistic effects of one disturbance encouraging another (e.g. windthrow on steep slopes leading to subsequent landslides).

It is important to be aware that disturbance as the cause of environmental heterogeneity is scale-dependent (Whitmore, 1984; 1991; Kolasa & Rollo, 1991), and that scale has to be applied to space as well as time. Therefore, patterns of spatial heterogeneity after forest disturbance can be studied at the landscape, community, seedling, or cellular scale, and, for instance, a forest patch can be described on the temporal scale of centuries, years, seasons, hours and seconds. The disturbance hypothesis has predominantly been applied

at the between-patch scale (β -diversity), as for instance, between the intact understorey and a gap environment, and has been given less attention at the within-patch scale (α -diversity), as for example, when investigating internal heterogeneity of gaps. The between-patch scale addresses landscape/community-scale issues, whereby the overall disturbance regime is important in influencing species' coarse-scale distributions, dynamics, and coexistence. The within-patch scale investigate finer-scale patterns created by a single disturbance event, which is arguably related to species' resource partitioning, coexistence and niche characteristics (Bazzaz & Wayne, 1994).

Despite the fact that the niche diversification hypothesis belongs to a different paradigm, the difference between the focus of the disturbance and the niche hypotheses seems to a considerable extent to be a question of scale. The niche diversification hypothesis postulates fine-tuned adaptations to explain the high species richness. By doing so, it concentrates on within-patch, internal heterogeneity of gaps (e.g. Orians, 1982; Brandani *et al.*, 1988), and also between-patch heterogeneity of gaps and understoreys, which is argued to be partially defined by gap-size (Denslow, 1980). The between-patch scale evaluation of environmental heterogeneity of the niche diversification hypothesis, however, only addresses the species level, and not the community level. Moreover, this scale appears to be too coarse since within-gap heterogeneity in, for instance, microclimatic conditions between the centre and the gap edge, can be as great or greater than between gaps of markedly different sizes (Brown, 1993). Thus, gaps of the same size may in fact favour the regeneration and growth of species with different autoecological characteristics.

At the between-patch and within-patch scale, disturbance of different size and severity is argued by Bazzaz (1984) to influence gap-fill by favouring regeneration using different regeneration pathways (Fig. 1.2). These pathways range from branch ingrowth (not true regeneration), sprouting and advance regeneration (suppressed seedlings and saplings), to germination from the seed bank and seed immigration. It seems intuitive that with increasing size and/or severity of disturbance the relative contribution of advance regeneration and sprouting is reduced, and germination from the seed bank and seed immigration enhanced. This means progressively more pioneer species should be favoured with increasing size and/or severity of disturbance. However, severity of disturbance (e.g. whether mineral soil is exposed), seems to be more important than size, because even in multiple treefall gaps of large sizes, seedlings of shade-tolerant species from advanced

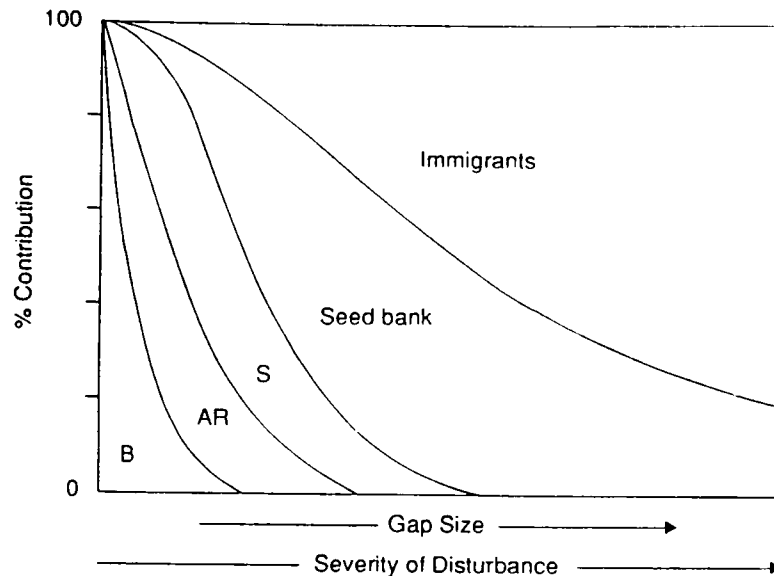


Fig. 1.2: Relationship between gap size and severity and the relative contribution of different pathways of regeneration. These are branch ingrowth (B), advance regeneration (AR), sprouts (S), and regeneration from the seed bank and from immigration (from Bazzaz, 1984)

regeneration often survive and can even constitute the majority of the regeneration layer (Uhl *et al.*, 1988).

It is difficult to ascertain which regeneration pathway yields the highest α -diversity in terms of woody species in a gap. For instance, advance regeneration often consists of very clumped patches of only a few seedling species (Brown & Whitmore, 1992), and sometimes the initial colonisation of bare soil surfaces, such as on landslides, only involves a few pioneer tree and shrub species (Garwood, 1985; Guariguata, 1990). However, as already pointed out above, treefall gaps in general provide opportunities for several different regeneration pathways to be followed simultaneously. Thereby the internal heterogeneity of disturbance severity in gaps can lead to increased levels of gap-fill diversity, although interspecific differences in mortality rates in the various life-cycle stages have to be considered. This is one of the examples where the niche diversification and the disturbance hypothesis coincide. However, it appears that only broad regeneration guilds are involved and timing with respect to dispersal, and chance in terms of location of treefall with respect to advance regeneration diversity, all influence the species composition of the gap-fill.

At the landscape-scale community diversity is influenced by the overall disturbance regime. The forests of Kolombangara island in the Solomons are a good example where regular cyclonic disturbance can be seen as repeatedly setting back succession, and thereby leading to forests with a high pioneer index (Whitmore, 1974; Whitmore, 1989). One of the crucial findings of the Kolombangara study is that spatial and time scales are important. For example, over the whole sample area the pioneer index dropped slightly over the 21 years of monitoring, and average disturbance was only 1.6% of the area per year, which was insufficient to maintain the overall floristic composition present at the start of the project. This result, however, conceals great variation in disturbance between periods (e.g. 67% of the area over the period 0.9 years was disturbed in the early 1970s) and between forest types, which can lead to substantial β -diversity increases, by increasing habitat diversity. Moreover, recruitment and mortality were also very variable between periods, species groups, and individual species. Thus, the regime of disturbance often reflects the interplay between the properties of organisms in the community and the characteristics of the physical forces that cause them (Sousa, 1984).

The islands of the West Indies are another example where periodic intense disturbance by hurricanes modifies structure and function of the forest ecosystem (Lugo & Waide, 1993), through direct impact from large-scale defoliation, branch damage and tree death, and by triggering other disturbance such as landslides and soil erosion (Guariguata, 1990; Dalling & Tanner, 1995; Lugo & Scatena, 1996). Lugo & Waide (1993) found in the Luquillo Experimental Forest of Puerto Rico that background disturbance (simple tree death) is more important in determining population turnover. Yet, catastrophic disturbance, such as hurricanes, and also landslides in a more severe but more localised way, significantly modify stand conditions. These phenomena have all been argued to influence forest succession, and therefore, allow the establishment of new combinations of species, although many species have been found to maintain their presence, even after severe disturbance, by sprouting (Sugden, 1992; Bellingham *et al.*, 1994; Vandermeer *et al.*, 1995). In particular non-pioneer species have been found to recover most quickly by sprouting, whereas the immediate impact on pioneer species was strongly negative. Yet, at a later stage pioneer abundance increased substantially, as a result of ideal regeneration conditions from increased light levels (Fernandez & Fetcher, 1991), and many areas of exposed soil from tree uprooting (Zimmerman *et al.*, 1994). In the case of landslides the succession is set back to the primary stage by usually causing 100% tree death and burial of the seed bank (Guariguata, 1990). Therefore, as indicated by Whitmore's (1974)

findings, both hurricanes and landslides seem to lead to habitat diversification on the landscape scale, and additionally such forests probably never approach a species equilibrium at the stand-level (Clark, 1990).

In contrast, tropical rain forests which are not subject to high frequencies of gap creation and periodic severe disturbances, provide different regeneration conditions in time and space. The Dipterocarp forests of Borneo are generally good examples of tropical forests rarely experiencing larger-scale disturbance, and therefore, favouring more shade-tolerant species. Thus, instead of gap-size governing the success of regeneration of climax species of different light requirement, the frequency of gap occurrence (Brown & Whitmore, 1992; Canham, 1989), and the spatial distribution of gaps on the landscape-scale appear very important.

The relevance of the Niche Diversification Hypothesis and the Disturbance Hypothesis to Krakatau

There are various implications of the preceding discussion for the study of the successional, and in particular the regeneration dynamics of the Krakatau islands. The proposed fine-tuning of species to particular gap-sizes seems particularly problematic, because being an isolated small island setting, still in the early stages of primary succession, (i) the tree flora does not contain the full spectrum from early pioneers to climax species (*sensu* Swaine & Whitmore, 1988); and (ii) many species seem to occupy different habitats and/or more than the 'realised niche' they would on the mainland of Sumatra or Java (Docters van Leeuwen, 1936), in so far as this information is known. Therefore, the likelihood of fine-tuned adaptation to, for instance, certain light conditions, can be anticipated to be small. However, that an interaction of many physical factors, such as soil texture, nutrient status, water-holding capacity and light can play a vital role is demonstrated by the preferred location of certain species, such as *Crypteronia paniculata* Bl. on ridge tops, and the palm *Oncosperma tigillarum* in moister areas (T. Partomihardjo pers. comm.). If biotic factors such as herbivory and dispersal, and stochastic stress factors such as periodic drought (pers. obs.), are also considered it can be seen that a synergism of different factors is influencing regeneration in gaps on Krakatau in time and space.

Bird data from Krakatau formed the first data set of island colonisation, with turnover apparently at equilibrium, considered by MacArthur & Wilson within *The Theory of Island Biogeography* (Mac Arthur & Wilson, 1967; Bush & Whittaker, 1993). The theory argues that island ecosystems arrive at a dynamic equilibrium of immigration and extinction of species mainly influenced by area and isolation. However, as Bush & Whittaker (1993) pointed out, plant data from Krakatau also provided the first exception that had to be explained, as it clearly demonstrates that dynamic equilibrium had not been reached as of 1930 - nor since for that matter. The colonisation of these islands has involved non-monotonic rate changes of observed immigration and extinction (Fig. 1.3).

As an explanation for the characteristics of the Krakatau assemblage of plant species various factors have been identified by Whittaker and colleagues. For instance, life-history factors are very important, and in the island colonisation context dispersal characteristics, as one aspect of life-history, are crucial (Whittaker *et al.*, 1989; Whittaker & Jones, 1994ab). This is clearly expressed in Fig. 1.4 which shows the structure related to dispersal which underlies island colonisation (Whittaker & Jones, 1994b). Furthermore, hierarchical links of plants and animals in food web relationships affect patterns of colonisation and turnover. These are ultimately governed by the population and community dynamics of the dominant life-forms, which in the Krakatau case are trees. Given the generational times of trees and the slow pace of later successional changes, the attainment of a dynamic equilibrium is unlikely for long-lived taxa in an island ecosystem with regular, and relatively severe disturbance events (Bush & Whittaker, 1991; Whittaker, 1995).

MacArthur and Wilson (1967) invoked a diffuse competition mechanism to explain turnover and species-area relationships (Whittaker, 1992). They acknowledged the potential influence of disturbance events such as storms, on extinction, immigration and successional turnover, but their theory does not allow for the fact that disturbance can play a very significant role in determining, and periodically changing, the structure and function, of some island ecosystems. In fact, disturbance creates opportunities for so-called 'successional turnover' due to induced habitat changes (Whittaker, 1995).

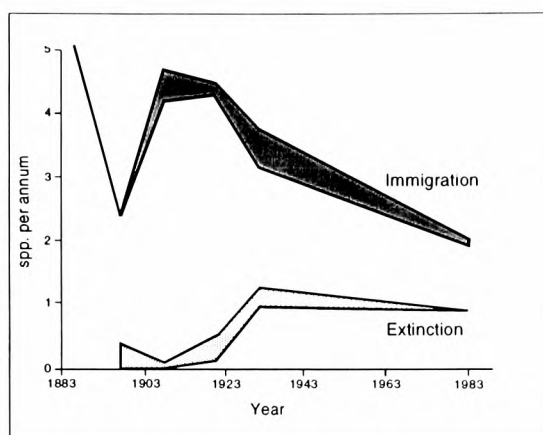


Fig. 1.3: Non-monotonic immigration/extinction curves for spermatophyte species on Rakata between 1883-1989. Data presented in this diagram assumes minimum turnover, i.e. species are only counted as going extinct if they fail to be found in all subsequent surveys (from Bush & Whittaker, 1991).

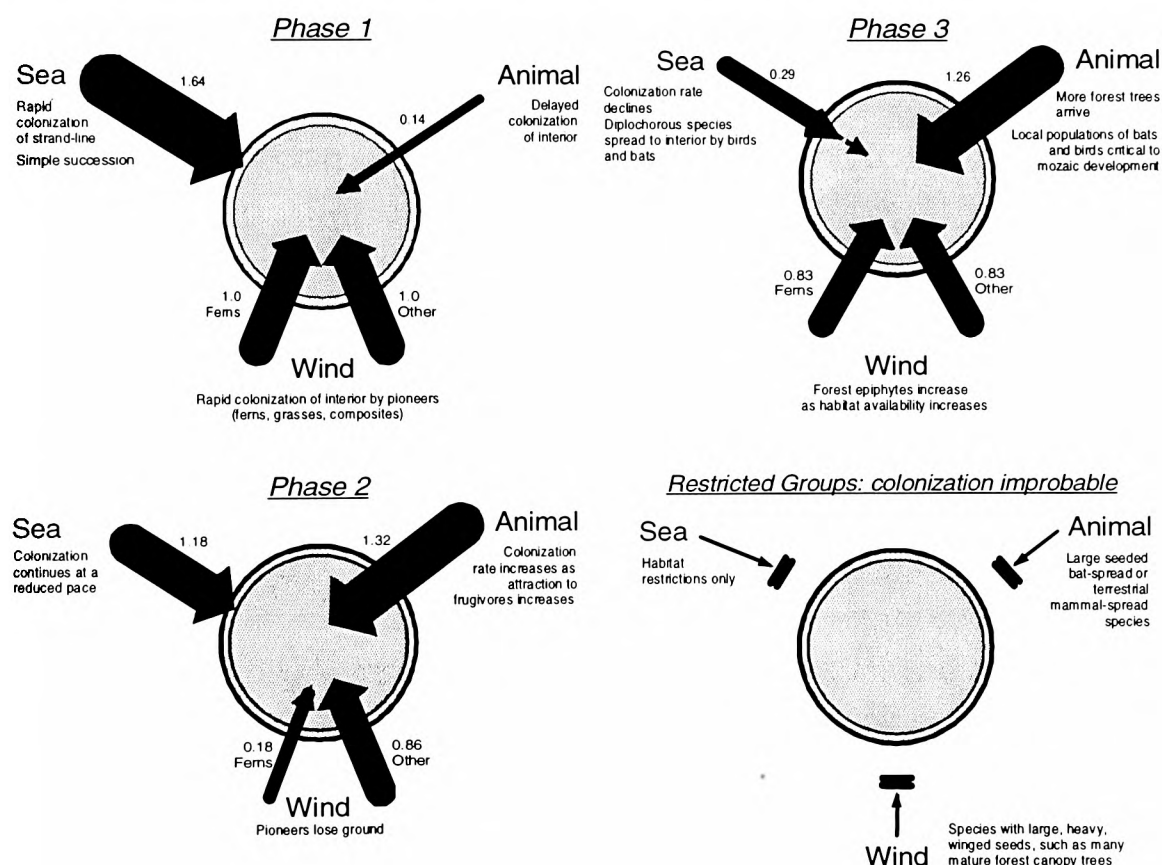


Fig. 1.4: Whittaker & Jones' (1994b; Fig. 2) dispersal-structured model of island colonisation, based on the recolonisation of Rakata by plants after sterilisation in 1883. Three phases are depicted: phase 1 1883-1897, phase 2 1897-1919, phase 3 1919-1989. The primary dispersal categories, of sea-, animal- and wind-dispersed are distinguished, whereby the latter is divided into ferns and flowering plants. Arrow widths are proportional to the increase in cumulative species number in species per year (values next to arrow; data from Whittaker *et al.* 1992a; Fig. 3b). Strand-line and interior habitats are distinguished by an outer and inner circle, and the fourth figure identifies constraints on further colonisation.

Examples of the impact of hurricanes and cyclones on the forests of the Caribbean and the Solomon islands have demonstrated the occurrence of interactions between habitat dynamics and disturbance. Such interactions are increasingly being recognised as an important part of island biogeography (Seagle & Shugart, 1985; Villa *et al.*, 1992), and in the case of Krakatau, disturbance plays an integral part in shaping the recolonisation process. For instance, since Anak Krakatau's emergence in 1930 several episodes of intense volcanic disturbance have drastically impacted on the successional development, affecting large areas of Sertung and Panjang. It has been claimed to have led to a set-back and divergence of their succession (Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker *et al.*, 1992a), with an associated reduction or at least slowing of their diversification.

1.3 History of vegetation succession and description of present vegetation

The history of volcanic activity is described in CHAPTER 2, and it need only be mentioned here that the catastrophic eruptions, which culminated on the 27th of August 1883, left the Krakatau islands much altered in shape, mantled in pyroclastic deposits, and effectively sterilised. A unique natural experiment of biogeographical and ecological importance was created (Whittaker *et al.*, 1989; Thornton, 1996). It was recognised as such and immediately attracted interest from geologists, botanists and zoologists. With Verbeek's first visit in October 1883 a phase of scientific exploration was initiated which was to last until the mid 1930s. Between then and 1979 only one more significant survey of the flora was carried out by Borssum Waalkes (1960) in 1951/52, and two brief surveys of Anak Krakatau in 1958 and 1963 took place (Fosberg, 1985). The 1979 Hull University 'Krakatoa Centenary Expedition' in collaboration with the Herbarium Bogoriense and the Institute Pertanian Bogor initiated renewed intensive studies of the flora and fauna which continued throughout the 1980s, and up to the present day. Apart from Whittaker's group at Oxford University and the Herbarium Bogoriense, other institutions involved in the study of the Krakatau islands have been Kagoshima University, Japan, King's College, London, UK, Leeds University, UK, and La Trobe University, Australia, and others.

First visits by Verbeek in October 1883 (Verbeek, 1885), who was the first to reach the summit of Rakata after the eruption, and Cotteau in May 1884 (Whittaker *et al.*, 1989) failed to find any plant life on the islands, and concluded that the eruption with its deposition of vast quantities of hot ash and pumice totally sterilised the island group. This

view was largely unchallenged until Backer's 'polemic publication' (Schröter, 1935) was issued in 1929 (see below).

The history of vegetation succession will be described for Rakata, Sertung, Panjang and Anak Krakatau in turn. For Panjang and Sertung the vegetation succession for the period after Anak Krakatau's emergence in 1930 will be described separately. Reference will be made to the various debates concerning the causal factors of forest divergence between Rakata, and Sertung and Panjang.

Rakata (1883-1995)

After Cotteau's visit in 1884 the next biologist to visit the islands was Treub in 1886. He was the first to find plant life, and in the interior it consisted of blue-green algae, ferns, and some grass species. In total he found 24 vascular plant species of which 11 were ferns. He also found six species of the blue-green algae (Cyanophyceae). These formed a gelatinous and hygroscopic layer, which he regarded as crucial in providing a colonisation medium for the first fern spores, by ameliorating the harsh conditions on the pumice substrate (Penzig, 1902; Backer, 1929; Docters van Leeuwen, 1936). In general Treub's collection was restricted to the beach on the West side of Zwarte Hoek, and to some lower ravines and ridges of the North-west of Rakata (Fig. 1.5; Fig. 2.2). The development of beach vegetation seemed to have only just started, and only nine species, which later became part of a beach association, were found (e.g. *Erythrina orientalis*, *Calophyllum inophyllum*, *Scaevola konigii*, *Ipomea pes-caprae*, *Hernandia peltata*, and two *Cyperaceae*). The higher altitudes were not explored, but it was judged from observation with field glasses that vegetation cover consisted predominantly of ferns.

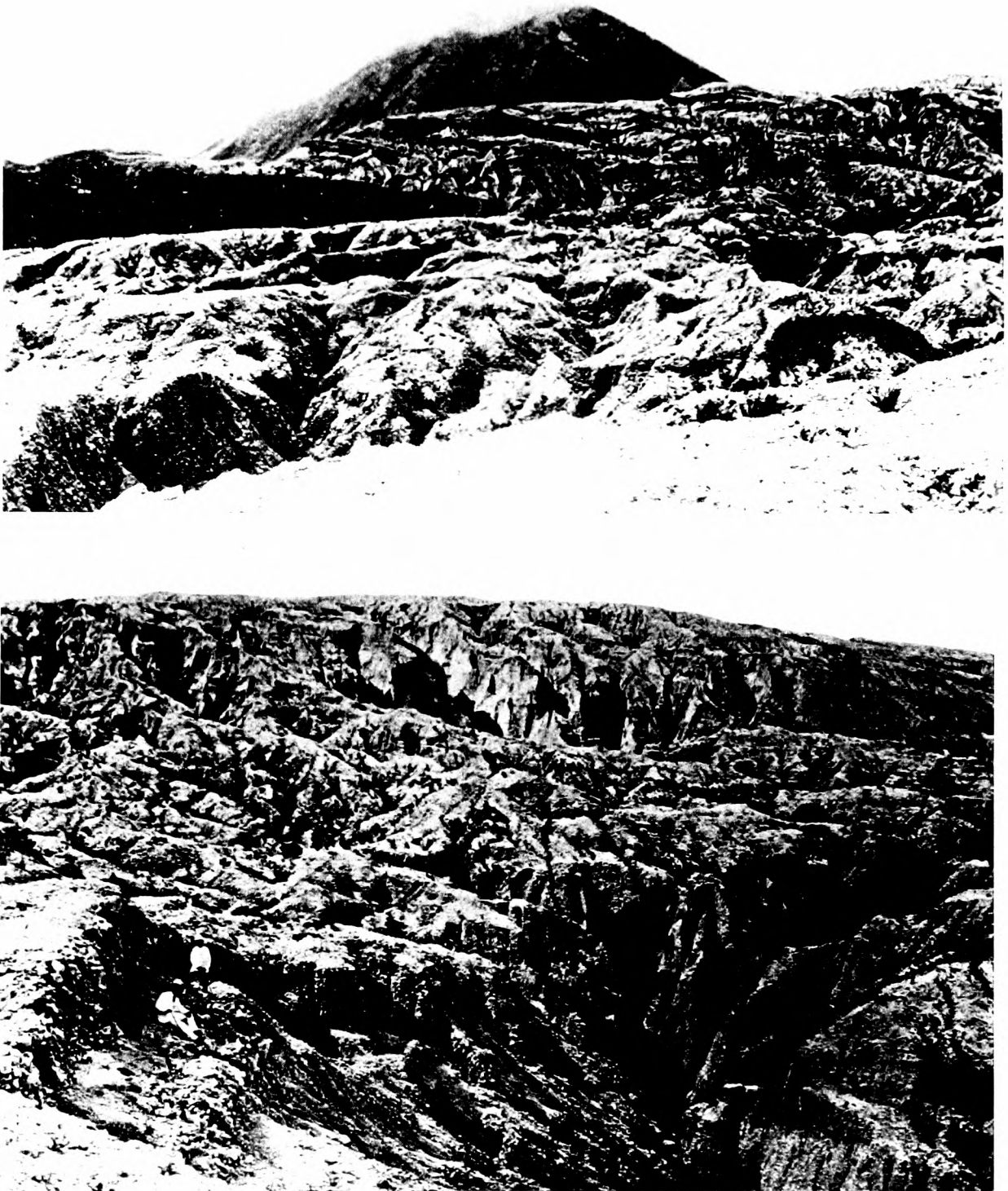


Fig. 1.5: The North-western side of Rakata near Zwarte Hoek in June 1886 during Treub's expedition. Note the general lack of vegetation and the heavy erosion of the pyroclastic deposits in the short span of three years (reproduced from Docters van Leeuwen, 1936). See Fig. 2.2 for the location of Zwarte Hoek.

Backer (1929) declared this survey as unrepresentative and argued that many species could have been missed particularly on the South and South-eastern slopes, which he thought were more protected from the effects of the 1883 eruption. In response to this criticism, Docters van Leeuwen argues that "up to 1919 and even later it was a striking fact that the vegetation was very monotonous". One could wander for hours through the ravines and over ridges without finding a new species, after having collected everything at the beginning of the excursion" (Docters van Leeuwen, 1936; p. 86). This coincides with Treub's observation that the significance of the plants in the recolonisation did not lie in the number of species, but in the large number of individuals (Docters van Leeuwen, 1936; p.95). One cannot, however, claim that the species totals of any of the surveys of the older islands are complete (Whittaker *et al.*, 1989).

In the interior of Rakata, eight phanerogams were found 'isolated here and there' (Docters van Leeuwen, 1936: p. 95) and Docters van Leeuwen was particularly interested in the fact that two true littoral species were found inland (e.g. *Messerschmidia argentea* and *Widelia biflora*). This was most likely due to the enlargement of the beaches in numerous places. However, he generally noted that on Krakatau many species often grow in places where they are never found in Java (Docters van Leeuwen, 1936; p. 90 & p. 248). This can largely be attributed to the initial lack of competition, which means that species can grow in habitats other than their realised niche on the mainland. This is illustrated by *Cyrtandra sulcata* which normally grows in the understorey, but which was part of the early vegetation of Krakatau (first recorded 1908), growing in full sunlight from 300 m to the summit until it was subsequently crowded out mostly by *Neonauclea calycina* (see below).

Schimper & Faber (1935) and Docters van Leeuwen (1936) hailed Treub's early findings of predominantly wind-dispersed inland species (six out of eight species; Ernst, 1907) as very important. They argue that it refuted the view held until then that succession on isolated islands proceeds from the initial colonisation of the beach, with plants then spreading inland and not simultaneously on the beach and the interior by different plants (Ernst, 1907). However, just this process was found on Krakatau, and thus colonisation appeared not to have followed the previously assumed order of thalassochorous, zoochorous and then anemochorous plants. Similar to the facilitation idea of Clements (Connell & Slatyer, 1977), Treub thought that the ferns were crucial in improving the conditions for more phanerogams to take hold on the island.

By 1897, when Penzig (1902) visited all three Krakatau islands, distinct plant-associations were already discernible. Nearly three times as many vascular plants were found as in 1886, and many changes not only in species but also in physiognomy had taken place within the 11 years. However, Penzig (1902) regarded the development as rather slow, and Docters van Leeuwen thought this understandable considering that in the beginning only plants adapted to harsh and very sunny conditions could grow (Docters van Leeuwen, 1936; p.109). In the lowland interior most of the ferns had been replaced by a dense savanna grassland made up of three grass species (*Saccharum spontaneum*, *Pennisetum macrostachyum*, and *Neyraudia madagascariensis*; Docters van Leeuwen, 1936), none of which were mentioned to be dominant. According to Backer (1929) the new grassland had "much the same aspect as young secondary vegetation in Java in rather moist climates" (p. 127). Ernst (1907) describes this association as 'jungle-like' and often over 2 m high, and Penzig (1902) points out that trailers, such as *Ipomea pes-caprae* which are normally found on the beach, hampered progress. Further up in the hills, an association was formed by smaller grasses with numerous ferns and a few scattered phanerogams.

Penzig suggested that of the 53 phanerogams present in 1897, 32 (60%) were sea-, 17 (32%) were wind-, and 4 (7.5%) animal-dispersed, whereas in 1886 Treub found no animal dispersed species. These figures show the initial great dominance of the sea- and wind-dispersed component, and Docters van Leeuwen (1936) suggests that sufficient trees and fruiting plants were not present to attract a large number of frugivorous birds. Thus, the animal-dispersed component of the flora was at that time still the smallest.

A brief visit by Valeton took place in 1905. Apart from collecting at Zwarte Hoek, it was the first time plants were collected on the South-east coast of Rakata. It was not a complete botanical survey, but 17 new species were found. For example, *Ficus fistulosa*, and *Neonauclea calycina* were new to the island group, while *Macaranga tanarius*, and *Ficus fulva* were new to Rakata, having already been found in Panjang 1896. These were to become the most important components of the earliest closed forests on the islands. Also it seems that considerable changes must have taken place in the span of a few years. For instance, most of these new species were woody and eight of them endozoically dispersed.

In 1906, a survey was carried out by Ernst who was accompanied by Backer and others (Ernst, 1907). They visited Rakata and very briefly Sertung (approx. one hour). For the first time collecting was carried out on the East-coast of Rakata and Ernst expressed great

surprise at finding the island covered by dense vegetation (Ernst, 1907; Docters van Leeuwen, 1936). The development of plant-associations had further continued, and instead of three associations it was now possible to distinguish five. The *Pes-caprae*, and the *Barringtonia* formation, a mixed forest zone with *Casuarina equisetifolia*, the grass-steppe, and the fern association which had been pushed further up the mountain (Docters van Leeuwen, 1923). The *Barringtonia* and the mixed forest zones were the additions since 1897. The composition of the *Barringtonia* zone had, however, not reached the species richness of the same formation found in either Java or Sumatra (Docters van Leeuwen, 1936), and the mixed zone consisted of only very few tree species such as, *Terminalia catappa*, *Ficus fulva*, and *Ficus fistulosa*.

On the South-east coast of Rakata a zone of woodland with many 12-15 m high *Casuarina*, had developed discontinuously behind the *Pes-caprae* zone. These were densely covered in climbers, such as *Cassytha*, *Vigna* and *Canavalia*. *Cocos nucifera* were also found. There was a large drift-zone area on the South-east-coast and the beach seemed to be enlarging, since the beach vegetation was composed of elements of different ages with the youngest nearest to the beach (Docters van Leeuwen, 1936). The grass-steppe formed a very wide band reaching from behind the beach formation up to the hills, and the isolated clusters of trees were more numerous than at the time of Penzig's visit; Docters van Leeuwen (1923). Forest-like patches formed half-way up the mountain in the ravines, and shrubs and trees were seen scattered right up to the summit. An attempt was made to climb to the summit, but they only reached an altitude of approximately 50 m, hampered by dense grassland inhabited by biting red and black ants. From his findings of the 1906 expedition, Ernst (1907) comments that the addition of new phanerogam species was still equally divided between interior and beach species, and that the species were of a generally wide distribution in the Malesian region.

Backer and the topographical service visited the islands in 1908. During this visit he came to the same conclusion as everybody else, namely that "the results of all researches have fully confirmed the presumption that the old flora has been totally destroyed, so that the new flora must exclusively consist of introduced elements" (Jacobson, 1908 in Docters van Leeuwen, 1936). However, he later totally rejected that sterilisation had taken place and tried to prove the opposite (see Backer, 1929).

The 1908 expedition also tried to climb to the summit, but they only reached an altitude of 400 m. Nevertheless, contrary to his claims that "tens or hundreds of new species" must have been missed when only exploring the lowlands (Backer, 1929; Docters van Leeuwen, 1936, p. 118), only 10 new species were found. As mentioned earlier, the ravines were wooded and Backer found them to be very dense and species poor, with many individuals of *Macaranga tanarius*, *Pipturus argenteus* and *Ficus fistulosa*. A striking fact is that the trees between 300-400 m were much taller (15-20 m) than lower down (10-15 m). This, Backer (1929) argued later, was supposed to confirm his claim that at higher altitudes, where the ash-cover was thinner, plants had survived and resprouted or germinated from the seed bank, and then spread downwards. Whittaker *et al.* (1995) found viable seeds of mainly *Villebrunea rubescens* in Sertung and Panjang soils that were buried by eruptions of Anak Krakatau between 1930-1935. However, the exposure of many buried carbonised tree remains on Rakata is testimony to the intense heat of the 1883 ejecta unlike the ash-fall of Anak Krakatau's subsequent eruptions. So, while some propagules may have survived, it is generally regarded as very doubtful that a regeneration from pre-1883 flora could have taken place to the extent claimed by Backer (Flenley & Richards, 1982; Whittaker *et al.*, 1989). Moreover, incomplete sterilisation does not, as claimed by Backer (1929), invalidate the importance of Krakatau as a unique natural experiment of recolonisation and succession of an isolated island habitat (Whittaker *et al.*, 1995).

Between 1919 and 1932, one of the most intensive and regular periods of study took place under Doctor van Leeuwen's initiative. In this period he probably observed the most important changes in the vegetation development: the change from an open grass-steppe inland formation to closed secondary forest.

By 1919, the greater part of Rakata was still covered in grass-steppe (Fig. 1.6), whereas the higher parts and the ravines were covered with woodland and considerably fewer ferns. In 1919, the summit was also reached for the first time by a botanist, since Verbeek's visit in October 1883, and above 400 m a.s.l. a new community was found. It was dominated by *Cyrtandra sulcata* with a thriving epiphytic flora. On Rakata Docters van Leeuwen (1936) found the plains and slopes of the South and South-east part to be most developed. This coincides both with Backer's (1929) claim and with many later observations (R.J. Whittaker, pers. comm.; Partomihardjo, pers. comm.; pers. obs.). Furthermore, the vegetation in the moist ravines appeared to have developed faster. Initially, woods dominated by *Macaranga tanarius*, *Pipturus argenteus*, *Ficus fulva*, *Homalanthus populneus*, and *Leucosyke*



Fig. 1.6: South-east side of Rakata in 1919 showing the savanna-like vegetation in the lowlands with clumps of trees (mainly *Macaranga tanarius*, *Ficus fistulosa*, and *Pipturus argenteus*; reproduced from Docters van Leeuwen, 1936)

capitellata were present in the lower altitudes, whereas above 150 m other *Ficus* species, *Neonauclea calycina*, and *Radermachera glandulosa* (with many shrubs in the understorey) had become more important. With forest closure occurring in the lowlands by the late 1920s, the more heliophilous ferns, such as *Nephrolepis biserrata*, were crowded out (Docters van Leeuwen, 1923; 1936). Instead, many new species of ferns, which were adapted to moist and shady conditions, increased rapidly in importance (Whittaker *et al.*, 1989).

The *Cyrtandra* formation quickly declined in importance and was, by 1924, displaced to habitats above 600 m altitude, and replaced by forests dominated by *Neonauclea calycina*. By 1929, *Cyrtandra* could only be found above 700 m a.s.l. but even there it was largely replaced by *Ficus fistulosa* and *Neonauclea*. As mentioned *Neonauclea* was first found in 1905 by Valeton, and in 1908 one specimen was discovered at 330 m a.s.l. by Backer (1929). It increased rapidly in importance, and by 1924 the forest above 400 m a.s.l. was

largely dominated by *Neonauclea*. Below that altitude young *Macaranga-Ficus fulva* forest could be found, which by 1928 had almost completely replaced the grassland areas.

No botanical work was carried out on Rakata after visits in 1933/34 by Boedijn (who mainly collected lower plants, Whittaker *et al.*, 1989) , until 1951/52 under van Borssum Waalkes (1954; 1960). He found that the so-called *Pes-caprae* formation had not changed since the 1930s. Even today this formation is essentially still the same, with few new immigrations and hardly any species loss (Whittaker *et al.*, 1989). It can be seen as an 'auto-succession' constantly replacing itself (Whittaker & Jones, 1994b).

A noteworthy development was the rapid decline of the *Casuarina* forest on the South coast. *Casuarina equisetifolia* is a true pioneer species that can not perpetuate itself unless open habitat with bare soil is regularly being created. Therefore, already in 1922 the *Casuarina* woods had largely been superseded by *Terminalia catappa*, *Macaranga tanarius*, *Hibiscus tiliaceus*, etc., and only a few specimens, which were heavily infested with climbers (e.g. *Ipomoea gracilis*), were left. However, on a newly formed strand-bank many young *Casuarina* of between 0.5 to 3 m tall had already formed a dense new wood in front of the old one, and, as speculated by van Borssum Waalkes (1960; p.22), might have been the '40 cm thick' specimens observed by him in 1951. The *Casuarina* on the South coast today are very much like the old ones found by 1922 and are probably the third or fourth generation, with the only difference that no new *Casuarina* seem to be able to develop due to the continued rapid erosion of the coastline (pers. obs.).

Curiously, in 1952 Borssum Waalkes (1960) did not find solely closed forest behind the stands of *Casuarina*, on the western part of the South-east side, instead open areas with *Saccharum spontaneum*, and *Nephrolepis biserrata* were present. Yet, Docters van Leeuwen (1936) indicates that the area had become closed forest in 1928 with *Saccharum* steppe only remaining in areas disturbed by landslides. However, the area found by Borssum Waalkes was on the flat ground, and he attributes this regression in vegetation largely to human influences. The flat area near the South-east coast today also has a very disturbed and stressed character, which does, however, not seem attributable to human disturbance. This was the area that suffered particularly under the 1994 drought (see CHAPTERS 2, 4 and 5).

Borssum Waalkes (1960) observed that it was nearly impossible in 1952 to distinguish sharply between the different vegetation types, but he divided the Rakata vegetation into five zones according to altitude. The first one reached from the coast to 50 m a.s.l., within it *Terminalia catappa* and also *Neonauclea calycina* were common. Throughout the 1920s the latter species gradually increased in abundance, and Docters van Leeuwen (1936) argues that the dense shade cast by its crown was the most important factor in the crowding out of the *Cyrtandra sulcata* association. By 1951, however, it had also become by far the most common tree species all the way from the coast to the summit, and the second zone from 50-200 m a.s.l. was indeed dominated by larger *Neonauclea*. The third zone from 200-500 m a.s.l. had in addition other tree species; mainly *Ficus variegata*, *F. retusa*, *F. tinctoria*, and *F. pubinervis*. The fourth zone from 500-750 m a.s.l., which is enveloped in cloud for most of the day, and therefore very humid, was characterised by thick moss covering on the trees. The tree layer had basically the same composition, but the individuals of the *Ficus* species were generally much larger than in the preceding zone. In the fifth zone between 750 -813 m a.s.l., he found mainly dense thickets of shrubs, with only scattered, stunted trees and some dense tussocks of *Saccharum spontaneum*. The most striking change was that instead of *Cyrtandra sulcata* as the absolute dominant, the semi-epiphytic shrub *Schefflera polybotrya*, had by then become very common. In addition to those two species, *Leucosyke capitellata*, *Clidemia hirta* and young specimens of *Neonauclea calycina* and *Macaranga tanarius* were also quite common. He reported the moss and epiphyte flora to be relatively rich.

Today, *Schefflera polybotrya*, is still common, though not as common as Borssum Waalkes (1960) suggested it to be in 1951. The dominant tree species of the summit area today is *Saurauia nudiflora* (first found on Rakata in 1929) , with *Vernonia arborea* (first found on Rakata in 1922 at 400 m a.s.l.) also being common (Jones *et al.*, 1993). These species were not mentioned by Borssum Waalkes (1960), and must have increased in abundance since his last visit.

On Rakata, *Neonauclea calycina* is still today the canopy dominant (Fig. 1.7) of the areas between 50 and 500 m a.s.l., in three permanent plots ranging from 30% at 500 m a.s.l., and 42% at 100 m a.s.l. on the eastern side, up to 68% species frequency at 190 m a.s.l. in the North-west near Zwarte Hoek (dbh $\geq$ 5 cm ; Whittaker & Jones, 1993). However, the fairly even-aged stands of this medium stature (20-25 m), wind-dispersed tree, do not



Fig. 1.7: *Neonauclea calycina* dominated forest in lowland Rakata today. Picture was taken in Whittaker and colleagues' permanent plot R1.

appear to be replacing themselves in so far as can be judged from the understorey (Bush *et al.*, 1992). In the 500 m a.s.l., 100 m a.s.l., and the 190 m a.s.l. permanent sample plots, the sapling layer only contains 3, 2 and 12% of *Neonauclea* respectively, and maybe only in the vicinity of the latter plot can a fairly high abundance of *Neonauclea* be maintained in the near future. Instead, *Ficus* species seem to play an important role in the regeneration layer of these forests. For instance, in 1992, 31% of the sapling individuals in the 100 m a.s.l. plot were made up of six *Ficus* species. At the 500 m plot 25% of the saplings were *Ficus* species, but 18% of the saplings were represented by *Vernonia arborea*, a typical higher altitude component (Whittaker & Jones, 1993). These figures are likely to be much changed now, particularly after major disturbance to the 500 m plot in 1993, and generally for all plots because of the drought in 1994.

This evidence seems to indicate that a very significant reduction in *Neonauclea*'s importance on Rakata is likely in the future, and Bush *et al.* (1992) suggest that no single species is likely to attain the same dominance. They do not agree with Tagawa *et al.*'s (1985) suggestion that *Dysoxylum* forest is the most advanced community, and that both *Timonius compressicaulis* and *Neonauclea calycina* forests are going to change into *Dysoxylum* forest. *Dysoxylum* is the canopy dominant of large stretches of Panjang and Sertung, and the development of this dominance pattern has been argued to be linked to successional set-back from volcanic disturbance from Anak Krakatau (Whittaker *et al.*, 1989; Bush *et al.*, 1992; see below). Rakata has, however, been unaffected by ash-fall, and its development has been uninterrupted since 1883 (Whittaker *et al.*, 1992a). Thus, the disturbance regime and its potential influence on succession on Rakata have been very different from that of the other two islands. *Dysoxylum* appears to be increasing on Rakata, mainly in the near coastal areas, but is part of a more diverse mosaic, not comparable to Panjang and Sertung (Bush *et al.*, 1992). The question of *Dysoxylum gaudichaudianum* performance, abundance and distribution will be addressed in CHAPTERS 4 and 5.

Sertung and Panjang (1883-1930)

Sertung and Panjang have less habitat diversity than Rakata because of their much lower altitude. Therefore, no high altitude component of the flora could develop. Without actually visiting these two islands in 1886, Treub suggested that Sertung and Panjang were still without vegetation (Ernst, 1907). However, as all three islands suffered the same fate and are equally isolated from the mainland, it is difficult to believe that Panjang and Sertung should still be bare when Rakata had already begun to develop a fern cover and strandline vegetation.

As mentioned above, the first brief botanical visit to Sertung took place in 1897 when Penzig (1902) landed on the North-east coast. It is a flat area forming a spit, which was at that point still small, but was constantly being enlarged from long-shore drift of pumice material, eroded from the pumice-cliffs of the South- and West-coast (Bird & Rosengren, 1984; see CHAPTER 2 and Fig 2.11). As at the Zwarte Hoek beach a *Pes-caprae* formation had already developed and additionally a small *Casuarina* wood of 5-6 m height was found. The interior was not visited by Penzig (1902), but he describes it as a closed grassland, very similar to Rakata.

After a brief visit to Sertung in 1906, Ernst (1907) concluded that the succession on Sertung proceeded much the same way as on Rakata. However, Panjang he thought to have developed slower, although he did not actually land there. He found many *Carica papaya* near the North-east beach of Sertung, and it seemed that the beach vegetation, which consisted of a well-developed *Pes-caprae*, and developing *Barringtonia* formation, was much the same as on Rakata. Following his visit in 1919, Docters van Leeuwen (1936) had a similar impression to that of Ernst in 1906, i.e. the successional development of Sertung was proceeding along the same lines as on Rakata, except that he thought it was slower than Rakata.

Backer (1929), during his brief visit to the flat North-east tip of Sertung in 1908, found that 7 patches of *Casuarina* wood had developed. By 1919, *Casuarina* woods covered the flat area completely, but were comprised of different aged stands. On the constantly enlarging eastern side the youngest trees were found, whereas on the eroding western side the oldest specimens were found. Docters van Leeuwen (1936) commented that no mixed woodland would be able to develop on the West side, since the area wears away constantly. Still today the spit - or the remainders of it, after its breach in 1994, and its almost complete disappearance in 1995 - is covered with *Casuarina*. The constant shifting and changing in shape has always provided new, sandy areas for colonisation, whereas in the stable habitat *Casuarina* were quickly replaced by species such as *Macaranga tanarius*, *Pipturus argenteus*, *Terminalia catappa*, and *Morinda citrifolia*, and later on also by *Neonauclea calycina*. By 1920, 12-20 m tall *Casuarina* found further inland were already standing further apart, and many dead ones littered the ground. *Macaranga tanarius* at that time was by far the most abundant tree species in the regeneration layer. By 1929, this flat area was replaced by "an impenetrable mixed forest" (Docters van Leeuwen, 1936; p.176). The heliophilous fern *Nephrolepis biserrata* was generally very common in the more open areas, and is still ubiquitous today.

In 1920, Docters van Leeuwen (1936) explored for the first time the hills of the interior of Sertung, which is dissected by many deep ravines. Most of the area was still covered by grass-steppe, but some *Macaranga tanarius*, and higher up also some *Ficus* spp. were found. Docters van Leeuwen (1936) suggested that *Macaranga tanarius* was the pioneer that first formed small groves and shaded out the grasses, and then allowed other species, such as *Pipturus argenteus*, *Ficus fulva*, and *Ficus fistulosa*, to grow in the grass free patches. In 1920, on the level part on the North point and in the hills, *Neonauclea calycina*

was already present, and a specimen of 40 cm girth was found. By 1930 this species was quite frequent, although not as common as on Rakata. An excursion to some ravines near the South of Sertung in 1929 found the same species mix as in the North, except that *Calophyllum inophyllum* and *Terminalia catappa* were more common. By then, trees occurred up to the upper edges of the gully walls and *Saccharum spontaneum* had nearly completely disappeared.

One very interesting feature of Sertung was the development of a saltwater lagoon in the area of the spit, where a small patch of mangrove (including *Excoecaria agallocha* and *Lumnitzera racemosa*) occurred for a while. By 1920 another lake, but this time with fresh water, had come into existence close to the other lake (see Fig. 2.11). Due to the constantly changing shape and movement of the spit (Bush *et al.*, 1992) the lakes and the mangrove community were eventually lost. In general, the absence of accreting beaches has prevented the development of a permanent mangrove community on the Krakatau islands.

As indicated above, the exploration of Panjang seemed to have been somewhat neglected initially, and visits were never as frequent as on Rakata (Table 1.2). Nevertheless, it is the smallest, and most accessible island, and one can assume that survey coverage was fairly good. The first collecting on Panjang was undertaken in 1896 by Boerlage, and some further collecting was carried out by the topographer Nolthenius, who was part of a survey team that stayed on Panjang until the beginning of 1897 (Backer, 1929; Docters van Leeuwen, 1936). This was followed by a visit by Penzig (1902) in 1897. Docters van Leeuwen did not land there until 1928, and it was only in the period between 1928 and 1932 that better vegetation descriptions of Panjang became available.

Several comments by Ernst (1907), and Docters van Leeuwen (1936) seem to indicate that successional development on Panjang was initially slower than on the Rakata and Sertung. Yet, Ernst never went there and Docters van Leeuwen first visited only in 1928. Important animal dispersed pioneer species, such as, *Macaranga tanarius*, *Ficus hispida*, and *Ficus septica*, were, however, found there as early as in 1896/7. At that time, the *Pes-caprae* formation, and a few areas of *Casuarina* forest were comparable in their development to Rakata, but ferns seemed less important. In 1906, the interior grass-steppe gave from a distance the impression of having fewer trees and shrubs than on Rakata (Ernst, 1907).

Table 1.2: Plant collecting surveys on the Krakatau islands (adapted from Whittaker *et al.*, 1989, and pers. comm., T. Partomihardjo pers. comm; and own data)

<i>Collection period</i>	<i>Principal collector*</i>	<i>Year</i>	<i>Rakata</i>	<i>Panjang</i>	<i>Sertung</i>	<i>Anak Krakatau</i>
<i>Time spent by collector (days**)</i>						
no plant seen	(Verbeek)	1883	+			
1886	(Cotteau)	1884	<2	0.5	0.5	
	Treub	1886	3 or 4			
1897	Boerlage	1896			1	
	Penzig	1897	0.5	<1	2	
1908	Ernst	1905	+			
	Ernst	1906	1	1h		
	Backer	1908	2	<1	1	
1920	DvL	1919	5.5	3		
	DvL	1920		7		
1922	DvL	1921		<1		
	DvL	1922	7			
1924	DvL	1924	7			
1929	DvL	1928	9	2	1	
	DvL	1929	3	1	2	
1932	DvL	1931	2	1		
		1932			3	1h
1934	Boedijn	1933/34	+	+	+	1h
1951	vBW	1951	9	2h	0.4h	1h
	vBW	1952		2h		1h
1979	Hull 1	1979	16			
1982	Tagawa	1982	7	<11	<7	<5
1983	Hull 2	1983	6	9	3	7
	Bush	1984	+	+		
1989	Partomihardjo & Whittaker <i>et al.</i>	1989	c.7	3	3	1
1992	Partomihardjo & Whittaker <i>et al.</i>	1992	c.7	2	3	2
1993-1996	Partomihardjo (Oxford)	1993	c. 12	c. 7	c. 4	
	Partomihardjo (Oxford)	1994	c. 7	c. 4	c. 3	2h
	Partomihardjo (Leeds & Oxford))	1995	9	1		1
	Partomihardjo (Leeds & Oxford)	1996	12	9	2	1

* DvL = Docters van Leeuwen; in 1932-34 Boedijn made six visits to the group, each of 5 or 6 d, but collected predominantly lower plants; vBW = van Borssum Waalkes; Bush collected a few species as part of the 1984 La Trobe Expedition, which have been included in the 1983 survey.

** units are days unless marked h = hour or + = short but unspecified time.

note: from 1989 full species list was available and Dr Partomihardjo (Botanist; Herbarium Bogor) had accumulated knowledge of the flora, so that through the 1989-1996 period especially new species and 'lost' species were targeted; BUT particularly between 1993-1996 plant collection was not the main focus of the work, and in that period days on the islands are representative of Partomihardjo's time spent on the Islands with involvement in other vegetation sampling.

During his first visit in 1928, Docters van Leeuwen (1936) found, behind the North-east beach, a similar mixed woodland as on Rakata. Yet, he did not think the interior vegetation quite as developed, and suggested that it gave "the same impression as that of Verlaten [Sertung] island a few years before" (Docters van Leeuwen, 1936; p.180). He also observed that most of the grass-steppe was found to occur on the steep southern and western slopes. Open patches of grassland could also be discerned from film footage of the team of volcanologist observing the birth of Krakatau in 1927 from an observation post on top of Panjang (Bemmelen, 1929). *Nephrolepis biserrata* was growing vigorously, and was often responsible for the crowding out of the grasses. In 1929, he observed in most areas transitional stages between the grass-steppe and mixed forest, and by 1932 forest closure was more or less complete except on a few ridges and landslide sites. Also (as with Sertung) the mixed forest near the coast was found to be much more diverse than in the hills, which is probably explicable by the movement of dispersers.

As suggested by Whittaker & Jones (1994a), it is plausible that birds and bats would have first been attracted to beach forest that developed early on in the succession, and that then the more diverse seed rain subsequently led to the establishment of mixed forest in areas adjacent to the beachline. Bats would have been attracted for instance to *Terminalia catappa* and *Calophyllum inophyllum*, and would have helped to spread these diplochorous species inland, and at the same time this may have led to increased dispersal of *Ficus* and other seed species. In contrast, for birds the strandline forest may have provided an attractive stop-over place and perches, also contributing to the increase in diversity in near-coastal forests, when seeds, probably carried from Sebesi or the mainland, were defecated. However, similar to Rakata many bird-dispersed species also appeared in the hills of Panjang, and included, apart from the early pioneers, species such as *Antidesma montanum*, *Ficus callosa* and *Timonius compressicaulis* (now also known to be bat dispersed; L. Shilton, pers. comm.). The latter was described as ubiquitous, whereas on Rakata it was only found on the North-west side at this time. In 1932, the large canopy tree *Dysoxylum gaudichaudianum* was also recorded for the first time, and adult and young specimens were found to grow 'gregariously' (Docters van Leeuwen, 1936). This species and *Timonius compressicaulis* had become the canopy dominants of large areas of Panjang and Sertung by 1982, when the next survey was carried out by Tagawa *et al.* (1985). At the beginning of the 1930s, comparable to the situation on Sertung, *Neonauclea calycina* was found on Panjang. It was predominantly growing in the darker ravines.

Anak Krakatau (1930-1995)

The vegetation of Anak Krakatau was not studied as part of this research. Thus, its vegetation development will only briefly be described from the literature.

After the events of 1883, volcanic activity recommenced in June 1927, and after the development of three temporary cones, Anak Krakatau - the Child of Krakatau - established itself permanently in 1930. Since that time, intermittent severe volcanic disturbance, and frequent ash-fall (Whittaker *et al.* 1989, 1992) has affected the vegetation of Sertung and Panjang. These islands are both the closest to Anak Krakatau, and downwind from it during the West and East monsoon season respectively. In contrast, Rakata has not been directly affected. The history of Anak Krakatau's eruptions is described in CHAPTER 2, and its postulated effect on the successional development of Sertung and Panjang is described in a separate section below. This section describes the vegetation development and the intermittent setbacks on Anak Krakatau itself. It is illustrative to the understanding of the successional history of the Krakatau islands as a whole to describe Anak Krakatau's history of vegetation development, and the theoretical importance attached to it.

There has been great interest in studying the vegetation development of this new habitat for recolonisation and succession within the Krakatau archipelago. Some researchers have attached considerable value to seeing Anak Krakatau as an analogue to the other island's development directly after the eruption in 1883 (Thornton, 1984; Thornton *et al.*, 1992; Zann *et al.*, 1990). However, Whittaker and colleagues have stressed that there are differences of history, environment, and ecology (Bush & Whittaker, 1991; Whittaker *et al.*, 1989). For instance, since 1930 the developing vegetation has several times been either totally destroyed or severely damaged by further eruptions (e.g. in 1932, 1939, 1952/53, 1960/61, 1972, 1979-81, and 1992-1995; (Borssum Waalkes, 1960; Whittaker *et al.*, 1989; Whittaker *et al.*, 1992a; Thornton *et al.*, 1994; pers. obs.), and the island has grown substantially in size and height, from 40 m a.s.l. in 1930 to some 280 m a.s.l. in 1993, and by 1995 estimated to be more than 300 m high (Fig. 1.8; Thornton *et al.*, 1994; pers. obs.). It has also been suggested that the emergence of Anak Krakatau provides new habitat, and may act as a 'window' for survival and/or immigration for open ground species, whose niche availability has been reduced on the other islands because of forest closure (Thornton & Rosengren, 1988; Thornton *et al.*, 1988).

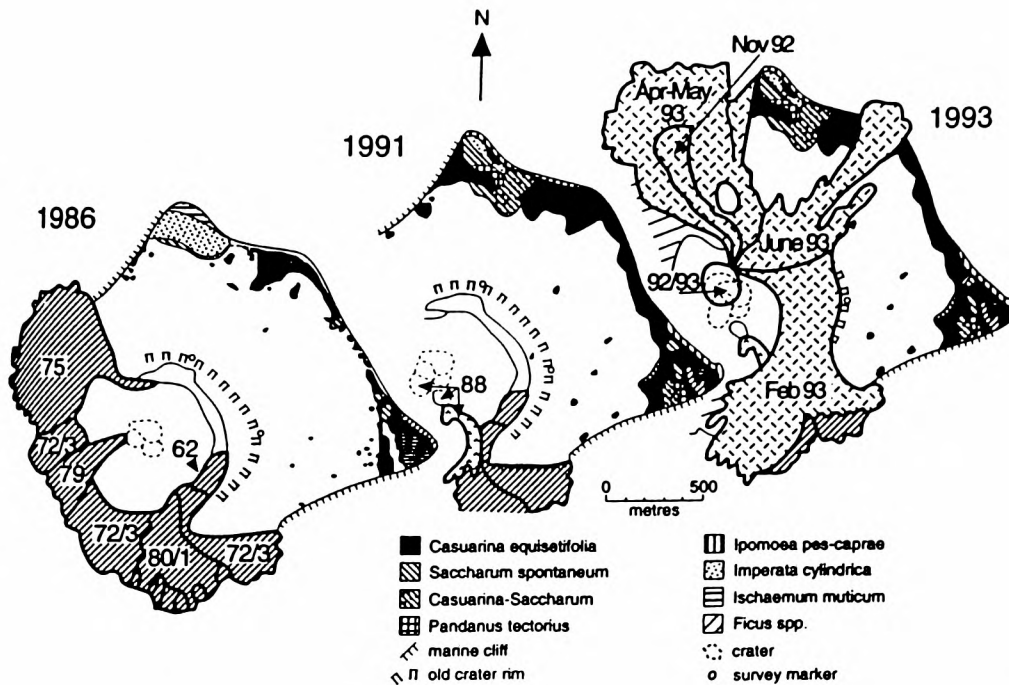


Fig. 1.8: Map showing the different lava flows and the vegetation types of Anak Krakatau (from Thornton, 1996).

Near the beaches and on the northern, north-eastern, and eastern foreland, *Ipomoea pes-caprae* formation and *Casuarina equisetifolia* woodland with *Ficus septica* and *Ficus fulva* have developed (Partomihardjo *et al.*, 1992; Fig 1.9). The slow development of the interior vegetation cover on Anak Krakatau may not wholly be due to the direct effect of eruptions. In fact, the interior is largely unvegetated apart from some *Saccharum spontaneum* clumps. There is a very sharp boundary between the vegetation along the coastal margin on the Panjang side, and the interior. Various hypotheses trying to explain this phenomenon have been advanced. For example, it has been suggested that strong physical (especially hydrological), and/or chemical conditions may be responsible (Whittaker *et al.*, 1989; Whittaker & Bush, 1993). In the case of the former hypothesis, it may be possible that the water-table only rises close enough to the surface near the beaches, and the water availability on the highly permeable ash slopes is insufficient to support vegetation (R.J. Whittaker, pers. comm.). Almost certainly, the lack of inland forest cover, is not due to lack of propagule immigration. The actual rate of immigration during inactive periods has been quite fast; for example, during the period 1983-1991, 53 new plant species were recorded, which represents a 38% increase (Partomihardjo *et al.*, 1992).

In 1932 Docters van Leeuwen and Boedjin (Docters van Leeuwen, 1936) found a few seedlings of typical coastal species on the beaches of Anak Krakatau. Much of that vegetation was killed by the 1932-33 eruptions. In 1947, 3 m tall *Casuarina equisetifolia* were recorded which indicated a previous calmer period, although between 1935 and 1947 it is known that there was at least one totally destructive eruption which occurred in 1939 (Borssum Waalkes, 1960). The *Casuarina* had reached a height of 10 m in 1951 but were reduced to skeletons by 3-5 m of ash-fall in 1952 (Borssum Waalkes, 1954). Much of the recovering vegetation was also reported dead by Fosberg (1985) after the 1960-63 eruptive period, although about 25 species were recorded by him. In 1972-73 heavy eruptions took place, which must have had a substantial impact since 42 species were found in 1971 and only 44 in 1979. It is striking, however, that since then the species totals rose rapidly to 90 by 1983 and 138 by 1991. This is despite the fact that there were two eruptive periods, in 1979-81 and in 1988 (Partomihardjo *et al.*, 1992).

Anak Krakatau's vegetation development is also seen to be different from the older islands in the proportion of its species belonging to different dispersal modes. For example, Anak Krakatau has a very large sea-dispersed component, 52% (1989-1991 data) in comparison to 22% for Rakata (1979-1989 data). On Rakata the sea-dispersed component remained dominant only until about 1920, since when the species number of this component have remained constant at about 50-55 species. Due to its high number of sea-dispersed species, Anak Krakatau has a very well developed littoral flora. Yet, in 1991 Anak Krakatau's wind-dispersed (23%) and animal-dispersed (24%) components (which are most important for the inland flora on the other islands), were only about two-thirds and one-half, respectively, of the size of Rakata's (Partomihardjo *et al.*, 1992). The animal-dispersed component (the most important dispersal type for inland forest species) has, however, grown rapidly throughout the 1980s. For instance, *Canarium hirsutum*, *Dysoxylum gaudichaudianum*, and *Timonius compressicaulis* could be found in 1991. The proximity of Rakata, Sertung and Panjang is likely to influence the development of inland plant communities should the volcano acquiesce for a sustained period. Therefore, it has been suggested that a rather different successional sequence may be anticipated from those recorded post-1883 (Partomihardjo *et al.* 1992), when the nearest source of propagules were the island of Sebesi (12 km distance) and Sebuksu (and some others) and the mainland, Fig. 1.1).

The general colonisation pattern of the Krakatau islands

By 1983, a cumulative total of 455-488 (the range due to uncertain taxonomy) vascular plant species had been found on all Krakatau islands. This compares to 24 by 1886, 69 by 1897, 130 by 1908, 325-326 by 1934, and 352-357 by 1951 (Whittaker *et al.*, 1989). This demonstrates a very rapid increase in the 1920s, and it was shown by the analysis of survey interval effects by Whittaker *et al.* (1989) that this was not just an artefact of increased survey effort. This rapid increase has been attributed to the advent of canopy closure because new habitat for shade-loving species was then created. This led particularly to an increase in the number of pteridophyta from 19 in 1908 to 61 species in 1934. Since at the same time several of the heliophilous pteridophyta were lost, this was a very substantial increase.

Furthermore, throughout the 1920s, the increasing abundance of potential food sources (e.g. the *Ficus* species) is argued to have made the islands a progressively more suitable habitat for birds and bats. This has to be understood as a mutually reinforcing effect (Hoogerwerf, 1953; Thornton, 1984), and is thought to explain the substantial increase in bird and bat dispersed species during this time. Today, the animal-dispersed component is, with 47% of all species, the most specious (Partomihardjo *et al.*, 1992). Nevertheless, the forests have not yet attained maturity. Bush & Whittaker (1991; 1993), argued that hierarchical links between flora and fauna, and habitat diversity and availability conditioned by the disturbance regime; are the most important determinants of island recolonisation. Changes in these variables can thus yield non-monotonic changes of immigration- and extinction-rates. Extinctions have been relatively rare and were shown to be mainly linked to successional processes, such as the loss of many heliophilous species when the open savanna habitat was replaced by closed forest around the late 1920s. Whittaker & Bush (1991; 1993; Fig. 1.3) therefore, questioned the applicability of MacArthur and Wilson's (1967) 'equilibrium theory of island biogeography' and its suggested monotonic rate changes.

The effect of volcanic disturbance on Sertung and Panjang

The birth of Anak Krakatau in 1930 has probably been the single most important event in the shaping of the successional history of Sertung and Panjang. Since then, Anak Krakatau's volcanic activity has been a major factor of disturbance to the forests of these islands and is argued to have deflected their succession (Bush, 1986a; Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker *et al.*, 1992a). Rakata, however, has been seen as an uninterrupted succession, since it gets spared from ash-falls due to the prevailing winds blowing towards Sertung in the dry-season (East monsoon) and Panjang in the wet-season (West monsoon; Dammerman, 1948; Whittaker *et al.* 1989; Bush *et al.*, 1992)

Sertung's forest were the first to be affected by Anak Krakatau. Already by 1928 damage to the north-eastern coastal forest from high waves was reported (Stehn, 1929), and after the 1930 eruptions "the middle part of the island gave the impression as of a European wood in winter" (Docters van Leeuwen, 1936; p.275; Fig. 1.9 & Fig 1.10). Docters van Leeuwen (1936), however, also reported that the ash-fall was not great, and thought not to have been very harmful. Most of the damage was attributed to the effect of sulphur dioxide gas, which he suggested led eventually to large-scale leaf-loss, and death of branches. Yet, synergistic effects of both forms of disturbance can not be ruled out. Moreover, the damage caused by the volcanic activity of Anak Krakatau during that time was not limited to the effects of ash-fall, gas damage or wave action. Earth tremors (22358 were recorded on Panjang in 1928; Whittaker *et al.*, 1992a) and local whirlwinds were thought and observed -to have substantial effects on the vegetation by, respectively, causing landslides in the narrow and steep gullies, and windthrows on the ridges or flat areas, respectively (Docters van Leeuwen, 1936; Whittaker *et al.*, 1989; see CHAPTER 2).

By 1931, it was evident that overall the number of dead trees and shrubs was not actually very great. However, there were large inter-specific differences; for instance, *Carica papaya* suffered up to 50% losses, whereas *Calophyllum inophyllum* seemed to be particularly resistant. Many resprouting species, such as larger specimens of *Macaranga tanarius*, *Ficus septica*, *Ficus fulva*, and *Pipturus argenteus* could be found. In most cases, the damage seemed to have acted much more like the influence of a large gap creation, and a great number of seedlings were reported to have sprung up. *Macaranga tanarius* seedlings were particularly common and were thought by Docters van Leeuwen

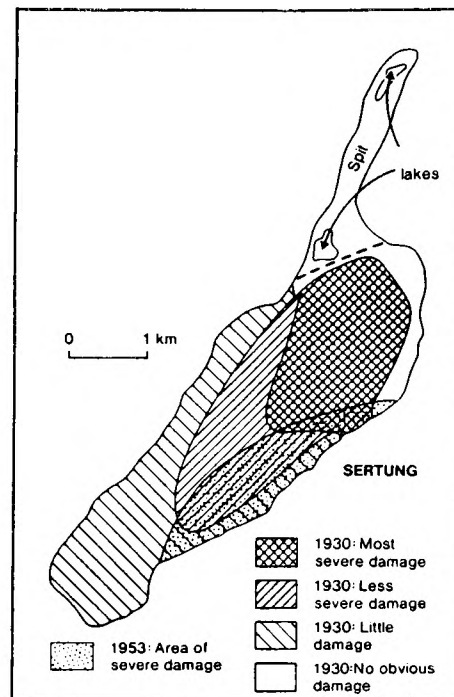


Fig. 1.9: Map of approximate areas of damage on Sertung in 1930 and 1953 as noted by Docters van Leeuwen (1936) and De Neve (in lit, 1984) respectively (figure adapted from Whittaker *et al.* 1989).



Fig. 1.10: Damage from the 1930s eruption to the North-eastern areas of Sertung. Note defoliation and toppling of some trees (reproduced from Docters van Leeuwen, 1936)

(1936) to have come from the seed bank (see CHAPTER 6 for comments on *M. tanarius* seed bank representation). *Saccharum spontaneum* also started to sprout gregariously. It had previously been shaded out from most areas, but rhizomes must have survived (Docters van Leeuwen, 1936). In 1934 and 1935 Sertung incurred blast damage and suffered from ash-fall (Dammerman, 1948; Docters van Leeuwen, 1936), but the state of the vegetation was not directly examined. Only statements such as from Stehn (1935; in Docters van Leeuwen, 1936) that Sertung "looked grey and disconsolate" and that "heavy showers of ash and sand have swept across it" (p.279), give an impression of the immediate damage.

Panjang does not seem to have suffered any substantial damage from the 1930 eruption, and severe damage was only noted after ash falls in 1932 (Dammerman, 1948; see Table 2.2 for chronology). As inferred from the ash stratigraphy, no large-scale deposits of ash, and therefore, presumably no further damage to Panjang's forests appeared to have occurred during the time of eruption in 1934/35 (Whittaker et al. 1992a).

It is unclear whether the eruptions that occurred between the mid 1930s and the 1952/53 eruptions had any effect on Panjang and Sertung, but it is known that a violent eruption in 1939 buried the vegetation of Anak Krakatau (Dammerman, 1948). Both Sertung and Panjang have, however, suffered considerably from ash-fall, gas- and blast-damage, during the eruptions in 1952 and 1953 (de Neve, 1953; Hoogerwerf, 1953; Borssum Waalkes, 1954; 1960; Bush & Whittaker, 1993;). Yet, the damage episodes were neither necessarily simultaneous nor of the same intensity within each island (Whittaker *et al.*, 1992a; CHAPTER 2). Borssum Waalkes (1954) reports that Sertung turned from being entirely green to looking "desolate as if a great fire had swept over it; everything was brown and scorched, and of the trees only the trunks and the stoutest branches were left" (de Neve, 1985; p. 98). He indicated that during these episodes up to 90% of the vegetation was damaged, and that half of Sertung was severely affected (Fig. 1.9), including the highest part, nearest to Anak Krakatau, as was the southern end of Panjang. The *Casuarina* forest of the spit of Sertung was found to be damaged by violent wave-action that was linked to one or more eruptions. Panjang gave a very similar impression to that of Sertung, but on closer inspection the damage was found to be not quite as severe. Also, one month after the 1952 eruption, Borssum Waalkes (1954) observed from the boat that some green patches were left and that on the east-side of Panjang, which faces away from Anak Krakatau, much less tree death had occurred. Near the East coast of Panjang in particular,

Terminalia catappa, and *Casuarina equisetifolia* remained almost unaffected (Borssum Waalkes, 1954; 1960). In contrast to both Panjang and Sertung, Rakata escaped totally unscathed.

Forest divergence

In 1982 (and confirmed in 1983) it was discovered that during the span of 30 years since the last fairly extensive botanical visit by Borssum Waalkes (1960; Table 1.2), the forest composition of Sertung and Panjang had strongly diverged from that of Rakata (Bush, 1986a; Tagawa *et al.*, 1985). However, since the surveys of Borssum Waalkes on Panjang and Sertung were very short (Table 1.2), and he did not penetrate the interior it is possible that the divergence process already began in the 1930s. In 1982, the forests of Rakata were still, as already seen in the 1950s (Borssum Waalkes, 1954; 1960), dominated by *Neonauclea calycina*, whereas large tracts of Sertung and Panjang were found to be dominated by *Timonius compressicaulis* or *Dysoxylum gaudichaudianum* forest (Fig. 1.11 & Fig. 1.12).

Before Anak Krakatau's emergence, Sertung's and Panjang's successional development was in line with compositional changes in lowland Rakata, although perhaps a little slower and there were differences in commonness of particular species. For instance, *Timonius compressicaulis* was found to be more widespread on Panjang than on Rakata (where it was mostly found in the North-west), and at that time it had not been found on Sertung. *Neonauclea calycina* was already quite frequent in the northern flat and hilly parts of Sertung (Docters van Leeuwen, 1936). By 1930, it was also frequently found on Panjang, but appeared generally not as common as in the upper reaches of Rakata. Yet, no evidence of significant forest divergence in the lowland associations was remarked upon by Docters van Leeuwen (1936).

“one will have noticed that in the three islands the associations in the lower parts and the various successions are alike. The vegetation of the higher parts of Mt. Rakata is different, and is absent in the other two islands, since these are no higher than 180 m and 147 m respectively.” (Docters van Leeuwen, 1936; p.256).



Fig. 1.11: An example of *Timonius compressicaulis* forest on the main ridge of Panjang. Note the flaky bark of the *Timonius* trunk and a large specimen of *Elaeagnus latifolia*, a common spiny vine on Panjang.

Despite the absence of botanical observation between 1953 and 1983, the knowledge of the history of volcanic disturbance during that time (Walden *et al.* 1991; Whittaker *et al.* 1992a), and the knowledge of the damage that the severe eruptions of the early 1930, and the 1952/3 events inflicted upon the vegetation of Panjang and Sertung, a set-back and deflection of succession seems very plausible (Fig. 1.13). This argument has been advanced by Whittaker and colleagues, and although direct evidence is not available, studies on the vegetation structure, diversity, and biomass are very indicative of Panjang's



Fig. 1.12: *Dysoxylum gaudichaudianum* with a peduncle of nearly ripe fruits.

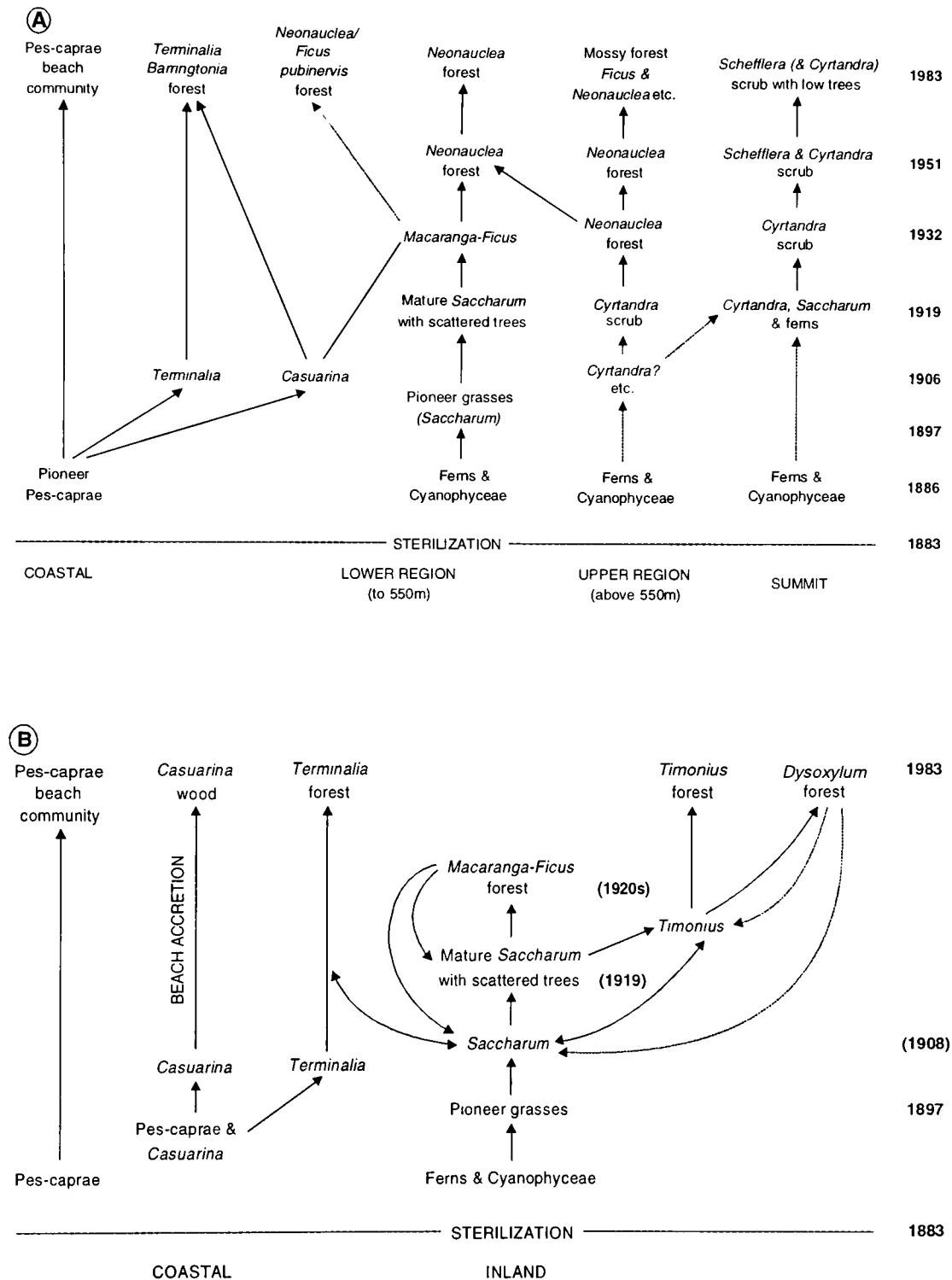


Fig. 1.13: Principal successional pathways on (A) Rakata and (B) Sertung and Panjang. The pathways are depicted separately for the coast and the interior and, for (A) Rakata, also for the lower, upper and summit regions. Note, in (B), the deflection from the *Macaranga-Ficus* pathway to *Timonius* followed by *Dysoxylum* forest types. Whether *Dysoxylum* generally replaced *Timonius* is not clear. Dates indicate the time at which vegetation types were first recorded (adapted from Whittaker *et al.* 1989).

and Sertung's forests being of an earlier successional stage than the forests on Rakata (Bush, 1986a; Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker *et al.*, 1992a). However, the cause of forest divergence has been a much debated issue by the various Krakatau researchers.

As already suggested, Whittaker and colleagues are mainly in favour of a disturbance argument, although they do acknowledge that early establishment can play an important role in influencing the course of succession (Whittaker *et al.* 1989, Bush *et al.* 1992). In contrast to the disturbance hypothesis, a group led by H. Tagawa advance the argument that the differences in forest dominance, and the sharp boundaries between *Dysoxylum* and the *Timonius* forest areas, are due to differences in the timing of species arrival, and differences in edaphic factors (Tagawa *et al.*, 1985; Bush, 1986a; Higashi *et al.*, 1987). In the case of the edaphic argument, they suggested that *Dysoxylum* is adapted to moister, and more humus-rich soils which should be characteristic of more advanced soil development, whereas *Timonius* is supposed to occupy drier areas. However, the recent expansion of the *Dysoxylum* forest area on Panjang and on Sertung (Bush *et al.*, 1992) gives no indication of an edaphic equilibrium, and any correlation with edaphic factors should be seen as a product, but not a cause of forest development. In any case, the intermittent deposition of ash, although of varying quantities between and within Panjang and Sertung, results in a mixture of soil and ash on both islands.

Later on, the much stronger argument of the importance of early arrival was fully embraced by Thornton and his group (Thornton *et al.* 1988). That differences in the time of arrival of different species on each island may explain some of the differences in commonness and composition of the main associations between the island, was already recognised by Docters van Leeuwen (1936) in the 1930s. He states, for instance, "one species of tree, *Timonius compressicaulis*, which in Krakatau [Rakata] is only found on the NW side, occurs everywhere [on Panjang]" (Docters van Leeuwen, 1936; p. 181). Thornton (1996) takes this as implying that differences in the sequence of arrival may lead to forest divergence. However, this seems to ignore various factors. For example, it is difficult to comprehend how, on the basis of earlier arrival alone, such extreme dominance patterns, uniform-age structure, and specific physiognomy could have developed on these islands. Also, how could such an early successional character have been maintained over more than 50 years? Moreover, one is generally not able to determine the date of first arrival. The date for the first record of a species for the islands often involves finding fairly long-established

specimens (Whittaker *et al.*, 1989). For instance, the first record of *Neonauclea calycina* was for Rakata in 1905. In 1920 it was found on Sertung for the first time, in the form of a specimen with a girth of 40 cm. Also the first *Dysoxylum gaudichaudianum* record on Panjang in 1932 involved mature as well as young trees, but it had not at that time been found on Sertung nor on Rakata. Moreover, *Timonius* was not found on Sertung until 1982, when it already dominated most of its area. For the early arrival argument to hold, one would assume that *Timonius* should have been as common on Sertung as it was on Panjang in the 1930s given that today it exhibits a similar dominance pattern on both islands.

Bush (1986a) suggested that the Panjang areas covered by ash in 1953 include those areas now dominated by *Timonius compressicaulis*. He argued that the 1953 eruption could have been particularly significant in influencing the succession since the damaged trees were already weakened by the 1952 eruption, and might therefore, have finally been killed, thereby making space for new colonisers. However, to reach the degree of dominance as found on Sertung and Panjang, the coloniser would need to have had abundant seeds available at the time of disturbance. *Timonius compressicaulis* which is animal dispersed, known to be highly invasive, and can flower when only 1 m tall (Corner, 1952), seems the right candidate for rapid colonisation (Bush, 1986a). Moreover, stress-induced flowering has been observed in this species (T. Partomihardjo, pers. comm.). Obviously, commonness at the time of disturbance should bestow an additional advantage.

On Sertung, *Dysoxylum gaudichaudianum* forest now dominates north-eastern and eastern areas which were most affected by the 1930s and 1952/53 eruptions (see Fig. 1.9; Fig. 1.14a). The rest of the area (except for the spit) is dominated by *Timonius compressicaulis*. It seems, however, most likely that the *Dysoxylum* dominance in these areas developed after 1953 or even later, since van Borssum Waalkes (1960) still observed *Terminalia* and *Neonauclea* to be common in the higher areas of Sertung in 1953. *Dysoxylum* is also a prolifically fruiting bird-dispersed species. Its autoecology is still little understood, but it is quite shade-tolerant as a seedling and sapling, and does not seem to fruit until it reaches the canopy (Whittaker & Jones, 1994; Whittaker & Turner, 1994). Under high light conditions it is able to grow very fast and reaches heights of ≥ 35 m. *Timonius* can also grow extremely fast in high light conditions, but can not regenerate in shady conditions, and only grows up to about 22 m height. Therefore, *Dysoxylum* can frequently be found regenerating beneath the thin canopy of *Timonius* which it eventually overtops (Whittaker,

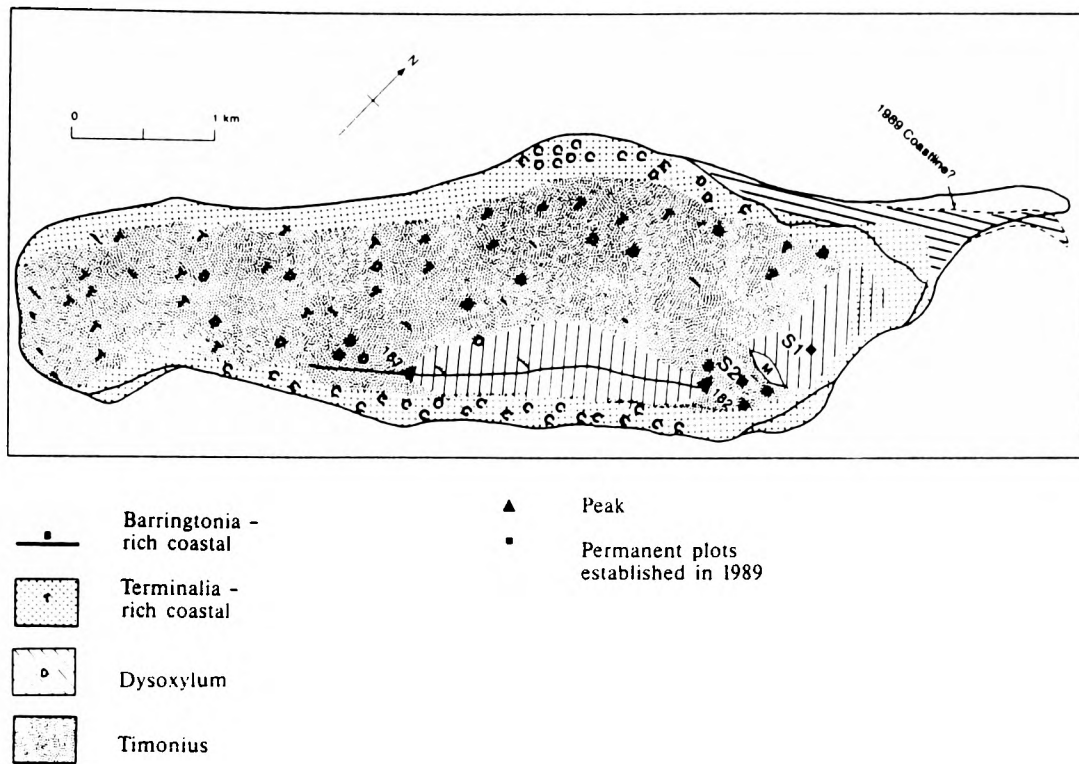
et al. 1989; Bush *et al.*, 1992). This process seems to be taking place on Sertung and Panjang, and on Panjang there has been a particularly noticeable expansion of *Dysoxylum*; it is roughly estimated to have increased its area of dominance from 50% in 1983 to 75% by 1989 (Bush *et al.*, 1992; Fig. 1.14b). Due to both the slightly later successional characteristics of *Dysoxylum*, and to its recent expansion, *Dysoxylum* forest seems to be the more mature stage of development. During the same timespan *Timonius* forest has put on considerable growth from 11-13 m canopy height to about 20 m, suggesting rapid early successional growth (Bush *et al.*, 1992).

On Panjang, the *Timonius* forests appear to be more mature. They are lush, not as open as in some of the *Timonius* areas on Sertung, and the trees are of greater size. Bush *et al.* (1992) suggested that from the relative extents and the character of *Dysoxylum* and *Timonius* forests, Panjang appears at a more advanced stage of recovery from disturbance than Sertung. In fact, in the southern areas of Panjang *Timonius* seems to be senescing (pers. obs.), and *Dysoxylum* is well on its way to take over the canopy. In contrast to Panjang, *Timonius* forests on Sertung may have suffered from repeated successional setback, as seen by the soil stratigraphic record which shows a greater number of ash-fall episodes (particularly in the post-1953 period; Walden *et al.*, 1991; Whittaker *et al.*, 1992a). Also, in one of Whittaker and colleague's permanent plots, widespread tree damage at uniform heights suggests that an even-aged stand of *Timonius* was hit twice by some major disturbance (possibly gas poisoning or ash-fall events). It has also been hypothesised that an additional drought following a volcanic disturbance may have killed or damaged the apical buds, producing wolfing (Bush *et al.* 1992).

Bush *et al.* (1992) stated that

"a simple relationship does not exist in which eruption 1 gives rise to vegetation 'a' and eruption 2 gives rise to vegetation 'b' and so forth. Rather, it is the cumulative impacts of eruptions coupled with variation in local seed availability and growing conditions, that produced the present mosaic of vegetation types on Sertung and Panjang." (p. 196)

a)



b)

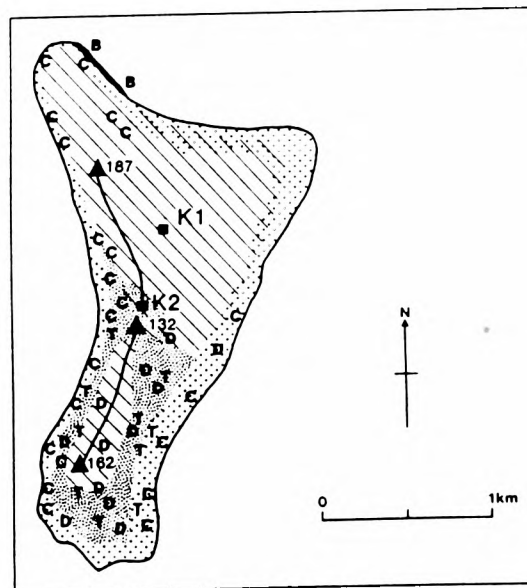


Fig. 1.14: Vegetation maps of (a) Sertung and (b) Panjang, depicting the vegetation distribution as recorded, and estimated in 1989 (from Bush *et al.*, 1992).

1.4 The main succession theories and models and their relevance to the development of the Krakatau forests

The climax theory of succession as developed by Clements (1916) was, despite the early criticism of Gleason (1926), the dominant view of succession for 50-60 years. Within this holistic theory, successional change is thought to be due to autogenic processes, that are orderly, predictable and thus deterministic, and which converge from various different starting points to a climatic climax community. In contrast, Gleason interprets a plant community as a chance assemblage of species populations, each of which has a unique behaviour (Matthews, 1996). Facilitation, as stressed in Clement's theory, is not seen to be important, and autogenic changes are considered to be neutral or inhibitory factors (Finegan, 1984). Connell & Slatyer (1977) made an attempt to describe mechanisms of succession and developed out of the existing body of theory and evidence three alternative models of succession: (i) facilitation; (ii) tolerance, and (iii) inhibition. The models have provided a constructive focus for research on plant succession, and have provided a theoretical framework for experimental studies. Yet, it is not possible to accommodate all successional studies within the framework of these three models, because they largely ignore allogenic changes, as, for instance, affected by disturbance and weather variations, and biotic effects such as dispersal. Furthermore, many successional processes often occur simultaneously, and so far no unified theory of succession has been achieved (Walker, 1987).

Types of succession fitting all three models can indeed be found on Krakatau either sequentially or simultaneously. For instance, in the initial phases of the primary succession blue-green algae were reported to be the rooting medium of the first fern spores (Treub, 1888). The blue-green algae may have ameliorated the xeric conditions on the bare ash. Initial colonising grasses, and pioneer shrubs and trees have also contributed to the amelioration of environmental conditions by providing shade and leading to the accumulation of organic matter. Thus, the establishment of more shade-loving, later successional species may have been facilitated. Inhibition could be argued to have occurred after forest closure, when the monodominant, uniformly aged stands of the long-lived pioneer *Neonauclea calycina* cast dense shade, as suggested by Docters van Leeuwen (1936). With senescence of the *Neonauclea* forest apparently now in progress, a replacement with other more later successional species should take place (see CHAPTER 5). Within the *Timonius compressicaulis* forest, however, mechanisms of 'tolerance' seem

to be important whereby *Dysoxylum gaudichaudianum* can grow to maturity beneath the sparse *Timonius* canopy and eventually overtop and replace this species (Bush *et al.* 1992; see CHAPTER 5).

Another major criticism of the Connell and Slatyer (1977) models is that, apart from the focus on species entry into the succession, mechanisms by which species persist and yield space are not explicitly considered. Furthermore, while they mention both the importance of disturbance, as the starting point of succession, and the fact that succession can be interrupted by disturbance, they do not consider the importance of the nature of disturbance (Pickett *et al.*, 1987). Interpretation of successional processes is also strongly affected by the level of organisation (e.g. the population or community level) at which it is studied. Pickett *et al.* (1987), for instance, suggest that the Connell and Slatyer (1977) models can only be applied to plant-by-plant interactions.

Recognising the combination of problems associated with the above successional models, Pickett *et al.* (1987) proposed a hierarchical model of the causes and mechanisms of succession. Its advantages are that the hierarchy covers all levels of enquiry. The top level presents a general explanation of succession, while the lowest level comprises specific predictive factors; consequently all causes that operate at all levels of ecological organisation are encompassed by the hierarchy. Thus, Pickett *et al.* (1987) argue that specific research questions and objectives determine where in the hierarchy causes are examined, but this does not mean that all possible mechanisms and causes of succession have to be incorporated in any one particular study. Table 1.3 gives an overview of the hierarchy of successional causes. The highest most general level lists the main causes of succession: (i) site availability, (ii) species availability, and (iii) species performance. The intermediate level covers the contributing processes, such as, for instance, disturbance as the determinant of site availability, and dispersal and propagule pool being the determinants for species availability. Species performance is listed as a function of a large number of processes, such as competition, stochastic environmental stress, and resource availability. The lowest level encompasses defining factors that must be assessed or modelled to make specific predictions about the course of succession. In the case of disturbance, they are, for example, the severity, size, timing, frequency, and spatial distribution of disturbance. Within this framework it is possible to accommodate many aspects of other successional models and theories as different as Clement's holistic climax theory, and Gleason's reductionist theory of succession.

Given the complexity of the factors influencing the Krakatau succession, the Pickett *et al.* (1987) model was seen as ideal for providing a clear framework and research agenda. It has, therefore, been adopted as the main framework ordering and guiding this research of disturbance and succession on the Krakatau islands.

The Krakatau islands are a famous case study of primary succession, and the vegetation change on the islands was, as shown in section 1.3, reasonably well documented between the period of 1888 to 1934 (Treub, 1888; Ernst, 1907; 1934; Backer, 1929; Docters van Leeuwen, 1936), but with a long hiatus until 1979 when intensive research resumed. Almost all the botanical studies conducted prior to the 1990s were concerned predominantly with surveying the islands to enumerate plant species numbers, and to ascertain which plant associations have existed and replaced each other to form certain pathways of succession (Ernst, 1907; 1934; Docters van Leeuwen, 1936; Richards, 1952; Whittaker *et al.*, 1989). Whittaker and colleagues (Bush, 1986a; Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker *et al.*, 1992a) have drawn attention to the potential deflection of the pathways because of intermittent volcanic disturbance by Anak Krakatau, and modified Richard's (1952) representation of Krakatau successional pathways to take into account the altered pathways of Sertung and Panjang (Fig. 1.13). However, study of the actual processes of the succession that have been taking place over more than a century since Krakatau's eruption, has been more or less absent. Permanent sampling plots to monitor turnover have been set up on all islands only relatively recently, in 1989 (Bush *et al.*, 1992; Whittaker & Jones, 1993), and my study is still one of the first attempts at quantifying, documenting, and drawing inferences on not only the pathways but also the processes involved in succession on Krakatau.

Table 1.3 A hierarchy of successional causes *sensu* Pickett *et al.* (1987). The highest level of the hierarchy represents the broadest, minimal defining phenomena: general causes of succession. The second or intermediate level contains mechanisms of change: contributing processes or conditions. The third and lowest level of the hierarchy consist of the particular factors that determine the outcome of the intermediate-level processes (adapted from Pickett *et al.* 1987).

General causes of succession	Contributing processes or conditions	Defining factors
site availability	coarse-scale disturbance	size, severity, time, dispersion
differential species availability	dispersal	landscape configuration
	propagule pool	dispersal agents, time since disturbance, land use
differential species performance	resource availability	microclimate, site history, soil conditions, topography
	ecophysiology	germination requirements, growth rates, population differentiation
	life history strategy	allocation pattern, reproductive timing, reproductive mode
	stochastic environmental stress	climate cycles, site history, prior occupants
	competition	presence of competitors, identity of competitors, resource base
	allelopathy	soil characteristics, neighbouring plants
	herbivory, disease and predation	climate cycles, consumer cycles, plant vigour, plant defence, community composition, patchiness

Successional processes on Krakatau at present are different from those during the initial phases of the succession directly after sterilisation (Walker, 1987). Forest cover has long been established (see above), and the processes involved after disturbances of variable size and severity (e.g. treefalls, landslides, lightning strikes, volcanic disturbance) are better described as those of a secondary succession superimposed on the overall *prisere*. Thus, the main focus of this research is on quantifying some of the processes of secondary succession, by concentrating in particular on their relationship to species compositional changes and diversity trends in space and over time. The quantification of these processes is necessarily restricted to the short-term due to the time constraints of doctoral research.

Fig. 1.15 represents the equivalent to Whittaker *et al.*'s (1989) pathway representation of the succession (Fig. 1.13), stressing the importance of volcanic disturbance and its impact on the succession of Panjang and Sertung. However, by using the Pickett *et al.* (1987) framework, Fig. 1.15 concentrates more on what influence volcanic disturbance has on successional processes rather than concentrating on describing possible pathways. As a preview of the main focus and results of this study, Fig 1.16 depicts the revised version of Fig. 1.15. Apart from volcanism it stresses the importance of climatic and human disturbance, and shows their links to the 'general causes and mechanism of succession' *sensu* Pickett *et al.* (1987; Table 1.3). Throughout the following data chapters reference will be made to the schematic representation in Fig. 1.16 of the successional processes and the influencing factors. However, before going on to describing the main aims and objectives of the thesis in section 1.6, I feel it is important to add a section (1.5) on the process involved in arriving at the final focus of this research.

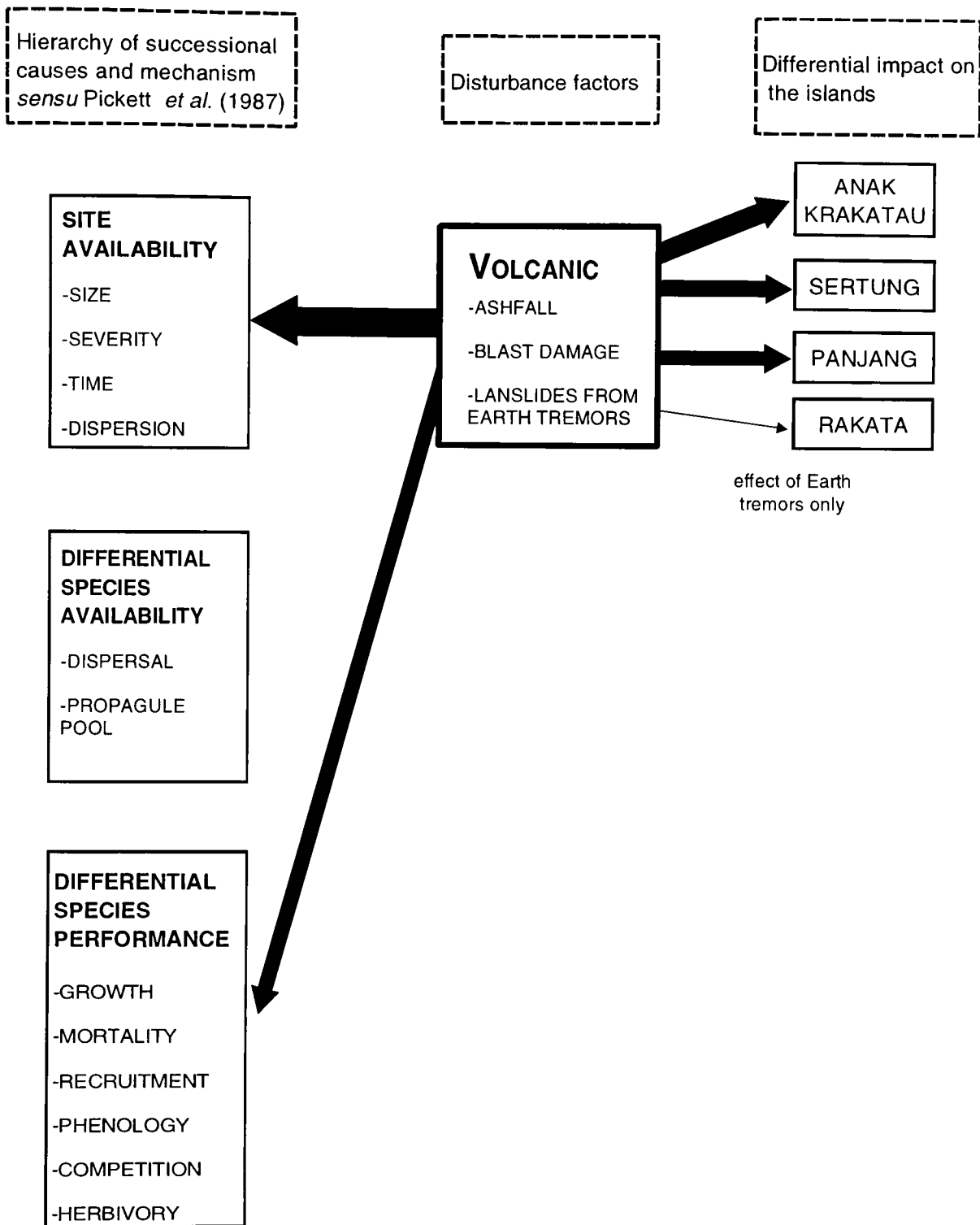


Fig 1.15: A hierarchical representation of successional processes on Krakatau using the Pickett *et al.* (1987) framework. The special significance of volcanic disturbance in the Krakatau context is recognised, and the model is an alternative representation of the pathway representation of Whittaker *et al.* (1989) presented in Fig. 1.13. Thickness of the arrows indicates the relative importance of this disturbance factor in relation to the different causes and mechanisms of succession. The arrow thickness also indicates the perceived strength of the differential impact on the islands.

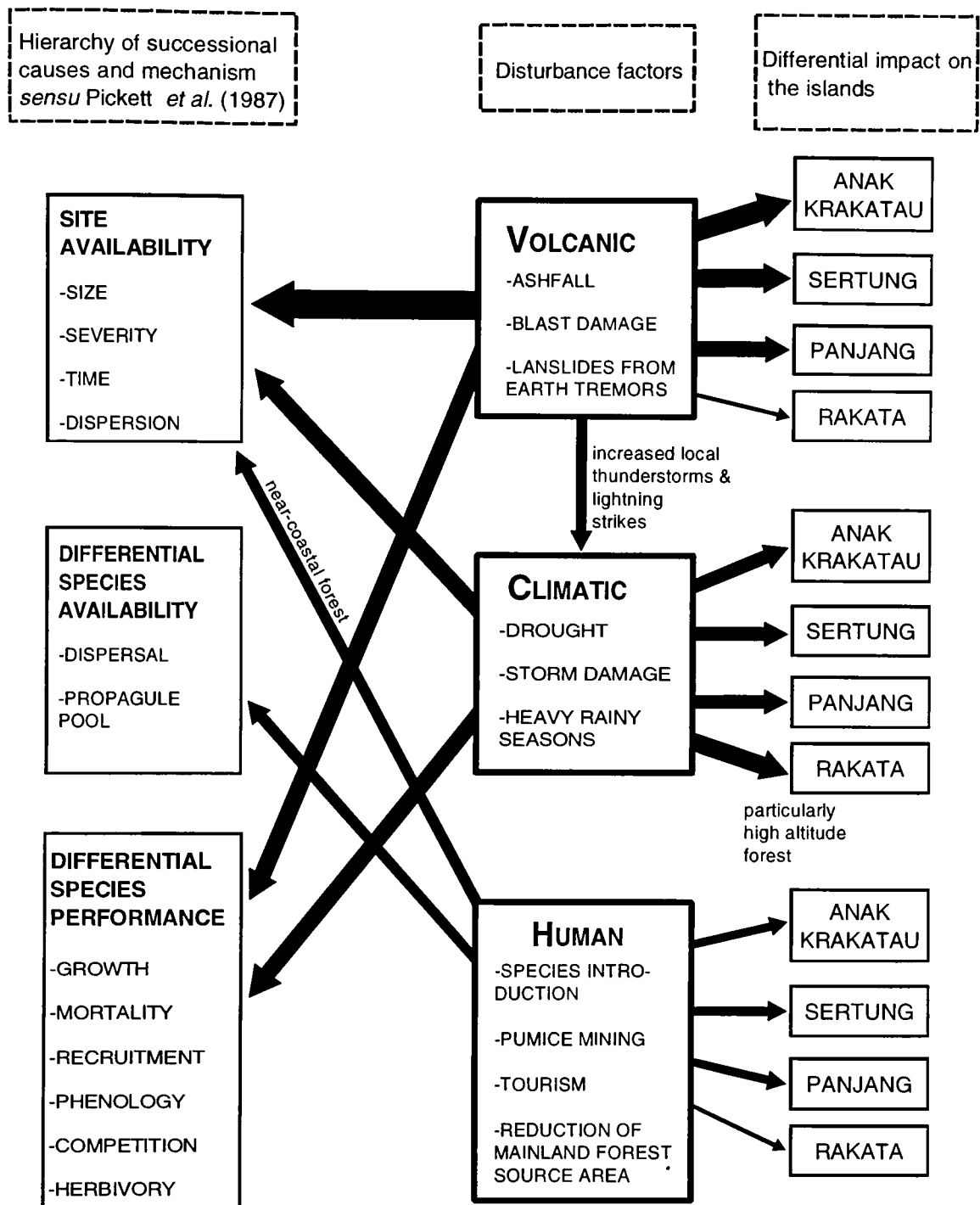


Fig. 1.16: A revised hierarchical representation of successional processes on Krakatau (see Fig. 1.15), emphasising the significance of not only volcanism, but also climatic and human disturbance and their potential influence on successional processes on the islands. Thickness of the arrows indicates the relative importance of these disturbance factors in relation to the different causes and mechanisms of succession. The thickness of the arrows also indicates the perceived strength of the differential impact on the different islands.

1.5 Development of thesis focus

It is probably true of most theses, that more questions are asked at the beginning than can realistically be pursued, and several attempted avenues of investigation turn out to be 'dead ends' for various unpredictable reasons. This certainly was the case in this thesis. Furthermore, the remoteness of the fieldwork site and the fact that for each field season only a very short time was available meant that the spreading of risk was important. Thus, I proposed several separate sub-projects in case one or the other could not be pursued or failed in-between three different field seasons.

The initial research outline was much more focused on the patch-scale. Gap ecological studies were in particular intended to investigate what factors influence the differential performance of saplings. Although this is still a main part of the thesis, the investigation was reduced to the investigation of rather fewer environmental variables than initially envisaged. Also the measurement of the variables that were investigated was less sophisticated than initially planned. The key physical variable of investigation was intended to be light (quantity related to gap size) and the key biotic variable was herbivory (leaf damage and seed predation).

Light was chosen as the main variable because it is one of the key resources necessary for plant growth and one of the resource that increases dramatically with gap openings (Brown, 1993; Whitmore, 1984). As described in more detail in CHAPTER 4, the quantification of the light environment using hemispherical photography was hampered by lack of equipment during the 1993 field period when all the gap monitoring sites were set-up. Moreover, the subsequent attempts at relating light measurements to each other were not totally satisfactory. Furthermore, the available Sunfleck Ceptometer (AT Delta-T devices) light measuring instrument, which integrates light from 80 linearly arranged sensors, was not sufficient to characterise the light environment of the different gaps. The alternative technique using ozalid light meters, assembled from light-sensitive diazo paper, seemed promising particularly with respect to quantifying spatial differences in the light environment in gaps, and the understoreys of the different forest types. However, despite extensive experimentation, the inherent problems with the technique remained, and the publication of the article by Bardon *et al.* (1995; two years into my study) clarified and confirmed the problems encountered. PAR values derived from ozalid light measurement

thus, had to be disregarded. See APPENDIX 1 for a description of the techniques and its associated problems.

Herbivory has frequently been identified as significantly affecting plants at the regeneration stage (Harper, 1977; Grime, 1979; Verkaar, 1987; Bazzaz, 1991), and may therefore influence succession (Connell & Slatyer, 1977; Brown, 1984; 1985; 1991). Specifically, temporal and intraspecific differences in herbivory pressure can be an important selective factor changing the species composition of the regeneration layer, with potential long-term effects on gap-fill and succession. On Krakatau insect herbivory rather than vertebrate herbivory is likely to be even more important than in other tropical forests (Leigh & Smythe, 1978) because of the lack of vertebrate herbivores (there are only rats). The only other potential herbivores are land crabs and molluscs.

Bush (1986b) argued that Krakatau provides a rare opportunity to study animal-plant interactions because of the archipelago's discrete, and definable tropical biota. Thus, one of the specific objectives with regard to herbivory was to investigate if more recently colonising tree species may be at a competitive advantage compared with long established and common species (Root, 1973; Morrow, 1977). This means seeking evidence to show signs of ecological release from predators (herbivores). Additionally, a quantification of how herbivory may affect plant fitness differently for different species, and ultimately what influence this may have on the succession and diversification process, was also intended.

The main aspects that hampered herbivory work were that it was too time consuming to be carried out during only three relatively short periods of field work. Ideally also herbivory work requires regular monitoring to quantify seasonal differences in damage, and is beset with many problems of measurement (Lowman, 1984; 1985; Sterck *et al.*, 1992). Furthermore, there is a considerable risk of not deriving a clear signal, particularly since it is very difficult to quantify inter-specific differences in the impact of herbivory, unless a controlled experiment is carried out. Artificial defoliation experiments and seed predation work (as a specific form of herbivory) were seen to be the best options to obtain relatively discrete results. Experiments were initiated but were not particularly successful. Therefore, this part of the programme was scaled down (see APPENDIX 3 for some results of artificial defoliation of *Dysoxylum* saplings).

A change of emphasis in this study towards quantifying more of the larger-scale dynamics, as well as the planned patch-scale investigation of regeneration dynamics in gaps, took place in parts to seize the opportunity presented by the coincidence of the fieldwork period with extreme events. These were the sustained period of ash-deposition on Panjang and Sertung from the volcanic activity of Anak Krakatau, and the drought in 1994. For instance, the coincidence of three consecutive dry season field phases with volcanic activity and ash-fall presented the unique opportunity to quantify its impact on the disturbance regime and sapling performance, and the event of the drought drew more attention to the importance of extreme climatic events. So far the latter has been a neglected aspect of investigation.

1.6 Aim and central research objectives

The overall aim of this study is to elucidate the importance and the effect of disturbance on the successional development of the forests of the Krakatau islands. The main research objective is to achieve this by concentrating on the quantification and evaluation of successional processes rather than by focusing on pathways. This will be attempted by concentrating on the landscape- (meso-) as well as the patch-scale, whereby the research agenda is largely provided by the framework of the Pickett *et al.* (1987) hierarchical model of causes and mechanisms of succession, as described in section 1.4 and used in Fig. 1.15 and 1.16. The three 'general causes of succession', site availability, species availability and species performance provide the focus for the central research objectives.

- (i) The first objective is to quantify the disturbance regime of the islands, and thus the potential 'site availability' and its defining factors, and to assess how volcanic activity modifies the disturbance regime of the Krakatau forests (CHAPTER 3).
- (ii) The second objective is to determine how far differential 'species performance' at the regeneration stage may influence species composition of gap-fill, and ultimately diversity of the Krakatau forests (CHAPTER 4), and whether the physical characteristics of gaps are the most important factors influencing gap species composition.
- (iii) The third objective is to investigate inter- and intra-island differences in diversity and composition at the meso- and patch-scale. This is in order to achieve some idea of 'species availability' and changing dominance patterns within the archipelago and how this may

affect the succession in future, as well as to evaluate the importance of volcanic disturbance for forest divergence (CHAPTER 5);

(iv) The fourth objective attempts a quantification of the composition and density of seeds in Krakatau top-soils, and to establish spatial variation in relation to differences in habitat types (gap and understorey), islands, and/or forest types. Seed bank presence or absence of species is also investigated for its usefulness as an indicator of autoecological characteristics, and thus another form of indicator of 'species performance' (CHAPTER 6).

CHAPTER 2:

DESCRIPTION OF THE STUDY SITE

Summary:

1. This chapter provides a description of the physical environment of the Krakatau islands. This includes a description of the history of the volcanic activity pre-1883 and post-1883, the derived soils, climate, the geomorphology and topography, and the history of administration and extent of human impact on the island group.

2. Intermittent volcanic eruptions of Anak Krakatau have led to the damage of the forests of Sertung and Panjang from ash-fall, blast and gas damage. A likely link of eruption events with more severe local climate, causing higher incidences of lightning, rainfall, and high winds, is stressed. Thus Rakata, if not directly affected by ash-fall, is argued to be indirectly affected and to experience a more dynamic disturbance regime during times of volcanic activity.

3. Soils are described. Almost all soils on Rakata are derived from 1883 pyroclastic deposits, whereas on Sertung and Panjang substantial ash deposits from Anak Krakatau have led to interruptions and the re-starting of pedogenesis. Permeability of soils on Krakatau is in general high, due to low bulk densities. Except for some recent evidence of low levels of plant available phosphorus, other major nutrients do not seem to pose a problem for plant growth as both the 1883 and Anak Krakatau ashes contain sufficient primary minerals or weather rapidly.

3. Apart from the description of the available data on the local and regional climate, attention is also drawn to the importance of extreme climatic events such as ENSO events in influencing vegetation dynamics.

4. The history of human impact, as well as current and potential future impact is described. It is suggested that human disturbance factors are more prevalent and extensive in the accessible coastal areas than previously thought. Pumice mining is the most destructive of all human forms of disturbance on these islands.

2.1 Introduction and geographical context

The Krakatau islands lie in the Sunda Straits (6°06' S, 105° 25' E; Fig. 1.1) nearly equidistant between Java and Sumatra with a distance to the mainland of c. 40 km. The nearest island is Sebesi, being 12 km to the north-east of the archipelago.

The archipelago consists of the three remnant islands Rakata, Sertung and Panjang, and Anak Krakatau, a new volcanic island that emerged at the edge of the old caldera in 1931. The altitudes and areas are given in Table 2.1. For Rakata altitude measurements have varied considerably between different researchers. Although some reduction in altitude through erosion may have taken place (e.g. rockfalls have been observed; Ernst, 1907; Docters van Leeuwen, 1936) the differences seem to be too substantial, and it can be assumed that measurement error has also played a role (R.J. Whittaker, pers. comm.). However, the altitude of 735 m a.s.l., which was regarded by Whittaker *et al.* (1989) as provisional, was confirmed by Hafkenschied (1994).

CHAPTER 1 has already described the successional history of the vegetation and the status of the present vegetation. This chapter describes the physical environment of the islands, in particular reporting on the known information about the pre-1883 volcanic history, and the history of renewed volcanic activity after the emergence of Anak Krakatau in 1930, the composition and formation of Krakatau soils, the general climatic conditions, and the geomorphology and topography. An introduction to the administrative history, and a description of the influence of humans on the islands in the century since sterilisation are also given.

Table 2.1: Area and altitudes of the Krakatau islands, Rakata, Sertung, Panjang and Anak Krakatau

<i>Island</i>	<i>Area in km²</i>	<i>Altitude in m a.s.l.</i>	<i>Source</i>
Rakata	17	830	Verbeek (1885)
		813	Stehn (1929)
		735	Whittaker <i>et al.</i> (1989)
			Hafkenschied (1994)
Sertung	13	182	Whittaker <i>et al.</i> (1989)
Panjang	3	142	Whittaker <i>et al.</i> (1989)
Anak Krakatau*	c.3	c. 280	in 1993, Thornton <i>et al.</i> (1994)
	> 3	>300	in 1995, pers. obs.;

* area approximated to that of a circle from the 2 km diameter measure;

2.2 Volcanic history and geology

Pre-1883 volcanic activity and island configuration

The possible volcanic and geological history of the Krakatau archipelago is presented in Fig. 2.1. Verbeek (1885) suggested that the islands pre-1883 Krakatau, Sertung and Panjang resulted from the “basal-wreck” (Judd, 1884 in Thornton, 1996) of an earlier eruption event of the so called ‘ancient Krakatau’ $\pm 60\,000$ years ago (Ninkovich, 1979), or as recent as 416 A.D. if old records from the Javanese Book of Kings (Pustaka Raja) are to be believed (Thornton, 1996). Ancient Krakatau was a large, andesitic, stratovolcano of approximately 11 km diameter and about 2000 m height (Thornton, 1996). After its destruction, a basement of coarse-grained tridymite andesite, volcanic ashes, and lava remained. This became overlain by volcanic products, such as basaltic lavas, bombs, lapilli and fine ashes, of several eruption events (7-9 reported in the Strait between the 9th - 16th century, Thornton, 1996). This led to the formation of two more cones apart from Rakata. They were Danan and Perbuatan and they eventually coalesced to form a single compound island with Rakata being the tallest cone in the South (822 m a.s.l.), Danan in the middle (450 m a.s.l.), and Perbuatan the smallest (120 m a.s.l.) and northernmost.

By the seventeenth century Krakatau island was well forested. However a major eruption, which lasted several months during 1680, is said to have left the island ‘burned and barren’ (Berg, 1884 in Thornton, 1996). The eruption produced augite hypersthene andesitic lavas, andesitic scoriae, hypersthene andesite and basaltic ashes (Neumann van Padang, 1951). It is documented that prior to the “reawakening” of Krakatau in May 1883 no further eruption had taken place since 1680, and that the islands were again fully forested.

The 1883 eruption

Activity resumed in May 1883 and continued over the following months, culminating in the catastrophic eruption on August 27th of that year. On 26th of August several major explosions occurred with smaller localised tsunamis. The greatest explosion and the largest tsunami occurred at around 10.00 am on August 27th and marked the climax of the eruptions. Another very large eruption followed at 10.52 am by which time a mud rain that lasted for three or four hours had begun. The massive tsunamis (e.g. 36 m high at Anyer, West Java; Kusumadinata, 1979) that followed the most severe eruption events, and the

final collapse of the caldera are estimated to have killed >36 000 people inhabiting the near-coastal areas of the Sunda Straits. It was also reported that throughout the eruption frequent lightning occurred in the eruption column, and at 11.10 am on the 27th of August lightning struck the lighthouse at Java's first point 'burning convict labourers through their irons' (Thornton, 1996; p.14). At Ketimbang, South Sumatra, more than 40 km distance from Krakatau, some 1000 people were killed by 'burning ashes', which were not just falling hot ashes but a horizontal ignimbrite-producing, pyroclastic flow or *nuée ardente* (Thornton, 1996). The eruptions ceased on the morning of August 28th 1883.

The islands were left much altered in shape and size. Two-thirds of the old Krakatau island had disappeared (Fig. 2.1). The only remaining parts of the old Krakatau were the southern half of Rakata, and the small outcrop of Bootsmansrots. The latter are thought to be the volcanic plug of a Danan vent (Judd, 1884, in Thornton, 1996). Rakata's cone was practically cut in half and the vertical cliff extended from the 830 m a.s.l. peak (Verbeek, 1885) down to 200 m below the sea's surface, whereby the collapsed caldera now forms the deepest point of the Sunda Straits (Thornton, 1996).

The deposition of pumice and ash was between 60-80 m deep on average, but might have reached up to 150 m in places (Whittaker *et al.*, 1989). It led to a significant enlargement of the islands of Panjang and Sertung, and the West and Southern areas of Rakata. In fact, Sertung's area tripled in size, which meant an increase of 7 km², and the extension of the South and West of Rakata was almost 5 km². However, immediate and rapid coastal erosion occurred, which was presumably slowed only as lava basements were encountered (Bird & Rosengren, 1984; Thornton & Rosengren, 1988). This process has removed large amounts of material and further reshaped the islands (see Fig. 2.2; see below). Pre-1883 lava-flows and rocks are frequently exposed at the northern and north-eastern cliff edges on Rakata, the southern cliffs of Panjang, and eastern cliffs of Sertung. Sometimes these are also exposed in gully bottoms, and at higher altitudes. The rest of the islands were, and remain today, completely mantled in thick pyroclastic deposits. These are made up of various shapes and sizes of pumice and ash layers of different thickness and size of scoriae, as well as material from the old volcanoes (Richards, 1982). The very deep V-shaped gullies noted today are remnants of an early exceedingly active erosive phase.

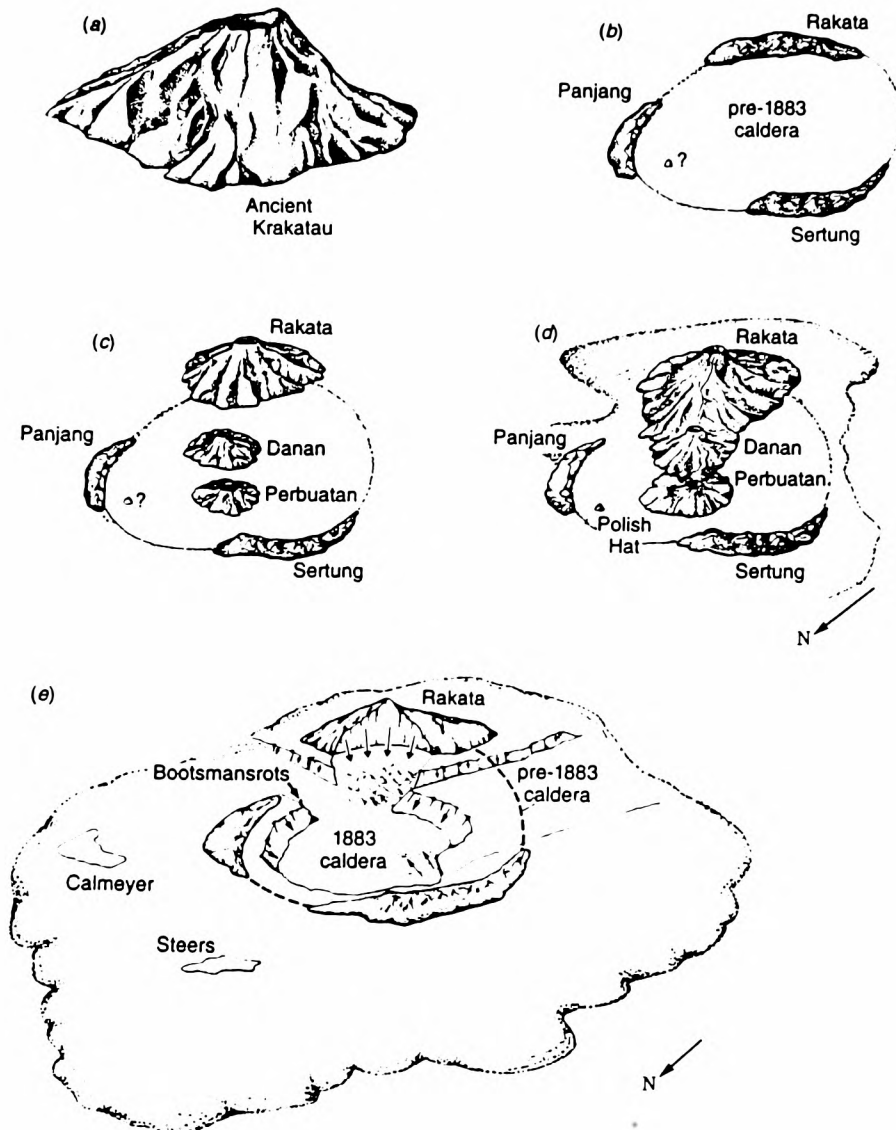


Fig. 2.1: The assumed geological history of the Krakatau archipelago depicting (a) Ancient Krakatau; (b) remnant islands around the prehistoric caldera after the explosive eruption of Ancient Krakatau; (c) renewed volcanic activity within the pre-1883 caldera and the emergence of the islands of Danan and Perbuatan; (d) fusion of the three volcanoes as on island, Krakatau; (e) the archipelago immediately after the August 27, 1883 eruption. (reproduced from Thornton, 1996; originally modified from Francis & Self, 1983)

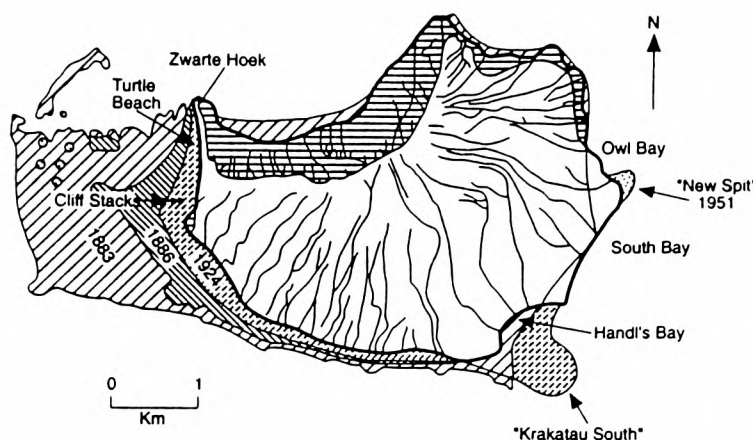


Fig. 2.2: Map showing the change in size and shape of Rakata over the last century. The thick black line is equivalent to the 1984 coast. The horizontal hatching represents pre-1883 lavas, and the extent of the island in 1882, 1886, and 1924 is indicated by the different cross-hatching patterns (reproduced from Thornton, 1996; Fig. 12)

Anak Krakatau and the post-1883 volcanic activity

Renewed volcanic activity commenced in 1927, and after the formation of several temporary cones (Anak Krakatau I-III) resulted, in August 1930 in the formation of a new island at the edge of the old caldera (Whittaker *et al.*, 1989). It was named Anak Krakatau (IV), which literally translated means 'Child of Krakatau'. The term 'anak' seems in general to be used for new cones produced by existing volcanoes. By 1932 it had already reached 47 m in height, and continued to grow rapidly and reached c. 200 m a.s.l. and c. 2 km in diameter by 1992 (Thornton, 1996). As a result of one of the most prolonged eruption periods since its emergence, and one of the most productive in terms of volume of lava (>4.3 million m^3 by July 1993), the new island has grown in height substantially, and was estimated to have a height of c. 280 m a.s.l. by 1993 (Thornton *et al.*, 1994). It has since grown further (pers. obs.), and is today estimated at c. 300 m a.s.l. by far the second highest island after Rakata (Table 2.1).

Very severe eruptions which caused much damage to Sertung's and Panjang's forests occurred between 1930/31, 1934/35, and 1952/53 (Table 2.2). During all of these eruption events, substantial amounts of ash fell on Sertung and Panjang, and blast damage was also reported to have affected the vegetation, particularly on Sertung. Moreover, it was suggested that gas damage was incurred in 1930 by Sertung and on both Sertung and

Panjang between 1952 and 1953 (see Fig. 1.9 & 1.11; Docters van Leeuwen, 1936; Borssum Waalkes, 1954, 1960). However, there is evidence that the pattern of damage varied between and within both islands. For instance, it was reported that the forests of Panjang were not much affected by Anak Krakatau's eruptions until 1932. Moreover, the eastern side of Panjang facing away from the volcano was reported to be less affected on this occasion (see CHAPTER 1).

During World War II, eruptions took place but no information on the effects on the vegetation exists (Borssum Waalkes, 1960), except that violent eruptions in 1939 destroyed the pioneer vegetation on Anak Krakatau (Dammerman, 1948). The visits by Borssum Waalkes just prior to, and just after, the major eruptions in 1952/53 represent more or less the last observation on the ecological impacts of the eruptions until 1982, with the exception of several brief surveys of Anak Krakatau (de Neve, 1982ab; Fosberg, 1985). A chronology and some descriptions of the eruption events between 1953 and 1982 (Table 2.2) are generally the only information available. Thus, it is not possible to reconstruct the ecological impact for this period from direct historical accounts.

Despite the long gap between surveys, a tentative reconstruction was produced from data on ash stratigraphies from various locations on Panjang and Sertung, involving the application of mineral magnetic techniques. Thus, not only the chronology, but also the inter- and intra-island differences in the amount of ash received by Sertung and Panjang could be reconstructed by Whittaker *et al.* (1992a). This analysis revealed that both these islands suffered numerous incidences of ash deposition since the birth of Anak Krakatau. According to these analyses, the largest total amount of deposits has been received by Sertung, and the most significant deposits were received in the early 1930s and during the 1952/53 events. The interpretation is concomitant with the historical accounts of the damage of these events (Docters van Leeuwen, 1936; Borssum Waalkes, 1954, 1960). For instance, with regard to the 1952/53 event, de Neve (1953) reports that Panjang and Sertung were covered in ash deposits between 0.5-1.5 m thick, and that practically the whole vegetation on Sertung and Panjang was either destroyed or severely damaged, whereas Rakata remained completely undisturbed. However, the study of ash stratigraphies also showed that significant disturbances must have occurred post-1953, in particular on Sertung. The measurement of the ash thickness in different places on Panjang and Sertung bears witness of this. For instance, the horizon depth on Panjang

Table 2.2: Record of the most severe or notable phases of volcanic activity of Anak Krakatau. Particular reference is made to effects on the other islands of the Krakatau group (adapted from Whittaker *et al.*, 1992a).

1927	Sub-marine activity (Stehn, 1929). Formation of Anak Krakatau begins.
1928	Northern coastal forests of Sertung damaged by waves associated with eruption (Stehn, 1929); Panjang received ash but damage not reported upon. Landslides are common on Rakata, and most likely also on the other islands because of earthquake activity; 22358 tremors recorded on Panjang and eruption columns to 1200 m high (1929).
1930	Extensive ash-fall, gas and water spout damage to Sertung (Docters van Leeuwen, 1936; Neumann van Padang, 1951), ash collected from Panjang (de Neve, 1981). No activity from 15th August until September 23rd 1931.
1931	In March Sertung described as looking seriously damaged, many dead trees (Docters van Leeuwen, 1936). Ash eruptions in September.
1932	Damaging ash-fall on Panjang (Dammerman, 1948).
1934	Blast damage to Sertung and island said to have a "wintry aspect" (Docters van Leeuwen, 1936).
1935	Blast damage to Sertung (Dammerman, 1948).
1939	Violent eruptions bury Anak Krakatau's vegetation (Dammerman, 1948); eruption clouds to 3000 m (Neumann van Padang, 1963).
1940-45	During World War II activity, but little hard data (Borssum Waalkes, 1960).
1952	Extensive ash-fall, blast and possibly gas damage to Panjang (ash depth of 0.7 m estimated by de Neve) and Sertung (ash depth estimated 0.5 to >1.5 m in places; de Neve 1953 ab). (Hoogerwerf, 1953; Borssum Waalkes (1960).
1953	Ash-fall, blast and possible gas damage to Panjang and Sertung caused damage to parts of both islands (Hoogerwerf, 1953; Borssum Waalkes, 1960). October 25-28th was main period of activity, ash clouds reached 4000 m.
1952-53	de Neve (1985 a) indicates damage to 90% of both Panjang and Sertung. Most severely affected the half of Sertung nearest to Anak Krakatau, and the southern end of Panjang.
1960	Extensive activity (e.g. 4000 registered eruptions in April, clouds to 2000 m), pyroclastic fall-out, great reshaping of the volcano (de Neve, 1982ab; de Neve, 1985)
1961	Eruptions continued into 1961 when first lava-flows and Pyroclastic fall-out occurred (de Neve, 1982a; Fosberg, 1985).
1972-73	Tall eruption clouds (3500 m), ash, lava, and other ejecta. Vegetation of Anak damaged (Barker & Richards, 1982; Fosberg, 1985).
1979	Eruptive activity, ejecta, lava and ash clouds (Siswowardjojo, 1985; Sumartadipura, 1985; R.J. Whittaker pers. comm.).
1980-81	Further activity, partly more intensive activity than 1979, ash-eruptions to a height of 1000 m in 1980 (Siswowardjojo, 1985), and in 1981 light fall of ash on Sertung (Simkin & Fiske 1983: 359), and ash observed drifting to Panjang (photograph by Partomihardjo), as well as lave flows.
1988	Lava-flows to lower South-west region, land explosions, ash and bombs ejected to a column height of 800 m as reported by Thornton (pers. comm. to R.J. Whittaker).
1992-1996	November 1992 resumption of activity with ash columns >1000 m, extensive lava-flows to the North-west, East and South (>4.6 million m ³ by July 1993; Thornton, 1996); 1993 many new landslides observed; substantial ash deposition on both Panjang and Sertung but Sertung receiving more (pers. observation); vegetation on Sertung and Panjang particularly stressed during 1994 in conjunction with drought; weight of ash led to snapping of small trees on Sertung; only a short lull of activity between Sept. 1993 and Feb. 1994, in August 1994 300-400 eruptions per day (Thornton, 1996); in September 1996 still active with ash depositions on Panjang and Sertung (L.A. Shilton, pers. com).

ranged from 54-108 cm, and on Sertung from 87-165 cm to the apparently unaltered grey 1883 ash and/or ash and soil layer (Whittaker *et al.*, 1992a).

These studies also showed that the sites closest to Anak, and/or directly downwind of the main seasonal wind directions, typically showed evidence of the largest number, and depth of different ashes. Using the ash stratigraphy as a method of reconstructing disturbance from volcanism is limited in that it reveals no information on disturbance caused by blast damage, gas poisoning, and localised wave-action (Whittaker *et al.*, 1992a). Moreover, problems of interpretation exist regarding possible rapid erosion of ash layers directly after deposition. Equally, additional gain of material will have occurred from slumping or wash-down of material in the lowland or gully sites. In addition, depth of ash layers may not correlate precisely with the actual extent of forest damage. However, in the absence of detailed historical accounts it is currently the best method for gleanings the possible chronology and impact of stress from ash depositions, especially for the period between 1953 and 1982. Shinagawa *et al.* (1992) report some small amounts of dark coloured scorias on Rakata, and attribute their origin to Anak Krakatau. This has not been substantiated. In fact, it is highly unlikely that material of the coarseness of scorias could reach Rakata without a far greater quantity of finer matrix ashes also being deposited: no such deposits can be found. Rakata can therefore be assumed to have been unaffected by direct volcanic disturbance. Rakata is spared from deposits because of the prevailing wind directions which are from the West to South-west during the rainy season (carrying material towards Panjang) and East to North-east during the dry season (carrying ash towards Sertung; Dammerman, 1948).

Lava-flows and pyroclastic fallout were first recorded during the 1961 Vulcanian and Strombolian eruption events (de Neve, 1982a) prior to which the ejecta usually consisted of ash particles. During the 1990s major eruptions have generally been accompanied by lava-flows, which have substantially enlarged the island, and led to the protection of some of its pure ash and pumice coast from further erosion (Thornton, 1996; see Fig. 1.8).

2.3 Soils

Soil formation and characteristics

In general, soil formation began on the 1883 pyroclastic flows mainly composed of vitric ash, which is lithologically andesitic and geochemically dacitic (Miyauchi *et al.*, 1986). Newsome (1982) suggested that biotic factors are of particular importance for soil development on Rakata, and particularly in the more stable areas, organic matter accumulation, incorporation and decomposition has been an important soil forming process (Hardjowigeno *et al.*, 1983; Newsome, 1986). Weathering and translocation as the other major factors involved in soil development in general, have been identified as less prominent. This has been argued to be due to the relatively short period of time (114 years) since the start of soil formation. In the more stable locations well developed, but thin (2-8 cm) A1 horizons with high biological activity were found to overlie weak gravely silt/loam AC horizons, and in some places even a B1 or weak B2 horizon could be distinguished (Subagjo & van Reuler, 1985). Soil depth was found to be between 20-30 cm and occasionally as much as 35-40 cm.

In the less stable areas, however, processes of erosion are of great importance in influencing soil development on Krakatau. This may be attributed to a combination of high rainfall, steep topography, and loose, excessively drained parent material of pumice and ash (Newsome, 1982). Thus, in some of the higher altitude areas of Rakata, and some of the gully bottoms, pre-1883 soil was quickly exposed after gully erosion, and the deposition of such eroded material has in other places led to gully infill and to mixing with 1883 deposits.

Whereas the soil formation on Rakata has in most places been continuous since the 1883 eruption, on Sertung and Panjang several buried horizons, or horizons mixed with ash from Anak Krakatau eruptions exist (see above). Whittaker *et al.* (1992a) found that the simplest soil profile recorded only one major disruptive event on North-east Panjang, whereas the most complicated profile had more than 11 post-1927 horizons and was found on North-east Sertung. That means pedogenesis was interrupted and re-started several times after major ash depositions, whereby the '1883-1927 soil' is overlaid with sequences of black ashes and scorias. These are interspersed with thin brown horizons that suggest periods of soil development (Whittaker *et al.*, 1992), but have during the course of further studies

largely been identified as layers of partially decomposed leaves (Whittaker *et al.*, 1995). These can be presumed to have been dropped under the stress of heavy ash-fall, which, in some instance, might have been combined with a drought period (pers. obs. of leaf loss under drought and ash-fall conditions in 1994 on Sertung and to a lesser extent Panjang; also see Fig. 1.10; Fig. A2.2 & Fig. A2.3 in APPENDIX 2). In contrast to the 1883 ash, the post-1883 ash deposits are basaltic andesite both lithologically and geochemically, and characterised by relatively larger amounts of heavy minerals (e.g. Mg-rich olivine forsterite, hypersthene, augite), and they contain smaller amounts of clay fractions (Miyauchi *et al.*, 1986).

Soil mineral content

An important contribution of Ernst (1907) is the investigation of the soil fertility status and micro-organism content of the Krakatau soils in 1906. This was the first time such a study was carried out, and it found the soil to contain sufficient nutrients in generally soluble form and the porous ash seemed to be a good rooting medium (Newsome, 1982). Yet, organic matter was then still lacking, and in general some nutrients may not have been available in soluble form (Baren, 1931). Interestingly, however, the Krakatau soils then already contained as many bacteria as the soil in Bogor. Ernst also suggested that the 16 species of Legumes should have contributed considerably to the accumulation of Nitrogen in the soil, but failed to point out that these only occurred in the beach zone and the immediate hinterland.

Soil samples collected in 1982 from Sertung and Panjang revealed lower amounts of soil organic matter, clay and free iron and aluminium hydroxides than for Rakata soils (Shinagawa *et al.*, 1985). For instance, average carbon content of Rakata surface soils was found to be >9%, whereas the average carbon content of the surface soils on Sertung, Panjang and Anak Krakatau was <1.5% (Shinagawa *et al.*, 1986). The amount of carbon, exchangeable and water-soluble potassium, and clay and silt contents decreased from Rakata, to Panjang followed by Sertung, with the least amounts found in Anak Krakatau soils. However, average phosphorus was found to be higher on Sertung and Panjang than Rakata, and all of these had substantially higher levels than Anak Krakatau (Shinagawa *et al.*, 1985). This result is indirectly supported by findings of a recent soil study by Schlesinger *et al.* (submitted) on Rakata. They found phosphorus the only major nutrient

that may be limiting to plant growth, because of a high rate of accumulation of organic P which binds to Al, which then becomes unavailable to plants. Unfortunately no study of Panjang and Sertung soils was carried out.

It has been suggested that the high amount of exchangeable bases in Rakata soils is predominantly derived from decomposition of easily weathered primary minerals and amorphous volcanic glass found in the 1883 ash-deposits (Newsome, 1986). In contrast, the origin of the clay minerals, which mainly consist of smectite, was not attributed to pedogenic processes. Newsome (1982) suggested a geohydrothermal origin, whereas Harjosoesastro & Dai (1985) proposed they originated from the oceanic crust and the cone of Krakatau. The most common bases are Ca, Mg, K and Na, and pH varies around neutral. Evidence of a slight translocatory process only exists for Fe and some clay particles (Newsome, 1982; 1986). However, at altitudes >600 m, base saturation, and pH and weatherable minerals were found to be lower, whereas Al and H content was higher than at lower altitudes. The former is suggested to be due to greater soil leaching under conditions of higher precipitation, whereas the latter is related to the decreasing pH which increases the solubility of Al and H (Hardjowigeno, 1992). As mentioned above, particularly in the upland areas (>400 m), pre-1883 brown-soils are sometimes exposed, and compared to the post-1883 soils they are more weathered and have a higher clay content (7-15%).

Soil texture and water retention

Soil texture can vary quite considerably within and between the islands. In the more stable areas on Rakata top soils are organic rich and crumbly with some of the highest clay/silt contents found on the islands. In contrast, losses of organic and mineral matter from the soil often occur in the steeper areas where, in combination with the loose soil material and high rainfall, soil erosion is a common feature. Thus, coarser textured soils are produced, whereby the gully bottoms are generally covered in the coarsest material, mainly consisting of pumice blocks (Hardjowigeno, 1992; pers. obs.).

Table 2.3: Bulk density values for the humic, transition and pumice layer at 110 m and 710 m (from Hafkenscheid, 1994).

<i>horizon samples</i>	<i>depth (cm)</i>	<i>bulk density (g cm⁻³)</i>
110 m		
humic (n=5)	0-5	0.58±0.08
transition (n=1)	10-20	0.69
pumice (n=2)	20-50	0.85±0.09
710 m		
humic (n=4)	0-5	0.68±0.07
transition (n=2)	10-20	0.56±0.03
pumice (n=4)	20-50	0.86±0.06

Due to the fact that the majority of Rakata soils are made up of pumice, bulk densities are generally rather low (Table 2.3), which means that the soils are very permeable particularly in areas with a thin or no humic layer. The average porosity ranges from 57% for the humic layer to 70% for the pumice layer at 110 m a.s.l. on Rakata (Hafkenscheid, 1994). Yet, the micro-pores of this relatively silt-rich soil have higher capacity for water retention than, for instance, the sandy soils (particles >50 µm) in the vegetated parts of Anak Krakatau. No bulk density figures for Panjang and Sertung soils are available, but in general the high ash, and low clay content of the soils again make them very permeable and prone to rapid desiccation.

2.4 Climate

General climatic conditions

No long-term meteorological observations are available from Krakatau. Therefore, the general climatic regime has to be deduced from records of weather stations from coastal regions of West Java and South Sumatra. The climate of the Sunda Strait area has been classified as 'Afa' under the Koeppens World System, which means it is a tropical rainy climate with few dry months (Subagjo & van Reuler, 1985), whereby the west monsoon brings heavy rainfalls from the Indian Ocean and the east monsoon relatively dry air from Australia (Dammerman, 1948).

The longest rainfall observation for Krakatau to date was reported in Dammermann (1948) for Rakata for 1929 and 1930, and for 1929 for Panjang (Table 2.4). For Panjang temperature as well as rainfall data were collected by van Stehn in 1929 (Baren, 1931, Fig. 2.3). Mean monthly temperatures were almost constant throughout the year varying from 26.9° C (July and December) to 28.7° C (October). These data also roughly demonstrate the wettest periods to be during the West monsoon from November to April, and the driest period during the East monsoon which extends from May to October. However, 1929 was very much drier than 1930 (Table 2.4) with a very pronounced dry season, and 1929 has been suggested to have been a particularly dry year (L. Bruijnzeel, pers. comm.). Hoogerwerf's data (1971, in Thornton *et al.* 1988) for Ujung Kulon found that many years have a pronounced dry season, whereas in other years the dry season barely differs in the amount of precipitation from that of the wet season. Concluding from his data and the Krakatau data Hoogerwerf argues that the dry seasons in the Sunda Straits are unpredictable, and that annual rainfall can also vary considerably (Thornton & Rosengren, 1988).

The rainfall data for 1929 and 1930 can be supplemented by observations from weather stations around the Sunda Straits. Listed in Table 2.5 are data that were compiled by Hafkenschied (1994) from various sources, and locations are mapped in Fig. 2.4. This figure also depicts approximate isohyets in millimetres of mean annual rainfall, as well as two Gaussen system illustrations of mean monthly rainfall for Tanjung Karang, Sumatra, and Anyer, West Java. This additional information was extracted from Thornton & Rosengren (1988; Fig. 5). From these combined data one can suggest that Krakatau's average annual precipitation at sea level is between 2500 and 3000 mm.

Table 2.4: Monthly rainfall on Panjang (1929) and Rakata (1929 and 1930; adapted from Dammerman, 1948).

<i>Months</i>	<i>Panjang</i>	<i>Rakata</i>	
	1929	1929	1930
January	357	210	230
February	620	266	354
March	267	267	463
April	178	179	225
May	72	72	422
June	138	138	112
July	9	9	168
August	79	81	67
September		0	61
October	68	68	281
November	245	245	341
December	589	612	384
Total	2620	2145	3117

Table 2.5: Mean monthly rainfall and temperature data for Panjang island (1929), Branti airport, Labuan (1961-1970), Kalianda (1913-1923), Java's First Point (40 years), Cilegon and Malingping (adapted from Hafkenscheid, 1994). See Fig. 2.4 for the location of the weather stations.

<i>Months</i>	<i>Panjang</i> (40 m a.s.l.)		<i>Branti</i> (10 m a.s.l.)		<i>Labuan</i> (4 m a.s.l.)	<i>Kalianda</i> (35 m a.s.l.)	<i>Java's F.P.</i> (40 m a.s.l.)	<i>Cilegon'</i>	<i>Malingping'</i>
	mm	°C	mm	°C	mm	mm	mm	mm	mm
January	357	27.7	278	25.2	394	311	443	327	459
February	620	27.9	281	25.3	320	235	377	254	348
March	267	27.4	291	25.9	317	203	325	295	362
April	178	27.8	151	26.2	176	187	258	143	334
May	72	28.2	95	25.6	141	177	171	125	223
June	138	27.3	38	25.3	62	146	178	90	143
July	9	26.9	51	25.2	38	96	130	90	143
August	79	27.6	211	25.0	67	90	138	66	104
September		28.6	150	25.1	51	109	141	59	118
October	68	28.7	145	25.7	95	114	263	92	250
November	245	28.2	123	26.0	245	214	351	132	397
December	589	26.9	216	25.4	436	227	474	243	484
Annual	2620	27.8	2030	25.5	2305	2109	3249	1811	3319

a: Shinagawa *et al.* (1986) from a rainfall map for West Java (Publisher: P.T. Stranico, Jl. Cempaka Barul A. No.2);

note: annual values represent the total yearly rainfall but monthly average temperature.

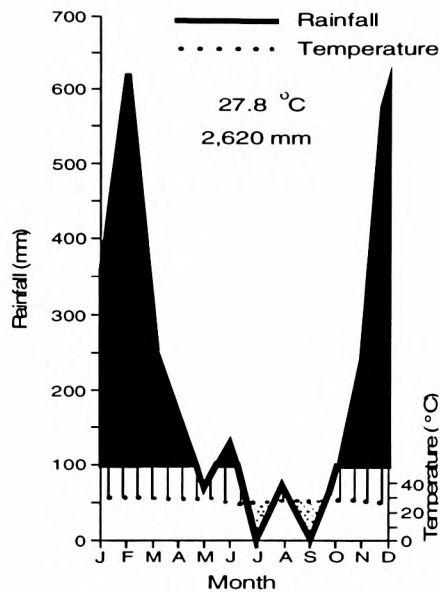


Fig. 2.3: Climate diagram of Panjang from observations by Stehn in 1929 (adapted from Thornton *et al.*, 1988).

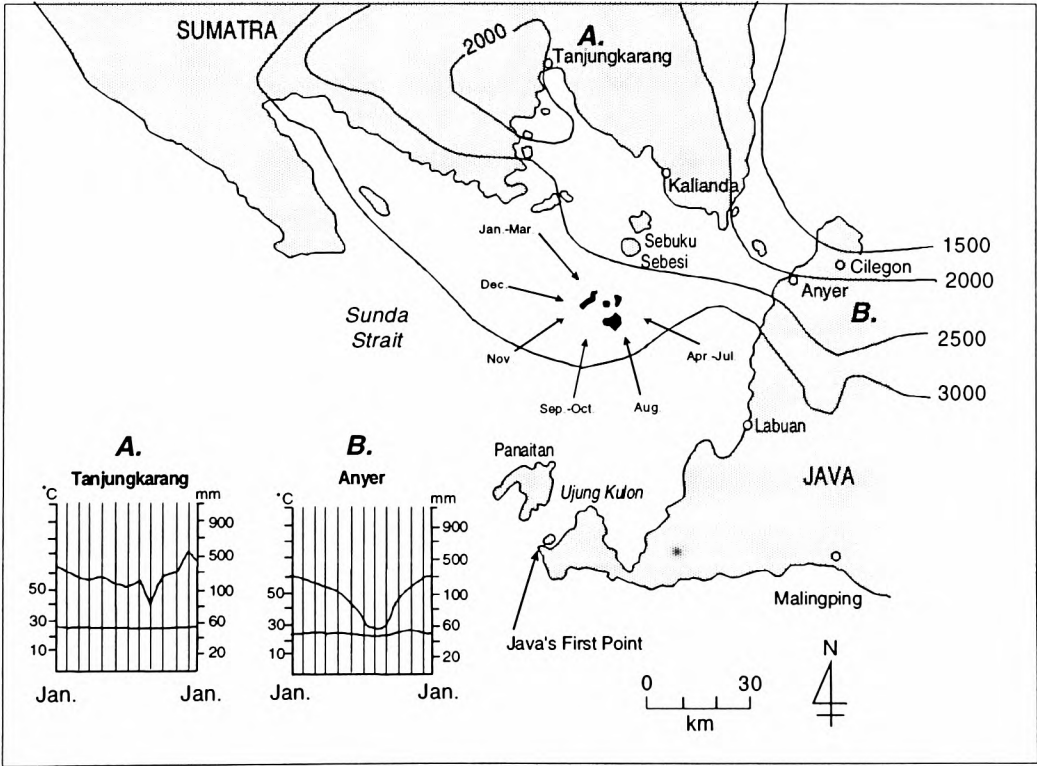


Fig. 2.4: Map of mean annual rainfall for the Sunda Strait from 1941-1975 data. Isohyets in millimetres and short arrows show approximate wind directions in different months. Climate diagrams with mean monthly temperature and rainfall for **A.** Tanjungkarang, South Sumatra and **B.** Anyer, West Java (adapted from Thornton *et al.*, 1988).

Influence of extreme events: the ENSO scenario

Indonesia lies in a region that is regularly and profoundly affected by El Niño Southern Oscillation events (ENSO), which can cause extreme droughts in some tropical regions and bring torrential rains to others (Nicholls, 1991; Diaz & Markgraf, 1992;). Several studies have shown that the Indonesian region and Papua New Guinea has been affected by major El Niño related droughts (Leighton, 1986; Allen, 1988; Allen *et al.*, 1989; Nicholls, 1993). They occur approximately every two to seven years, typically lasting for 18 to 24 months. The years 1990-1995 have all been under ENSO influence making it an unusually long period, which was not, however, of equal strength spatially throughout the region and over the five year period (R. Washington, pers. comm.). During my study period the Krakatau islands were worst affected by drought during 1994, when almost no rain fell for 5 months (M. Clarbrough, pers. comm.; pers. obs). The whole region of Kalimantan, Sumatra and Java was also severely affected during that year, leading to widespread forest fires in the former two regions, whereby heavy smoke pollution led to the temporary closure of several airports, including Singapore (Jakarta Post, articles in August and September 1994 editions).

Data collated by Walsh (1996) on drought frequency changes in Sabah and adjacent parts of northern Borneo show that between the periods 1878-1915 and 1967-to-date the area was subject to longer and more intense drought periods, whereas the intervening period 1916-1967 was relatively drought free. These findings are concordant with the result of extensive studies by R. Washington (pers. comm.) who has looked at ENSO frequencies since 1900 and their link to rainfall in Sub-Saharan Africa.

ENSO phenomena are triggered by complex, and still imperfectly understood, atmospheric and oceanic anomalies in pressure, atmospheric circulation, and sea-surface temperatures of the Pacific Ocean (Walsh, 1996). During an ENSO event, anomalously high pressure persists over the Indonesian-northern Australian region and sea-surface temperatures are higher than normal, whereas surface pressure in the south-eastern Pacific Ocean is abnormally low (Allen, 1988). El Niño drought events are often, but not always, followed by a pluvial La Niña period. La Niña is the counterpart of El Niño and presents the other extreme of the ENSO cycle, during which sea surface temperatures of the equatorial Pacific Ocean drop well below normal levels and advect to the west while the trade winds are unusually intense rather than weak (information from

http://enso.unl.edu/ndmc/enigma/el_nino.htm; 1996).

The long-term ecological implications of extreme droughts, depending on the frequency and duration, and whether accompanied by fire, are likely to be very significant. However, the direct effect on rain forest character and dynamics is still poorly understood (Walsh, 1996). In the context of the early successional forests of Krakatau extreme events such as drought may have long-lasting effects on the succession, and have thus been included in the revised model introduced in CHAPTER 1 (Fig. 1.16). Droughts induce mortalities of both trees and saplings, and consequently favour the regeneration of light demanding species in many simultaneously created gaps (cf. Woods, 1989). Thus, regenerating forest may have an unusual tree age and dbh distribution with fewer than normal large trees and a substantial number of trees of similar dbh and age (Newbery *et al.*, 1992; Walsh, 1996). Data on the effect of the 1994 drought on sapling composition, survival and growth, and the general impact on the Krakatau forests, is presented in CHAPTER 4 & 5.

Lightning and thunderstorms

Although very little literature exists, gap creation by lightning has been argued to be fairly frequent in tropical forests (Brünig, 1964; Whitmore, 1984; Johns, 1986; Tutin *et al.*, 1996). It may, therefore, be argued to be an important aspect of forest dynamics and succession. However, lightning damage has to be seen as spatially and temporally heterogeneous, whereby certain areas are likely to be more prone to lightning damage due to possible favourable coincidences of a number of physiographic, edaphic, climatic and biotic factors (Brünig, 1964). For instance, even-canopied and mono-specific stands such as *Shorea albida* peat swamp forest (Brünig, 1964; Anderson, 1964), and mangrove and *Nothofagus* forest in Papua New Guinea (Johns, 1986), have been found to be more susceptible. In the latter forest types the commonness of root grafting between similar or related species, has been suggested to allow the lightning to travel laterally from the central tree, and thus increase the area of damage (up to 50 m diameter; Johns, 1986).

Thunderstorms were said to occur more often in the Sunda Straits than in any other region of the Malay archipelago (Van der Stok in Braak, 1925), and frequent lightning and some lightning strikes have been observed on the Krakatau islands (Borssum Waalkes, 1960; Whittaker & Jones, 1993; pers. obs.). Bush *et al.* (1992) report of areas of circular tree death in north-eastern and southern Sertung. These areas looked as if repeated damage

from lightning had occurred, which is apparently not an uncommon phenomenon according to Brünig (1964). Moreover, these areas are covered in mono-dominant, and even-canopied stands of *Timonius compressicaulis*, thus fitting the suggestions of greater susceptibility of dominant stands made above.

Furthermore, it is reasonable to suppose that the electrical discharges often observed in eruption clouds (e.g. as observed by Ernst, 1934; pers. obs.; Fig. 2.5), together with the large amounts of ash projected into the atmosphere, may spawn a greater number of local thunderstorms with associated lightning, heavy rainfalls, and high winds (A. Robock, pers. comm.; S. Self, pers. comm.; see CHAPTER 3). It is suggested here that during times of volcanic activity, lightning damage and gap formation from windthrows are likely to increase. Some casual observational evidence suggests this and, for instance, Docters van Leeuwen (1936) observed increased windthrows after the 1931 eruptions. In the case of Rakata, cloud forms around the peak on more or less a daily basis, and even during times when the volcano is relatively inactive, lightning flashes in the cloud band have been observed by visiting scientists (Borssum Waalkes, 1960). As the summit of Rakata (735 m a.s.l.) exceeds the maximum elevation of the other islands by > 500 m, lightning may more frequently discharge to the higher altitudes of this island (see CHAPTER 3)

Hydrology and rainfall

The Krakatau islands have no perennial streams, as drainage in the porous substrate is too rapid (section 2.3). Temporary streams begin to flow during heavy rainfall events, but tend to cease shortly after precipitation has stopped (Newsome, 1982; R.J. Whittaker pers. comm.).

Some work on the forest hydrology was carried out by Bruijnzeel *et al.* (in prep.) and Hafkenscheid (1994) with the main purpose of investigating the possible causes of forest stunting at higher altitudes. During these studies hydro-meteorological data on water retention, plant available water, and evapotranspiration etc., were collected on Rakata at the altitudes of 110 and 720 m a.s.l., during the dry season in July 1992. The average evapotranspiration rate was estimated to be 3.3 mm day⁻¹ at 110 m a.s.l., and 1.2 mm day⁻¹ at 720 m a.s.l. With these figures and the assumption that most plant roots are concentrated in the upper 50 cm of soil, Hafkenscheid (1994) calculated that soil moisture

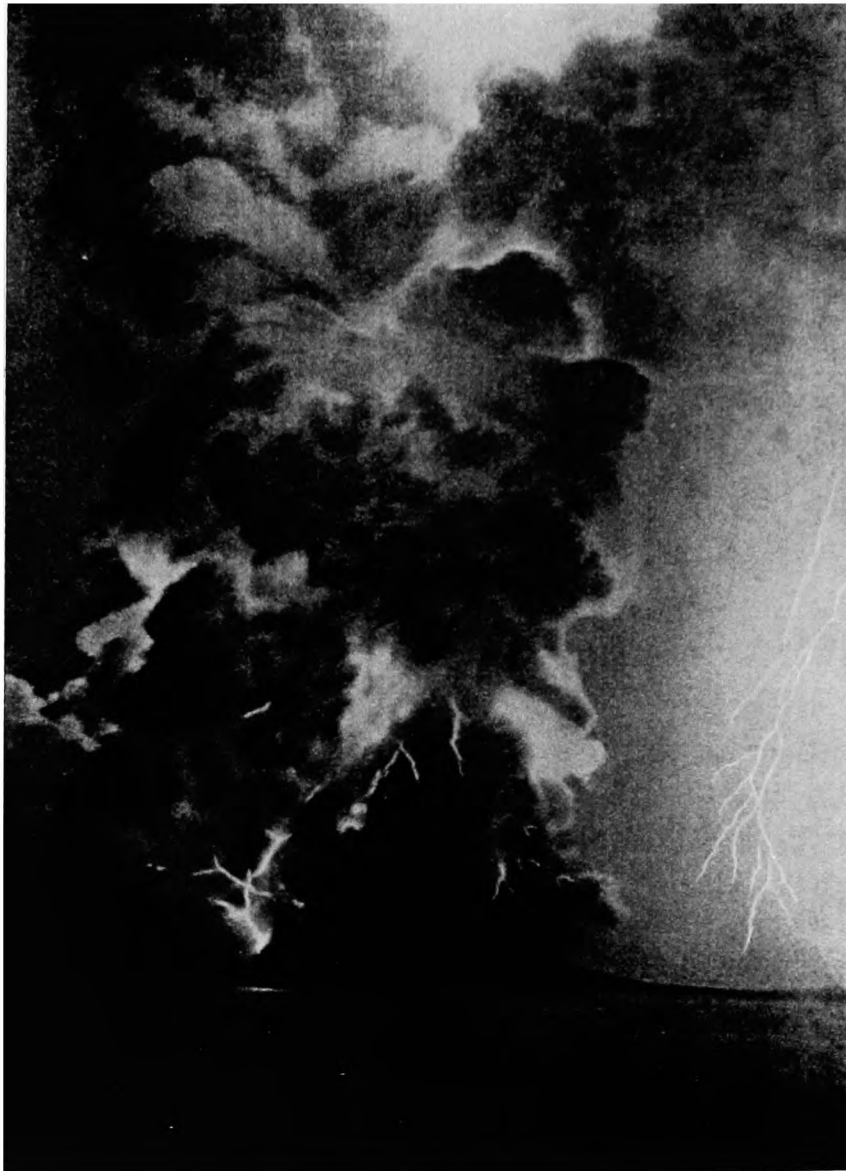


Fig. 2.5: The formation of Anak Krakatau in 1930 showing electrical discharges within the ash clouds (reproduced from Umbgrove, 1949).

should be depleted within 4 to 5 weeks at 110 m a.s.l. and c. 3 month at 720 m a.s.l. He suggested that water stress is unlikely to ever occur at the higher altitudes, and only occasionally at the lower altitude. Yet, the prolonged drought of 1994, with almost no rain for 5 months (M. Clarbrough, pers. comm.; pers. obs.), has shown that severe water stress can even be experienced by the higher altitude vegetation.

No quantitative information on water retention, or other hydrological measurements, however, exists for the South-east coast area of Rakata. Such data would be particularly interesting in order to explain why this area seemed to suffer particularly under the 1994 drought. One can speculate on excessive drainage of the very pumice rich soil, with little or no organic layer in this area, and/or rapid underground drainage of run-off from the steep slopes of Rakata by way of rapid flow in soil pipes. Evidence of piping has previously been observed on Rakata (Richards, 1982), as well as on Panjang after collapse or slope erosion (pers. obs.; Fig. 2.6). Walsh & Howells (1988) found that pipes contributed 14-16 percent of stream flow in a small catchment on the volcanic island of Dominica, West Indies. Under-supply with soil water in the drought prone area of South-east Rakata may also be a result of sub-terranean drainage lines cutting off this particular wedge of lowland from upland flow. Furthermore, the very flat topography may act in conjunction with the above, and seems to play an important role, since the drought impact was much reduced as soon as the more hilly terrain started towards the interior. As this area is very close to a rapidly eroding coastline, saltwater incursion due to capillary suction during times of water deficit has also been suggested as a possible cause of extremity of the drought impact. This is particularly so, because normally drought can be expected to first affect vegetation on ridges and upper slopes (L. Bruijnzeel, pers. comm.). Increased evapotranspiration due to the flat topography, and greater wind exposure near the coast may also play an important role.

In contrast to the South-east Rakata area, during the 1994 drought gully areas on Panjang appeared much more moist and the vegetation much lusher. This seems to contradict the suggestions made in section 2.3 that the high ash content of the soils should make them very permeable. However, after the wet-season following the 1994 drought, erosional down-cutting revealed a thick, impermeable clay layer at the gully bottoms in the East and North-east of Panjang. These layers should lead to greater water retention, at least near the gully bottoms. Sertung generally appeared very parched during the 1994 drought, as it additionally suffered from large amounts of ash-fall that was carried to Sertung particularly during the dry season.



Fig. 2.7: Rakata island with the characteristic cloud cap. Clouds form almost daily above 500 m a.s.l.

On Rakata in particular, intra-island differences in rainfall are to be expected due to its higher altitude. Above 500 m a.s.l. Rakata is generally in clouds for most of the day and substantially more rainfall and occult precipitation from fog is received than at lower altitudes (Fig. 2.7). For instance, Hafkenscheid (1994) calculated that occult precipitation near the summit accounts for more than 5-7 percent of annual precipitation, depending on whether the calculation is based on 2305 mm per year for Labuan, West Java (10 year average) or that of 3250 mm per year for Java's First Point, Ujung Kulon (40 year average; Table 2.5). Moreover, the estimate is likely to be an underestimation as measurements were taken during the driest period of the year. Intra-island differences in precipitation are also likely to be great on Rakata due to the large cone causing a rain-shadow effect for the east side of the island during the wet North-west monsoon (November to April). However, as the western side of the island is little studied due to difficulty of access, and the general difficulty of working on the islands during the wet-season, no quantitative data exist.

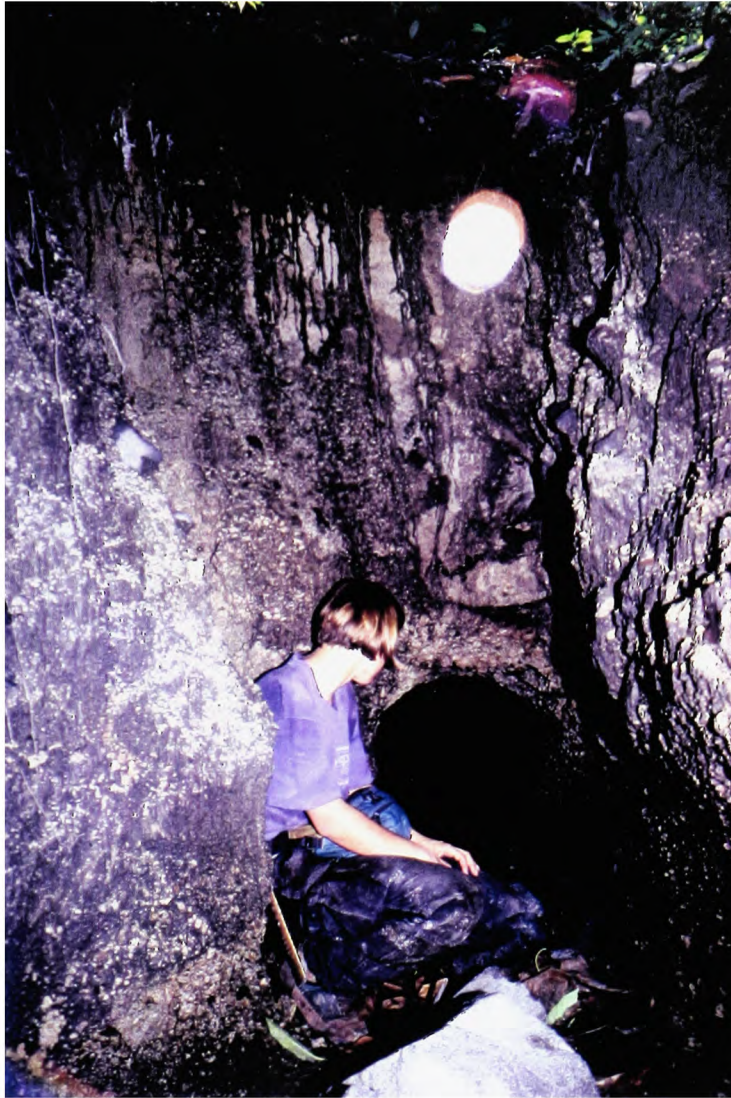


Fig. 2.6: Example of a soil pipe found on Panjang in 1995. The pipe was exposed through erosion of the steep, lower slopes of a narrow gully (photo: Paul Jepson).

Inter- and intra-island differences in the amount of rainfall received might also account for some of the observed difference in drought impact, and possibly vegetation composition and stature. Differences in rainfall received have been reported for Panjang and Rakata, with Panjang receiving twice as much average rainfall than Rakata during the month of February in 1929 (Baren, 1931; Table 2.4). Also in 1996, considerable differences in rainfall between Rakata and Panjang were measured (L. Shilton, pers. comm.), whereby Rakata lowlands in the months of April to July received less than Panjang. However, this situation suddenly reversed during August and September. Thus, although monthly totals may differ, over a yearly average these differences might disappear. But judging by the 1929 data, differences in annual receipt between islands may exist, as Panjang received 465 mm more rainfall than Rakata.

It was suggested above that there may be increased thunderstorm activity during times of Anak Krakatau's activity. Not only would this increase the incidence of lightning, but it would also increase the amount of rainfall received by the island group, since ash particles may act as condensation nuclei for rain drop formation. One can suggest that this should at least be the case if activity coincides with average years when, for instance, during the 1993 dry season relative humidity is >75% (pers. obs.), in comparison to a range of between 55-70% measured during the 1994 drought. Thus, even in the dry season of normal years enough moisture for condensation on the small ash particles should be available.

2.5 Geomorphology and topography

"Changes still take place constantly. Large pieces slide down again and again, new ravines are eroded, others are filled with materials which are washed down along them. The coast-line is shifted continuously owing to the wash of the sea. The main direction of the successions, however, is not changed by it." (Docters van Leeuwen, 1936; p. 260)

Of all the scientific disciplines studying the Krakatau islands, probably the least active has been the discipline of geomorphology. A substantial amount of descriptive information of the ash-cover and its initial erosion exists. However, except for the study of coastal erosion (Bird & Rosengren, 1984; Rosengren, 1985; Rosengren & Suwardi, 1985), and a pilot study assessing the development of the morphology of a tephra drainage basin and some of the processes involved (Swabey *et al.*, in prep.), no in-depth study of the geomorphological development of the remnant islands has been made.

The configuration of all three remaining islands was determined both by residual pre-1883 terrain, and by the dissection of the thick mantle of pyroclastic deposits consisting of different sized pumice blocks and fine porous ash that buried the existing topography during the 1883 eruption (Verbeek, 1885). Rapid erosion downslope and erosion of the new deposits along the coast took place after the 1883 eruption. It formed deep V-shaped gullies separated by narrow ridges. At the western and southern coastline of Rakata and Sertung these end as hanging gullies at the rapidly receding cliff edges (Fig 2.8). Mostly, as the channel floors of the gullies were eroded down to the resistant pre-1883 lavas (Thornton & Rosengren, 1988), and/or new vegetation started clothing the slopes and



Fig. 2.8: West side of Rakata with pumice cliffs and hanging gullies from rapidly receding cliff edges.

ridges, gully erosion consequently slowed down. Thus, the deep gully systems of these islands are essentially fossil features of an intense early post-eruption phase of erosion (Stehn, 1929; Newsome, 1982; Whittaker *et al.*, 1989; see Fig. 1.5). Nevertheless, the Krakatau geomorphology can still be seen as very active, as gully widening, interfluvial breaching and headward erosion still takes place. Also, during fieldwork between 1992 and 1995 evidence of often very heavy down-cutting, as well as redeposition during the wet season, was found. Thus, further down-cutting of the gully bottoms is still possible in places (Fig. 2.9), and may actually amount to the removal of material previously deposited from down-wash of erosion material. Down-cutting of this material of up to 2 m was observed. This produces a stepped gully morphology in places. In other areas, such as the lower parts of the main South-east gully on Rakata, c. 1.3 m of pumice and soil was washed down and deposited between 1993 and 1994. This could be measured, since a treelet



Fig. 2.9: Example of down-cutting of a gully bottom near the South-coast of Rakata. The erosion took place during the 1993/1994 wet season.

marked at a certain height in 1993 was found buried in 1994, and the excavation revealed the depth of burial (Fig. 2.10). In some gullies infilling has taken place from slope retreat which results in interfluvies frequently reduced to very narrow ash walls that are only maintained by the forest cover (Richards, 1982).

Such an active geomorphological regime has a profound effect on the disturbance regime of Krakatau forests. For instance, it can frequently be observed that trees on ridges and slopes have had their roots undermined by erosion, and that this has predisposed them to falling, often causing a small landslide. Furthermore, after periods of drought, the reduction of understorey vegetation cover and death of trees makes Krakatau soils even more susceptible to erosion. This was demonstrated by the fact that the greatest amount of erosion was observed after the wet season immediately following the drought of 1994.



Fig. 2.10: Between 1993 and 1994 this treelet was partly buried by c.1.3 m thick depositional material transported down the gully.

Landslides

All three islands are very prone to landslides due to their topographic and geomorphologic characteristics. They possess many narrow V-shaped gullies with extremely steep and, because of the loose pumice substrate, often unstable gully walls. Above 400 m, Rakata has particularly steep slopes of 40-70 percent, and some of the Sertung and Panjang gullies have near vertical walls. This combination makes landslides common events, and Docters van Leeuwen (1936) reported that "new ravines are constantly formed and ravine-walls tumble down" (p. 144). Also, according to his evidence, landslides are often indirectly related to volcanic activity which is generally accompanied by frequent earth tremors (Whittaker *et al.*, 1992a; see CHAPTER 3). For instance, after the 1930 eruption of Anak

Krakatau, Docters van Leeuwen found many landslides in the gullies of Sertung. These caused severe damage to the forests, and he suggested that by the late 1920s landslide sites were often the only areas where *Saccharum spontaneum* could still maintain itself (particularly relevant to South-east Rakata). This shows that these sites are important in locally setting back the succession, maintaining areas for early colonisers, and in offering opportunities for possible new colonisers to the islands (see CHAPTER 3).

Coastal erosion

Coastal erosion and the constant reshaping of the coast line is a very characteristic disturbance factor of the Krakatau islands. For instance, coastal retreat of up to 2.5 km has taken place in certain areas since 1883 (Bird and Rosengren, 1984; Fig. 2.2). Between 1884 and 1887 alone, up to 2-3 km² of the new deposits were removed (Thornton, 1996). The steep tuff-walls in the West and South of Rakata, and the South, and South-west, of Sertung are known to erode fast with rates of up to 3 m per month (Rosengren & Suwardi, 1985) due to the powerful swells from the Indian Ocean. The eroded material, largely consisting of sand and pumice, is often re-deposited by longshore drift. In this way the spit of Sertung was formed and evolved, the first stages of which were noted in 1897 (Penzig, 1902), and the fully formed spit was first noted and mapped in 1908 (Thornton, 1996). Fig. 2.11 shows the drastic changes in shape and size of the spit, and in fact the spit was broken in 1994 and had completely disappeared by 1995 (pers. obs.). Some evidence of rebuilding has, however, been noted in 1996 (T. Partomihardjo, pers. comm.).

The spit on the South coast of Rakata was documented on maps and charts between 1903 and 1940 (Fig. 2.2). It was the location of a landing stage used by Händl who ran a pumice extraction operation between 1916-1919 (section 2.6). Already in 1924 Docters van Leeuwen (1936) found that the South-Rakata spit had become smaller and that the South coast was shifting inland. An aerial photograph from 1946 showed that the spit was replaced by a shallow embayment (Thornton, 1996). Borssum Waalkes (1960) also reported that in 1951 the spit had suffered a large reduction from the 1930s, and that at the same time a new spit on the East side, which is now Owl Bay, began to form. All this demonstrates that the coastal geomorphology of the Krakatau archipelago is still very active today.

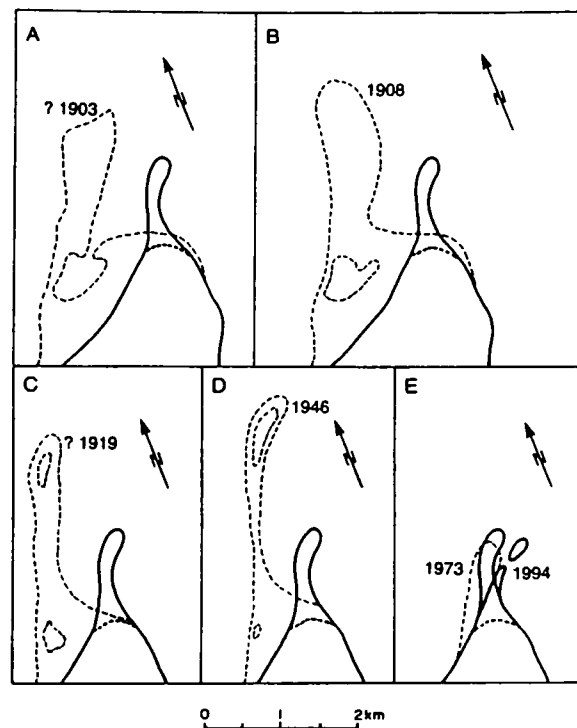


Fig. 2.11: Since the eruption in 1883 the shape, size, and position of the Sertung spit has constantly been changing. The bold outline shows the spit's coastline in 1984. The additional bold outline in E shows the fragmentation of the spit in May 1994. Its isolated portion was completely awash 4-5 month later (reproduced from Thornton, 1996). By 1995 the remainder of the spit was cut-back further by c. 80 m (pers. obs.)

Clearly such active coastal erosion influences the vegetation by, for instance, not allowing a littoral zone to develop on the narrow beaches at the bottom of the retreating cliffs. Also the plant communities on the tops of the constantly receding cliff edges often show little coastal influence, but are rather occupied by inland species since the erosion is faster than the regeneration. The higher light incidence at the unstable edge allows exploitation by heliophilous herbs such as *Eupatorium odoratum* and *Lantana camara* (Bush, 1986a). This may also contribute to the occurrence of a band of the Sertung and Panjang dominant, and pioneer tree species *Timonius compressicaulis*, along cliff-edges of the South and West side of Rakata (T. Partomihardjo, pers. comm.)

2.6 History of administration and extent of human impact

The Krakatau islands attracted almost immediate interest from scientists of various disciplines, the geologist Verbeek being one of the first to visit the islands in 1884. Botanists especially recognised the sterilised islands as a 'natural experiment' for studying the process of primary succession during a period of preoccupation amongst plant geographers with the question of dispersal of propagules to off-shore and oceanic islands. As early as 1914 was it proposed that Rakata be designated a nature reserve. In 1919, the western half of Rakata, and the whole of Sertung were declared a National Monument, and in 1925 the area covered by this designation was extended to include the eastern half of Rakata. In 1925, Rakata and Sertung were also included in the Ujung Kulon Nature Reserve, lying some 45 km South of the island group, and the legal status of the islands became that of Strict Nature Reserve (Cagar Alam). In 1982, the Ujung Kulon Nature Reserve was declared a National Park and the Krakataus were included in the proposed boundaries. In Indonesia, the status "declared" National Park means that the management status of the land is in accordance with national park guidelines, but the legal status of the land remains that of the earlier designation, until the park is formally designated by decree of the Ministry of Forestry. In this case, the "declared" park boundaries crossed two provinces : West Java (Ujung Kulon) and Lampung (Krakatau). A national park management unit based in West Java would face significant logistical difficulties in co-ordinating with Provincial and Regency authorities in Lampung . For this reason, when the Ujung Kulon National Park was designated Krakatau was excluded to be managed as a Strict Nature Reserve under the provincial conservation office of the Directorate General of Nature Conservation and Forest Protection (PHPA) in Lampung (P. Jepson, pers. comm.)

The status of Strict Nature Reserve means that access is only permitted for the purpose of scientific research (Sumardja *et al.*, 1984; Government of Indonesia, 1990). In practice, however, a presence of PHPA guards was established on the islands only in the late 1980s, and even since then the lack of facilities (e.g. patrol boats) makes a no-access policy difficult to enforce. PHPA does allow limited tourist access by permits obtained from offices in Tanjung Karang (Sumatra) and in Labuan (West Java). Tourist visits are mainly restricted to circling the islands by boat, and landing on the beaches of Anak Krakatau, occasionally Owl Bay on Rakata (see Fig. 2.2 for location), and on North-east Sertung, where a PHPA guard post is established. During the absence of volcanic activity people

often climb the open slopes of Anak Krakatau. Tourists in general do not penetrate far inland on the other islands, although the popularity of Krakatau for student groups and groups of adventurers seems to be increasing (pers. obs.).

In 1995, a workshop and conference was held at Lampung University to assess eco-tourism potential. Some suggestion of building accommodation on Sertung was made, despite the lack of adequate water resources, problems of waste-disposal, and the general volcanic hazard. Such operations would conflict with the current status as a Strict Nature Reserve, unless the protection status of the islands were to be changed.

So far the islands have always been seen as very little affected by human disturbance. However, it is suggested here that human impact has probably been greater than previously anticipated, and it seems to have increased in recent years. It has therefore, been included as another disturbance factor in the revised successional model outlined in CHAPTER 1 (Fig 1.16).

The fact that no long-term permanent settlement has existed on the islands since 1883 seems to support the suggestion that human impact may be regarded as very small. Yet, it is still important to examine what potential impact the various human visitations have had on the islands.

The longest continuous period of stay on Rakata was that by Händl and a group of workers. He was granted a 30-year lease for the extraction of pumice over a 870 ha area covering the eastern part of Rakata, and lived near the South-east coast of Rakata between 1916-1919. His lease was cancelled in 1917 as he did not keep to its terms and Händl apparently left and abandoned his house in 1919 (Whittaker *et al.*, 1989; Thornton, 1996). However, some form of operation of unknown effect still continued until 1922. During this time a small garden was established, but it is very likely that the area occupied was on the South spit which has now almost disappeared. In any case, Docters van Leeuwen (1936) reported that the area of disturbance quickly overgrew, and that introduced crop species were rapidly shaded out.

In 1951, Borssum Waalkes (1960) found patches of *Saccharum spontaneum* behind the strandline forest in South-east Rakata and thought them to be linked to human disturbance, because Docters van Leeuwen (1936) had already reported this area to be covered in

mixed forest. Also in 1951, some cleared areas planted with coconuts and other crops were found in northern Sertung, but these and large areas of the forest were subsequently destroyed by the substantial eruptions of Anak Krakatau in 1952 (Borssum Waalkes, 1960). Panjang experienced most of the temporary habitation, when, for instance, a small topographical survey team was stationed on Panjang between August 1896 to January 1897, and the Volcanological Service maintained an official observation post there between June 1927 and sometime in 1931, the period of Anak Krakatau's emergence (Bemmelen, 1929; Ernst, 1934). These visits led to the introduction of a few weeds, but Docters van Leeuwen (1936) suggested that none survived.

In 1919, a visiting member of the Pan-Pacific Science Congress accidentally started a fire which burnt a large area of the North-west of Rakata which was then covered in savanna vegetation with scattered clumps of small trees. Docters van Leeuwen (1936) suggested that the fire did little damage, and that the vegetation recovered quickly. However, the fire must have had a temporary if not a longer lasting effect on the succession, and may well have altered the species composition and the competitive balance of the species within the affected area.

Temporary camps of fisherman can always be found on the islands. They collect firewood, camp-building material, and turtle eggs, and search the lowlands for land-crabs (Bush *et al.*, 1986). The latter fetch around 2500 Rupiah (c. £0.8) each in the local markets. They are thus a lucrative source of additional income encouraging over-exploitation. Indeed a significant decline in densities was noted between 1992 and 1995, and the specimens found in 1995 were mainly very small, except in more inaccessible inland areas (pers. obs.). Since land-crabs act as secondary dispersers for various seeds (e.g. *Terminalia catappa*), their decline may affect regeneration dynamics in the more accessible areas of the Krakatau islands.

Although scientific expeditions over the years have always tried to minimise the impact on the environment, and avoid accidental introduction of plant and animal species, some impact is unavoidable. For example, during the fieldwork for this study, the frequently used paths along narrow ridges, and on slopes of steep and loose substrate suffered considerable erosion. The maintenance of trails also causes damage due to cutting of brush.

Pumice mining was not restricted to Händl's time. There are reports of this activity taking place in 1951 (Borssum Waalkes, 1954), and presumably extraction has continued throughout the intervening period. However, it appears that in recent years pumice mining has become more extensive, and it is suggested to be the most noticeable and destructive form of exploitation on the islands (pers. obs.). An increase in extraction might be a function of several variables such as greater accessibility with motorised boats, increased demand and higher price for pumice, as well as lack of enforcement of reserve regulations. In 1994, workers obtained 750 Rupiah per sack (c. £0.25), which then fetched c. 6000 Rupiah in Jakarta (T. Partomihardjo, pers. comm.). Pumice in ground form is used as a component in washing powder, toothpaste, and other cosmetics, as well as being used for making building material. Large quantities, predominantly from Lombok, but possibly also from Krakatau, are exported to Hong Kong (Jakarta Post, 29th August, 1995).

Observations and informal surveys revealed that the areas most affected by extraction are the North and North-east near-coastal gullies, and the North-western cliff-face on Panjang, and the gullies and cliff-faces in particular on the West-coast of Sertung. On two occasions between July and August 1994, pumice mining activities were observed during fieldwork on Panjang and Sertung respectively (see CHAPTER 3). Loading operations of more than 150 large rice sacks filled with pumice (normally holding 50 kg of rice) onto boats were observed twice in both 1994 and 1995, and apparently take place at least once every two weeks during the dry season. As the extraction is illegal the loading is usually timed to coincide with the absence of PHPA reserve wardens during staff change-over.

In 1995, a survey of the damage around the northern area of Panjang revealed that large quantities of pumice were removed in several gullies (Fig 2.12). This process usually starts from the top of ridges downwards, cutting back the gully walls, and/or digging out the pumice from underneath tree roots, where pumice seems most concentrated. This process involves the undermining of large numbers of trees (leading to their subsequent fall), and the creation of large areas of bare mineral soil and pumice. In general, this kind of disturbance to the gullies also alters the geomorphological and hydrological regime on the local scale. It causes gully erosion and large amounts of run-off and downslope transport of fine pumice material which is deposited either as fans at the gully entrances, or into the sea during more heavy rainfall events.



Fig. 2.12: Examples of pumice digging damage in near-coastal gullies of North-east Panjang.

Digging in both the small area of the coastal plain in eastern and northern Panjang, and in the South-east of Rakata, has also taken place over a number of years. During the 1993-95 study period, fresh evidence for this type of pumice extraction was found in particular on Panjang. For example, in 1994 one of the gap study sites (site P13, see CHAPTER 4) was found to be severely re-disturbed by digging and undermining of roots. It led to six treefalls (15-40 cm dbh) and the creation of many holes (up to 1.8 m depth), and bare mineral soil surfaces that began to be colonised by pioneer vegetation, such as *Macaranga*, *Pipturus* and *Hernandia peltata*. The coastal plain is also covered in a large number of holes, all of which are remnants of pumice digging operations in the past. These can also be found in a more confined area of the South-east coast of Rakata. Some of the older holes were observed to form temporary pools after heavy rainfalls, and during the wet-season (pers. obs.).

Collection of pumice on the beaches also takes place. This form of extraction is particularly common on the West-coast of Sertung. It is the least destructive extraction method although it is not clear how much the removal of pumice along the west-coast and the beach area of the Sertung spit may have contributed to altering the erosional regime of this very active coastline.

The direct destructive impact of pumice mining is obvious, however, the presence of large numbers of people for several weeks a few times a year also has an impact on the near-coastal forest of the islands. For instance, workers cut poles for building camps, they collect firewood, and they are the source for potential introductions of plants and animals. Near one camp, some planting of cassava had taken place, and useful trees such as *Mangifera indica* and *Tamarindus indica* had been planted. In 1994, 15 camps with c.10 people in each were counted on the long stretch of the West-coast of Sertung (T. Partomihardjo, pers. comm.), and in 1995 the remains of 18 camps were counted in northern Panjang, with more than half of them recently occupied.

Overall, it appears that the human impact on the islands has increased, and that now additional threats of further interference are posed by plans to develop eco-tourism. However, the Krakatau islands are a unique and internationally important site for the study of primary succession and ecosystem recovery from major disturbance. The primary objective of declaring the islands a Strict Nature Reserve was to provide a site for scientific

investigation, consequently human interference should be strictly controlled in order to ensure the perpetuation of the islands' scientific value.

2.7 Conclusions:

This chapter has outlined the main characteristics of Krakatau's volcanic history and its physical geography, it also confirms suggestions that there is both a very dynamic physical environment and a very active disturbance regime. It has been highlighted that disturbance from intermittent volcanic activity is the most distinctive element of the disturbance regime. However, for the first time attention has also been drawn to the importance of occasional extreme climatic events. This consideration is further illustrated in the data chapters, where, for instance, the impact of the 1994 drought on the vegetation and the regeneration dynamics is investigated in great detail. Moreover, attention has been drawn to the fact that human impact on the islands, particularly in the more accessible coastal areas, is not as negligible as previously thought.

CHAPTER 3:

DISTURBANCE AND GAP FORMATION: A MESO-SCALE INVESTIGATION*

"The concept of disturbance regime is a means of organising spatial and temporal information about a range of disturbances affecting a particular landscape."....."To understand the role of disturbance in creating broad landscape patterns, the full range of disturbances affecting a particular landscape must be considered." (Veblen, 1992; p. 175)

Summary

1. There is no lack of regeneration opportunities, i.e. the rate of gap formation seems to be sufficient or more than sufficient to offer regeneration opportunities or 'site availability' *sensu* Pickett *et al.* (1987).
2. Since the volcanic activity commenced in 1992 the forests of the Krakatau islands have experienced increased rates of gap formation in comparison to the previous decade. This is particularly found for Sertung, and does not exclude Rakata.
3. Diversification, and succession on Sertung and Panjang are very likely to be hampered during more severe volcanic eruptions in the future (ash deposits or even blast damage), although the degree of disturbance and the chronology may differ between the two islands. This is in line with Whittaker *et al.*'s disturbance driven model for succession on Krakatau. However, this model is extended here by suggesting that Rakata does not remain unaffected, as volcanic activity may go hand in hand with more severe weather conditions, and an increased number of earth tremors. Therefore, landslides, windthrows and lightning strikes seem to increase particularly in the higher altitudes of Rakata, but also in other areas of the islands. Thus, it is also possible to suggest that during eruptive activity the rate of gap-formation will increase overall.
4. Interactions with extreme climatic events on the regional scale (e.g. ENSO events) may add additional disturbance factors acting archipelago wide.

* Data presented in this chapter have been published in summarised form in Schmitt & Partomihardjo (in press), Schmitt & Whittaker (in press), and Whittaker *et al.* (submitted).

3.1 Introduction

Natural regeneration and succession are complex processes dependent on a multitude of variables and changes in resource availability in time and space. The formation of gaps in the vegetation has for decades been recognised as crucial events for regeneration (Watt, 1923, 1947; Sernander, 1936; Richards, 1952; Bray, 1956; Veblen, 1992). In forest ecosystems, the death of one or more trees, due to a variety of possible gap creating triggers (e.g. treefalls, landslides, lightning strikes, etc.) exemplifies the single most drastic event with respect to the release of, and reduced competition for, vital resources for plant growth (Ricklefs, 1977; Hartstorn, 1978; Whitmore, 1984; Richards, 1996; Veblen, 1992). These are foremost physical regeneration space ('site-availability'), light, plant available moisture and nutrients. A large literature (see CHAPTERS 1 & 4) now exists on the importance of light and it has also been established that the temporary reduction of root competition (Sandford Jr., 1989; Wilczynski & Pickett, 1993) after gap creation can mean a substantial increase of plant available moisture (Veenendal *et al.*, 1996). This has been found particularly in the case of severe disturbance by landslides (Dalling & Tanner, 1995). The evidence of greater nutrient availability after gap creation is equivocal, and one can only say that there is little or no evidence of increasing or decreasing nutrient contents in the soil or in the leached water. Nevertheless, short-term pulses of nutrients have been recorded and differences in the amount of debris in gaps influences the amount of nutrient release and causes heterogeneity in gaps (Vitousek & Denslow, 1986; Uhl *et al.*, 1988).

Gap opening creates the critical precondition for succession, i.e. 'site availability' *sensu* Pickett *et al.* (1987), for onward growth of surviving advance regeneration, and/or colonisation of species from the seed bank or seed immigration (see CHAPTER 6). It is thus crucial to quantify the frequency of gap occurrence in time and space, and as many as possible of the other key descriptors of the disturbance regime (Sousa, 1984; see section 1.2), such as area, and type and severity of disturbance. Although spatial quantification of gap occurrence can be achieved by either applying a plot based or a transect approach, quantification over time is difficult since long-term monitoring is often not feasible, and even the longest running studies on changes in floristic composition and successional dynamics in tropical forest have hardly managed to cover the life-span of primary forest species (Swaine *et al.*, 1987; Manokaran & Swaine, 1995; Sheil & May, 1996). Quantification of short-term temporal frequency of disturbance can be attempted by trying to date the age of disturbances encountered. This approach has been adopted here. It is necessarily crude

and only covers a very short time-span (4 years). Nevertheless, in this study it happened to cover a crucial period that allows some comparison of the disturbance regime during volcanic activity with that of a period of no activity. Comparison of mortality data of permanent plots of Whittaker and colleagues for the period prior to and during the most recent volcanic activity will also shed more light on the potential differences in the disturbance regime of Krakatau forests.

The aim of this chapter is to provide some baseline information on the most recent characteristics and dynamics of the disturbance regime of the forests on the three study islands. It will make reference to recent spatial and temporal frequencies, and the approximate areal extent of disturbance for areas covered by the transect surveys. The results on total frequency, area, inter- and intra-island differences and differences between the disturbance regime during and without volcanic activity, will aid prediction of successional development, as well as highlight the potential for successional set-back.

3.2 Objectives

An investigation into how disturbance may influence successional development and diversification of vegetation on the Krakatau islands, needs baseline information on the spatio-temporal frequency of gap occurrence on the meso- or landscape-scale. Furthermore, because this study coincides with a period of volcanic activity of Anak Krakatau, the past and future impact of this additional source of disturbance to the Krakatau forests can be examined. The objectives of this chapter therefore are:

- (i) to gain insights into the disturbance regime of the Krakatau forests at the meso spatial scale through quantification of gap occurrence, area in gap phase, and age-class distribution, using a transect approach;
- (ii) to compare directly turnover between the volcanically active period between 1992-1995, and the preceding inactive period 1989-1992 with the help of permanent plots;
- (iii) to draw attention to the potential impact of human disturbance - in particular pumice mining- on succession in near-coastal areas;

(iv) with the findings of (i), (ii) and (iii) to obtain more understanding of the nature of, and differences between the disturbance regimes of Rakata, Sertung and Panjang, and in particular their characteristics during volcanically active periods.

3.3 Methods

Transect disturbance survey

Disturbance frequency was quantified in 1994, using transects aligned in two ways: (i) six were 'cross-country' transects which ran from a chosen starting point along a compass bearing, and (ii) nine were 'gully transects' which followed gullies, mainly for ease of survey (Fig. 3.1). Due to the fact that most of the Krakatau area is dominated by steep gullies with often narrow ridges, 'cross-country' transects generally traverse many gullies. Moreover, the 'gully transects' also incorporate some flat areas where the gullies end in near-coastal areas. Thus, the potential influence of topography on the disturbance regime is more or less comparable for the different transect types. In the case of (ii) the transects were in some cases combined from several transect parts of adjacent gullies when the survey led to an abrupt gully end. This may have been due to a vertical gully wall or the approach of the transect to the coast. The transects ranged in length from 450 to 1080 m (total lengths surveyed: 5850 m on Rakata; 3480 m on Panjang; 3000 m on Sertung), and their location was principally determined by ease of access. All canopy disturbances within approximately 10 m of either side of the transect line and of greater than approximately 10 m² were recorded. The disturbances, which included tree-falls, lightning strikes, and landslides, were then classified into four age-classes according to the criteria set out in Table 3.1 to enable assessment of recent patterns of gap creation within and between islands. To determine gap area per ha of surveyed transect the area of each gap was approximated by an ellipse calculated from the width and length of the direct physical disturbance on the ground (gap area = πab ; $a=0.5$ width; $b=0.5$ length in m). Due to the progression of trunk and debris decay in older gaps (class 3 and 4; Table 3.1) this method results in an underestimation of the area of disturbance at the point of gap creation. Thus, for classes 3 and 4, calculated gap areas of <10 m² are also included in the determination of total gap area per ha. In contrast, for some of the large disturbances the true extent of the disturbance was measured even if this extended to more than 10 m either side of the transect. Thus, in this case, an over-estimation of the area disturbed per ha is possible. It is

important to see this survey as providing merely a preliminary indication of the nature and extent of the disturbance regime, and not as a precise quantification of disturbance. It should also be noted that information on areal extent, age-class differentiation for gaps older than 2 years (>class 1), and identification of different types of gap creating events was not collected for 'cross-country' transects. Initially the main objective of the latter was the quantification of species presence/absence (see CHAPTER 5), and frequency of gap occurrence was more casually recorded.

Table 3.1: Subjective age-class (range: 1-4) determination from the decay stage of fallen trees, and the stage of regeneration, for the estimation of short-term temporal frequency of disturbance in forests on Rakata, Panjang, and Sertung. For landslides the stage of re-vegetation of the landslide scar was used to assess the age-class of the disturbance. Also, gap creation from standing dead treefalls can usually be distinguished by the advanced stage of decay of the trunk, and the presence of fresh disturbance, and/or very young regeneration.

<i>Age-class with year's since disturbance</i>	<i>scoring criteria</i>
1 ≤ 2 years	fallen tree mostly intact, still with twigs or even leaves; bark intact; new regeneration small or absent.
2 = 2-3 years	trunk still firm but beginning to break-down; bark starting to flake/ already flaked; only major branches left; regeneration of pioneers >2 m depending on size and type of disturbance.
3 = 3-4 years	trunk softening and breaking up fast; no bark left; major branches broken off and very decayed; regeneration >3 m depending on size and type of disturbance;
4 >4 years	trunk breaking apart; all debris decayed; gap filled by regeneration forming a low canopy in medium to large gaps; gap-closure from ingrowth and regeneration in small gaps.

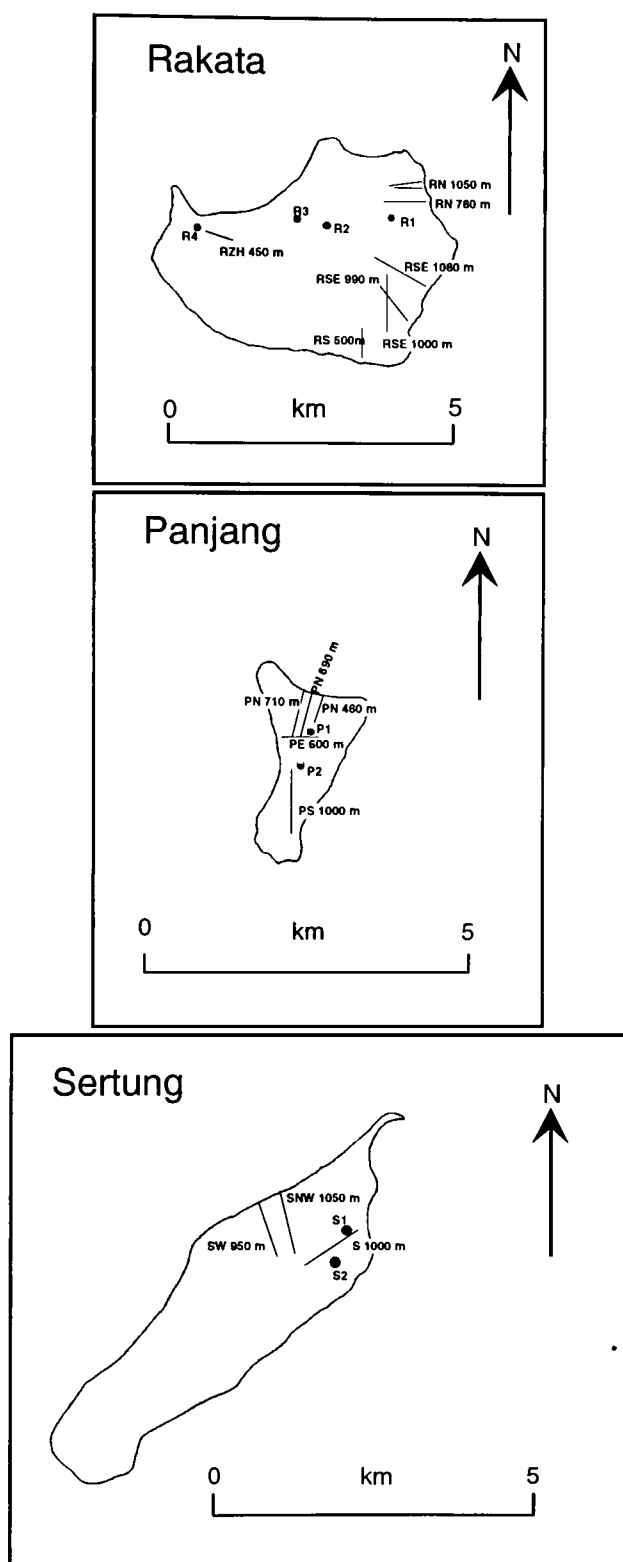


Fig. 3.1: Map showing all transects and the locations of the permanent plots of Whittaker *et al.* (Whittaker *et al.* 1989; Whittaker & Jones, 1993) on Rakata, Panjang and Sertung. Note: for clarity transects are generally represented by one line only, despite some gully transects being compounds of surveys in two or three adjacent short gullies. See GLOSSARY for transect codes, and identification of compound transects.

Tree mortality

Six small permanent plots that were established on the islands in 1989 (Fig. 3.1) by Whittaker and colleagues (Whittaker *et al.*, 1990; Bush *et al.*, 1992). These were re-surveyed in 1992, when two others were installed on Rakata (R3 and R4; Whittaker & Jones, 1993). An examination for mortalities in all plots (except R4) took place in 1994/95. Therefore, a calculation of an albeit short base-line for mortality rate from the tree layer in a period of volcanic inactivity (1989-1992) is possible, and can be compared with that for the active period (1992-95). Percentage mortality is calculated on the 1989 baseline, as the percentage of 1989 recorded trees (dbh ≥ 5 cm) dying by 1992 and 1995. The exceptions are Rakata 3, which uses the 1992 baseline, and for R2, the second period was 1992-1994.

Pumice mining

Observations from informal surveys, and information from the Krakatau literature on pumice mining damage that has taken place in recent years and in the past, were described in detail in CHAPTER 2.

3.4 Results

Historically, direct volcanic impacts since 1930 have been somewhat greater on Sertung than on Panjang, and have not been evident on Rakata (Whittaker *et al.*, 1992a). After several years of inactivity, Anak Krakatau commenced a continuous eruption phase from November 1992 to August 1995 (see also: Thornton *et al.*, 1994). This study ended in 1995, but it is known that after a short lull of activity between November 1995 and spring 1996 Anak Krakatau has been active again, with substantial new lava-flows to the North and West of the island (L. Shilton pers. comm., 1996).

Between visits of August 1992 and June 1993, a large number of new disturbances to the canopies of each island had taken place, coincident with this renewed volcanism. Ash fell on Sertung and to a lesser extent on Panjang, but not on Rakata, throughout this period. All three islands were affected by other forms of disturbance, such as wind-throws, lightning strikes, and landslips. The islands were also affected by drought conditions in the extreme dry season of 1994 (see CHAPTER 2).

Transect disturbance surveys

It is difficult to judge what might be an appropriate baseline figure for the frequency of new disturbances (class 1) at times when Anak Krakatau is not active. The expectation, based on historical and stratigraphic data (Borssum Waalkes, 1954; Docters van Leeuwen, 1936; Whittaker *et al.*, 1992), was that the volcano would have caused increased gap formation, and that this would be evident in greater proportions of disturbances 1-2 years old in a trend from Rakata to Panjang to Sertung. The results of the disturbance survey support this expectation (Fig. 3.2; Table 3.2a), although Rakata's proportion of class 1 gaps is nearly as high as Panjang's, and for 'gully-transects' only, Panjang's distribution of age-classes of disturbance, contrary to expectation, has a lower frequency of recent disturbances than both Sertung and Rakata (Fig. 3.3). The relatively high figure of class 1 disturbances that were found for the combined analysis on Rakata, and the fact that gully disturbance surveys on Panjang returned a lower frequency of recent disturbances, indicates a role for events other than direct volcanic impacts in spatial and temporal patterning of disturbance phenomena within these islands.

Further results of the disturbance survey presented in Table 3.2a also demonstrate that Sertung was not only found to have the highest proportion of most recent (class 1) gaps of all islands (Fig. 3.2; 40.9%), but also to have the highest number of class 1 gaps per ha for all 'gully' and 'cross-country' transects combined (8.7 gaps/ha). Sertung's percentage values for class 1 gaps is significantly greater than those of Rakata transects (one tailed t-test; $p < 0.05$), but was not significantly different from Panjang (one-tailed t-test; $p = 0.084$), although there was a trend towards Panjang values being smaller. Yet, differences between islands were not significant for a comparison of number of class 1 gaps per ha.

The greatest area of disturbance per ha ($3172 \text{ m}^2/\text{ha}$ or 31.7 %) for both all gaps and for the most recently created gaps ($2430 \text{ m}^2/\text{ha}$ or 24.3 %) was found for a Rakata gully transect (RS 1080 m). However, most of the disturbed area along this transect is the result of three very large recent treefalls (c. $900\text{--}1200 \text{ m}^2$) of strangler figs and a very large specimen of *Casuarina equisetifolia* in close proximity to each other (Fig. 3.4). Together their falls make up more than half of the total disturbance area of the transect.

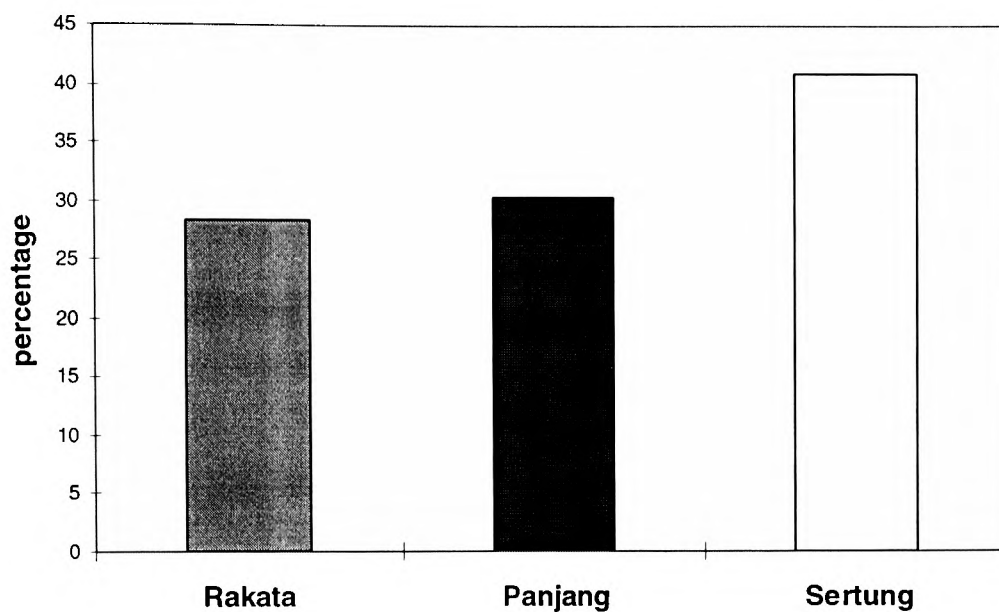


Fig. 3.2: Histogram depicting class 1 (< 2 year) disturbances as percentage of the total number of disturbances recorded for transect surveys on Rakata, Panjang and Sertung ('gully' and 'cross-country' transects were combined).

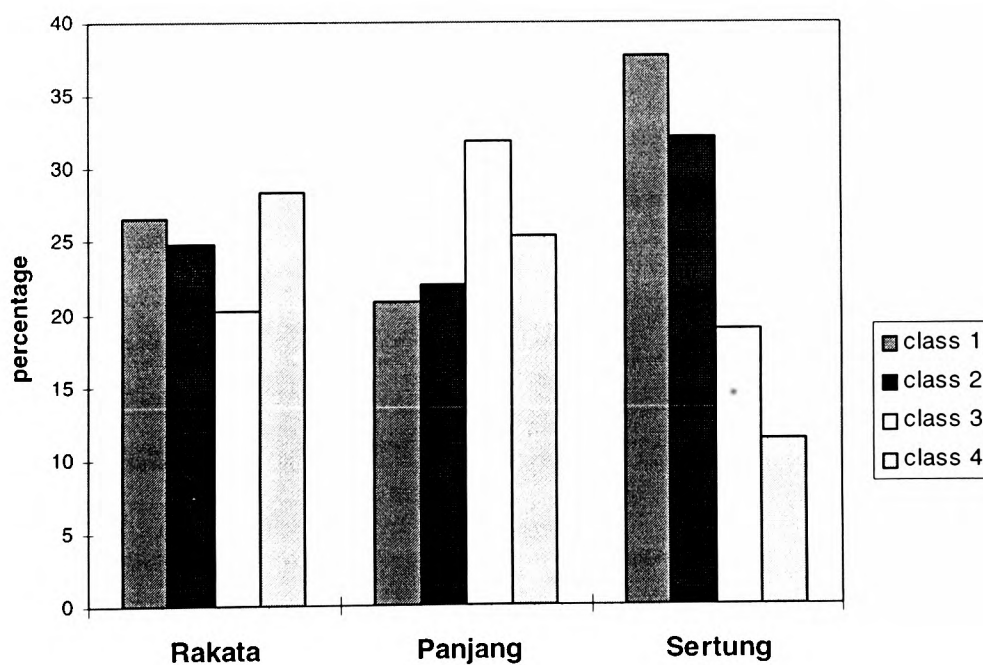


Fig. 3.3: Age-class distribution of disturbances (in percentage of all disturbances) for gully transects on Rakata, Panjang and Sertung.

Table 3.2a: Disturbance survey summary table listing the age-class distribution of disturbances in percent (class 1-4) of all disturbances of all transects combined and per transects separately, number of gap occurrences per hectare (ha) for all disturbances and differentiated by age-class, area in m² of gap phase per hectare of the surveyed transects. Note: see glossary for explanation of transect codes; the gray shaded areas indicate absence of data for 'cross-country' transects.

	Rakata								Panjang					Sertung				
	all transects	RSE 1000m	RS 500m	RZH 450m	RSE 1080m	RSE 990 m	RN 780m	RN 1050 m	all transects	PS 1000 m	PE 600 m	PN 710 m	PN 480 m	PN 690 m	all transects	S 1000m	SNW 1050 m	SW 950 m
% of all disturbances																		
class 1	28.3	43.2	20	0	31.4	21.2	23.1	32.3	30.2	43.5	75	29.2	10.8	26.7	40.9	57.1	44.3	28.9
class 2					13.7	25.0	33.3	32.3				29.2	21.6	16.7			34.4	28.9
class 3					15.7	19.2	25.6	22.6				37.5	37.8	20.0			11.5	28.9
class 4					39.2	34.6	17.9	12.9				4.2	29.7	36.7			9.8	13.3
no of gaps																		
per ha																		
total	19.7	18.5	15	5.5	23.6	26.3	25.0	14.8	18.1	11.5	10	16.9	38.5	21.7	21.2	10.5	29.0	23.7
class 1	5.5	8	3	0	7.4	5.1	4.2	4.6	5.5	5	7.5	5.1	4.2	5.8	8.7	6	12.9	6.8
class 2					3.2	6.0	6.0	4.6				5.1	8.3	3.6			10.0	6.8
class 3					3.7	4.6	4.6	3.2				6.5	14.6	4.3			3.3	6.8
class 4					9.3	8.3	3.2	1.9				0.7	11.5	8.0			2.9	3.2
gap area in																		
m ² /ha																		
total					3172	2296	1959	1745				1409	1641	2708			2569	2187
class1					2430	491	648	662				1066	148	1319			1787	321
% gap area																		
per ha																		
total					31.7	23	19.6	17.5				14.1	16.4	27.1			25.7	21.9
class 1					24.3	4.9	6.5	6.6				10.7	1.5	13.2			17.9	3.2

Table 3.2b: Frequency of different types of gap creation caused by either branchfalls (BF), treefalls (TF), multiple treefalls (MTF), landslides, or lightning strikes. In the cases of landslides it was sometimes difficult to distinguish between a treefall or multiple treefall and a landslide. These cases are indicated as TF/LS or MTF/LS. The pumice mining disturbance (pum.) is classified under a landslide disturbance. Note: these data were only collected for 'gully-transects'; see GLOSSARY for transect codes.

number of	<i>Rakata</i>				<i>Panjang</i>			<i>Sertung</i>	
	RS 1080m	RSE 990 m	RN 780 m	RN 1050 m	PN 710 m	PN 480 m	PN 690 m	SNW 1050 m	SW 950 m
all gaps	51	52	39	31	24	37	30	61	45
BF	9	3	3	0	3	4	4	1	0
TF	28	32	18	13	15 (1TF/LS)	29	16	31	33 (1 TF/LS)
MTF	12	17	5	10	4 (1MTF/LS)	3	6 (2MTF/LS)	25 (4 MTF/Ls)	5 (1 MTF/LS)
LS	2	0	12 (3LS/TF)	8	2 (LS/TF)	1 (pum.)	4 (2LS/TF)	4	7 (5 LS/TF)
LNG			1	0	0	0	0	0	0

The second largest total area of disturbance per ha (2708 m²/ha or 27.1 %/ha) of all transects was found for the Panjang gully transect PN 690 m. Yet, a Sertung gully transect (SN 1050 m) near the North-west coast had the second largest area of recent disturbance (1787 m²/ha or 17.9 %/ha) after Rakata. That the frequency of gaps does not necessarily give much indication of the area affected is demonstrated by one Panjang gully transect, which had the highest frequency of gap occurrence per ha (38.5), but the second smallest total area of disturbance, as the majority of disturbances were made up of very small, and relatively old falls (class 3 and 4, see methods).

As methods of determining disturbance/gap area vary widely (Pompa *et al.*, 1988; van der Meer & Bongers, 1996), and problems such as multiple disturbance to the same area is in general a common feature in many tropical forests (Young & Hubbell, 1991; Veblen, 1992), only a tentative comparison with other studies can be made. Comparison also has to be very tentative because these forest are very different from the early successional forests of Krakatau. Nevertheless, it is striking how much higher the percentage gap area per ha is than the 1-3 % per ha for most published studies (Yavitt *et al.*, 1995). Even if only the most recent gaps (class 1) are considered, only one transect on Panjang falls within this range of values.

The summary table (Table 3.2a) also reveals the great variability of results which characterise the disturbance regime (e.g. number of gaps per ha, gap area per ha, and different gap types). It is very noticeable that within-island variability in the survey results might be as large as that between the different islands. Thus, any interpretation of average figures describing the disturbance regime of one island may disguise great spatial variability in the areal extent, frequency, and dispersion of disturbance: a finding which also seems to apply to variability in time as indicated by the differences in age-class distribution within and between islands. Obviously this method only covers a very short time period, but supports suggestions made by Whittaker and colleagues (Bush & Whittaker, 1993; Whittaker, 1995) of a rather pulse-driven nature of canopy turnover and succession, i.e. pulses are largely driven by Anak Krakatau's activity, and this in particular with regard to Sertung and Panjang's disturbance regime.

For all the transects surveyed, single treefalls were the most common type of disturbance, usually followed by multiple treefalls (Table 3.2b). The latter included single disturbance events and multiple-aged gaps, although the single events were more commonly found. Landslides (Fig. 3.4) were the third, and branchfalls were after lightning strikes the least common type of disturbance. However, in the case of landslides it is sometimes difficult to distinguish between a treefall or multiple treefall and a landslide. It was also frequently noted that great intra-island differences in the proportional importance of landslides existed, and in particular how high the number of landslides along two transects in the North-east of Rakata was (Table 3.2b). The former is likely to have to do with the average steepness of slopes, and other geomorphological characteristics, but is also likely to be influenced by age-and health status of the particular forest area (Sousa, 1984; Veblen, 1992). Surprisingly, it was also Rakata that was found to have the highest proportion of disturbances being caused by landslides, and not, as expected, the very steep slopes of the Sertung West-coast transects. However, it has to be mentioned that the majority of the Rakata landslides were extremely small, whereas some of the landslides in the Sertung West-coast gullies were very extensive (Fig. 3.4). One disturbance classified as a landslide in the PN 480 m transect was in fact a gap created by pumice digging (see below). However, both disturbance types are comparable in severity of disruption. Also, this form of human disturbance should now be recognised as part of the near-coastal disturbance regime (see below, and Chapter 2) and was, thus, not excluded from this analysis.

b)



a)



Fig. 3.5: Pictures show the effect of a lightning strike experienced by the higher altitude permanent plot R2 at 500 m a.s.l. Between 1993-1994 a lightning strike killed a large *Ficus pubinervis* tree and surrounding vegetation: (a) shows the dead or half-dead surrounding vegetation in 1994 (*F. pubinervis* in top right-hand corner) and; (b) depicts the disintegrating trunk of the standing dead *F. pubinervis* in 1995. Note the vigorous re-growth and that some epiphytes are still alive on the dead trunk.



a)



b)

Fig. 3.4: Examples of disturbances encountered during transect surveys. (a) Recent fall of large strangling fig with very large and old specimen of *Casuarina equisetifolia* (not visible in this picture). These two treefalls created a gap opening of approximately 1200 m² along transect RS 1080 m in South Rakata. The picture was taken on top of the 'trunk' of the strangler fig (possibly *Ficus sumatrana*). (b) An example of a large landslide along transect SNW 1050 m in Northwest Sertung. Note the drought- and ash-stressed herbaceous cover on the landslide surface.

Tree mortality

Another means of quantifying variability of turnover in space and in particular between different periods is via the mortality data from the permanent plots (Table 3.3). These data demonstrate increased mortality of trees ≥ 5 cm dbh coincident with the period of Anak Krakatau's activity. Indeed, permanent plots on all islands showed raised percentage mortality of the trees enumerated in 1989, by a factor of 1.2 to 3.9, over the period 1992-1995 compared with 1989-1992. This applied notably within the larger size classes of tree (Table 3.4), and the three plots with the greatest mortality in 1992-1995 in declining order were Rakata 2, Sertung 1, and Panjang 1. On Rakata, the transect data discussed above were from regions below 100 m a.s.l. Partly in contrast to this, the observations on tree mortality from the higher regions (>300 m a.s.l.), suggest a phase of accelerated tree death from canopy disruption coincident with the eruptive period. Unlike in the lowlands these disturbances have frequently taken the form of lightning strikes, followed by subsequent extension of the gaps into large areas by further wind-throws and by the erosion of the soil surface leading in turn to undercutting and landslips. Illustration of the local impacts in upland Rakata comes from both upland permanent plots, each of which serendipitously received a lightning strike (Fig. 3.5). Plot Rakata 2 at c. 470 m a.s.l. experienced 9% mortality between 1989 and 1992, mostly of smaller stems, and at the time the forest structure suggested a fairly lengthy period without major disruption. By 1994, as a result of the form of storm damage described, mortality had risen to 46% judged by the 1989 baseline (i.e. a further 37% of the 1989 number of trees died between 1992-1994). These losses included several of the largest trees (e.g. the largest tree in the plots, a *Ficus pubinervis* with 88 cm dbh). The second site (Rakata plot 3), at c. 680 m a.s.l., a small plot of mostly short-stature multiple-stemmed trees, experienced 43% mortality between 1992 and 1995. This degree of disruption appeared fairly typical of the disturbance to much of the summit region.

Table 3.3: Mortality from the tree layer (dbh $\geq$ 5.0 cm) in permanent plots in a period without (1989-1992) and with (1992-1995) volcanic activity. The plots were established in 1989 (Bush *et al.* 1992). Percentage mortality is calculated on the 1989 baseline except for Rakata 3, which uses the 1992 baseline. To derive total percentage mortality both figures for the periods 1989-1992 and 1992-1994 were combined. See Fig. 3.1 for the location of the permanent plots; * = for Rakata 2, the second period was 1992-1994; **= Rakata 3 was only set up in 1992 (adapted from Whittaker *et al.*, submitted).

<i>Permanent sample plot</i>	<i>no of trees in 1989</i>	<i>%M between 1989-1992</i>	<i>%M between 1992-1995</i>	<i>total % M 1989-1995</i>
Rakata 1 (110 m a.s.l.)	112	8	13	21
Rakata 2* (470 m a.s.l.)	108	9	37	46
Rakata 3** (680 m a.s.l.)	114		43	43
Panjang 1 (75 m a.s.l.)	137	6.5	13.5	20
Panjang 2 (130 m a.s.l.)	157	8	17	25
Sertung 1 (80 m a.s.l.)	125	14	23	37
Sertung 2 (140 m a.s.l.)	158	11	13	24

Table 3.4: Mortalities of different size-classes of trees summed across the six permanent plots establish on the Krakatau islands in 1989. Note the values for 1992-1995 include the data form Rakata 2 plot, which was sampled in 1994 rather than 1995 (data from Whittaker *et al.*, submitted).

<i>dbh class (cm)</i>	<i>5-7.49</i>	<i>7.5-9.9</i>	<i>10-19.9</i>	<i>20-29.9</i>	<i>30-39.9</i>	<i>>40</i>
n in 1989	242	123	259	79	57	34
% mortality 1989-1992	14	12	8	6	2	0
% mortality 1992-1995	26	25	17	15	16	27

Pumice mining

As described in CHAPTER 2 observations and informal surveys of pumice mining revealed a significant, and apparently increasing amount of disruption to the near-coastal forests over recent years. Pumice mining in particular and human disturbance in general is mentioned in this chapter because it can no longer be ignored as having an impact on the succession of the coastal forests. Increasing pressures from future tourism development may also be anticipated to have a greater impact on the Krakatau environment. Apart from direct physical damage to the forest, the possibility of increased numbers of deliberate and accidental introductions of plants and animals also needs consideration.

3.5 Discussion

In Fig. 1.15 and 1.16, 'site availability' is an important cause of succession in the hierarchy of successional determinants (Pickett *et al.*, 1987). In forests in general, and in mature tropical rain forest in particular, the creation of a gap releases light and other resources. Thus, the growth of saplings and regeneration is increased, and on the patch-scale a secondary succession takes place. However, 'site availability' in these mature forests may not necessarily have to be equated with a visible gap creation, as small increases in light (e.g. caused by a small branch fall or the death of an understorey shrub or tree) are often enough to allow the regeneration and rapid growth of many different shade-tolerant species (Swaine, 1996; S. Jennings pers. comm.). Judged from this study gaps are also not absolutely necessary for succession to take place as the forests possess a fairly open canopy (particularly *Timonius compressicaulis* forest on Panjang and Sertung) in comparison to mature rain forests. For instance, in a Costa Rican rain forest the total daily photosynthetically active radiation (PAR) received in the understorey is only 1-2% of that in a the open (Chazdon & Fetcher, 1984). *Dysoxylum gaudichaudianum*'s ability to regenerate and grow into the canopy beneath *Timonius* (see CHAPTER 4 & 5) provides a good example and one may argue that some of the rarer more shade-tolerant tree species may not necessarily be constraint by the lack of light. This study has, however, shown that 'site availability' is, in any case, sufficient or more than sufficient for fast turnover and succession to take place. This means that in more severe cases of disturbance it can actually lead to successional set back. For instance, in the period since its emergence in 1930, Anak Krakatau's activities are known to have impacted on Sertung and Panjang, principally through ash deposition or even blast damage, notably in 1932/33, and 1952/53 (CHAPTER 1&2), when large areas were defoliated. Lighter falls of ash, similar to those of 1992-1995 have occurred intermittently throughout the post-1930 period (Whittaker *et al.*, 1992). The data on the high proportion of recently created gaps, and their high total spatial frequency on Sertung, and of the increase in mortality within the permanent plots provide evidence for an important role of the volcano in gap creation during the 1992-1995 eruption period. In particular the results of the disturbance surveys suggest that during that period Sertung's forests have been more dynamic than those of the other two islands (Fig. 3.2 and Fig. 3.3); a result which lends further support to the hypothesis that volcanic disturbance has a significant impact on turnover and succession through the creation of gaps.

Ash-affected Panjang, which was also expected to show an increase in recent disturbance, showed somewhat conflicting results. In the combined analysis (Fig. 3.2), it was found to have only a slightly higher proportion of recent disturbances than Rakata, whereas the analysis of only the gully transects, shows no evidence of increased disturbance since the beginning of the eruptions in 1992 (Fig. 3.3). Within-island differences in disturbance dynamics have been demonstrated (Table 3.2a), which may be important in determining vegetation structure and composition. Additionally part of the explanation might lie in the fact that Panjang is not necessarily affected by the eruptions at the same time, and not to the same degree as Sertung. The differences in the thickness and, partly the chronology of the ash-profiles as shown by Whittaker *et al.* (1992a), and casual observations on differences of ash-thickness during the recent eruptive phase (c. 8-10 cm for Panjang and 10-15 cm for Sertung) support this argument. This may largely be explained by the timing, and duration of eruptions in relation to dominant seasonal wind directions; whereas, Sertung lies down-wind of the active vents during the dry season (May-October; easterly winds), Panjang receives most ash during the wet season (November-April; westerly winds; Ernst, 1907; Dammerman, 1948; Fig. 2.4). Ash-fall received during the wet season might result in less volcanicity-related disturbance, as a build-up of heavy ash-loads is avoided due to regular rainfall. Thus, branch and stem snapping, as was observed on Sertung, does not occur so frequently on Panjang.

As shown above, the expectation of much greater increases in canopy opening on the ash-affected islands of Sertung and Panjang relative to Rakata was only partially fulfilled, and the results point to the significance of other possible disturbance factors apart from volcanism. These can be climatic fluctuations, as well as a combination of a multitude of external and internal factors (van der Meer & Bongers, 1996), such as slope angle, substrate stability (cf. Kapos *et al.*, 1990), health status, age and composition of the forest patch, predominant wind-direction and exposure, all acting together in various ways and combinations. During this study the obvious other disturbance factor apart from volcanism was the 1994 El Niño Southern Oscillation (ENSO) related drought. Observational evidence suggested an increase in mortality attributable to drought weakening trees and reducing canopy cover (cf. Becker & Smith, 1990; see Fig. A2.2 - A2.4 in APPENDIX 2). In general, tree-falls are more likely during the wet season (Oldeman, 1974; Brokaw, 1982; Brandani *et al.*, 1988), particularly on more susceptible, loose, and steep substrates, such as are found on the Krakatau islands. Yet, storms in the wet season may well have been

more extreme than usual, because an El Niño event of below average rainfall is often preceded and/or followed by a pluvial period (La Niña; Nicholls, 1993). This can lead to increased numbers of wind throws and to the erosion of exposed soils (cf. Nicholls 1993). Evidence of such a phase of enhanced geomorphological activity was presented in CHAPTER 2.

Despite not receiving any significant quantities of ash-fall, it is also argued that the dynamism of Rakata's forests might indirectly be linked to Anak Krakatau's activity (Fig. 1.15). One form of tectonic activity which has affected Rakata, especially during eruptive periods has been earth tremors (Docters van Leeuwen, 1936; Tagawa, 1992; S. G. Compton, pers. comm.) leading to landslides, which might partly explain the high frequency of recent landslips, albeit small ones, in the gullies of Rakata's North-east. Another possibility is that there may be a link between volcanic and climatic phenomena. For instance, storm and lightning damage to the forest, especially the upper regions, was intense and widespread during Anak Krakatau's active phase between 1992 and 1995 (Fig. 3.5). The volcano was ejecting large quantities of eruptive material to heights in excess of 1000 m into the local atmosphere, often associated with strong electrical discharges in the eruption clouds (as Ernst, 1934; pers. obs.; see Fig. 2.5). As already mentioned in CHAPTER 2, this may lead to interactions between the volcano and local climate and precipitate increased numbers, and more severe, thunderstorms with associated lightning events and wind-throw of trees (A. Robock pers. comm.; S. Self pers. comm.). This seems to have been a feature of the 1992-1995 period, and the high altitude areas on Rakata seemed most affected although strikes were noted on each island. Distinguishing between a regional climatic signal, a volcanic explanation and a synergistic interaction between the two is likely to be problematic. However, research elsewhere has demonstrated that climatic disturbance phenomena are of general significance in rain forest dynamics, and that the role of extreme weather phenomena is confined neither to islands, nor to the recognised cyclone belt (e.g. Whitmore, 1974, 1989; Johns, 1986; Nelson *et al.*, 1994). Climatic impact (e.g. increasing or decreasing trend in precipitation, and/or higher frequency of extreme droughts) does not even have to manifest itself directly in increased physical disturbance (e.g. as from hurricane damage; Lugo, 1988; Lugo & Waide, 1993). It can nonetheless influence mortality and growth of all strata, and in this way leave a lasting imprint in the form of altered competitive balances between species, and ultimately changed species composition (Condit *et al.*, 1995; Condit *et al.*, 1996), which altogether affects the progress of successional development.

New evidence on the apparently increasing importance of human disturbance on the Krakatau islands has been presented in CHAPTER 2, and highlighted here as a disturbance factor that requires recognition. Pumice mining is the most drastic form of human disturbance encountered and has direct impact on the near-coastal forest ecosystem by locally changing its structure and function. The presence of large numbers of people for a considerable period of time also increases the likelihood of deliberate and accidental introductions of plant and animal species. The former is in particular a plausible factor, as the mining activity creates large open areas that might easily be colonised by, for instance, new weed species. These activities add another locally severe element to the disturbance regime, setting back the succession to a pioneering stage. Moreover, if any of the plans regarding eco-tourism development go ahead the likelihood of further influence and disruption on the Krakatau forests will increase. It has already been found that the number of species introductions by tourists to Anak Krakatau has significantly increased in recent years (Partomihardjo *et al.*, 1992).

It has been suggested previously that while volcanism has at times set-back the successions of Panjang and Sertung, Rakata may continue to be considered as an essentially uninterrupted primary succession (Bush *et al.*, 1992; Whittaker *et al.*, 1989; Whittaker *et al.*, 1992a). This binary divide has here been shown to be over-simplistic: the notion of an 'uninterrupted prisiere' is no longer tenable. Particularly during Anak Krakatau's active periods the differences between the islands are of scale and type of disturbance, but each experiences, in general, an active disturbance regime and variable weather conditions. At present, 'site availability' would not appear to present a major constraint on the spread of later successional species; on the contrary, disturbance in some areas may well have been strong enough to selectively weed out some components, thereby reducing diversity, and resulting in the disparities in forest composition, age-structure and physiognomy (see CHAPTER 5).

3.6 Conclusion

The results of the disturbance survey lend further support to suggestions that the Krakatau forests experience a very active disturbance regime. It follows that lack of 'site availability' is posing no constraint to the increase in diversity and successional development. In fact, the disturbance regime on Krakatau has recently and historically provided plenty of 'safe sites' (Harper, 1977) for pioneer species, and in the case of the ash-affected islands of Panjang and Sertung may actually have hampered the increase in diversity of shade-tolerant species (see CHAPTER 5). Furthermore, it has for the first time been directly demonstrated that during times of volcanic activity of Anak Krakatau a greater incidence of disturbance is experienced by the forests of Sertung in particular, and the Krakatau forests in general. Thus, more support to the disturbance driven model of succession (Bush *et al.*, 1992; Whittaker *et al.*, 1989; Whittaker *et al.*, 1992a) is provided, but at the same time it is suggested that the model is too simplistic because Rakata is no longer viewed as being unaffected by volcanic activity of Anak Krakatau. That is to say that the primary succession on Rakata is subject to disturbance factors that are indirectly linked to Anak Krakatau's activity, but which may nevertheless be of considerable relevance to the unfolding of this island's successional pathways.

In line with many other studies of tropical rain forest dynamics (Whitmore, 1974, 1989; Condit *et al.*, 1995; Condit *et al.*, 1996), there is an increasing realisation that extreme climatic events such as the 1994 drought experienced during this study, can have very significant impacts on turnover and successional dynamics on these islands (e.g. affecting sapling performance; see CHAPTER 4). This also calls for modification of the successional model for the Krakatau islands. Similarly the human disturbance factor, taking various different forms and having different impacts, can no longer be ignored as an integral part of the successional dynamics on these islands. Thus, in Fig. 1.16 both these disturbance factors are now incorporated in the hierarchical model of succession for the Krakatau islands, and interactions between volcanism and climate are also stressed.

CHAPTER 4:

SAPLING PERFORMANCE*

Summary

1. This chapter investigates 'species performance' of the regeneration layer as one of the general causes of succession *sensu* Pickett *et al.* (1987). A subset of defining factors of species performance, i.e. growth, mortality, and recruitment, were investigated for two different size-classes of saplings, in relation to island (ash- or not ash-affected), gap-size, type and severity of disturbance. The often small numbers of saplings did not allow extensive comparisons between species. However, species compositional changes as an indirect expression of 'species performance' of the regeneration layer, could be assessed in various ways (e.g. gap- and understorey distribution changes, rank-abundance tables and plots).

2. Both island and gap size, and their interactions have been identified as an influence on growth of saplings in gaps. In general saplings on Rakata grew better than saplings on the ash-affected islands, and the island factor was the strongest and most consistent influence on growth for both small and tall saplings. The effect of gap size was less clear, and only for small saplings did it yield the expected result of higher growth in larger gaps. During 1994-1995, the effect of the drought seemed to be the overriding stress factor, particularly on the ash-affected islands. Possibly due to the greater light availability in Sertung forests, understorey small saplings grew significantly more in height than on Rakata, despite the ash.

3. Growth performance of *Dysoxylum gaudichaudianum*, one of the canopy dominants, was investigated separately in the tall sapling analysis. This species was relatively indifferent to the stress of ash-fall. On Sertung, the most ash-stressed island, it even showed a tendency to perform best in comparison to Panjang and Rakata.

* Some of the data in this chapter are presented in summarised form in Schmitt & Whittaker (in press).

4. Contrary to expectation, mortality was not higher on the ash-affected islands, and interactions between island and gap size could not be detected. That the saplings were negatively affected by ash mainly seemed to manifest itself in reduced recruitment and net change of number of individuals. Some competitive release for the apparently ash- and drought-tolerant *Dysoxylum gaudichaudianum* saplings in the taller size-class may thus have been provided.

5. There was no significant influence of gap size on mortality in general. Only for small saplings could an indication of higher mortality in larger gaps be detected. Similarly for gap type and severity of disturbance the results are mainly non-significant, except in the mesic period of 1993-94 (for small saplings only), when light- to medium-disturbed gaps experienced less mortality.

6. The pioneer species *Macaranga tanarius* and *Pipturus argenteus* were shown to have much higher turnover than the more shade-tolerant species. High growth rates enable them to exploit favourable open conditions fast, but they quickly perish under physical stress (e.g. ash-fall and drought) when still in the sapling stage.

8. Of the current canopy dominants only *Dysoxylum gaudichaudianum* was found to regenerate very well. Particularly in the tall sapling layer, this species is a very common gap regeneration component on Panjang and Sertung, and in the near-coastal plots on Rakata. In contrast, saplings of *Neonauclea calycina* and *Timonius compressicaulis* were rarely found. This supports the suggestions, and mounting evidence (Bush *et al.* , 1992; CHAPTER 5; CHAPTER 6), of their rapid decline, and their early pioneer regeneration ecology. Specific regeneration requirements may explain their absence, because if their regeneration niche was very similar to that of the other pioneer species (e.g. *Macaranga tanarius*, *Pipturus argenteus*) they should be just as commonly found regenerating in gaps.

4.1 Introduction

It has been argued that the creation of gaps in the forest canopy is important in maintaining species diversity (Ricklefs, 1977; Denslow, 1980; Orians, 1982; Brokaw, 1985) as most potential canopy and/or late successional species need a gap during some of their life-cycle in order to reach the canopy (Hartshorn, 1978). This theory is now much contested (Brown & Whitmore, 1992; Whitmore, 1996; Brown & Jennings, in press; see section 1.2). In the successional context of the Krakatau islands the main interest lies not in how important gaps could be for maintaining high diversity, but actually how important they are for encouraging the increase in diversity. That means whether the development from an early successional, low-diversity forest with heavy canopy dominance of one or a few species to a more diverse later successional forest might be encouraged by increased availability of regeneration space ('site availability' *sensu* Pickett *et al.*, 1987) through canopy gaps.

In theory, one would expect the process of gap-fill to be a rather smooth progression from initially dense seedling and sapling stands, slowly thinning out with increasing size of the saplings, until one or more - depending on gap size - individual(s) succeed to reach the canopy and fill the gap. In parallel, one would expect there to be a large component of saplings with a high pioneer affinity, and fast growth rates in the early stages of gap regeneration being partly replaced by a more shade-tolerant component over the course of gap-fill (Harper, 1977; Silvertown, 1987; Richards, 1996).

Not every gap-fill process is that simple. For instance, Bazzaz (1984; Fig. 1.2) suggests there to be five contributing factors to gap-fill: branch ingrowth, more shade-tolerant advance regeneration, sprouts, seed bank, and seed immigration. The relative contributions of each in order from branch ingrowth to seed immigration is supposed to increase from small gaps of light severity of disturbance (e.g. a branch fall) to large gaps created by a severe disturbance (e.g. a large landslide). The pioneer component is in general assumed to increase in the same direction. This model and ideas are a simplification, as for example, several severity levels of disturbance can be found in the same gap, leading to significantly different species composition between different gap zones (root zone, bole zone, crown zone; Brandani *et al.*, 1988; Núñez-Farfán & Dirzo,

1988). Thus, within-gap heterogeneity can be as great as between-gap variation (Brown, 1993).

Several studies in tropical forests (Hubbell & Foster, 1986; Lawton & Putz, 1988; Pompa *et al.*, 1988; Young & Hubbell, 1991) have, furthermore, shown that existing gaps are often more likely to be redisturbed than previously undisturbed forest. Thus, a supposedly simple progression can be interrupted, and followed by a potential new recruitment wave. In some cases the interruption can even take the form of an arrested succession when, for example, the gap regrowth is prevented by smothering with climbers (Whitmore, 1990). Furthermore, and crucially, gaps can vary enormously in physical (Brown, 1993) and biotic (e.g. herbivory damage; Brown & Whitmore, 1992) characteristics which potentially influence the outcome of gap-fill. Thus, investigations of gap regeneration have attempted to take these multivariate factors into account with the aim of improving the understanding of gap-fill processes, and the predictability of which species is to fill the gap. Increased understanding can have important implications for commercial forestry, and to a degree also biodiversity conservation. In the case of the former, for instance, autoecological knowledge of the regeneration requirements of many valuable timber species is still scarce, and their study under different regeneration conditions in gaps is an important area of enquiry (Swaine, 1996).

There are numerous examples in the literature of the importance of the light environment for seedling and sapling regeneration. It is one of the crucial physical factors influencing species performance (Hartstorn, 1978; Whitmore, 1978; Denslow *et al.*, 1990). Fewer studies have investigated other physical variables, such as, temperature, relative humidity, plant available nutrients and moisture (Vitousek & Denslow, 1986; Uhl *et al.*, 1988; Brown, 1993), and biotic variables, such as herbivory (Becker, 1983; Coley, 1983; Brown, 1990; Brown & Whitmore, 1992), and pathogens (Augspurger, 1984) on regeneration in gaps. Most of these and other variables are likely to work synergistically, and vary in space and time. In a field experiment it is very difficult to study and isolate the effect of each individual variable on species performance. Thus, caution is needed in attributing an observed demographic or physiological response to one environmental factor only (Bazzaz & Wayne, 1994). The development and increased use of multivariate techniques has helped, but their main utility is in detecting pattern.

Detailed ecological investigations of several variables in a field situation remain difficult, given which this chapter concentrates on the importance of what was judged a feasible sub-set of physical variables of gaps. These are size, type of gap (e.g. treefall, multiple treefall, landslide, lightning strike), and severity of disturbance (e.g. area of bare soil), which are the defining factors of one of the causes site availability - of the Pickett *et al.* (1987; see Table 1.3) hierarchy of successional determinants. These variables are not completely independent from each other as, for instance, a severely disturbed site with a large area of bare soil is often a landslide gap. But most importantly, these variables are likely to have an impact on resource availability (e.g. microclimate, soil conditions, site history), and the importance of competition in influencing species performance as the third level in the hierarchy of causes and mechanisms of succession *sensu* Pickett *et al.* (1987).

Gap sites were also selected in different island locations and surrounding forest types, as these are also factors that are likely to be important in influencing not only the species composition (CHAPTERS 5 & 6), but also species performance. This was especially so as the beginning of this study coincided with the renewed activity of Anak Krakatau, which led to large amounts of ash being deposited on the forests of Panjang and in particular Sertung. It was hypothesised that species performance of the regeneration layer might be negatively affected on these islands, whereas Rakata being the island unaffected by ash, was seen as a baseline for comparison of mortality and regeneration as well as growth performance.

The main indicators of species performance measured in this study are survival and recruitment, and growth. These are quantified for two different size-classes: small saplings and tall saplings (see methods and GLOSSARY for definitions).

One of the main aims is to establish if there are significant inter-site differences in species performance on the whole-site and/or on the most-common-species level, due to one or more of the physical variables. Very importantly, the ash-fall coinciding with the fieldwork period of this study allows for the first time some direct testing of the suggestion that volcanic activity and ash-fall have affected or in more extreme cases deflected the succession in the past (Bush *et al.*, 1992; Whittaker *et al.*, 1989). Variations in relative abundance and performance of species between different size-classes, and for small saplings, between gap and understorey environments, might also yield some important clues on differences in life-history characteristics. Overall, the variation in growth and

survival between species will be interpreted in the light of the previous findings and autoecological interpretations of the tree layer (Docters van Leeuwen, 1936; Tagawa *et al.*, 1985; Whittaker *et al.*, 1989; Tagawa, 1992; Whittaker *et al.*, 1992b; Whittaker & Jones, 1994; Whittaker & Turner, 1994; Partomihardjo, 1995), and an attempt at predicting future importance of the current dominant species *versus* some of the rarer species found regenerating in the gaps will also be made.

4.2 Objectives

As stated in CHAPTER 1 the main aim of this study is to elucidate how disturbance can influence the successional development and diversification of the Krakatau forests. Chapter 3 investigated the main question at the meso-scale, whereas this chapter deals with the patch-scale. The specific objectives of this chapter are:

(i) to investigate how sapling growth, survival and recruitment (aspects of 'species performance' *sensu* Pickett *et al.*; 1987) in gaps on Krakatau are influenced by the variables of size, gap type and severity of disturbance, and island. The effect of ash-fall on the islands of Panjang and Sertung will be of particular interest.

(ii) by studying the inter-specific differences in response to canopy gaps, and the distribution of species between gap and understorey environment to increase information on the autoecology of a sub-set of Krakatau woody species.

(iii) with the information from (i) and (ii), and information on abundance, commonness, diversity and evenness of gap regeneration, to make some suggestions on possible trends in the successional development of the Krakatau forests. This will focus particularly on the dominant species (*Dysoxylum gaudichaudianum*, *Neonuclea calycina*, *Timonius compressicaulis*), and the occurrence of extreme events (e.g. climatic, volcanic).

4.3 Methods

Gap sites of recent age (generally estimated as less than one year) were located on each island (Fig. 4.1), and from the three main forest types previously identified, i.e. canopies rich in one or other of *Neonauclea calycina*, *Timonius compressicaulis*, and *Dysoxylum gaudichaudianum*. In 1993, fifteen sites were selected, incorporating varying sizes and disturbance types. Two recent landslide sites were added in 1994 (Table 4.1). Gaps were divided into two broad disturbance types. The more severe disturbance type (score 2) had a considerable area of bare soil resulting from landslips, a number of root zones from multiple tree-fall, or indeed from human disturbance due to pumice digging, as was found for one near-coastal Panjang site. Lightning strikes that kill not only canopy trees, but additionally the sapling layer, would also count as severe disturbances. A lightly disturbed gap site would in general be created by a large branch- or tree-fall, with relatively little disturbance to the soil, and survival of much of the sapling layer.

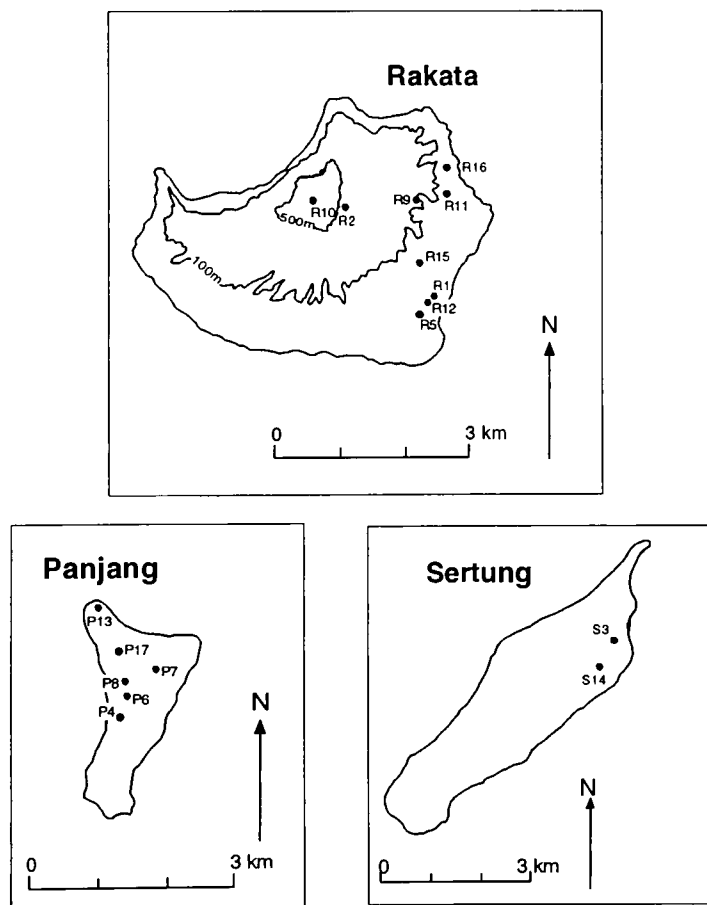


Fig. 4.1: Map of the islands with all studied gap sites marked.

Table 4.1: Summary table listing the physical characteristics of all gap sites applicable to both small- and tall-sapling studies. See glossary and below for gap codes, acronyms, and definitions.

site	size in m ²	size- class ^a	sev. score ^b	disturbance type	age ^c	forest type	aspect	slope angle (degrees)	altitude (m a.s.l.)	aver. canopy height (m) ^d	%CO93 ^e 16mm	%CO93 ^f (8 mm)	%CO94	%CO95	prev. disturb. ^g	94 new disturb.	95 new disturb.
R1	361	1	1	STD/LNG MTF	<1y	Nc/Dg	SE-NW	0	15	20	11.53	19.00	9.56	8.16	N		N
R2	3016	4	2	MTF/LNG	<1y	Nc/Va	E	35	470	19.5	25.62	35.49	27.26	15.77	N	N (LNG part)	Y
S3	2297	4	1	TF	<6m	Dg	SE-NW	0	90	22.4	12.62	20.28	28.65	14.68	N	Y	N
P4	2209	4	2	MTF	<6m	Tcl	W-SW	<10	120	17.8	25.99	35.92	9.17	23.56	N	Y (US)	N
R5	830	2	1	LBF	<6m	coastal Dg	S-N	0	20	17.6	12.04	19.60	26.04	20.33	Y	N	Y
P6	829	2	1	MTF	<6m	Tcl/Nc	SW-NE	25	90	22.4	10.27	17.53	8.38	12.91	N	Y	N
P7	447	2	2	LS	<6m	Nc/Tcl/Dg	E-W; plot NE	>35	30	21.5	8.03	14.91	12.93		N	Y	Y
P8	724	2	1	MTF	<1	Nc/Tcl	E-W	<5	80	18.3	8.23	15.14	5.11	8.42	Y	N	Y
R9	486	2	1	MTF	<1	Nc	NW-SE; plot S	30	90	17.2	6.94	13.63	6.75	10.98	Y	N	N
R10	1084	3	2	MTF/LNG	<1y	Sn/Va	SE-NE	20	650	10	23.80	33.36	42.57	37.70	N	Y	Y
R11	368	2	2	TF	1m	Nc/Dg	SSW-NNE	0	20	16.6	10.27	17.52	6.79	19.73	Y	N	Y
R12	1492	3	1	LBF	<6m	coastal Dg	NNW-SSE	0	20	22.5	7.07	15.01	15.65	15.02	Y	N	N
P13	721	2	2	LBF	<6m	coastal Dg	E-W	0	5	19.7	7.05	13.76	16.77	12.31	N	Y (human)	Y (small TF)
S14	1487	3	1	LNG	c.1y	Tcl	NNE-SSW	0	140	13.6	5.46	11.89	16.64	21.68	Y	N	N
R15	485	2	1	TF (STD)	<1	Nc/Tca/Fp	W-E	26	70	18.3	7.53	14.32	7.17	9.18	Y	Y (edge)	N
R16	491	2	2	LS	<1	Nc/Tca	SW-NE	47/67 ^h	10	18.3	*****	*****	9.72		N?		N
P17	589	2	2	LS	<1	Tcl/Nc/Dg	NNW-SSE	32/47	50	20	*****	*****	17.47	10.71	Y?		N

^a: size classes are defined as, 0-400 m² = small = 1, 400-1000 m² = medium = 2, 1000-2000 m² = large = 3; >2000 m² = very large = 4

^b: severity score: 1 = light to medium disturbed; 2 = severely disturbed; see methods for further explanation

^c: y = year; m = month;

^d: average canopy height derived from trees measured around the immediate gap perimeter;

^e: 1993 %CO values from semi-fisheye lens images;

^f: %CO93 (8mm) was calculated using regression equation $y = 1.17x + 5.5$ (see methods section);

^g: prev. disturb. = there is evidence that the gap area has experienced disturbance previously (e.g., decayed tree trunk); N = no; Y = yes;

^h: the first value is the slope angle of the actual landslide surface and the second value is the slope angle measure to the top of the gully.

Eight gap sites (plus one in 1994) were located on Rakata, five (plus one in 1994) on Panjang and two on Sertung. Gap selection attempted to achieve replication in island representation, size, severity of disturbance, and also age. This, however, proved more difficult than initially anticipated. Firstly, as the Krakatau islands are a Strict Nature Reserve and a unique 'natural experiment', it was not appropriate to create gaps artificially to achieve a same age baseline, and accurate replication of different sizes. Secondly, even with the attempt at replication from the selection of very recent and different size-classes of gaps, it turned out that the impacts of the unexpected drought and ash-fall that occurred during the study period varied considerably between the different sites. This rendered the attempted replication to be relatively ineffective, and even the selection of many more sites would not have resolved the replication problem completely. Thirdly the difficulty of access to certain areas on the islands (e.g. the western slopes of Rakata, and the southern part of Sertung), and the general time constraints of the project did not allow the detailed quantification of more sites.

In each gap site, two transect lines were set out through the gap centre, one along the long-axis, and the other at right angles to it. Gap size was approximated to that of an ellipse using the transect lengths (Fig. 4.2) as diameters, and ranged from 361 m² to 3016 m². The end points of the ellipse's diameters, i.e. the approximate gap edges, were determined as the point where photosynthetically active radiation (PAR) level dropped to the understorey equivalent for more than two readings (readings taken every 2.5 m using a Sunfleck Ceptometer; AT Delta-T Devices). Percentage canopy openness was also measured (see below).

Two size-classes of regenerating woody species were enumerated: small and tall saplings. As the tallest saplings are likely to be at a competitive advantage (Brown & Whitmore, 1992) information on their performance should be particularly valuable in predicting gap-fill.

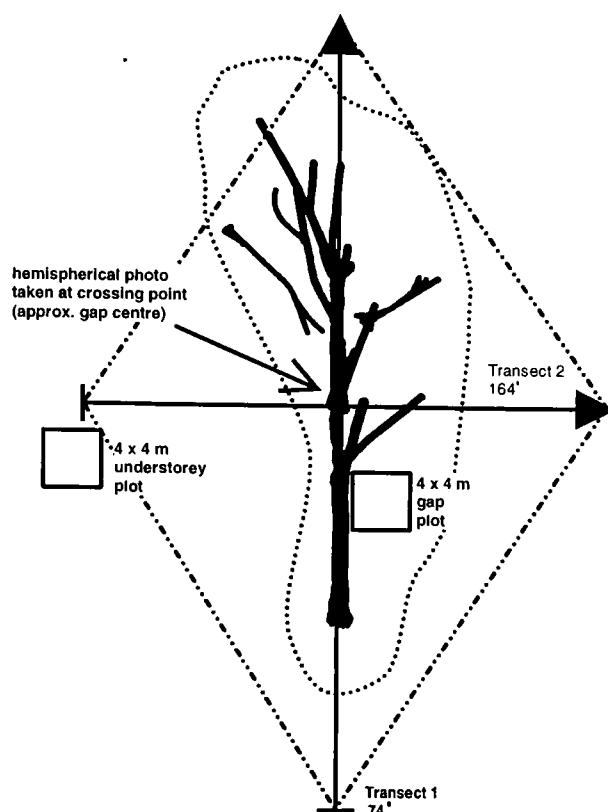


Fig. 4.2: Sketch map of a typical gap site (here based on S3; see Table 4.1) with the layout of all 4 x 4 m plots and transects. The rhomboid shape is the area in which tall saplings were enumerated. The dotted line around the treefalls indicates the approximate extent of physical damage.

Small saplings in 4 x 4 m plots

In 1993, 4 x 4 m small sapling monitoring plots were set up in 15 gap sites, near the centre of the gap, and in the adjacent understorey (sites G1 to G15; Table 4.1; Fig. 4.2). The effect of a canopy opening can extend far into the understorey. Therefore, the understorey plots were located beyond the end of either one of the transect lines, as these were defined as the gap edge, i.e. the absence of gap influence. Small sapling (>50 cm <5 m) enumeration involved tagging, identifying and mapping of individuals, and then measuring their height and diameter (dbh). All plots, except P7G and R10G, were re-measured in both 1994 and 1995. P7G, the gap plot of the landslide site on Panjang, could not be re-measured, as all its seedlings were killed by erosion and further slippage during the 1993-94 wet-season. The gap plot of site R10, at 680 m a.s.l. near the summit, was re-measured in 1994 despite redistribution. However, in 1995 it could not be relocated and re-measured due to very heavy overgrowth of this large and steep gap site. Between 1993-1994 site R1 was redistributed by the fall of the standing dead trees that initially formed the

gap. In 1994 this allowed only the enumeration of the 4 x 4 m gap plot mortality, and height growth measurement. Recruitment was not determined in that year.

Due to the involvement of different helpers in measurements taken at three points in time, problems with dbh measuring consistency arose. Shrinkages or grossly inflated dbh growth rates were therefore a frequent problem. Thus, it was decided that for the small sapling growth analysis only height growth measures would be used, as this is the most accurate, and ecologically important measure of growth available for this size-class. Reductions in height were often due to physical damage or the top of shoots dying-off. If the measured shoot died and was replaced by a new shoot this individual was excluded from growth analysis, but counted as alive.

Tall saplings

Additional to the small sapling enumeration, a study of tall sapling/sub-adults (>1.5 m height and between 1 cm and 10 cm dbh) performance in gaps was initiated in 1994. This was with the intention of quantifying how growth and turnover related to gap size, character, and island (ash- or non ash-affected). Species compositional dynamics and changes in diversity and evenness were also investigated after what turned out to be an extreme drought year (1994-1995).

In contrast to the small sapling investigation, the area of enumeration was proportional to gap size, and determined by connecting the end points of the transect lines. This yielded a rhomboid sample area, proportional to gap size (Fig. 4.2). All saplings were tagged, mapped, and marked with red paint at c.1.3 m height. Sapling identities, dbh, height, mortality and recruitment were recorded in 1994 and 1995 in 15 gap sites, omitting the high altitude sites (R2 and R10), but adding the two landslide sites newly enumerated in 1994 (R16 and P17).

Using red paint to mark the exact dbh measuring point proved very useful, avoiding most of the data quality problems encountered with the small saplings. The exception were Panjang and Sertung sites where prolific ash-fall in the intervening period generally obscured, and/or scoured off the paint on most saplings. Also, the bark of some species (e.g. *Macaranga tanarius*) tends to flake off more than for other species. Therefore, the following data-handling procedure was applied to dbh measurement errors or inconsistency

in the data: tall saplings were excluded from growth analysis if dbh shrinkage was >3 mm, or if the originally measured shoot died and a new shoot replaced it. However, the shoot that died was counted as mortality, and the new shoot as recruitment to the site if it was >1 cm dbh, the definition point of tall saplings.

Height was generally measured with a measuring stick (extension up to 10 m), but on occasion the measuring stick was unavailable due to repeated breakage. Then heights >3 m had to be estimated (average of 2-3 people's estimations). Developing a strict data-handling procedure for height growth is more difficult than for dbh. Often genuine height shrinkages are due to loss from physical damage (Clark & Clark, 1989; Clark & Clark, 1991). Height reductions due to such damage can normally be recognised, yet height overestimation is also possible. Therefore, some of the large reductions, or excessive height growth, could be due to these measurement problems. However, very considerable real growth increments can be observed, particularly when dealing with well-lit saplings of pioneer species such as *Pipturus argenteus* or *Macaranga tanarius*. Thus, in the case of the tall sapling enumeration dbh growth analysis is a more reliable measure of growth performance than height growth. However, in order to compare small sapling and tall sapling performance height growth analysis has to be used.

Light quantification

Arbitrarily defined measures of gap size (e.g. Brokaw, 1982; see section 1.2) are not good predictors of microclimate experienced by seedlings and saplings in gaps (Pompa *et al.*, 1988). This applies in particular to the crucial variable: photosynthetically active radiation (PAR). PAR is generally highly variable in time and space (Mitchell & Whitmore, 1993). This applies to the light environment of gap areas (Brown, 1993), but also that of the understorey. In fact, the dichotomy between gap and non-gap sites is somewhat arbitrary, given the continuum of variation in light levels within the forest (Canham, 1989; Lieberman *et al.*, 1989). Thus, in order to be ecologically meaningful, measurement of PAR in gaps should ideally involve many measurement points in the gap area and the gap-understorey transition (see APPENDIX 1 for description of the ozalid method, and its associated problems), as well as PAR should be monitored for a considerable length of time (e.g. a year), to integrate the light environment spatially and temporally. Apart from being very cost-intensive, and often liable to equipment failure under tropical conditions, monitoring over long periods of time was not possible in this study.

Hemispherical photography has proven a useful method for integrating light over space and time (Mitchell & Whitmore, 1993; Whitmore *et al.*, 1993), and it is relatively cheap, and easy to handle in difficult field situations. A large body of literature describing the use of hemispherical photography, and some of its limitations, has been published in recent years (e.g. Chazdon & Field, 1987; Becker *et al.*, 1989; Rich, 1990; Mitchell & Whitmore, 1993; Whitmore *et al.*, 1993), although little has so far been published on the size of the errors involved (S. Jennings, pers. comm.). There is no space here to elaborate on all of the problems and advantages associated with this method. Therefore, only aspects directly relevant to this study will be described.

With scanned 180 degree canopy images obtained from hemispherical photographs it is possible to calculate direct and indirect site factors, and percentage canopy openness. All tend to be highly correlated to most microclimatic parameters, including total PAR received (Whitmore *et al.*, 1993). PAR can be calculated from data on direct and indirect site factors. These measurements could not be used here, because the required records of light conditions in the open in a nearby site, over a period of at least one year (Mitchell & Whitmore, 1993) were not available for the Krakatau islands.

At the beginning of the fieldwork period in 1993 only a semi-fisheye lens (Nikorr 16 mm; f 2.8) was available. In contrast to the full fisheye lens (Nikorr 8 mm; f 2.8) that was obtained for the 1994, and 1995 field-phase, the semi-fisheye lens does not capture the whole canopy hemisphere, and does not produce a circular image. Thus, 180 degrees are covered only for the longest side of the rectangular negative, which leads to an underestimation of the true canopy openness. Yet, the amount of PAR contributed from degrees close to the horizon are small, except when gap sites are located on steep slopes (see slope angles in Table 4.1), which applies to several gaps. Most of these are, however, in narrow gullies, for which the whole 180 degrees are not visible in any case.

In order to compare relationships of growth and survival with respect to canopy openness between years, and over the whole monitoring period, the 1993 canopy openness values were calculated using regression analysis. The regression equation was obtained by relating 1995 semi-fisheye and full-fisheye lens values. The regression equation $y=1.17x+5.5$ with a satisfactory regression coefficient of $R^2=0.72$ was obtained.

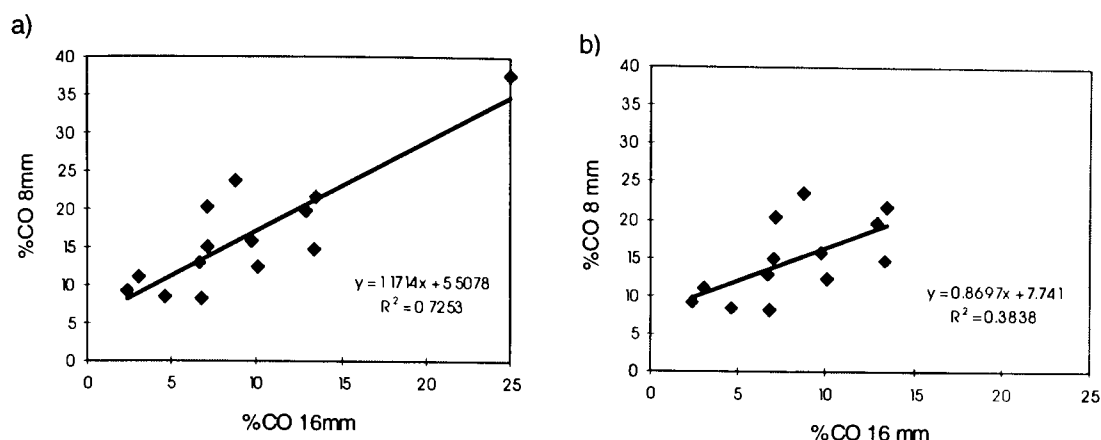


Fig. 4.3: Regression analyses of percentage canopy openness values (%CO) derived from canopy pictures taken with a semi-fisheye (16 mm) and full-fisheye (8 mm) Nikorr lens in 1995. (a) The regression line and coefficient for %CO values from all gap sites, and (b) the regression line and the reduction in the regression coefficient when the large R10 site is excluded (see Table 4.1 for %CO values).

However, with the removal of the data point for the very large R10 gap the regression coefficient only has the value of 0.38 (Fig. 4.3). One of the explanations for the low regression coefficient might be related to the problem of steep slopes stated above. The usefulness of the 1993 measurement of percentage canopy openness is therefore in question and relationships to growth, survival and recruitment should be interpreted with caution.

Photographs were taken in each gap at the crossing point of the gap transects, which in each case was located to coincide with the estimated gap centre. Two pictures were taken parallel to each of the two transects at a height of 1.3 m. Generally, however, only the picture parallel to the same transect of the initial 1993 semi-fisheye photograph was analysed, to insure greatest correspondence between percentage canopy openness measures of the two different lenses. Negatives were scanned and digitised with the Canon ION Video (PAL highband HIVE) system, and potential inaccuracies due to occasional leaf and trunk reflectance were corrected using the image editing software FLAMINGO (version 1.2; Hamlet Software Systems). Percentage canopy openness was then calculated using WINPHOT (ter Steege, 1994).

Data analysis

Growth performance

Small saplings were monitored over two years in gap as well as understorey plots, and data analysed for the whole two year period (1993-1995), and for the 1993-94 and 1994-95 periods separately. Two-year and between-year results were compared.

To investigate which factors (island, size, severity) are likely to affect height growth of small saplings in gaps most, a General Linear Model (GLM) was employed. GLM as an analysis method was chosen because of the unbalanced, and nested design of the data set (Sokal & Rohlf, 1981; Dobson, 1990). Exploratory analysis on the data set has, however, shown that using a GLM violates the assumptions of normality and homogeneity of variance. The removal of 'negative growth values' with subsequent transformation of the data could circumvent this problem. However, it was felt that this would reduce the ecological meaningfulness of the data, because loss in height can indicate various forms of stress, such as physiological stress causing shoot die-off, physical damage causing breakage, or loss of top-shoots from herbivory. The negative values were therefore kept. With the knowledge of non-fulfilled assumptions, alternative analysis was also pursued using the non-parametric Mann-Whitney-U tests (one-tailed) to compare islands, and different size and severity classes pairwise. For these analyses, the sapling height growth data were combined across different plots. This was done with the awareness that it leads to pseudo-replication. Given the slightly problematic data set, however, it has not been possible to find an ideal statistical solution. Thus, both methods were employed, and results compared to show the most robust trends in the data set.

The analysis of understorey height growth did not require the use of GLM as gap size and severity of disturbance was of no influence. Therefore, only the pairwise comparison between islands, using one-tailed Mann-Whitney-U tests was applied.

Tall saplings were only monitored over one year (1994-95), and the growth analysis included both dbh and height growth. The same analytical steps were applied as above with the exception that GLM analysis included additional analysis for covariance of sampling area, which in the tall sapling case was proportional to gap size (see above). Understorey plots for this size class were not enumerated. Height growth performance was

compared to that of small saplings in that year. Furthermore, for saplings in this larger size-class, *Dysoxylum gaudichaudianum* occurred in all gaps, and achieved 'common' species status (arbitrarily defined as density of ≥ 1.25 individuals/100 m²) in 12 out of the 15 gap sites. This species' performance was analysed separately and its growth performance (dbh and height) compared to the overall performance of all sapling species (excluding *Dysoxylum*). For small saplings sample sizes did not allow a comparative analysis of single species performances by inferential statistics. Yet, general inferences on individual species success can be drawn from changes in abundance due to mortality and recruitment.

Sapling mortality and recruitment

Small sapling mortality, recruitment, and net change in numbers were calculated for each year and over the whole two year period in both gap and understorey plots. Tall saplings were only monitored over one year (1994-1995).

Mortality included dead and missing saplings. It was not estimated as an annual mortality rate (see Primack *et al.*, 1985; Swaine & Lieberman, 1987; Sheil *et al.*, 1995; Sheil & May, 1996 for associated problems with estimated rates), but rather calculated as percentage absolute mortality. For small saplings this was calculated for the periods 1993-1994, 1994-1995 and 1993-1995. For the 1994-1995 period the calculation was done on the 1994 baseline, which included the 1993 sapling survivors plus the new recruits into the small sapling size-class. The percentage mortality calculation for 1993-1995 was meant to express the total mortality of the 1993 saplings, and was thus expressed as the proportion of 1993 saplings dead. See APPENDIX 2 for formulae.

The results for mortality, recruitment and net change in number of individuals were modelled against the factors of island, gap size and severity of disturbance using the GLM. For the small sapling data this was carried out for each year separately and for the whole two year period. For the tall saplings the same analyses were carried out for the one year of monitoring. To show the direction of the relationship with particular factors, pairwise analyses using a one-tailed t-test were also applied. Parametric analyses were justified in these cases because percentage mortality and recruitment appeared normally distributed.

Percentage canopy openness and small sapling performance

Correlation analyses were performed on growth, mortality and recruitment of small saplings in relation to percentage canopy openness. Hemispherical photographs were taken at 1.3 m. Thus, this measurement of gap size and proxy for microclimate was a meaningful representation of light conditions for most small saplings in gap plots, but not for the tall sapling analysis (individuals >1.5 m height). This was one of the reasons why it was decided to use very broad size-class categories of gaps, based on the gap size approximation from the gap transects. Additional aspects influencing the accuracy and repeatability of the canopy openness measure, further justified this choice (see below).

Species compositional changes and habitat preferences

For small saplings species compositional changes over the two year period and changes in understorey to gap representation were also quantified. Tall sapling analyses involved the calculation of percentage frequency of each species as a measure of relative abundance, enabling comparison between gaps of different size and thus of different sample area. From percentage frequency data of sapling species in gaps, rank abundance plots (Whittaker, 1965; Hubbell, 1979) were computed as a method of showing short-term dynamics in changes of species importance, and of evenness and diversity of the sapling layer as a whole, between initial enumeration and re-measurement after one year, and between gaps. These trends are demonstrated on two very distinct sites (R5 and S3) in particular.

4.4 Results

Hemispherical photography

Percentage canopy openness values of all gap sites are listed in Table 4.1 for 1993, 1994 and 1995. Comparing these values suggests that the gap environment was in general very dynamic over this period. These changes did not always involve the progressive reduction in canopy openness as one would expect with gap infill over time. Several gaps showed a substantial increase in canopy openness from 1993 to 1994 due to drought impact, and/or redisturbance (e.g. S3, R5, R10, P13). Others, however, showed large reductions in openness even in the drought year, which is mainly due to the rapid formation of a dense

pioneer canopy reducing light levels at 1.3 m (e.g. P4, R1; the latter despite redisturbance), the height at which photographs were taken.

Inaccuracies related to the image quality, and repeatability have to be taken into account, however, and percentage canopy openness figures treated with caution. For instance, apart from the change in lens (relevant for 1993 pictures only; see above), there were some problems associated with the quality of images, and sometimes with the position of the camera for the gap photos. The former were due to the fact that pictures could not always be taken in the early morning or late afternoon, and in overcast conditions. The latter was due to slight alterations of transect crossings between years, particularly in heavily overgrown gaps or redisturbed gaps. However, that the forests and their canopy cover were highly dynamic between years can simply be demonstrated by comparing hemispherical photographs of the same understorey sampling spots between the drought year and the year prior and after the drought (see Fig. A2.1 to Fig. A2.3 in APPENDIX 2 for *Neonauclea*, *Timonius*, and *Dysoxylum* forest types).

Percentage canopy openness values from understorey hemispherical photographs were not calculated. This was because the errors associated with the analysis of images of small values of percentage canopy openness are potentially very large. For instance, even for images of ideal contrast and exposure, the error from repeat analysis of images of <5% canopy openness can be 30% of the mean (S. Jennings, pers. comm.). Considering this, and the fact that in this study hemispherical photographs were taken along the 'cross-country' transects under less than ideal conditions, understorey images were not analysed for an investigation of between-year differences in canopy structure.

The considerable changes from very open conditions in 1994 to more closed canopy conditions, and the differences between forest types can largely be attributed to recovery of canopy cover after the drought in 1994. The drought had varying effects, depending on forest type and local conditions (e.g. compare Fig. A2.1b with A2.2b in APPENDIX 2). Synergistic effects with the stress from ash-fall were also likely in the case of Panjang and Sertung forests. Thus, despite some problems with the comparability of the gap images, the large differences between gap percentage canopy openness values between years were largely attributable to the general dynamics of the Krakatau forest.

Percentage canopy openness was only used in correlation analysis with small sapling height growth in gaps, as well as percentage mortality, recruitment and net recruitment of small saplings. 1993-1994 and 1993-1995 growth, mortality and recruitment results were correlated to 1993 percentage canopy openness values of all gap sites. The correlation coefficients were derived using percentage canopy openness values both directly derived from the 1993 semi-fisheye lens images, and 1993 values calculated from regression analysis. These were compared for differences and results are presented below.

Sapling performance

Small sapling height growth in gap plots

Data on mean and maximum height growth in all gap plots for all years are given in Table A2.1a in APPENDIX 2.

Although General Linear Modelling (GLM) is able to deal with an unbalanced and nested sample design, too many empty cells existed in the small sapling study for analysis of interaction effects. GLM analysis of single factors was, nevertheless, possible. It showed that island and size, but not the severity of disturbance exerted a significant effect on the total height growth of survivors over the 1993-95 period. This was also shown for the sapling growth in the first year (1993-94), but the size effect became non-significant during the second year (1994-95; Table 4.2).

The one-tailed Mann-Whitney-U tests comparing height growth of the small saplings in gap plots also showed that the island effect is significant (Table 4.3a). It generally confirmed the expectation that growth is suppressed on the ash-affected islands of Panjang and Sertung in comparison to the unaffected island of Rakata. The exceptions were the nearly significant result of the 1993-1994 comparison of Rakata and Panjang height growth, and the non-significant result of the 1994-1995 comparison of Rakata and Sertung height growth. This analysis also corroborated the GLM results regarding the effect of gap size on height growth (Table 4.2). It showed that small saplings were growing more in large (size

Table 4.2: General Linear Modelling (GLM) of the factors island, gap size, and severity of disturbance with respect to *small sapling* height growth in *gaps*. Interactions could not be modelled because of too many missing values, i.e. the sample design was too unbalanced. Note small sapling height is measured in centimetres (cm).

1993-1994						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	148928	74464.0	3.957952	0.0211867	*
size	1	120131	120130.8	6.385258	0.0125726	**
severity	1	1399	1398.7	0.074346	0.7854963	
Residuals	146	2746811	18813.8			
1994-1995						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	62373.1	31186.55	7.991980	0.0006195	***
size	1	62.7	62.66	0.016058	0.8994283	
severity	1	905.2	905.20	0.231969	0.6311751	
Residuals	95	370712.0	3902.23			
1993-1995						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	117166	58583.2	4.24028	0.0171915	*
size	1	260357	260356.6	18.84476	0.0000351	***
severity	1	5152	5152.5	0.37294	0.5428503	
Residuals	96	1326323	13815.9			

3&4) than in small gaps (size 1&2), but that during the drought year no significant difference in these two size-classes could be found (Table 4.3a). Panjang and Rakata have more size 2 gaps than any other size, and a comparison of the growth performance in these gaps with Mann-Whitney-U tests provided a check on the island effect independent of gap size. It demonstrates that small saplings in gap plots on Panjang were performing consistently less well than those on Rakata for all years (Table 4.3 a). Thus, this seems to confirm that the island effect is significant and that the effect of ash deposition seems to have a significant negative effect on small sapling growth in gaps.

The GLM single factor analysis established that gap type and severity of disturbance had no significant effect on height growth in any of the years. However, the Mann-Whitney-U test results suggest that height growth in more severely disturbed gaps is significantly greater during the 1993-94 period, but not in the drought year (1994-1995) and over the whole period (1993-1995). Caution in interpreting these results is, however, recommended as gap size and severity of disturbance are not independent of each other (see methods).

Table 4.3: Small sapling height growth performance in 4x4 m (a) *gap* and (b) *understorey* plots is compared between the islands Rakata, Panjang and Sertung, and between different size, and disturbance type and severity classes, using one-tailed Mann-Whitney-U tests on combined data. These analyses are carried out for the 1993-1994, the 1994-95 and the whole two year period 1993-1995. Small saplings were recorded in plots on Rakata = 8, Panjang = 5, Sertung = 2 sites, and size-classes are defined in Table 4.1. NB: no size 2, and sev 2 gaps on Sertung;

Table 4.3a: Comparison of height growth of *gap* saplings.

	1993-1994	1994-1995	1993-1995
Island	R v P $\wedge$ NS R > S ** S v P NS	R > P *** R v S NS S v P NS	R > P ** R > S * S v P NS
Gap size	size 1+2 < size 3+4 **	size 1+2 v size 3+4 NS	size 1+2 < size 3+4 *
Size 2 gaps	R > P *	R > P **	R > P **
Disturbance type and severity	sev 1 < sev 2 *	sev 1 v sev 2 NS	sev 1 v sev 2 NS

*** = $p < 0.001$

** = $p < 0.01$

* = $p < 0.05$

$\wedge$ = R > P but only at the $p < 0.1$ ($p = 0.065$)

note: 1993-94: P7G (size 2; sev. 1) gap plot lost due to erosion;

1994-95 and 1993-1995: additionally R10G (size 3; sev. 2) plot could not be remeasured; R5G (size 2; sev 1) had no survivors. If R10G plot is excluded in the 1993-94 analysis the results for the island and size comparison remain the same.

Sample sizes of surviving small saplings were:

1993-94: R=73; P=63; S=16; size 1+2 = 76; size 3+4 = 77; Rakata size 2 gap = 27; Panjang size 2 gap = 41; sev 1 = 79, sev 2 = 72;

1994-95: R=43; P=48; S=10; size 1+2 = 72; size 3+4 = 29; Rakata gap size 2=24; Panjang gap size 2=36; sev 1 = 68; sev 2 = 33;

1993-95: R=43; P=48; S=10; size 1+2 = 72; size 3 & 4 = 29; Rakata gap size 2=24; Panjang gap size 2=36; sev 1 = 68; sev 2 = 33;

Table 4.3b: Comparison of height growth of *understorey* saplings.

	1993-1994	1994-1995	1993-1995
Island	R > P *** R v S NS S v P NS	R v P NS S > R * S > P *	R v P NS S > R * S > P **

*** = $p < 0.001$

** = $p < 0.01$

* = $p < 0.05$

Sample sizes of surviving small saplings were:

1993-94: Rakata = 163; Panjang = 143; Sertung = 20;

1994-95: Rakata = 116; Panjang = 116; Sertung = 17;

1993-95: Rakata = 116; Panjang = 116; Sertung = 17;

An overall comparison of height growth of small saplings in gap plots (combined data; one-tailed Mann-Whitney-U test) between the mesic (1993-94) and the drought year (1994-95), surprisingly, revealed no significant difference. There was, however, a trend towards higher growth during 1993-94, but only at the 90% significance level.

Small sapling height growth in understorey plots

Small sapling height growth data are presented in Table A2.1b in APPENDIX 2.

The analysis of understorey height growth performance only involved the comparison between islands (using one-tailed Mann-Whitney-U tests) as the factors of gap size and severity are not relevant (Table 4.3b). Understorey height growth results, mostly show different trends from the gap plots. For instance, unlike in the gap plots, Rakata and Panjang's height increments were not significantly different, except in the mesic year of 1993-1994. During that year there was only a trend towards greater height growth in gap plots on Rakata. In the case of Sertung, height growth of small saplings in understorey plots was significantly greater than for saplings on Rakata, except in the mesic year 1993-94 when no significant difference was found. Furthermore, instead of showing no significant difference as for gap plots, Sertung's understorey saplings out-performed Panjang's in height growth, except in 1993-94. Overall, it appears that the understorey environment on the ash-affected island of Sertung was more conducive to height growth than on Rakata, or Panjang.

Height growth of small saplings in gap plots (combined data) was, as one would expect, significantly greater (one-tailed Mann-Whitney-U test; $p < 0.001$) than that of small saplings in understorey plots (combined data) for the first year (1993-94) and over the whole two year period. The significance of the growth differences of gap and understorey saplings was, however, reduced ($p < 0.05$) during the drought year (1994-95). Comparing the overall differences of understorey height growth of small saplings between the mesic (1993-94) and the drought year (1994-95) no significant difference could, however, be detected.

Density and small sapling growth in gap plots

With the awareness that density dependence is likely to be most apparent in the small seedling stage, the density of individuals may nevertheless still affect the growth performance of small saplings. If density dependent forces were influencing growth performance of saplings in gap plots, for instance, than one would expect a negative correlation between density and mean or maximum growth. Calculating Spearman's rank correlation coefficients, no significant relationship was found between density and height growth in any of the years, and for the whole two year period (Table 4.4).

Table 4.4: Spearman's rank correlation coefficients between small sapling density in gap plots and mean and maximum height growth for 1993-1994, 1994-1995, and 1993-1995.

	<i>df</i>	<i>mean height growth</i>	<i>maximum height growth</i>
1993-1994	14 ^a	0.32 ^{NS}	0.34 ^{NS}
1994-1995	12 ^b	-0.15 ^{NS}	-0.05 ^{NS}
1993-1995	12	-0.04 ^{NS}	0.28 ^{NS}

a: P7G lost through erosion;

b: additionally R5G no survivors, R10G could not be remeasured;

Percentage canopy openness and small sapling height growth in gap plots

Spearman's rank correlation coefficients between percentage canopy openness and mean and maximum height growth for 1993-94, 1994-95, and the whole period 1993-95 showed that very little of the variation in the height growth data could be explained by the influence of percentage canopy openness in general. Percentage canopy openness against maximum height growth returned a relatively high correlation coefficient in the 1993-94 period (Table 4.5; significant only at the 90% level). The correlation coefficients were lowest for the 1994-1995 period suggesting again that the drought had an overriding effect. These analyses only partly confirm the results of the GLM and the Mann-Whitney-U test analyses using the arbitrary division of gap into different size-classes, but the results support the suggestion that gap size is less important than island effect in influencing height growth of small saplings.

Table 4.5: Spearman's rank correlation analysis between percentage canopy openness as a proxy for gap size and microclimate and mean and maximum height growth of small saplings in 4 x 4 m gap plots. Note: the correlation coefficient remains unchanged using either the percentage canopy openness value of the semi-fisheye lens or the derived value from regression analysis. The values from the correlation with the derived percentage canopy openness values are presented here.

	<i>df</i>	<i>mean height growth</i>	<i>maximum height growth</i>
1993-94	14 ^b	0.29 ^{NS}	0.52 [^]
1994-95	12 ^c	0.16 ^{NS}	0.06 ^{NS}
1993-95	12 ^c	0.23 ^{NS}	0.39 ^{NS}

[^]: $p < 0.1$ only

a: number of sites in which sapling growth in the 4x4 m gap plot was correlated;

b: P7G was destroyed;

c: P7G destroyed, R5G no survivors, and R10G could not be remeasured in 1995;

Mortality and recruitment in gap plots

It was hypothesised that the increased stress from ash-fall should not only be reflected in depressed growth performance but also in the mortality and recruitment data, which in turn might provide some insight into the performance data presented above. However, the size of the gap and the severity of the disturbance that created it may also have had an impact on mortality and recruitment. For all analyses, the results from the ash-affected islands Panjang and Sertung were treated as a single set (P+S), because of the small sample size of Sertung plots ($n=2$). Percentage mortality, recruitment and net change in the number of individuals (net recruitment) of small saplings in 4 x 4 m gap plots are given in Table A2.2a in APPENDIX 2, the results of the GLM analyses are given in Table 4.6, and those of the one-tailed t-tests are presented in Table 4.7a.

The GLM results show that percentage mortality has no significant relationship with island, size and severity of disturbance and their various interactions, and that this is the case for all years. For percentage recruitment and percentage net change in number of individuals (net recruitment) the only significant result ($p < 0.05$) is with the island factor, and this is only the case for the 1993-1994 period. No interactions were significant. These results are confirmed by the one-tailed t-tests, which additionally show that percentage recruitment and percentage net recruitment was greater on Rakata than on the ash-affected islands of Panjang and Sertung. For the 1993-1994 period these results were significant at $p < 0.01$ for recruitment, and $p < 0.001$ for percentage net recruitment. Although not shown by the GLM analysis the t-test also indicated that Rakata was performing significantly better than

Panjang and Sertung for the whole 1993-1995 period ($p < 0.05$). During the drought year (1994-1995) no significant difference in percentage recruitment and net recruitment could be found (Table 4.7a).

It thus appears that small sapling mortality in gaps was not significantly increased due to ash stress, but that this kind of stress negatively affected recruitment and the net change in the number of individuals. The drought conditions (1994-1995) served to obscure these inter-island differences.

In the GLM analyses differences in the sizes of gaps, and the severity of disturbance failed to return a significant result for mortality, recruitment or net recruitment. However, the one-tailed t-tests comparing the results of the different size- and severity classes did find that mortality was significantly greater in larger gaps for the whole 1993-1995 period ($p < 0.05$), and that mortality in the 1993-1994 period was greater in the more severely disturbed gaps ($p < 0.05$; Table 4.7a).

Table 4.6: Results of the GLM analyses of percent mortality, percentage recruitment, and percentage net recruitment of *small saplings* in *gap* plots. Analyses were carried out for the 1993-1994, 1994-1995 and the whole 1993-1995 periods.

Mortality

1993-1994					
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	175.993	175.993	0.206055	0.6658342
size	1	490.480	490.480	0.574262	0.4772679
severity	1	1130.425	1130.425	1.323518	0.2937393
island:size	1	207.379	207.379	0.242802	0.6397006
island:severity	1	46.574	46.574	0.054530	0.8231238
size:severity	1	18.450	18.450	0.021601	0.8879678
island:size:severity	1	308.941	308.941	0.361713	0.5695666
Residuals	6	5124.635	854.106		
1994-1995					
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	1480.741	1480.741	1.184484	0.3376282
size	1	1504.435	1504.435	1.203438	0.3342425
severity	1	25.648	25.648	0.020516	0.8930305
island:size	1	68.043	68.043	0.054429	0.8269809
island:severity	1	21.401	21.401	0.017119	0.9022176
size:severity	1	120.079	120.079	0.096054	0.7720924
island:size:severity	1	4.664	4.664	0.003731	0.9542246
Residuals	4	5000.460	1250.115		
1993-1995					
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	0.103	0.103	0.000072	0.9935509
size	1	2583.773	2583.773	1.809692	0.2363330
severity	1	218.178	218.178	0.152813	0.7119630
island:size	1	0.153	0.153	0.000107	0.9921323
island:severity	1	281.939	281.939	0.197472	0.6753434
size:severity	1	153.213	153.213	0.107311	0.7564978
island:size:severity	1	1.690	1.690	0.001184	0.9738856
Residuals	5	7138.710	1427.742		

Table 4.6: continued.....

Recruitment**1993-1994**

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	18516.45	18516.45	8.752400	0.0315756 *
size	1	1141.60	1141.60	0.539612	0.4955780
severity	1	189.52	189.52	0.089584	0.7767490
island:size	1	517.33	517.33	0.244531	0.6419109
island:severity	1	467.31	467.31	0.220890	0.6581477
size:severity	1	1938.69	1938.69	0.916386	0.3823894
island:size:severity	1	1510.82	1510.82	0.714140	0.4366319
Residuals	5	10577.93	2115.59		

1994-1995

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	273434	273433.8	0.5489433	0.4998858
size	1	63378	63378.0	0.1272372	0.7393351
severity	1	149056	149056.0	0.2992435	0.6134437
island:size	1	89382	89381.9	0.1794423	0.6936385
island:severity	1	92832	92831.8	0.1863684	0.6882075
size:severity	1	22581	22581.1	0.0453336	0.8418027
island:size:severity	1	47227	47226.5	0.0948116	0.7735147
Residuals	4	1992438	498109.4		

1993-1995

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	43810.8	43810.82	1.401349	0.2897047
size	1	181.2	181.20	0.005796	0.9422679
severity	1	12081.3	12081.27	0.386436	0.5614216
island:size	1	36.5	36.48	0.001167	0.9740725
island:severity	1	7191.4	7191.40	0.230027	0.6517480
size:severity	1	1393.8	1393.82	0.044583	0.8411084
island:size:severity	1	6.6	6.63	0.000212	0.9889438
Residuals	5	156316.6	31263.33		

Net Recruitment**1993-1994**

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	16158.98	16158.98	8.207914	0.0352021 *
size	1	3615.76	3615.76	1.836615	0.2333544
severity	1	589.07	589.07	0.299215	0.6078929
island:size	1	164.12	164.12	0.083362	0.7843791
island:severity	1	631.23	631.23	0.320630	0.5956987
size:severity	1	1334.84	1334.84	0.678028	0.4477467
island:size:severity	1	2854.88	2854.88	1.450130	0.2823975
Residuals	5	9843.53	1968.71		

1994-1995

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	234671	234671.1	0.5205920	0.5105112
size	1	84412	84411.8	0.1872582	0.6875187
severity	1	152992	152992.1	0.3393962	0.5914385 *
island:size	1	84518	84517.7	0.1874932	0.6873371
island:severity	1	95672	95672.3	0.2122384	0.6689522
size:severity	1	19408	19407.9	0.0430542	0.8457590
island:size:severity	1	46293	46292.6	0.1026949	0.7646619
Residuals	4	1803110	450777.4		

1993-1995

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	43945.3	43945.29	1.997761	0.2166564
size	1	4133.4	4133.42	0.187906	0.6827293
severity	1	15546.5	15546.52	0.706748	0.4388668
island:size	1	41.4	41.36	0.001880	0.9670910
island:severity	1	4625.5	4625.51	0.210276	0.6657935
size:severity	1	622.8	622.80	0.028313	0.8729705
island:size:severity	1	15.0	15.02	0.000683	0.9801668
Residuals	5	109986.3	21997.26		

Table 4.7a: Comparison of percentage mortality (%M), recruitment (%R), and net change (%net R) in the number of small saplings in 4 x 4 m *gap* plots between Rakata, and the ash-affected islands of Panjang and Sertung (P+S), between different gaps size-, and disturbance type and severity-classes. Student's t-tests are used; sample sizes: R = 8, P+S = 7, but sample sizes vary between years, and mortality and recruitment calculation due to exclusions (see below).

		1993-1994	1994-1995	1993-1995
%M	Island Gap size Disturbance type & severity	R v P+S ^{NS} size 1+2 v size 3+4 ^{NS} sev 1 < sev 2 *	R v P+S ^{NS} size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}	R v P+S ^{NS} size 1+2 < size 3+4 * sev 1 v sev 2 ^{NS}
%R	Island Gap size Disturbance type & severity	R > P+S ** size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}	R v P+S ^{NS} size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}	R v P+S ^{NS} size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}
%net R	Island Gap size Disturbance type & severity	R > P+S *** size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}	R v P+S ^{NS} size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}	R > P+S * size 1+2 v size 3+4 ^{NS} sev 1 v sev 2 ^{NS}

*** = p<0.001

** = p<0.01

* = p<0.05

^ = R>P+S only significant at p<0.1 (p=0.062)

Sample sizes:

1993-1994: P7G (size 2; sev. 2) destroyed by erosion; R1G (size 1; sev. 1) recruitment and net recruitment could not be determined.

1994-1995: additionally R10G (size 3; sev. 2) excluded, could not be remeasured.

1993-1995: P7G lost, R10G excluded; R1G recruitment and net change in number of individuals enumerated over the whole two year period.

Table 4.7b: Comparison of percentage mortality (%M), recruitment (%R), and net change (%net R) in the number of small saplings in 4 x 4 m *understorey* plots between Rakata, and the ash-affected islands of Panjang and Sertung (P+S). Student's t-tests are used; samples sizes: R=8; P+S = 7; note: no exclusions for understorey plots.

	1993-1994	1994-1995	1993-1995
%M	R v P+S ^{NS}	R v P+S ^{NS}	R v P+S ^{NS}
%R	R v P+S ^{NS}	R v P+S ^{NS}	R v P+S ^{NS}
%net R	R v P+S ^{NS}	R v P+S ^{NS}	R v P+S ^{NS}

Despite the apparent strong effect of the drought in 1994 no significant difference in mortality and recruitment could be found for an overall comparison between 1993-1994 and 1994-1995. However, inter-site variability might obscure such an effect, as very high mortality was only observed for some of the gap sites (see Table A2.2a in APPENDIX 2).

Mortality and recruitment in understorey plots

Mortality and recruitment data for small saplings in understorey are given in Table 2.2.b in APPENDIX 2.

A comparison of percentage mortality, recruitment and net change in the number of small saplings in understorey plots (Table 4.7b) was carried out between Rakata and Panjang and Sertung, and between the first and second year of monitoring.

The results of the one-tailed t-tests reveal that inter-island differences were non-significant for mortality, and unlike in the gap plots, recruitment and the net change in the number of individuals also showed no significant differences between islands (Table 4.7b). No significant difference could be found for mortality and recruitment trends in understorey plots between the first and second year of monitoring.

Density and small sapling mortality and recruitment dynamics in gap plots

Table 4.8 shows the Pearson's Product Moment correlation coefficients for percentage mortality and recruitment for 1993-1994, 1994-1995, and 1993-1995 and the sapling densities of the relevant years. The correlation between percentage mortality of 1993-1994 and density is just significant ($p < 0.05$), but no other significant correlation between density and mortality could be found. For the correlation between 1993 sapling density and recruitment over the whole 1993-1995 period the coefficient shows a trend towards a negative effect of density on sapling recruitment in gaps at the 90% level. Since, however, no significant correlation between recruitment and density was found for the first year, the high correlation coefficient for the whole monitoring period may not represent a true causal relationship. It can be speculated that apart from the physical redistribution, the effect of the 1994 drought, and the ash-fall on some plots over the whole period generally acted as an important factor for density independent mortality and recruitment. This is further

Table 4.8: Pearson's product moment correlation coefficients between small sapling density in gap plots and percentage mortality and recruitment.

	<i>df</i> %M ^a	%M	<i>df</i> %R ^b	%R
1993-1994	14	0.496 *	13	-0.357 ^{NS}
1994-1995	13	0.086 ^{NS}	12	-0.264 ^{NS}
1993-1995	13	0.110 ^{NS}	13	-0.481 ^{NS}

* = $p < 0.05$;^ = $p < 0.1$;

a: 1993-1994 P7G lost through erosion; 1994-1995 R10G could not be remeasured, the same applies to the 1993-1995 period.

b: 1993-1994 and 1994-1995 same as for %M, except that R1 was redisturbed and only %M could be enumerated; for the whole 1993-1995 period the overall surviving recruitment could be determined in R1, otherwise the same as for %M

supported by the fact that gap and understorey mortality are significantly correlated (Spearman's rank correlation, $r=0.57$, $n=13$, $p < 0.05$).

Percentage canopy openness and small sapling mortality and recruitment in gap plots

Percentage mortality and recruitment of small saplings in gap plots were correlated with percentage canopy openness values using Pearson's Product Moment correlation coefficient (Table 4.10). For the 1993-1994 and the whole 1993-1995 period the 1993 percentage canopy openness values were used (derived from the regression analysis; see methods), and the 1994-1995 findings were correlated to the percentage canopy openness values from 1994 images. No significant correlation between percentage canopy openness and percentage mortality was found for the 1993-1994 period, and for the whole 1993-1995 period. However, for the 1994-1995 period this relationship was significant, indicating that percentage mortality increased with increasing gap size, whereas in the arbitrary gap size comparison for that year the large gap sizes were not found to have significantly higher mortality (Table 4.7a). No significant correlation between percentage recruitment and net recruitment was found for any year.

Table 4.10: Pearson's product moment correlation coefficients between percentage canopy openness and percentage mortality, recruitment, and net recruitment of small saplings in 4 x4 m gap plots. Values are compared between years and over the whole two year period. Note: if the analysis for 1993-94 and 1993-95 is carried out with percentage canopy openness values of the semi-fisheye lens, only slight differences in the correlation coefficients are found. These do not change the significance relationships.

	<i>df</i> %M ^a	%M	<i>df</i> %R, %net R ^b	%R	%net R
1993-1994	14	0.401 ^{NS}	13	0.006 ^{NS}	-0.184 ^{NS}
1994-1995	13	0.643 ^{**}	12	0.422 ^{NS}	0.412 ^{NS}
1993-1995	13	0.374 ^{NS}	13	-0.112 ^{NS}	-0.213 ^{NS}

^{**} = p<0.01

^{*} = p<0.05

a: 1993-94 period P7 was destroyed; additionally in 1994-1995 R10G could not be remeasured; the same applies to 1993-1995.

b: 1993-1994 and 1994-1995 same as for %M, except that R1 was redisturbed and only %M could be enumerated; for the whole 1993-1995 period the overall surviving recruitment could be determined in R1, otherwise the same as for %M

Tall sapling growth performance in gaps

Mean dbh and height growth data are presented in Table A2.3 in APPENDIX 2.

For tall sapling dbh and height growth, responses to the factors island, gap size and disturbance type and severity were tested using General Linear Modelling (GLM). Analysis for interaction of island and size and island and severity was possible in most cases (Table 4.10a&b), although interaction between size and severity could only be calculated once. It can, however, be assumed that they are not independent from each other (see methods), and size and severity interactions are not discussed further. Exploratory analyses identified site R12 (the only size 3 site on Rakata) as an extreme site. Height reductions, as well as small growth increments for both dbh and height of saplings were common (see Table A2.3 in APPENDIX 2). This may be attributed to problems with measurement specific to this site, but also to evidence of physical damage and more extreme drought impact in this near-coastal area in the South-east of Rakata (Fig. 4.1). All GLM (Table 4.10a&b) and Mann-Whitney-U analyses (Table 4.11a-c) were therefore, carried out with and without R12 in order to detect the influence of this site on the results.

Since the plot area for tall sapling enumeration varied with gap size, initial GLM analyses for height and dbh growth were carried out with sampling area as a covariant. It was, however, shown that sampling area influenced neither dbh nor height growth (Fig. A2.4 in APPENDIX 2).

The GLM analyses for 'all saplings' were intended to show the general trends in growth performance of all tall sapling species in the gap sites with respect to the factors island, gap size and severity of disturbance, and their interactions. These analyses identified that for both height and dbh growth the single factor of island was always significantly influencing growth performance, and that the results were particularly significant with the exclusion of R12 (Table 4.10a&b). The influence of gap size showed mixed results for height and dbh growth, but if judged by the result for 'all saplings excluding R12', gap size seemed to influence dbh growth more than height growth. These results indicate that the island effect on growth is stronger and more consistent than the gap size effect.

The additional Mann-Whitney-U analyses for 'all saplings' (Table 4.11a) support the hypothesis that growth tends to be suppressed on the ash-affected islands, and that this is irrespective of gap size. The latter can be tested by comparing size 2 gaps on Rakata and Panjang (the gap size most common on these islands), whereby both dbh and height growth were significantly lower on the ash-affected Panjang in comparison to Rakata (Table 4.11a). Nevertheless, a significant interaction between island and gap size occurred for both dbh and height growth as shown by the GLM for all saplings (Table 4.10a&b). This result was not identifiable when site R12 was excluded. Severity and type of disturbance had no significant influence on growth in all cases, and showed no significant interaction with island (Table 4.10a&b).

Thus, it appears that overall inter-island differences in tall sapling growth were not a simple function of differences in size of gap, nor of the nature of the gap-initiating events (landslides, versus tree-falls, etc.). The poor growth performance of Panjang's saplings relative to those of Rakata (Table 4.11a) provided some support for the proposition that ash-fall has a detrimental effect on sapling growth performance. The results for Sertung, however, partly conflict with it. Historically, it is believed that Sertung has experienced the most severe impacts from Anak Krakatau (Walden *et al.*, 1991; Whittaker *et al.*, 1992), and during the 1992-1995 period of volcanic activity, casual observation and measurements of ash-depths appeared to confirm this pattern. Rakata did show higher dbh increments than Sertung, and Sertung performed equally well in dbh growth as Panjang. However, Sertung's saplings generally out-performed those on Panjang in height growth, and they did not show any significant difference to Rakata in height increment, whereas one would expect Sertung's sapling growth to be most suppressed. Without the exclusion of site R12

in Rakata gaps. This is attributable to the poor performance and the problematic nature of this site.

Table 4.10: GLM results for *tall sapling* (a) height and (b) dbh growth modelled with respect to factors island, gap size, and disturbance type and severity, and their interactions. Listed are the analyses for all saplings, all saplings excluding *Dysoxylum gaudichaudianum* (All Dg), and *Dysoxylum gaudichaudianum* only (Dg only). Additionally the analysis of all saplings was performed excluding the extreme site R12. Note: tall saplings height measured in metres, and dbh in centimetres.

Table 4.10a: Tall sapling dbh growth

All saplings						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	4.2026	2.10129	4.53357	0.0109711	*
size	1	0.0048	0.00482	0.01039	0.9188339	
severity	1	0.0384	0.03835	0.08275	0.7736709	
island:size	1	10.8759	10.87587	23.46490	0.0000015	***
island:severity	1	0.0005	0.00047	0.00101	0.9746878	
Residuals	969	449.1269	0.46350			
All saplings excluding R12						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	7.0396	3.519806	7.16518	0.0008185	***
size	1	5.3314	5.331372	10.85294	0.0010254	**
severity	1	0.4680	0.468038	0.95277	0.3292803	
island:severity	1	0.0528	0.052758	0.10740	0.7432027	
Residuals	888	436.2191	0.491238			
All - Dg						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	1	4.9405	4.940535	9.96575	0.0016535	**
size	1	1.5072	1.507229	3.04029	0.0815985	
severity	1	0.1880	0.188046	0.37932	0.5381418	
island:size	1	2.6008	2.600791	5.24616	0.022499	*
island:severity	1	0.1174	0.117374	0.23676	0.6266864	
severity:size	1	7.1893	7.189315	14.50185	0.0001505	***
Residuals	815	404.0376	0.495752			
All - Dg excluding R12						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	1	5.9253	5.925273	11.49550	0.0007332	***
size	1	6.8978	6.897841	13.38236	0.0002713	***
severity	1	0.7759	0.775943	1.50539	0.2202192	
island:size	1	2.5003	2.500270	4.85072	0.0279306	*
island:severity	1	0.0488	0.048818	0.09471	0.7583551	
Residuals	769	396.3754	0.515443			
Dg only						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	1.02725	0.513623	1.975368	0.1423752	
size	1	2.35208	2.352081	9.045976	0.0030979	**
severity	1	0.45524	0.455238	1.750821	0.1878280	
island:size	1	0.90244	0.902440	3.470734	0.0644590	
island:severity	1	0.02353	0.023528	0.090486	0.7639847	
Residuals	147	38.22206	0.260014			
Dg only excluding R12						
	Df	Sum of Sq	Mean Sq	F Value	Pr(F)	
island	2	2.77831	1.389157	4.659932	0.0113593	*
size	1	0.07183	0.071826	0.240941	0.6244793	
severity	1	0.00187	0.001874	0.006286	0.9369443	
island:severity	1	0.01587	0.015870	0.053238	0.8179397	
Residuals	113	33.68606	0.298107			

Table 4.10b: Tall sapling height growth**All saplings**

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)	
island	2	16.599	8.29931	5.55144	0.0040063	*
size	1	30.770	30.76987	20.58210	0.0000064	***
severity	1	3.127	3.12702	2.09167	0.1484270	
island:size	1	22.114	22.11379	14.79201	0.0001279	***
island:severity	1	1.927	1.92725	1.28915	0.2564862	
Residuals	969	1448.638	1.49498			

All saplings excluding R12

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)	
island	2	31.418	15.70905	10.56618	0.0000292	***
size	1	0.343	0.34256	0.23041	0.6313380	
severity	1	0.049	0.04923	0.03311	0.8556493	
island:severity	1	3.036	3.03619	2.04219	0.1533406	
Residuals	888	1320.216	1.48673			

All - Dg

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)	
island	1	4.388	4.38808	2.91183	0.0883132	*
size	1	22.618	22.61767	15.00854	0.0001156	***
severity	1	0.931	0.93057	0.61750	0.4322046	
island:size	1	26.753	26.75286	17.75255	0.0000280	***
island:severity	1	19.361	19.36119	12.84762	0.0003580	***
severity:size	1	0.460	0.46046	0.30555	0.5805759	
Residuals	815	1228.194	1.50699			

All - Dg excluding R12

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)	
island	1	12.169	12.16867	8.170774	0.0043722	**
size	1	0.450	0.45014	0.302251	0.5826344	
severity	1	5.098	5.09758	3.422821	0.0646845	*
island:size	1	11.070	11.07025	7.433229	0.0654880	*
island:severity	1	14.197	14.19748	9.533038	0.0020906	**
Residuals	769	1145.266	1.48929			

Dg only

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)	
island	2	7.7879	3.89397	3.126696	0.0467931	*
size	1	0.9770	0.97703	0.784510	0.3772119	
severity	1	8.2812	8.28122	6.649474	0.0109005	*
island:size	1	10.8135	10.81351	8.682799	0.0037367	**
island:severity	1	3.5770	3.57699	2.872169	0.0922407	
Residuals	147	183.0731	1.24540			

Dg only excluding R12

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)	
island	2	3.7990	1.899497	1.527572	0.2215102	
size	1	3.3134	3.313437	2.664659	0.1053834	
severity	1	2.5651	2.565130	2.062873	0.1536881	
island:severity	1	3.9409	3.940893	3.169259	0.0777241	
Residuals	113	140.5126	1.243475			

Table 4.11. *Tall sapling* dbh and height growth performance for the period 1994-1995, from 15 gap sites. Pairwise island comparisons, and between different size-classes were carried out using one-tailed Mann-Whitney-U tests. A comparison of different disturbance types and severity classes is omitted in these analyses as it was a consistently non-significant factor in the GLM (Table 4.10a&b). For the island and size comparison additional analyses are carried out excluding the extreme site R12, which for the tall sapling enumeration is the only size 3 gap on Rakata. Refer to Table 4.1 for size-class definitions. Number of sites: R = 7, P = 6, S = 2. Note: there were no size 2 gaps on Sertung.

Table 4.11a: Comparison of dbh and height increment of all saplings.

	ALL SAPLINGS	
	<i>dbh growth</i>	<i>height growth</i>
Island	R > P *** R > S * S v. P NS R > P *** R > S *	R > P * S > R * S > P ** R > P *** R v S NS
Island excl. R12		
Gap size	size 1+2 v size 3+4 NS	size 1+2 > size 3+4 **
Gap size excl. R12	size 1+2 v size 3+4 NS	size 1+2 v size 3+4 NS
Size 2 gaps	R > P ***	R > P ***

*** = p<0.001

** = p<0.01

* = p<0.05

Sample sizes:

island comparison: R = 468; R excluding R12 = 386; P = 423, S = 85; gap size comparison: size 1+2 = 705, size 3+4 = 271, size 3+4 excluding R12 = 189; size 2 gaps comparison: R = 311, P = 319.

Table 4.11b Comparison of dbh and height increment of all saplings excluding *Dysoxylum gaudichaudianum* ('All - Dg').

	ALL SAPLINGS (excluding <i>Dysoxylum gaudichaudianum</i>)	
	<i>dbh growth</i>	<i>height growth</i>
Island	R > P *** R > S ** S v P NS R > P *** R > S **	R > P *** R v S NS S > P *** R > P *** R v S NS
Island excl. R12		
Gap size	size 1+2 v size 3+4 NS	size 1+2 > size 3+4 ***
Gap size excl. R12	size 1+2 v size 3+4 NS	size 1+2 > size 3+4 *
size 2 gaps	R > P ***	R > P ***

*** = p<0.001

** = p<0.01

* = p<0.05

Sample sizes:

island comparison: R = 399, R excluding R12 = 352; P = 358, S = 65; gap size comparison: size 1+2 = 645, size 3+4 = 177, size 3+4 excluding R12 = 130; size 2 gaps comparison: R = 286, P = 293.

Table 4.11c: Comparisons of *Dysoxylum gaudichaudianum* sapling performance ('Dg only'). Note that site R12 was the most *Dysoxylum* rich site on Rakata.

	DYSOXYLUM GAUDICHAUDIANUM	
	dbh growth	height growth
Island	R v P NS R v S NS S v P NS	R v P NS S > R ** S > P *
Island excl. R12	R > P ** R v S NS	R v P NS R v S NS
Gap size	size 1+2 > size 3+4 **	size 1+2 v size 3+4 NS
Gap size excl. R12	size 1+2 v size 3+4 NS	size 1+2 < size 3+4 *
Size 2 gaps	R v P NS	R v P NS

*** = $p < 0.001$

** = $p < 0.01$

* = $p < 0.05$

Sample sizes:

island comparison, R = 67; R excluding R12 = 31; P = 67; S = 20; gap size comparison, size 1+2 = 60; size 3+4 = 94, size 3+4 excluding R12 = 59; size 2 gaps comparison: R = 22, P = 28.

Single species performance: the case of the dominant Dysoxylum gaudichaudianum

The analysis of all tall saplings may, of course, disguise considerable variations in performance between species. In illustration, the performance of *Dysoxylum gaudichaudianum*, the only really abundant canopy species in the gap data set (n=154 out of 976 saplings), was investigated. To compare with the performance of *Dysoxylum*, analyses also considered all other sapling species combined (All Dg). As >50% of saplings in R12 were *Dysoxylum*, analysis excluding R12 was also performed.

The results of the GLM, and the Mann-Whitney-U analyses indicate that *Dysoxylum* performance differs quite considerably from that of all other species (Table 4.10a&b; Table 4.13b&c). This is particularly the case when site R12 is excluded. For instance, for *Dysoxylum* (Dg only excluding R12) height growth the island factor is non-significant, and no interaction with size takes place, whereas for all other sapling species (All-Dg excluding R12), island as a single factor significantly influences height growth (Table 4.10b). For dbh growth of *Dysoxylum* the GLM shows significant influence of the gap size and island factor when R12 is included and excluded from the analysis respectively (Table 4.10a). The Mann-Whitney-U analyses support these findings. They suggest that for all other sapling species (All-Dg), Rakata saplings are in general performing better than those on Panjang and Sertung, but that this is not the case for *Dysoxylum* saplings. Additionally these

analyses show that Sertung's saplings perform better than Panjang's in height growth, and also tend to perform better than or equally as well as saplings on Rakata (both height and dbh growth), depending on whether R12 is excluded or not (Table 4.11b&c). This compares well with the general signal for Sertung in the 'all saplings' analyses described above.

The one-tailed Mann-Whitney-U analyses, comparing height and dbh growth of only size 2 gaps on Rakata and Panjang, demonstrate clearly that there is a marked difference in performance between all other species and *Dysoxylum* with regard to the island factor, and independent of any possible gap size factor (Table 4.11b&c). With potential gap size effects ruled out, the analyses for dbh and height growth of only *Dysoxylum* saplings showed no significant difference between Rakata and the ash-affected island of Panjang (Table 4.11c). In contrast, for all other species (All -Dg) the growth of Rakata saplings is highly significantly greater than that of saplings on Panjang (Table 4.11b). Whilst there is a possibility that the *Dysoxylum* data reflect some site specific factors, it can be suggested that *Dysoxylum* saplings grew as well on the ash-affected islands as on Rakata (Table 4.11c).

The relatively good growth performance of *Dysoxylum* under the stress of ash-fall also has to be set in the context of the changing frequencies of species between 1994 and 1995. The mortality and recruitment data provides evidence that *Dysoxylum* has gained significantly in relative abundance in sites on Panjang and Sertung in comparison to Rakata sites (one-tailed Mann-Whitney-U tests; $p < 0.05$). It has lost in importance in all but one Rakata site. Its best gains in relative abundance were 11.6% and 7.1%, achieved in gaps on Sertung and Panjang respectively. In the former, *Dysoxylum gaudichaudianum* became the numerical dominant of the sapling layer, whereas in the latter it served merely to reinforce its existing dominance. This trend seemed apparently unrelated to the type and size of gap, since the former was created by a lightning strike leaving a multi-stemmed *Timonius compressicaulis* tree standing dead, and the latter by a multiple tree fall, creating a very large gap.

In short, it appears that in this size-class *Dysoxylum gaudichaudianum* has done disproportionately well on the ash-affected islands by increasing its relative abundance, and in terms of growth increments it has not been affected by ash-fall. It might be hypothesised that *Dysoxylum gaudichaudianum* possesses a better than average capacity

to tolerate the polluting and physically damaging effects of ash-fall. The deposition of these ejecta has led to reduced net recruitment of the other species collectively, so it is possible that part of the explanation for unaffected growth of surviving *Dysoxylum gaudichaudianum* saplings lies in the reduction of inter-specific competition. Percentage net recruitment of saplings of all species (collectively) was generally negative for Panjang and Sertung, and significantly lower for these islands than for Rakata sites (see below, Table 4.13). Another contributory factor could be reduced herbivory on particular species. Some evidence for this has emerged from a pilot study in 1995 (L.T. White, 1995, in lit.), which found that less herbivorous ant activity, and fewer stem entry holes occurred on *Dysoxylum gaudichaudianum* in the ash-affected forests of Panjang, and Sertung, in comparison to Rakata. However, *Dysoxylum* at the sapling and tall sapling stage seems to be in general quite tolerant to even severe herbivory damage. This was shown by artificial defoliation experiments of *Dysoxylum* saplings on Rakata (see APPENDIX 3).

Mortality and recruitment of tall saplings

Mortality and recruitment data for tall saplings are given in Table A2.3 in APPENDIX 2

Percentage mortality, recruitment and net change in the number of tall sapling individuals (net recruitment) was again carried out using GLM. To show the potential directions of the relationships one-tailed t-test for pairwise comparisons between island (Panjang and Sertung treated as a single set), gap size and severity were executed.

The GLM analyses established that percentage mortality and recruitment were not significantly affected by the island or gap size factors. The only significant result was for net recruitment with respect to island (Table 4.12). In this case Rakata sites were found to have significantly higher net recruitment (one-tailed t-test; $p < 0.01$; Table 4.13). In fact only three out of eight Sertung and Panjang sites returned a net percentage increase in sapling numbers between 1994 and 1995 (Table A2.3 in APPENDIX 2). Although there was a significant trend for small saplings in gap plots to show higher recruitment and net recruitment on Rakata, this was not found for the 1994-1995 period, which is the period of tall sapling monitoring. GLM analyses also found no significant influence of the severity of disturbance (Table 4.12), but the comparison with one-tailed t-tests indicated that there was at least a significant difference for recruitment, which was greater in lightly disturbed gaps ($p < 0.05$; Table 4.13).

Table 4.12: GLM analyses of percentage mortality, recruitment and net recruitment of *tall saplings* in the period 1994-1995.**Mortality**

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	173.774	173.7736	0.7029857	0.4261226
size	1	26.212	26.2116	0.1060368	0.7530560
severity	1	150.527	150.5273	0.6089448	0.4576505
island:size	1	218.936	218.9360	0.8856863	0.3741939
island:severity	1	60.163	60.1627	0.2433828	0.6350300
size:severity	1	127.601	127.6007	0.5161974	0.4929152
Residuals	8	1977.549	247.1937		

Recruitment

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	269.484	269.4841	1.643991	0.2356836
size	1	0.008	0.0078	0.000048	0.9946618
severity	1	709.827	709.8268	4.330307	0.0710115
island:size	1	53.100	53.1000	0.323937	0.5848722
island:severity	1	358.346	358.3463	2.186096	0.1775204
size:severity	1	89.013	89.0126	0.543023	0.4822316
Residuals	8	1311.365	163.9207		

Net Recruitment

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
island	1	876.059	876.0589	6.094590	0.0387876 *
size	1	27.124	27.1243	0.188699	0.6754800
severity	1	206.601	206.6009	1.437287	0.2648827
island:size	1	56.393	56.3928	0.392315	0.5485359
island:severity	1	124.849	124.8488	0.868551	0.3786241
size:severity	1	3.465	3.4648	0.024104	0.8804662
Residuals	8	1149.949	143.7437		

Table 4.13: Comparison of percentage mortality (%M), recruitment (%R), and percentage net change in number of individuals (%net R) using one-tailed Mann-Whitney-U tests. Note: no size 2 gaps on Sertung, and the small number of size 3+4 gaps;

	%M	%R	%net R
Island	R v P+S ^{NS}	R v P+S ^{NS}	R > P+S ^{**}
Gap size	size 1+2 v size 3+4 ^{NS}	size 1+2 v size 3+4 ^{NS}	size 1+2 v size 3+4 ^{NS}
Disturbance type & severity	sev 1 v sev 2 ^{NS}	sev 1 > sev 2 *	sev 1 v sev 2 ^{^NS}

** = p<0.01

* = p<0.05

^ = p<0.1 only, sev 1 > sev 2

sample sizes: R = 7; P+S = 8; size 1+2 = 11; size 3+4 = 4; sev 1 = 9; sev 2 = 6;

Thus, overall it appears that tall sapling mortality was not significantly affected by the potential stress from ash-fall, as was hypothesised at the outset. This may be speculated to be due to the drought conditions experienced during that year (1994-1995), which may have been the overriding factor. Nevertheless, the stress from ash-fall seems to have had a significant negative effect on net recruitment. Under the multitude of extreme circumstances (ash-fall and drought year), no evidence for density dependent mortality or recruitment could be detected.

Species compositional changes of the regeneration layer

Dynamics and habitat preferences of the small sapling species

Data above have shown that apart from ash-fall, the stress from drought was an important influence on sapling performance. The impact of this extreme climatic event is also reflected by twice as large a decrease in the net abundance of small saplings (gap and understorey) between 1994 and 1995 (8.9%) than the previous year (3.6%; Table 4.14a total of all species). The losses were mostly incurred in understorey plots, whereas gap sapling numbers were higher in 1995 than 1994 (Table 4.14a). However, these results again disguise considerable variation in net recruitment trends between plots for both gap and understorey saplings (see Table A2.2a&b in APPENDIX 2)

Over the two years, five species that were present in 1993 were lost and one new species recruited, leaving a total of 39 species in 1995. The highest net loss of species was incurred between 1994 and 1995 (3 species; Table 4.14a). In 1993 the plot of rank order of abundance of small sapling species provides a relatively smooth J-shaped curve (Fig. 4.4a). This changed over the two years with the curve becoming more broken, which was due to the steady increase in *Antidesma montanum* abundance, and the steady decrease in *Leea sambucina*, *Semecarpus heterophylla* (Bl.), and *Dysoxylum gaudichaudianum* abundance (Fig. 4.4b&c). The decline in *Dysoxylum* small sapling numbers is contrary to the trend for tall saplings (see above). This possibly points to a difference in performance in the different size-classes, i.e. stress tolerance of *Dysoxylum* seems to be enhanced in the larger size-classes. The lack of recruitment of small *Dysoxylum* saplings during the study period, but the considerable amount of *Dysoxylum* seedling recruitment found in 1995 after prolific fruiting in 1994, seems to indicate that its recruitment is periodic.

These trends seem to indicate that there was progressive decline in overall diversity of small sapling regeneration, involving both reduction in species numbers, and in particular a decrease in evenness.

Table 4.14a: Number of individuals of the 10 most abundant *small sapling* species in 4 x 4 m gap and understorey plots on all islands in 1993, 1994, and 1995. The distribution of abundance between gap and understorey is also given, and comparison to total number of small saplings in the different categories can be made. For each year the total number of species enumerated and the number of species exclusively occurring in either gap or understorey plots are listed. See GLOSSARY for species abbreviations.

rank	1993				1994				1995			
	sp	total n	n G	n U	sp	total n	n G	n U	sp	total n	n G	n U
1	Am	96	46	50	Am	101	46	55	Am	112	50	62
2	Sh	87	2	85	Sh	89	3	86	Sh	72	3	69
3	Dg	66	18	48	Ls	56	25	31	Mt	66	38	28
4	Ls	58	23	35	Dg	54	19	35	Dg	45	17	28
5	Mt	35	27	8	Mt	23	22	1	Ls	44	20	24
6	Ah	30	9	21	Ah	23	5	18	Pag	15	15	0
7	Fm	26	3	23	Ba	20	2	18	Ba	14	8	6
8	Ba	22	1	21	Pag	15	15	0	Ah	14	3	11
9	Pag	20	20	0	Pd	14	1	13	Ch	14	1	13
10	Pd	14	1	13	Pad	13	12	1	Fh	12	12	0
total 10 highest ranking sp.		454	150	304		408	150	258		408	167	241
total all sp		583	217	366		562	227	335		510	221	289
no sp		43				42				39		
sp exclusive in G and U			8	6			10	5			11	7

NB: excluding P7, R10; n=13 sites.

Table 4.14b: Proportions of individuals of the 10 highest ranking species, and all species found in gap and understorey plots in 1993, 1994, and 1995

	1993		1994		1995	
	%G	%U	%G	%U	%G	%U
top 10 species	33.04	66.96	36.76	63.24	40.93	59.07
all species	37.22	62.78	40.39	59.61	43.33	56.67

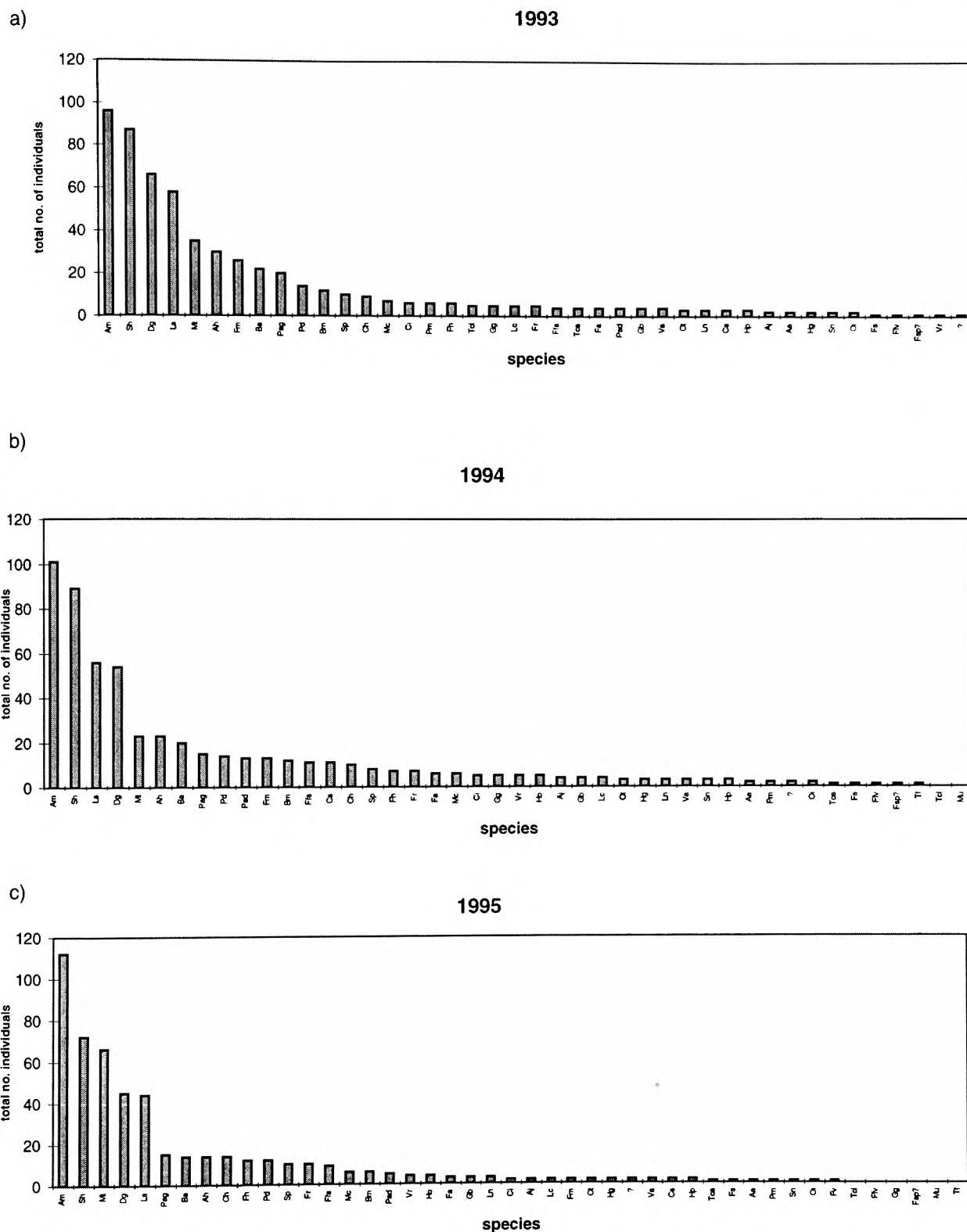


Fig. 4.4: Rank order of abundance of gap and understorey small sapling species in (a) 1993, (b) 1994, and (c) 1995.

Of the 10 most numerous small sapling species in 1993 the typical pioneers *Macaranga tanarius* and *Pipturus argenteus* were the only species with a majority of their individuals in gaps. Indeed *Pipturus* was through all three years exclusively found in gaps, whereas *Macaranga* had more than a quarter of its individuals in the understorey. This figure was drastically reduced in 1994, but rose to over 40% of *Macaranga* individuals found in the understorey in 1995. This trend is suggested to be due to the increase in understorey light-levels from temporary leaf-loss, and branch and tree death caused by the drought, and thus increased recruitment chance for *Macaranga*. In any case, *Macaranga tanarius* showed the greatest increase in numbers (threefold) of all species between 1994 to 1995. This was, however, concentrated mainly in two gap sites (e.g. R5 and S14; see CHAPTER 5).

It is also notable that the proportion of saplings occurring in gaps rose steadily over the two years (Table 4.14b). The gap proportion of 'all species' in 1995 is 6.1% higher than in 1993, and the gap proportion of saplings of the 10 most commonly found gap species in this study even rose by 7.9%. Although there has been some change in the composition of the 10 highest ranking species almost all of the gain in gap individuals was due to the increase in *Macaranga tanarius*, and the loss of saplings in the understorey was mainly due to the death of *Semecarpus heterophylla*, *Buchanania arborescens*, *Leea sambucina* and *Dysoxylum gaudichaudianum*. All of these species were in the category of the 10 most common species over the two years.

In 1994, through rapid recruitment, *Piper aduncum* entered the list of the ten most common species, and was predominantly found in gap plots. In fact, almost exclusively in the 500m gap R2TF, which also indicates, its apparent preference for the higher altitude environment on Rakata. Similar habitat preference for gaps was found for *Ficus hispida* which replaced *Piper aduncum* in the list of the ten most common species. Habitat preference for shadier conditions was found for *Dysoxylum gaudichaudianum*, *Ardisia humilis*, and *Planchonella duclitan*, as examples of common species that were predominantly found in the understorey. In the case of *Buchanania arborescens*, which was predominantly found in the understorey in 1993 and 1994, the distribution became more or less even between gap and understorey, as all 1993 individuals except one died and were replaced by new recruits. Other species which were more or less equally common in gaps or the understorey were *Antidesma montanum*, and *Leea sambucina*, both of which seem to persist as advance regeneration in the understorey. However, whereas *Leea* benefited from greater

height increments in gaps (one-tailed t-test; $p < 0.001$; combined data of all survivors), *Antidesma* did not show significantly higher growth increments in gaps (one-tailed t-test; $p = 0.065$; combined data of all survivors). Unfortunately, it was not possible to investigate the habitat preferences and growth responses of more species in detail because of the generally very small sample sizes of the surviving individuals. Even for *Leea sambucina* and *Antidesma montanum* the data had to be combined across sites. Yet, in the light of the previous dearth of quantified autoecological information on even the common species on Krakatau this investigation has nevertheless been able to provide useful information.

The data also indicates that the majority of sapling individuals is found in the understorey (Table 4.14a&b). At first this seems quite surprising since one expects that apart from surviving saplings a large number of new recruits would add to the sapling number in gaps. In fact the trends are very varied, and it is important to note that the PG8 understorey site is a very extreme site in that it has a very high density of *Semecarpus heterophylla* saplings. Thus, 28% of all understorey sapling species are found in this plot alone. Nevertheless, this result does point to the importance of regeneration beneath the canopy, which subsequently is likely to play a significant role in gap regeneration as the advance regeneration component (AR); see CHAPTER 5 & 6). Understorey regeneration on Krakatau might in any case be encouraged by the relatively high light levels in some of the forest types; in particular the *Timonius* forest has a relatively sparse canopy (Bush *et al.*, 1992).

Species compositional changes in the tall sapling layer

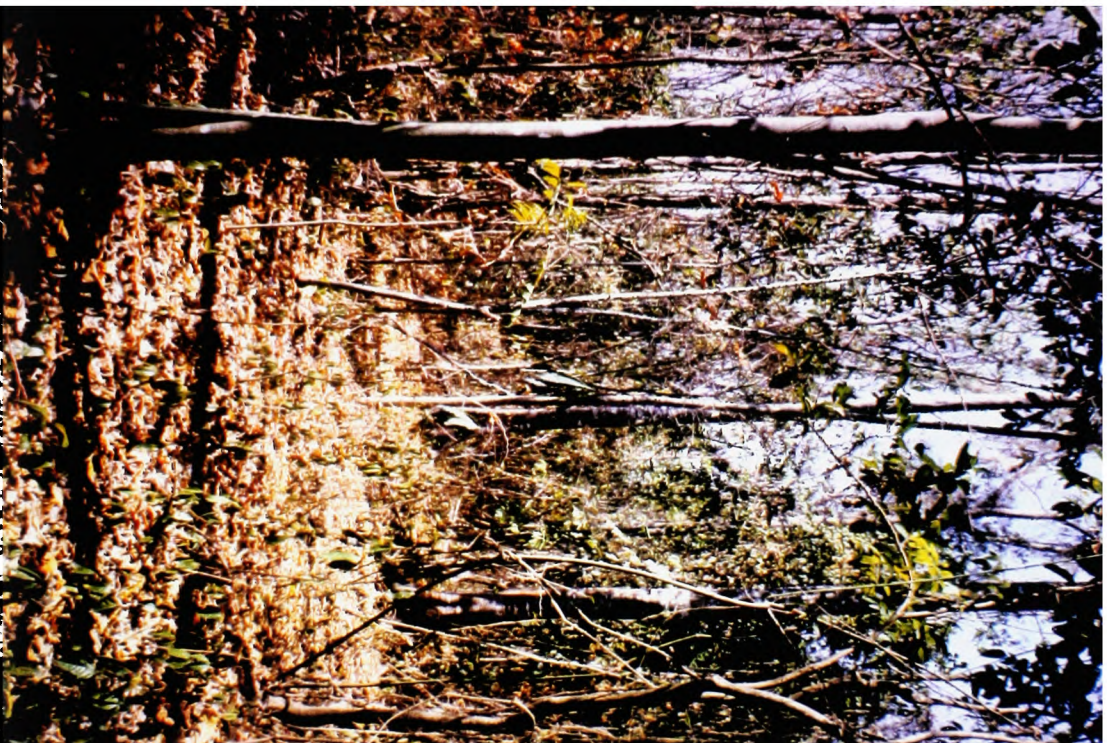
Species compositional changes within the tall sapling layer during gap-fill can be dramatic, and can illustrate widely differing conditions among sites, but also autoecological differences in performance, and availability of propagules, etc. To a greater or lesser degree these aspects are illustrated by two sites, both of which appeared severely stressed. Sertung site S3 was affected by very heavy ash-fall, in combination with the drought (Fig. 4.5), and Rakata site R5 by a combination of the severe drought, and hydrological conditions which appeared to under-supply this area of the near-coastal plain of South-east Rakata (Fig. 4.6). Even large trees suffered mortality in this vicinity. A comparison of the rank-abundance curves (Fig. 4.7) of 1994 and 1995 for S3 shows that *Pipturus argenteus* moved from first to the last rank, as all 19 individuals died, and only one recruited. This allowed *Buchanania arborescens* to become the most abundant sapling



Fig. 4.5: Sertung forest near S3 gap site during the drought and heavy ash-fall in 1994. Note the *Dysoxylum* tall sapling on the left (photo: R.J. Whittaker)

species in this gap. Two species were lost from the site and one gained, with only minor alteration in the steepness and shape of the rank-abundance curve, thus evenness and diversity did not change very much between 1994 and 1995. This contrasts with R5 in which the most abundant species, *Macaranga tanarius*, increased in importance from 25% in 1994 to 40% in 1995, despite all but one of its 1994 representatives dying (compare to results in Table 4.14a; Fig. 4.6). In this case the rank order does not look very different between the two years, but it disguises a high amount of turnover and dynamism in the recruitment layer from one year to the next. Moreover, as indicated by the considerable steepening of the rank-abundance curve, it also disguises considerable change in

a)



b)



Fig. 4.6: Near-coastal South-east Rakata forest in 1994 during the drought and in the following dry season of 1995. Photograph (a) clearly shows that the drought caused substantial death of the understorey, and leafloss that opened the canopy. The photograph was taken close to R5. Photograph (b) depicts the understorey vegetation adjacent to R5. The R5 nan area adjacent to (b) was even more

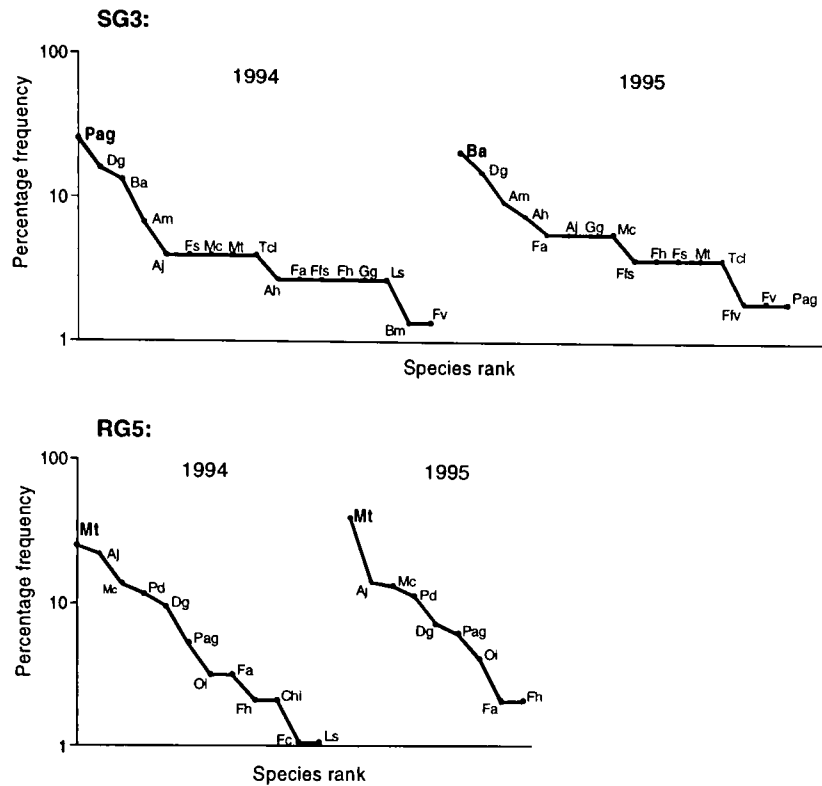


Fig. 4.7: Rank abundance plots of tall saplings for S3 and R5: a comparison of two dynamic plots in which turnover had a very different impact on diversity and evenness. See Glossary for species abbreviations.

evenness and diversity, that is caused by the increased dominance of *Macaranga tanarius*, and the loss of three (*Canarium hirsutum*, *Ficus callosa*, and *Leea sambucina*) out of twelve species by 1995. The first two still being rare canopy species on Krakatau.

These examples show that rapid species compositional changes and turnover are not necessarily confined to the small size-classes of saplings, although there is still a difference in degree. For instance, small saplings in the gap plot of R5 suffered 100% mortality but the plot also experienced a fivefold increase in sapling numbers in comparison to the 1993 baseline.

4.5 Discussion

Following on from considerations of the disturbance regime and 'site availability' in CHAPTER 3, this chapter has concentrated on differential species performance as one of the main causes of succession in the hierarchical model of Pickett *et al.* (1987). It was investigated at the local scale, in terms of a sub-set of the differentiating factors recognised in Fig. 1.16, focusing mostly on turnover and growth. Small sample sizes of saplings of individual species largely prevented the comparison of growth and turnover of many different species. However, initial species composition, abundance, and habitat preferences (gap or understorey) of the regeneration layer were studied as indirect expressions of species performance linked to life-history characteristics, propagule availability, and physical and other biotic variables.

The tall sapling data for all saplings (excluding *Dysoxylum gaudichaudianum*) provided some evidence of the significance of the effects of ash-fall on Sertung and Panjang, as depressed growth for both dbh and height increment were found. Sertung's results were slightly conflicting, as for height growth no significant difference was found compared to Rakata. Small saplings growing in gap plots, also showed depressed height growth on the two ash-affected islands. The understorey height growth trend of small saplings showed mixed results, but indicated that Sertung understorey saplings mostly performed better than those growing on Rakata over the two year period.

From the small sapling results in gap plots it appears that under the environmental conditions prevailing during the study period, density independent factors were more important in influencing growth of small saplings in gap plots. However, density dependent effects may have already occurred before the plots were measured, and the nearest neighbour of a small sapling may be more important than density in influencing growth (Connell *et al.*, 1984).

Some of the conflicting results might in part be due to the severity of the drought impact in certain Rakata sites, and in part to the confounding effects of changing sapling density as a function of differential recruitment and mortality. Indeed, the turnover of tall and small saplings was pronounced in many gaps. Clearly, also, different species exhibit varying responses to ash and drought. This could only be tested for tall sapling data of *Dysoxylum*

not represented in many gaps. However, the performance of *Dysoxylum*, compared to that of all other sapling species combined exemplified these varying responses. Not only was this species growing equally well or better on the ash-affected islands, but it was found in the tall sapling sample of all the gaps studied, and was often the first or second ranking species in abundance. This underscored the results of the landscape-scale evaluation (CHAPTER 5), providing further evidence of the continuing significance of the species in canopy fill in the lowland forests of Panjang and Sertung, and of its rise on Rakata. It is striking, however, that in terms of growth of survivors this species has done as well on ash-affected islands as on Rakata, and that generally it has increased its relative abundance in comparison to other species on the two ash-affected islands. This provides a mechanism to explain its success on Panjang and Sertung, consistent with the volcanic disturbance-affected pathways of Whittaker *et al.* (1989). Other species appear to be relatively intolerant of ash-fall, as exemplified by the data from S3 in which all 19 members of the cohort of *Pipturus argenteus* died, with just one recruit appearing the following year. Further examples include *Bridelia monoica* and *Arthrophyllum javanicum* which, were seemingly badly affected by ash-fall (Whittaker *et al.*, submitted). In contrast to which, both *Dysoxylum gaudichaudianum* (larger sapling size-classes and adults) and *Timonius compressicaulis* (if not already very mature or even senescing), appeared able to withstand ash damage relatively well, as anticipated from the analyses of past successional changes on Panjang and Sertung (Whittaker *et al.*, 1989; Bush *et al.*, 1992).

It seems reasonable to suggest that physical disturbance factors, such as volcanism and climatic fluctuations, alter the competitive balance between species within these islands, and must have done so in the past. Whereas, at least during and after the drought in the 1994-95 period of the study, factors such as gap size and type did not have an obvious or simple relation to sapling species performance. These properties of the gap itself, rather than external forcing factors, were shown to be more important in the mesic period of 1993-94 (see small sapling data), and are likely to be of greater significance in forests of a more mature character, where the full spectrum from pioneer to climax species (*sensu* Swaine & Whitmore 1988) would be present.

That is not to say that the regeneration requirements of different canopy species on Krakatau are indistinguishable. The three most significant canopy dominants on these islands illustrate this point. Each is clearly an early successional species, but in contrast to *Dysoxylum gaudichaudianum*, both *Neonauclea calycina* and *Timonius compressicaulis*

were rare in the sapling layer of the gaps in this study. Of the six tall sapling species which achieved 'common' status (see: methods): *Antidesma montanum*, *Dysoxylum gaudichaudianum*, *Ficus fistulosa*, *Leea sambucina*, *Macaranga tanarius*, and *Pipturus argenteus*, only *Dysoxylum gaudichaudianum* is a large canopy tree at maturity. Similarly for the 10 most abundant small sapling species found in the 15 gap plots (Table 4.14a) *Buchanania arborescens* was the only other canopy species apart from *Dysoxylum*. In contrast, in the tall sapling layer, *Neonauclea calycina* was only represented by one or two individuals in each of eight sites in 1994, and was reduced to 5 sites in 1995. *Timonius compressicaulis* was found in only four sites, in each as just one or two individuals. In the small sapling layer both species were even more insignificant, with *Neonauclea calycina* not being present in any of the small sapling plots, and the only small *Timonius compressicaulis* sapling dying by 1994. It is important to take life-history characteristics into account in evaluating such data, as some species may have a high probability of survival once in the sapling layer (I suspect *Terminalia catappa*, *Planchonella duclitan*, and *Buchanania arborescens* to be in this category), some only recruit periodically (e.g. *Dysoxylum gaudichaudianum* to some degree), and others (e.g. *Macaranga tanarius*, *Pipturus argenteus*) are ephemeral, and of earlier successional character. However, observations from the permanent plots do not suggest that either *Neonauclea calycina* or *Timonius compressicaulis* have unusually high rates of survivorship from sapling to canopy layer. The *Neonauclea calycina* stands on Rakata show signs of senescence, as do some of the older *Timonius compressicaulis* stands on Panjang. In interaction with extreme weather conditions, such as droughts and storms, the older specimens of both species appear particularly vulnerable to mortality and wind-throw. Reversal of their decline would appear to require a far more severe disruption to canopy cover than has been provided by the relatively modest ash deposition of 1992-1995 (c. 10-15 cm, contrasting with depths of 50-150 cm for the 1952/53 eruptions; Whittaker *et al.* 1992a). *Neonauclea calycina*, in particular appears to require bare mineral soil and high light conditions for successful establishment (C. Ridsdale pers. comm.; pers. obs.). Even then, the outcome of such large-scale canopy opening would be dependent on the timing of disturbance and on seed-supply coincident with gap availability, which is unlikely to mimic precisely that of the early phase of forest formation earlier this century.

4.6 Conclusion

In conclusion, one can say that gap-fill processes on the Krakatau islands, observed during this study, were not a smooth progression, rather the dynamics of gap regeneration on Krakatau were found to be responsive to a variety of controls. The trajectories of gap-fill were altered frequently, and marked differences could be found between and within islands, and between years. Volcanic pollution and regional climatic fluctuations provide obvious forcing factors. Particularly when in combination, as in 1994-95, their influence was more readily detectable in the analyses of species performance than differences related to gap size, type and so forth. However, variations in factors such as initial species composition, gap geometry, soil conditions, further canopy disturbances (very frequent), herbivory, and hydrology, render each site in some way distinctive. For instance, the present study would have benefited from monitoring the variability of plant available moisture, particularly as the unforeseen drought in 1994 severely affected the vegetation. Unfortunately this was not possible as this would have required monitoring over the full two years, and logistical difficulties (work on all three islands, very rugged terrain, no research station and no permanent fresh water on the islands), and limited resources and time made this unfeasible. Thus, constraints are necessarily placed on the generality of the present findings, which should best be seen as an account of events at one point in time, and in a limited number of places within the islands.

Several lines of evidence in this chapter have highlighted the performance of the canopy dominant *Dysoxylum gaudichaudianum*, which has been identified as stress-tolerant with respect to ash-fall as well as drought (at least in the tall sapling size-class). Given these life-history characteristics combined with plentiful (though sometimes periodic) fruit-supply, the ability to germinate in shady as well as high-light environments (Bush *et al.* 1992, pers. obs.), and the high growth potential allowing rapid gap-fill, helps to explain its success on the ash-affected islands. Its relatively restricted near-coastal and lowland distribution on Rakata has, however, raised questions about its future fate on this island (Bush *et al.*, 1992; Whittaker & Turner, 1994). CHAPTER 5 will provide more information on the representation of *Dysoxylum* in the regeneration layer on the landscape-scale.

CHAPTER 5:

DIFFERENCES IN INTER- AND INTRA-ISLAND DIVERSITY AND COMPOSITIONAL PATCHINESS *

Summary

1. Quantification by transects at the meso-scale (c. 2 ha area) revealed markedly lower cumulative species totals and a more uniform nature (lower beta-diversity) for the canopy and lower canopy for Panjang and Sertung than for comparable areas of Rakata. These findings are in line with previous plot-based and whole island analyses by Whittaker and colleagues. However, canopy composition of forests on Panjang was much more patchy than on Sertung, and a previously unrecognised forest type with almost equal proportions of *Timonius compressicaulis* and *Neonauclea calycina* in the canopy layer was found on this island.

2. For all transects, *Dysoxylum gaudichaudianum* had the highest number of occurrences of all species when all strata were considered. In the Rakata transect, *Dysoxylum* was the canopy dominant in the near-coastal forest. After a rapid transition to *Neonauclea calycina* dominated canopy, *Dysoxylum* was still continuously present in the understorey. It is, therefore, clearly shown that successful regeneration of *Dysoxylum* is occurring under *Neonauclea calycina*, as well as under *Timonius compressicaulis* canopy. Moreover, the almost complete absence of regeneration of *Neonauclea calycina* and *Timonius compressicaulis* does not suggest their perpetuation. Greater importance of *Dysoxylum gaudichaudianum* as a canopy component not only on Panjang and Sertung but also the lowlands of Rakata is indicated. However, convergence of *all* lowland forest areas on *all* islands towards a *Dysoxylum gaudichaudianum* 'climax' community as proposed by Tagawa *et al.* (1995) is not suggested. Whilst this species may dominate large areas of Sertung and Panjang it is not likely to do to the same degree in the more species rich forests of Rakata, where several other species may compete for a place in the canopy.

* some of the analyses presented in this chapter have been published in summarised form in Schmitt & Partomihardjo (in press), and Schmitt & Whittaker (in press).

3. At the patch-scale (16 m²) DCA ordination of compositional data of the regeneration layer of young gaps in 1993 showed trends of greatest dissimilarity from the neighbouring understorey for the gap plot which suffered very severe disturbance (e.g. a landslide site). However, otherwise no clearly discernible trends in relation to broad gap size, and severity classes of disturbance could be detected. Instead, advance regeneration (AR) is suggested to be of greater significance in gap regeneration, whereby in the early successional forests on Krakatau the composition of the advanced AR seems to be influenced mainly by island affinity and forest type.

4. DCA analysis, applied to the combined patch-scale data-set of 1993, 1994, and 1995, showed that some gap and understorey plots experienced substantial changes in composition over the two years. Others remained more or less unchanged, as expressed by the distances between successive points in ordination space. The plots with the greatest compositional changes generally became more early successional in character including both gap and understorey plots, whereby in most cases the greatest changes were observed in the aftermath of the 1994 drought.

5. The direct comparison of gap and understorey composition using percentage similarity showed no uniform trend in initial similarity and changes in similarity over time with respect to gap size, severity and island. Great variability in the magnitude and direction of change in similarities over time was noted, and seems to a large part to be influenced by the local variability in drought impact. This variability can be seen as a function of the susceptibility of the local canopy dominant to drought, as well as the local hydrological and topographic conditions. Overall, the mean percentage similarity of pairs of plots increased from 30 to 36.2% over the study period, which can be attributed not so much to successional development of the gap-fill as to the drastic increase in pioneer affinity in some areas of the islands.

6. Diversity (species richness and evenness) trends of small saplings at the patch-scale were also very variable between plots and over time. The understorey plots showed a mean reduction in diversity and evenness between 1993-1995. No significant relationship of diversity with gap size could be found. More severely disturbed gaps were shown to be more diverse in the mesic years but the difference was lost in the extreme year of the drought.

5.1 Introduction

Plant recolonisation of the Krakatau islands began swiftly after the cessation of the sterilising eruptions of 1883 (section 1.3). All islands passed through a savanna stage with scattered clumps of trees and shrubs, typically *Macaranga tanarius*, *Ficus septica*, and *Ficus fulva*. These clumps eventually coalesced so that by around 1930 a species-poor closed forest covered each island. On Rakata large areas became dominated by the early successional, anemochorous tree species, *Neonauclea calycina* (see CHAPTER 1; Ernst, 1934; Docters van Leeuwen, 1936; Whittaker *et al.*, 1989).

Based on fieldwork in 1982, Tagawa *et al.* (1985) were the first to describe clear differences in forest types between the islands. Sertung and Panjang were found to be dominated by *Timonius compressicaulis* and *Dysoxylum gaudichaudianum*, and the present pattern of distribution of these species was attributed to the order of arrival and to edaphic factors (Tagawa *et al.*, 1985; Tagawa, 1992; Thornton, 1996). However, Tagawa *et al.* (1985) failed to recognise the possible influence of volcanism which resumed in c. 1930 with the emergence of Anak Krakatau in the centre of the island group. As reported in CHAPTER 2 and CHAPTER 3 disturbance from intermittent volcanic activity has since then been an integral part of the Krakatau islands' disturbance regime. Ash-fall and, during severe eruptions (e.g. 1931-5 and 1952/3), blast and gas damage (Docters van Leeuwen, 1936; Borssum Waalkes, 1954; Whittaker, 1989) has directly affected Panjang and Sertung but not Rakata. A history of these episodes can be reconstructed from stratified ash deposits in the soil profiles of Sertung and Panjang (Whittaker *et al.*, 1992a; see section 2.2). Forest divergence has been argued by Whittaker and colleagues to have occurred, at least in part, as a result. Thus, the current forest dominance by *Timonius compressicaulis* and *Dysoxylum gaudichaudianum* on Panjang and Sertung, rather than *Neonauclea calycina*, as on Rakata, has been suggested to be due in part to a deflection of succession by volcanic disturbance to the former (Whittaker *et al.*, 1989; Bush *et al.*, 1992). Further support to this suggestion was given by the discovery in 1983 of low and rather uniform canopy height, very sharp boundaries between the *Timonius* and *Dysoxylum* forest types, as well as the frequent occurrence of multiple trunks on *Timonius* individuals, many of which also currently show signs of former damage at uniform heights (Bush *et al.*, 1992; R.J. Whittaker, pers. comm.; see section 1.3).

Overall, the forests are still early successional in nature, as indicated by their general pattern of dominance by a small number of early or relatively early successional tree species such as *Neonauclea calycina*, *Timonius compressicaulis*, and *Dysoxylum gaudichaudianum*. Typically, within plots of c.400-2500 m², >50% of basal area is accounted for by one of these three species (Whittaker *et al.*, 1989; Bush *et al.*, 1992). At this spatial scale Panjang's, and particularly Sertung's forests have frequently been found to be species poorer. However, surveys over the last 17 years suggest that the flora continues to increase in size, and change in terms of the balance of different ecological and taxonomic groups (Whittaker *et al.*, 1992b; Bush & Whittaker, 1993; Whittaker & Jones, 1994).

While there is direct evidence now that Anak Krakatau's activity increases disturbance and gap formation even during episodes of relatively light ash-fall (see CHAPTER 3), and there is much historical and circumstantial evidence supporting the disturbance-driven successional model (Bush *et al.*, 1992; Whittaker *et al.*, 1989; Whittaker *et al.*, 1992a), most of the evidence indicating forest divergence and reduced diversity on the smaller islands has come from plot-based vegetation and general floristic surveys. These have therefore concentrated on quantification at the small scale (400-2500 m²) or the whole island-scale (3-17 km²). This chapter presents data on diversity and species composition at the meso-scale (c. 2 ha), and for the gap regeneration layer on the patch-scale (16 m²).

The basic tenets of the disturbance-driven model suggest that (i) ash-fall and/or blast damage has at different intervals, and to a different degree, enhanced the disturbance regime of Panjang and Sertung; and (ii) that this has led to a deflection of succession causing dominance and diversity patterns to differ from comparable lowland areas of Rakata. In CHAPTER 3 the validity of (i), even under moderate amounts of ash-fall, was demonstrated, whereas results from this chapter should help to elucidate if (ii) is also valid, and how the differential impact of disturbance is reflected in the forest mosaic structure and species-richness of each island at the meso-scale.

It is, therefore, hypothesised that (i) on the meso-scale suppressed diversity on Panjang and Sertung can be shown, and (ii) that the ash-affected islands are less patchy in their species composition than Rakata. Thus, this chapter aims to clarify whether inferences drawn from the plot based studies with regard to successional pathways can be corroborated at the meso-scale.

A patch-scale analysis of species composition and diversity (species richness and evenness) of the regeneration layer is also carried out. Whereas in CHAPTER 4 species performance in relation to broad size classes of gaps and severity classes of the gap-creating disturbance was investigated, this chapter tries to ascertain if these physical characteristics of gaps are the dominant influence on species composition of the regeneration layer of gaps or whether island and surrounding forest type are more important. This analysis is aided by the comparison of the gap species composition with that of the adjacent understorey, whereby the level of similarity between the plot pairs should be a good indicator of the importance of gap-size-specific recruitment versus AR. If recruitment of species specifically adapted to a particular gap size (Denslow, 1980; Oriens, 1982) was important, then information on the average gap size distribution on the different island should be a good predictor of the species composition of the gap-fill, and therefore of successional development. Special attention will be paid to patterns and changes in species compositional similarities of the different plots that may be linked to the 1994 drought, which has already been shown to have a major effect on sapling performance (CHAPTER 4).

It is specifically hypothesised that at the patch-scale (i) physical characteristics of the gap are less important in determining patch-scale diversity and species composition, and that (ii) the drought had a considerable effect on species composition and diversity in the gap and understorey environments, stressing the importance of extreme climatic events.

5.2 Objectives

The objectives of this chapter are:

(i) to investigate how the differential impact of disturbance is reflected in the forest mosaic structure and species richness of each island at the meso-scale, and thus to test if the inferences drawn from plot based studies with regard to successional pathways, and the disturbance-driven successional model, will be corroborated at this spatial scale.

(ii) to use the transect data on species presence/absence patterns in the understorey and canopy/lower canopy strata, respectively, to assess the forest development as known from historical accounts and from survey work in the 1980s and 1990s. Implications for future changes in canopy composition on the three islands will also be considered, and special attention will be paid to the patterning and presence of the current canopy dominants *Neonauclea calycina*, *Timonius compressicaulis*, and *Dysoxylum gaudichaudianum*.

(iii) To investigate if at the patch-scale spatial trends in species composition and temporal trends in species compositional changes in gap plots is primarily determined by the physical characteristics of the gap site (e.g. size and severity of disturbance). It will also be investigated if changes in the species composition and diversity show detectable successional trends over the 1993-95 period.

5.3 Methods

The meso-scale

In 1994, on each island, one 1000 m 'cross-country' transect from the disturbance survey was also used to enumerate species presence/absence (RSE 1000 m; PS 1000 m; S 1000 m). For methods and for location of the transects, see CHAPTER 3 and Fig. 3.1 respectively, and for transect abbreviation see GLOSSARY. Scoring of woody species (excluding climbers) in the understorey (c.0.5-5 m), lower canopy (c.5-15 m, depending on total height of canopy) and canopy (>15 m) took place for every 10 m section of the approximately 20 m wide transects. The total number of sampling points in each case was 100. Species-area curves for all strata were calculated based on 0.1 ha sections derived by combining five 10

x 20 m sections together. Although the presence/absence scoring was rapid, and misidentification or missing of species may be seen as a problem, the joint scoring work with the botanist Dr T. Partomihardjo, who has extensive knowledge of the Krakatau flora, ensured best possible data quality.

This method of survey has the advantage of being less liable to the subjective bias affecting site positioning within plot-based methods, and enables small-scale plot-based studies to be put into the context of medium-scale forest patterning. The larger scale patterns for all strata combined are further explored by using multivariate ordination and classification, in the form respectively of Detrended Correspondence Analysis (DCA, as provided by the CANOCO package of ter Braak, 1988), and Two Way Indicator Species Analysis (TWINSpan; Hill, 1979). For each 0.1 ha section each species was awarded a score between 0 and 5 as a function of presence in each 10 m section. These scores were used as input for the DCA and TWINSpan analyses. For the latter, the pseudo-species cut-levels (Hill, 1979; Kent & Coker, 1992) corresponded to the scores, and division to the third level (8 groups) was carried out. DCA scales the ordination axes into average standard deviations of species turnover (SD), whereby a complete turnover in the species occurrence in the transect sections takes place over about 4SD, and 1SD roughly equates to a 50 percent change in species composition (Kent & Coker, 1994).

For the major canopy dominants *Neonauclea calycina*, *Dysoxylum gaudichaudianum*, and *Timonius compressicaulis*, further analyses quantifying spatial occurrence patterns, as well as total occurrence in the canopy/lower canopy *versus* the understorey strata along the transect is carried out. Occurrence pattern is assessed in 50 m sections for which the maximum score of the number of occurrences is 5. This analysis allows tentative suggestions to be made with regard to the likely future importance of these species in the canopy. Furthermore, the trends of these meso-scale results for understorey distribution and occurrence can be compared to those found for the regeneration layer in gaps (see CHAPTER 4).

The patch-scale

For method of enumeration of the small sapling layer in 4 x 4 m plots, and measurement of percentage canopy openness see CHAPTER 4 (methods). See Table A4.1 in APPENDIX 4 for a summary of details on species numbers, and Simpson index values for all gap and understorey plots in 1993, 1994, and 1995.

Spatial analyses

The 1993 species compositional data of 4 x 4 m gap and understorey plots, measured in absolute abundance, were also analysed using DCA and TWINSpan analyses. For the latter the pseudo-species cut levels were set at 0, 2, 5, 10, and 20, for total number of saplings recorded in the plots, otherwise default settings were used (Kent & Coker, 1992). The only exception was the exclusion of P8U understorey plot as it was an extreme site with very high density of the rare species *Semecarpus heterophylla* and low species richness. Its presence in the data matrix distorted the ordination producing a second axis of no general ecological relevance. It was therefore omitted.

The assumption underlying the analysis of 1993 data is that if type and scale of disturbance are more important than the island context and the surrounding forest type in influencing diversity and species composition of the gap plots, then these should be separated in ordination space and/or placed into different main TWINSpan groups from their understorey plots. Main TWINSpan groups are defined in this study by the second level of the division (4 groups). This low level of division should be successful in showing substantial compositional differences between gap and understorey plots. The differences in composition should be the greater the larger the scale of disturbance, as that would, according to Bazzaz (1984), result in an increasing component of recruitment from the seed bank and seed immigration rather than a more shade-tolerant AR component (see CHAPTER 6).

DCA and TWINSpan were used as they give a community emphasis, and because each allow identification indirectly of environmental conditions by identifying the major gradients in the data set (Gauch, 1982). With existing knowledge of the environmental conditions and the characteristics of the surrounding forest types of the sites, interpretation of the results

with regard to the importance of physical characteristics of the gap can be attempted. Compared with other ordination techniques, the distances between samples along the DCA axes are a better equivalent to changes in species composition (Hill & Gauch, 1980). Canonical correspondence analysis would have allowed the identification of more direct relationships between species composition and environmental variables, but could not be used in this study, because an insufficient number of environmental variables were quantified due to constraints described in CHAPTER 4. Kent and Coker (1994) suggest that, in the absence of a good set of environmental data, DCA analysis is currently the best ordination method available.

Temporal analyses

DCA analyses were also carried out on the combined data set (1993, 1994, 1995) of species composition and abundance of the small sapling layer of 4 x 4 m gap and understorey plots. The aim of the combined analysis is to quantify, in community compositional terms, the short-term dynamics of the small sapling layer, and to elucidate whether the observed compositional changes may be seen as essentially successional, and/or whether gap type and size influenced compositional trends occurring during the gap-fill process. Thus, ordination was supposed to reveal potential successional pathways of the pairs of plots. In this context, potential divergence or convergence in composition can be portrayed graphically by the changing positions of relevés in ordination space over time (Belsky, 1986; Halpern, 1988; Whittaker, 1991). The increased or decreased distance of plot pairs over time can be interpreted as increased or decreased similarity in species composition of gap and understorey plots, because distances in the ordination space represent standard deviations of species turnover (SD; see above). Therefore, the inherent complexity of successional data may be reduced by ordination (Halpern, 1988), aiding the interpretation of the short-term compositional response of the regeneration layer to disturbance. It is important to note that for the plots P7G, R2LNG, and R10G only an incomplete data set exists. As already mentioned in CHAPTER 4, P7G was destroyed by erosion between 1993-94, and R2LNG and R10G could not be remeasured in 1995. In the cases of P7 and R10, understorey data are available, but due to the inability to compare gap and understorey for all years these sites were excluded. In the case of R2LNG, the data for the second gap plot (R2TF) in the treefall area of site R2 was still available for all years. The R2 site was therefore, kept.

For all three years P8U understorey plots, which were heavily dominated by *Semecarpus heterophylla*, were omitted from the analysis, and so were the P8G plots.

Direct comparison between gap and understorey sapling composition was carried out for 1993, 1994, and 1995 pairs of plots using percentage similarity indices. These are presented in diagrammatic form and ordered by increasing size, and grouped by severity and island. These representations allow detection of any trend in similarity of pairs of plots (see above), and provide insight as to whether percentage similarity changes over time may be influenced by these variables.

Patch-scale diversity trends

Diversity has often simply been equated with species richness, although many ecologists hold that the concept of diversity should incorporate a measure of evenness, i.e. the relative abundance of species within a sample or the community (Hurlbert, 1971). Diversity indices are often used, and a vast array of indices with varying degrees of weaknesses and strength, depending on the need of discriminatory ability, sensitivity to sample size, species-richness and evenness or simply the ease of calculation, exists. For this study the Simpson index was chosen as it has a relatively good discriminatory ability between different samples, and a low sensitivity to sample size (Magurran, 1988). This was appropriate as the number of individuals in the plots could vary considerably. The Simpson index has been suggested to be more biologically meaningful than, for instance, the very widely used Shannon-Wiener index. The assumptions for the latter, such as complete random sampling from an 'infinitely' large population, and that all species of the community are included in the sample (May, 1975; Magurran, 1988; Kent & Coker, 1992), are almost impossible to meet. However, the disadvantages of the Simpson index are that it is weighted towards the most abundant species in the sample, and is less sensitive to species richness (Magurran, 1988).

Yet, since the number of species in gap and understorey plots rarely exceed the suggested threshold of 10, the underlying species abundance distribution is not important in influencing the value of the index in this study (May, 1975). The index was calculated using the MVSP programme (Kovach, 1993), according to the following formula:

$$D = \sum \left(\frac{n(n_i - 1)}{N(N - 1)} \right)$$

(1-D) is used to ensure that the index increases with increasing diversity (Magurran, 1988).

Species richness and the Simpson index values were used: (i) to compare diversity between the gap and adjacent understorey plots; (ii) to compare diversity between different gap plots to establish if patterns may be related to gap size and/or type and severity of disturbance, and; (iii) to compare the relationships between diversity and gap-size and severity of disturbance between years.

5.4 Results

The meso-scale

The Rakata 1000 m transect has the highest cumulative species richness for the 2 ha area, followed by Panjang and then by Sertung. The curves for Panjang and Sertung also flatten earlier than that of Rakata, from which they differ significantly (Fig. 5.1). These observations are consistent with the view that past disturbance to Sertung and Panjang has resulted in successional set-backs and has restricted the process of diversification (Whittaker *et al.*, 1989). These data provide the first meso-scale evidence of this pattern. This has been suggested previously from whole-island species richness and from plot-based analyses (Table 5.1). The analysis presented here is arguably more convincing than the latter. The varying form of the species-area curves, depending on which end of the transect is used to start the plot, demonstrates the danger of relying on very small plots for such analyses.

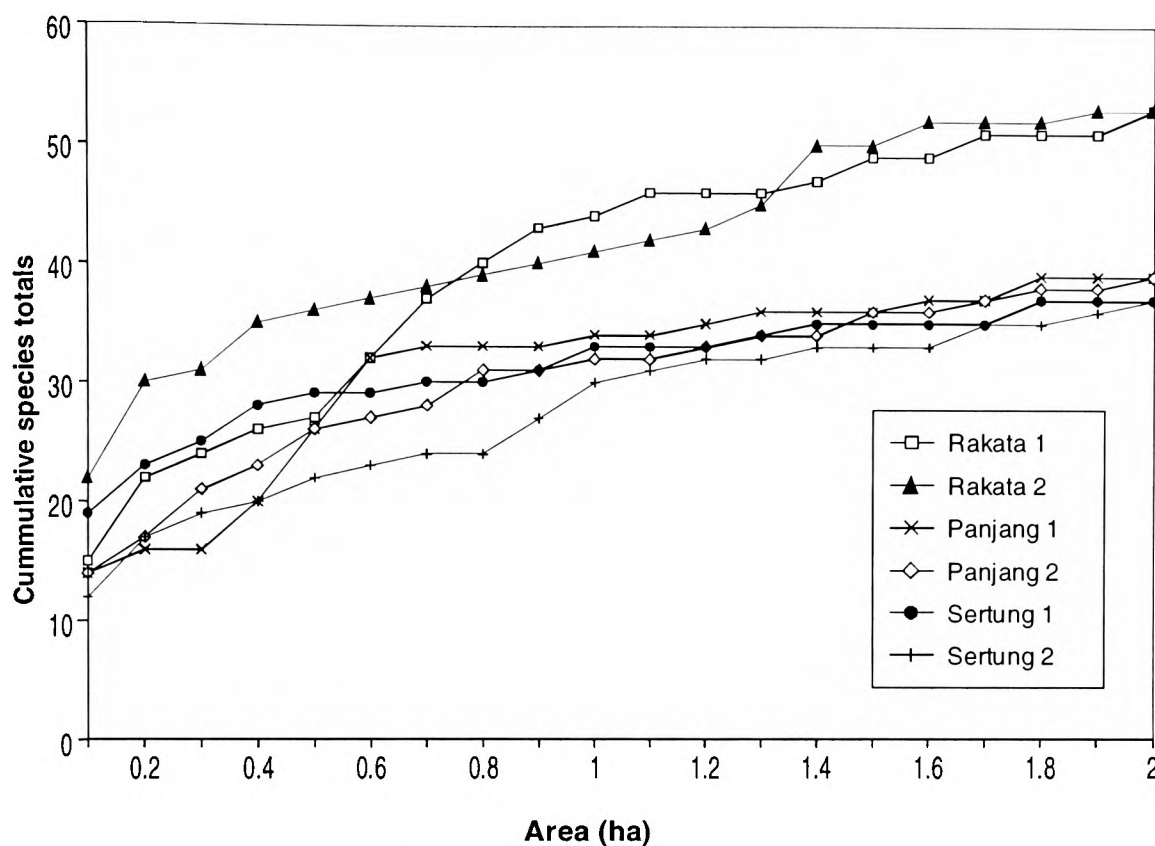


Fig. 5.1: Species-area curves for woody species (excluding climbers) of all strata. For this chapter, one 1000 m 'cross-country' transect (RSE 1000 m, PS 1000 m and S 1000 m); see section 5.3) was enumerated on Rakata, Sertung, and Panjang respectively. Approximate area covered is 20 x 1000 m (2 ha). The alternative forms of the curves were derived by calculating the cumulative species totals in turn from each end of the three transects. The great variation in the shape of the 0-0.6 ha sections of the alternative versions of the same transect demonstrate the danger of relying on very small plots for species richness comparisons.

Table 5.1: Average species total for trees >9.5 cm dbh for Rakata, Sertung, and Panjang on the plot scale, and tree and shrub species totals for the whole island scale from surveys up to 1994 (Data source: Bush *et al.* 1986; Whittaker *et al.*, 1989; Partomihardjo, 1995; R.J. Whittaker, pers. comm.)

	<i>plot scale (900 m² lowland plots only): average species total for trees >9.5 cm dbh (n = number of plots)</i>	<i>number of inland tree and shrub species on the whole island scale.</i>
Rakata (17 km²)	9.5	139
	n=2	
Panjang (3 km²)	7.8	80
	n=5	
Sertung (13 km²)	4.83	94
	n=6	
All islands (excl. Anak Krakatau)	N/A	170

The results of the multivariate analyses of the transect data are presented in Fig. 5.2. TWINSpan groupings at the third divisive level are superimposed on to the first two DCA axes. The principal forest types distinguished are: (i) *000 early phase *Timonius* forest, characterised by typical gap-fill species such as *Macaranga tanarius*, *Pipturus argenteus*, *Ficus septica* and in which *Bridelia monoica* is also frequent; (ii) *001 forest in which *Timonius compressicaulis*, *Neonauclea calycina* and *Dysoxylum gaudichaudianum* share the canopy in fairly even proportions, and in which other common species include *Buchanania arborescens*, *Oncosperma tigillarium*, and *Ardisia humilis*; (iii) *010 Sertung *Dysoxylum* forest, in which *Dysoxylum gaudichaudianum* heavily dominates the canopy, and in which *Terminalia catappa*, *Ficus septica*, *Bridelia monoica* and *Morinda citrifolia* are also consistent components; (iv) *011 disturbed near-coastal forest on Rakata in which *Dysoxylum gaudichaudianum* forms much of the canopy, and consistent species include *Arthrophyllum javanicum*, and *Ficus ampelas*; (v-viii) *100, 101, 110, 111 represent local variation within *Neonauclea* forest, in which a higher number of locally occurring species, some generally rare, such as *Planchonella duclitan* (Blanco) Bakh.f. and *Horsfieldia glabra* (Bl.) Warb., are to be found along a transect which has been subdivided to a greater extent in the TWINSpan analyses than those of Panjang and Sertung (Table 5.2).

Dysoxylum gaudichaudianum was the most frequently occurring species in the canopy/lower canopy and/or the understorey layer within each of the transects, occurring at a total of 99 and 97 of the 100 sampling points (every 10 m) of Sertung and Panjang respectively, and 82 points of the Rakata transect. In the Rakata transect, seven species occur at >50 sampling points (Fig. 5.3), in declining order of occurrence they are: *Dysoxylum gaudichaudianum*, *Leea sambucina*, *Antidesma montanum*, *Neonauclea calycina*, *Ficus fistulosa*, *Buchanania arborescens*, and *Ficus ampelas*. The equivalent set for Panjang is: *Dysoxylum gaudichaudianum*, *Timonius compressicaulis*, *Ardisia humilis*, *Antidesma montanum*, *Buchanania arborescens* and *Neonauclea calycina*; and for Sertung, there are only three species in the set, *Dysoxylum gaudichaudianum*, *Bridelia monoica* and *Ficus septica*. Of the species listed, only *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, *Buchanania arborescens* and *Timonius compressicaulis* are canopy species.

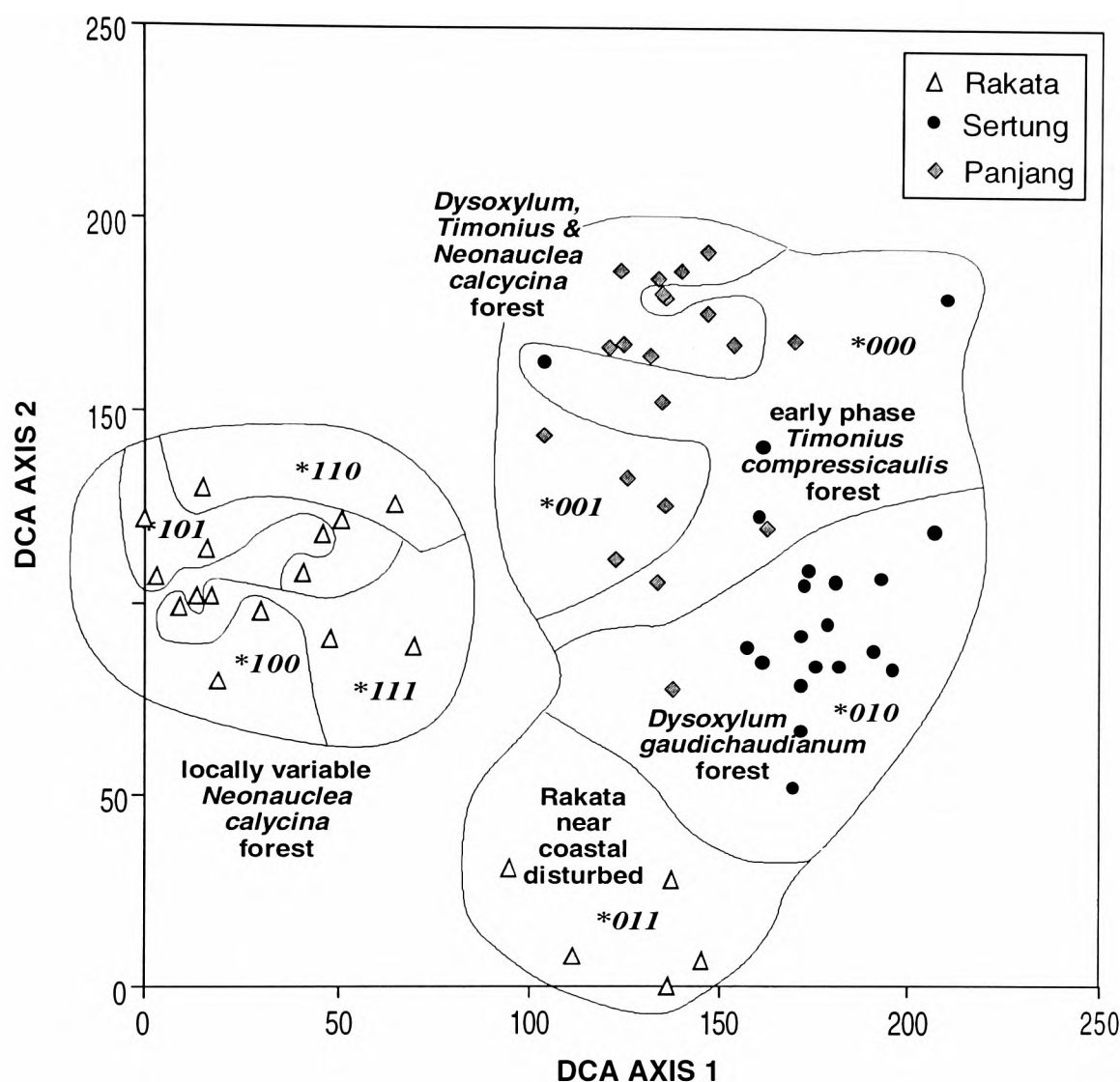


Fig 5.2: DCA ordination and TWINSpan classification of woody species occurrence in 0.1 ha sections of the 1000 m 'cross-country' transects on Rakata, Sertung and Panjang respectively.

Table 5.2: Summary statistics from the multivariate analyses of the 1000 m transects. DCA values are in standard deviations of species turnover, providing a standardised measure of community variation within islands. TWINSpan groupings and transitions between groups encountered in a traverse of each transect are given for the 8-group level of the analysis (as Fig. 5.2).

	DCA				TWINSpan	
	Axis 1	Axis 2	Axis 3	Axis 4	Groups	Transitions
Rakata	146	130	146	64	5	6
Sertung	106	128	96	111	2	1
Panjang	66	114	63	103	3	8
eigenvalues	0.302	0.177	0.095	0.072	-	-

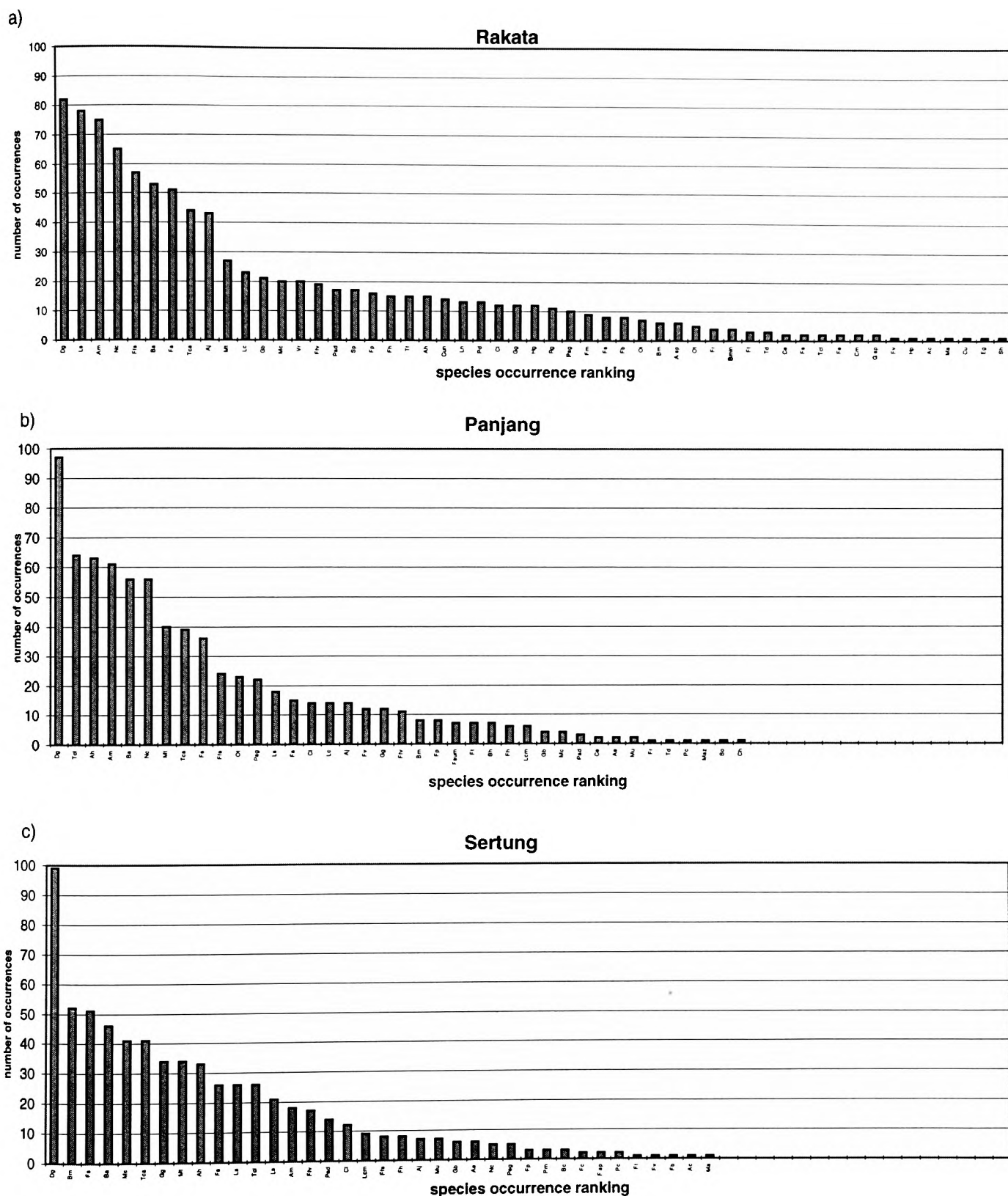


Fig. 5.3: Histogram ranking the number of occurrences (100 sampling points) of species enumerated in all strata (understorey, lower canopy and canopy) along the 1000 m 'cross-country' transects on (a) Rakata, (b) Sertung and (c) Panjang respectively. All graph demonstrate the overwhelming importance of *Dysoxylum gaudichaudianum*. See Glossary for species abbreviations.

Within the Rakata transect, only in the sites of group *011 is *Dysoxylum* currently a major canopy species, but the data show that it is ubiquitous in the understorey. Fig. 5.4a&b show the spatial occurrence of *Dysoxylum* and *Neonauclea calycina* in both canopy/lower canopy and the understorey layer. These figures demonstrate the continuous *Dysoxylum gaudichaudianum* dominance of the canopy, and almost continuous presence in the understorey moving from the near-coastal area up to the 240 m section of the former (corresponding to group *011). Then, a very rapid transition to the inland forest takes place, possibly to a certain degree linked with the start of hilly topography, and marked by the appearance of *Neonauclea calycina* as a canopy component. When moving further inland *Neonauclea* first shares (340 - 490 m section; *111) and then takes over the canopy/lower canopy dominance from *Dysoxylum*. In the last third of the transect *Neonauclea* occasionally shares the canopy with other species, in particular with *Terminalia catappa*, but also some rarer *Ficus* species (e.g. *Ficus sumatrana*), and towards the end of the transect *Dysoxylum* again features as a canopy component. The most striking find for the Rakata transect, however, is that *Dysoxylum* had not only continuous, but generally high frequencies of occurrence (Fig. 5.5), which was particularly so for the understorey throughout the *Neonauclea calycina* dominated area. This not only demonstrates that *Dysoxylum* can regenerate under *Neonauclea* canopy but, given moderately good survival that it is likely to be a common, if not dominant component, of the canopy layer in the future. This suggestion is further supported by the extremely low number of occurrences of *Neonauclea* saplings in the understorey (Fig. 5.5). The diagrams also show the near complete absence of *Timonius compressicaulis* which is one of the dominant species on Sertung and Panjang.

As noted earlier, Rakata's transect is richer in species than that of Sertung and Panjang, and the patchy occurrence of canopy species such as *Litsea noronhae* (Bl.) , *Oroxylum indicum* (L.) Vent., *Planchonella duclitan*, *Syzygium polyanthum* (Wight) Walp. and *Horsfieldia glabra* explains the greater degree of subdivision in the TWINSpan analysis than of the other transects (Table 5.2). This means it has arguably a larger number of fairly distinct forest types, although in the inland part of the transect (>240 m; groups *100-111; Fig. 5.2) the distinction would largely be due to the understorey component, as *Neonauclea calycina* is the almost exclusive canopy dominant. However, both Rakata and Panjang transects are locally patchy, as indicated by the relatively high number of transitions from one forest type to another along the transect line.

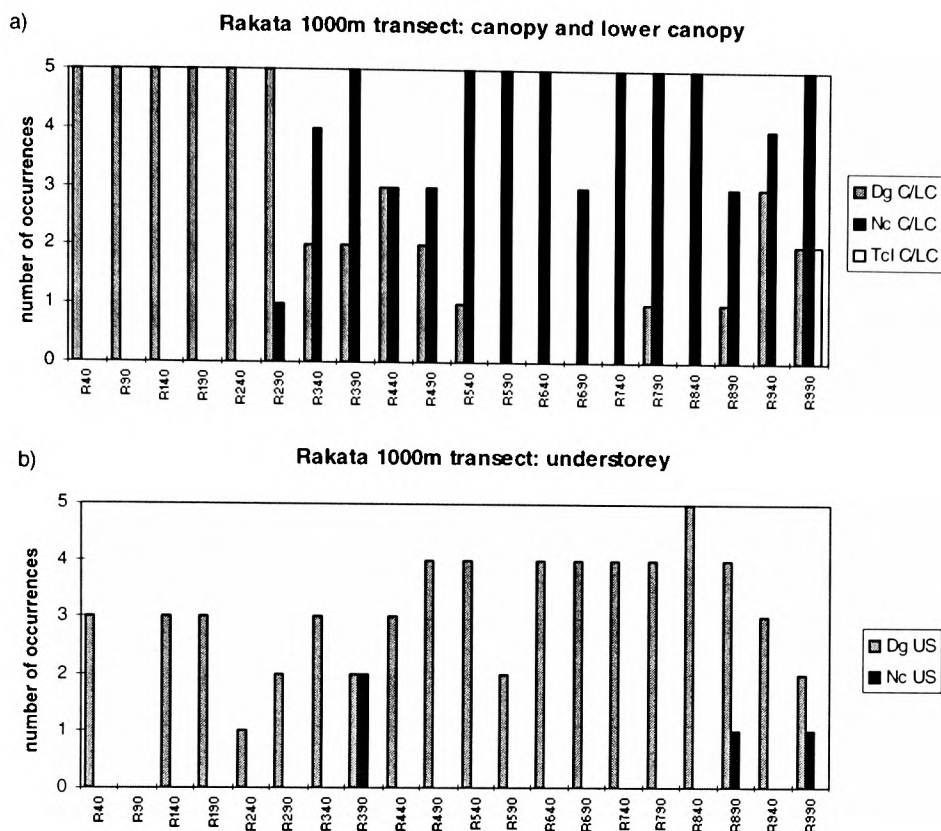


Fig. 5.4: The occurrence of *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, and *Timonius compressicaulis* in 50 m sections along the Rakata transect (RSE 1000 m) in (a) the canopy/lower canopy and (b) the understorey. Presence/absence of these species was scored at every 10 m for the understorey and the canopy/lower canopy layer (maximum score for 50 m section equals 5).

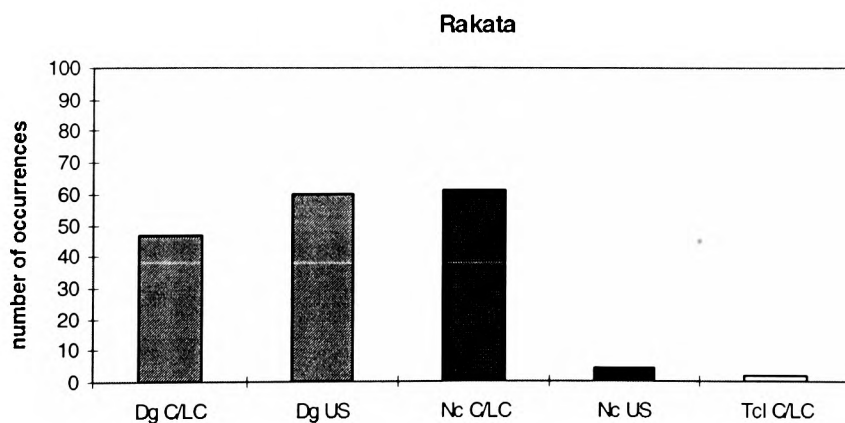


Fig. 5.5: The total number of occurrences of *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, and *Timonius compressicaulis* in the canopy/lower canopy and the understorey strata along the Rakata transect (RSE 1000m). *Dysoxylum* occurrence in the canopy and particularly the understorey is very high (all strata combined 82 out of 100 occurrences). Note the very low occurrences of *Timonius*, which is the canopy dominant in large areas of Sertung and Panjang.

In Fig 5.6a it is shown that *Neonauclea calycina* is a major canopy/lower canopy component of the transect on Panjang, and the DCA/TWINSPAN analyses clearly identifies these Panjang sections as a separate group (*001; Fig. 5.2) from the early phase *Timonius* forest found on Sertung and from other sections of the Panjang transect. It is therefore suggested that another forest type exists on Panjang, characterised by more or less equal proportions of *Neonauclea calycina* and *Timonius compressicaulis* and slightly greater proportions of *Dysoxylum* in the canopy/lower canopy strata (Fig. 5.7). *Dysoxylum* usually overtops *Neonauclea* and *Timonius*. This is a forest type which can now be considered to be of sufficient areal extent to be recognised as an additional forest type, but which has previously been neglected in plot-based sampling by Whittaker *et al.* (1989) and Bush *et al.* (1992). Moreover, in the more central part of the island *Neonauclea* and *Timonius* occupy more or less equal proportions of the canopy, but *Dysoxylum* plays a much less important role. That Panjang's forest are becoming more patchy was also supported by the recent discovery of another distinct forest type dominated by *Buchanania arborescens* by Dr T. Partomihardjo (1995).

The data also confirm the general trend towards almost complete absence of *Neonauclea calycina* and *Timonius compressicaulis* regeneration. Only in the last quarter of the Panjang transect does some recruitment of *Timonius* and *Neonauclea* take place. In contrast, and as found in the Rakata transect, *Dysoxylum gaudichaudianum* seems to be ubiquitous and regenerating particularly well in the last quarter of the transect where *Timonius* was generally a more important canopy component than both *Dysoxylum* and *Neonauclea* (Fig. 5.6b; Fig. 5.7). Successful regeneration and growth of *Dysoxylum gaudichaudianum* into the canopy in *Timonius compressicaulis* dominated forest has previously been noted, and attributed to the sparse canopy cover characteristic of this tree (Whittaker *et al.*, 1989; Bush *et al.*, 1992). This was also frequently observed during the present study. The growth and relative frequency data of tall saplings presented in CHAPTER 4, for instance, showed that *Dysoxylum* saplings were performing particularly well in *Timonius* forest areas.

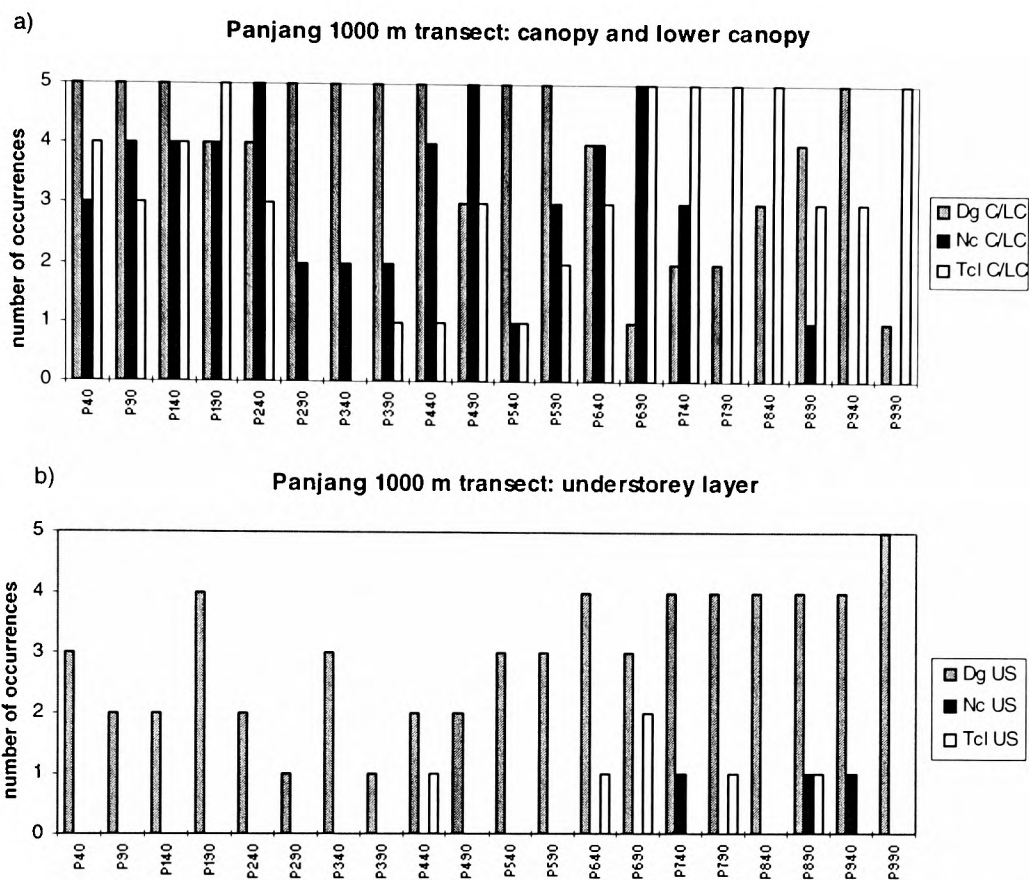


Fig. 5.6: The occurrence of *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, and *Timonius compressicaulis* in 50 m sections along the Panjang transect (PS 1000 m) in (a) the canopy/lower canopy and (b) the understorey. Presence/absence of these species was scored at every 10 m for the understorey and the canopy/lower canopy layer (maximum score for 50 m section equals 5).

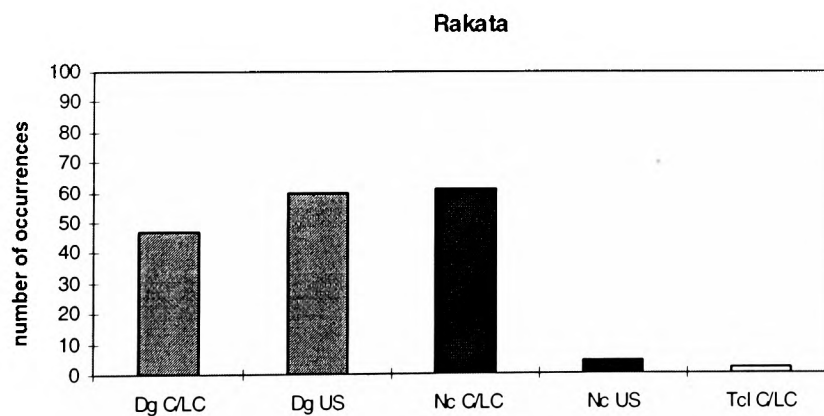


Fig. 5.7: The total number of occurrences of *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, and *Timonius compressicaulis* in the canopy/lower canopy and the understorey strata along the Panjang transect (PS 1000 m). *Dysoxylum* occurred in 97 out of 100 sampling points (all strata combined).

The Sertung transect sections display a greater spread of points in the DCA ordination space than Panjang (Table 5.2, Fig. 5.2). Yet, this is mainly determined by two extreme points in group *000, and all the Sertung transect sections have been placed into one of only two TWINSpan groups, with only one transition between groups occurring along the transect line. This indicates that while the difference between the extremes of the *Dysoxylum* forest, occupying three quarters of the transect, and the *Timonius* forest block which makes up the remainder, must be fairly distinct (see also Fig. 5.8a), little patchiness exists within either stand type. That *Timonius compressicaulis* has such a low number of occurrences as a canopy component is simply an artefact of the location of the transect. Almost all of the southern part of Sertung extending beyond the transect is covered by *Timonius* forest. The plotting of understorey species occurrence along the transect revealed that *Dysoxylum* is again occurring in high numbers all along the transect in both the *Dysoxylum* and the *Timonius* forest sections, whereas *Timonius* is hardly found regenerating (Fig. 5.8b; Fig. 5.9). All evidence on gap regeneration gathered so far, suggests that *Dysoxylum* is the strongest gap-fill candidate on Sertung, as well as Panjang. However, in 1995, in the most disturbed areas of ash and drought stressed *Timonius* forest on Sertung, there was an indication that it may pass through a *Macaranga tanarius* stage first (see below, section 4.4, and CHAPTER 6)

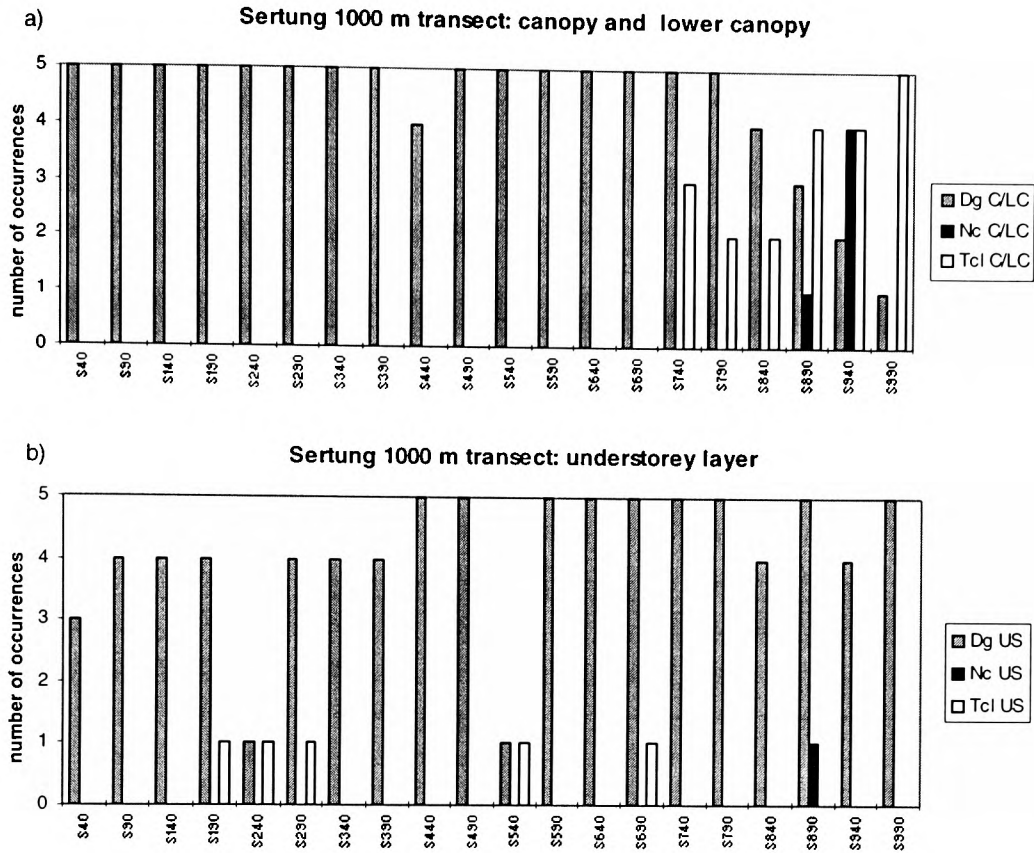


Fig. 5.8: The occurrence of *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, and *Timonius compressicaulis*, in 50 m sections along the Sertung transect (S 1000 m) in (a) the canopy/lower canopy and (b) the understorey. Presence/absence of these species was scored at every 10 m for the understorey and the canopy/lower canopy layer (maximum score for 50 m section equals 5).

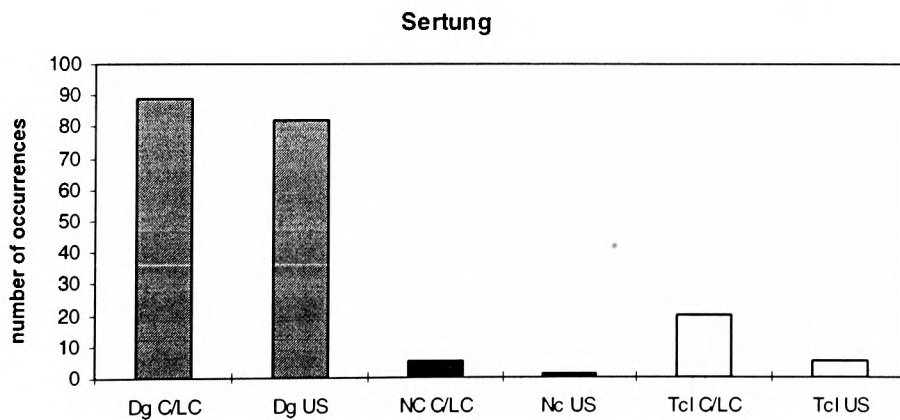


Fig. 5.9: The total number of occurrences of *Dysoxylum gaudichaudianum*, *Neonauclea calycina*, and *Timonius compressicaulis* in the canopy/lower canopy and the understorey strata along the Sertung transect (PS 1000 m). *Dysoxylum* occurred in 99 out of 100 sampling points (all strata combined).

The patch-scale

Species composition in space

After applying the DCA ordination to the 1993 gap and understorey data set (inclusive of P7G, R10G, R2LNG sites), TWINSpan divisive classification to the second level of the division results in four groups. Sub-groups of plots are formed at the third level of the division (Fig. 5.10). It is important to note that the data set is very noisy, and only a weak gradient is identified (only 11.3% of cumulative variance for DCA AXIS 1 and 28.4% for all four Axis). Therefore, interpretation and identification of relevés forming associations is difficult. The only strong differentiation displayed by the ordination is that between the group almost exclusively comprised of Rakata high altitude plots (*10), and the rest of the relevés. No clear separation of gap and understorey plots in relation to their size and severity of disturbance was observed for most sites (see Table 4.1 for gap size- and severity-classes; Fig. 5.10). When the TWINSpan divisive classification was overlain, R1G, S3G, P4G, P7G and R9G were the only plots placed into separate second level groups from their respective understorey plots. They ranged widely in size and disturbance severity and belonged to all three islands. P7G was so different in species composition and abundance from the other plots that it formed a second level TWINSpan group by itself (*11). R9G was the only other plot of this group which was very distant in ordination space from its understorey plot. It was classified with the high altitude group (*01) by TWINSpan. Other gap plots relatively distant in ordination space from their understorey plots were R12G, and S14G. Yet, they were similar enough in composition to remain in the same second level group, or in the case of R12 even in the same third level TWINSpan group (*011).

The remaining second level groups can be characterised as follows: Group *01 was in general comprised of gap and understorey plots with some *Dysoxylum gaudichaudianum* regeneration. In particular its third level sub-group *010 was made up of gap plots that had a considerable *Macaranga tanarius* and *Pipturus argenteus* component. TWINSpan group *00 consisted of plots which contained a significant *Antidesma montanum* component, except S14G which in 1993 had very low sapling abundance and was characterised by *Bridelia monoica*. It formed its own third level sub-group *000. *Antidesma montanum* is a very characteristic understorey tree species of Panjang's forests (both in Panjang's

Dysoxylum gaudichaudianum and *Timonius/Neonauclea* forests), but also a common understorey tree species in many parts of lowland Rakata.

In the large second level groups (*00 and *01), TWINSpan classification mostly led to a separation of gap and understorey plots only at the third or fourth level of the division. Where the gap and understorey plots were highly similar they remained in a single group even at the third or fourth level, as in the case of two Panjang gaps P6 and P13 (see direct comparison of plot pairs below). Both were lightly disturbed gaps (P13G only became severely disturbed by pumice digging in 1994) of medium size with a very large component of *Antidesma montanum* surviving as AR.

Overall, ordination and classification results of the 1993 data suggest that differentiation between gap and understorey plots is only partly affected by differences in gap size and types of gap creating events. This is with the exception of very severely disturbed gaps such as P7G. In other cases some of the differentiation is likely to be due to clumped distribution of AR species, and/or colonisation by a less common species.

Short-term species compositional trends

The combined analysis for all years (Fig. 5.11) shows great differences in the trends and the degree of compositional changes of the different plots in the period between 1993-95. No uniform trend that may be attributed to a general maturation of gap-fill and succession could be detected, nor was there a trend in the compositional changes explained by the size of the gap. Some plots remained extremely stable in their species composition whereas others were highly dynamic. It was striking that some understorey plots were as, or more, dynamic than their respective gap plots, and most of the highly dynamic gaps as well as understorey plots regressed, i.e. they became of more early successional character.

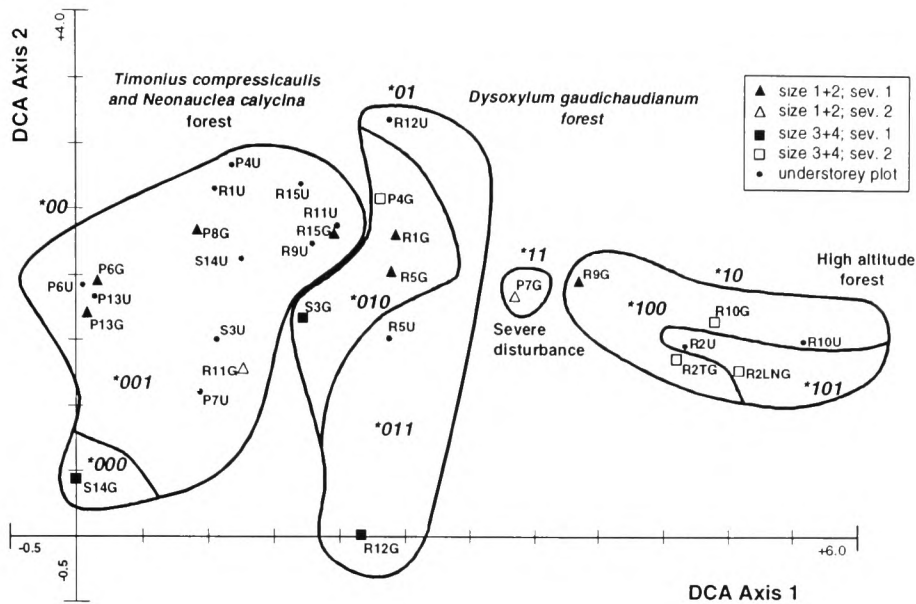
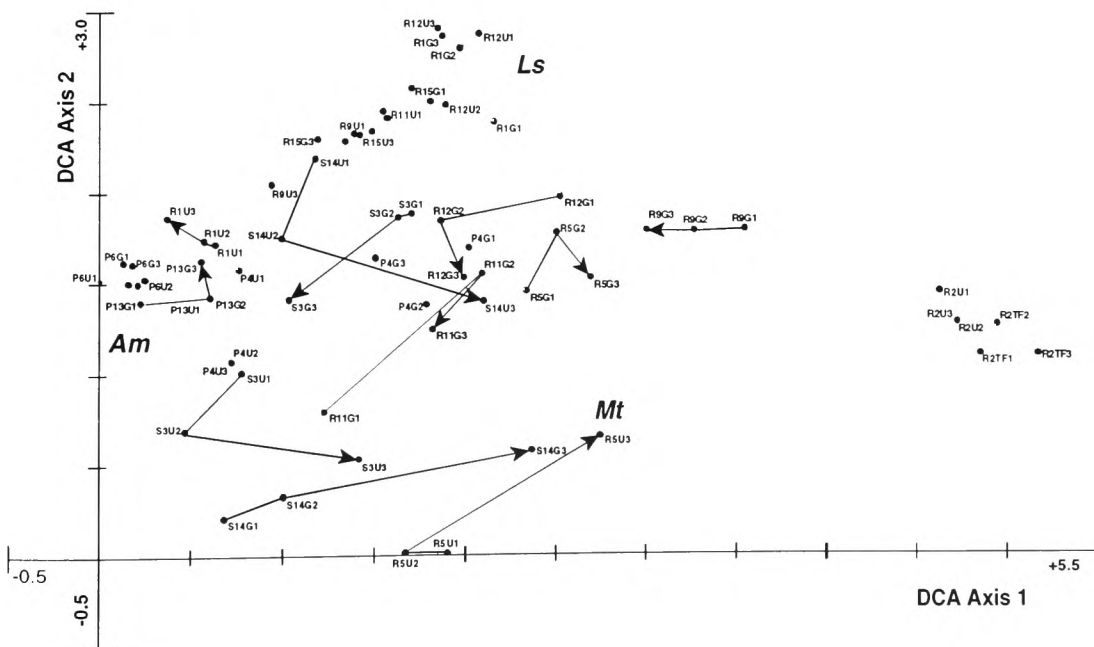


Fig. 5.10: DCA ordination and TWINSpan classification of the 1993 sapling abundance data of 4 x 4 m gap and understorey pairs of plots from Rakata, Sertung, and Panjang. The distance in ordination space and the TWINSpan groupings of plots illustrates the relative similarity in species composition of plots. See legend for classification into different size- and severity-classes. Note: P8U plot was excluded because of the heavy dominance of the rare *Semecarpus heterophylla* which unduly distorts the ordination; P13G plot was still classified as sev. 1 as redisturbance only occurred between 1993-1994 making it a sev. 2 site;



As already indicated in CHAPTER 4, most of the population and compositional turnover took place after the 1994 drought, which caused wide-spread death of saplings, and led to subsequent new recruitment. The latter was predominantly of pioneer character and most prominent were saplings of *Macaranga tanarius*. In this context it is very noteworthy that in some areas (Rakata near-coastal forest; Sertung *Timonius compressicaulis* forest) the canopies were opened so much as to allow pioneer recruitment in some of the understorey plots. Two of the most dynamic plots were S14G and S14U, which seemed to have become more similar over time as suggested by the greater proximity of their 1995 (year 3) plots in ordination space (see below and Fig. 5.11). S14G was the gap plot which moved most in ordination space: almost exclusively along Axis 1, and mostly after the drought in 1994, i.e. from y_2 to y_3 (gross SD = 167; y_1 - y_2 SD = 33; y_2 - y_3 SD = 134). R5U (gross SD = 126; y_1 - y_2 SD = -23; y_2 - y_3 SD = 103) was also very dynamic, and the large numbers of *Macaranga tanarius* recruits in both the gap and understorey plot after the drought also meant greater similarity between the gap and understorey plots for both these sites (see below). The figures show clearly that the changes in species composition was greatest between 1994 and 1995 (y_2 - y_3).

The sites with the least change in species composition, as apparently indicated by little movement within the ordination space, were the high-altitude Rakata sites (R2U and R2TF), and the majority of Panjang sites. The latter were characterised by high abundances of *Antidesma montanum*, which had very high survival rates. In addition, this species often recruited new individuals (see Table 4.14a). It was surprising, however, that P13G gap plot, which suffered from high levels of disturbance from pumice digging between 1993 and 1994 still remained similar in its composition between years. The P4U plot, which was disturbed by a treefall between 1993 and 1994, also did not change as much in composition as the plots mentioned above. Rakata inland plots, and the near coastal plots of R1 and R12, constitute the other set of sites with relative compositional stability. However, the gap plot of R12 is a slight exception, as is the gap plot of R11. The latter showed very considerable species turnover between 1993 and 1994, which is partly due to the fact that half of the plot was a very new root-zone rapidly recruiting new saplings. Moreover, pseudo-turnover is a problem in this gap as the sprawling *Ficus montana* saplings were very hard to relocate and survivors may have been overlooked.

To equate proximity of plots over time with absence of turnover can lead to misinterpretations. Careful inspection of the raw data is required as the ordination detects species turnover within the data matrix, but not necessarily to the same degree *population* turnover which happens to involve the same set of species. This is illustrated in the case of R5G and partially in the case of R2G. R5G's small sapling dynamics were very similar to that of its tall saplings (see CHAPTER 4). Both size-classes experienced tremendous mortality of saplings but recruited individuals of largely the same species over and above the abundances in the first year. Thus, although the distances in ordination space are small, the plots were highly dynamic in population terms. Absence of species as well as population turnover may, however, also be suggested as only two dimensions of the ordination are represented, whereas turnover in the third and fourth dimension might have been important for some plots, even if the variances involved were small.

The percentage similarity results for 1993, 1994, 1995 for each gap-understorey pair were graphed and ordered by size of gap, expressed in percentage canopy openness (1993 semi-fisheye lens values), and grouped by island and severity of disturbance (Fig. 5.12a-c). It was postulated that similarity between the gap and understorey regeneration layer, should decrease with increasing gap size as the AR component becomes less and less important (Bazzaz, 1984; 1991; Fig. 1.2). No such trend was detected for the 1993 data set. This corroborates the findings from the 1993 DCA/TWINSpan analysis (Fig. 5.10). Results also depend on the severity of the disturbance; e.g. PG7 and R2LNG were severely disturbed, both have low similarity in 1993, but one is a small and the other a very large gap respectively (note: only 1993 data existed for the former, and 1993 and 1994 for the latter plot). This finding is in line with Bazzaz's (1984) model which also emphasises the decline in the importance of the AR component with increasing severity of disturbance (Fig. 1.2). However, other sites classified as severely disturbed (severity 2; Fig. 5.12b) showed high similarity in 1993 (e.g. R2TF, R10). Comparing R2LNG and R2TF gap plots of the same gap site, it becomes clear that the heterogeneity in severity of disturbance within the same gap can play a crucial role in affecting species composition. In this case, the gap plot in the actual lightning-hit part of the gap (R2LNG) was more severely damaged (with much mineral soil) than R2TF gap plot in the bole zone of one of the treefalls in this large gap. Therefore, the crude classification into severity classes for the whole gap site may not directly reflect the very localised conditions experienced in different parts of the gap.

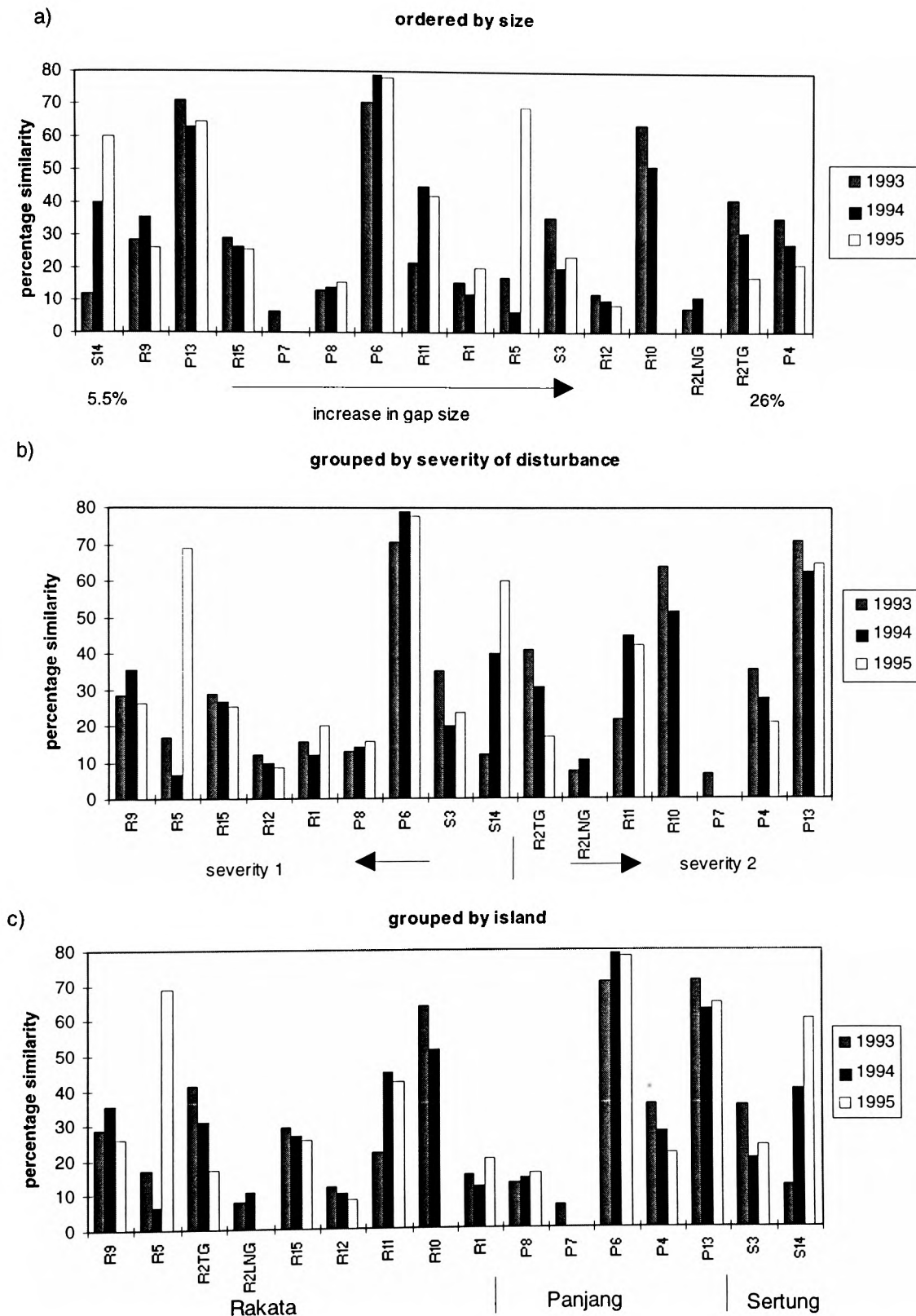


Fig. 5.12: Percentage similarity values between gap and understorey pairs of plots for 1993, 1994 and 1995 (a) ordered by gap size (in percentage canopy openness), and grouped by (b) severity of disturbance, and (c) by island.

Grouping by island also revealed no trend that may be related to the drastically different conditions encountered between Rakata and the ash-affected islands (Fig. 5.12c). Panjang, as one of the ash-affected islands, even had two gap sites with the greatest similarity in gap and understorey composition. This high similarity was maintained throughout the monitoring period, despite the ash-fall and the drought, apparently contradicting the previous suggestions that ash-fall and drought significantly affected species composition. However, in other sites (e.g. R5, S14) great changes in similarity could be observed, indicating great inter-site, but not necessarily inter-island variation.

One of the factors that could be of importance is the forest type, and its particular understorey/advance regeneration composition. For instance, the understorey and gap pair of plots of the large summit site had very high similarity, a result which appeared to be due to a dominant high altitude component in the sapling layer. Very high similarities to their respective understorey plots are also displayed by the two Panjang gap plots P6 and P13 just mentioned, and which were already identified in the DCA/TWINSPAN analysis above. The very high similarity is here due to Panjang's generally ubiquitous understorey component of *Antidesma montanum*, which survived as AR (even in P13G which was severely redisturbed).

Substantial increases in similarity between gap and understorey pairs can be achieved over time, as is displayed by S14 and R5 gap sites, confirming the DCA analysis (Fig. 5.11). It is noteworthy that the mean percentage similarity value for all pairs of the different sites has increased steadily between 1993-1995 from 30 to 36.2%. This result supports the finding of an increase in the number of sites that had both their gap and understorey plots in the same third level TWINSPAN group when 1995 data were analysed separately.

The sites with the most substantial increases in similarity (e.g. R5 on Rakata and S14 on Sertung) experienced substantial secondary canopy opening. This was caused by the 1994 drought, and in case of the Sertung site by both drought and the stress from ash. It appeared that the particularly severe drought effect in these sites was due to a combination of local hydrological regime and/or the susceptibility of the forest type to the drought. In the case of Rakata this was the flat, near-coastal *Dysoxylum gaudichaudianum* forest area which has in normal years a very broken canopy with lower layers of *Pipturus argenteus*, *Ficus hispida*, and *Macaranga tanarius*. All of these species have the characteristics of rapid leaf shedding under drought conditions, and in fact many trees died. This led to the

temporary opening of the canopy, allowing the recruitment of large numbers of *Macaranga tanarius* in both the gap and the understorey. A similar situation could be detected for the Sertung site S14 located in *Timonius compressicaulis* forest, whereby the forest already having a rather sparse canopy, opened up with the drought effect. *Macaranga tanarius* recruitment then took place throughout the understorey (see also section 4.4). It is noteworthy, that *Macaranga* recruitment did not take place to the same degree in the understorey of Sertung's *Dysoxylum* forests. This might be due to the fact that *Dysoxylum*'s shade is more dense, although during the drought *Dysoxylum* was shedding even more leaves than *Timonius*. Maybe the recovery of the pre-drought canopy cover was faster so that *Macaranga* was immediately shaded out except in gaps. However, there was not much *Macaranga* recruitment in S3G, the other Sertung gap, which is very sizeable and located in *Dysoxylum* forest. One might, therefore, speculate that a local seed source could be important, even though *Macaranga tanarius* is a rapidly, and widely dispersed species on account of abundant, and frequent fruit production, and (in the Krakatau case in particular) several resident bird dispersers (see CHAPTER 6; Taylor, 1982; Mitchell, 1994, S. Davis pers. comm.; pers. obs.).

Patch-scale diversity trends

Gap and understorey plot comparison

Overall species richness in understorey plots in 1993 was not found to be significantly different to that in gap plots ($p=0.63$; one-tailed t-test; Fig. 5.13a&b). By 1994 the mean number of gap species rose ($N_{93}=6.0$, $N_{94}=7.3$; with P7G excluded), and at the same time mean understorey richness fell significantly ($N_{93}=6.3$; $N_{94}=4.4$; P7U excluded). Thus, gap species richness had become significantly greater than understorey richness ($p<0.01$), but by 1995 significance had fallen to the 90% level ($p=0.069$; sites P7, R10 were excluded as full data sets were unavailable).

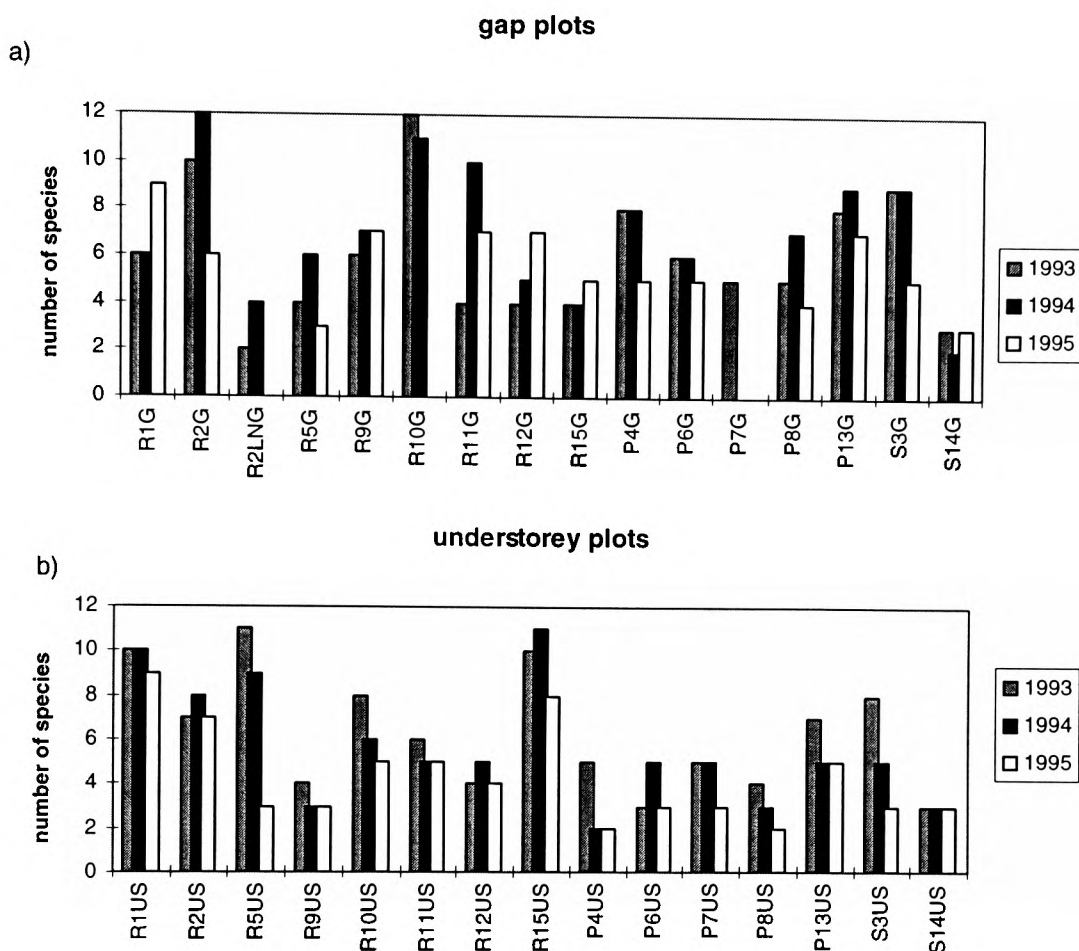


Fig. 5.13: Species richness trends between 1993, 1994, and 1995 for (a) all gap plots and (b) all understorey plots. Note: P7G, R2LNG and R10G have only incomplete data sets.

In general, the understorey diversity and evenness as measured with the Simpson index showed a decline between 1993 and 1995 which was nearly significant at the 95% level ($p=0.058$; one tailed Mann-Whitney-U test; Fig. 5.14b). The decline in the mean understorey Simpson index was greatest between 1994 and 1995. However, it was not significant as the variation between different plots was great. Whereas for understorey plots a declining trend in diversity and evenness was detectable no such trend was found for the Simpson indices of gap plots between 1993 and 1995 or 1994 and 1995 (Fig. 5.14a). Gap plots showed varied trends, whereby some plots showed an increase in diversity and evenness (e.g. R1G and R12G), others showed a continued decrease (e.g. R5G and P6G; Fig. 5.14a). This might be explicable by the rapid replacement of individuals and species after mortality.

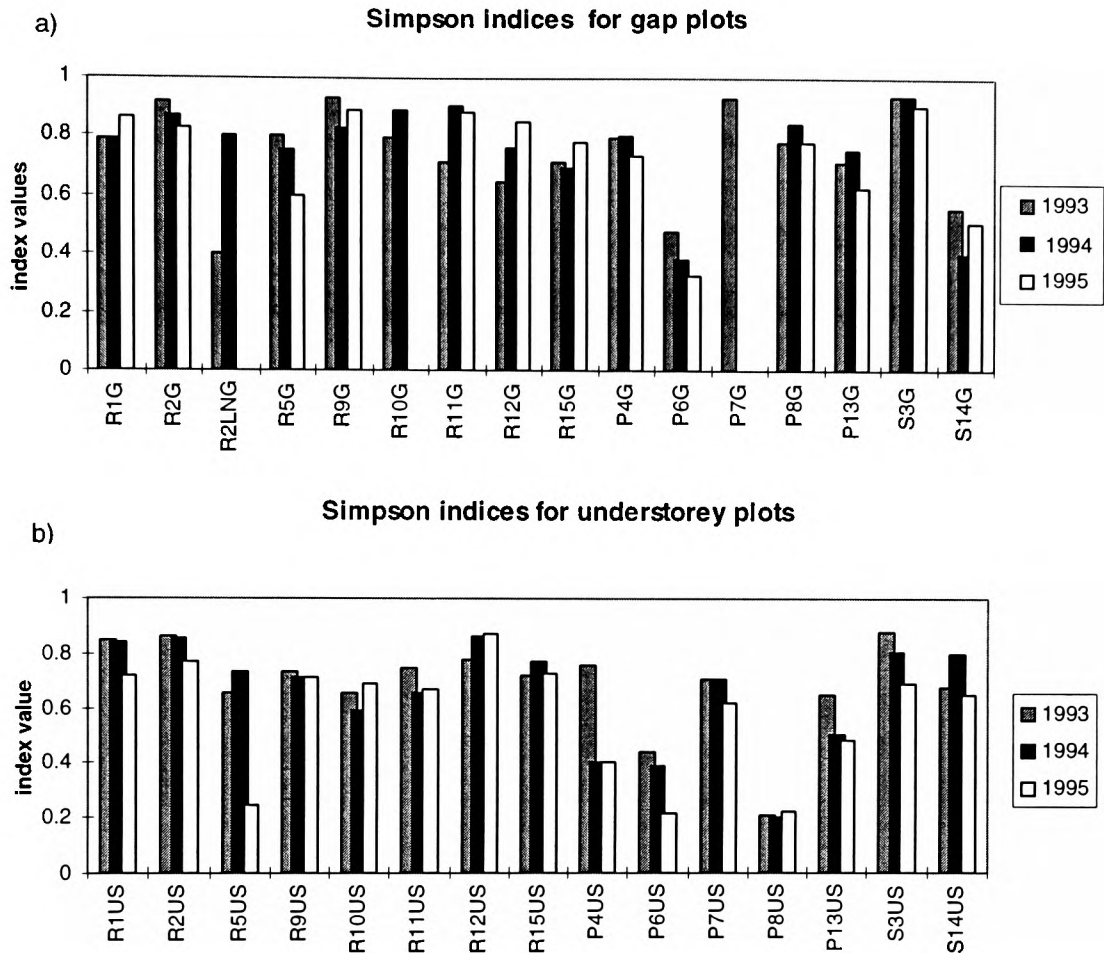


Fig. 5.14: Simpson index values for 1993, 1994, and 1995 for (a) all gap plots and (b) all understorey plots. Note: P7G, R2LNG and R10G have only incomplete data sets.

Significantly lower numbers of sapling species in previously disturbed gaps (see Table 4.1) were found in 1993 ($p < 0.01$). This may have been due to the previous disturbance wiping out the AR component. However, in single disturbance gaps (medium to lightly disturbed sites) surviving AR together with new recruitment after gap creation increased species numbers. However, by 1994 the trend was only significant at the 90% level ($p = 0.06$), and was undetectable in 1995 ($p = 0.16$; all one-tailed t-tests). This may be attributable to redisturbance of some plots, the effects of general recruitment, and again the overruling effect of the drought.

Diversity and gap-size and severity of disturbance

Regression analysis found that there was a weak positive, but non-significant relationship between gap size (measured as percentage canopy openness derived from the 1993 semi-fisheye values) and species richness in 4 x 4 m gap plots in 1993 ($R^2 = 0.20$; $p=0.079$), and 1994 ($R^2 = 0.19$; $p=0.104$). No relationship between the 1995 species richness in gap plots and gap size could be discerned at all ($R^2=0.024$; Fig. A4.1 in APPENDIX 4). Regression analyses between the Simpson indices and gap size also found no significant trends for any of the years. One-tailed t-tests between the arbitrary gap size-classes showed that there was no significant difference between size 1+2 and size 3+4 gaps for all years (Table A4.1; Fig. A4.2 in APPENDIX 4). In these analyses sites P7 and R10 and gap plot R2LNG were excluded for all years as their data sets were incomplete after the first or second year of monitoring. Even without the exclusion of these sites 1993 species richness in the large size-classes was only significantly higher at the 90% level. Therefore, one can conclude that gap-size does not significantly influence species richness in the present data-set.

The more severely disturbed gaps had a higher number of sapling species in both 1993 and 1994 ($p<0.05$ and $p<0.001$ respectively; one-tailed t-tests), without the exclusion of P7G, R10G and R2LNG gap plots (both are sev 2; Fig. A4.3 in APPENDIX 4). With the exclusion the difference was only significant at the 90% level for 1993 ($p=0.089$), but still significant for 1994 ($p<0.01$). By 1995, the difference became non-significant which was partly due to the absence of the data for P7G, R10G and R2LNG in this year, but also due to a general trend of reduced species numbers (Fig. A4.3 in APPENDIX 4). The Simpson indices for more severely disturbed gaps were only found to be significantly higher in 1994 ($p<0.05$; one-tailed t-test; Fig. A4.4 in APPENDIX 4), but not in 1993 and 1995. Again the 1994 significance was reduced to the 90% level ($p=0.061$) with the absence of R10G and R2LNG (P7G was already lost between 1993-1994). This indicates that there must have been a substantial increase in diversity in more severely disturbed gap plots between 1993 and 1994, which was not sustained or even partly reversed between 1994 and 1995 in the aftermath of the drought.

5.5 Discussion

The meso-scale

Through the 1000 m transects it was possible to show that more patchiness on the beta-scale exists on Rakata than on Panjang, with Sertung showing the least varied mosaic pattern. This is suggested to be a reflection of interactions between disturbance histories and local species availability. The latter is another important causative factor in the hierarchy of successional determinants according to Pickett *et al.* (1987; Table 1.3; Fig. 1.16). The transect on Rakata contained more species in general, and in particular, more canopy species. Thus, the findings of lower species richness and lower patchiness at the meso-scale for the forests of Sertung and less so Panjang, add support to the suggested importance of (particularly volcanic) disturbance as a key factor influencing the succession on the Krakatau islands (Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker *et al.*, 1992a). Also if one accepts that Rakata's forests are in general the most mature in the island group, the finding of higher beta-diversity conforms with the widely accepted notion that compositional differentiation along environmental gradients typically increases during succession, and is highest in the most mature forests (Matthews, 1979 for herb-dominated ecosystems; Christensen & Peet, 1984;).

Lower species richness on the ash-affected islands today (Bush, 1986a; Whittaker *et al.*, 1989; Whittaker & Jones, 1993) contrasts with the time prior to Anak Krakatau's emergence. Then more species were known from the forests of Sertung than from Panjang, but fewer than from Rakata (whole island scale; see Table 4 in Whittaker *et al.*, 1989; Table 5.1). Taking differences in survey efforts into account (Whittaker *et al.*, 1989; Table 1.2) this may simply be explained by species-area relationships, as Sertung (13 km²) is more than three times the size of Panjang (3 km²), but smaller than Rakata (17 km²). Additionally, the greater height of Rakata added a high altitude component to its flora. Furthermore, successional development of Sertung and Panjang up to c.1930, was in line with compositional changes in lowland Rakata, although perhaps a little slower and there were differences in commonness of particular species (Ernst, 1907; Docters van Leeuwen, 1936). For instance, *Timonius compressicaulis* was found to be more widespread on Panjang than on Rakata (there mostly found in the North-west), and at that time had not been found on Sertung. *Neonauclea calycina* was already quite frequent in the northern flat and hilly parts of Sertung, and was frequently found on Panjang by 1930, but appeared

by *Buchanania aborescens* as the canopy species was recently identified (Partomihardjo, 1995). Thus, although Panjang's forests are dominated by *Dysoxylum gaudichaudianum* and *Timonius compressicaulis*, and despite documented trends of *Dysoxylum* expansion, Panjang's forest are rather less uniform than anticipated from permanent plot studies. In fact, if these newly identified forest types were to be recognised as significant elements of Panjang's forests, it would require revision of the successional summary diagrams of Whittaker *et al.* (1989), which distinguish between pathways followed on Rakata on the one hand, and Sertung & Panjang considered jointly on the other (Fig. 1.13). While this form of representation, as offered by Richards (1952), Whittaker *et al.* (1989) and Tagawa *et al.* (1985) has its uses, it must be recognised that such diagrams over-simplify, placing artificial stress on the development of community types, or 'associations' (as in the earlier 20th Century tradition, Ernst, 1907; Richards, 1952), whereas, in practice, successional pathways vary from patch to patch and over time as a function of the sorts of factors identified in Fig. 1.16. This may also partly account for the fact that there is, as yet, no evidence to support Ernst's (1907) prediction of interior forest associations becoming 'closed' through competition as more species have colonised.

During studies in the 1980s it was established that *Dysoxylum gaudichaudianum* is the canopy dominant in large areas of Panjang, and in the North of Sertung (Tagawa *et al.*, 1985; Whittaker *et al.*, 1989). It has also been suggested that *Dysoxylum* is rapidly spreading into *Timonius* forest areas on both of those islands. For instance, on Panjang the island area dominated by *Dysoxylum* has increased from c. 50 to about 75 percent between 1983 and 1989 (Bush *et al.*, 1992), and data on the increase in relative importance of the *Dysoxylum* component in gap regeneration specifically in *Timonius* forest areas (CHAPTER 4), further supports this suggestion. Moreover, the apparent ability to withstand ash-fall stress makes *Dysoxylum* a successful candidate for invading more areas of Panjang and Sertung in particular during times of volcanic activity. There has, however, been debate as to the future prominence of *Dysoxylum gaudichaudianum* in the lowlands of Rakata, in which at present *Neonauclea calycina* remains the numerical dominant. The transect data demonstrate unequivocally that *Dysoxylum gaudichaudianum* is widespread in the understorey of this area of lowland Rakata. It does, however, remain predominantly lowland on Rakata. Thus, it has been shown that *Dysoxylum* has the ability to regenerate under *Timonius compressicaulis* as well as *Neonauclea calycina* canopy, and that it is in the process of invading the lowland *Neonauclea* forest. This is despite the fact that *Dysoxylum* supposedly arrived much later than *Neonauclea*, as its first record on

Rakata was in 1979 in the South-east coast area (Whittaker *et al.*, 1989). Yet, the fact that Borssum Waalkes in 1951 and 1952 carried out the only botanical surveys between 1932 and 1979, and the fact that these were only partial surveys, means that *Dysoxylum* specimens on Rakata may well have been overlooked.

The new evidence on *Dysoxylum*'s increased importance in the Rakata lowlands concords with the predictions of a rise in its importance (Tagawa *et al.*, 1985, Whittaker *et al.*, 1989; Tagawa, 1992). In Tagawa *et al.*'s (1985) model, this is represented diagrammatically as a general convergence of forest types towards a single forest type dominated by *Dysoxylum*. However, whilst *Dysoxylum gaudichaudianum* may in general be extremely successful and rising to greater prominence in lowland Rakata, a general compositional convergence of *all* lowland forests towards mono-dominance of *Dysoxylum* is not implied by the data in this chapter. The lowland forests of Rakata contain more species on the meso-scale, and it appears that many of them are managing to spread at least locally, and thus to contribute to a richer forest than has as yet developed on Sertung, and Panjang. Thus, *Dysoxylum gaudichaudianum* is not the sole contender for a position in the canopy. For instance, *Buchanania arborescens* was found to be quite common on all islands (Table 4.14a; Fig 5.3). This was more so in the regeneration layer than the canopy layer, but as this species can grow to canopy height (20-25 m), and had very good survival over the 1993-95 period (see Table 4.14a), one might suggest that it will be of greater future importance as a canopy component.

There are also a considerable number of other potential canopy species present on the Krakatau islands. For instance, approximately half of the 47 tall sapling species encountered in the gap sites (see CHAPTER 4) could be potential canopy species. Yet, more than one third of the species enumerated occurred in only one or two sites. These might come to fill the gap in question. However, they are not likely to become of major importance on the Krakatau islands in the short term due to apparent dispersal constraints. This and the general difficulty for new immigrants of late successional character to reach the archipelago (Whittaker & Jones, 1994ab) influences 'species availability' according to the Pickett *et al.* (1987) hierarchy of successional causes and mechanisms, and can slow successional development even if site availability is not a problem. The dispersal syndrome of species of late successional character often requires mammal or large bird dispersers which are not able to cross the sea-barrier, moreover a large proportion of the seeds of such species are recalcitrant, and may thus not be able to reach the islands in a viable

state. At the archipelago scale, these factors are without doubt a general constraint on successional development on these islands (Whittaker & Jones 1994ab; Fig. 1.4). Furthermore, while many species are shared between all three islands some, for no obvious reason of their ecology, are restricted to a sub-set, and others, while locally abundant on an island, have yet to spread widely (1995; Whittaker *et al.*, 1992b; Whittaker *et al.*, 1989; Bush & Whittaker).

Potential canopy species are, for instance, *Planchonella duclitan*, *Horsfieldia glabra*, and *Semecarpus heterophylla*. They are recruiting successfully locally (e.g. *Planchonella duclitan* and *Horsfieldia glabra* in the South-east area of Rakata), but mostly are failing to spread rapidly and extensively (see CHAPTER 6). Thus, the major constraint in these cases appears to be one of dispersal. These constraints might be caused by the low density of dispersers, or the lack of a more specialised disperser. The latter might be relevant to the case of *Semecarpus heterophylla*, in the Anacardiaceae, a family known for its high amounts of secondary, often allergenic compounds in its leaves and fruits (Umavedi *et al.*, 1988). It displays a distinctly under-dispersed distribution, concentrated around a small number of large parent trees in North-eastern Panjang. In extreme cases the lack of a specific pollinator, as required by *Ficus* species, may also act to constrain species spread (Compton *et al.*, 1994), as might be the case in some of the rare *Ficus* spp (e.g. *Ficus virens*, *F. callosa*, *F. benjamina*).

The patch scale

Spatial analysis of sapling composition

The second level TWINSpan groupings (four main groups) of the 4 x 4 m gap and understorey plots of the 1993 analysis predominantly appeared to reflect differences in forest types (Fig. 5.10). The size of the gap and type of the gap-creating disturbance at that level of the division does not appear to be the predominant factor involved in differentiating the gap and understorey composition, except in the extreme landslide case (P7G). First, even the small to medium sized gaps (e.g. RG1, size 1+2) were large enough to recruit extreme pioneers such as *Pipturus argenteus*, differentiating them from the understorey composition at the second level of the division. Second, although PG4 (size 3+4), was very different in its composition to its understorey plot, other very large gaps such as the high altitude site R2 have gap plot compositions similar enough to their understorey pair to be retained in the same second level group. In contrast, R9G, a small to medium sized gap (size 1+2), that was not very severely disturbed, was found to be very different from its

understorey plot. For the majority of gaps, irrespective of size and disturbance type, AR appeared to play an important role (cf. Uhl *et al.* 1988) in the initial phase of gap-fill. Otherwise gap and understorey plots would have more often been separated into different TWINSpan groups. However, the clumped distribution of AR, which is largely a matter of chance, may be a problem, such as, for instance, clumped establishment beneath rare parent trees (e.g. the case of *Semecarpus heterophylla* in P8U) or clumped dispersal (e.g. observed in the case of *Calophyllum inophyllum* below bat roosts; pers. obs.). Also, the fact that only a single 4 x 4 m plot was enumerated for each gap and its understorey may, under conditions of such patchiness, lead to the chance sampling of such very distinct patches. Except for the sites indicated, however, the species composition of the AR component seemed relatively homogenous, with the only very strong gradient being exhibited between the lowland and high altitude plots, and a less strong gradient largely between some inland Rakata and Panjang plots.

Short-term species compositional trends

The short-term changes in species compositional similarity between gap and understorey pairs of plots during the study period (1993-95), as expressed in percentage similarity values, suggests there to be very mixed trends in the direction of change (Fig. 5.12). Some plots decreased or remained very dissimilar, whereas some others drastically increased in similarity. The latter was, in general, not due to the gap plot recruiting more shade-tolerant species, but rather the opposite. In several instances the plots with the largest compositional and population turnover (e.g. S3U, R5U, S14G, S14U) became more open due to the effects of drought, ash-fall, and redisturbance by further treefalls. In the combined DCA ordination (Fig. 5.11), they have usually moved towards the middle of Axis 1 and the lower part of Axis 2, which is the part of the ordination space occupied by *Macaranga tanarius*. Thus, these plots have become of more early successional character over the study period. In contrast, the lower end of Axis 1 and the middle and upper section of Axis 2 was occupied by sites with generally little compositional turnover. That area of the ordination space is occupied by common, apparently more shade-tolerant species such as the understorey tree *Antidesma montanum*, and the canopy species *Buchanania arborescens*, and *Dysoxylum gaudichaudianum*. Comparable trends were observed by Condit *et al.* (1996) who found that rapid increases of some 'colonising species' (i.e. species with higher pioneer affinity) on Barro Colorado Island (BCI) could be attributed to the severe 1982/83 El Niño drought temporarily opening the canopy, and thus improving

recruitment chances. However, under average climatic circumstances the species that preferentially colonise gaps on BCI were found more likely to decrease in abundance over time.

Overall, these results do not suggest that gap size is of importance in relation to recruitment pattern (Denslow, 1980). This is not surprising given that in this primary successional, insular context there is a lack of a full successional spectrum of pioneer and mature forest species (*sensu* Swaine & Whitmore 1988). With the exception of the extreme pioneers (e.g. *Macaranga tanarius*, *Pipturus argenteus*, *Neonauclea calycina*, *Timonius compressicaulis*, etc.), Krakatau's woody flora is dominated by secondary species, with an apparently broad tolerance of environmental factors (Richards, 1996). The common ones include, *Dysoxylum gaudichaudianum*, *Buchanania arborescens*, and *Ficus ampelas*, whereas rare and/or localised secondary tree species include, *Planchonella duclitan*, *Syzygium polyanthum* and *Semecarpus heterophylla*. Their presence or absence, and continued survival in gap regeneration is much more likely to be influenced by dispersal, chance and site history (i.e. frequency and scale of disturbance). The latter is strongly influenced by the occurrence of extreme events, such as periods of volcanic activity, storms or droughts.

Indeed, in CHAPTER 4, the extreme event of the 1994 drought has been identified to have had an important influence on the species compositional turnover of the small sapling layer at the patch-scale. This is scarcely surprising given that the same conclusion was drawn in relation to patterns at the species population level. However, the important finding is that the effect is not uniform and of the same degree across all islands, and within the same island. At least part of the differences in the effect appeared to have been the result of variable combinations of drought susceptibility of the canopy dominant in the respective forest area, stress from ash-fall, and/or the local hydrological conditions (possibly variations of poor water retention, drainage pattern and rainshadow effect) of that area. Therefore, it can be argued that this extreme event, as well as redisturbance in some plots has further encouraged multiple path-ways of regeneration and succession and helped to enhance inter-and intra-island heterogeneity of the regeneration layer. In future, this may translate into increased canopy heterogeneity or patchiness (beta-diversity). However, it is important to bear in mind that this was only a very short-term study, and some of the compositional changes, and in some cases apparent 'convergence' to an earlier successional sapling composition, may be of a rather transient nature, with possible rapid divergence to follow

(cf. Halpern, 1988; Inouye & Tilman, 1988). This is particularly relevant in the case of some understorey plots, where a period of mesic conditions with renewed closure of the canopy cover is likely to result in the shading out of the light-demanding pioneer component.

Patch-scale diversity trends

Gap and understorey plot comparison

The environmental differences between the approximate gap centres, where the gap plots were located, and the understorey environment were not reflected in an overall difference in gap and understorey species richness at the beginning of monitoring in 1993. At first this seems a rather surprising result as gaps are known to increase resource availability (e.g. light and available moisture) and to reduce competition, and therefore to provide an important cue for the recruitment of more light-demanding species. Together with surviving advance regeneration this should boost the number of species. This expected result was however, achieved in 1994 when some of the very recently created gaps (e.g. R11G, R2G) had experienced a period of recruitment. Why at the same time mean understorey species richness fell was not directly evident, except in the case of P4U which lost three species due to a treefall. Sertung understorey plot S3U also lost three out of eight species between 1993 and 1994, which may have been due to a combination of ash-fall and drought. As it was only the beginning of the drought period its effect seemed to have manifested itself more rapidly on Sertung than in some other parts of the archipelago.

The fact that understorey diversity and evenness, as measured by species richness and the Simpson index, declined over the study period might be explicable by the fact that the forests as a whole had suffered stress (drought and/or ash). In general, it is possible that the effect of the drought was felt earlier in the understorey plots, and also drought stress in the understorey may have been greater. Veenendal *et al.* (1996) found that in the moist tropical forests of Ghana dry season water stress was greater for shaded seedlings than for those growing in gaps. In conjunction with such an effect, understorey plots may not have been able to rebound and recruit new species as quickly as some of the gap plots. As shown in CHAPTER 4, after the 1994 drought there was a general trend in both the gap and the understorey towards reduced woody species diversity of the regeneration layer and

rapid recruitment of pioneers such as *Macaranga tanarius*, which benefited from more open conditions (see R5 understorey plot in Fig. 4.6).

Previous disturbance of the gap site appeared an important determinant of species richness in the 4 x 4 m gap plots in 1993. The greater survival of AR plus some additional recruitment of new species might, explain the significantly higher number of species in previously undisturbed gap plots. However, if previous disturbance really was important in influencing species richness of the gap regeneration then its significance rapidly disappeared. The obvious controlling factor in this study seems to be the impact of the drought. It is unclear, however, if under less extreme circumstance this difference may also have disappeared as a result of inter-specific differences in mortality and recruitment.

Diversity and gap-size and severity of disturbance

Gap size was shown to have only a weak influence on species richness in the young gaps enumerated in this study, and this influence disappeared over the two year monitoring period. The Simpson diversity indices also showed no significant relationship with gap size. That even the weak positive trend disappeared may have been due to the extreme influence of the drought causing a reduction (at least short-term) in the diversity of the regeneration layer, but may also have been due to general selective mortality with time, as competition for resources increases. However, it is also important to bear in mind that gap size (especially if measured by geometric means) is a poor representation of the light environment and the microclimate experienced in different areas of the gap and by different sapling individuals (Brown & Jennings, in press). It is therefore, difficult to ascertain which particular physical variable is influencing the species composition and diversity of a gap site. Additionally, with respect to sapling populations, the history of the site in terms of local diversity, dispersal, successful germination and survival beneath the canopy are probably more important in determining the sapling composition and diversity of the early phases of gap regeneration. However, it has been shown here that extreme events have the potential to modify this initial regeneration 'make-up' considerably.

The severity and type of disturbance usually determines how much bare mineral soil is available in a gap. The more severely disturbed the gap the more bare soil surfaces are available (see methods). These surfaces are known to encourage the germination and colonisation by different suits of species than in the crown or bole zone (cf. Brandani *et al.*,

1988; Núñez-Farfán & Dirzo, 1988). Thus, internal heterogeneity in more severely disturbed gaps is generally greater. This means that apart from some surviving AR, pioneer species will be favoured in particular in the bare mineral soil areas, where they germinate from either the seed bank or seed immigration. Thus, the tendency for higher diversity in more severely disturbed gaps becomes more understandable (Fig. A4.3 & Fig. A4.4 in APPENDIX 4). These differences between lightly and severely disturbed gaps disappeared, however, during the drought year (1994-1995). Although in CHAPTER 4 it was established that during the drought mortality was not necessarily higher in more severely disturbed gaps (Table 4.7a), mortality may have selectively weeded out the new species and thus reduced diversity in these types of gaps.

Gap size as one of the physical characteristics was thus shown to have no effect on diversity (species richness and evenness). However, the severity of disturbance was shown to have some positive relationship with diversity in the gap environment (given that the disturbance is not so severe as to wipe out all AR). However, it seems that this is only the case under mesic conditions and not during the extremes of a drought.

5.6 Conclusion

For the meso-scale this chapter has presented evidence of suppressed diversity on Panjang and Sertung. This evidence is in agreement with suggestions made by Whittaker and colleagues who have emphasised a volcanic disturbance related set-back in succession based on plot-scale and whole island studies. However, whereas Panjang's woody species richness on the meso-scale is very similar to that of Sertung, its forest composition, particularly with respect to the canopy, is much more heterogeneous than that of Sertung, but still less so than on Rakata.

The meso-scale study also emphasised the imminent decline of the current canopy dominants *Neonauclea calycina* and *Timonius compressicaulis*, due to the nearly complete absence of regeneration. However, in contrast, *Dysoxylum gaudichaudianum* is extremely likely to further expand its importance, not only on Sertung and Panjang, but also in lowland Rakata. The difference on Rakata is, however, that it is likely to face greater competition with a higher number of potential canopy species in the struggle for a place in

the canopy. Thus, no general convergence of forest types between islands is suggested, but great similarity may exist between small areas of forest on all islands.

The patch-scale analyses suggest that a gap creating event only has a significant effect on the species composition if the disturbance was extremely severe and/or repeat disturbance to the same plot has taken place. Then AR does not play an important role, and the gap-fill is likely to differ from the surrounding forest type, as it will mainly consist of light demanding pioneer species recruited from either seed immigration or the seed bank (see CHAPTER 6). The number of species regenerating in the gap are then also likely to be lower. It was also established that there were great difference in the degree of compositional changes in the small sapling layer between different gap sites, but with no detectable trend related to the physical characteristics of the gap. The extreme event of the 1994 drought was identified as being one of the most dramatic influences on not only population turnover as reported in CHAPTER 4, but also compositional turnover during the study period. Its effect was neither uniform within nor between islands, but in the areas affected it led to significant compositional turnover in both the gap and the understorey plots. Thus, it increased the heterogeneity of the regeneration layer with potential lasting effects on the future canopy composition. It was, however, surprising that the drought, in conjunction with ash-fall, did not seem to have a very drastic effect on the short-term dynamics of Panjang plots. Sertung plots appeared to have been much more dynamic and affected.

CHAPTER 6:

SEED BANK CHARACTERISTICS ON THE KRAKATAU ISLANDS

"The composition of viable seeds in soils beneath a plant community is one indicator of the regrowth potential of that community." (Hopkins & Graham, 1983; p. 90)

Summary

1. This study examines the species composition of Krakatau top-soil seed banks and how it varies with respect to habitat type (gap or understorey), gap size and severity of disturbance, island, and local forest type. Density and species composition of the seed bank also provide autoecological information.
2. From 15 gap sites, 32 top-soil samples from gap and adjacent understorey sites were used for germination trials in 1993. They yielded 55 species of spermatophytes and 3 pteridophytes with a total of 3732 seedlings and 8 ferns respectively. The two most abundant seed bank components were the two pioneer species *Pipturus argenteus*, and *Leucosyke capitellata*, with 859 and 849 seedlings respectively. 59% of species had <10, and 26% had only one individual germinating from all samples.
3. Seed densities ranged from 144 to 5744 seeds per m². No significant differences between gap and understorey seed densities were found, which might be due to depletion of the gap seed bank and/or addition to it from seed rain in gaps of slightly different ages. Panjang had significantly lower top-soil seed bank densities, which may be attributable to considerable quantities of seasonal ash deposition prior to sampling.
4. After the 1994 drought, *Macaranga tanarius*, a common pioneer on the islands, invaded large areas of South-east Rakata, and *Timonius compressicaulis* forest areas of Sertung. However, it had very poor representation in the 1993 seed bank samples (0.3% of all seeds). It is suggested that *Macaranga tanarius* has a very transient seed bank and that regeneration is mostly from abundant seed rain.

5. In a previous study, undertaken in 1992, *Neonauclea calycina*, the long-lived pioneer tree species, and canopy dominant on Rakata, was absent in all 13 top-soil samples (Whittaker *et al.*, 1995). In the 1993 seed bank samples of this study, it was relatively common, although it occurred in a highly patchy distribution.

6. *Ficus* species were well represented with 11 of 25 currently known *Ficus* species in the seed bank, and contributed four of only five large canopy species found in the seed bank (*F. pubinervis*, *F. variegata*, *F. sumatrana*, and *F. tinctoria*). The small seed sizes (1-2 mm) of *Ficus* species seem to be particularly suited for seed bank storage, and asynchronous fruiting provides seed input throughout the year albeit with high spatial variability.

7. Cluster analysis of percentage similarity measures between seed bank samples from gap and understorey plots showed a clear separation into three main clusters: samples characterised respectively by *Leucosyke capitellata*, *Neonauclea calycina*, and *Pipturus argenteus* seedlings. Paired gap and understorey seed bank composition was generally quite similar, and the surrounding forest type appeared the most significant factor influencing seed bank composition.

8. Seed bank presence seemed to be closely related to seed size: (i) only very small seeded (<3 mm) species were present; (ii) slightly larger sized seeds were rare in all seed bank samples even if common in the tree and shrub layer (e.g. *Antidesma montanum*, *Leea sambucina*); (iii) large-sized seeds were completely absent. It is suggested that species in the category (ii) and (iii) predominantly rely on direct regeneration after dispersal. For the more shade-tolerant species this means the formation of a seedling bank (advance regeneration).

6.1 Introduction

The primary succession on the Krakatau islands (6°06' S, 105°25' E) has become a famous case-study with one of the longest data series of primary succession in the tropics (Richards, 1996). However, data on the process of turnover and species replacement within the forests are still very scarce. An attempt was made in CHAPTER 4 to elucidate some aspects of the short-term performance of saplings in gaps and understorey plots, and CHAPTER 5, apart from clarifying meso-scale patterns, established spatial and short-term trends in species composition at the patch-scale. The purpose of the present chapter is to document the species composition and density of seeds in the seed bank in the 1993 dry season, and from that to draw some conclusions with respect to the importance of gap size and severity of disturbance, island context and the local forest type in influencing these characteristics.

Opinions regarding the relative importance of seed bank regeneration to secondary succession in tropical forests vary widely (Garwood, 1989; Mitchell, 1994). For instance, it has been argued that the initial stages of secondary succession (e.g. the process of gap-fill) are already imprinted on a forest because of the soil seed bank (Guevara & Gomez-Pompa, 1972), whereas Whitmore (1983) stressed more the importance of the timing and composition of the pioneer seed rain. He argues that this is the reason for the largely uniform composition of pioneers within, but not between gaps created at different times of the year. Evidence supporting both of these positions exist, and they are not necessarily mutually exclusive. One may, for instance, interpret the conceptual framework of Bazzaz (1984) as an attempt at reconciliation of the two positions. He suggests that the relative contribution of regeneration pathways to gap-fill depends on the gap size and severity of disturbance, whereby with increasing size and severity the pathways range from branch-ingrowth, advance regeneration (AR), sprouting, to germination from the seed bank and immigration from seed rain (Fig. 1.2).

Of course, many other factors can influence future gap-fill by affecting colonisation, and growth and mortality of regeneration (e.g. dispersal, chance, site history, competition, microclimate), and Bazzaz's model makes no statement about the frequency of disturbance encountered by a particular forest. However, frequency of disturbance has been identified as being positively correlated to soil seed density, as long as the gaps created are large enough to allow pioneer regeneration (Saulei & Swaine, 1988).

The main aim of the study is to quantify the spatial variation in species composition and density of the seed bank with respect to habitat type, island, and/or forest type, as well as assessing if seed bank densities bear any relation to the frequency of disturbance (e.g. Sertung and Panjang; see CHAPTER 3 & 5; Whittaker *et al.*, 1989; Bush *et al.*, 1992). The seed bank results are also discussed in the light of a recent seed bank pilot study by Whittaker *et al.* (1995), and some comparisons to other soil seed bank studies in the tropics are made. Information on seed bank presence or absence, as well as data on species' seed densities provides additional information on the little known autoecology of Krakatau's species.

This study was carried out in close collaboration with Dr T. Partomihardjo who helped with the identification and enumeration of seedlings germinated from the seed bank. He presented some aspects of the seed bank data in his doctoral thesis (Partomihardjo, 1995), but this study analysed the data independently and asked somewhat different questions.

6.2 Objectives

The specific objectives of CHAPTER 6 are:

- (i) to quantify the density and composition of seeds in the top-soil seed bank on the Krakatau islands, and compare them to the pilot study of Whittaker *et al.* (1995) and other studies in tropical rain forest;
- (ii) and more specifically to investigate if significant spatial variation exists, e.g. between different habitat types (gap and understorey), between islands, and/or forest types;
- (iii) and to improve the autoecological knowledge of some Krakatau species.

6.3 Methods

Sampling was undertaken in 1993 on all three islands, in 15 gap sites of varying degrees of disturbance and size. Ideally, for the estimation of seed density and composition, sampling should be repeated to account for seasonal variation (Thompson, 1992). However, time constraints and the unavailability of suitable greenhouse space made a repeat sampling in 1994 impossible. Moreover, fieldwork was only possible in the dry season so that seasonal variation in the seed bank could not have been detected in any case.

Spatial variation in seed bank composition is also potentially high (Thompson, 1992; Warr *et al.*, 1993), but again time constraints and space constraints in the germination site only allowed one top-soil sample to be taken next to the pair of gap and understorey 4 x 4 m plots. As already described in CHAPTER 4, in these plots small saplings (>50 cm) were enumerated, and additionally for the seed bank study seedlings were recorded (<50 cm height) in five 1 x 1 m sub-plots. The sampled area in each case was 25 x 25 cm and soil was taken down to 5 cm depth. Samples varied in volume due to variable soil texture, and ash- and pumice content in different sites. Gap sites R2 and R11 had two 4 x 4 m gap plots, and extra seed bank samples were therefore collected to check for heterogeneity of seed banks associated with different gap zones. In R2 gap these samples were taken from the area affected by lightning, the bole zone of the treefalls, and additionally from a small area of landslide, and a root zone (the latter two not associated with a 4 x 4 m plot). In gap R11 samples were taken adjacent to the 4 x 4 m plot located mostly in the root zone of the treefall, whereas the second sample was taken from the crown zone. R2 is the only gap site that had no understorey sample collected.

Soil samples of four sites were collected between 12/6/1993 and 1/7/1993, and between 24/7/1993 and 20/8/1993. The widely used technique of enumerating the soil seed bank by germination was employed (Hopkins & Graham, 1983; Saulei & Swaine, 1988; Whittaker *et al.*, 1995), despite the fact that the relationship between seedling emergence and the actual composition of the seed bank is poorly known. The alternative technique, of seed extraction, generally also leads to biased estimates (Warr *et al.*, 1993). Foreseeable greater problems of seed rather than seedling identification, and the difficulty of checking for viability led to the rejection of this technique.

Until sowing took place, all samples were stored in plastic bags in the dark. The first batch was sown in plastic trays on 3/7/1993, the second on 26/8/1993. The soil was spread (approx. 2 cm deep) on sterilised sand, to ensure good drainage, and for the germination trials the seed-trays were placed in an enclosure on the roof-top of the Herbarium Bogoriense, Bogor (Fig. 6.1). Splash-damage from rainfall was prevented by a clear plastic roof, and to avoid contamination the sides of the enclosure were screened with nylon netting of a 2 x 2 mm mesh size. Furthermore, to ensure that no contamination had occurred, seedtrays with sterilised soil were placed between the planted samples. Until approximately 3 pm the enclosure was in full sun, but the plastic roofing and screen is likely to have affected the red/far red ratio which can be important in influencing germination of seeds (Vasquez-Yanes & Orozco-Segovia, 1993; Vazques-Yanes & Orozco-Segovia, 1994).



Fig. 6.1: Seed bank germination experiment. Note the largest seedlings are *Pipturus argenteus*, and the empty trays are control trays filled with a sterilised soil mixture.

Unfortunately no equipment to quantify the potential change in light quality was available. Hopkins & Graham (1983) found that a similar enclosure led to about 30% shade. Seedtrays were watered every second day, or daily during sunny weather, and were moved around regularly to ensure that the same light and temperature conditions were experienced by all samples.

All germinating seedlings were marked with toothpicks, with different colour-codes for each week (cf. Mitchell, 1994), and first identified and counted between 5/10 -10/10/1993. Final enumeration took place between 14/1/ -17/1/1994. The first count was conducted by myself, and Dr T. Partomihardjo helped with the identification of seedlings, and together with Cecilia Luttrell, carried out the last count of seedlings after my return to the UK.

An overall description of the seed bank composition, and seed bank size (density per m²) will be given in the results section. Particular attention will be paid to inter-island differences, and potential differences between seed bank samples from gap plots versus those from the understorey. Cluster analysis using percentage similarity was performed (Kovach, 1993; see section 5.3 for justification of using percentage similarity index) as one way to detect the degree of overall compositional similarity between the species composition of gap and understorey seed bank samples, and samples of different sites in general. To quantify the compositional similarity between the sapling layer in 4 x 4 m plots and the respective seed bank samples, Sorensen similarity index scores were calculated as an alternative similarity measure that allowed the comparison of a large number of seed bank seedlings with a small number of seedlings and saplings in the gap and understorey plots (Magurran, 1988). The following formula was used:

$$C_s = 2j/(a+b)$$

where j = the number of species found in both sites; a = number of species in site A (e.g. gap plot saplings); b = number of species in site B (e.g. the seed bank sample)

The index scores were calculated for each site for: (i) paired seed bank gap and understorey samples; (ii) all gap seed bank samples and their respective sapling plots, and; (iii) all gap seed bank samples and their respective seedling plots. It was then tested if gap and understorey seed bank sample pairs were more similar in species composition to each other than to the extant regeneration layer in the sapling and seedling plots in gaps. Furthermore, if Bazzaz's model (1984; Fig. 1.2) is applicable one would expect that the similarity between the gap regeneration layer and the gap seed bank composition should

increase with increasing gap size and severity of disturbance, with the exception of disturbances that involve removal of top-soil (e.g. landslide sites). Therefore, it was tested whether the sapling compositions of small, and lightly disturbed gaps were less similar to their seed bank composition than those of large, and more severely disturbed gaps (see Table 4.1 for size- and severity classifications).

Although only one sample was taken from each gap and adjacent understorey pairing, a comparison of similarities between the seed bank composition and the seedling and sapling species composition of the 4 x 4 m monitoring plots may be justified since possible spatial variation (Warr *et al.*, 1993) should be minimal due to the immediate proximity of soil sampling to the plots. Unidentified, herbaceous and climbing species were not included in the Sorensen indices and cluster analysis.

On a more general level, the species composition and seed densities of top-soil samples of this study are compared to those of the top-soil samples of Whittaker *et al.*, (1995), and other seed bank studies in tropical forest. Whittaker *et al.* (1995) also sampled buried soils, and soil from crab burrow samples but the result from these samples are not directly considered here.

6.4 Results

Seed bank densities

Across all samples, seed density estimates varied from 144 to 5744 seeds per m² (Table 6.1; mean = 1863 per m²), whereby the former was a soil sample from a fresh landslide surface on Panjang and the latter was from a very large lightning/treefall gap site at 500 m a.s.l. on Rakata (R2). No significant difference in the number of seedlings germinating from gap *versus* understorey samples was detected, when assessed separately for all islands (including unidentified individuals: Rakata $p=0.101$; Panjang $p=0.32$; Sertung $p=0.45$, for one-tailed Mann-Whitney-U-tests; Table 6.1). This also holds when all samples from all 15 gap sites were combined. Furthermore, the number of species found in gap and understorey samples was identical except for Sertung, where the understorey samples had one more species (Table 6.1). However, as a considerable number of individuals could not be identified it is possible that a study of greater length might have revealed some differences.

Table 6.1: Comparison of (a) number of seedlings, and (b) number of species germinating from the seed bank samples of gap and understorey plots on Rakata (n = 7), Panjang (n = 5), and Sertung (n = 2).

<i>a) No. individuals</i>	<i>Rakata</i>	<i>Panjang</i>	<i>Sertung</i>	<i>total</i>
gap	779	313	288	1380
understorey	950	310	268	1528
gap, unidentified	91	30	33	154
US, unidentified	54	97	33	184
Total	1874	750	622	3246
b) Species number				
gap	36	17	15	
understorey	36	17	16	
Total	47	25	21	

Note: R2 gap samples (R2TF, R2LNG, R2LS) were excluded as no understorey sample for comparison could be taken; R11 crown zone sample, as the second gap sample for this site, was also excluded.

Table 6.2: Seed densities for all gap and understorey seed bank samples.

<i>gap site</i>	<i>gap density seed/m²</i>	<i>understorey density seeds/ m²</i>
R1	1088	1088
R2LNG	5744	-
R2LS	3952	-
R2TF	2272	
R5	2000	4960
R9	2400	1296
R10	1264	1088
R11root	2016	880
R11crown	1168	880
R12	944	1104
R15	2752	4784
P4	2992	1296
P6	960	1104
P7	144	704
P8	576	171
P13	326	1648
S3	1344	864
S14	3264	3424

note: for R2LNG, R2LS, and R2TF no understorey sample; for R11root and R11crown only one understorey sample was collected.

Overall, Panjang samples (gap and understorey; $n=10$) had significantly lower seedling densities than Sertung ($n=4$; $p<0.05$) and Rakata ($n=18$; $p<0.01$) samples, whereas Sertung densities showed no significant difference to those of Rakata. For the Panjang result no obvious reason could immediately be detected (see Table 6.2 for list of seed densities).

A significant correlation was found between gap size measured in the form of percentage canopy openness (1993 semi-fisheye lens values) and gap sample seed density ($r=0.51$; $n=18$; $p<0.05$ for one-tailed Spearman's rank correlation). With the exclusion of the additional, high density, gap samples in R2 (R2LNG, R2LS) and the crown sample in R11 (R11crown; Table 6.2) the correlation was non-significant ($r=0.27$; $n=15$). Similarly, a significant difference ($p<0.05$; one-tailed Mann-Whitney-U test) between seed bank densities was found when comparing samples divided by arbitrary gap size classes (size 1+2 and size 3+4), but with the exclusion of the additional gap samples in R2 and R11 the difference was only significant at the 90% level ($p = 0.07$). With or without inclusion of these extra gap samples, no significant difference was found between the seed bank densities of severely- *versus* light- to medium-disturbed gaps. Severely disturbed gaps had, however, the greatest density range, including P7G landslide site which must have lost most of its existing seed bank (144 seeds per m^2), and the lightning site R2LNG with 5744 seeds per m^2 .

Seed bank species composition

In total 55 species of spermatophytes and 3 pteridophytes germinated from the 32 top-soil samples (18 Rakata, 10 Panjang, 4 Sertung; Table 6.3). The number of individuals were 3732 and 8 respectively. This compares to 34 spermatophytes and 2 pteridophytes from 13 top-soil samples from Whittaker *et al.*'s (1995) study, which yielded 664 seedlings and 87 ferns. The average seedling density per sample of this study (116) was more than twice as high as in the study of Whittaker and colleagues (51), despite comparable time of sampling, and sampling and germination procedures. However, slight differences in the volume of soil taken and the germination set-up between the two studies cannot be completely discounted as an explanation for this. For instance, the large number of ferns in Whittaker *et al.*'s study may partly be accounted for by contamination. In this study the 55

Table 6.3: Summary table of the 1993 Krakatau seed bank experiment: total number of samples N=32; R=18; P=10, S=4; H=herb; S=shrub; ST=small tree; T=tree; LT=large tree; F=fern, hC=herbaceous climber; C=climber (woody); (n) denotes species found in n samples. For some species seed sizes were available (data from Whittaker et al. 1995; Partomihardjo, 1995; pers.obs.). For authorities see Whittaker *et al.* (1989) and Backer and Bakhuizen Vol I-III (1963-1968).

	life-form	seed size ln mm	family	Island	R (n=18)	P (n=10)	S (n=4)	total (total no. samples)
<i>Ageratum conyzoides</i>	H	0.5	Compositae	R,S	1(1)			1 (1)
<i>Antidesma montanum</i>	ST	3-5	Euphorbiaceae	P		1 (1)		1 (1)
<i>Antigonon leptopus</i>	hC		Polygonaceae	R	2(2)			2(2)
<i>Arthrophyllum javanicum</i>	ST	1-2	Araliaceae	R,P	7(5)	1(1)		8 (6)
<i>Breynia cernua</i>	S		Euphorbiaceae	R	5 (2)			5 (2)
<i>Bridelia monoica</i>	ST	5	Euphorbiaceae	S			1(1)	1 (1)
<i>Capsicum frutescens</i>	H		Solanaceae	R	1 (1)			1 (1)
<i>Casuarina equisetifolia</i>	LT		Casuarinaceae	R	14 (3)			14 (3)
<i>Cayratia trifolia</i>	C		Vitaceae	R	3(2)			3(2)
<i>Clidemia hirta</i>	S	1	Melastomataceae	R	30 (6)			30(6)
<i>Cyclea barbata</i>	hC		Menispermaceae	R,S	4 (2)		2 (1)	6 (3)
<i>Cyrtandra sulcata</i>	S	1	Gesneriaceae	R	8 (1)			8 (1)
<i>Digitaria rhopalotricha</i>	H		Gramineae	R	1 (1)			1 (1)
<i>Dioscorea bulbifera</i>	C		Dioscoreaceae	R	4 (3)			4 (3)
<i>Eleusine indica</i>	H		Gramineae	P		1 (1)		1 (1)
<i>Ficus ampelas</i>	ST	1-2	Moraceae	R,S	11(7)		2 (2)	13 (9)
<i>F. fistulosa</i>	ST	1-2	Moraceae	R,S,P	12 (6)	2 (2)	2 (1)	16 (9)
<i>F. fulva</i>	ST	1-2	Moraceae	S,P		2 (1)	1 (1)	3 (2)
<i>F. hispida</i>	ST	1-2	Moraceae	R,S,P	13 (4)	1 (1)	6 (2)	20 (7)
<i>F. lepicaarpa</i>	ST	1-2	Moraceae	R	4 (3)			4 (3)
<i>F. pubinervis</i>	LT	1-2	Moraceae	R	31(9)			31 (9)
<i>F. ribes</i>	ST	1-2	Moraceae	R,P	26 (12)	1 (1)		27 (13)
<i>F. septica</i>	ST	1-2	Moraceae	R,S,P	10 (5)	15 (6)	19 (4)	44 (15)
<i>F. sumatrana</i>	LT	1-2	Moraceae	R,P	2 (1)	2 (2)		4 (3)
<i>F. tinctoria</i>	LT	1-2	Moraceae	P	0	1 (1)		1 (1)
<i>F. variegata</i>	LT	1-2	Moraceae	R,S,P	10 (3)	14 (2)	6 (2)	30 (7)
<i>Gnaphalium purpureum</i>	H		Compositae	R	1 (1)			1 (1)
<i>Hedyotis corimbosa*</i>	H		Rubiaceae	S,P		8 (1)	1 (1)	9 (2)
<i>Leea sambucina</i>	S	4-5	Leeaceae	R	5 (4)			5 (4)
<i>Leucosyke capitellata</i>	S	0.5-1	Urticaceae	R,S,P	697 (15)	80 (7)	72 (3)	849 (25)
<i>Macaranga tanarius</i>	ST	4-5	Euphorbiaceae	R,S	8 (5)		2 (2)	10 (7)
<i>Medinella exima**</i>	S		Melastomataceae	S,P			3 (1)	3 (1)
<i>Melastoma affine</i>	S	0.5-1	Melastomataceae	S	1 (1)	1 (1)	22 (1)	24 (3)
<i>Melochia umbellata</i>	ST		Sterculiaceae	R	1 (1)			1 (1)
<i>Mikania cordata</i>	hC		Compositae	R,S,P	38 (5)	2 (1)	95 (4)	135 (10)
<i>Neonauclea calycina</i>	T	0.5-1	Rubiaceae	R,S,P	154 (12)	33 (6)	2 (1)	189 (19)
<i>Nephrolepis biserrata</i>	F		Oleandraceae	S			2 (1)	2 (1)
<i>Nervillia aragoana</i>	H	<0.5	Orchidaceae	R	1 (1)			1 (1)
<i>Omalanthus populneus</i>	ST		Euphorbiaceae	R	1 (1)			1 (1)
<i>Opismenus compositus</i>	H		Gramineae	R	1 (1)			1 (1)
<i>Peperomia pelusida***</i>	H		Peperomiaceae	R	39 (1)			39 (1)
<i>Piper aduncum</i>	S?	2	Piperaceae	R,S,P	246 (11)	6 (3)	70 (4)	322 (18)
<i>Pipturus argenteus</i>	ST	0.5	Urticaceae	R,S,P	416 (18)	288 (8)	155 (4)	859 (30)
<i>Pityrogramma calomelanos</i>	F		Pteridaceae	P		10 (1)		10 (1)
<i>Pogonatherum paniceum</i>	H		Gramineae	R	2 (2)			2 (2)
<i>Pollia secundiflora</i>	H		Commelinaceae	R	17 (3)			17 (3)
<i>Polycias nodosa</i>	T		Araliaceae	R	1 (1)			1 (1)
<i>Radermachera glandulosa</i>	T	0.5	Blignoniaceae	R	230 (13)			230 (13)
<i>Sauraula nudiflora</i>	ST	0.5-1	Sauraulaceae	R	15 (2)			15 (2)
<i>Selaginella plana</i>	F		Selaginellaceae	R	4 (1)			4 (1)
<i>Tarenna dasyphylla</i>	ST		Rubiaceae	R,S,P	15 (7)	1 (1)	1 (1)	17 (9)
<i>Tarenna fragrans</i>	ST		Rubaceae	P		2 (1)		2 (1)
<i>Tetragstigma lanceolarium</i>	C		Vitaceae	R	1 (1)			1 (1)
<i>Timonius compressicaulis</i>	T	1 x 3	Rubiaceae	R,S,P	5 (4)	16 (6)	7 (2)	28 (12)
<i>Trema orientalis</i>	T	1-2	Ulmaceae	R,P	1 (1)	2 (1)		3 (2)
<i>Tylophora asthmatica</i>	hC		Asclepiadaceae	R	3 (1)			3 (1)
<i>Villebrunea rubescens</i>	ST	0.5-1	Urticaceae	R,S,P	238 (13)	5 (2)	18 (2)	261 (17)
<i>Widelia bliflora</i>	H		Compositae	P		1 (1)		1 (1)
unidentified					221 (14)	127 (7)	66 (3)	414 (24)
total					2561	623	556	3740

note: * possible contaminant; ** previously only recorded from Rakata; *** not previously recorded on Krakatau

spermatophyte species included 17 herbs, 1 woody liana, 1 orchid, 8 shrubs, and 28 trees. This compares to a Krakatau total of 313 spermatophytes, of which 99 are tree species, and 88 pteridophytes (Partomihardjo, 1995). As in other seed bank studies in tropical rain forest (Garwood, 1989; Thompson, 1992) trees and shrubs are the largest component in the number of species and individuals germinating in this study. However, only five of the tree species are large canopy species. They are *Ficus pubinervis* (31 seedlings all from Rakata), *F. variegata* (30; 16 on Rakata; 14 on Panjang; 0 on Sertung) which were also found in Whittaker *et al.*'s (1995) study, and *F. sumatrana* (4; 2 Rakata; 2 Panjang; 0 Sertung), and *F. tinctoria* (1 Panjang), with the latter two having a strangling habit (Backer & Bakhuizen van den Brink, 1963-68). The only other potential large canopy species is the very early pioneer tree *Casuarina equisetifolia* (14 Rakata) of which some very large individuals of up to 35 m can still be found in the flat, near-coastal area of South-east Rakata. Indeed, the seedlings of this species only germinated from two samples from this particular area. *Casuarina* was also recorded in seed trap samples from the South-east coast area in 1993 and again in 1994 (total of 50 seedlings germinated).

Considering the results by island: Rakata top-soils yielded 47 species of spermatophytes and 1 fern from 19 samples; 25 species of spermatophytes and 1 fern species germinated from 10 Panjang samples, and; 21 species of spermatophyte and 1 fern species germinated from 4 Sertung samples (Table 6.3).

For all samples combined, the six most abundant woody species were: *Pipturus argenteus* (859), *Leucosyke capitellata* (849), *Piper aduncum* (322), *Villebrunea rubescens* (261), *Radermachera glandulosa* (230), and *Neonauclea calycina* (189). All of them can be classified as pioneers (see Table 6.3 for life-form).

Rakata had the highest number of herbaceous species (12 of 16, including herbaceous climbers), of which 11 were exclusive to that island. Unfortunately, a relatively high number of 414 seedlings, including some dead individuals, remained unidentified at the end of the experiment. Removal and planting of unidentified seedlings in separate pots would have helped to lower the number of unidentified seedlings, but could not be carried out due to time and space constraints. 34 out of a total of 58 species (59%) had less than 10 seedlings for all samples, and 15 species (26%) were only represented by one individual. These figures demonstrate that the seed bank is characterised by only one or a few common, small seeded pioneers, which coincides with Whittaker *et al.*'s (1995), and other findings in tropical seed bank studies (Garwood, 1989). Furthermore, the two most

common species in the top-soil samples of Whittaker *et al.* (1995) were also *Pipturus* and *Leucosyke*. However, *Macaranga tanarius*, the other very typical pioneer found regenerating in gaps on Krakatau, was barely represented in the seed bank of this (0.3% of all seedlings) and Whittaker *et al.*'s (1995) study (0.15% of all seedlings). In the latter case only one individual germinated from 13 top-soil samples on Rakata, and two individuals germinated from the >60 years old buried soil layer from Panjang.

An island comparison identifies *Leucosyke capitellata* (697), *Pipturus argenteus* (416), *Piper aduncum* (246), *Villebrunea rubescens* (238), *Radermachera glandulosa* (230), and *Neonauclea calycina* (154) as the six most abundant woody species for Rakata (total of 1981 identified seedlings). The six most abundant woody species for Panjang, of a total of 623 identified seedlings, were *Pipturus argenteus* (288), *Leucosyke capitellata* (80), *Neonauclea calycina* (33), *Timonius compressicaulis* (16), *Ficus septica* (14), and *Ficus variegata* (14), revealing a heavy dominance of *Pipturus argenteus*. Also on Sertung (total of 556 identified seedlings) *Pipturus argenteus* (155) is the most numerous followed by *Leucosyke capitellata* (72), *Piper aduncum* (70), *Melastoma affine* (22), *Ficus septica* (19), and *Villebrunea rubescens* (18).

Seed bank similarity

The dendrogram produced by the cluster analysis of percentage similarity values for all gap and understorey seed bank samples showed three major clusters of sites (Fig. 6.2) of greater than 50% similarity. Each of these is characterised respectively by substantial numbers of seedlings of the tree species *Neonauclea calycina*, *Pipturus argenteus*, and *Leucosyke capitellata*. The *Neonauclea* group shows high similarity (57 and 60.7%) between the gap plots of two Panjang sites (P6G and P8G), and a gap and understorey pair of samples from a lowland Rakata site (R1G and R1U). All sites of this cluster have *Neonauclea* as a significant component in the canopy. The *Pipturus argenteus* cluster predominantly consists of Panjang and Sertung samples, and Rakata samples from the South-east coast; the latter area has substantial amounts of *Pipturus* in the canopy. A characteristic of this group is the general *Dysoxylum gaudichaudianum* dominance in the canopy, except for S14G, a gap sample from an area of *Timonius* forest on Sertung. The whole of the *Leucosyke capitellata* group is made up of Rakata samples, again with the

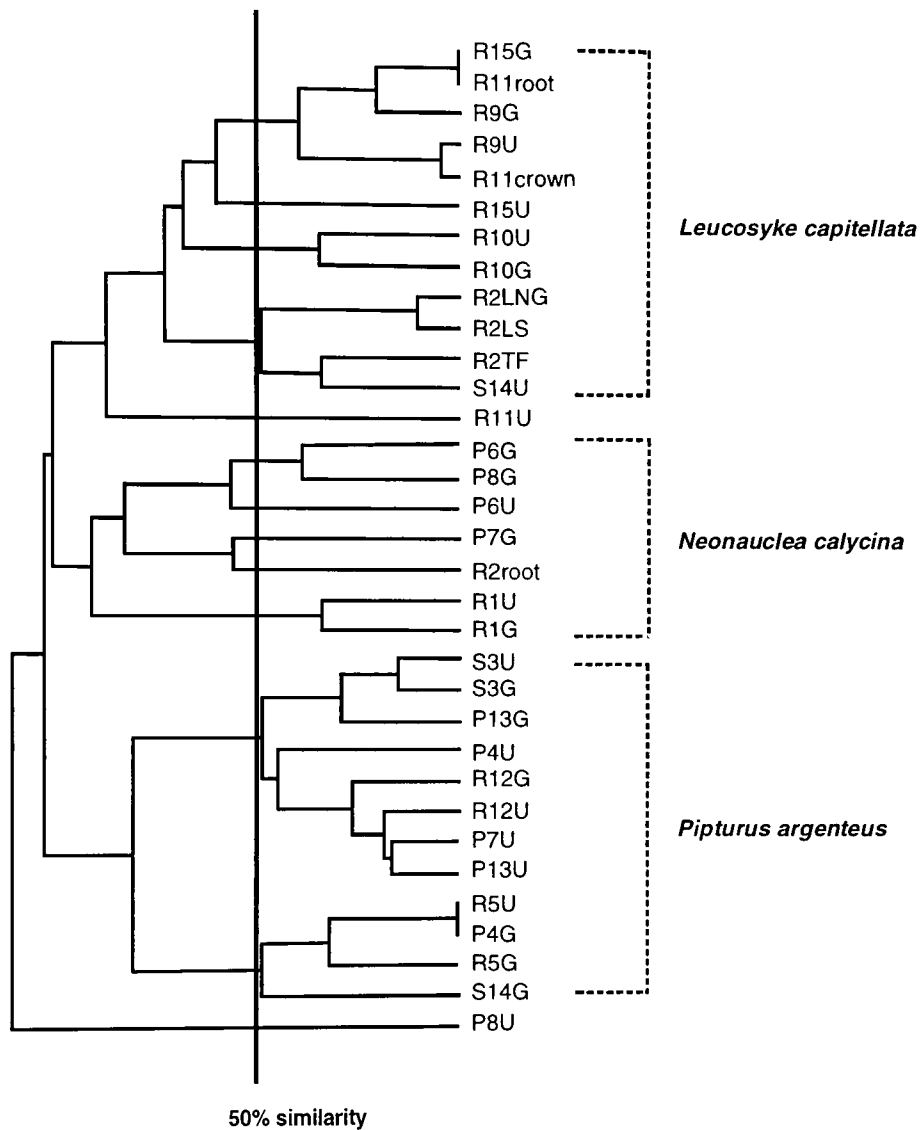


Fig. 6.2: Dendrogram of the cluster analysis of percentage similarity of all gap and understorey seed bank samples. Particular attention is drawn to the samples of >50% similarity. Their seed bank composition is in general associated with the pioneer shrub species *Leucosyke capitellata* (Lc), the long-lived pioneer tree *Neonauclea calycina* (Nc), or the small pioneer tree *Pipturus argenteus* (Pag). The Lc dominated samples are from inland and high-altitude Rakata plots, which are rich in Nc as a canopy species, and have Lc scattered in the understorey (except S14U in *Timonius compressicaulis* (Tcl) forest on Sertung). The Nc rich samples have Nc in the canopy as a co-dominant (e.g. the Panjang samples from the Tcl/Nc forest areas). The Pag rich seed bank samples are generally from forest dominated by *Dysoxylum gaudichaudianum* (except S14G which is dominated by Tcl).

exception of one Sertung sample (S14U). It can be further subdivided in groups of co-dominance with other pioneers such as *Piper aduncum*, and *Radermachera glandulosa*. In particular, the high altitude area (R2 gap site) was noted for having a considerable *Piper* component. The *Radermachera* sub-cluster consists of inland Rakata plots, with this species locally abundant (e.g. R15G, R11root, R9G, R9U, R11crown, R15U). However, that significant local variability in the seed bank composition between gap and understorey occurred for some sites is demonstrated by several sample pairs which were placed into very different groups (e.g. P7, S14, R2root) or by one of the pair being very dissimilar even from other samples (P8U, R11U; Fig. 6.2).

Similarities between: (i) the composition of seed bank gap and understorey pairs of samples and; (ii) the composition of gap seed bank samples and gap sapling and seedling plots, were examined with the help of the Sorensen index (Table 6.4). The indices calculated for (i) and (ii) were compared and tested for significant differences by applying a one-tailed t-test. These analyses established that, as is to be expected given the difference in life-cycle stage under study, seed bank samples are highly significantly more similar to each other than the gap seed bank composition is to the gap sapling and seedling composition ($p=0.0001$ for saplings; $p=0.0009$ for seedlings).

Table 6.4: Sorensen index comparison for seed bank gap and understorey samples, seed bank and gap sapling/seedling similarity.

Gap code	G & U seed bank similarity	G seed bank and gap regeneration similarity	
		saplings	seedlings
R1	0.57	0.32	
R2TF	-	0.46	0.59
R5	0.25	0.18	
R9	0.63	0.4	0
R10	0.6	0.29	-
R11root	0.29	0	0.12
R11crown	0.32	-	-
R12	0.4	0.15	0.21
R15	0.75	0	0
P4	0.67	0.24	
P6	0.53	0	0.13
P7	0	0	0
P8	0.62	0	0
P13	0.29	0.18	0.36
S3	0.53	0.29	0.33
S14	0.48	0.14	0

Note: R2 has no understorey seed bank sample, and only R2TF sample could be compared to the sapling and seedling layer of the equivalent 4 x 4 m plot; R1, R5, R10, R12, and P4 have no seedling plots; in R11crown no regeneration was found;

Some support for the Bazzaz model was found when Sorensen similarity values between gap seed bank and gap sapling composition of small *versus* large and lightly *versus* severely disturbed gaps were compared. The results showed that the gap regeneration layer of small gaps was significantly less similar to the gap seed bank composition than that of large gaps ($p < 0.05$ for saplings but only $p = 0.091$ for seedlings; one-tailed t-test), and that there was a tendency towards the less severely disturbed gap sites showing less similarity of gap saplings to the gap seed bank composition. However, in the latter case the results were not significant. This may partly be due to the fact that the very severely disturbed and very young landslide gap P7, which will have lost most of its seed bank through erosion and burial, was included.

6.5 Discussion

Seed density estimates

It appears that Krakatau top-soils, with 144-5744 seedlings per m^2 , and a mean number of 1863 seedlings per m^2 (including herbaceous species) have a large range of different seed densities, and a relatively high mean seed density in comparison to other 'mature' tropical forests (Garwood, 1989; Table 6.5). High variability in seed density in different tropical forest types and in different continents (Thompson, 1992) was shown to be related to magnitude and frequency of canopy disturbance (Vazques-Yanes & Orozco-Segovia, 1994), and characteristically undisturbed tropical forests have lower seed densities than frequently disturbed forests (Putz & Appanah, 1987; Young *et al.*, 1987; Saulei & Swaine, 1988). For instance, Chandrashekara & Ramakrishnan (1993) reported seed densities from 55-243 seeds per m^2 in undisturbed forests in the western Ghats, India, whereas in Papua New Guinea Saulei and Swaine (1988) found seed densities of up to 9230 seeds per m^2 (largely herbaceous species) for a cleared area after 17 month of regeneration, with initial heavy depletion of the seed bank immediately after logging. Therefore, in the Krakatau context, high spatial variability, and a relatively high mean value for seed densities might be due to the fact that sampling took place in very contrasting sites, varying from relatively undisturbed to heavily disturbed sites (e.g. from the understorey to large gaps and landslides), from both low and higher altitudes, as well as from different forest types, in what are still early successional forests. Timing of sampling is, of course, also crucial. On

Table 6.5: Comparison of seed densities, and species richness of seed banks of a selection of published studies (adapted from Garwood, 1989), with the results of this study. All studies sampled the top 5 cm of soil.

<i>location</i>	<i>vegetation type</i>	<i>altitude (in m)</i>	<i>edge'</i>	<i>mean seed density per m²</i>	<i>CV^b</i>	<i>N^c</i>	<i>no of species^d (total area sampled in cm²)</i>	<i>Reference</i>
Krakatau (Indonesia)	Early successional forest	10-500		1863	77	32	58 (20 000)	own data
Krakatau (Indonesia)	"	"	G & U-					
Krakatau (Indonesia)	"	"	G	1956	72	18	46 (11 250)	"
Krakatau (Indonesia)	"	"	U	1744	87	14	44 (8750)	"
La Selva (Costa Rica)	Lowland evergreen	<100	E	2340	94	-	-	Soderstrom (1986; unpubl. data)
"	"	"	CD	4700-2000	46-70	-	-	"
San Carlos (Venezuela)	Caatinga forest	120-170	-	200	88	30	14 (12 000)	Cheke <i>et al.</i> (1979)
Dol Suthep (Thailand)	Lower montane (yr. 1)	1350	C	243	-	1	27 (7500)	"
"	" (yr. 2)	"	CD	2-49	-	6	2-9 (60 000)	"
"	Lower montae (yr. 1)	1000	D	161	-	1	22 (7500)	"
Kade (Ghana)	Moist semi-deciduous	150	D	900	22	25	-	Epp (1987)
Queensland, Australia	Evergreen	60	-	588	41	12	64 (30 000)	Hopkins & Graham (1983)
"	Semi-deciduous	80	-	1069	42	12	60 (30 000)	"
"	Evergreen	<70	-	592	12	4	30 (5000)	Hopkins & Graham (1984)

a: distance of seed bank sample to nearest gap, early successional forest, or agricultural land: for Krakatau G = gap, U = understory samples; for other samples C= <50 m; D = 100-200 m; E= >>500 m ; x = ≥ 20 from treefall (notation taken from Garwood);

b: Coefficient of variation (SD* 100/mean)

c: number of seed bank samples; note the gap samples on Krakatau include all multiple samples;

Krakatau one can expect to find higher seed densities in the wet-season as most fruiting seems to be taking place just prior or during the wet-season (October to April; L. Shilton pers. comm.).

The higher seed densities mostly associated with forest suffering more frequent disturbance (Saulei & Swaine, 1988; Warr *et al.*, 1993) were, however, not substantiated for the more frequently disturbed islands of Panjang and Sertung. Instead, significantly lower average seed densities were found on Panjang, and the seed densities of Sertung were not significantly different from those of Rakata. The Panjang results may have been due to the fact that Panjang temporarily received more ash-fall than Sertung, whereby the addition of the ash may have had a 'diluting' effect on the top-soil seed bank density. A seasonally greater deposition of ash on Panjang during the wet-season is possible, because the predominant wind direction is then South-west to West towards Panjang (see CHAPTER 2 & 4 and Fig. 2.4), and the 1993 field season was directly preceded by the 1992/93 wet-season during which Anak Krakatau began its current active phase.

Furthermore, during the initial months the eruptions were particularly frequent and strong, and accompanied by heavy ash-falls (M. Clarbrough, pers. comm.). It is also noteworthy that some Rakata sites may, during times of volcanic activity, also have suffered more frequent disturbance (see CHAPTER 3), and in general there seems to be great intra-island variability in frequency of disturbance. For instance, R5 in the near-coastal South-eastern area of Rakata seems to be a frequently disturbed site judging by the structure and physiognomy of the forest, and the high proportion of pioneer trees in the canopy (e.g. *Pipturus argenteus*, *Macaranga tanarius*). Its understorey density of seeds is very high (4960 m², Table 6.2).

A surprising result when comparing the seed density of Krakatau seed bank samples between years was that the seed densities of top soils in this study (1993; n=32) were significantly greater ($p < 0.01$; one-tailed Mann-Whitney-U test) than those of the top-soils in the 1992 study (n=13) by Whittaker *et al.* (1995). This is despite the fact that sampling took place in the same season and the same methods were used, although, as mentioned above, some unknown differences in germination conditions, and a less precise sample volume in the earlier study (R.J. Whittaker, pers. comm.) may account for some of the difference in seed bank size between the two studies. The fact that in this study sampling also took place in gap sites can largely be ruled out as a reason for this apparently large

increase, since no significant difference was found between the gap and understorey seed bank size. Contributing factors probably include inter-annual differences in fruiting phenology and crop size, and greenhouse conditions may for unknown reasons have differed between the two studies. Furthermore, this study sampled the top-soil from a greater number of sites than Whittaker *et al.*'s (1995) study, but not necessarily a wider variety of habitats. Large between-year differences in densities were found by (Cheke *et al.*, 1979; Table 6.5), who reported up to five-fold inter-annual differences in seed bank size of the same sample sites, but evidence for between as well as within-year differences in seed bank densities in tropical forests is still limited (Garwood, 1989).

Differences in top-soil seed densities between the habitat types of gap and understorey were not significant. However, as the gaps were not artificially created, and therefore the age is only roughly known as 'recent' (<1 year), it is difficult to know how much depletion of, or new addition to, the seed bank from seed rain has taken place since gap creation. Thus, samples suffering from depletion *versus* others that have already received seed bank additions might cancel each other out. Had repeat sampling been possible some of the temporal dynamics of Krakatau seed bank densities could have been quantified.

The size of gap seed banks should be independent of gap size at the time of gap creation (Garwood, 1989). However, after sufficient time for the gap-fill species to reach maturity, one may postulate densities to be greater in larger gaps, because of large numbers of recruited pioneers providing direct seed input. Given the recent age of the gaps sampled in this study it is, therefore, not surprising that seed densities showed mixed results with respect to gap size. Some tendency towards greater seed densities with larger gap sizes did exist. However, comparing the densities of several samples from the same gap (e.g. in R2 and R11 gap; Table 6.2) demonstrates that even within the same gap site the heterogeneity can be great. For instance, with the exclusion of the extra gap samples (R2LNG, R2LS, and R11crown), the correlation between gap size and gap seed bank density became non-significant. In any case, apart from the size of the gap and the time since the last disturbance, the density of the seed bank in a particular site reflects numerous factors including the distance to the nearest seed sources, time since the last fruiting event, soil texture and slope (Mitchell, 1994). The latter two factors may, for example, be responsible for some of the within-gap differences of the seed bank samples of R2 gap. These samples were taken from areas of very different soil texture and two from up- and two from down-slope of this very large gap site located on a 35° slope.

Dalling *et al.* (1994) have questioned whether the great variability in seed densities found in different studies in the tropic is a true reflection of seasonal, annual or geographic variation in seed banks, or whether it may be partly due to differences in methodology. They found that soil depth had a considerable effect on seedling emergence, and that a thickness of >0.5 cm may lead to considerable underestimation of seed density. Since the soil-thickness in the germination trays in this study was considerably higher than this recommended figure, and, for instance, additional stirring of soil and removal of seedlings did not take place, one can assume considerable underestimation of seed bank densities.

Seed bank species composition

As found by Whittaker *et al.* (1995), the top-soil samples in the present study were dominated numerically by shrub and small to medium tree species. The total number of herbaceous species (17) was fairly high, but abundances were mostly low. The only abundant herbaceous species was the climber *Mikania cordata* (135) which was predominantly found in Sertung samples (95), followed by Rakata (38) and Panjang (2). After the rainy season following the 1994 drought this species smothered regenerating vegetation, particularly in gaps in the *Dysoxylum* forest areas of Sertung (Fig. 6.3), but also the South-east coast disturbed areas of Rakata (R5) and the large disturbance near the summit (R10), but it was not a common feature in gaps on Panjang except in one of the very large gaps (P4). Thus, the 1993 seed bank distribution and density of this species appeared well reflected in the post-drought herbaceous vegetation of gap sites.

The proportional representation of different life-forms in the Krakatau seed banks is comparable to that found under mature and secondary tropical forest. Only in young regrowth from large-scale clearings (at least in the first few years if close to forest; cf. Saulei & Swaine, 1988), and in forest close to agricultural land, is the seed bank dominated by herbaceous species (Table 6 in Garwood, 1989).



Fig. 6.3: Regenerating vegetation smothered mostly by the herbaceous climber *Mikania cordata* in a gap in the *Dysoxylum* forest on Sertung in July 1995. This gap site was created by lightning in the wet-season following the 1994 drought, and this dense cover must have been the result of only a few months growth. Note the sparse number of saplings; the sapling in the centre is a specimen of *Macaranga tanarius*.

Amongst the germinating tree species, large canopy trees (>30 m) were not common (5 species), and were of low abundance. Interestingly, out of the five large canopy species all except *Casuarina equisetifolia* were from the fig genus. The small seeds (1-2 mm; Table 6.3) of this genus appear well-suited for storage in the seed bank, and asynchronous (Janzen, 1979; Compton *et al.*, 1996) fruiting at the population level should provide fig seed input throughout the year albeit with high spatial variability. In contrast, canopy species such as *Dysoxylum gaudichaudianum*, or the rarer species *Semecarpus heterophylla*, and *Horsfieldia glabra* fruit only seasonally. The Moraceae has the largest number of tree

species of any family on Krakatau (except for two *Artocarpus* species all are figs). As the Moraceae was represented by 11 of the 25 species of figs currently known from the archipelago (Partomihardjo, 1995), it can be said to be well represented in the seed bank samples. The most abundant fig species in the seed bank were *Ficus septica* (small short-lived pioneer), *Ficus variegata* (large, long-lived pioneer) and *Ficus pubinervis* (large secondary species). This largely reflects their general commonness in comparison to other fig species, but there was a tendency for them only to be abundant in areas with substantial numbers of adult trees in the vicinity.

The data revealed a tendency for particular species to germinate from samples taken from sites with parent plants in the close vicinity, particularly for *Radermachera glandulosa*, but also for the two most common species *Pipturus argenteus* and *Leucosyke capitellata*. In the case of *Radermachera*, the concentration seems more surprising as it is a wind dispersed species with tiny winged seeds. One might, therefore, expect a wider, less clumped distribution than for strictly animal-dispersed species. Ants can act as dispersers as well as seed predators (Levey & Byrne, 1993), and were in this study observed to move *Radermachera* seeds. Thus, secondary dispersal of some of the seeds by ants may explain some of the clumping, but should not be overstressed. It is also noteworthy that *Radermachera glandulosa* was found exclusively in Rakata seed banks. This appears a direct reflection of the fact that *Radermachera* has not so far been found on Sertung and is rare on Panjang, where it was first recorded in 1920 (Whittaker *et al.*, 1989). It is surprising, however, that this typical pioneer should hardly be represented on the other islands as dispersal is unlikely to be a constraint, and frequent disturbance to Panjang and Sertung since Anak Krakatau's emergence should have provided ideal conditions for colonisation.

Pipturus and *Leucosyke* seeds, were found in most samples (30 and 25 out of 32 respectively), but particularly high concentrations were found in areas where these species are locally common (i.e. near-coastal area of South-east Rakata, and inland and high-altitude Rakata respectively; often old gaps; Fig. 6.2). For instance, *Leucosyke*, not only had the highest number of seedlings on Rakata (27% of Rakata seedlings; 15 of 18 samples), but they were highly concentrated in two samples taken near the very large, 500 m a.s.l. lightning/treefall gap (52% of *Leucosyke* total for Rakata). In this area *Leucosyke* was frequently found in the understorey and made up 11% of Whittaker and colleagues' permanent plot sample (Whittaker & Jones, 1993) of saplings before the R2 gap was created (the gap area overlaps with the permanent plot). *Pipturus argenteus* seeds tended

to be even more concentrated in just a few samples. For instance, on Panjang, where *Pipturus* was by far the most common seed bank component (46% of all seedlings germinating from Panjang samples), more than half of them germinated from a single gap sample from a large gap site (P4) located in disturbed *Timonius/Dysoxylum* forest with a considerable *Pipturus* component in the canopy.

These findings support those of many other studies which have suggested frequent spatial clumping of seeds in top-soil seed banks, due mainly to uneven dispersal, leading to a high density seed shadow close to parent plants (Hopkins & Graham, 1983; Young *et al.* 1987; Saulei & Swaine, 1988). Moreover, old gaps have been found to be focal points for frugivorous birds that feed on surrounding trees and shrubs, which in turn have been shown to fruit more prolifically after a gap opening (Schupp *et al.*, 1989; Levey, 1990). Therefore, increased dispersal of seeds into gaps, and particularly gap edges where birds preferentially perch (Schupp *et al.*, 1989), is likely. This is supported by several studies which revealed greater seed densities in old gaps than in the adjacent understorey (Garwood, 1989; see above). However, with respect to the potential composition of the seed bank Loiselle *et al.* (1996) found that the composition of the seed rain, which in general largely consists of animal dispersed species, was more similar between different habitat types in one area (i.e. between a gap and its adjacent understorey) than between the same habitat types from different forest areas. This indirectly suggests that spatial foraging activity and habitat preference of seed dispersers result in non-random patterns of seed rain, and a tendency towards more local dispersal. In contrast, Denslow & Gomez-Diaz (1990) found that in the vicinity of four recent treefall gaps in lowland tropical rain forest in La Selva, Costa Rica, abundant seed input to the seed bank, came from widely distributed sources. They found that 65% of species and 45-81% of seeds were dispersed from distances of generally > 50 m, and pioneers from second growth vegetation from at least 750 m away.

Clumping of seeds can occur because of habitat preferences of dispersers (e.g. other feeding trees, nest sites, calling perches for birds, and day and night roost for bats; Fleming & Heithaus, 1981; L. Shilton pers. comm. pers. obs.). Thus, in the case of bird dispersed species such as *Pipturus argenteus* and *Leucosyke capitellata* clumping may not only occur beneath their own canopies, but also under the canopies of other preferred food shrub and tree species, which may in this way serve as recruitment foci for seeds of species fruiting at the same time (Stiles, 1992).

Typical bird-dispersed species on Krakatau include the canopy trees *Dysoxylum gaudichaudianum* and *Timonius compressicaulis* (Whittaker & Jones, 1994a), which are frequently visited by, for instance, pigeons (e.g. *Ducula aenea*, and *Ptilinopus melanospila*; Whittaker & Jones, 1994a; Whittaker & Turner, 1994). These are likely to defecate considerable quantities of seeds other than those of *Dysoxylum* and *Timonius* (e.g. *Pipturus argenteus* seeds). For instance, Fleming & Heithaus (1981) found this to be the case for bats. This hypothesis seems to be supported by the result of the cluster analysis that shows the *Pipturus argenteus* cluster to be predominantly comprised of sites located in forest areas with a *Dysoxylum* or *Timonius* canopy, but also relatively local availability of *Pipturus* parent plants. Furthermore, *Dysoxylum* seeds themselves are, for instance, commonly dispersed beneath *Timonius* canopies, where they are able to germinate and grow, leading apparently to the eventual replacement of *Timonius* forests on Panjang and Sertung (Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker pers. comm.; see below). This is largely due to the fact that *Timonius compressicaulis* does not seem to germinate and cannot grow beneath its own canopy or that of other species. This species' regeneration pathway involves the exploitation of open sites by either germination from the seed bank or immediate seed rain. However, this study and Whittaker *et al.*'s (1995) study have shown that its seed bank representation appears to be small, possibly suggesting short seed longevity, and thus a reliance on seed rain. The latter is plausible given that *Timonius* appears to be flowering all year round (Partomihardjo, pers. comm.), it can fruit from a very early age (e.g. one meter tall specimen observed fruiting by Corner, 1952), and that seeds are small (1 x 3 mm; Whittaker *et al.*, 1995) and abundant within fig-like fruits. Furthermore, efficient dispersal should be ensured as the species is not only bird- but also bat-dispersed (L. Shilton, pers. comm.). In addition, its ability to colonise sites should be enhanced as fruiting may be induced under conditions of stress (T. Partomihardjo, pers. comm.). *Dysoxylum gaudichaudianum*, in contrast, is fairly large seeded (8-12 mm; Whittaker *et al.* 1995) with short seed viability (Whittaker & Turner, 1994; pers. obs.) but with the ability to germinate underneath relatively dense canopy. CHAPTER 4 has highlighted its potential tolerance to stress from drought, ash and herbivory (see also APPENDIX 3), and its ability for rapid growth under high light conditions, all of which make it a very successful gap-filling species.

Seed bank composition and succession on Krakatau

The importance of the seed bank for regeneration in gaps or forest edges is still a somewhat contentious issue with some studies finding the seed bank to be a major contributor to regeneration, whereas other studies suggest AR to be more important (Brokaw, 1985; Sarukhan *et al.*, 1985; Uhl *et al.*, 1988; Raich & Christensen, 1989) and others stress the role of seed rain (Whitmore, 1983; Young *et al.*, 1987). For instance, in Panama Williams-Linera (1990) found the composition of pioneer vegetation emerging at forest edges to be the same as the seed bank. Putz & Appanah (1987) tried to distinguish between the importance of the seed rain and the seed bank and found that even with a relatively small seed bank (131 seeds per m²) the number of seedlings germinating from the seed bank was seven times greater in the first nine months than seedlings from the seed rain. In contrast, the occurrence of monodominant stands of pioneers and differences in species composition among gaps created at different times of the year each point to the importance of high seed input just before or after the creation of a gap (Whitmore, 1983). Thus, the composition of the regrowth, according to Whitmore's view, is not predictable from the seed bank, but is largely due to chance (Swaine & Hall, 1983), e.g. the coincidence of timing of seed production and gap creation, and the quantity and quality of dispersal. Since dominance of a single pioneer species in the seed bank is quite common (Table 6 in Garwood, 1989), and seed bank compositions are very patchy, single species dominance of different species in different gaps may, nevertheless, be possible from the seed bank.

In this study I would have liked to establish the relative importance of regeneration from the seed bank in gaps of various sizes and types of disturbance. However, this was not directly possible, as explained above. The low similarities found between the gap seed bank samples and the gap seedling and sapling layers in this study cannot be interpreted as direct evidence of an insignificant seed bank contribution to gap regeneration on Krakatau. AR has been suggested to play a considerable role in the regeneration of gaps of a range of different sizes and types and severity of disturbance (CHAPTER 5). It has also been shown that the similarity between the gap seed bank composition and the gap sapling and seedling composition is greater in the larger size-classes of gaps (although still very small), and that very severely disturbed gaps had little or no similarity (e.g. P7G). Thus, it may be deduced that the seed bank contribution increases with increasing gap size, and decreases again when the disturbance is very severe, as suggested by Bazzaz's (1984; Fig. 1.2)

intuitive model. In general, however, an important factor influencing how much the seed bank can *potentially* contribute to regeneration, is the maturity of the forest and/or the proximity to disturbed areas acting as source pools for pioneer propagules (Hopkins & Graham, 1983; Saulei & Swaine, 1988). Since the Krakatau forests are still early successional, and highly dynamic with frequent disturbances creating opportunities for pioneer regeneration (see CHAPTER 3) a plentiful supply of pioneer propagules can be assumed.

Seed bank samples of the gap and adjacent understorey were found to be much more similar to each other than to the immediate seedling and sapling layer. As already established above, part of this may be due to loss of seedlings derived from the seed bank through mortality in the intervening period. However, part of this result is also explicable by the fact that only a sub-set of species found in the regeneration layer are actually suitable for storage in the seed bank. These species with short seed viabilities and immediate regeneration beneath the canopy (e.g. larger seeded species such as *Dysoxylum gaudichaudianum*), often form a major component of gap regeneration in the form of AR (Uhl *et al.*, 1988). Competition from AR for light and nutrients (Uhl *et al.*, 1988; Connell, 1989) may also have prevented successful germination from the seed bank in the first place.

The case of Macaranga tanarius

After the drought in 1994 *Macaranga tanarius* invaded large parts of the near-coastal, South-east area of Rakata and the forests of Sertung (particularly *Timonius compressicaulis* forest; see CHAPTER 4&5). However, as reported above, the very low abundance of *Macaranga tanarius* seedlings germinating during the seed bank experiment raises the question of the regeneration pathway of *Macaranga*. Although seeds of the genus *Macaranga* have frequently been found in the seed banks of tropical forests in the Palaeotropics (Symington, 1933; Liew, 1973; Cheke *et al.*, 1979; Hall & Swaine, 1980; Hopkins & Graham, 1983; Saulei & Swaine, 1988) *Macaranga tanarius* seeds are relatively large (4-5 mm; Whittaker *et al.*, 1995) for a pioneer *Macaranga* species and are susceptible to desiccation (S. Davis, pers. comm.). One would therefore expect relatively short periods of viability, as has, for instance, been found for the Neotropical pioneers *Didymopanax morotoni* (Aubl.) Decne & Planch (Araliaceae), *Jacaranda copaia* (Aubl.) D. Don. (Bignoniaceae; Viana, 1989), and *Cecropia obtusifolia* Bertol (Moraceae). The latter has a high turnover and achieves constant representation in the seed bank only from continuous seed rain (Alvarez-Buylla & Martinez-Ramos, 1990; Alvarez-Buylla & Garcia-Barrios, 1991).

Thus short viability might partly explain the very low abundance of *Macaranga tanarius* in this and Whittaker *et al.*'s (1995) study of Krakatau top soil seed banks. Seeds may be particularly susceptible to desiccation in areas, such as the South-east coast of Rakata with pumice rich soils of excessive drainage. Evidence contradicting this suggestion was, however, found in the Whittaker *et al.* (1995) study when two *Macaranga tanarius* seedlings emerged from a >60 year old buried soil sample on Panjang. This could suggest short viability to be a consequence of environmental conditions rather than an inherent property of the seed, whereby in the case of the buried soil moister conditions of this soil layer (R.J. Whittaker, pers. comm.), and/or rapid burial may have maintained viability and prevented germination. However, contamination of the buried soil sample can also not be ruled out.

Primack & Lee (1991) reported that the rapid appearance of *Macaranga* after disturbance suggests that either the seeds of this genus can remain dormant in the soil until there is a disturbance or that there is a more-or-less constant seed rain. Persistent seed banks have been found for other *Macaranga* species (e.g. *M. hoseii*, *M. winkleri*), and Whitmore (1983) reports that all 20 of the *Macaranga* species in Malaya fruit frequently if not continuously. Thus, if the findings of this and the Whittaker *et al.* (1995) study are generally correct, and a persistent seed bank is not an important regeneration pathway for *Macaranga tanarius*, then abundant seed rain and efficient dispersal should be a necessary trait giving this pioneer species the ability to invade open areas, such as landslides, bare ash (e.g. on Sertung in conjunction with post drought opening of the canopy), or rootzones, with little or no seed bank. The production of an abundant *Macaranga tanarius* seed rain does appear feasible as this species was reported to fruit in 3-4 monthly bursts (Pasoh, Malaysia: Taylor, 1982) or even more or less continuously (Sumatra: Schaik, 1986; Sabah: S. Davis, pers. comm.). Moreover, its widespread occurrence from sea-level to the summit seems predominantly achieved by dispersal of the arilated seeds by flocks of yellow-vented bulbuls (*Pycnonotus goiavier*, cf. Taylor, 1982 and Mitchell, 1994 reporting various species of bulbuls as important dispersers of *Macaranga* elsewhere). Glossy starlings (*Aplonis panayensis*) and other birds have also been observed to take its fruits on the islands (Docters van Leeuwen, 1936; Partomihardjo, 1995; pers. obs.).

Taylor (1982) observed that flowering of *Macaranga* species may be stimulated by prevailing drought conditions. This is consistent with the rapid and extensive invasion of *Macaranga tanarius* into open *Timonius compressicaulis* forest on Sertung, and into the

disturbed South-east coast forest area of Rakata with the onset of the rainy season after the 1994 drought. Nevertheless, even with short viability of seeds, one would under the conditions of continuous flowering and/or the frequent fruiting periods, expect there to be a considerable transient seed bank. In fact, in comparison to several seed bank studies that found *Macaranga tanarius* in their samples, the concentration of number of seeds per m² was an order of magnitude higher in this study (Table 6.6). This might be an expression of the early successional status of Krakatau forests and their disturbance regime, which means that a considerable proportion of pioneer species, such as *Macaranga tanarius* are still in the canopy. However, relative to other pioneer species in this study (e.g. *Pipturus argenteus*, *Leucosyke capitellata*) *Macaranga* had a very low density in the seed bank.

In conclusion, it is suggested that for *Macaranga tanarius* the most important pathway of regeneration is from a transient seed bank laid down by abundant seed rain. The apparent contradictory result of the survival of *Macaranga* in a >60 year old buried soil (Whittaker *et al.*, 1995) could be due to several reasons: (i) the buried soil provided moister conditions enhancing seed viability; and/or (ii) fast burial prevented rapid germination or (iii) possible contamination of samples.

The current canopy dominants *Neonauclea calycina*, *Timonius compressicaulis*, and *Dysoxylum gaudichaudianum*

The seed bank experiments provide some information on the presence or absence, density and spatial coverage, of propagules of the three dominant canopy species in the top-soil. *Neonauclea calycina*, the Rakata canopy dominant, is a long-lived pioneer tree with tiny, wind-dispersed seeds (see above; Whittaker *et al.*, 1995). *Timonius compressicaulis* is a low-stature, shorter-lived pioneer species with small seeds which are dispersed by birds and bats (Whittaker & Jones, 1994a; L. Shilton pers. comm.). *Dysoxylum gaudichaudianum* is a large canopy tree species of early to intermediate seral status whose medium-sized seeds are bird-dispersed (Whittaker & Jones, 1994a; Whittaker & Turner, 1994). Thus, further autoecological information was gained which is helpful in explaining current and future trends in these species' representation in Krakatau forests. *Neonauclea calycina* was found to have relatively high densities, but very clumped distributions in the top soils of this

Table 6.6: Comparison of the Krakatau seed bank density of *Macaranga tanarius* with that of two studies in the Palaeotropics. Note that the other two studies found several *Macaranga* species, but *Macaranga tanarius* always had the lowest density (Table adapted from Mitchell, 1994). Density was calculated as the total number of *Macaranga tanarius* germinating from all samples (see Table 6.3) divided by the total area of soil sampled expressed in m². Depth of sampling was 5 cm in all studies.

Density number m ²	Quantity of soil sampled (m ²)	Forest type	Location	Comments	Source
4.85	2.06	Early successional tropical forest	Krakatau, Indonesia	<i>Macaranga tanarius</i> is the only species in this genus present; very low density in comparison to other pioneers <i>Pipturus argenteus</i> and <i>Leucoyske capitellata</i> etc.	own data
0.25	12	Meso- and Notophyll vine forest	North Queensland, Australia.	some of the sites may have been selectively logged >15 years ago	Hopkins & Graham (1983)
0.6	5	Lowland tropical forest	Gogol Valley, Papua New Guinea	0.85 ha closed forest site approx. 55 years old, surrounded by secondary forest	Saulei & Swaine (1988)

study. It was found in 19 samples (Table 6.3), but two samples from the gap and understorey of one gap site in South-east Rakata alone contained 41% of all the *Neonauclea* seeds germinating. The finding of relatively high densities of seeds contrasts with the germination of only three individuals from a crab burrow sample, and none from the 13 top soil samples of the 1992 study of Whittaker *et al.* (1995). This may point to inter-annual or even intra-annual variation (flowering June-September; Backer and Bakhuizen, 1963-68) in availability of *Neonauclea* seeds in the seed bank, but could also be the result of considerable patchiness of seed distribution of this species as observed in this study. Despite the heavy dominance in the canopy, the extreme patchiness in distribution of *Neonauclea* seeds in the seed bank does not seem to correspond well, however, with the observed ability to colonise uniformly large areas of disturbance. In general, very little or no *Neonauclea* regeneration was observed in the gap studies (even in very large gaps; see CHAPTER 4), except for high densities of small seedlings on bare landslide surfaces (Fig. 6.4), and occasionally in root-zones, for both of which seed banks are largely unimportant. *Neonauclea calycina* has also been observed to blanket road building and spoil areas in



Fig. 6.4: *Neonauclea calycina* seedlings on a bare landslide surface on Rakata

the Philippines (C. Ridsdale, pers. comm). The mono-dominance and the apparently more or less uniform age-structure of *Neonauclea* forests on Rakata (Whittaker *et al.*, 1989) seem to indicate that this species spread on the island in a similar fashion in the 1910s and 1920s. These findings suggest the existence of only a transient seed bank with a heavy reliance on seed rain, and the requirement of bare soil for germination. Thus, the present scarcity of *Neonauclea* regeneration may be explained by the fact that landslides and root-zones, despite being relatively common on Krakatau, are not the dominant disturbance type, and the fact that the surrounding forests are more mature than in the past. In the latter case, this means that a greater number of species are competing for colonisation space, light and resources than in the early phases of succession. *Neonauclea*'s preference of bare soil may largely have to do with the absence of leaf litter (Vázquez-

(Vázquez-Yanes *et al.*, 1990; Molofsky & Augspurger, 1992), but differences in soil chemistry may also play a role. Schlesinger *et al.* (submitted) have recently shown that phosphorus is limiting to plant growth in Rakata soils, but concentrations of plant-available phosphorus has higher concentration in sub-surface horizons. Thus, mineral soils exposed in rootzones and landslides may provided a nutrient related germination trigger for *Neonauclea* seeds.

The findings for *Neonauclea calycina* can more or less be applied to the case of *Timonius compressicaulis*, which also had a fluctuating, but poorer representation in the seed bank (28 individuals in this study, Table 6.3; 1 individual in Whittaker *et al.*'s (1995) study). It also appears to require very open conditions and bare mineral soil for germination. Although in smaller numbers than *Neonauclea*, it was also observed as small seedlings on landslides and in root-zones, and matching the typical pioneer syndrome, it appears not to be able to regenerate under its own canopy. However, as already highlighted in CHAPTER 4 and CHAPTER 5, *Dysoxylum gaudichaudianum* is very well able to regenerate beneath a *Timonius* canopy, and eventually overtop it. *Dysoxylum* was also found to be able to regenerate under *Neonauclea calycina* canopy. Its main regeneration pathway is, therefore, AR, or as also observed, direct colonisation of a gap from seed rain (e.g. in a landslide site on Panjang). The absence of *Dysoxylum* seeds in the seed bank further supports these findings, and is largely explained by the fact that *Dysoxylum* seeds have very short viability, and suffer significantly from seed predation by rats, land- and hermit-crabs. Ants did not predate on the seeds but quickly remove the aril if still present (Whittaker and Turner, 1994; pers. obs.). Under favourable conditions it germinates rapidly, but appears to suffer from fungal attack when germinating in high density beneath its own canopy (pers. obs.). Nevertheless, it is spreading and regenerating successfully in most lowland areas on the Krakatau island. This is aided by a large annual seed crop, with occasional mast-years, dispersal by pigeons and other common birds on the islands, and tolerance of a wide range of different light conditions, as well as of stress from ash, drought and herbivory at the sapling stage and beyond (see CHAPTER 4 and APPENDIX 3).

Some observations on seed-size and seed bank representation

This study and that of Whittaker *et al.* (1995) coincide not only in finding roughly the same life-form distribution and the prevalence of small-seeded species, but both studies also have in common that the species of slightly larger seed sizes, such as *Macaranga tanarius* (4-5 mm) and *Bridelia monoica* (5 mm) have very low densities in the seed bank despite being common on Krakatau (particularly on Sertung). Moreover, *Antidesma montanum*, an ubiquitous understorey tree on Panjang, and *Leea sambucina*, a very common shrub on Rakata both have slightly larger seeds (3-5 mm, and 4-5 mm respectively), and between them produced only six individuals in this study (Table 6.3). In the study by Whittaker *et al.* (1995) these species were completely absent. In contrast, *Villebrunea rubescens* which is very small-seeded (0.5-1 mm), but is relatively less common than both of the mentioned species, is the fourth most common species in the seed bank. The following pattern seems to be emerging: (i) in line with other seed bank studies in the tropics, most tree and shrub species in the seed bank are small-seeded (1-2 mm); (ii) species with slightly larger sized seeds (e.g. 3-5 mm) are rare in the seed bank even if common in the tree and shrub layer; and (iii) relatively large-seeded species (e.g. >6 mm) are completely absent from the seed bank in both studies (Table 6.3; Table 2 in Whittaker *et al.* 1995).

Points (ii) and (iii) cover most of the rarer species that often display clumped distributions and/or only spread locally. Examples include *Planchonella duclitan* (8 x 15 mm), *Horsfieldia glabra* (10-12 mm), *Semecarpus heterophylla* (c. 10 mm), and *Syzygium polyanthum* (c. 4-5 mm; pers. obs.; Partomihardjo, 1995). This may indicate that these species largely rely on direct regeneration after seed fall and dispersal. Absence of such species could however, be due to several other reasons. First, small numbers of samples that may miss clumped distribution of seeds. Second, great temporal variation in seed production and size of seed crop (Mukhtar *et al.* 1992; pers. obs.) combined with short viabilities may produce a transient seed bank or no seed bank at all (viabilities of canopy rain forest species can be <6 weeks, Hopkins & Graham, 1987). Third, seed predation can also lead to the depletion of the seed bank, and fourth greenhouse conditions may not meet the germination requirements of some larger-seeded species (Raich & Khoon, 1990).

6.6 Conclusions

This chapter has shown that seed bank density on Krakatau can be very variable in space, and by comparison with Whittaker *et al.* (1995), also apparently in time. These results seem to confirm general findings of other seed bank studies in the tropics. However, spatial differences in composition were less pronounced than variations in density. The fairly high similarity values between paired gap and understorey seed bank composition seemed to show this, and may be a reflection of the still depauperate woody flora of the islands. In general, the seed bank composition was found to be broadly linked to the predominant forest type although some exceptions occurred.

Some insight into the potential importance of regeneration from the seed bank was gained, although the limitation of the methods used did not allow determination of the precise importance of regeneration from the seed bank as a regeneration pathway in Krakatau gaps. There was some indication that the seed bank contributes little to the regeneration in small to medium-sized gaps, but that its importance increases somewhat in larger gaps. These results seem to confirm suggestions made in CHAPTER 4 and CHAPTER 5 that AR may be seen as the dominant pathway of regeneration for a broad range of gap sizes and severities of disturbance. The exceptions were very severely disturbed gaps or parts of gaps (e.g. landslides and root zones), and very large gaps. In the former, seed rain must have been the most important pathway, as the seed bank is largely eroded or buried. In the latter case, a mixture of AR together with regeneration from both the seed bank and seed rain was suggested to contribute to regeneration. However, to identify clearly the relative importance of each of these pathways, a more extended study including more frequent seed bank sampling, regular monitoring of seed rain, and/or monitoring of germination in autoclaved soil (Putz & Appanah, 1987) would have to be carried out. More extended spatial coverage would also be desirable to identify clearly spatial variation in density and composition of the seed bank. However, if the contribution of the seed bank to gap regeneration is to be quantified, it is very important to know the seedling bank composition before gap creation, and to extract soil samples prior to and just after gap opening, as well as to monitor seed rain and germination from day one after gap creation. This can realistically only be achieved if gaps are created artificially (cf. Kennedy & Swaine, 1992).

The conceptual framework of gap regeneration proposed by Bazzaz (1984) broadly describes the relative contributions of the various pathways with increasing gap size and severity of disturbance. Bazzaz (1991) furthermore suggested that AR is probably the most important means of regeneration of primary forests. Yet, the Krakatau data indicate that, even in early successional forests with a dynamic disturbance regime, AR plays an important role. This is at least the case in the more stable forest areas of Krakatau that are, for instance, less susceptible to severe drought impacts, or landslides, and that do not get severely disturbed by volcanism. However, a knowledge of the predominant size and severity of disturbance is far from sufficient in predicting the predominant regeneration pathways and the composition of gap-fill. Numerous factors, such as the timing of disturbance in relation to seed availability in the seed bank and from seed rain (Whitmore, 1983), chance dispersal, prevailing climatic conditions (see CHAPTER 4), are also of crucial importance in influencing the composition of the early stages of gap regeneration. On Krakatau the best predictive factor of not only the seed bank, but also the AR (CHAPTER 5) seems to be the composition of the local forest type.

From the seed bank experiments, in conjunction with the gap-ecological study and general observations, further autoecological information on the current canopy dominants, *Neonauclea calycina*, *Timonius compressicaulis*, and *Dysoxylum gaudichaudianum*, was gleaned. This information supports the notion that *Neonauclea* and *Timonius* dominance is likely to, and/or already in the process of decline, which might only be reversed in the event of a large-scale disturbance. However, recruitment may then largely depend on the timing of the disturbance in relation to pioneer seed availability. Furthermore, the seed bank may only play a role if, for instance, no burial from ash takes place, as the tiny *Neonauclea* seeds (probably also the small *Timonius* seeds) could be very sensitive to burial (cf. Molofsky & Augspurger, 1992, for small-seeded pioneers; and Drake, 1993, for the small-seeded *Metrosideros polymorpha*). The finding of fairly high densities of *Neonauclea calycina* in the top-soil seed bank in this study in 1993 contrasts with that of Whittaker *et al.* (1995) in 1992, who found no *Neonauclea* representation in the top-soil. Two main scenarios may be involved to produce this result: (i) great inter-year variability in seed production in combination with a transient seed bank; or (ii) the result may be a product of great spatial variability in density as far as that can be deduced from the relatively small number of samples. *Dysoxylum gaudichaudianum* absence from the seed bank coincided with findings of Whittaker *et al.* (1995) and provided additional support to suggestions of its

predominant reliance on the AR pathway of regeneration, or under fortuitous timing, on direct colonisation of gaps from the seed rain.

In general, noting the presence or absence of certain tree species or categories of tree species can give important insights into their autoecology, although any conclusions have to be tentative as the spatial and temporal representativeness of Krakatau seed bank studies is so far limited. Nevertheless, in line with the majority of seed bank studies in the tropics the seedlings that germinated from seed bank samples in this study are predominantly from very small-seeded species (e.g. < 3 mm), and interestingly not only were the large-seeded species absent from the top-soil seed bank, but even relatively small-seeded species (e.g. 3-6 mm) were found to be rare in both Krakatau seed bank studies conducted so far. This even applies to ubiquitous and readily dispersed species such the understorey tree *Antidesma montanum*, and the common bird-dispersed shrub *Leea sambucina*. Also none of the rarer species with seeds of larger size seem to be able to benefit from storage in the seed bank until ideal regeneration conditions arise. Although various factors that may cause seed bank absence have to be taken into account one may suggest that unless seeds of tree and shrub species are small-seeded, the direct regeneration pathway predominates. Whether this occurs mostly in gap environments or in the understorey probably varies between species. Again this is a commonly found result in other seed bank studies in the tropics, but it is additionally interesting to note that in terms of seed size the cut-off point for a common representation in the seed bank seems to be at quite a small seed size.

CHAPTER 7:

CONCLUSIONS, RELEVANCE TO OTHER STUDIES, AND SUGGESTIONS FOR FURTHER RESEARCH

Krakatau represents "a very rare natural situation that provides insights into one of the most difficult and important questions in ecology, the way in which a natural ecosystem (in this case tropical forest) is formed." (Thornton, 1996, p.273)

This chapter summarises the main findings of the thesis, and discusses their relevance to other studies. A section is also devoted to highlighting avenues of further research.

7.1 Main findings and relevance to other studies

Disturbance, dominance and diversity

"Canopy turnover rates may be enhanced by a variety of endogenous and exogenous processes, with results which may suppress or encourage diversity depending on scale" (Whittaker & Jones, 1993, p. 21)

The meso-scale work of this study provided the main new contributions to understanding some of the processes, and predicting the course of succession on the Krakatau islands. Meso-scale methods were the disturbance- and species-transect surveys. These provided base-line information on the spatio-temporal frequency of gap occurrence (CHAPTER 3), and established that gap frequency and areal extent of disturbance is generally high. Therefore, gap openings as regeneration foci are sufficient for succession to take place, i.e. the site availability *sensu* Pickett *et al.* (1987) is no constraint. Indeed, in some cases the disturbances are too large and severe, and/or frequent for succession to progress beyond the early stages (e.g. areas of Sertung and Panjang, the near-coastal area in the South-east of Rakata, and the Sertung spit).

This study gathered the first direct evidence on the impact of volcanic activity on the disturbance regime of Panjang and Sertung, and the findings of an increase in disturbance and associated tree/sapling mortality between the non-active and active period add further support to Whittaker and colleagues' disturbance-driven model of succession on Krakatau (Whittaker *et al.* 1989, Whittaker *et al.* 1992a; Bush *et al.* 1992). However, this study demonstrated that the disturbance-driven model, as previously articulated, is somewhat

simplistic. The model assumes that only Panjang and Sertung, the islands that receive ash-fall and are closest to Anak Krakatau, suffer increased disturbance. Instead, all islands were found to have a more active disturbance regime during the most recent phase of volcanic activity (1992-1995) than in the preceding inactive phase. In the case of Rakata, this meant that despite the fact that it does not receive ash-fall and blast damage, it may experience more disturbances in the form of landslides, lightning strikes and windthrows, from an increased number of earth tremors and from local thunderstorms during volcanic activity (Fig. 1.16).

Previous plot-based and whole-island studies indicate suppressed diversity (species richness and patchiness) on Panjang and Sertung. This can now also be confirmed for the meso-scale. However, this does not mean that Panjang and Sertung should be seen as equally species poor and uniform in canopy composition. At the meso-scale Panjang is more patchy and locally species rich than Sertung, and apart from the previously identified forest types with mono-dominance of *Dysoxylum* and *Timonius*, a new forest type with equal importance of *Neonauclea calycina* and *Timonius compressicaulis* forming the canopy was recognised in this study (CHAPTER 5). A greater patchiness and degree of diversification on Panjang is further supported by the recent finding by Partomihardjo (1995) of another forest type dominated by *Buchanania arborescens*. It is suggested that the slightly more mature impression and the differences in forest types and diversity patterns of Panjang are a result of less severe and frequent and/or more patchy impacts of volcanic disturbance than on Sertung (see CHAPTER 2, Table 2.2). Furthermore, it is believed that the newly recognised forest types on Panjang are not recent phenomena, and that their existence had been missed by previous plot-based sampling in the 1980s.

In addition to the somewhat serendipitous coincidence of the study period with prolonged volcanic activity of Anak Krakatau, a major El Niño drought was experienced in 1994. This drew particular attention to the importance of extreme climatic events in influencing successional processes, and was thus included in the revised hierarchical model of causes and mechanisms of succession presented in Fig. 1.16. The 1994 drought, for instance, had a major influence on the species composition of the regeneration layer (CHAPTERS 4 & 5). However, a substantial proportion of the drought impact has only been temporary, involving ephemeral species. Even so, some longer-term shifts in species composition may occur due to increased mortality in general, and inter-specific differences in mortality of sub-adult and adult trees, and in particular due to differential recruitment of replacement species. Drought causes impacts similar to those of a gap (cf. for BCI, Becker & Smith, 1990), in the sense that it opens the canopy and temporarily increases light levels on the ground. Obviously, these impacts are less localised than a gap opening, and become particularly

apparent in areas of greater drought susceptibility, which can be a function of several factors, such as a more susceptible species-mix or excessively drained soil.

Observations made during this study have also raised awareness of anthropogenic disturbance to the islands (CHAPTERS 2 & 3), and highlighted in particular the case of pumice mining in the near-coastal forests. It is advocated here that human disturbance should no longer be ignored as an influence on the succession on Krakatau. In the hierarchical model of succession on the islands depicted in Fig. 1.16, human impact was thus included as another major disturbance factor besides volcanism and climate.

As Krakatau is a Strict Nature Reserve (Cagar Alam), such anthropogenic disturbance events are technically illegal (Sumardja *et al.* 1984; Government of Indonesia, 1990). The Directorate General of Nature Conservation and Forest Protection (PHPA) was informed of these activities and their apparent increase in recent years. It was stressed in particular that human disturbance of such a degree conflicts with the reserves' primary value as a unique site for the study of primary succession and the reassembly of a tropical ecosystem. However, it should be recognised that PHPA's capacity to enforce a no-access and zero-utilisation policy on Krakatau is limited (Bush, 1986b; P. Jepson, pers. com.). Although minimum human impact should be the goal to safe-guard Krakatau's value as a study site of primary succession, a more pragmatic approach may be to accept that some form of human impact has and will always be present on the islands (e.g. pumice mining in the 1910s-20s; general species introductions). Therefore, any model of succession on Krakatau can not ignore human impact as part of the ecology of the islands. In any case, human activities have influenced the Krakatau succession even if the impact is not directly destructive to the islands themselves. This is clearly the case, for instance, with the progressive reduction of the mainland species pool from forest loss due to agricultural expansion and logging.

The meso-scale study of the species transects, and the patch-scale study of gap regeneration identified that *Neonauclea calycina* and *Timonius compressicaulis* are barely regenerating, and it can be stated with confidence that these species are in the process of losing their dominance. Even in the event of large-scale disturbance it is not necessarily these species that would again come to dominate. This is because several tree species with rapid colonising abilities are now present in the flora, and the outcome would depend on factors such as timing of disturbance in relation to season and seed availability.

A series of observations during this study suggest that the tiny seeds of *Neonauclea calycina* need bare soil and high light conditions for germination (C. Ridsdale, pers. comm.; pers. obs.). However, if this is indeed the case, then it would be difficult to explain how *Neonauclea* could expand from the higher altitudes of Rakata and come to dominate all lowland areas of this island between by 1951 (Borssum Waalkes, 1960; Whittaker *et al.*, 1989), as when *Neonauclea* started its expansion in the 1920s, Rakata was already covered by savanna grasslands with scattered clumps of trees, which developed rapidly into mixed *Macaranga-Ficus* forest (Whittaker *et al.*, 1989). Thus, high light environments, but in particular bare soil surfaces for germination, must have been limited. However, it could be that the apparent preference of *Neonauclea* to germinate on bare soil, has more to do with the chemical properties of a mineral substrate than, for instance, with absence of litter cover allowing the germination of the tiny seeds (cf. Molofsky & Augspurger, 1992). For instance, a recent study suggests that on Rakata phosphorus may be limiting to plant growth (CHAPTER 2). However, it was also found that the sub-surface horizons have higher concentrations of plant available P. Thus, the chemical properties of mineral soil from sub-surface horizons, may not only provide more P, but may also resemble more those of soils during the early stages of soil development when P may have been more readily available in surface horizons. This is consistent with the pattern of occurrence of *Neonauclea* seedlings (e.g. in root-zones and landslide surfaces) as were observed in this study.

Considering the fact that grassland habitats are also very prone to burning in seasonally dry climates, one could also hypothesise that the effect of natural- or human-caused fires during Krakatau's savanna stage of development may have created ideal conditions for *Neonauclea*'s expansion. This said, there are no reports of fires in the Krakatau literature except for the accidentally lit fire in North-west Rakata in 1919 (see CHAPTER 1). Docters van Leeuwen (1936) claims, however, that the fire had little or no effect on the successional development in this area, which is a claim that is difficult to substantiate in the absence of subsequent study of compositional changes in the aftermath.

Whereas *Neonauclea* and *Timonius* appear in decline, the previously suggested process of expansion of *Dysoxylum gaudichaudianum* (in particular on Panjang; Bush *et al.*, 1992), is supported by both the meso-scale study of the species transects and the patch-scale study of gap regeneration. This study also confirmed many of the suggested autoecological traits of *Dysoxylum* (see Bush *et al.*, 1992; Whittaker & Turner, 1994), and added new information on its tolerance to environmental stress (drought, ash-fall, and herbivory; see APPENDIX 3 for herbivory). Most strikingly, and to a greater extent than suggested by Whittaker & Turner (1994), *Dysoxylum* is a very important and common component in the near-coastal and lowland inland forest of Rakata. It is often the canopy dominant near the

East and South-east coast, and has a ubiquitous presence as an understorey component of the inland *Neonauclea* forest of South-east Rakata (CHAPTER 5).

Despite the continued expansion of *Dysoxylum* on Panjang and Sertung (CHAPTERS 4 & 5), and despite the fact that *Dysoxylum* appears to have recently increased its presence in the lowlands of Rakata, a convergence of *all* lowland forest types on *all* islands towards a single forest type dominated by *Dysoxylum*, as proposed by Tagawa *et al.* (1985), is considered unlikely. This is mainly because, in the more species rich forests on Rakata, *Dysoxylum* has to compete with more species for a place in the canopy. Therefore, *Dysoxylum* dominance on Rakata might only be possible in patches, whereas most areas in lowland Rakata are likely to be of a richer species mix in future. Furthermore, *Dysoxylum* expansion on Panjang and Sertung may be abruptly halted in the event of severe volcanic disturbance to these islands.

Tagawa *et al.* (1985) suggested that *Dysoxylum* forest is currently the most advanced forest community on the islands, and that the climax state would be a tropical monsoon forest type similar to that found on the island of Panaitan, Ujung Kulon (Fig. 1.1). There are two main problems with the interpretations of Tagawa *et al.* (1985). First, the concept of a 'climax' forest in the Clementian sense implies that equilibrium can be reached. Yet, this study and those of Whittaker and colleagues (Whittaker *et al.*, 1989; Whittaker *et al.* 1992a; Bush *et al.* 1992) have shown that Krakatau forests experience a very active disturbance regime with the likelihood of intermittent successional set-back. Therefore, under these conditions an equilibrium may never be reached (Bush & Whittaker, 1993). Second, when Tagawa *et al.* (1985) developed their model in the early 1980s *Dysoxylum gaudichaudianum* was still misidentified as *D. caulostachyum*. The latter is a primary forest species (Whitmore, 1984), and knowledge of this species' life-history characteristics may have influenced projections of Tagawa *et al.* (1985) concerning successional pathways which were argued to move towards a later-successional *D. caulostachyum* dominated community, and consequently that *Dysoxylum* forests as found on Panjang and Sertung is the most mature stage of development on the islands. However, *D. gaudichaudianum* is a widely dispersed, early to intermediate seral tree species (Mabberley, pers. comm. to R.J. Whittaker; Backer and Bakhuizen 1963-1968). Its heavy dominance on Sertung and Panjang is viewed here as a result of recovery from successional set-back caused by volcanic disturbance, and not as a generally more mature stage of development than for instance *Neonauclea* forests. However, *Dysoxylum* forests might be less mature in terms of their age and diversity in comparison to *Neonauclea* forests, but in terms of the life-history characteristics of *Dysoxylum gaudichaudianum* it is a more advanced successional species than both *Neonauclea* and *Timonius*.

In this context, the existence of mono-dominant *Neonauclea*, *Timonius*, and *Dysoxylum* forests on the Krakatau islands is an expression of early successional development, and successional set-back. As already suggested for the case of *Neonauclea* and *Timonius* forests, mono-dominance in the Krakatau case should not be seen as a persistent state. This is because these species cannot regenerate beneath their own canopy. *Dysoxylum* seems to be able to regenerate beneath the canopy of *Timonius* and *Neonauclea*. Thus, persistence of mono-dominance, albeit with differing species mixes, is favoured by catastrophic disturbance such as from intermittent volcanism. In the absence of such disturbance, mono-dominance on Krakatau is liable to be reduced.

As mechanisms involved in mono-dominance on Krakatau are disturbance driven, they contrast, for instance, with those found on Hawaii, where mono-dominance is largely due to an extremely impoverished tree flora and synchronous stand die-back allowing auto-succession of *Metrosideros polymorpha* (Mueller-Dombois, 1991, 1992). Other reasons that have been implicated in causing persistent mono-dominance in tropical forests are also not relevant to Krakatau; these include for instance: edaphic characteristics such as permanently water-logged soils (e.g. *Pterocarpus officinalis* forests in Costa Rica; Janzen, 1978), and reasons related to above average ability of tree species to persist in the understorey (e.g. *Gilbertiodendron dewevrei* in forests of Central Africa, and *Dryobalanops aromatica* forests in Malaya and Sumatra; Hart, 1995; Kachi *et al.*, 1993). Higher degrees of ectomycorrhizal associations have also been suggested to cause persistence of mono-dominant forests (Connell & Lowman, 1989)

Regeneration dynamics and pathways

Sapling growth was generally negatively affected by ash-fall, and the drought in 1994 combined with ash-stress appeared to override the importance of the effects of physical characteristics of gaps (gap size and type of disturbance) on sapling growth. Contrary to expectations, mortality was not higher on ash-affected islands. Rather, the effect of ash manifested itself in reduced recruitment, and thus, the net change in number of individuals. In turn, reduced recruitment may have provided some competitive release for the surviving saplings of the relatively stress tolerant *Dysoxylum gaudichaudianum*, which would partly explain its good performance on the ash-affected islands.

After the wet season following the 1994 drought, blanket recruitment of *Macaranga tanarius* was a significant feature in other gaps, or even the understorey of the *Timonius compressicaulis* forest on Panjang, and the near-coastal open forests of South-east

compressicaulis forest on Panjang, and the near-coastal open forests of South-east Rakata. Much of this *Macaranga* recruitment is likely to be ephemeral due to the restoration of canopy cover after the end of the drought. However, in more permanent gaps *Macaranga* is expected to form a uniform canopy. A considerable number of mature *Macaranga tanarius* forest patches on the main ridge of Sertung may thus be seen as a result of intermittent severe disturbance. Such disturbance may be from volcanism (particularly on Sertung), large windthrows, lightning, or drought, or an interaction of more than one of these factors.

The physical disturbance factors of ash-fall and drought seem to have altered the competitive balance between species within the islands of Panjang and Sertung, and this must have been the case in the past. Some evidence was found that gap size influences growth dynamics of saplings (particularly in the small size-class, all species combined) in the mesic year. However, the properties of the gap itself are likely to be of greater significance in mainland forests of a more mature character, because a greater range of the pioneer to climax spectrum of species (*sensu* Swaine & Whitmore, 1988) is present, and inter-specific competition is likely to be of greater importance.

It is nevertheless important to take differences in life-history characteristics of species into account when evaluating regeneration dynamics in gaps on Krakatau, because some species have a high probability of survival once in the sapling layer (e.g. *Terminalia catappa* appears to have this characteristic) whereas others (e.g. *Pipturus argenteus*) are ephemeral (cf. Lieberman, 1996). In general, however, it is now widely recognised that in recent years the emphasis of research on regeneration in gaps has been excessive (Lieberman *et al.*, 1989; Ashton *et al.*, 1995; Veenendal *et al.*, 1996; Brown & Jennings, in press), and the monitoring of species performance in all different environments of the gap-understorey continuum, and the associated environmental gradients (i.e. not only light, but also moisture, nutrients) has been advocated.

It is also recognised that it is difficult to predict floristic change after disturbance because considerable overlap in the environmental tolerances of seedlings of different species, in terms, for instance, of light, has been shown (Lieberman *et al.*, 1995). Moreover, the patterns of change may reflect more the proximity of potential seed sources, the timing of fruit production and the presence of advanced regeneration at the time of disturbance (Lieberman, 1996). Under the absence of severe disturbance from Anak Krakatau and related stress from ash-fall, these factors, rather than characteristics of a specific gap environment may be argued to be particularly relevant to the limited inland tree flora of Krakatau. This can be argued in particular, because inland tree species appear to have

fairly broad environmental tolerances. Differences in tolerance to stress from extremes in climate or to stress from such factors as ash-fall is likely to be more influential in affecting species compositional patterning on Krakatau.

In line with the argument that species-specific adaptations to different physical characteristics of gaps are not very important here, the gap regeneration and the seed bank data indicated that advanced regeneration is the most important regeneration pathway in small to medium sized and moderately disturbed gaps on Krakatau (CHAPTERS 4, 5, and 6). Furthermore, the data presented suggests that the species composition of the advanced regeneration varies with, and is largely determined by, the composition of the surrounding forest type, i.e. local dispersal is very important. This was, for instance, highlighted by the general absence of regeneration of the less common species in gaps, unless some adult specimens were in relatively close vicinity of the gaps studied (e.g. for *Horsfieldia glabra*, and *Semecarpus heterophylla*). Thus, the dispersability of a species is likely to be an important factor affecting the process of diversification of the Krakatau forests. This is not only restricted to the dispersal of new species to the islands, but also the spread of already established but rare species between and within the islands.

With respect to *Dysoxylum* dispersal, the limited data available were interpreted by Whittaker & Turner (1994) to suggest that the behaviour and abundance of various avian dispersal agents may be significant in determining the rate of *Dysoxylum*'s spread inland on Rakata. The species presence/absence data of this study provides strong indications that *Dysoxylum* is spreading better in areas of inland Rakata (see CHAPTER 5) than realised by Whittaker & Turner (1994).

The comments about the relationship between the rate of spread and behaviour and abundance of dispersal agents are nonetheless relevant to other bird- or bat-dispersed species. For example, the clumped and/or localised distributions of *Horsfieldia glabra*, *Semecarpus heterophylla*, and *Planchonella duclitan*, are apparently not a result of shortages of 'safe sites' but rather a sign of distinctly under-dispersed distributions. Whittaker & Turner (1994) suggested with respect to *Dysoxylum* that some dispersers may only produce very concentrated seed shadows, and that dispersal may be dependent on a very restricted sub-set of potential dispersers to found disjunct populations in the interior of the islands. What is suggested here is that this does not so much apply to *Dysoxylum*, but appears a plausible explanation for the clumped distributions of some of the rarer species. No observations on dispersal are available for *Semecarpus*, but in support of the dispersal

species in the Anacardiaceae family (Umavedi, 1988), may make it an unattractive food source to other than specialist dispersers. In apparent contradiction to the suggestions by Whittaker & Turner (1994), however, I have observed that both *Horsfieldia*, and *Planchonella* fruits are eaten in large quantities by Imperial pigeons, e.g. *Ducula bicolor* and *Ducula aenea*, both of which are not seed predators, and excellent dispersers. Only further research on dispersal (e.g. determining the disperser community; their abundance and behaviour) of the examples above and other species, can shed more light on these hypotheses and apparent contradictions.

The pathway analysis of succession as applied to the Krakatau islands by Richards (1952), and in modified form by Whittaker and colleagues, largely conforms with the early 20th century preoccupation with the study of the development of community types and associations. For instance, Ernst (1907) predicted that the interior forest associations would with time become closed through competition. As yet, this has not taken place as new species are still colonising, and given the dynamic nature of the Krakatau environment, it is not likely to be the case in the near future. The results and observations of this study suggest that successional pathways vary from patch to patch and over time as a function of a number of abiotic and biotic factors. The abiotic factors prominent in this study and particularly relevant in the Krakatau context are intermittent volcanic disturbance and the influence of extreme climatic events. Biotic factors include, for instance, dispersal and herbivory.

Rather than concentrating on successional pathways, the Pickett *et al.* (1987) framework of succession is concerned with processes. As applied to this study it has been able to accommodate all of the different aspects addressed at the appropriate level of organisation. At the meso-scale this was the community-level and for the gap regeneration studies this was the population-level. The differential impact of the identified disturbance factors (e.g. volcanic, climatic, human) on the different islands, as well as links between these and the general causes and mechanisms of succession as identified by Pickett *et al.* (1987) was represented in diagrammatic form as a new model of succession on the Krakatau islands (Fig. 1.16).

The main topics of the role of disturbance, dispersal constraints, and differential species performance have long been recognised as important in the Krakatau literature (Ernst, 1907; 1934; Docters van Leeuwen, 1936; Borssum Waalkes, 1954; 1960; Whittaker *et al.*, 1989; Whittaker & Jones, 1994ab). It is also these factors affecting the succession in various combinations that make predicting the Krakatau succession in terms of floristic pathways difficult in other than broad terms. An enhanced predictive understanding of the succession requires an understanding of the processes, in which documenting pathways is but a small part. The use of the Pickett *et al.* (1987) model has provided a hierarchical framework into which to place the various processes involved. It has helped to illuminate the complexities and inter-relationships outlined throughout the thesis, and served very well as a research agenda.

The wider picture

"Anyone who sets about to repair or restore any object, whether it is a clock, an old engine, or an eroded savanna, soon realises that in order to do a good job he or she needs to know something about that object, the nature of its parts, how it was put together in the first place, and how the whole thing works." (Bradshaw, 1987; p. 53)

As the quote at the beginning of the chapter highlights, Krakatau represents a natural experiment of ecosystem rebuilding in the tropics. Closely studying the processes involved is of great intrinsic value and interest. Yet, because Krakatau research is concerned with the study of 'how the object is put together' it is of direct practical relevance to restoration ecology; a branch of ecology that is more and more in demand in the face of increased destruction and fragmentation of forest habitats from logging, mining, and agricultural activity (Jordan *et al.*, 1987). Research on the successional processes on Krakatau may provide important parts of the blueprint needed in tropical ecosystem restoration.

The issues of natural colonisation and restoration of an isolated island (e.g. oceanic shelf or habitat island), and the establishment and diversification of forest, and its animal community, are of particular interest to restoration ecology. To date the Krakatau studies have managed to provide the baseline of understanding of the different stages, and the order of reassembly of plant and animal communities on the islands (Thornton *et al.*, 1988; Whittaker *et al.*, 1989; Bush *et al.*, 1992; Whittaker & Jones, 1994a). However, less knowledge has been accumulated about the actual processes involved in recolonisation and succession.

As outlined above, this study was in large measure concerned with understanding some of these processes, in particular the process of regeneration after disturbance and gap creation. In other, non-tropical ecosystems, with a lower diversity of the source pool, predictability of successional development and recovery on the landscape-scale may be more straightforward. In the case of the Krakatau islands, it is becoming increasingly clear that predicting the succession and species composition after major disturbances is difficult, other than in terms of broad characteristics, such as functional attributes (e.g. growth-form and dispersal spectra; Whittaker & Jones, 1994b). On the patch-scale, gap-fill seems slightly more predictable as the regeneration layer in moderately disturbed gaps appears to be largely a combination of the common species in close vicinity of the gap, and not 'hot spots' for the establishment of new and rare species. Indirectly this finding on the patch-scale, stresses further the importance of local seed sources in the recovery from disturbance, as dispersal constraints may prevent the wide-spread dispersal of new or rare species. Attempts at restoring a natural forest ecosystems, are likely to suffer from such dispersal constraints unless seed sources are relatively near, and animal dispersers are present in sufficient numbers.

On the landscape scale, this study has further demonstrated the need to understand the effect of intermittent disturbance on the process of rebuilding and succession of island ecosystems as suggested by Whittaker (1995), and the complicated and often unpredictable nature of the resulting plant communities. In the context of the Krakatau islands, attention has so far been concentrated on the impact of volcanic disturbance on the rebuilding process. However, this study has also highlighted the general importance of disturbance and stress to tropical forests from extreme climatic events such as, for instance, those linked to major ENSO events, and/or hurricanes and cyclones. Increasingly, ecological and climatological studies, have documented the significance of such events in altering forest dynamics and composition depending on the intensity, length of, and area affected by such extreme events (Whitmore, 1974; 1989; Walker, 1991; Walker *et al.*, 1991; Lugo & Waide, 1993; Nicholls, 1993; Lugo, 1995; Walsh, 1996;). Even slight differences in dry season rainfall can have a considerable effect on plant stress and mortality in tropical forest (e.g. Wright, 1991), thus the effect of extreme events may be an order of magnitude higher in the degree of impact. For instance, the Bornean forest fires during the very severe 1982/83 El Niño drought (Walsh, 1996) brought home the fact that even wet tropical forests, away from the hurricane and cyclone belts, may be subject to intermittent catastrophic disturbance that has an effect on forest dynamics, and composition for several tree generations. In the context of increasingly fragmented forests and low population densities of plant or animal species, such extreme events may push some species over the edge towards extinction (Whittaker, 1995), unless sufficiently large

and viable populations are maintained. How large these forest areas or networks of forest areas have to be to conserve populations of particular plants and animals is a matter of intense debate and current research (Pickett *et al.*, 1997).

Apart from the hierarchical framework of Pickett *et al.* (1987) the ideas encapsulated in the intermediate disturbance hypothesis (IDH; Connell, 1978) have provided the other main conceptual framework for this study. Sheil (1996), however, suggests that the IDH is arguably a truism as the introduction of pioneers into late successional vegetation inevitably increases diversity and a sufficiently destructive event will cause local extinctions and reduce diversity. After remeasuring and analysing the existing data on the permanent plots (established in the 1920s and 1930s) in Budongo forest (the forest site that was used as an example by Connell, 1978), he argued that the model was insufficient in explaining the relative differences observed between sites and over time. He suggests that apart from disturbance, the nature of the species pool itself is likely to be a major factor influencing diversity in time and space (i.e. potential species availability as one of the general causes of succession, Pickett *et al.*, 1987).

With the continuing reduction of natural forest in the vicinity, and the surrounding areas of Budongo being turned into agricultural land, drastic reductions in the wider species pool have taken place. Thus, Budongo is likely to become a habitat island, whereas Krakatau is a real island surrounded by sea. Possible differences in constraints imposed by the nature of the species pool for a habitat island rather than a real island will to a large extent, depend on the distance of isolation and the differences between the characteristics of agricultural land or non-natural forest in comparison to the sea as a barrier to dispersers. However, applying the IDH to a forest which is still early successional, as well as subject to considerable isolation in a small island setting, is quite a different matter. In effect, Krakatau forests are depauperate, and it is not a question of maintaining early successional species in a late successional forest. The interest of the Krakatau study lies in how the forest is diversifying with respect to the accumulation of later successional species. Transferable from the IDH, however, is the principle that this is likely to be encouraged if the disturbance regime is 'intermediate', providing sufficient regeneration opportunities in gaps of medium severity of disturbance.

The possibility on Krakatau, at least on Sertung and Panjang, is that the disturbance regime experienced is too severe and disturbance occurs too frequently for diversification

to take place or that the pace of diversification will be slowed significantly. Whittaker and colleagues (Bush, 1986a; Whittaker *et al.*, 1989; Bush *et al.*, 1992) were the first to suggest that intermittent volcanic disturbance has led to the divergence in forest types and a set-back of succession on Panjang and Sertung, and this study has provided further evidence in support of this. Despite the fact that Rakata's forests have been shown to experience increased disturbance during times of volcanic activity (CHAPTER 3), there is a difference in the frequency, severity and areal extent of disturbance in comparison to the other two islands. Thus, one may argue that Rakata experiences an 'intermediate disturbance' regime, and in line with the IDH its forests boast the highest diversity of all islands on all spatial scales. In fact, one may argue that times of increased disturbance, such as recently experienced, could contribute to a more rapid demise of the senescing *Neonauclea* stands on Rakata. Thus, enhanced opportunities for an increase in diversity may be provided due to the removal of an inhibition effect by early successional species occupying the site.

The data have shown that *Neonauclea* stands on Rakata have locally experienced quite rapid turnover (CHAPTER 3), but there is no clear evidence that this in turn will lead to a rapid increase in species richness of this island. On all islands, the regeneration layer in gaps was not found to be distinctly different in species composition to the understorey layer, except for the fact that more of the common pioneer species were recruited in the gap sites studied (CHAPTER 4 & 5). Gaps certainly were not 'hot spots' for regeneration of rarer species. Thus, it can be hypothesised that the next generation of canopy species on Rakata are likely to be stands with a reduced dominance of *Neonauclea*, and that these stands will be comprised of a matrix of different, but already common species (e.g. *Dysoxylum* and various *Ficus* spp.). These mixed stands may be complemented by more localised areas of higher alpha-diversity that, for instance, coincide in space with the clumps of rarer canopy species (e.g. *Planchonella duclitan*, *Semecarpus heterophylla*, *Horsfieldia glabra*, *Syzygium polyanthum*, as mentioned above). Such areas were identified in the South-east of Rakata, and some areas of Panjang. This means that beta-diversity is likely to increase on Rakata in the near future, but that species totals on the island scale might not increase rapidly. All these suggestion still have to be seen as tentative until more studies monitoring the species compositional changes on all spatial scales are carried out.

In the Krakatau context of today (unlike the conditions directly post-1883), the real problem is not it seems the lack of suitable 'safe sites' (Harper, 1977) for regeneration, but rather the fact that, in the cases of Panjang and Sertung, excessive disturbance seems to have

weeded out later successional species, reduced beta-diversity and prevented the stratification of the forests. Nevertheless, one of the top constraints on diversification of all Krakatau forests is imposed by the distance to the source pool of potential new colonists, as well as the continuing shrinkage of mainland forest areas and, in conjunction, the availability of animal dispersal vectors. Of course, aspects of habitat availability also set limits to diversification. For instance, the low altitudes of Panjang (146 m a.s.l.) and Sertung (180 m a.s.l.) mean that these islands simply cannot support a higher altitude vegetation component, and in terms of species-area relationships these islands cannot acquire as many species as Rakata (e.g. Panjang < Sertung < Rakata).

The examples of Sheil's (1996) study and that of Krakatau seem to emphasise the argument that 'conservation of context' (Pickett *et al.*, 1992) is necessary to provide a source of propagules and/or dispersers and pollinators to maintain diversity in the increasing number of tropical forest 'islands', as well as trying to reconstruct tropical forest ecosystems after incidences of severe disturbance. In the case of the former, source pool supply is important, but management practices that provide some form of artificial disturbance to initiate sufficient successional habitat may also have to be considered (Sheil, 1996; Rogers, 1997). In the latter case, i.e. an effort to reconstruct natural tropical forest, such as after logging, or agricultural conversion, the isolation from source pools of propagules is likely to be one of *the* top constraints apart from the multitude of other variables linked to the autoecology of species. As many studies have shown (e.g. Walker *et al.*, 1991; Whitmore, 1974; 1989), tropical rain forests do have the potential to recover naturally from major disturbance, such as caused by extreme climatic events (e.g. hurricanes, and cyclones). This may for instance take place by direct regeneration, i.e. from resprouting of stems (Vandermeer *et al.*, 1995). Nevertheless, erosion of diversity over time can only be prevented if sufficient 'undisturbed' source areas remain available.

7.2 Recommendation for further research

"Although species surveys should be continued in order to monitor such changes, it is information on species interactions that will provide evidence of the progressive ecological integration of the biota as its diversity increases."
Thornton (1996) p.283

This quote expresses concisely what one of the major areas of focus should be for further studies on Krakatau. More specifically, out of this study the need for many more studies in the fields of ecology, but also hydrology, and geomorphology became evident. During this research I was able to study and monitor only a small part of the successional dynamics of the Krakatau islands over a very short period of time. It would be extremely useful to extend this work, and to test some of the claims made by myself and other researchers who have worked on the islands. Suggestions of possible extensions to this work and other research avenues are made below.

First, on the patch-scale, growth and survival of sapling populations in gap and understorey areas should be monitored over longer periods of time, i.e. from gap creation, via building phase to complete gap fill. Longer-term monitoring would make it possible to document if major species compositional changes, and increases in diversity are likely, in the absence of further major disturbance events. The monitoring of tree dynamics in all life-history stages is according to Clark & Clark (1992) crucial in the attempt to understand the maintenance of tree species diversity. In this case, the concern is not the maintenance, but the future increase of diversity. Yet, to a large degree the same principles should apply.

Second, as this gap ecological study was not able to measure a large array of environmental variables, in particular soil water availability, and nutrient dynamics, and more reliable light measurements, further studies that quantify these variables in detail are recommended. However, it is suggested that the regeneration conditions should be quantified across a large variety of sites in the gap-understorey continuum and if possible with greater spatial coverage and replication. Yet, practical constraints of carrying out such detailed patch-scale work that requires regular monitoring, are great. Only the ability to stay for longer and throughout the wet-season on the islands would allow a comprehensive study to be carried out. This is unlikely to happen unless sufficient funds were available to allow monthly trips to the islands or more ideally if a research station could be established, and a boat was always available.

Third, it is clear that one of the major barriers to an increase in diversity on Krakatau is the fact that some species have difficulties reaching the islands or possess dispersal strategies that do not allow long-distance dispersal across a sea barrier (Whittaker & Jones, 1994a,b; see Fig. 1.4). However, this study has identified that dispersal constraints may also be implicated in slowing the spread within and between islands of some of the already established species. Therefore, specific studies on the dispersal ecology, in particular of the species with identified clumped distributions, is proposed (e.g. *Semecarpus heterophylla*, *Horsfieldia glabra*). Such studies would provide information additional to a current study by L. Shilton on aspects of bat- and bird- dispersal of common tree and shrub species on Krakatau.

Fourth, on Panjang and Sertung, the ability to predict successional development is largely constrained by the unpredictability of the future impact of volcanic eruptions. This study has managed to contribute some information on the regeneration behaviour of a number of the common tree and shrub species, and shed some light on the distribution of the rare canopy species *Semecarpus heterophylla*, *Planchonella duclitan* and *Horsfieldia glabra*. However, in general the ability to make some predictions on future canopy composition is still constrained by the lack of autoecological knowledge of most of the potential canopy species. The constraint of limited information on dispersal ecology has been stressed above, but information on other autoecological aspects such as fruiting phenology, germination requirements, and stress tolerance, amongst others, is also very limited. Therefore, studies investigating these aspects are strongly recommended.

Fifth, more studies at the meso-scale investigating broad compositional patterns and diversity through transect surveys are called for. This concerns in particular areas so far under-sampled by this and other studies. The areas that should be targeted in particular are the West and higher altitudes of Rakata, and the South of Sertung. Difficulty of access poses a considerable problem, but such investigations would allow the quantification of observations such as those by Partomihardjo (1995) who suggested that *Timonius compressicaulis* is an important component in the near-coastal forest on the cliff-tops of the West of Rakata. On Sertung, an investigation of species composition and diversity of the southern part of the island could assess whether the forest composition on this island is still strictly divided between *Timonius* and *Dysoxylum* forest, and whether intra-island differences in diversity and species composition, particularly of the regeneration layer, are noticeable.

Sixth, it has been suggested that *Dysoxylum gaudichaudianum* is to a considerable extent stress tolerant to ash-fall, drought and herbivory, and that it is in the process of expanding its area of dominance in particular on Sertung, but also on Panjang. From results of the meso-scale study it was concluded that its importance in lowland Rakata is also likely to increase. Nevertheless, the claim of Tagawa *et al.* (1985) that all lowland forests on all islands are moving towards *Dysoxylum* dominance was rejected here, because in particular on Rakata *Dysoxylum* has to compete with a considerable number of other potential canopy species. To test the validity of their claim it would be necessary to quantify *Dysoxylum*'s abundance and spread at regular intervals. I suggest that further study would be particularly informative if carried out in about five to 10 years time. Within this period, the *Dysoxylum* understorey found in many near-coastal areas of Rakata will have had time to develop, whereas on Panjang and Sertung further volcanic disturbance may have influenced the course of *Dysoxylum*'s current expansion.

Seventh, a study concerned with establishing the importance of inter-specific differences in herbivory was initially intended as part of this research, but as described in section 1.5, difficulties encountered in this, and the opportunity to study the effects of volcanism on the vegetation, led to a change in focus. However, it still is an important area of investigation that may provide interesting insights into the differences in leaf damage and seed predation suffered by different species on the island, and how this may affect their future success. For instance, it would be interesting to establish whether inter-specific differences in herbivory favour the rarer species, and whether herbivore diversity and host-specificity play a significant role in influencing the amount of herbivory suffered. Thus, it could be investigated whether 'predation' is already a significant limiting factor for some species which in turn may affect the successional dynamics and diversification of the Krakatau islands (Connell & Slatyer, 1977; Brown, 1985; 1991). Some pilot studies have been carried out by Dr B. Turner and myself, and initial results indicated that, for instance, the Rakata dominant *Neonauclea* suffers from many more damage types than other species, and that this may be an indication of increased stress. However, one of the difficulties with herbivory studies is whether there is direct correlation with the amount of damage, and the number of different damage types and the impact on plant fitness. Different species have very different tolerances to herbivory, and in a field situation it is notoriously difficult to isolate which factor is most responsible for the reduction in the fitness of individuals of a particular tree species.

Eighth, other avenues of further research on the islands lie in the fields of forest hydrology as well as geomorphology, information on both of which would aid the understanding of vegetation dynamics on the islands. On forest hydrology, some studies have been carried out by Bruijnzeel (in prep.) and Hafkenscheid (1994). These were, however, mainly concerned with the question of forest stunting in the higher altitude of Rakata. Yet, during my study the great need for in-depth investigation of the general hydrological regime in the different areas of the islands became clear. This was brought to my attention particularly during the 1994 drought and as a result of the differential impact it seemed to have in different areas within the islands. Piping was found on several occasions (Fig. 2.6), and an investigation into its significance in influencing the speed, and quantity of drainage from particular areas would be very worthwhile. Furthermore, an extensive study on all islands on the differences in soil permeability, infiltration, and water holding capacities may be able to highlight areas of excessive *versus* moderate drainage and could aid in the prediction of future drought impact.

Ninth, closely linked to hydrological studies, intensive studies of the geomorphological dynamics would enhance our knowledge of the relative importance of, for instance, erosional processes in the disturbance regime of the islands. That the geomorphological regime is dynamic and appears to be a major factor influencing the disturbance regime has been observed frequently in this and other studies (CHAPTER 2; Docters van Leeuwen, 1936; Whittaker *et al.* 1989; Swabey, in lit), but no quantitative information exists. Observations from this study has also suggested that there is a link between the effects of drought reducing plant cover and erosion, as the signs of erosion, after the wet-season which followed the 1994 drought, were particularly pronounced. Quantification of such links would be highly desirable.

In general Bazzaz (1991) has stressed the great need for demographic studies, detailed physiological studies in relation to drought, and to high and low light intensities, the effect of pathogens, and nutrient availability. Most of these areas of ecological study have been stressed as valuable pathways for future study on the Krakatau islands. In the case of this study some of the most basic questions, such as an attempt at quantifying the disturbance regime, investigating the species composition and short term dynamics of gap regeneration, and increasing the knowledge on the mosaic nature of the forests on the different islands, still needed addressing.

Concluding remarks

This study has attempted to provide more insight into the process of regeneration and diversification in relation to disturbance of varying types and severities. It has further contributed to establishing the broad picture of the successional dynamics in a landscape ecological sense. For the first time, also, attention was drawn to the importance of extreme climatic events, and anthropogenic disturbance factors on the succession of Krakatau. Further evidence was found on all spatial scales that the mono-dominance of *Neonauclea* and *Timonius* is in decline, but that *Dysoxylum* is one of the most successfully spreading species on the island. In relation to volcanic disturbance from ash-fall and the drought, extreme short-term dynamics could be observed, of which the post-drought invasion by *Macaranga tanarius* was one of the most striking elements. Findings of this study have also contributed to the autoecological knowledge of some of the dominants as well as some of the rare species. However, within the scope of this study it was not possible to address questions concerning, for instance, complicated interactions (e.g. mycorrhizal associations, allelopathic inhibitions, and herbivory) that may influence the successional development. Thus, there are still manifold avenues of research that are needed in the pursuit of a more complete understanding of the rebuilding of this tropical island ecosystem.

BIBLIOGRAPHY

- Allen, B., Brookfield, H. & Byron, Y. (1989). Frost and drought through time and space. Part II: the written oral and proxy records and their meaning. *Mountain Research and Development* **9**: 279-305.
- Allen, R. J. (1988). El Niño southern Oscillation influences in the Australasian region. *Progress in Physical Geography* **12**: 313-348.
- Alvarez-Buylla, E. R. & Garcia-Barrios, R. (1991). Seed and forest dynamics: a theoretical framework and an example from the Neotropics. *The American Naturalist* **137**: 133-154.
- Alvarez-Buylla, E. R. & Martinez-Ramos, M. (1990). Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia (Berlin)* **84**: 314-325.
- Anderson, J. A. R. (1964). Observations on climatic damage in peat swamp forests in Sarawak. *Commonwealth Forestry Review* **43**: 145-149.
- Ashton, P. M. S., Gunatilleke, C. V. S. & Gunatilleke, I. A. U. N. (1995). Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. *Journal of Tropical Ecology* **11**: 263-279.
- Ashton, P. S. (1969). Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* **1**: 155-196.
- Aubréville, A. (1938). La forêt coloniale; les forêts de l'Afrique occidentale française. *Annales Académie des Sciences Coloniales Paris*: **9**.
- Augspurger, C. K. (1984). Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* **65**: 1705-1712.
- Backer, C. A. (1929). *The problem of Krakatao as seen by a botanist*. Surabaya, by the author.
- Backer, C. A. & Bakhuizen van den Brink, R. C. (1963-68). *The flora of Java*. Groningen, N.V.P. Noordhoff.
- Bardon, R. E., Countryman, D. W. & Hall, R. B. (1995). A reassessment of using light-sensitive diazo paper for measuring integrated light in the field. *Ecology* **76**: 1013-1016.
- Baren, J. v. (1931). Properties and constitution of a volcanic soil, built in 50 years in the East-Indien Archipelago. *Medeelingen van de Landbouwhoogeschool te Wageningen* **35**: 6.
- Barker, N. & Richards, K. (1982). The vegetation of Anak Krakatau. *The Krakatoa Centenary Expedition: final report*. Flenley, J. R. and Richards, K. Hull, University of Hull, Department of Geography. Miscellaneous Series No. 25: 143-164.
- Barton, A. M. (1984). Neotropical pioneer and shade-tolerant tree species: do they partition tree-fall gaps? *Tropical Ecology* **25**: 196-202.

- Bazzaz, F. A. (1984). Dynamics of wet tropical forests and their species strategies. *Physiological ecology of plants of the wet tropics*. Medina, E., Mooney, H. A. and Vazques-Yanes, C. The Hague, Dr. W. Junk Publishers: 233-243.
- Bazzaz, F. A. (1991). Regeneration of tropical forests: physiological responses of pioneer and secondary species. *Rain forest regeneration and management*. Gomez-Pompa, A., Whitmore, T. C. and Hadley, M. Paris, UNESCO: 91-117.
- Bazzaz, F. A. & Wayne, P. M. (1994). Coping with Environmental heterogeneity: The physiological ecology of tree seedling regeneration across the gap-understorey continuum. *Exploitation of environmental heterogeneity*. Caldwell, M. M. and Pearcy, R. W. San Diego, Academic Press: 349-390.
- Becker, P. (1983). Effect of insect herbivory and artificial defoliation on survival of *Shorea* seedlings. *Tropical rain forest: ecology and management*. Sutton, S. L., Whitmore, T. C. and Chadwick, A. C. Oxford, Blackwell Scientific Publications.
- Becker, P., Erhart, D. W. & Smith, A. P. (1989). Analysis of forest light environments part I. computerised estimation of solar radiation from hemispherical canopy photographs. *Agricultural and Forest Meteorology* **44**: 217-232.
- Becker, P. & Smith, A. P. (1990). Spatial autocorrelation of solar radiation in a tropical moist forest understorey. *Agricultural and Forest Meteorology* **52**: 373-379.
- Bellingham, P. J., Tanner, E. V. J. & Healey, J. R. (1994). Sprouting of trees in Jamaican montane forests after a hurricane. *Journal of Ecology* **82**: 747-758.
- Belsky, A. J. (1986). Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. II. Five years of successional change. *Journal of Ecology* **74**: 937-951.
- Bemmelen, R. W. v. (1929). The Krakatau volcano and its eruptions since December 1927. Video film. Utrecht, Geological Institute of the University of Utrecht.
- Bird, E. C. F. & Rosengren, N. J. (1984). The changing coastline of the Krakatau Islands, Indonesia. *Zeitschrift fuer Geomorphologie* **28**: 347-366.
- Borssum Waalkes, J. v. (1954). The Krakatau islands after the eruption of October 1952. *Penggemar Alam* **34**: 97-104.
- Borssum Waalkes, J. v. (1960). Botanical observations on the Krakatau Islands in 1951 and 1952. *Annales Bogorienses* **4**: 1-64.
- Braak, C. (1925). The climate of the Netherlands Indies. *Vehandelingen van het Koninklijk Magnetisch en Meteorologisch Observatorium te Batavia*. **8**: 1-497.
- Bradshaw, A. D. (1987). The reclamation of derelict land and the ecology of ecosystems. *Restoration ecology: a synthetic approach to ecological research*. Jordan, W. R. I., Gilpin, M. E. and Aber, J. D. New York, Cambridge University Press: 53-83.

Brandani, A., Hartshorn, G. S. & Orians, G. H. (1988). Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *Journal of Tropical Ecology* **4**: 99-119.

Bray, J. R. (1956). Gap phase replacement in a maple-basswood forest. *Ecology* **37**: 598-600.

Brokaw, N. V. L. (1982). The definition of treefall gap and its effects on measures of forest dynamics. *Biotropica* **14**: 158-160.

Brokaw, N. V. L. (1985). Treefalls, regrowth and community structure in tropical forests. *Natural disturbance: an evolutionary perspective*. Pickett, S. T. A. and White, P. S. New York, Academic Press: 53-69.

Brokaw, N. V. L. (1987). Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology, UK* **75**: 9-19.

Brown, N. D. (1990). *Dipterocarp regeneration in tropical rainforest gaps of different sizes*. D.Phil. thesis, Oxford Forestry Institute, Department of Plant Sciences, University of Oxford.

Brown, N. D. (1993). The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology* **9**: 153-168.

Brown, N. D. & Jennings, S. (in press). Gap size niche differentiation by tropical rain forest trees: a testable hypothesis or a broken-down bandwagon? *Population and community dynamics in the tropics*. Newbery, D. M., Prins, H. and Brown, N. D. Oxford, Blackwells. British Ecological Society Symposium no. **34**.

Brown, N. D. & Whitmore, T. C. (1992). Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society London B* **335**: 369-378.

Brown, V. K. (1984). Secondary succession: insect plant relationships. *Bioscience* **34**: 711-716.

Brown, V. K. (1985). Insect herbivores and succession. *Oikos* **44**: 17-22.

Brown, V. K. (1991). Insect herbivores, herbivory and plant succession. *Genetics, Evolution, and co-ordination of insect life-cycles*. Gilber, F. New York, Springer: 183-196.

Brünig, E. F. (1964). A study of damage attributed to lightning in two areas of *Shorea albida* forest in Sarawak. *Commonwealth Forestry Review* **43**: 134-144.

Bush, M. (1986a). Some effects of physical processes on the redevelopment of the forests of Krakatau. *Krakatoa Centenary Expedition 1983: final report*. Bush, M., Jones, P. and Richards, K. Hull, England, Department of Geography, University of Hull. Miscellaneous Series No. **33**: 57-76.

Bush, M. (1986b). A biogeographical appraisal of the butterflies of Krakatau. *Krakatoa Centenary expedition 1983: final report*. Bush, M. D., Jones, P. and Richards, K. Hull, England, Department of Geography, University of Hull. Miscellaneous Series No. **33**: 97-112.

- Bush, M., Jones, P. A. & Richards, K. (1986). Conservation of Krakatau. *Krakatoa Centenary Expedition 1983: final report*. Bush, M., Jones, P. A. and Richards, K. Hull, England University of Hull, Department of Geography. Miscellaneous Series No. **33**: 157-166.
- Bush, M. B. & Whittaker, R. J. (1991). Krakatau: colonisation patterns and hierarchies. *Journal of Biogeography* **18**: 341-356.
- Bush, M. B. & Whittaker, R. J. (1993). Non-equilibrium in island theory of Krakatau. *Journal of Biogeography* **20**: 453-457.
- Bush, M. B. & Whittaker, R. J. (1995). Colonisation and succession on Krakatau: an analysis of the guild of vining plants. *Biotropica* **27**: 355-372.
- Bush, M. B., Whittaker, R. J. & Partomihardjo, T. (1992). Forest development on Rakata, Panjang and Sertung: Contemporary dynamics (1979-1989). *GeoJournal* **28**: 185-199.
- Canham, C. D. (1989). Different responses to gaps among shade-tolerant tree species. *Ecology* **70**: 548-550.
- Challinor, J. (1964). *A dictionary of geology*. 2nd ed. Cardiff, University of Wales Press.
- Chandrashekara, U. M. & Ramakrishnan, P. S. (1993). Germinable soil seed bank dynamics during the gap phase of a humid tropical forest in the Western Ghats of Kerala, India. *Journal of Tropical Ecology* **9**: 455-467.
- Chazdon, R. L. (1988). Sunflecks and their importance to forest understorey plants. *Advances in Ecological Research* **18**: 2-54.
- Chazdon, R. L. & Fetcher, N. (1984). Photosynthetic light environment in a tropical rain forest in Costa Rica. *Journal of Ecology* **72**: 553-564.
- Chazdon, R. L. & Field, C. B. (1987). Photographic estimation of photosynthetically active radiation : evaluation of a computerised technique. *Oecologia* **73**: 525-532.
- Cheke, A. S., Nanakorn, W. & Yankoses, C. (1979). Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in Northern Thailand. *Biotropica* **11**: 88-95.
- Christensen, N. L. & Peet, R. K. (1984). Convergence during secondary forest succession. *Journal of Ecology* **72**: 25-36.
- Clark, D. A. & Clark, D. B. (1992). Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecological Monographs* **62**: 315-344.
- Clark, D. B. (1990). The role of disturbance in the regeneration of Neotropical moist forests. *Reproductive ecology of tropical forest plants*. Bawa, K. S. and Hadley, M. Paris, UNESCO. **7**: 291-315.
- Clark, D. B. & Clark, D. A. (1989). The role of physical damage in the seedling mortality regime of a Neotropical rain forest. *Oikos* **55**: 225-230.

- Clark, D. B. & Clark, D. A. (1991). The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* **79**: 447-457.
- Clark, D. B., Clark, D. A. & Rich, P. M. (1993). Comparative analysis of microhabitat utilisation by saplings of nine tree species in Neotropical rain forest. *Biotropica* **25**: 397-407.
- Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation*. Washington, D.C., Carnegie Institution of Washington.
- Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* **53**: 209-233.
- Compton, S. G., Ross, S. J. & Thornton, I. W. B. (1994). Pollinator limitation of fig tree reproduction on the island of Anak Krakatau (Indonesia). *Biotropica* **26**: 180-186.
- Compton, S. G., Wiebes, J. T. & Berg, C. C. (1996). The biology of fig trees and their associated animals. *Journal of Biogeography* **23**: 405-407.
- Condit, R., Hubbell, S. P. & Foster, R. B. (1995). Mortality rates of 205 Neotropical tree species and the responses to a severe drought. *Ecological Monographs* **65**: 419-439.
- Condit, R., Hubbell, S. P. & Foster, R. P. (1996). Changes in tree species abundance in a Neotropical forest: impact of climate change. *Journal of Tropical Ecology* **12**: 231-256.
- Condit, R., Hubbell, S. P., Lafrankie, J. V., Sukumar, N., Manokaran, N., Foster, R. B. & Ashton, P.S. (1996). Species-area and species individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* **84**: 549-562.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1310.
- Connell, J. H. (1989). Some processes affecting the species composition in forest gaps. *Ecology* **70**: 560-562.
- Connell, J. H. & Lowman, D. (1989). Low-diversity tropical rain forests: some possible mechanisms for their existence. *The American Naturalist* **134**: 88-119.
- Connell, J. H. & Slatyer, I. C. (1977). Mechanisms of succession in natural communities and their role in community structure and organisation. *The American Naturalist* **111**: 1119-1144.
- Connell, J. H., Tracey, J. G. & Webb, L. J. (1984). Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs* **54**: 141-164.
- Corner, E. J. H. (1952). *Wayside trees of Malaya*. Singapore, Government Printer.
- Dalling, J. W. (1992). Regeneration on landslides in the Blue Mountains, Jamaica. Ph.D. thesis. University of Cambridge, Cambridge, UK.
- Dalling, J. W. & Tanner, E. V. (1995). An experimental study of regeneration on landslides in montane rain forest in Jamaica. *Journal of Ecology* **83**: 55-64.

- Dalling, J. W., Swaine, M. D. & Garwood, N. C. (1994). Effect of soil depth on seedling emergence in tropical soil seed-bank investigations. *Functional Ecology* **9**: 119-121.
- Dammerman, K. W. (1948). The fauna of Krakatau 1883-1933. *Vehandelingen der Koninklijke Nederlandse Akademie van Wetenschappen Afdeling Natuurkunde (Tweede Sectie)* **44**: 1-594.
- de Neve, G. A. (1953). *Krakatoa and Anak Krakatoa, with a communication on the latest investigation in October 1953*. 8th Pacific Science Congress, Manila, Philippines. National Research Council of the Philippines, Queson City.
- de Neve, G. A. (1982a). Anak Krakatau (1930-1980): fifty years of geomorphological development and growth with the petrographically derived consequences. *Proceedings PIT X Ikatan Ahli Geologi Indonesia*. Bandung 8-10 December 1981, Indonesian Association of Geologists.
- de Neve, G. A. (1982b). The Krakatau group and Anak Krakatau's eruptivity. Snapshot of 1981. *Berita Geologi/Geosurvey Newsletter* **14**: 195-211.
- de Neve, G. A. (1985). Geovolcanology of the Krakatau group in the Sunda Strait Region - review of a hundred years development (1883-1983). *Proceedings of the Symposium on 100 years development of Krakatau and its surrounding*. Jakarta, LIPI, Indonesian Institute of Sciences.: 20-34.
- Denslow, J. S. (1980). Gap partitioning among tropical rainforest trees. *Biotropica* **12**: 47-55.
- Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**: 431-451.
- Denslow, J. S. & Gomez-Diaz, A. E. (1990). Seed rain to tree-fall gaps in a neotropical rain forest. *Canadian Journal of Forest Research* **20**: 642-648.
- Denslow, J. S., Schultz, J. C., Vitousek, P. M. & Strain, B. R. (1990). Growth responses of tropical shrubs to treefall gap environments. *Ecology* **71**: 165-179.
- Diaz, H. F. & Markgraf, V., Eds. (1992). *El Niño: historical and paleoclimatic aspects of the Southern Oscillation*. Cambridge, Cambridge University Press.
- Dobson, A. J. (1990). *An introduction to general linear modelling*. London, Chapman and Hall.
- Docters van Leeuwen, W. M. (1923). On the present state of the vegetation of the islands of the Krakatau Group and of the island of Sebesi. *Proceedings of the second Pan Pacific science conference*, Australia.: 313-318.
- Docters van Leeuwen, W. M. (1936). Krakatau 1883-1933. *Annales du Jardin Botanique de Buitenzorg* **46-47**: 1-507.
- Drake, D. R. (1993). Germination requirements of *Metrosideros polymorpha*, the dominant tree of Hawaiian lava flows and rain forests. *Biotropica* **25**: 461-467.

- Ernst, A. (1907). *Die neue Flora der Vulkaninsel Krakatau*. Zuerich, Faesi & Beer.
- Ernst, A. (1934). Das biologische Krakatauprobem. *Vierteljahresschrift der Naturforschenden Gesellschaft in Zuerich* **22**: 1-187.
- Fernandez, D. S. & Fetcher, N. (1991). Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica* **23**: 393-399.
- Finegan, B. (1984). Forest succession. *Nature* **312**: 109-114.
- Fleming, T. H. & Heithaus, E. R. (1981). Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica* **13**: 45-53.
- Flenley, J. R. & Richards, K. (1982). The Krakatoa Centenary Expedition: final report, University of Hull, Department of Geography.
- Fosberg, F. R. (1985). Botanical visits to Krakatau in 1958 and 1963. *Atoll Research Bulletin* **292**: 39-45.
- Friend, D. T. C. (1961). A simple method of measuring integrated light values in the field. *Ecology* **42**: 577-580.
- Garwood, N. C. (1985). Earthquake-caused landslides in Panama: recovery of vegetation. *National Geographic Society Research Reports* **21**: 181-184.
- Garwood, N. C. (1989). Tropical soil seed banks: a review. *Ecology of soil seed banks*. Leck, M. A., Parker, V. T. and Simpson, R. L. San Diego, Academic Press, Inc.: 149-210.
- Gauch, H. G. (1982). *Multivariate analysis in community ecology* Cambridge, Cambridge University Press.
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 1-20.
- Government of Indonesia (1990). *Act of the Republic of Indonesia No. 5 of 1990 concerning the conservation of living resources and their ecosystems*.
- Grime, J. P. (1979). *Plant strategies and vegetation processes* New York, John Wiley & Son.
- Grubb, P. J. (1977). The maintenance of high species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**: 107-145.
- Guariguata, M. R. (1990). Landslide disturbance and forest regeneration in the upper Luquillo mountains of Puerto Rico. *Journal of Ecology* **78**: 814-832.
- Guevara, S. & Gomez-Pompa, A. (1972). Seeds from surface soils in a tropical region of Vera Cruz, Mexico. *Journal of the Arnold Arboretum* **53**: 312-335.

- Hafkenscheid, R. L. L. J. (1994). *Hydrological observations in rain forest of contrasting stature on Gunung Rakata (Krakatau), Indonesia, with special reference to the "Massenerhebung" effect*. M.Sc thesis. Faculty of Earth Sciences, Amsterdam, Vrije Universiteit.
- Hall, J. B. & Swaine, M. D. (1980). Seed stocks in Ghanaian forest soils. *Biotropica* **12**: 256-263.
- Halpern, C. B. (1988). Early successional pathways and the resistance and resilience of forest communities. *Ecology* **69**: 1703-1715.
- Hardjowigeno, S. (1992). The development and nature of soils on Rakata. *GeoJournal* **28**: 131-138.
- Hardjowigeno, S., Subagyo, H., Satari, A. M. & Wiranegara, H. (1983). Properties and the development of soils derived from pumiceous tuff of the 1883 eruption. *Proceedings of the symposium on 100 years of development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 281-287.
- Harjosoesastro, R. & Dai, J. (1985). Pumiceous tuff of the eruption of Krakatau in 1883 on Rakata island and its development. *Proceedings of the symposium on 100 years development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 72-83.
- Harper, J. L. (1977). *Population biology of plants*. London, Academic Press.
- Hart, T. B. (1995). Seed, seedling and sub-canopy survival in monodominant and mixed forests of the Ituri Forest, Africa. *Journal of Tropical Ecology* **11**: 443-459.
- Hartstorn, G. S. (1978). Treefalls and tropical forest dynamics. *Tropical trees as a living system*. Tomlinson, P. B. and Zimmermann, M. H. Cambridge, Cambridge University Press: 617-616.
- Higashi, T., Miyauchi, N., Shinagawa, A., Djuwansh, M. R. & Sule, A. (1987). Forest vegetation and the nutritional status of soils on the Krakatau Islands, Indonesia. *Soil Science and Plant Nutrition* **33**: 103-122.
- Hill, M. O. (1979). TWINSpan - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Ithaca, N.Y., Cornell University.
- Hill, M. O. & Gauch, H. G. (1980). Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42**: 47-58.
- Hopkins, M. S. & Graham, A. W. (1983). The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica* **15**: 90-99.
- Hopkins, M. S. & Graham, A. W. (1987). The viability of seeds of rainforest species after experimental soil burials under tropical wet lowland forest in north-eastern Australia. *Australian Journal of Ecology* **12**: 97-108.

- Hoogerwerf, A. (1953). Notes on the vertebrate fauna of the Krakatau islands, with special reference to the birds. *Treubia* **22**: 319-348.
- Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**: 1299-1309.
- Hubbell, S. P. & Foster, R. B. (1986a). Canopy gaps and the dynamics of a Neotropical forest. *Plant ecology*. Crawley, M. J. Oxford, Blackwell Scientific Publications: 77-96.
- Hubbell, S. P. & Foster, R. B. (1986b). Biology, chance and history and the structure of tropical rain forest tree communities. *Community Ecology*. Diamond, J. and Case, T. J. New York, Harper and Row: 314-329.
- Hubbell, S. P. & Foster, R. B. (1986c). Commonness and rarity in a Neotropical forest: implications for tropical tree conservation. *Conservation Biology: the science of scarcity and diversity*. Soulé, M. E. Sunderland, MA, Sinauer: 205-231.
- Hurlbert, S. H. (1971). The non-concept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577-586.
- Inouye, R. S. & Tilman, D. (1988). Convergence and divergence of old-field plant communities along experimental nitrogen gradients. *Ecology* **69**: 995-1004.
- Janzen, D. H. (1978). Description of a *Pterocarpus officinalis* (Leguminosae) monoculture in Corcovado National Park, Costa Rica. *Bresnia* **14**: 305-309.
- Janzen, D. H. (1979). How to be a fig. *Annual Review of Ecology and Sytematics* **10**: 13-51.
- Johns, R. J. (1986). The instability of the tropical ecosystem in New Guinea. *Blumea* **31**: 341-371.
- Jones, S. H., Whittaker, R. J. & Partomihardjo, T. (1993). Forest composition and dynamics: spatial variation in forest composition within the Sunda Strait region and changes over three years in forest permanent plots on Krakatau. *The recovery of tropical forest ecosystems from major disturbances: Krakatau, Sunda Straits, Indonesia*. Whittaker, R. J. and Jones, S. H. Final Report to ODA Forest Research Programme, School of Geography, University of Oxford, Oxford.: 1-24.
- Jordan, W. R. I., Gilpin, M. E. & Aber, J. D. (1987). *Restoration ecology: a synthetic approach to ecological research*. New York, Cambridge University Press.
- Kachi, N., Okuda, T. & Yap, S. K. (1993). Seedling establishment of a canopy tree species in Malaysian tropical rain forest. *Plant Species Biology* **8**: 167-174.
- Kapos, V., Pallant, E., Bien, A. & Freskos, S. (1990). Gap frequencies in lowland rain forest sites on contrasting soils in Amazonian Ecuador. *Biotropica* **22**: 218-225.
- Keddy, P. A. (1989). *Competition*. London, Chapman & Hall.

- Kennedy, D. N. & Swaine, M. D. (1992). Germination and growth of colonising species in artificial gaps of different sizes in dipterocarp rain forest. *Philosophical Transactions of the Royal Society London B* **335**: 357-366.
- Kent, M. & Coker, P. (1992). *Vegetation description and analysis: a practical approach*. London, Belhaven Press.
- Kitajima, K. & Augspurger, C. (1989). Seed and seedling ecology of a monocarpic tropical tree. *Ecology* **70**: 1102-1115.
- Kolasa, J. & Rollo, C. D. (1991). Introduction: The heterogeneity of heterogeneity: A glossary. *Ecological Heterogeneity*. Kolasa, J. and Pickett, S. T. A. New York, Springer-Verlag.
- Kovach, W.L. (1993). MSP Plus multivariate statistical package. Version 2.1. Abermagwr, Wales.
- Kusumadinata, K. ed. (1979). *Data dasar gunung api Indonesia*. Dir. Jen. Pertambangan Umum.
- Lambert, F.R.L. (1989). Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology* **5**: 401-412.
- Lambert, F.R.L. & Marshall, A.G. (1991). Keystone characteristics of bird-dispersed *Ficus* in Malaysian lowland rain forest. *Journal of Ecology* **79**: 793-809.
- Lawton, R. O. & Putz, F. E. (1988). Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology, USA* **69**: 764-777.
- Leibold, M. A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology* **76**: 1371-1382.
- Leigh, E. G. & Smythe, N. (1978). Leaf production, leaf consumption and the regulation of folivory on Barro Colorado Island. *The ecology of aboreal folivores*. Montgomery, G. G. Washington D.C., Smithsonian Press.: 33-50.
- Leighton, M. (1986). Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982-83 El Niño Southern Oscillation event . *Tropical rain forests and the world atmosphere*. Prance, G. T. Boulder, Westview.: 75-102.
- Levey, D. J. (1990). Habitat-dependent fruiting behaviour of an understory tree *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* **6**: 409-420.
- Levey, D. J. & Byrne, M. M. (1993). Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* **74**: 1802-1812.
- Lieberman, D. (1996). Demography of tropical tree seedlings: a review. *The ecology of tropical forest tree seedlings*. Swaine, M. D. Paris, UNESCO. 17: 131-138.
- Lieberman, M., Lieberman, D. & Peralta, R. (1989). Forests are not just 'Swiss Cheese': canopy stereogeometry of non-gaps in tropical forests. *Ecology* **70**: 550-552.

- Lieberman, M., Lieberman, D., Peralta, R. & Hartshorn, G. S. (1995). Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology* **11**: 161-178.
- Liew, C. T. (1973). Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. *Malayan Forester* **36**: 185-193.
- Loiselle, B. A., Ribbens, E. & Vargas, O. (1996). Spatial and temporal variation of seed rain in a tropical lowland wet forest. *Biotropica* **28**: 82-95.
- Lowman, M. D. (1984). An assessment of techniques for measuring herbivory: is rain forest defoliation more intense than we thought? *Biotropica* **16**: 264-268.
- Lowman, M. D. (1985). Temporal and spatial variability in insect grazing of the canopies of five Australian rain forest tree species. *Australian Journal of Ecology* **10**: 7-24.
- Lugo, A. E. (1988). Ecological aspects of catastrophes in Caribbean islands. *Acta Cientifica* **2**: 24-31.
- Lugo, A. E. (1995). Reconstructing hurricane passages over forests: a tool for understanding multiple scale responses to disturbance. *Trends in Ecology and Evolution* **10**: 1-3.
- Lugo, A. E. & Scatena, F. N. (1996). Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* **28**: 585-599.
- Lugo, A. E. & Waide, R. B. (1993). Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental forest. *Journal of Bioscience* **4**: 475-481.
- MacArthur, R. H. & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, New Jersey, Princeton University Press.
- MacDougall, A. & Kellman, M. (1992). The understorey light regime and patterns of tree seedlings in tropical riparian forest patches. *Journal of Biogeography* **19**: 667-675.
- Magurran, A. E. (1988). *Ecological diversity and its measurement*. London, Croom Helm.
- Manokaran, N. & Swaine, M. D. (1995). *Population dynamics of trees in Dipterocarp forests of Peninsular Malaysia*. Kuala Lumpur, Forest Research Institute Malaysia. Malaysian Forest Records No. **40**.
- Marshall, A.G. (1985). Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society* **83**: 351-369.
- Matthews, J. A. (1979). A study of the variability of some successional and climax plant assemblage-types using multiple discriminant analysis. *Journal of Ecology* **67**: 255-271.
- Matthews, J. A. (1996). Classics in physical geography revisited: Gleason, H.A. (1939) The individualistic concept of the plant association. *The American Midland Naturalist* **21**, 92-110. *Progress in Physical Geography* **20**: 193-203.

- May, R. M. (1975). Patterns of species abundance and diversity. *Ecology and Evolution of Communities*. Cody, M. L. and Diamond, J. M. Cambridge, MA., Harvard University Press: 81-120.
- Mitchell, P. L. & Whitmore, T. C. (1993). Use of hemispherical photographs in forest ecology, Oxford Forestry Institute. *O.F.I Occasional Papers*. **44**
- Mitchell, T. (1994). *The ecology of Macaranga (Euphorbiaceae) trees in primary lowland mixed dipterocarp forest, Brunei*. Ph.D. Botany Department, University of Cambridge, Cambridge (UK).
- Miyauchi, N., Higashi, T., Shinagawa, A., Djuwansah, M. R. & Sule, A. (1986). The soils on the Krakatau islands: III. mineralogy of soils. *Memoirs of the Faculty of Agriculture. Kagoshima University*. **22**: 157-167.
- Molofsky, J. & Augspurger, C. K. (1992). The effect of litter on early seedling establishment in a tropical forest. *Ecology* **73**: 68-77.
- Morrow, P. A. (1977). The significance of phytophagous insects in the *Eucalyptus* forests of Australia. *The role of arthropods in forest ecosystems*. Mattson, W. J. New York, Springer.
- Mueller-Dombois, D. (1991). The mosaic theory and the spatial dynamics of natural dieback and regeneration Pacific forests. *The mosaic-cycle concept of ecosystems*. Remmert, H. Berlin, Springer-Verlag.: 46-60.
- Mueller-Dombois, D. (1992). Distributional dynamics in Hawaiian vegetation. *Pacific Science* **46**: 221-231.
- Mukhtar, E., Suzuki, E., Kohyama, T. & Rahman, M. (1992). Regeneration process of a climax species *Calophyllum* cf. *soulattri* in tropical rain forest of West Sumatra. *Tropics* **2**: 1-12.
- Nelson, B. W., Kapos, V., Adams, J. B., Oliveira, W. J., Braun, O. P. G. & do Amaral, I.L. (1994). Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* **75**: 853-858.
- Neumann van Padang, M. (1951). *Catalogue of the active volcanoes of the world including solfatara fields. Part I. Indonesia*. Naples, Italy, International Volcanic Association.
- Newbery, D. M., Campell, E. J. F., Lee, Y. F., Ridsdale, C: E. & Still, M. (1992). Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative, abundance and family composition. *Philosophical Transactions of the Royal Society of London B* **335**: 341-356.
- Newsome, D. (1982). Soil development on Rakata. *The Krakatoa Centenary Expedition: final report*. Flenley, J. R. and Richards, K. Hull, England, Department of Geography. Miscellaneous Series No. 25.: 83-102.
- Newsome, D. (1986). Aspects of soil surface characteristics on Rakata and Anak Krakatau. *Krakatoa Centenary Expedition 1983: final report*. Bush, M., Jones, P. and Richards, K. Hull, University of Hull, Department of Geography. Miscellaneous Series No. **33**: 134-156.

- Nicholls, N. (1991). The El Niño / Southern Oscillation and Australian vegetation. *Vegetatio* **91**: 21-36.
- Nicholls, N. (1993). ENSO, drought and flooding rain in South-East Asia. *South-east Asia's environmental future*. Brookfield, H. and Byron, Y. Tokyo, United Nations University Press: 154-175.
- Ninkovich, D. (1979). Distribution , age and chemical composition of tephra layers in deep-sea sediments off Western Indonesia. *Journal of Volcanology and Geothermal Research* **5**: 67-86.
- Núñez-Farfán, J. & Dirzo, R. (1988). Within-gap spatial heterogeneity and seedling performance in a Mexican tropical forest. *Oikos* **51**: 274-284.
- Oldeman, R. A. A. (1974). L'architecture de la foret Guyanaise. *Memoires ORSTOM* **73**: 1-204.
- Orians, G. H. (1982). The influence of treefalls on tropical forest tree species richness. *Tropical Ecology* **23**: 255-279.
- Partomihardjo, T. (1995). *Studies on the ecological succession of plants and their associated insects on the Krakatau islands, Indonesia*. PhD thesis. United Graduate School of Agricultural Sciences, Kagoshima University, Kagoshima, Japan.
- Partomihardjo, T., Mirmanto, E. & Whittaker, R. J. (1992). Anak Krakatau's vegetation and flora circa 1991, with observations on a decade of development and change. *Geojournal* **28**: 233-248.
- Penzig, O. (1902). Die Fortschritte der Flora des Krakatau. *Annales du Jardin Botanique de Buitenzorg* **18**: 92-113.
- Pickett, S. T. A. (1980). Non-equilibrium co-existence of plants. *Bulletin of the Torrey Botanical Club* **197**: 238-248.
- Pickett, S. T. A., Collins, S. L. & Armesto, J. J. (1987). A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**: 109-114.
- Pickett, S. T. A., Ostfeld, R. S., Shachak, M. & Likens, G. E., Eds. (1997). *The ecological basis of conservation*. New York, Chapman & Hall.
- Pickett, S. T. A., Parker, V. T. & Fiedler, P. L. (1992). The new paradigm in ecology: implications for conservation biology above the species level. *Conservation Biology: the theory and practice of nature conservation preservation and management*. Fiedler, P. L. and Jain, S. K. New York, Chapman and Hall: 66-88.
- Pickett, S. T. A. & White, P. S. (1985). *The ecology of natural disturbance and patch dynamics*. Orlando, Fl., Academic Press.
- Pompa, J., Bongers, F., Martinez-Ramos, M. & Veneklaas, E. (1988). Pioneer species distribution in treefall gaps in neotropical rain forest: a gap definition and its consequences. *Journal of Tropical Ecology* **4**: 77-88.

- Press, M. C., Brown, N. D., Barker, M. G. & Zipperlin, S. W. (1996). Photosynthetic responses to light in tropical rain forest tree seedlings. *Ecology of tropical tree seedlings*. Swaine, M. D. Paris, UNESCO and Parthenon: 41-58.
- Primack, R. & Lee, H. S. (1991). Population dynamics of pioneer (*Macaranga*) and understorey (*Mallotus*) trees (Euphorbiaceae) in primary and selectively logged Bornean rain forests. *Journal of Tropical Ecology* 7: 439-458.
- Primack, R. B., Ashton, P. S., Chai, P. & Lee, H. S. (1985). Growth rates and population structure of Moraceae trees in Sarawak, East Malaysia. *Ecology* 66: 954-958.
- Putz, E. E. & Appanah, S. (1987). Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19: 326-333.
- Raich, J. W. & Khoon, G. W. (1990). Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology* 6: 203-217.
- Raich, W. J. & Christensen, L. N. (1989). Malaysian dipterocarp forest: tree seedling and sapling species composition and small-scale disturbance patterns. *National Geographic Research* 5: 348-363.
- Rich, P. M. (1990). Characterising plant canopies with hemispherical photographs. *Remote Sensing Review* 5: 13-29.
- Richards, K. (1982). Notes on the geomorphology of Krakatau. *The Krakatoa Centenary Expedition: final report*. Flenley, J. R. and Richards, K. Hull, University of Hull, Department of Geography. Miscellaneous Series No. 25.: 184-187.
- Richards, P. W. (1952). *The tropical rain forest: an ecological study* Cambridge, Cambridge University Press.
- Richards, P. W. (1996). *The tropical rain forest: an ecological study*. 2nd ed., Cambridge, Cambridge University Press.
- Ricklefs, R. E. (1977). Environmental heterogeneity and plant species diversity: a hypothesis. *The American Naturalist* 111: 376-381.
- Robinson, J. V. & Dickerson, J., J.E. (1987). Does invasion sequence affect community structure? *Ecology* 68: 587-595.
- Rogers, K. H. (1997). Operationalizing ecology under a new paradigm: an African perspective. *The ecological basis of conservation*. Pickett, S. T. A., Ostfeld, R. S., Shachak, M. and Likens, G. E. New York, Chapman & Hall: 60-77.
- Root, R. B. (1973). Organisation of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43: 95-120.
- Rosengren, N. J. (1985). The changing outline of Sertung, Krakatau islands, Indonesia. *Zeitschrift für Geomorphology* 57: 105-119.

- Rosengren, N. J. & Suwardi, A. (1985). Coastal geomorphology of Anak Krakatau and Sertung. *Proceedings of the symposium on 100 years development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 1-17.
- Sandford Jr., R. L. (1989). Fine root biomass under a tropical forest light gap opening in Costa Rica. *Journal of Tropical Ecology* **5**: 251-256.
- Sarukhan, J., Pinero, D. & Martinez-Ramos, M. (1985). Plant demography: a community level interpretation. *Studies in plant demography: a festschrift for John L. Harper*. White, J. London, UK, Academic Press: 17-31.
- Saulei, S. M. & Swaine, M. D. (1988). Rain forest seed dynamics during succession at Gogol, Papua New Guinea. *Journal of Ecology* **76**: 1133-1152.
- Schimper, A.F.W. & Faber, P.S. (1935). *Pflanzen Geographie auf physiologischer Basis*. 2nd edition .
- Schlesinger, W. H., Bruijnzeel, L. A., Bush, M. B., Klein, E. M., Mace, K. A. *et al.* (submitted). The biogeochemistry of phosphorus after the first century of soil development on Rakata island, Krakatau, Indonesia. *Soil Science*.
- Schmitt, S. F. & Partomihardjo, T. (in press). Disturbance and its significance for forest succession and diversification on the Krakatau islands, Indonesia. *Proceedings of the third Flora Malesiana Symposium*. Dransfield, J., Coode, M. & Johns, R. Kew, Richmond, Surrey, UK, Royal Botanical Gardens Kew .
- Schmitt, S. F. & Whittaker, R. J. (in press). Disturbance and succession on the Krakatau islands, Indonesia. *Population and community dynamics in the tropics*. Newbery, D. M., Prins, H. and Brown, N. D. Oxford, Blackwells. British Ecological Society Symposium no. **34**.
- Schröter, C. (1935). Das biologische Krakatau problem. *Die Naturwissenschaften* **15**: 240-244.
- Schupp, E. W., Howe, H. F., Augspurger, C. K. & Levey, D. J. (1989). Arrival and survival in tropical treefall gaps. *Ecology* **70**: 562-564.
- Seagle, S. W. & Shugart, H. H. (1985). Faunal richness and turnover dynamic on landscapes: A simulation study. *Journal of Biogeography* **12**: 499-508.
- Sernander, R. (1936). Granskär och Fiby urskog (Swedish, with English summary: The primitive forests of Granskär and Fiby: a study of the part played by storm-gaps and dwarf trees in the regeneration of the Swedish spruce forest). *Acta Phytographica Suecica* **8**.
- Sheil, D. (1996). *The ecology and long term change in a Ugandan rain forest*. D.Phil thesis. Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, Oxford.
- Sheil, D., Burslem, D. F. R. P. & Alder, D. (1995). The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* **83**: 331-333.
- Sheil, D. & May, R. (1996). Mortality and recruitment rate evaluations in heterogeneous populations. *Journal of Ecology* **84**: 91-100.

- Shinagawa, A., Miyauchi, N. & Higashi, T. (1992). Cumulic soils on Rakata, Sertung and Panjang (Krakatau Is.) and properties of each solum. *GeoJournal* **28**: 139-151.
- Shinagawa, A., Miyauchi, N., Higashi, T., Djuwansah, M. R. & Sule, A. (1986). The soils on the Krakatau islands: IV accumulation and composition of humus. *Mem. Fac. Agr. Kagoshima Univ.* **22**: 169-176.
- Shinagawa, A., Miyauchi, N., Higashi, T., Djuwansah, R. & Sule, A. (1985). The soils on the Krakatau Islands. *Proceedings of the symposium on 100 years of development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 273-280.
- Shmida, A. & Wilson, M. A. (1985). Biological determinants of species diversity. *Journal of Biogeography* **12**: 1-20.
- Silvertown, J. (1987). *Introduction to plant population ecology*. 2nd ed., Oxford, Blackwell Scientific.
- Simkin, T. & Fiske, R.S. (1983). *Krakatau 1883: the volcanic eruption and its effects*. Washington, D.C., Smithsonian Institution Press.
- Siswowidjoyo, S. (1985). The renewed activity of Krakatau volcano after its catastrophic eruption of 1883. *Proceedings of the symposium on 100 years of development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 192-198.
- Smith, T. & Huston, M. (1989). A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* **83**: 49-69.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry: the principles and practice of statistics in biological research*. 2nd ed., New York, W.H. Freeman.
- Sousa, W. P. (1984). The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**: 353-391.
- Stehn, C. E. (1929). The geology and volcanism of the Krakatau Group. *Proceedings of the fourth Pan-Pacific Science Congress*, Batavia.: 1-55.
- Sterck, F., van der Meer, P. & Bongers, F. (1992). Herbivory in two rain forest canopies in French Guyana. *Biotropica* **24**: 97-99.
- Stiles, E. W. (1992). Animals as seed dispersers. *Seeds: the ecology of regeneration in plant communities*. Fenner, M. Wallingford, CAB International: 87-104.
- Subagjo, H. & van Reuler, H. (1985). Some characteristics of brown soils on Rakata Island developed in material originating prior to the 1883 Krakatau eruption. *Proceedings of the symposium on 100 years development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 288-295.
- Sugden, A. M. (1992). Hurricanes in tropical forests. *Trends in Ecology and Evolution* **7**: 146-147.

- Sullivan, T. J. & Mix, M. C. (1983). A simple and inexpensive method for measuring integrated light energy. *Environmental Science and Technology*. **17**: 127-128.
- Sumardja, E. A., Harsono & MacKinnon, J. (1984). Indonesia's network of protected areas. *National Parks, conservation and development: the role of protected areas in sustaining society*. McNeely, J. A. and Miller, K. R. Washington, D.C., IUCN/Smithsonian Institution Press.
- Sumartadipura, A. S. (1985). Brief review of the latest investigations and research regarding the geology and volcanism of Krakatau in the Sunda Straits Region (1979-1983). *Proceedings of the symposium on 100 years of development of Krakatau and its surroundings*. Jakarta, LIPI (Indonesian Institute of Sciences). 1: 7-10.
- Swaine, M. D. (1996). Foreword. *The ecology of tropical forest tree seedlings*. Swaine, M. D. Paris, UNESCO. 17: xxi-xxviii.
- Swaine, M. D. & Lieberman, D. (1987). Note on the calculation of mortality rates. *Journal of Tropical Ecology* **3**: 359-366.
- Swaine, M. D., Lieberman, D. & Putz, F. E. (1987). The dynamics of tree populations in tropical forest: a review. *Journal of Tropical Ecology* **3**: 359-366.
- Swaine, M. D. & Hall, J. B. (1983). Early succession on cleared forest land in Ghana. *Journal of Ecology* **71**: 601-627.
- Swaine, M. D. & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rainforests. *Vegetatio* **75**: 81-86.
- Symington, C. F. (1933). The study of secondary growth on rain forest sites. *Malaysian Forester* **2**: 107-117.
- Tagawa, H. (1992). Primary succession and the effect of first arrivals on subsequent development of forest types. *GeoJournal* **28**: 175-183.
- Tagawa, H., Suzuki, E., Partomihardjo, T. & Suriadarma, A. (1985). Vegetation succession on the Krakatau Islands, Indonesia. *Vegetatio* **60**: 131-145.
- Taylor, C. E. (1982). *Reproductive biology and ecology of some tropical pioneer trees*. PhD thesis, University of Aberdeen, Aberdeen.
- Terborgh, J. (1986). Keystone plant resources in tropical forests. *Conservation biology: the science of scarcity and diversity*. M.E. Soulé, Sunderland, MA, Sinauer Associates Inc. Publishers: 330-344.
- ter Braak, C. J. F. (1988). *CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis*. Wageningen, ITI-TNO.
- ter Steege, H. (1994). *Hemiphot: a programme to analyse vegetation indices, light and light quality from hemispherical photographs*. Wageningen, The Netherlands, Tropenbos Documents No 3, Tropenbos.

- Thompson, K. (1992). The functional ecology of seed banks. *Seeds: the ecology of regeneration in plant communities*. Fenner, M. Wallingford, CAB International: 231-258.
- Thornton, I. W. (1996). *Krakatau: the destruction and reassembly of an island ecosystem*. Cambridge, Massachusetts, Harvard University Press.
- Thornton, I. W. B. (1984). Krakatau the development and repair of a tropical ecosystem. *Ambio* **13**: 217-225.
- Thornton, I. W. B., Partomihardjo, T. & Yukawa, J. (1994). Observations on the effects, up to July 1993, of the current eruptive episode of Anak Krakatau. *Global Ecology and Biogeography Letters* **4**: 88-94.
- Thornton, I. W. B. & Rosengren, N. J. (1988). Zoological expeditions to the Krakatau islands, 1984 and 1985: general introduction. *Philosophical Transactions of the Royal Society B* **322**: 273-316.
- Thornton, I. W. B., Ward, S. A., Zann, R. A. & New, T. R. (1992). Anak Krakatau - a colonisation model within a colonisation model? *GeoJournal* **28**: 249-259.
- Thornton, I. W. B., Zann, R. A., Rawlinson, P. A., Tideman, C. R., Adikerana, A. S. *et al.* (1988). Colonisation of the Krakatau islands by vertebrates: equilibrium, succession and possible delayed extinction. *Proceedings of the National Academy of Sciences (USA)* **85**: 515-518.
- Treub, M. (1888). Notice sur la nouvelle flore de Krakatau. *Annales du Jardin Botanique de Buitenzorg* **7**: 213-223.
- Tutin, C. E. G., White, L. J. T. & Machanga-Missandzou, A. (1996). Lightning strike burns large forest tree in Lopé Reserve, Gabon. *Global Ecology and Biogeography Letters* **5**: 36-41.
- Uhl, C., Clark, K., Dezzio, N. & Marquirino (1988). Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**: 757-763.
- Umavedi, I., Daniel, M. & Sabnis, S. D. (1988). Chemotaxonomic studies on some members of Anacardiaceae. *Proceedings of the Indian Academy of Sciences, Plant Sciences* **98**: 205-208.
- Umbgrove, J. H. F. (1949). *Structural history of the East Indies*. Cambridge, Cambridge University Press.
- van der Meer, P. J. & Bongers, F. (1996). Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *Journal of Ecology* **84**: 19-29.
- Vandermeer, J., Mallona, M. A., Boucher, D., Yih, K. & Perfecto, Y. (1995). Three years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua: evidence in support of the direct regeneration hypothesis. *Journal of Tropical Ecology* **11**: 465-471.

- Vasquez-Yanes, C. & Orozco-Segovia, A. (1993). Patterns of seed longevity and germination in the tropical rain forest. *Annual Review of Ecology and Systematics* **24**: 69-87.
- Vazques-Yanes, C. & Orozco-Segovia, A. (1994). Signals for seeds to sense and respond to gaps. *Exploitation of environmental heterogeneity by plants*. Caldwell, M. M. and Pearcy, R. W. San Diego, Academic Press, Inc.: 209-236.
- Vázquez-Yanes, C., Orozco-Segovia, A., Rincón, E., Sánchez-Coronado, M. E., Huante, P. *et al.* (1990). Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* **71**: 1952-1958.
- Veblen, T. T. (1992). Regeneration dynamics. *Plant succession: theory and prediction*. Glenn-Lewin, D. C., Peet, R. K. and Veblen, T. T. London, Chapman & Hall.
- Veenendal, E. M., Swaine, M. D., Agyeman, V. K., Blay, D., Abebrese, I. K., Mullens, C.E. (1996). Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology* **84**: 83-90.
- Verbeek, R. D. M. (1885). Krakatau (original in Dutch, used here is partial translation into English). *Krakatau 1883 the volcanic eruption and its effects*. Simkin, T. and Fiske, R. S. Washington D.C., Smithsonian Institution Press. 169-201.
- Verkaar, H. J. (1987). Population dynamics - the influence of herbivory. *New Phytologist* **106**: 49-60.
- Viana, V. M. (1989). *Seed dispersal and gap regeneration: the case of three Amazonian tree species*. PhD thesis. Harvard University, Cambridge MA.
- Villa, F., Rossi, O. & Sartore, F. (1992). Understanding the role of chronic environmental disturbance in the context of island biogeographic theory. *Environmental Management* **16**: 653-666.
- Vitousek, P. M. & Denslow, J. S. (1986). Nitrogen and phosphorus availability in treefall gaps of a lowland tropical forest. *Journal of Ecology* **74**: 1167-1178.
- Walden, J., Whittaker, R. J. & Hill, J. (1991). The use of mineral magnetic analyses as an aid in investigating the recent volcanic disturbance history of the Krakatau Islands, Indonesia. *The Holocene* **1**: 262-268.
- Walker, L. R. (1987). Interactions among processes controlling successional change. *Oikos* **50**: 131-135.
- Walker, L. R. (1991). Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**: 379-385.
- Walker, L. R., Brokaw, N. V. L., Lodge, D. J. & Waide, R. B., Eds. (1991). *Special Issue: Ecosystem, plant, and animal responses to hurricanes in the Caribbean.*, Biotropica **23**.

- Walsh, R. P. D. (1996). Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* **12**: 385-407.
- Walsh, R. P. D. & Howells, K. A. (1988). Soil pipes and their role in runoff generation and chemical denudation in a humid tropical catchment in Dominica. *Earth Surface Processes and Landforms* **13**: 9-17.
- Warr, S. J., Thompson, K. & Kent, M. (1993). Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography* **17**: 329-347.
- Watt, A. S. (1923). On the ecology of British beechwoods with species reference to their regeneration. Part I. The causes of failure of natural regeneration of the beech (*Fagus sylvatica* L.). *Journal of Ecology* **11**: 1-48.
- Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology* **35**: 1-22.
- Welden, C. W., Hewett, S. W., Hubbell, S. P. & Foster, R. B. (1991). Sapling survival, growth, and recruitment: relationship to canopy height in a Neotropical forest. *Ecology* **72**: 35-50.
- Webb, L. J., Tracey, J.G. & Williams, W.T. (1972). Regeneration and pattern in the Subtropical rain forest. *Journal of Ecology* **60**: 675-696.
- Whitmore, T. C. (1974). *Change with time and the role of cyclones in tropical rainforest on Kolombangara, Solomon Islands*. Commonwealth Forestry Institute, Oxford.
- Whitmore, T. C. (1978). Gaps in the forest canopy. *Tropical trees as a living system*. Tomlinson, P. B. and Zimmermann, M. H. Cambridge, Cambridge University Press: 639-656.
- Whitmore, T. C. (1983). Secondary succession from seed in tropical rain forests. *Forestry Abstracts* **44**: 767-779
- Whitmore, T. C. (1984). Gap size and species richness in tropical rain forests. *Biotropica* **16**: 239.
- Whitmore, T. C. (1984). *Tropical rain forests of the Far East*. 2nd ed., Oxford, Clarendon Press.
- Whitmore, T. C. (1989). Changes over twenty-one years in the Kolombangara rain forests. *Journal of Ecology* **77**: 469-483.
- Whitmore, T. C. (1990). *An introduction to tropical rain forests* Oxford, Oxford University Press.
- Whitmore, T. C. (1991). Tropical rain forest dynamics and its implications for management. *Rain forest regeneration and management*. Gomez-Pompa, A., Whitmore, T. C. and Hadley, M. Paris, UNESCO: 67-90.

- Whitmore, T. C. (1996). A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. *Ecology of tropical tree seedlings*. Swaine, M. D. Paris, UNESCO and Parthenon: 3-39.
- Whitmore, T. C. & Brown, N. D. (1996). Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philosophical Transactions of the Royal Society London B* **351**: 1195-1203.
- Whitmore, T. C., Brown, N. D., Swaine, M. D., Kennedy, D. K., Goodwin-Bailey, C. I. *et al.* (1993). Use of hemisphere photography in forest ecology: II measurement of gap size and radiation totals in a Borneo tropical rain forest. *Journal of Tropical Ecology* **9**: 131-151.
- Whittaker, R. H. (1965). Dominance and diversity in land plant communities. *Science* **147**: 250-260.
- Whittaker, R. J. (1991). The vegetation of the Storbreen gletschervorfeld Jotunheimen, Norway. IV. Short-term vegetation change. *Journal of Biogeography* **18**: 41-42.
- Whittaker, R. J. (1992). Stochasticism and determinism in island ecology. *Journal of Biogeography* **19**: 587-591.
- Whittaker, R. J. (1995). Disturbed island ecology. *Trends in Ecology and Evolution* **10**: 421-425.
- Whittaker, R. J., Asquith, N. M. & Bush, M. B. (1990). *Krakatau Research Project 1989 Expedition Report*. Oxford, School of Geography, University of Oxford.
- Whittaker, R. J. & Bush, M. B. (1993). Dispersal and establishment of tropical forest assemblages, Krakatoa, Indonesia. *Primary succession on land*. Miles, J. and Walton, D. W. H. Oxford, Blackwells Scientific Publications. 12: 147-160.
- Whittaker, R. J., Bush, M. B., Partomihardjo, T., Asquith, N. M. & Richards, K. (1992b). Ecological Aspects of plant colonisation of the Krakatau islands. *GeoJournal* **28**: 201-211.
- Whittaker, R. J., Bush, M. B. & Richards, K. (1989). Plant recolonisation and vegetation succession on the Krakatau islands, Indonesia. *Ecological Monographs* **59**: 59-123.
- Whittaker, R. J. & Jones, S. H. (1993). *The recovery of tropical forest ecosystems from major disturbances: Krakatau, Sunda Straits, Indonesia*. Final Report to ODA Forest Research Programme, School of Geography, University of Oxford, Oxford.
- Whittaker, R. J. & Jones, S. H. (1994a). The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography* **21**: 245-258.
- Whittaker, R. J. & Jones, S. H. (1994b). Structure in re-building insular ecosystems: an empirically derived model. *Oikos* **69**: 524-529.
- Whittaker, R. J., Partomihardjo, T. & Riswan, S. (1995). Surface and buried seed banks from Krakatau, Indonesia: implications for the sterilization hypothesis. *Biotropica* **27**: 346-354.

- Whittaker, R. J., Richards, K., Wiriadinata, H. & Flenley, J. R. (1984). Krakatau 1883 to 1983: a biogeographical assessment. *Progress in Physical Geography* **8**: 61-81.
- Whittaker, R. J., Schmitt, S. F., Jones, S. H., Partomihardjo, T. & Bush, M. B. (submitted). Stand biomass and turnover of permanent forest plots on Krakatau, 1989-1995. *Biotropica*.
- Whittaker, R. J. & Turner, B. D. (1994). Dispersal, fruit utilisation and seed predation of *Dysoxylum gaudichaudianum* in early successional rainforest, Krakatau, Indonesia. *Journal of Tropical Ecology* **10**: 167-181.
- Whittaker, R. J., Walden, J. & Hill, J. (1992a). Post-1883 ash fall on Panjang and Sertung and its ecological impact. *GeoJournal* **28**: 153-171.
- Wilczynski, C. J. & Pickett, S. T. A. (1993). Fine root biomass within experimental canopy gaps: evidence for a below-ground gap. *Journal of Vegetation Science* **4**: 571-574.
- Williams-Linera, G. (1990). Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* **78**: 356-273.
- Woods, P. (1989). Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* **21**: 290-298.
- Wright, S. J. (1991). Seasonal drought and phenology of understorey shrubs in a tropical moist forest. *Ecology* **72**: 1643-1657.
- Yavitt, J. B., Battles, J. J., Lang, G. E. & Knight, D. H. (1995). The canopy gap regime in a secondary Neotropical forest in Panama. *Journal of Tropical Ecology* **11**: 391-402.
- Young, K. R., Ewel, J. J. & Brown, B. J. (1987). Seed dynamics during forest succession in Costa Rica. *Vegetatio* **71**: 157-173.
- Young, T. P. & Hubbell, S. P. (1991). Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* **72**: 1464-1471.
- Zann, R. A., Male, E. B. & Darjono (1990). Bird colonisation of Anak Krakatau, an emergent volcanic island. *Philosophical Transactions of the Royal Society of London B* **328**: 29-54.
- Zimmerman, J. K., Everham III, E. M., Waide, R. B., Lodge, D. J., Taylor, C. M., Brokaw, N. V. L. (1994). Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* **82**: 911-922.

APPENDIX 1:

THE OZALID LIGHT METERING TECHNIQUE AND ITS LIMITATIONS

Introduction to and apparent advantages of the technique

The ozalid paper technique for measuring integrated light values was first developed by Friend (1961). It involves the use of paper which is coated with light sensitive diazo compounds (Black 5, Medium, Standard Speed, manufactured by Ozalid (UK) Ltd., Loughton Essex, IG10 3TH) that form a deep blue colour on short exposure to ammonia vapour. On exposure to light unmasked areas of the paper are bleached. The use of the paper is best known from direct positive 'blue prints' used for making architectural drawings. The central assumption is that the number of diazo sheets exposed is a function of total quantity of radiation received (i.e. duration x intensity; Bardon *et al.*, 1995), and if used in little booklets, the number of sheets bleached was found to correlate very well to the log of incoming PAR (Friend, 1961).

The greatest advantage of the ozalid light meter technique was seen to lie in its low cost, easy assembly and use in the field, which allows a great number of simultaneous light measurements over the period of one to several days. In contrast, the use of large numbers of electronic light measuring devices for simultaneous measurements of the forest light regime is often too expensive, as well as liable to breakdown. The use of hemispherical photography is currently the most widely used and accepted way of integrating light over a longer time-period. However, the computation of absolute radiation rather than relative light measurements is only possible if the incident radiation and cloudiness of the site is measured over a long time period (section 4.3; Mitchell & Whitmore, 1993). Also spot samples of light, for instance, for a particular seedling or sapling are not possible using hemispherical photographs, and spatial heterogeneity in a relatively small area such as a gaps and in a small area of the understorey can not be quantified. In illustration of the latter, Chazdon (1988) recorded understorey light receipt of two sensors that were only 0.2 m apart, and found that they correlated very poorly. Furthermore, to reduce errors photographs with low reflectance and good contrast are required. This means that pictures need to be taken under ideal conditions (e.g. early morning or late afternoon, and overcast), which is sometimes difficult to achieve. In addition, the subjectivity of image analysis is particularly problematic for understorey environments of <10% canopy openness (Dalling 1992), and very little quantification of the size of various errors has so far been carried out (S. Jennings, pers. comm.).

The advantage of the ozalid technique was seen not only in its ability to integrate light over a period of at least 24 h, or up to several days with appropriate filtering, but also in the possibility of analysing spatial heterogeneity by placing large numbers of meters in a small area. An example of such a study is provided by MacDougall (1992), who used the ozalid method to quantify the understorey light regime directly above seedling canopies in order to measure its influence on individual tree seedling distribution in tropical riparian forest patches in Belize. The ozalid method was also used by Kitajima & Augspurger (1989) who tried to characterise the light environment beneath three different canopy types on Barro Colorado Island, Panama, and specifically to quantify the difference in PAR received by seedlings of the monocarpic tree *Tachigalia versicolor* growing in a gap and understorey environment.

For the present study, ozalid light metering was also seen as an additional light measuring technique to hemispherical photography, and a cheap alternative to expensive quantum sensors. Additional light metering was thought to be desirable, because in 1993 only a semi-fisheye lens was available (see section 4.3), and because of the inaccuracies inherent in relative light measurement of hemispherical photography, especially if photographs can only be taken in less than ideal conditions.

Method of assembly and use in the field

A large number of ozalid light meters can be assembled easily and cheaply by producing small (3 x 4 cm) stacks of 10-15 stapled sheets (depending on length of exposure required, and amount of filtering used). Following the suggestion of Kitajima and Augspurger (1989), the little booklets were wrapped in aluminium foil with a 0.5 cm diameter hole in the centre of the light sensitive side, but additionally the booklets were placed in small self-seal plastic bags to give protection from rain and humidity. Using aluminium foil and self-seal plastic bags is a modification of Friend's (1961) method of using petri dishes for protection and placing the lightmeters beneath black paper with a whole punched in the centre. The method used here proved cheaper, and less bulky so that large numbers could be produced before going to the field. The lightmeters were assembled in a darkroom and kept in light-tight containers until exposure. The standard procedure involved the calibration of the light meters against the 30-min. PAR averages of the Sunfleck Ceptometer (AT Delta T

Devices). Also, as recommended by Friend (1961), standards were produced to distinguish partially developed sheets as 0.25, 0.5 or 0.75 developed. After exposure, the light meters were removed to light-tight containers until development took place up to 48 h later. This was achieved by exposing the unwrapped booklets in ammonium vapour for 20-25 minutes.

The small plastic bags containing the ozalid booklet were attached to 1.5 m high bamboo sticks (Fig. A1.1), a height which was seen as suitable for the quantification of the light regime for the majority of small saplings in the 4 x 4 m plots. The sticks were placed every 2.5 m along the gap transects (Fig. 4.2), and at every corner and in the centre of the 4 x 4 m gap and understorey plots.

In 1993, 24h exposure periods (practical constraints sometimes led to 48h exposure) were used (Friend 1961; MacDougall & Kellman, 1992), which typically led to the bleaching of several ozalid sheets, with the last ozalid sheet being only partially developed. Scoring of partial development steps may be influenced by operator subjectivity. Therefore, scoring was only carried out by myself and one other trained person, after comparison of scoring results revealed only very little discrepancy in our scoring decisions. Nevertheless, in the 1993 field season it was impossible to determine a 'full development' step (e.g. 3.0 or 4.0) for the last sheet, since more than 0.75 bleaching of the last sheet always led to a slight bleaching on the next sheet below. This reduced the accuracy of the technique, especially for higher radiation inputs/lengths of exposure, and the size of potential errors increases logarithmically with increasing number of sheets developed (Fig. A1.2a).

Experimentation with the ozalid technique prior to the 1994 field season attempted to (i) improve the resolution, and; (ii) extend the period of exposure beyond 24h, to overcome the problem of representativeness from potential between-day variability in incident light. The latter was previously achieved by Sullivan & Mix (1983), who managed to extend the exposure period to 40 days using stacks of aluminium screens. A neutral density filter would have been another alternative. Both these filtering methods could not be replicated in this study because of assembly problems and supply and cost problems, respectively. Therefore, experimentation using several combinations of sheets of standard white typing paper as filters was carried out. Ideally, the result of the filtering would not only: (i) reduce the light sensitivity, i.e. lower the intercept of the regression curve for the number of sheets



Fig A1.1: Ozalid light meter attached to a 1.5 m high bamboo stick.

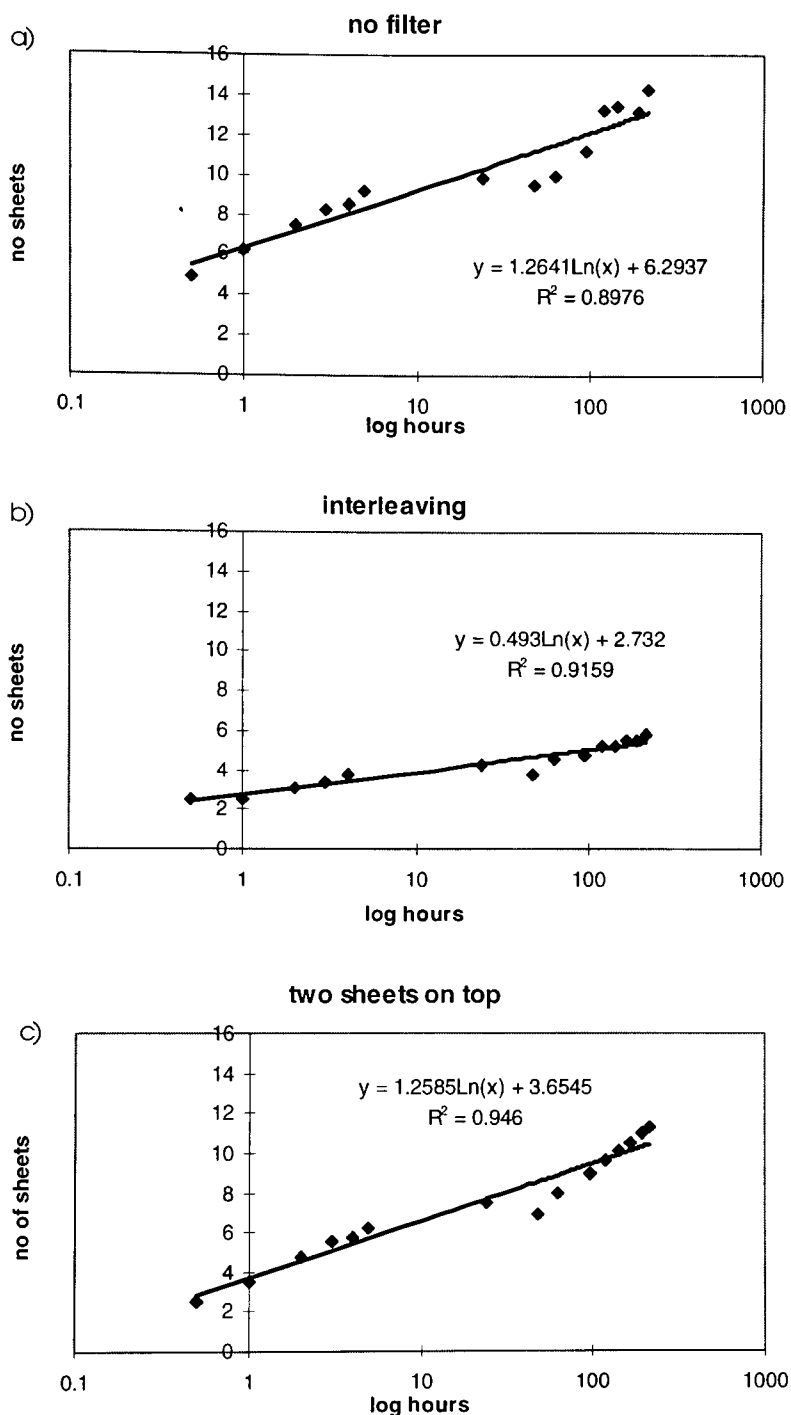


Fig. A1.2: Some results of the 1994 experimentation with the ozalid light metering technique. The objective was to achieve an extension of exposure time to 4-6 days, and to improve the ability to distinguish between development steps for longer periods of exposure. The graphs show regression curves of the log number of hours of exposure to natural light with the number sheets developed. The number of sheets developed are an average figure of the results of three ozalid light meters. Ozalid meters were made from 15 ozalid paper sheets with different filters: (a) no filtering; (b) 'interleaving' of ozalid paper with standard white typing paper; (c) two sheets of standard white typing paper on the top of the booklet of ozalid papers. Method (c) was used in the 1994 field season

developed and log hours of exposure, but (ii) also allow a 'full development step' to be distinguished, and improve the ease of recognising partial development steps, with increased length of exposure; and (iii) achieve the highest regression coefficient.

In May 1994 the test exposures were carried out in the open for 30 min, 1, 2, 3, 4, 5 hours, 1, 2, 3, 4, 5, 6, 7, 8, 9 days. Various filtering combinations were tried and placing of one copy paper sheet on top and after every ozalid sheet ('interleaving') lowered the sensitivity of the ozalid meters most substantially. However, for exposures of more than four days it was almost impossible to distinguish development steps, and in general the resolution was very poor. This is indicated in particular by the flat slope of the regression curve. As errors could be large this filtering method was rejected (Fig. A1.2b).

The optimal solution was found to be two sheets of standard typing paper on top of the ozalid stack, which decreased the sensitivity sufficiently to be able to extend exposure time to 4-6 days (Fig A1.2c). This filtering method also produced the highest regression coefficient, and resolution was improved by the fact that standards could be produced that allowed the identification of a 'full development' step. However, overall the regression curve was not steeper than that for ozalid meters with no filter, and the difference in number of sheets developed between different exposure times was not greater than when no filters were used. Thus, in this way the resolution was not drastically improved.

In 1993, 'full sunlight' measurements were made by exposing ozalid meters for 24h on the beach. The ceptometer could not be used for continuous measurement, because it was needed to set up the gap transects. In that year, the ceptometer was also used in an attempt to characterise the spatial heterogeneity of gap light environments (see CHAPTER 4), but the great temporal variability of PAR meant that these measurements were not representative. In 1994, in an attempt to increase the length of exposure and thus to reduce error from variability of total daily PAR, light meters were left in the field for five days. Depending on logistics, exposure time could, however, vary between four and six days. In that year, the ceptometer was available for the whole fieldwork period to measure continuously 'full sunlight' Photosynthetic Active Radiation (PAR) on the beach. It gave 30-min. average intensities of PAR in $\mu\text{molm}^{-2}\text{s}^{-1}$ for the whole fieldwork period except for the 31/7/94 and the 1/8/94 during which the ceptometer was accidentally switched off. These two days have been substituted by PAR measurements of two representative days, and should not lead to great inaccuracies since the whole fieldwork period was generally very

cloud-free (drought year). Daytime intensities ($>5 \mu\text{molm}^{-2}\text{s}^{-1}$) were converted into total PAR values of $\text{molm}^{-2}\text{s}^{-1}$. Daily total PAR in molm^{-2} are given in Fig. A1.3.

To be able to calculate total PAR from the developed ozalid light meters, calibration against the ceptometer readings was carried out. This was undertaken twice during both the 1993 and 1994 fieldwork season, in order to account for possible deterioration of the diazo compounds over time. The log-transformed regression-curves yielded correlation coefficients $r=0.95$ to $r=0.99$ for $n=16$. Percentage of full sunlight values were then obtained by calculating the ratio of total PAR from the gap and forest measurements and the 'full sunlight' PAR that was either calculated from exposed ozalids (1993) or direct recordings with the ceptometer (1994). If possible, two ozalid light readings per site were obtained in both 1993 and 1994, from which the average value of percentage full sunlight was calculated, to reduce errors from scoring and material variability.

In an attempt to characterise the typical understorey light regime of the three dominant forest types 30-36 ozalid light meters were placed in 6 x 6 m grids beneath the canopy of the Whittaker *et al.* (1989) permanent plots: Rakata plot 1 in *Neonauclea calycina* forest (1994 only), Panjang plot 1 and Sertung plot 1 in *Dysoxylum gaudichaudianum* forest, and Panjang plot 2 and Sertung plot 2 which are both *Timonius compressicaulis* forests.

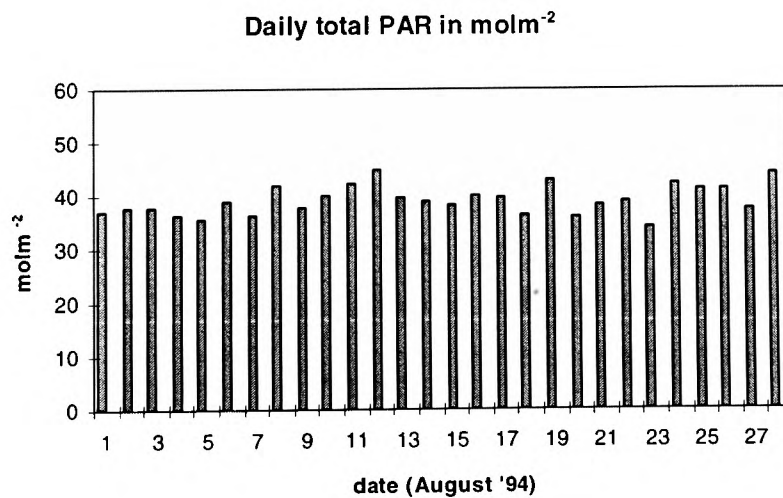


Fig. A1.3: Daily total PAR in molm^{-2} calculated from 30-min. averages of ceptometer measurements during August 1994, in the open, on the Owl Bay beach of Rakata. Note the relatively small variations between the very cloud-free days that were characteristic during the 1994 drought.

The limitations of the ozalid method

Unfortunately, the ozalid technique has been found to suffer from several limitations. These were partly in connection with field work logistics, but most of all due to inherent problems with the technique itself.

Information about the ozalid method was only obtained shortly before the start of the first field season in 1993, when it became apparent that only a semi-fisheye lens could be obtained and an alternative light metering method was seen to be necessary. Therefore, lengthy testing of the technique and planning of the logistics involving ozalid readings in the forest were not possible, with the result that several limitations were only detected during the 1993 fieldwork period. For example, one of the problems was that the ceptometer was only available for the brief calibration periods but not for continuous 'full sunlight' recording on the beach of Rakata. That meant that often 'full sunlight' readings using the ozalid meters were started early in the morning on the beach of Rakata, but often the actual light meters in the gap could not be installed until mid-morning to early afternoon, due to long travelling times to the sites in high altitude Rakata, as well as the other islands. In the meantime there might have been a very sunny or rainy morning (weather conditions were very variable in 1993), which was not exactly repeated the next day in the period until the light meters in the plots were taken in. Furthermore, initial bleaching of the sheets happens very fast, and high light intensity around midday would have led to a faster bleaching than for the full sunlight ozalids, and it seemed that unexplained discrepancies in the results may have been due to this reason (see below).

In 1993, this could overall have led to higher or lower 'full sunlight' measures on different days, not necessarily because of differences in total daily PAR, but due to inherent problems with the method. It was therefore thought that substantial variations in percentage full sunlight readings for the same site between days might be linked to this particular problem. However, in 1994, although (i) absolute full sunlight levels were measured with the ceptometer; (ii) days were generally very sunny throughout; and (iii) the measurement periods were extended to five days, all of which should have improved the accuracy of the method, percentage of full sunlight calculations for two periods still yielded very different results. The difference in results between periods also tended to be much larger (up to three times) with increasing number of sheets developed (e.g. in large gaps),

which seemed to be an expression of the increasing error associated with the log relationship.

With the longer exposure times achieved in 1994 it was assumed that these errors could not be attributed to possible differences in the timing of the start of exposure. However, a number of other potential sources of error were identified. First, errors may have been due to scoring inconsistencies, although only two trained persons scored the sheets, and standards were produced. Nevertheless, decisions on the partial development of sub-categories could still have been subject to variability, particularly for deciding between 0.75, fully, and 0.25 developed. Full bleaching (e.g. 6.0) was scored when the last sheets seemed less than 0.25 developed and the second to last more than 0.75. This was sometimes difficult to decide and scoring on different days could have influenced the decision. Second, another possible source of error could be slight variations in positioning of the light meters between periods, as well as change in their relative positioning (angle to the sun) during the time of exposure.

My suspicion that the rapid development of sheets under high light levels at the beginning of the measurement period is very important, was confirmed by Bardon *et al.* (1995). They found that the usefulness of the technique is severely limited by the fact that the diazo compound reacts to maximum rather than cumulative radiation, which means that after maximum incident radiation of the period has been received, no further development of sheets takes place. They tested this subjecting ozalid lightmeters to constant radiation, and another regime that provided 90 minutes of high radiation levels followed by a period of low radiation. The logarithmic curve of PAR versus number of sheets developed did not rise after the period of maximum radiation (Fig. A1.3). Thus, for instance, longer exposures are most likely to result in an under-estimation of total PAR received if maximum incident radiation occurs early on in the exposure period.

The discovered inconsistencies and experimental problems during this study, and the fact that recent testing of the technique by Bardon *et al.* (1995) revealed major limitations, led me to discard the ozalid light meter results as a measure of the light environment in the present study.

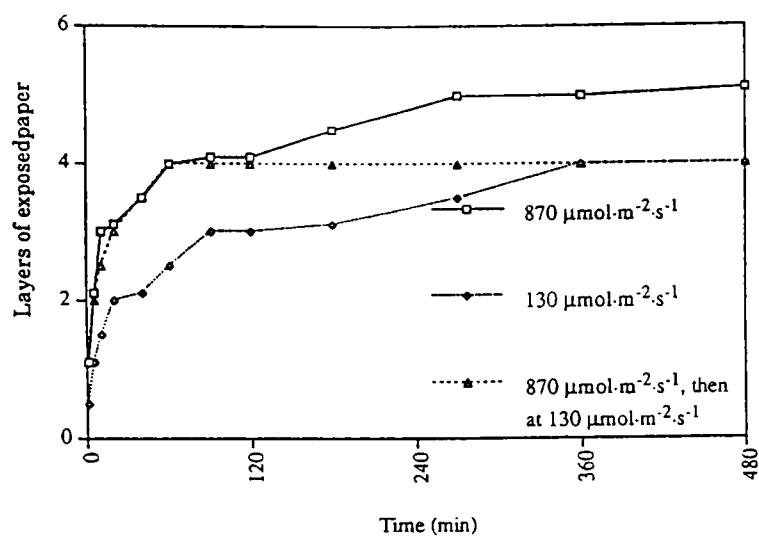


Fig. A1.4: Experimentation by Bardon *et al.* (1995) revealed that the diazo compounds of the ozalid paper react mainly to maximum instantaneous radiation rather than cumulative radiation. The number of layers of exposed paper at constant irradiance of $870 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $130 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and at a combination of $870 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (90 min) and $130 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (from Bardon *et al.* 1995).

APPENDIX 2:

FORMULAE, DATA TABLES AND GRAPHS FOR CHAPTER 4

Formulae for percentage mortality calculation of small and tall saplings

for small saplings (gap and understorey):

$$\begin{aligned} M_1 &= (N_1 - N_2 / N_1) * 100 \\ M_2 &= ((N_2 + r_1) - N_3 / (N_2 + r_1)) * 100 \\ M_3 &= (N_1 - N_4 / N_1) * 100 \end{aligned}$$

Where

M_1 = percentage mortality between 1993-1994;
 M_2 = percentage mortality between 1994-1995 (on the 1994 baseline);
 M_3 = percentage mortality between 1993-1995 (on the 1993 baseline);
 N_1 = number of saplings enumerated in 1993;
 N_2 = number of 1993 saplings surviving in 1994;
 N_3 = number of 1994 saplings ($N_2 + r_{s1}$) surviving in 1995;
 N_4 = number of 1993 saplings surviving in 1995;
 r_1 = number of saplings recruited between 1993-1994;

for tall saplings:

$$M = (N_5 - N_6 / N_5) * 100;$$

Where

M = percentage mortality of tall saplings;
 N_5 = number of tall saplings in 1994;
 N_6 = number of tall saplings in 1995;

Similarly recruitment was measured in percent and calculated as follows:

for small saplings (gap and understorey):

$$\begin{aligned} R_1 &= (r_1 / N_1) * 100; \\ R_2 &= (r_2 / (N_2 + r_1)) * 100; \\ R_3 &= (r_{s3} / N_1) * 100; \end{aligned}$$

Where

R_1 = percentage recruitment between 1993-1994;
 R_2 = percentage recruitment between 1994-1995 (on 1994 baseline);
 R_3 = percentage recruitment between 1993-1995 (total surviving recruitment on the 1993 baseline)
 r_1 = number of saplings recruited between 1993-1994;
 r_2 = number of saplings recruited between 1994-1995;
 r_{s3} = number of surviving saplings between 1993-1995;

for tall saplings:

$$R = (r/N) * 100$$

Where

R = percentage recruitment of tall saplings between 1994-1995;

r = number of tall sapling recruits between 1994-1995;

N = number of tall saplings in 1994;

Net change in number of individuals was measured in percent and calculated as follows:

for small saplings (gap and understorey):

$$\text{net}R_1 = R_1 - M_1;$$

$$\text{net}R_2 = R_2 - M_2;$$

$$\text{net}R_3 = R_3 - M_3;$$

Where

netR₁ = net percentage change of number of individuals between 1993-1994;

netR₂ = net percentage change of number of individuals between 1994-1995;

netR₃ = net percentage change of number of individuals between 1993-1995;

for tall saplings:

$$\text{net}R = R - M;$$

Where

netR = net percentage change of number of tall saplings between 1994-1995.

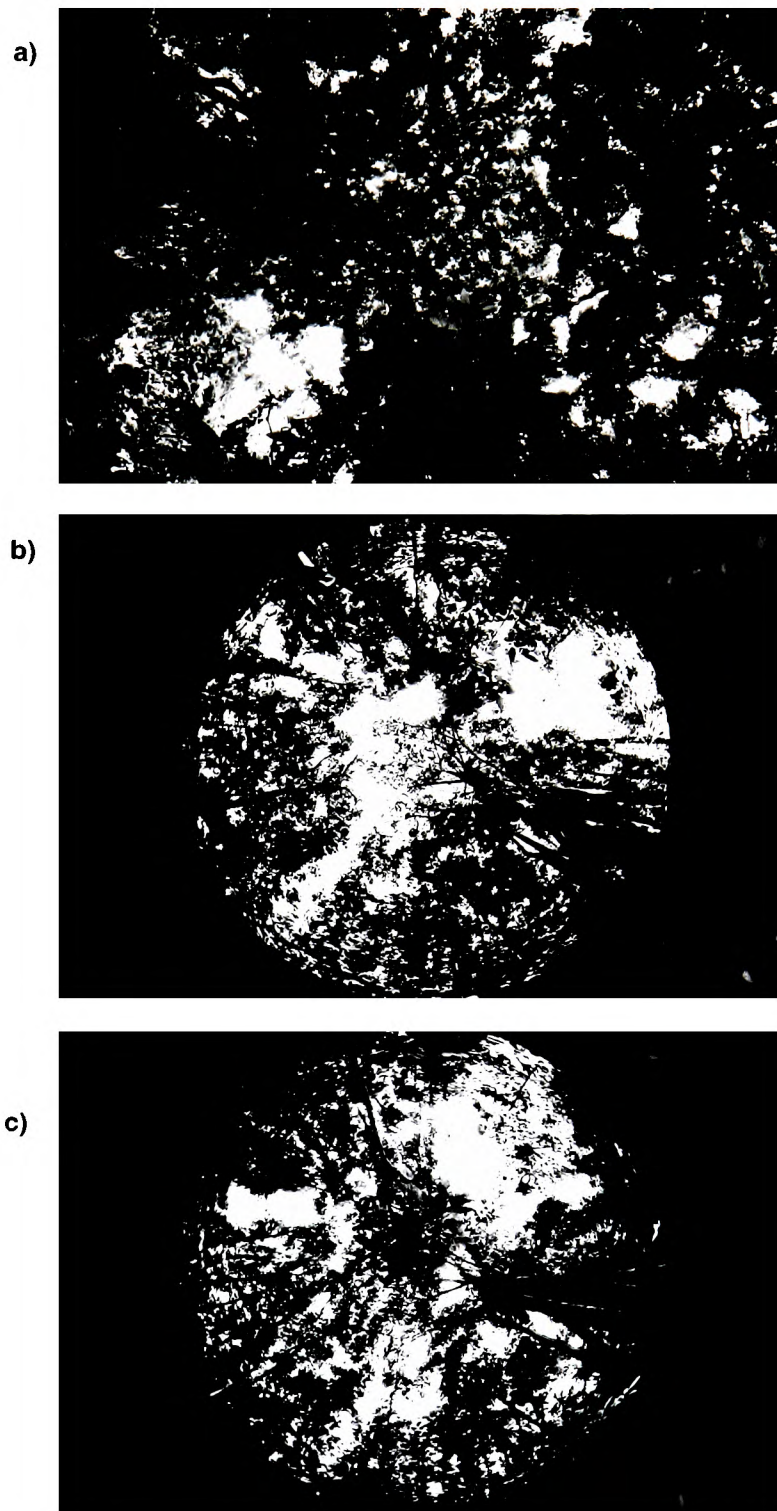


Fig. A2.1: Hemispherical photographs of *Neonauclea calycina* forest of inland Rakata (at 840 m point of RSE 1000 m transect; see Fig. 3.1 for location) in (a) 1993, when picture was taken with a semi-fisheye lens, (b) 1994 and (c) 1995. Picture (a) represents the central section of (b) and (c). Taking differences in light conditions into account, there is still a noticeable increase in open sky between 1993 and 1994. It also appears that the same degree of canopy closure as in 1993 was not yet achieved by 1995. However, the change in canopy cover between years in this forest type and under absence of ash is not as large as seen in Fig. A2.2. The multi-trunk tree on the right is a *Ficus sumatrana* strangler.

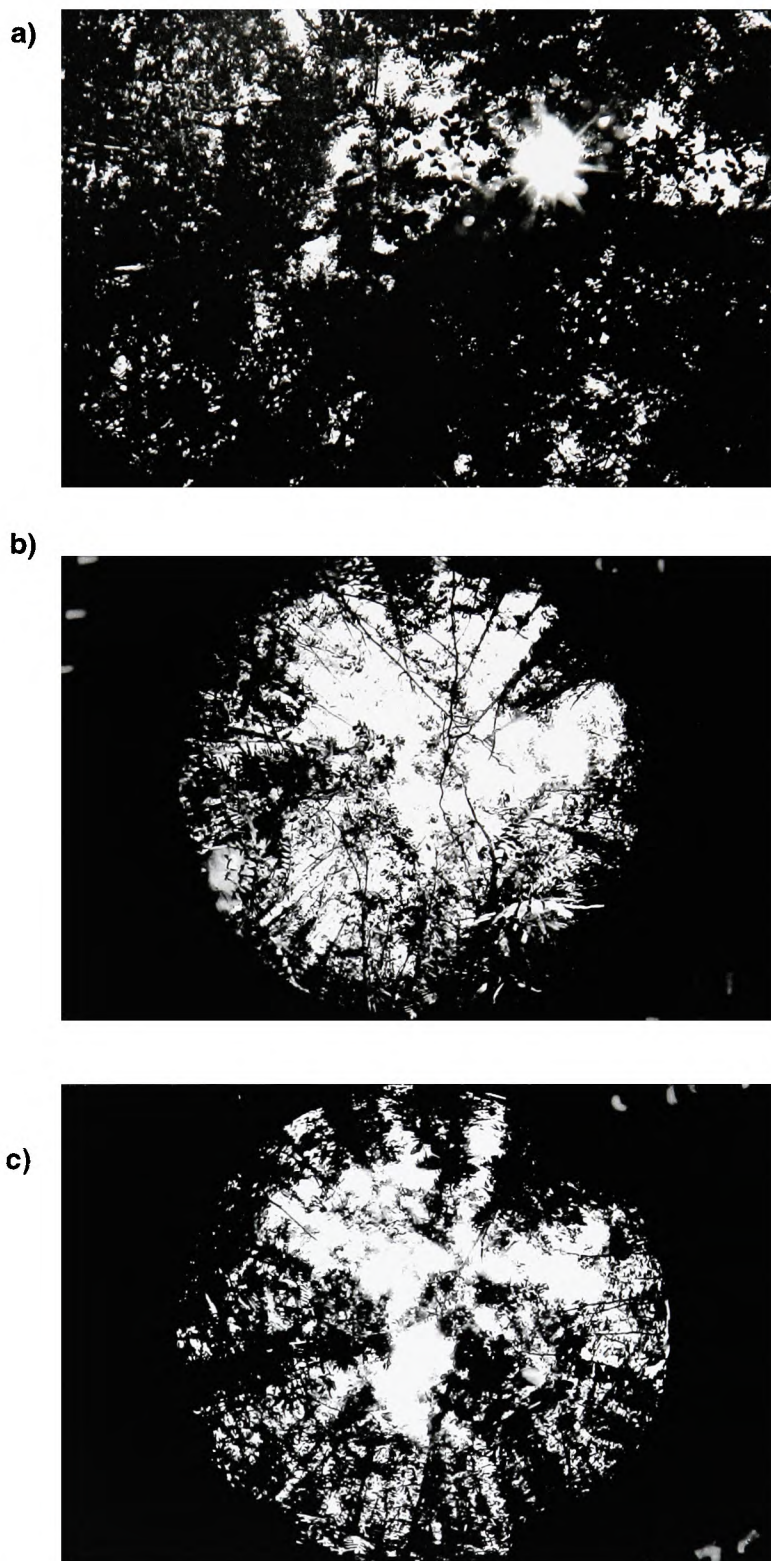
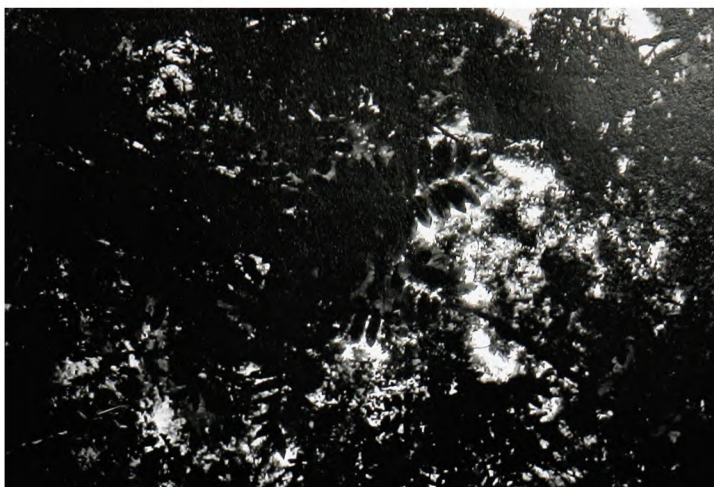
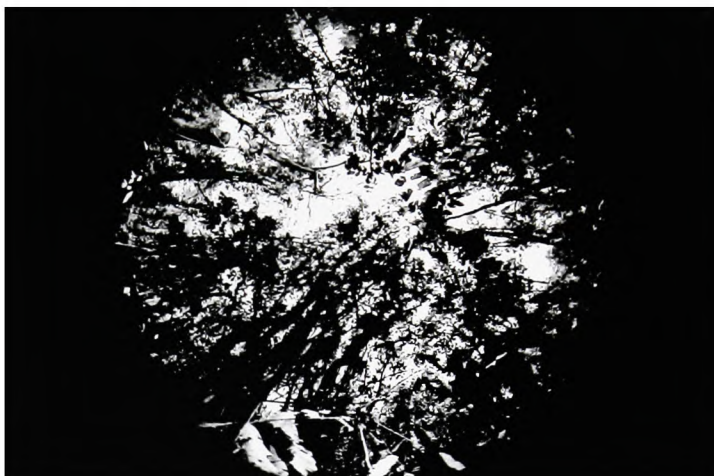


Fig. A2.2: Hemispherical photographs of *Dysoxylum gaudichaudianum* forest on Sertung (at 240 m point of S 1000 m transect; see Fig. 3.1 for location) in: (a) 1993 when picture was taken with a semi-fisheye lens; (b) in 1994 and; (c) in 1995. Note the drastic difference in canopy cover between years, with the 1994 picture taken during the drought period and showing the largest proportion of open sky. Drought and large amounts of ash-fall led to extensive leaf-shedding of *Dysoxylum*.

a)



b)



c)

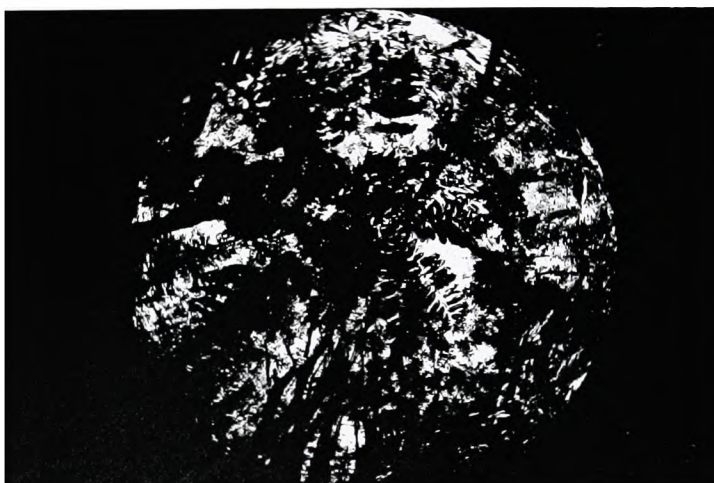
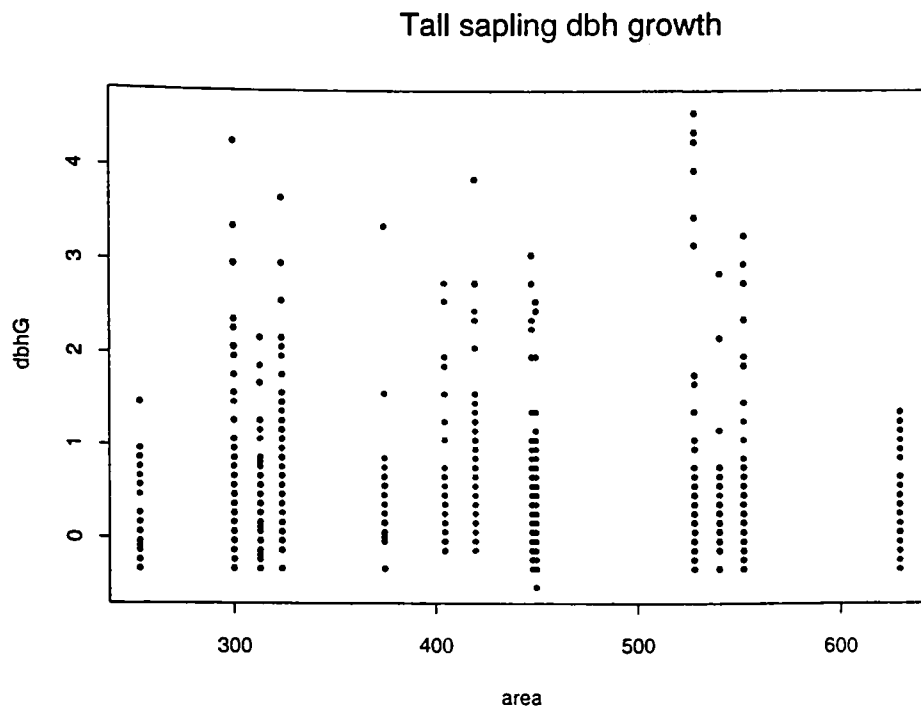


Fig. A2.3: Hemispherical photographs of *Timonius compressicaulis* forest on Sertung (at 860 m point of S 1000 m transect; see Fig. 3.1 for location) in: (a) 1993 when picture was taken with a semi-fisheye lens; (b) in 1994 and; (c) in 1995. The difference between years is not as drastic as for *Dysoxylum* forest on the same island, but note absence of the *Dysoxylum* sapling in 1994. In 1995 it must have either recovered or the sapling shown is a new recruit. Note that much of the drought-induced changes in the light environment were not only due to greater opening of the canopy, but also from wilting and death of the understorey layer. This must have reduced competition for light when regeneration resumed at the onset of the 1994/95 wet-season.

a)



b)

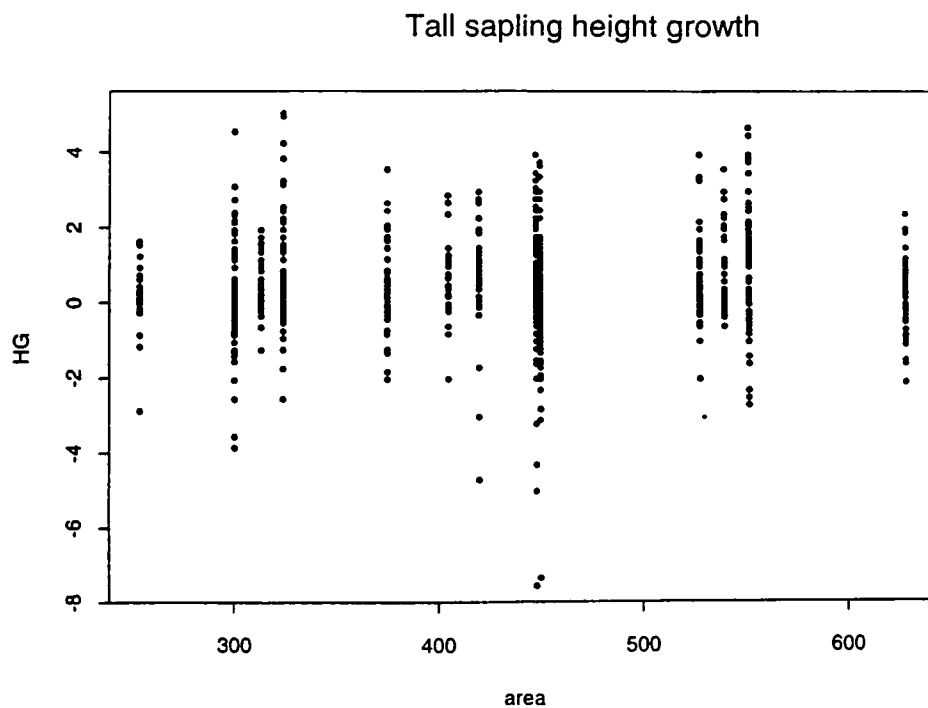


Fig. A2.4: Scatter plot for tall saplings enumerated in all gap sites (see Table A2.3): (a) dbh and; (b) height growth in each case *versus* area of sampling. It shows that no relationship between growth and area of sampling of tall saplings exists.

Table A2.1a: Height growth performance of small saplings in 4 x 4 m *gap* plots between 1993-1994, 1994-1995, and the whole 1993-1995 period.
Note the generally small sample sizes of saplings in gap plots.

site	mean HG ₁ ^a	HG ₁	Stdev	max. HG ₁	mean HG ₂	mean HG ₂	HG ₂	Stdev	max. HG ₂	mean HG ₃	HG ₃	Stdev	max. HG ₃
R1	290.17		174.22	550.00	48.25		164.00	60.91		147.50		189.52	517.00
R2 (TF)	106.69		80.34	265.00	115.83		165.00	56.96		272.50		81.16	415.00
S3	11.27		27.31	45.00	30.57		115.00	52.67		53.00		64.81	138.00
P4	152.95		218.06	585.00	0.75		140.00	87.87		174.50		211.59	525.00
R5	-30.00		289.91	175.00	-----		-----	-----		-----		-----	-----
P6	26.68		24.67	81.00	10.67		44.00	31.74		38.56		36.89	125.00
P7 ^b	-----		-----	-----	-----		-----	-----		-----		-----	-----
P8	2.58		69.59	135.00	11.00		26.00	13.92		32.78		56.09	155.00
R9	74.86		93.32	239.00	101.14		270.00	90.34		176.00		145.78	394.00
R10 ^c	67.47		159.15	620.00	-----		-----	-----		-----		-----	-----
R11	51.29		63.91	170.00	-8.00		14.00	27.65		41.33		54.12	144.00
R12 ^d	86.17		58.61	148.00	-83.00		-83.00	-----		57.00		-----	57.00
P13	4.30		61.09	130.00	19.56		62.00	42.06		38.44		51.10	92.00
S14	27.20		25.59	58.00	43.00		130.00	85.07		67.33		81.83	160.00
R15	17.82		57.84	82.00	70.00		165.00	59.30		87.82		63.82	180.00

a: height growth in centimeters; subscript 1 = 1993-1994; subscript 2 = 1994-1995; subscript 3 = 1993-1995 periods;

b: P7G lost between 1993-1994

c: R10G can not be remeasured in 1995, thus no data for 1994-1995 and 1993-1995 height growth;

d: R12 only has 1 survivor by 1995;

Table A2.1b: Height growth performance of small saplings in 4 x 4 m *understorey* plots between 1993-1994, 1994-1995, and the whole 1993-1995 period.

site	mean HG_1^a	H_1	Stdev	max. HG_1	mean HG_2	HG_2	Stdev	max. HG_2	mean HG_3	HG_3	Stdev	max. HG_3
R1	8.42		23.27	57.00	8.52		42.88	128.00	18.03		49.69	130.00
R2 (TF)	29.67		30.69	100.00	19.25		42.75	88.00	45.38		51.20	100.00
S3	10.47		17.75	38.00	35.23		42.97	105.00	49.38		50.32	143.00
P4 ^b	-32.50		55.45	5.00	28.25		49.18	100.00	-4.25		10.90	10.00
R5	23.50		52.53	118.00	112.33		56.54	170.00	112.33		56.54	170.00
P6	6.30		41.56	52.00	-14.43		36.88	38.00	0.43		32.02	43.00
P7	-4.75		30.53	48.00	7.17		47.60	161.00	5.94		43.98	150.00
P8	5.12		33.80	235.00	23.07		49.82	230.00	26.69		53.91	250.00
R9	21.63		28.30	70.00	2.75		15.68	20.00	24.11		30.41	90.00
R10 ^b	69.78		78.41	250.00	92.50		74.91	225.00	191.40		132.78	450.00
R11	20.65		22.40	65.00	7.91		25.41	55.00	23.77		38.44	84.00
R12	5.25		43.21	68.00	-24.00		66.59	48.00	-0.80		57.78	50.00
P13	23.83		21.29	60.00	13.24		29.29	86.00	37.29		32.29	84.00
S14	16.00		17.35	36.00	36.67		29.48	70.00	52.67		28.18	75.00
R15	4.18		28.87	60.00	-3.57		29.69	43.00	-7.10		29.15	80.00

a: height growth in centimeters; subscript 1 = 1993-1994; subscript 2 = 1994-1995; subscript 3 = 1993-1995 periods;

b: P4US and R10US suffered physical damage between 1993-1994.

Table A2.2a: Summary table of percentage mortality (%M), recruitment (%R), net change in number of gap saplings (%netR), and density of saplings in gap plots between 1993-94, 1994-1995, and the whole 1993-95 period. See glossary for gap codes, and below for further explanations. Calculations of %M, %R and %net R are explained in the methods section.

site	%M ₁ ^a	%R ₁	%netR	%M ₂	%R ₂	%netR ₂	%M ₃	%R ₃	net%R ₃	Den ₁ ^b	Den ₂	Den ₃
R1 ^c	51.72	*****	*****	0.00	*****	*****	51.72	27.59	-24.13	1.81	0.88	1.38
R2 (TF)	30.00	100	70.00	70.59	20.58	-50.01	65	50	-15	1.25	2.13	1.06
S3	21.43	14.29	-7.14	38.46	0.00	-38.46	50	0	-50	0.88	0.81	0.44
P4	45.24	2.38	-42.86	45.83	4.35	-41.48	69	2.4	-66.6	2.63	1.50	0.81
R5	71.43	142.9	71.47	100.00	1750.00	1650.00	100	500	400	0.44	0.75	2.19
P6	9.09	18.18	9.09	8.33	4.17	-4.16	18.2	22.7	4.5	1.38	1.50	1.44
P7 ^d	100.00	-----	-----	-----	-----	-----	100	-----	-----	0.38	-----	-----
P8	7.69	7.69	0.00	23.08	0.00	-23.08	30.8	15.4	-15.4	0.81	0.81	0.69
R9	0.00	71.43	71.43	25.00	44.44	19.44	0	114.3	114.3	0.44	0.75	0.94
R10 ^e	71.79	17.95	-53.84	-----	-----	-----	71.8	17.9	-----	4.88	2.25	2.25
R11	41.67	150	108.33	44.00	0.00	-44.00	41.7	66.7	25	0.75	1.56	0.94
R12	25.00	87.5	62.50	53.85	144.44	90.59	75	200	125	0.50	0.81	1.13
P13 ^f	47.83	13.04	-34.79	11.11	6.67	-4.44	52.18	26.1	-26.08	1.44	1.13	1.06
S14	44.44	0	-44.44	40.00	140.00	100.00	66.68	77.78	11.1	0.56	0.31	0.62
R15	0.00	25	25.00	6.67	7.14	0.47	0	25	25	0.75	0.94	0.94

a: subscript 1 = 1993-1994; subscript 2 = 1994-1995; subscript 3 = 1993-1995;

b: density per m²; subscript 1 = density in 1993; subscript 2 = density in 1994; subscript 3 = density in 1995;

c: missing values are due to inability to determine recruitment in 1994 because of redisturbance; complete recording in 1995 allowed the calculation of the overall 1993-1995 values.

d: gap plot lost between 1993-1994 due to erosion;

e: plot was redisturbed between 1993-1994, and by 1995 heavily overgrown with climbers making relocation of saplings impossible.

f: between 1993-1994 gap site disturbed by pumice digging; gap plot affected by covering with pumice;

Table A2.2b: Summary table of percentage mortality (%M), recruitment(%R) and the net change in the number of saplings (%net R) in 4 x 4 m understorey plots between 1993-1994, 1994-1995, and the whole 1993-1995 period. See glossary for gap codes and methods section for the calculation of %M,%R, %net R.

site	%M ₁ ^a	%R ₁	%netR ₁	%M ₂	%R ₂	%netR ₂	%M ₃	%R ₃	net%R ₃
R1	2.94	5.88	2.94	11.43	11.43	0.00	14.71	17.65	2.94
R2 (TF)	15.00	65.00	50.00	33.33	37.50	4.17	35	75	40
S3	19.05	9.52	-9.53	21.05	16.67	-4.38	33.33	19.04	-14.29
P4 ^b	64.29	0.00	-64.29	0.00	0.00	0.00	64.3	0	-64.3
R5	54.76	4.76	-50.00	85.71	105.26	19.55	92.86	47.6	-45.26
P6	6.25	25.00	18.75	16.67	16.67	0.00	25	30	5
P7	0.00	12.50	12.50	22.22	7.41	-14.81	25	16.7	-8.3
P8	6.12	5.10	-1.02	19.59	0.00	-19.59	23.5	3.1	-20.4
R9	23.08	15.38	-7.70	8.33	16.67	8.34	30.8	30.8	0
R10 ^b	43.48	19.57	-23.91	65.71	92.31	26.60	73.9	56.5	-17.4
R11	4.00	16.00	12.00	3.45	0.00	-3.45	25	20	-5
R12	11.11	11.11	0.00	27.27	0.00	-27.27	44.4	11.11	-33.29
P13	15.00	0.00	-15.00	5.26	11.76	6.50	20	10	-10
S14	20.00	20.00	0.00	20.00	175.00	155.00	40	160	120
R15	22.00	6.00	-16.00	21.43	7.32	-14.11	38	6	-32

a: subscript 1 = 1993-1994; subscript 2 = 1994-1995; subscript 3 = 1993-1995

b: P4U and R10U suffered physical damage between 1993-1994;

Table A2.3: Tall sapling summary table listing the number of saplings, the area sampled within the gap site, and density in 1994. Mean height and dbh growth, percentage mortality (%M), recruitment (%R) and net change in number of individuals (%netR) between 1994-1995 are also listed.

site	size	severity	N	area	density	mean HG ^a	Stdev HG	mean dbhG ^b	dbhG Stdev	%M	%R	%net R
R1	1	1	103	324	0.32	0.7	1.4	0.63	0.78	27.18	32.04	4.86
S3	4	1	76	540	0.14	0.94	1.06	0.3	0.61	48.64	21.62	-27.02
P4	4	2	148	300	0.49	0.18	1.29	0.51	0.84	21.77	8.16	-13.61
R5	2	1	95	420	0.23	0.51	1.37	0.6	0.88	53.13	57.29	4.16
P6	2	1	87	528	0.16	0.45	0.98	0.53	1.05	9.2	9.47	0.27
P7	2	2	51	254	0.20	0.25	0.75	0.21	0.37	27.45	5.88	-21.57
P8	2	1	108	450	0.24	0.23	1.23	0.15	0.47	32.41	23.15	-9.26
R9	2	1	40	405	0.10	0.61	1	0.7	0.76	7.5	32.5	25
R11	2	2	106	552	0.19	0.8	1.5	0.44	0.72	16.04	10.38	-5.66
R12	3	1	104	450	0.23	-0.25	1.25	0.17	0.4	10.58	20.19	9.61
P13	2	2	101	630	0.16	0.33	0.78	0.11	0.42	17.82	7.92	-9.9
S14	3	1	76	450	0.17	0.64	1.87	0.18	0.55	23.94	25.35	1.41
R15	2	1	105	448	0.23	0.42	1.14	0.25	0.58	10.1	19.19	9.09
R16	2	2	59	313	0.19	0.58	0.73	0.35	0.52	8.47	5.08	-3.39
P17	2	2	71	375	0.19	0.33	1.1	0.26	0.53	25.35	32.39	7.04

a: height growth in meters;

b: dbh growth in centimeters;

Note: in R2 and R10 high altitude sites no tall saplings could be enumerated, but the tall sapling analysis additionally includes landslide sites R16 and P17.

APPENDIX 3:

ARTIFICIAL DEFOLIATION EXPERIMENT ON *DYSOXYLUM GAUDICHAUDIANUM*

Introduction

Artificial defoliation experiments on *Dysoxylum gaudichaudianum* saplings were carried out in an attempt to quantify tolerance to damage from herbivory. Initially it was the intention to carry out more of these experiments on other species, but it proved very difficult to find sufficient numbers of saplings of one species growing in relatively close vicinity to each other (i.e. in relatively similar environmental conditions).

The objectives of this appendix are to:

- (i) present results on the effect of artificial defoliation on the growth and mortality of *Dysoxylum* saplings between 1993 and 1995;
- (ii) and to evaluate whether the results support the suggested stress-tolerance of *Dysoxylum* (see CHAPTER 4).

Methods

In 1993, in near-coastal forest of South-east Rakata, 45 saplings (>1 m and <2 m) of *Dysoxylum* were tagged and dbh and height measured. Most saplings were found beneath the canopy of two large semi-deciduous *Terminalia catappa* trees. Three different clipping treatments of 0, 50, and 75% leaf clipping were randomly assigned, and the single leaflets of the compound leaves were clipped with scissors accordingly. In 1994, all surviving saplings were remeasured and subjected to further clipping. The final enumeration was carried out in 1995.

Results

Mortality

Between 1993-1994 two saplings died; one from each of the 75 and 50% clipping treatments. None of the control saplings died. The mortality incurred between 1994-1995 was much higher. From the 75% clipping treatment five more saplings died increasing the number of dead saplings of this treatment to six. The control saplings lost three individuals, one of which was, however, crushed by a treefall. No more saplings of the 50% clipping treatment died.

1994-1995 was the period at the end of the drought and the wet-season following the drought, when substantial shifts in the species composition of this area occurred due to high mortality followed by rapid recruitment of pioneers such as *Macaranga tanarius* (see CHAPTER 4 & 5). In 1995, it was noticed that the health of the saplings seemed to be worse than in 1994, with slightly more evidence of herbivory, and fewer compound leaves on the top shoot. The 1995 result may be an expression of the more extreme conditions experienced due to the 1994 drought.

Table A3.1: Clipping treatments of 75, 50 and 0% as the control, and the number of saplings surviving in each treatment in 1994 and 1995.

	<i>75%</i>	<i>50%</i>	<i>0%</i>	<i>total</i>
1993	15	15	15	45
1994	14	14	15	43
1995	9	14	12	35

Height growth

For the 1993-1994 period comparison of height increments between 0, 50 and 75% clipped *Dysoxylum* saplings showed that the 50% clipped saplings achieved the greatest median growth, and that their growth was almost significantly different from that of the control group ($p=0.057$; Mann-Whitney-U test). The 75% clipped group were not significantly different in height growth from either the control or the 50% clipped saplings (Fig. A3.1 a). For the 1994-1995 period, no significant difference in height change could be found between any of the treatments (Fig. A3.1b).

Fig. A3.2 shows the distribution of change in height for all saplings for both the 1993-1994 and the 1994-1995 period. It demonstrates that most saplings grew between 0-10 cm, and that for the first year of monitoring more saplings grew between 0-10 cm and 10-20 cm than in the second year. In contrast to the mesic year 1993-1994, the range of height increments was much greater in 1994-1995, whereby several saplings achieved considerably greater height growth, and others were reduced considerably in height in that year (Fig. A3.1b; Fig. A3.2).

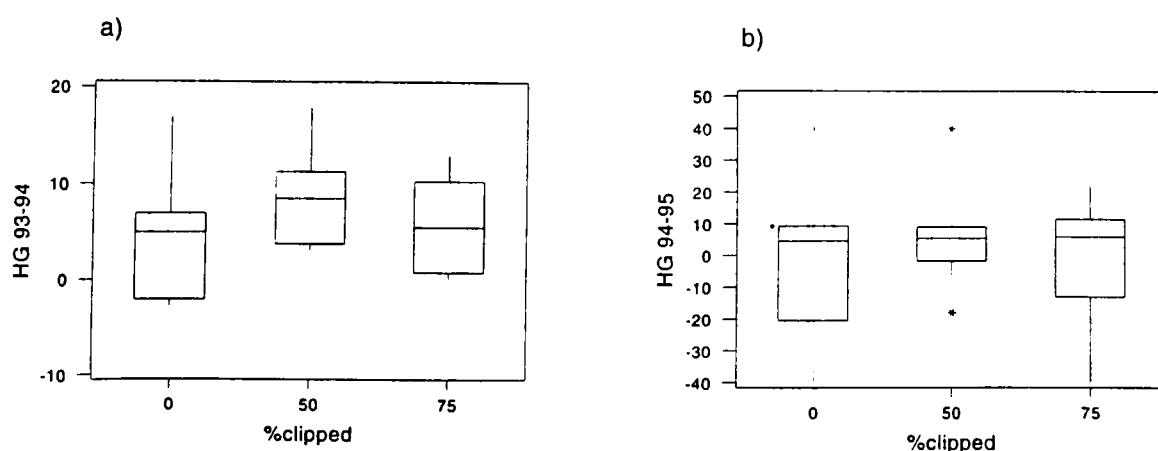


Fig. A3.1: Comparison of height change of *Dysoxylum gaudichaudianum* saplings 0, 50, and 75% clipped: (a) 1993-1994, and (b) for 1994-1995.

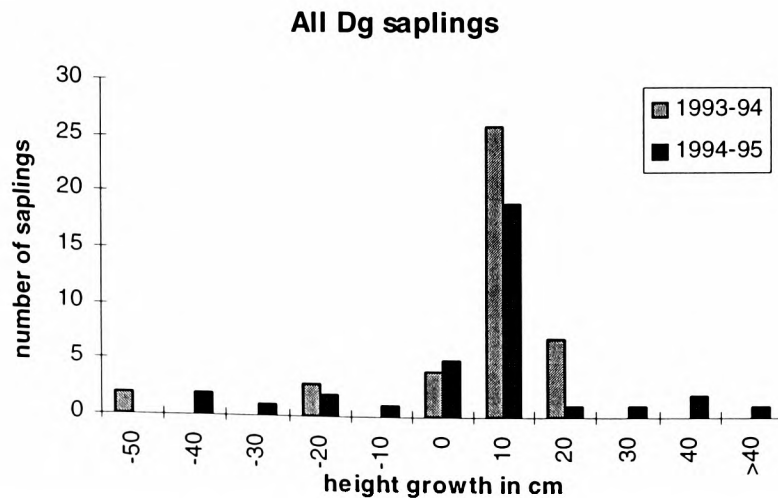


Fig. A3.2: Distribution of height change of all saplings of the *Dysoxylum* clipping experiment for the periods 1993-1994 (n=43) and 1994-1995 (n=35).

Discussion

These clipping treatments have subjected *Dysoxylum* saplings to artificial herbivory damage which was well above the average level of leaf-area loss that is in general found for other rain forests (e.g. 3-10%; Lowman, 1984). Moreover, the same high levels of defoliation were applied twice. Despite these unusually severe levels of herbivory, *Dysoxylum* saplings from the two different clipping treatments did not show significantly different height growth from those which were not defoliated. In fact, at least in the mesic year (1993-94), the 50% clipped saplings mostly had greater height increments than the control saplings. Sapling mortality showed similar results, whereby the 50% clipped saplings suffered from the smallest losses. However, after the second severe clipping of 75% considerable losses of saplings in this category resulted. It is likely that the additional stress of the 1994 drought was a contributing factor in the mortality of already weakened saplings. It appears that the 75% clipping is beyond the threshold of tolerance of *Dysoxylum* saplings, as the considerable leaf-area loss from 50% clipping did not increase mortality. In fact, the saplings from the 50% clipping treatment showed a tendency to perform better than even the control saplings.

Of course, it is important to bear in mind the small number of saplings and the absence of any replication. Nevertheless, the results presented here give further support to the suggested stress-tolerant life-history characteristics of *Dysoxylum* in this and taller sapling size-classes. Apart from the fact that severe herbivory is tolerated fairly well, a striking characteristic of *Dysoxylum* is also its ability to recover from substantial top-shoot loss. These may have been incurred from physical damage or, as observed in this study, from stem-boring activities of two species of ants. One species seems to use the shoots of *Dysoxylum* saplings as dormitaries. Eventually the sapling stems are chewed through, which might, however, involve another species of ant also observed on *Dysoxylum* saplings (L. White in lit; pers. obs.). This can lead to losses of more than half of the original sapling height, but resprouting generally resumes very quickly.

The characteristics reported above and in other chapters, make *Dysoxylum* saplings ideal candidates to survive occasional or even repeated stressful episodes of an abiotic as well as biotic nature. However, there seems to be a clear division between the tolerance of taller saplings (e.g. >1m) and small saplings, and seedlings (e.g. <50 cm). This was indicated by the results of another clipping experiment in 1993-1994. This involved 75 seedlings located in five plots in a small near-coastal area in the East of Rakata. The same treatments of 75, 50 and 0% clipping were applied. It was found that after one year a very high proportion of *Dysoxylum* seedlings were dead or missing (79%), and that the 75% clipped seedlings had the highest mortality (92%). Mortality of the control and of the 50% clipped seedlings were respectively 68% and 76%, i.e. considerably less than for the 75% clipping treatment. Thus, overall mortality levels were much higher than for *Dysoxylum* saplings in that year. This is to be expected as seedling mortality is in general high but, in contrast to the sapling clipping experiment in the same mesic year (1993-1994), the 75% clipping category caused much higher levels of mortality than in the sapling size-class. It appears therefore that the tolerance of *Dysoxylum* to herbivory is much lower at the seedling stage. That *Dysoxylum* seedlings are not as stress tolerant as the saplings, and in comparison to the seedlings of other species was also shown when none of 63 *Dysoxylum* seedlings survived the stress of ash-fall and the onset of the drought in the understorey plot of S3 on Sertung between 1993-1994. In contrast, seedlings of *Ardisia humilis* and *Morinda citrifolia* survived.

Conclusion

The results reported here lend further support to the suggested stress-tolerance of *Dysoxylum* to not only ashfall and drought but also to high levels of herbivory and shoot loss. However, there appears to be a great difference in tolerance between the seedling and the sapling stage (>1 m). From the limited information known about the autoecology of *Dysoxylum gaudichaudianum*, it appears that the most significant environmental filter (*sensu* Silvertown, 1987) acts at the seedling stage, and thereafter, at the sapling or sub-adult stage, *Dysoxylum* is able to survive considerable levels of stress. As seedling cohorts are usually large, the high mortalities at the seedling stage still leave a considerable sapling cohort. The saplings of these cohorts of *Dysoxylum* are then particularly suitable candidates to succeed into the canopy under intermittent stress from ashfall and other factors.

APPENDIX 4:

ADDITIONAL TABLES AND FIGURES FOR CHAPTER 5

Table A4.1: Summary table of gap and understorey species richness and Simpson indices for 1993, 1994, and 1995. Percentage canopy openness for 1993 derived from semi-fisheye images, and arbitrary gap size- and severity classes are also given.

gap code	G sp 93 ^a	U sp 93	G sp 94	U sp 94	G sp 95	U sp 95	G Sim 93 ^b	U Sim 93	G Sim 94	U Sim 94	G Sim 95	U Sim 95	%CO93 ^c	size ^d	severity ^d
R1	6	10	6	10	9	9	0.786	0.85	0.791	0.839	0.861	0.717	11.53	1	1
R2LNG ^e	2	7	4	8		7	0.919	0.863	0.872	0.856	0.831	0.768	25.62	2	2
R2TF	10	7	12	8	6	7	0.4	0.863	0.8	0.856		0.768	25.62	2	2
S3	9	8	9	5	5	3	0.936	0.876	0.936	0.809	0.905	0.689	12.62	2	1
P4	8	5	8	2	5	2	0.797	0.758	0.801	0.4	0.736	0.4	25.99	2	2
R5	4	11	6	9	3	3	0.8	0.656	0.758	0.731	0.598	0.245	12.04	1	1
P6	6	3	6	5	5	3	0.476	0.439	0.38	0.386	0.324	0.216	10.27	1	1
P7 ^f	5	5		5		3	0.933	0.703		0.702		0.617	8.03	1	2
P8	5	4	7	3	4	2	0.782	0.209	0.842	0.205	0.782	0.224	8.23	1	1
R9	6	4	7	3	7	3	0.929	0.731	0.833	0.712	0.894	0.709	6.94	1	1
R10 ^g	12	8	11	6		5	0.797	0.653	0.894	0.587		0.69	23.80	2	2
R11	4	6	10	5	7	5	0.712	0.747	0.907	0.652	0.886	0.668	10.27	1	2
R12	4	4	5	5	7	4	0.643	0.778	0.764	0.861	0.85	0.867	7.01	2	1
P13	8	7	9	5	7	5	0.711	0.645	0.758	0.507	0.625	0.484	7.05	1	2
S14	3	3	2	3	3	3	0.556	0.679	0.4	0.8	0.511	0.644	5.46	2	1
R15	4	10	4	11	4	8	0.712	0.72	0.695	0.77	0.781	0.725	7.53	1	1

a: G sp 93 = gap species richness in 1993; U sp 93 = understorey species richness in 1993; likewise for other years;

b: G Sim 93 = gap Simpson indices in 1993; likewise for the understorey and other years;

c: %CO 93 = percentage canopy openness in 1993 measured with the semi-fisheye lens;

d: size- and severity class definition see Table 4.1;

e: R2LNG is the second 4 x 4 m plot located in gap R2, but note that only one understorey plot for this gap site exists and values are therefore repeated for both R2TF and R2LNG; this plot could not be remeasured in 1995;

f: P7G plot destroyed between 1993-1994;

g: R10G plot could not be remeasured in 1995.

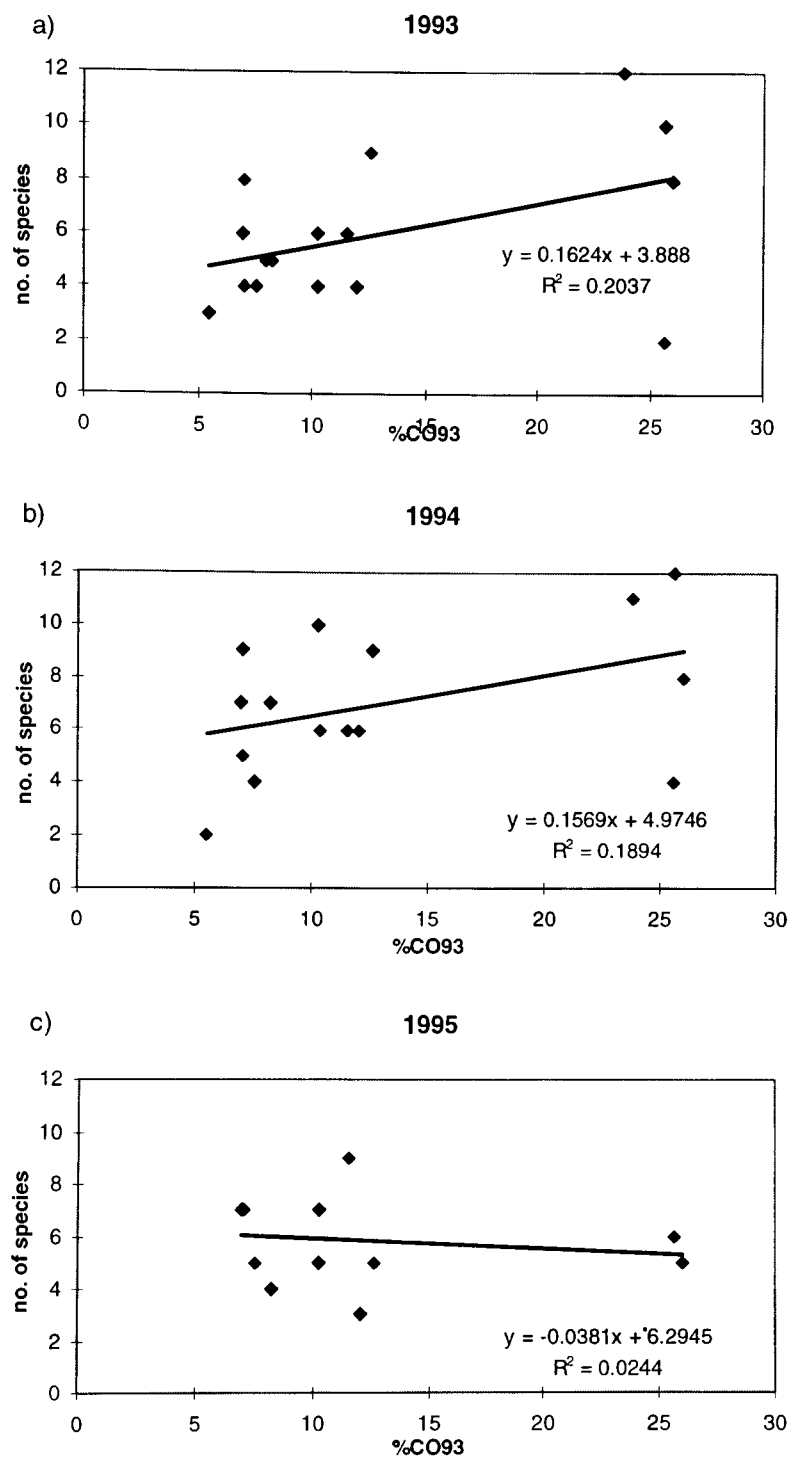


Fig A4.1: Regression analyses of gap species richness and gap size measured as 1993 percentage canopy openness (semi-fisheye values; %CO93) for: (a) 1993; (b) 1994 and; (c) 1995. It shows that no significant relationship with gap size existed for any of the years, but it should also be noted that gaps of intermediate size (as measured by %CO93) were not sufficient for adequate regression analyses.

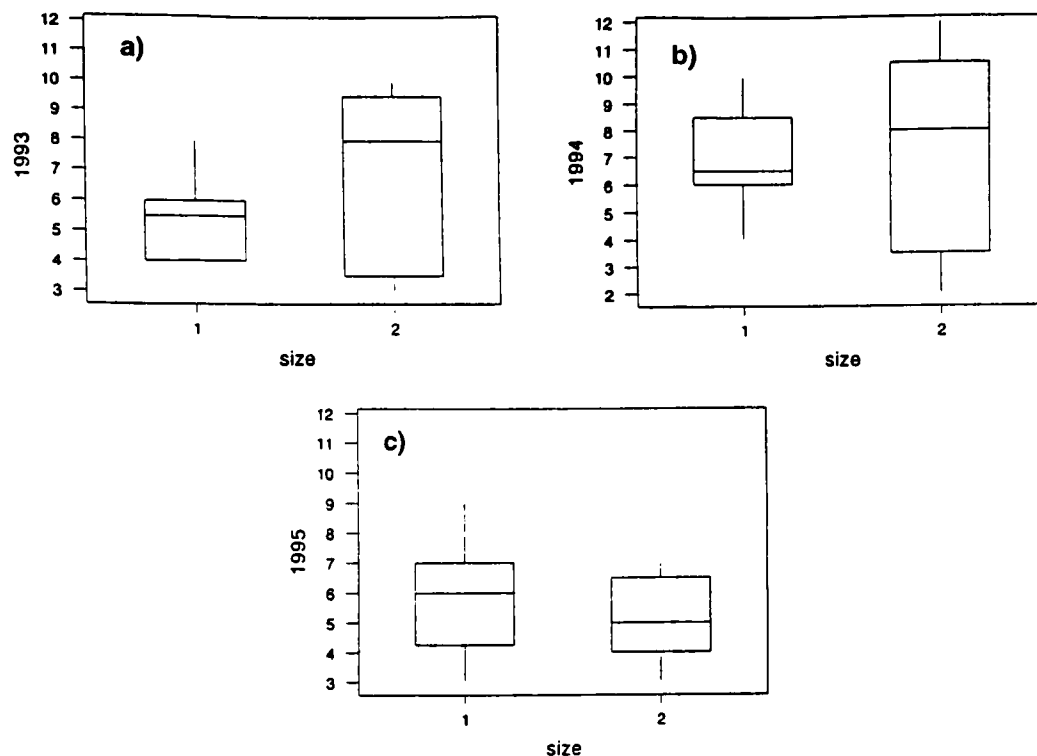


Fig. A4.2: Difference in the distributions of species richness between size 1+2 (1) and size 3+4 (2) gaps for: (a) 1993; (b) 1994 and; (c) 1995. See Table 4.1 for definitions of size-classes. Note that to allow comparison P7G, R10G and R2LNG were excluded for all years because of incomplete data sets after the first or second year of monitoring.

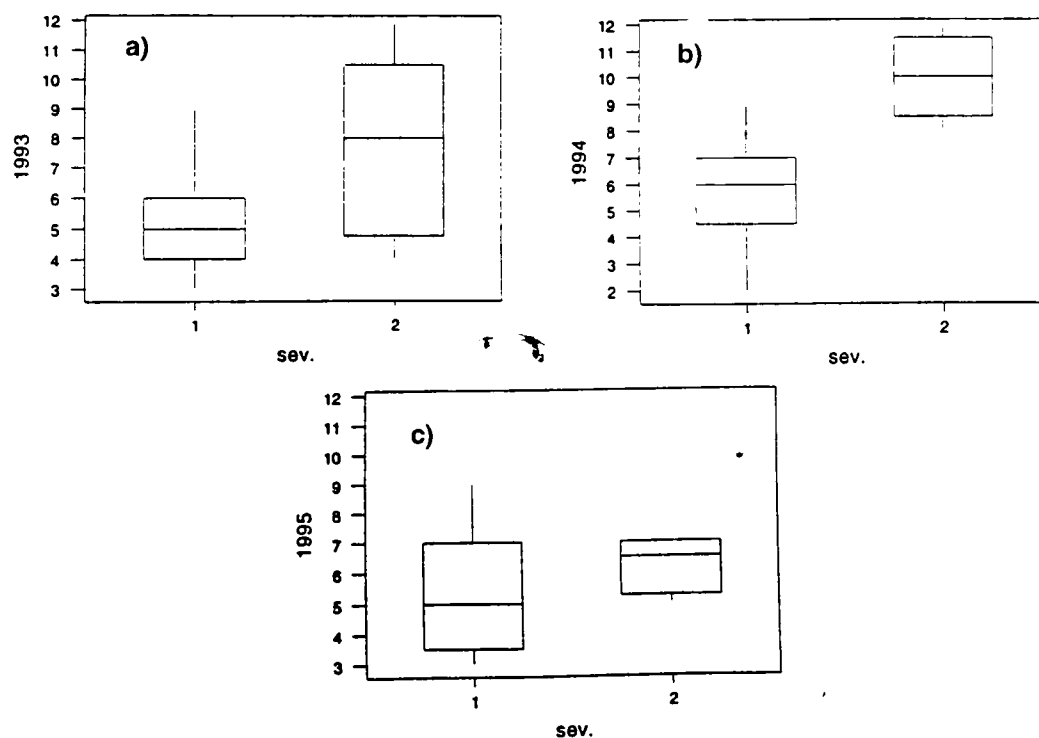


Fig. A4.3: Difference in the distribution of species richness between gaps of light to medium disturbance (sev. 1) and those of severe disturbance (sev. 2) for: (a) 1993; (b) 1994 and; (c) 1995. Note that P7G, R10G and R2LNG are *not* excluded here to show the significant difference in species richness in both 1993 and 1994. See section 4.3 for definition of the different severity classes.

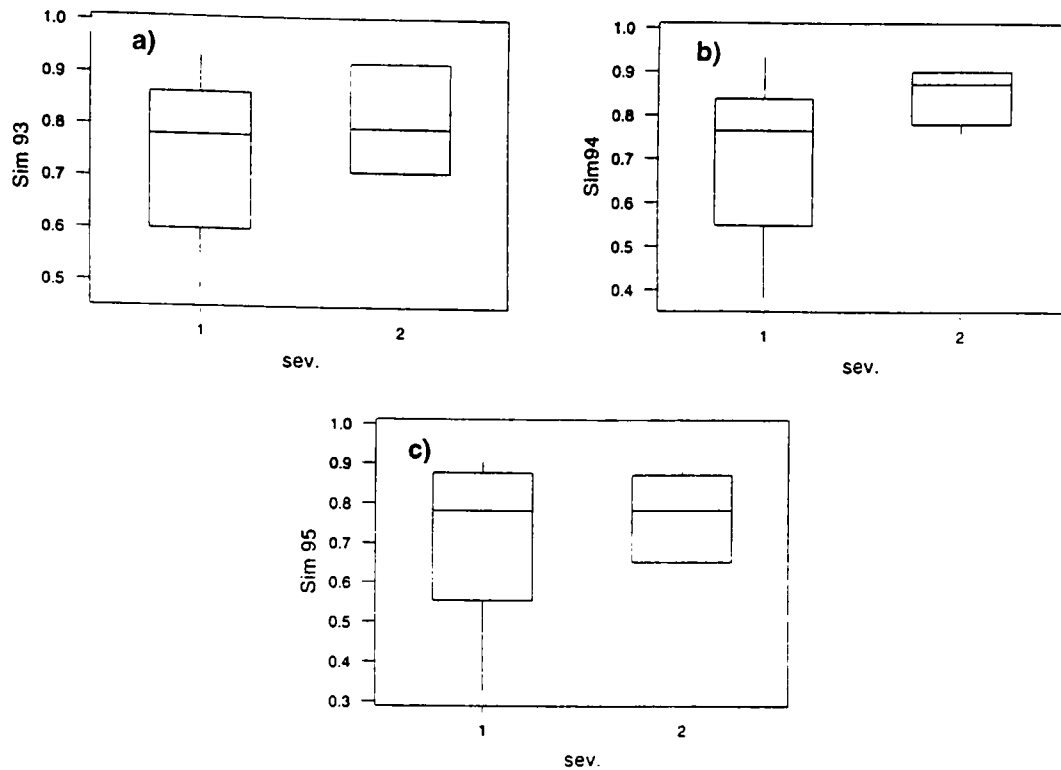


Fig. A4.4: Difference in the distribution of Simpson indices between gaps of light to medium disturbance (sev. 1) and those of severe disturbance (sev. 2) for: (a) 1993; (b) 1994 and; (c) 1995. Note that P7G, R10G and R2LNG are *not* excluded here to show the significant difference in the Simpson indices for 1994.

APPENDIX 5:
CURRENT BIOLOGICAL STUDIES ON THE KRAKATAU ISLANDS

Apart from the fact that the permanent plots of Whittaker *et al.* (1989) are remeasured every few years, several projects of shorter duration are currently in process.

Bird and bat dispersal

Whittaker & Jones (1994ab) have stressed the importance of dispersal studies for the understanding of the maintenance and restoration of forest in the region. Ms Louise Shilton (Leeds University) is currently undertaking research on bird and bat dispersal and the fruiting phenology of tree and shrub species on the islands. Her findings will make a valuable contribution to the autoecological knowledge of Krakatau tree and shrub species, and in particular to the little known information on the mechanisms of dispersal to and between the islands. Initial results have already provided further evidence that support the suggestion that figs are acting as 'keystone resources' providing food for the main bat and bird dispersers throughout the year and thus influencing the dispersal of other zoochorous species (Marshall, 1985; Terborgh, 1986; Lambert, 1989; Lambert & Marshall, 1991). Their role seems to become particularly important in the lean period of the dry season when fruit production of non-fig species seems to drop off markedly (Louise Shilton, pers. comm.). Initial analysis of her data on bat dispersal also indicates the great importance of these animals for inter-island dispersal, and that fig species are readily dispersed by these vertebrate frugivores. In 90% of the collected bat faecal samples she found fig seeds, and approximately 85% of the samples solely contained fig seeds. This initial analysis lends further support to the often suggested importance of bats as dispersers, and their potential significance in the restoration of tropical forest ecosystems.

Fig ecology on Krakatau

Recently further intensive studies on the Krakatau figs have been carried out by Dr N. Mawdsley, Dr S. Compton, and Dr R.J. Whittaker. These involved the study of pollination ratios to address the question of possible pollinator limitation, and how this may differ between species, and between islands. Furthermore, a comparison of fig diversity, distribution and abundance within and between islands has also been investigated and awaits analysis.

Founder effects in tree species

Studies have also been initiated by Dr P.J. van Dijk and Ms Tracey Parish at the Netherlands Institute of Ecological Research on genetic founder effects in tree species of the Krakatau islands. The project intends to provide important information on the population genetical aspects of the conservation of tropical forest trees, and the Krakatau islands are seen as an ideal study location for the investigation of genetic changes in tropical forest trees following expansion from bottlenecks. The genetic variation of five species is being quantified and compared to the levels in populations on Java and Sumatra, and (historical) migration patterns and rates are being assessed. These species are *Ficus fistulosa*, *F. pubinervis*, *Leucosyke capitellata*, *Leea sambucina*, and *Oroxylum indicum*, all except the latter are bird and/or bat dispersed tree or shrub species. The intention is to develop a stochastic metapopulation model to assess the long term effects of colonisation and migration in tropical forest trees (van Dyke, in lit.).