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O.F.I. OCCASIONAL PAPERS

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NO. 39

ECOLOGICAL EFFECTS OF FORESTRY
PRACTICES IN LONG-ESTABLISHED
WOODLAND AND THEIR IMPLICATIONS
FOR NATURE CONSERVATION

by

P.L. Mitchell and K.J. Kirby

1989

OXFORD FORESTRY INSTITUTE
Department of Plant Sciences
UNIVERSITY OF OXFORD



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PREFACE

The Nature Conservancy Council is concerned about the changes to British woodland caused by modern forestry practice. Consequently, as part of its research programme, it commissioned the Oxford Forestry Institute to review the literature relating to the ecological effects of forestry practices in long-established woodland. The review was carried out by P.L.M. between June 1985 and March 1987.

The nature of the subject means that it is difficult to choose keywords precisely enough to use a computerized database so Forestry Abstracts (1978 to date), Ecology Abstracts (1978-1985) and Ecological Abstracts (1974-1978, 1983-1984) were searched manually. This provided a core of references around which many more accumulated. The author index to Forestry Abstracts (cards for 1934-1983, microfiche thereafter) was particularly useful on occasion to trace work from the author's name only. There was never a shortage of reading material; the difficulty was to sift what was relevant and fit it into a coherent structured review.

The review concentrated on the soils and plants and is weaker with respect to the animal groups, partly because very little could be found on some subjects in the time available and partly because of our interests and expertise. For some animal groups other recent reviews are available.

The phrase "ecological effects" rather than conservation effects was chosen deliberately when the contract was set up. The aim was a review of the actual changes reported in soils or plant and animal communities under modern forestry practices without value judgements. Whether these ecological effects are good or bad depends on the viewpoint. For example, suppression of shrub regrowth is a "good" effect to the forester who wishes to establish a new tree crop on the site. It is a "bad" effect in nature conservation terms if the shrubs are part of the former semi-natural woodland cover. It has been the rôle of K.J.K. to add a nature conservation perspective on the changes described.

A number of technical terms are used which may not be familiar outside their particular fields. These are defined in Appendix 1. We have also used in places English names and standard abbreviations for some plants, whose scientific names are given in Appendix 2.

Peter Mitchell, Oxford.
Keith Kirby, Peterborough.

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If we have used any of their ideas without proper acknowledgement we apologize here. The remaining omissions and errors, of fact or of interpretation, are our own.

SUMMARY

Concern has been expressed about the damaging effects of modern forestry practices in Great Britain on the nature conservation values of long-established woodland. It is less often appreciated how far traditional forestry practices such as coppicing themselves altered the structure and composition of the original forests. This review compares the effects of modern and traditional forest practices on the soils, flora and fauna of British woods. Effects are allocated (as far as possible) between those due to a change of tree species, those caused by changes in stand or woodland structure and those due to other changes which take place under modern forestry management such as fertilization, or the application of pesticides.

A complex pattern emerges where no single forestry system (traditional or modern) is likely to favour all groups of organisms, so that it is essential for nature conservation objectives to be defined as precisely as possible for any given wood. This is particularly true in small woods (less than 10 hectares) where there is little opportunity to vary the treatments applied to different areas.

In general the review has confirmed that nature conservation interests are best served by systems which make use of trees and shrubs native to the site; use relatively small coupes, but contain also some larger open areas (either permanent glades or temporary clearings); keep some over-mature trees and dead wood; and minimize soil disturbance, fertilization, pesticide use and drainage. These tend to be more commonly associated with traditional systems of management such as coppice or coppice with standards than with modern forestry practice.

By contrast the practices that have been favoured in commercial forestry during the last forty years do tend to reduce the overall species or habitat diversity: the use of heavy shade-casting trees such as spruce, relatively large coupes (over 5 ha), few if any trees retained beyond maturity, a preponderance of stands all of a similar age, and intensive ground preparation techniques.

There is however some scope for offsetting the more damaging effects of modern forestry on nature conservation interests, for example by heavier thinning where a heavy shade-caster is used. Equally, traditional practices can be improved upon, by leaving some areas undisturbed to grow on to high forest. Hence it is worth analysing, for any site what elements of modern forestry are the most serious (in nature conservation terms), because it may be possible to change them without necessarily abandoning commercial management altogether. There will still be economic penalties (revenue forgone or cost increases) from so doing, but these are inevitable if nature conservation is genuinely to be accepted as an objective of woodland management.

There is a need for more monitoring of managed stands to improve our understanding of the effects of modern forestry, which should be combined with short-term experiments on some of the crucial issues and practices.

CONTENTS

Preface

Acknowledgements

Summary

INTRODUCTION	1
1.1 Forestry and nature conservation	1
1.1.1 Background	1
1.1.2 From wildwood to modern forestry	1
1.1.3 Management for nature conservation and for wood production	2
1.1.4 Nature conservation objectives in woodland management	3
1.1.5 The need to know about the effects of forestry practices	3
1.2 Scope	3
1.2.1 Ecological effects	4
1.2.2 Forestry practices	5
1.2.3 Long-established woods	7
1.3 Changes within stands and within the whole wood	7
1.3.1 The stand	8
1.3.2 Changes within a stand during the rotation	8
1.3.3 The wood	10
1.3.4 Silvicultural systems and woodland structure	11
1.3.5 Comparing effects of forestry practices between stands and woods	13
1.4 Structure of this review	14
1.4.1 General approach	14
1.4.2 Bias and gaps in the coverage	15
1.4.3 How to use this review	15
2 SOILS	17
2.1 Background	17
2.1.1 Soil and trees	17
2.1.2 Historical perspective	17
2.1.3 Variations in soil characteristics in space	18
2.1.4 Variations in soil characteristics through time	19
2.1.5 Variations in soil characteristics due to stocking	21
2.1.6 Effects of shrubs and ground vegetation on soil conditions	23
2.1.7 Effects of grazing and trampling	23
2.2 The effects on the soil of changing tree species	23
2.2.1 Other reviews	23
2.2.2 Organic matter	24
2.2.3 Soil pH	26
2.2.4 Nutrients and fertility	27
2.2.5 General changes in the soil	28
2.2.6 Hydrology and water relations	29
2.2.7 Soil flora and fauna	30
2.2.8 The effects on soils of mixtures of tree species	32
2.3 The effects on soils of changes in stand structure	32
2.4 The effects on soils of a change in woodland structure	33
2.4.1 The effect of silvicultural systems on soil conditions	33
2.4.2 The effects of road or ride creation	34

2.5	The effects on soils of changes on the site	34
2.5.1	Soil disturbance	34
2.5.2	Fertilization, drainage and woodland streams	36
2.5.3	The effects of weed control on soil properties	36
2.5.4	Increased intensity of harvesting	37
2.6	Discussion	39
2.6.1	Soil as a woodland feature of nature conservation value	39
2.6.2	Tree species and litter type	39
2.6.3	Soil disturbance	40
2.6.4	Soil conservation	40
2.7	Implications for nature conservation (soils)	40
3	FLORA	42
3.1	Background	42
3.1.1	Flora and vegetation	42
3.1.2	Groups within the woodland flora and their relationships	42
3.1.3	Changes during the rotation in worked coppice	44
3.1.4	Changes during the rotation in high forest	47
3.1.5	The effects on the flora of changes in stocking	50
3.2	The effects on the flora of a change of tree species	52
3.2.1	Trees and shrubs	52
3.2.2	Ground flora	52
3.2.3	The ground flora under mixtures of tree species	58
3.2.4	Bryophytes	60
3.2.5	Epiphytes	61
3.2.6	Effects of tree species on the ride flora	62
3.3	The effects on the flora of a change of stand structure	62
3.3.1	Trees and shrubs	62
3.3.2	Ground flora	64
3.3.3	Bryophytes and epiphytes	66
3.4	The effects on the flora of a change in woodland structure	67
3.4.1	Roads and rides	67
3.4.2	The effects of selection systems: the Bradford plan	67
3.4.3	Other silvicultural systems	69
3.4.4	The effects of coupe and stand size on plant diversity	70
3.5	The effects on the flora of changes on the site	71
3.5.1	Treatments to achieve natural regeneration	72
3.5.2	Effects of site preparation on existing trees and shrubs	72
3.5.3	Site preparation and the ground flora	73
3.6	Discussion	75
3.6.1	Summary of effects by groups of flora	76
3.6.2	Relative importance of the four types of change	77
3.6.3	Change of tree species	78
3.6.4	Changes on the site	81
3.6.5	Rides and their flora	82
3.7	Implications for nature conservation (flora)	83

4	FAUNA	85
4.1	Background	85
4.1.1	Approach and limitations	85
4.1.2	Mobility of species and habitat patch distribution	86
4.1.3	The effects on the fauna of variations in stocking	86
4.2	Effects of forestry practices on invertebrates (general)	87
4.2.1	Changes during the rotation	87
4.2.2	The effects on invertebrates of a change of tree species	88
4.2.3	The effects on invertebrates of a change in stand structure	90
4.2.4	The effects on invertebrates of a change in woodland structure	91
4.2.5	The effects on invertebrates of changes on the site	91
4.3	Effects of forestry practices on Lepidoptera	92
4.3.1	Introduction	92
4.3.2	The effects on Lepidoptera of a change of tree species	92
4.3.3	The effects on Lepidoptera of a change in stand structure	93
4.3.4	The effects on Lepidoptera of changes in woodland structure	93
4.3.5	The effects on Lepidoptera of changes on the site	94
4.4	Effects of forestry practices on molluscs	95
4.5	Effects of forestry practices on amphibians and reptiles	95
4.6	Effects of forestry practices on birds	96
4.6.1	Introduction	96
4.6.2	The effects on birds of a change of tree species	98
4.6.3	The effects on birds of a change in stand structure	99
4.6.4	The effects on birds of a change in woodland structure	101
4.6.5	The effects on birds of changes on the site	102
4.7	Effects of forestry practices on mammals	103
4.7.1	Introduction	103
4.7.2	The effects on mammals of a change of tree species	104
4.7.3	The effects on mammals of a change in stand structure	105
4.7.4	The effects on mammals of a change in woodland structure	105
4.7.5	The effects on mammals of changes on the site	106
4.8	Discussion	107
4.8.1	General points	107
4.8.2	Change of tree species	107
4.8.3	Change of stand structure	108
4.8.4	Change of woodland structure	108
4.8.5	Changes on the site	110
4.9	Implications for nature conservation (fauna)	110

5	DISCUSSION	112
5.1	Introduction	112
5.2	Generalizations about types of change	112
5.2.1	Change of tree species	112
5.2.2	Change in stand structure	114
5.2.3	Change in woodland structure	115
5.2.4	Changes on the site	117
5.3	Concepts and approaches	117
5.3.1	Nature conservation as an objective not a constraint	118
5.3.2	Nature conservation objectives must be defined	118
5.3.3	What is the level of acceptable change?	119
5.3.4	The long-term maintenance of habitat conditions	119
5.3.5	Inter-relations of site, treatment and tree species effects	120
5.3.6	A practical example of the changes that may occur	121
5.4	Further research	125
5.4.1	Long-term trials and short-term experiments	125
5.4.2	Research on the mechanisms of change	127
5.4.3	Research on ecological groups	128
5.5	Woodland management, preservation and conservation	129
	REFERENCES	131
	APPENDICES	161
	INDEX	165
	LIST OF TABLES	
1.1	Ecological groups and properties	4
1.2	Four types of change resulting from the forestry practice	6
1.3	Coverage of soils, flora and fauna	16
2.1	Tree crop and soil organic matter in Norway spruce stands	22
2.2	Grieve's (1975) sites in the Forest of Dean	29
3.1	The twenty widespread species in the Ovington plots	49
3.2	No. of species of lichens found on different tree species	62
3.3	Details of four silvicultural treatments in Michigan	69
4.1	Stand characteristics and no. of species of birds recorded	100
5.1	The initial state of a wood and the forestry proposals	122
5.2	The changes resulting from a particular forestry proposal	123
5.3	Treatment classes for broadleaved woods	130

LIST OF FIGURES

1.1	The structure of stands	8
1.2	Stages in a rotation	9
1.3	Woodland structure	11
1.4	Pattern and scale of woodland structure	11
1.5	Regular and irregular forest structures	12
1.6	One unit of the Bradford Plan selection system	13
2.1	The redistribution of precipitation by a tree canopy	17
2.2	Soil pH changes through the rotation	20
2.3	Dry weight of surface organic matter on Ovington's plots	25
3.1	Changes in the ground vegetation during a coppice rotation	46
3.2	Changes in the ground flora during a coppice rotation	46
3.3	Changes in the ground flora during a high forest rotation	48
3.4	Effects of stocking (basal area/ha) on ground vegetation	50
3.5	Effects of stocking on transmission of visible light	51
3.6	Above-ground dry weight of the ground vegetation	53
3.7	Number of species in the ground flora of Ovington's plots	54
3.8	The ground flora under alternating bands of oak and spruce	59
3.9	Seasonal change in photosynthetically active radiation	80
3.10	Assessing the total area treated by herbicide	83
4.1	No. of insects and mites associated with 28 tree species	88
4.2	A sequence of coppice cuts	93
4.3	Differentiation of habitat use by birds	99
4.4	Arrangement of stands to give maximum edge	110
5.1	Tree species grouped according to their generalized effects	113
5.2	Effects of tree mixtures on the species content of a stand	114
5.3	Size distribution of ancient woods in England and Wales	115
5.4	Shape and size of a coupe and the proportion of its area that is unshaded	116
5.5	The initial state of a wood and effects of proposed changes	122
5.6	Differentiation of forestry systems by their gap dynamics	126

"It would be surprising if our view were not improved by standing on our predecessors' shoulders, and any comments which appear critical should be taken in this vein."

(G.C. Evans, Journal of Ecology, 1956, 44, 392.)

1 INTRODUCTION

1.1 Forestry and nature conservation

1.1.1 Background

Over the last 40 years in Great Britain there have been dramatic changes in the appearance and composition of many ancient semi-natural woods, with some 20-30% being transformed from broadleaved coppices to young, mainly coniferous plantations (Kirby *et al.* 1984). Great concern has been expressed about the effects of these changes on our native woodland species and communities. On the other hand, owners and forest managers who wish to obtain an economic return from their woods have sometimes disputed the occurrence or significance of the effects of modern forestry practices on woodland nature conservation.

This report draws together information from the literature on the changes to the soils, flora and fauna that occur within woods managed to produce timber. The significance of these changes in nature conservation terms is outlined. There are gaps in our knowledge, inevitably, but we have tried to provide a basic framework into which further work may be fitted.

All woodland is structurally complex and provides habitats for a wide range of species (Steele 1975). In addition woodland of some kind or other is the natural climax vegetation cover for much of the British Isles under present climatic conditions. The great primaeval forests of the Atlantic period, the wildwood (Rackham 1976, 1988), have been destroyed, but a shadow of them survives, albeit heavily modified, in the many ancient woods that still exist. As such they are one of the most important habitats for wildlife because there is some continuity in their species and communities with the past-natural vegetation cover (Peterken 1977a). Some of these woods are also of great historical and archaeological value (Rackham 1980). Given the value of these areas for wildlife and that ancient and semi-natural woods now occupy no more than 2-3% of the land surface, even small changes in their total area or composition become important.

1.1.2 From wildwood to modern forestry

Even ancient semi-natural woods differ from the wildwood because of the treatment they have received (Bunce 1982). The woods are small (most much less than 50 ha) and often isolated. This fragmentation may not in itself have led to the complete extinction from Great Britain of any ground flora species. These are often patchily distributed even in large forest blocks (Middleton & Merriam 1983). However, local extinctions must have occurred. Some species, small-leaved lime for example, are much less widespread than formerly, while others such as sessile oak in western Britain, were favoured by past treatments. Many woods, being now more disturbed, may hold more plant species than a similar area of primaeval woodland would (Levenson 1981; Middleton & Merriam 1985; Swindel & Grosenbaugh 1988).

Some large mammals that would have affected woodland processes, such as boar, beaver, wild ox, are now extinct; other species have been introduced (grey squirrels, domestic stock, sika, muntjac and fallow deer) or their numbers, in relation to the area of the surviving woods, have greatly increased (red deer in Scotland for example). The role of herbivores in a near-natural forest is discussed by Falinski (1986).

In coppices there are few over-mature trees and the amounts of dead and dying wood are less than would be expected in undisturbed temperate deciduous forests (Falinski 1978; Harmon *et al.* 1986; Lang & Forman 1978), so that a large and important part of the invertebrate fauna is missing or at least much reduced (Girling 1982). In the old parks and former Royal Forests where dead and over-mature timber does often survive, the shrub and ground flora layers are reduced by centuries of grazing.

Thus our concern is not with the effect of introducing modern forestry practices to previously undisturbed woodland, but with a change to the management regime in sites that have already been modified by past treatments.

1.1.3 Management for nature conservation and for wood production

A natural wood might be defined as one in which Man's direct and indirect effects on the processes that go on within it are minimal. We cannot recreate the past-natural forests, the wildwood, anywhere in Great Britain, not least because we cannot bring back the fauna that has been lost and eliminate the introductions from a large enough block of land. Nevertheless we can and should set up minimum intervention woodland areas where, as far as is possible under present conditions, natural woodland processes may take place.

Such areas may range from a single compartment to large tracts depending on the objectives and circumstances (including the surrounding land use). They form essential control areas against which the effects of management on the woods elsewhere can be judged; dead wood can accumulate; and their soils will not be disturbed by machinery or timber extraction. Steele & Peterken (1982) suggest that about 22,000 ha of broadleaved woodland (plus large areas within the native pinewoods) should be set aside for this purpose. Peterken & Jones (1987) illustrate the changes that can be described in one such site (Lady Park Wood, Gloucestershire). Minimum intervention is thus one form of management for nature conservation, but it does not allow any production from the site.

Elsewhere some form of active woodland management is likely to take place (albeit often interspersed by periods of neglect). The aims of this management depend on the objectives of the owner and others who have an interest in the state of the wood. If the management is simply for nature conservation then only work which is necessary to maintain or enhance the natural features, species or communities on that site should be undertaken. Timber production is an incidental factor; in strict nature conservation terms there does not need to be a final crop to harvest.

In practice, the owner may not wish to have nature conservation as the sole objective. Traditional forms of management, such as coppicing or pollarding, may not provide either the products or the income that is required. There is an understandable desire to change to more profitable forms of woodland management and these are frequently thought to be more damaging to nature conservation interests than traditional practices.

The Nature Conservancy Council believes that some woodland should be treated as minimum intervention areas; that in other woods traditional management should be restored; but that in many woods there is scope for adapting modern commercial forestry in such a way that it is compatible with nature conservation needs. To do this we must have a sound scientific basis from which to offer advice, both on managing for nature

conservation and on integrating nature conservation with other objectives, particularly timber production.

1.1.4 Nature conservation objectives in woodland management

The nature conservation objectives for a site may be to maintain or enhance the relatively natural elements in the woodland; to protect or increase the populations of any rare species present; or to maintain or enhance the populations of all native woodland species in that area. However, the detail varies from site to site and priorities may also vary between different parts of the site.

For example, Cranborne Chase is an extensive area of ancient, mainly semi-natural woodland with a rich and varied ground flora typical of the southern chalk. The general conservation aim is to maintain the variety of native tree, shrub and ground flora communities over as wide an area as possible. Coppice or some forms of high forest treatment could achieve this objective. In addition, however, there are some areas identified as of high importance for lichens where it is crucial to maintain old trees generally and even specific individual trees. Other areas are particularly valuable for invertebrates. Where these are open ground species short rotation coppice or management of the rides should be encouraged, but for the dead wood species the need is to increase the stock of over-mature trees and not to clear fallen dead wood. In replanted areas the nature conservation priority is to encourage thinning and the opening up of stand edges to benefit the surviving ground flora and shrub layers.

1.1.5 The need to know about the effects of forestry practices

Within Cranborne Chase, as for most sites, no single prescription would be ideal for nature conservation over the whole area. The effects of any forestry proposal must be assessed at two levels. Firstly, is the silvicultural system likely to meet the general conservation aims? Secondly, what will be the effects of the individual practices or operations, within a given system, when applied to particular areas?

Recent changes in forestry policy (Forestry Commission 1985a, 1985b) mean that there is much more interest in the management of broadleaved woods than was the case ten years ago. Increasingly information is needed, not on whether an "extreme" form of modern commercial forestry (clear fellings of 20 ha, followed by planting of Norway spruce at 2m spacing) will be damaging to nature conservation interests, but whether 3 ha as opposed to 1 ha coupes will be damaging; whether planting of broadleaves at 3m rather than 1.5m spacing is to be preferred in a particular situation.

General management principles for woodland nature conservation already exist (Kirby 1984a; Peterken 1977b, 1981, 1987; Steele 1972). We must now move to an assessment of the effects of particular practices.

1.2 **Scope**

The aim of this review is to describe the ecological effects of modern forestry practices in long-established woodland in Great Britain, based as far as possible on published results. A subsidiary aim is to point out gaps in present knowledge and suggest where future research might be done. It is not a prescriptive guide to woodland nature

reserve management.

1.2.1 Ecological effects

The ecological effects considered are changes to the soils, flora and fauna. Effects on landscape, amenity and recreation are excluded. The management of woods for particular rare species is not covered, except in so far as it helps to illustrate more general principles, because the requirements of these species may be unique. The conservation of genetic resources (Ledig 1988) is not discussed either, although such resources are affected by modern forestry practices - most notably when trees of a different provenance are introduced to a site; more subtly when there is selection for just a few trees to form the parents of any natural regeneration. The genetic flows of shrubs, ground flora and animals are also affected by the imposition of "bottlenecks": temporary phases in the rotation that eliminate much of the population of a given species such that subsequent regeneration or colonization is from a reduced genetic base. (See Harris (1984) for the application of ideas on the conservation of genetic resources to the preservation of old-growth Douglas fir stands.) With a few exceptions (Forrest (1980) on Scots pine, Rackham (1980) on native oak populations) there appears to be very little information on this subject for British woodland species.

Table 1.1 Ecological groups and properties.

Soil	litter and type of organic matter	-	closely linked, together comprising soil fertility
	pH		
	nutrient levels		
	hydrology and water relations		
	soil flora and fauna		
Flora	trees and shrubs		
	vascular ground flora		
	ground bryophytes		
	epiphytes		
Fauna	invertebrates (general)		
	Lepidoptera		
	molluscs		
	amphibians and reptiles		
	birds		
	mammals		

The effects of forestry practices on the soil, flora and fauna of a wood have been broken down according to the headings in Table 1.1. The emphasis given to each topic depends on the amount of information available and the ready availability of other reviews. The vascular plants and especially the ground vegetation are dealt with in detail, because they are widely used to assess the nature conservation value of woods and support most of the fauna (Peterken 1981). The coverage of invertebrates was limited by the scattered literature. There are

several recent reviews on birds (Bibby 1987; Newton 1986; Smart & Andrews 1985). The coverage of mammals, especially deer on which much has been written (e.g. Prior 1983; Ratcliffe 1987), was limited by lack of time and expertise.

Effects on soils are included for two reasons. The composition, abundance and vigour of the vegetation, including the tree crop, depends partly on the properties of the soil. Also undisturbed soils under ancient woodland are of great intrinsic interest and worthy of preservation (Ball & Stevens 1981). These soils have been least altered, if at all, by agricultural use and so provide controls for comparative studies. The significance of woodland for retaining former soil characteristics may increase as the extent of past soil erosion in, for example, the downland of southern England is recognized (Collins 1978).

1.2.2 Forestry practices

A general definition of forestry is the art and science of managing trees to meet defined objectives, usually but not necessarily to produce wood or timber. Modern British experience is based largely on afforestation and often involves plantations of introduced species. Rackham (1976) distinguished this as "forestry", in contrast to "woodmanship": the traditional management of existing woods to provide underwood and timber using the ability of native broadleaved trees to regenerate after felling, mainly as coppice but also from seed. Woodmanship was well established by the Middle Ages and continues in a few places to the present day. Rackham (1976) traced the rise of modern forestry from the 17th century and pointed out that almost all of it was afforestation. Only recently have similar techniques come to be practised on a large scale in ancient semi-natural woods.

1.2.2.1 The effects of woodmanship

The change from the unmanaged wildwood to the Mediaeval systems of coppices, parks and fragmentary areas of high forest had dramatic consequences for the woodland ecosystem, particularly on the structure of the woodland and the occurrence of large mammals (1.1.2). (In this review cross-referencing is indicated by the relevant section number.) Thereafter traditional management did not cause rapid change in the woodland except for the inevitable progress through the rotation. Rackham (1976) regarded coppice management as "both intensive and conservative": intensive in that a continual yield of underwood was expected and taken (with short rotations in the Middle Ages) but conservative in the unchanging methods used and because coppicing tended to preserve the tree and shrub species composition.

Apart from the coppicing itself, the silvicultural input was minimal and output was limited to the yield that happened to be available when the underwood had reached the size or age required for cutting. Access for Man, oxen or horse and cart was provided initially by meandering paths between the stools and later by a system of grassy rides (Rackham 1976). These paths probably received comparatively light use most of the time, but it would be wrong to assume that no ground disturbance occurred, particularly where coppicing was more for industrial rather than domestic uses.

Short-term damage to the existing ground flora and bird communities must have occurred on the areas actually cut and some of the descriptions of 19th century coppicing in the uplands suggest cutting on

a scale that would raise an outcry today (Fell 1908). Rixon (1975) similarly comments on the digging of saw-pits, rutting of roads by waggons, building of temporary shelters and other activity associated with 17th, 18th and 19th century cutting in Bedford Purlieus.

1.2.2.2 The increased intensity of modern forestry

Modern forestry is more intensive in the sense that it is a high input system expecting a correspondingly high output. The extra input is in effort and money: management plans and accounts prepared, site preparation, planting, weeding, thinning, and all the routine tending against fire, pests and diseases. In addition good access for machinery is required so roads and rides have to be made and maintained. There is little doubt that the physical output can be much higher than in traditional systems, both as above-ground biomass and especially in wood utilizable by modern standards. Whether the economic output is always higher is a moot point (Lorrain-Smith 1982; Pryor 1982) and there may be adverse effects on non-monetary outputs such as nature conservation, the landscape and, less often, recreation.

1.2.2.3 Types of change associated with forest management

Table 1.2 Four types of change resulting from forestry practice.

CHANGE	CAUSE
A Changes in tree species composition	by planting* by selective thinning by selective thinning and planting
B Changes in the structure of stands**	existing structure changed to: simple coppice coppice with standards high forest*
C Changes in the structure of woodland**	involving the stands only: the pattern and the scale of different silvicultural systems involving other features: roads and rides* glades streams and ponds
D Changes on the site	site preparation: clearing site* clearing and grubbing site site amelioration: drainage fertilization cultivation, scarification control of herbaceous weeds* control of woody weeds* generally more intensive management: more frequent harvests increase in amount harvested use of machinery*

* the most probable changes in long-established woodland.

** stand and woodland structure are discussed in 1.3.1 and 1.3.3

The changes that forestry practices bring about have been classified into four types (Table 1.2). The types of change are in increasing order of intensity of management applied to the wood as a whole and in a hierarchy: the lower in the list the less likely it is to occur independently and the more likely to be associated with a change higher up. The types are conceptually independent and in theory any one type could occur without the others. For example, lengthening the rotation and grouping adjacent stands of existing coppice together for treatment changes only the structure of the woodland; drainage and fertilization to try and improve productivity of an existing stand would be changes on the site alone. However, usually certain types occur together, in a hierarchical fashion.

Changing the tree species thus very often involves changing stand and woodland structures and changes on the site as well. Change of stand structure is usually incidental to change of species, or to change of species and of woodland structure together. Change of woodland structure seldom occurs without changing species and stand structure. Changes on the site are usually associated with all the other types of changes. This hierarchical aspect should be remembered when the effects of any particular operation are considered: discussions may centre on the effects of a change of tree species, but changes to stand and woodland structure are likely to be involved without necessarily being specifically mentioned.

It is the cumulative effect of all proposed and associated changes that is important in nature conservation terms.

1.2.3 Long-established woods

This review is primarily concerned with the changes within long-established woodland, not those associated with afforestation of open ground (Good 1987; Jenkins 1986; Nature Conservancy Council 1986; Stroud *et al* 1987). The woods of most interest for nature conservation are ancient woods, known to have existed since before 1600 A.D. and probably primary, although woods that have developed from natural succession for 150 years or more also have considerable nature conservation value (Peterken 1977a). Studies dealing with more recent woods and plantations have been included where similar or analogous ecological processes may be involved, or when nothing much else was available. For the same reason relevant American and European examples have been cited.

1.3 Changes within stands and within the whole wood

For the most part British woods are isolated by non-woodland habitat, whether pasture, arable or moorland and the changes taking place within them can be considered in isolation. However, emigration from and immigration to a wood may be affected by the nature and treatment of the surrounding land and the significance of any particular change may be influenced by what is happening round about. Such "landscape scale" effects, for example the adverse effect on birds in some Finnish forest reserves of intensive forest management in adjacent areas (Helle 1986), have been largely ignored in this review.

Even a single wood, however, includes areas not covered by trees. The best way to deal with this complexity is to consider separately the stands of trees and the wood as a whole.

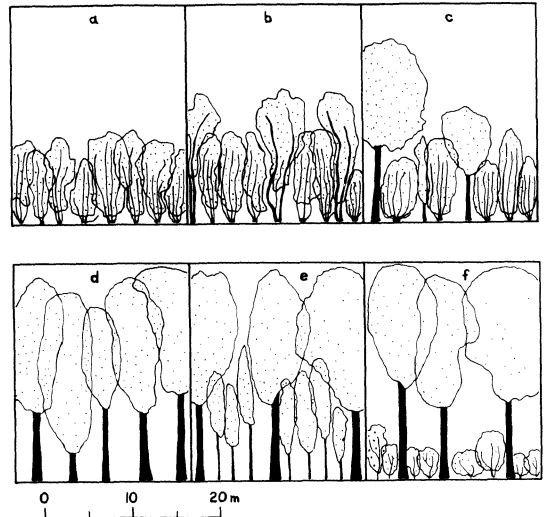
1.3.1 The stand

The stand is a recognizable unit of trees, more or less uniform in itself but differing from other stands in either species composition, age, structure, or past or present treatment (Kirby 1984a). The subcompartments of forestry stock maps are stands defined and used from the point of view of silviculture. For recognition as subcompartments, stands must usually be above a certain minimum area (0.5 ha in the Forestry Commission, for example) but our concept of the stand extends, as and when necessary, down to the area occupied by a single large tree. Thus a selection forest consists of many very small stands containing one large tree or several saplings or a patch of seedling regeneration. Stand structure is the vertical arrangement of the trees and underwood, and is described by its associated silvicultural system with qualifiers as necessary, e.g. high forest, high forest with a shrub layer, simple coppice, coppice with standards (Figure 1.1).

Figure 1.1

The structure of stands:

- (a) simple coppice;
- (b) two-storey coppice;
- (c) coppice with standards;
- (d) high forest;
- (e) two-storey high forest;
- (f) high forest with shrub layer.



Each type is shown at a late stage in the rotation when the differences in stand structure are fully developed. Vertical and horizontal scales are the same.

1.3.2 Changes within a stand during the rotation

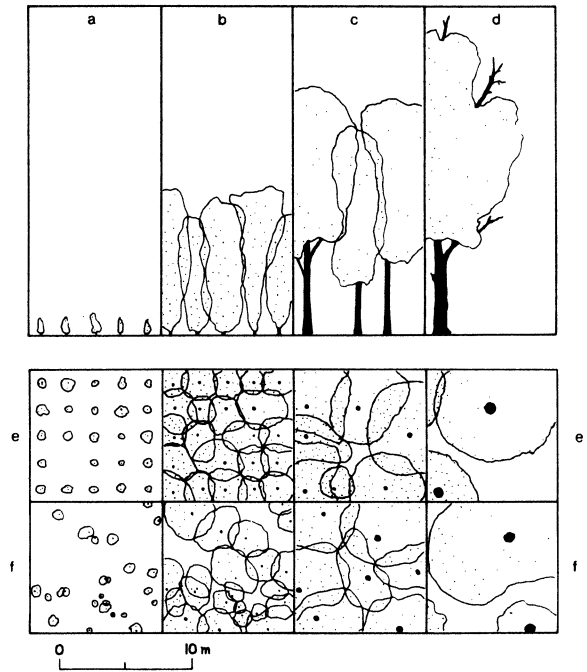
Conditions change greatly during the growth of a stand of trees. After felling the regeneration (natural regeneration from coppice or seed, or planted trees) takes several years before it starts to affect the conditions for other species on the site. The canopy then closes to form a "thicket". The green tree canopy moves upwards as the lower branches become increasingly shaded and die, leading to the pole stage at which the coppice is cut or thinning begins in high forest. This stage lasts until felling at the end of the rotation in managed high forests. If, however, the stand is left, a further stage develops in which tree growth slows and the trees are unable to close gaps left by thinning or natural loss of individual trees and large branches. Finally the over-mature stage may be reached when most of the trees start to die. This sequence of changes through the rotation (Figure 1.2) occurs under both traditional and modern forestry management, except in neither is the final senescent phase allowed to develop.

Figure 1.2

Stages in a rotation:

- (a) young trees;
- (b) thicket;
- (c) pole and mature;
- (d) over-mature.

The same stand is shown in plan form (row (e)) and compared with a naturally regenerated stand with irregular spacing (row (f)) at the same stocking level as the planted stand. Vertical and horizontal scales are the same.



Similar changes take place in natural forests where instead of felling, natural disturbances (windthrow, fire, landslip, insect or fungal plague) lead to regeneration (Oliver 1981; Whitmore 1982). The scales of these disturbances vary, even between different types in the same forest (Koop & Hilgren 1987), but they all produce more or less even-aged regeneration on areas from one-hundredth of a hectare, where a single tree is removed from the canopy, to hundreds of hectares after a fire or extensive windthrow. The large scale of clear felling in many British woods is not intrinsically unnatural if forests worldwide are considered (Jones 1945; Whitehead 1982). However, it bears little relation to the probable natural scales of disturbance for much British woodland and is therefore inappropriate where nature conservation is a high priority.

The sequence of changes in the ground flora (e.g. Ash & Barkham 1976; Alaback 1982) or in nesting birds during the rotation is often referred to as succession. However, the difference between succession, fluctuation and regeneration is one of scale, in time and space (Miles 1979). In the long term and on the large scale appropriate here changes within a rotation are fluctuations around an overall mean value or a longer-term trend. The conditions should return to their starting point at each restocking (assuming no change of species or treatment). Succession is the long-term directional change of vegetation or animal communities through a sequence of types such as abandoned chalk grassland to scrub to woodland or the switch from moorland to woodland bird communities during afforestation.

1.3.2.1 Rotational change within a coppice

Clear felling is not the same as deforestation (pace Blackie *et al.* 1980) provided that steps are taken to ensure or allow regeneration. Rackham (1976) emphasized that felling a broadleaved wood was a normal part of management and did not destroy it but renewed it. Under traditional coppice treatment the usual sequence was cutting followed by regrowth from stumps. The regrowth was probably variable and a mixture of species, and there was little or no intermediate treatment before the next coppicing. In coppice with standards the standards would remain

for several coppice rotations and in theory cover a range of ages so that only a few were felled at each coupe. In practice felling was probably more opportunistic so that from time to time all the standards would be felled during coppicing. The consequences of this were no doubt just as drastic then as they are now (1.2.2.1).

1.3.2.2 Rotational changes under modern forestry practice

After felling, modern British forestry generally involves planting, rather than stump regrowth to regenerate the stand, followed by weeding during the early stage to obtain good establishment (Evans 1984; Savill & Evans 1986). Little tending takes place in the thicket stage. Near the beginning of the pole stage thinning starts and it continues at intervals until clear felling at the end of the rotation. Silvicultural systems other than even-aged clear felling either overlap the ends of rotations, as in the uniform shelterwood system, or work with small stands, as in the group and strip shelterwood systems (Appendix 1; Pryor & Savill 1986; Troup 1952). In the selection or group selection systems the unit of working can be regarded as a miniature stand containing, at a late stage in the rotation, only one or a few trees. Even in the selection system the single tree arose from numerous seedlings and progressed through a stage with several saplings in the small gap made by felling one or two trees. In that small gap the earlier stages (young trees, thicket, pole) can still be recognized although environmental conditions are dominated by the surrounding taller trees.

1.3.3 The wood

The wood consists of the stands (including non-crop trees) and other features such as roads, rides, ponds, streams and glades (i.e. an area permanently without trees). The structure of woodland is the arrangement of the stands and these other features, i.e. structure in the horizontal dimension (Figure 1.3). Even without other features the stands alone give structure to a wood because they vary in species, age and stand structure and occur as a pattern and at a scale determined by the silvicultural system (Peterken 1981). This is especially clear in worked coppice where it is possible to have equal areas at each age (a normal forest with equal sustained annual yields) as a patchwork of stands on a scale of a few hectares.

The structure of the wood in terms of its pattern and scale of stands is important to animals, especially those of limited mobility and with strong preferences for particular stages (Figure 1.4). It is less important for plants because they are either more or less immobile (poorly dispersed shade species or species with a seed bank), or very mobile with well-dispersed seeds, so that contiguous or nearby suitable stands are not so necessary for their persistence in a wood. Woodland structure in terms of the arrangements of the stands has no relevance for soils as far as we know.

The margins of stands and of woods are different from the interior and so add further to the diversity of habitats, particularly if these margins are diffuse and irregular rather than sharp (Peterken 1981). Some plants often occur only or with higher cover at the edge and Ellenberg (1988) describes distinct edge assemblages. Internal margins may attract a different range of birds to those on the edge of the wood, for example some scavengers and raptors may use the moorland-woodland margin, whereas passerines may use the stand-ride margins. Margins are little studied because work is normally done either well inside the

stand, or in the glade, ride, or field adjoining the wood precisely to avoid edge effects. It is worth treating margins as a distinct element of the woodland because it is often possible to improve the wildlife habitat in a wood by manipulating the margins with little effort or expense (Anderson 1987a, Carter & Anderson 1987).

Figure 1.3

Woodland structure.

Apart from the stands of trees there are streams, a pond, a glade and a road and ride with verges. Small-scale woodland structure is shown in the bottom left corner with stands of about 0.5 ha, e.g. the groups in a subcompartment under the group selection silvicultural system. Large-scale structure is indicated north of the road with some stands of 10 ha or more.

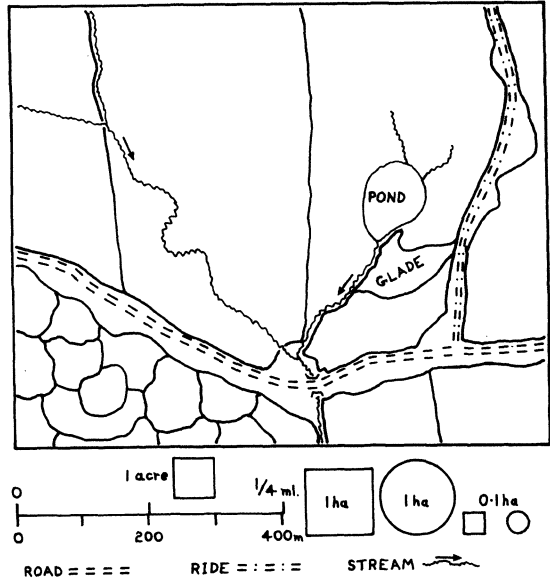
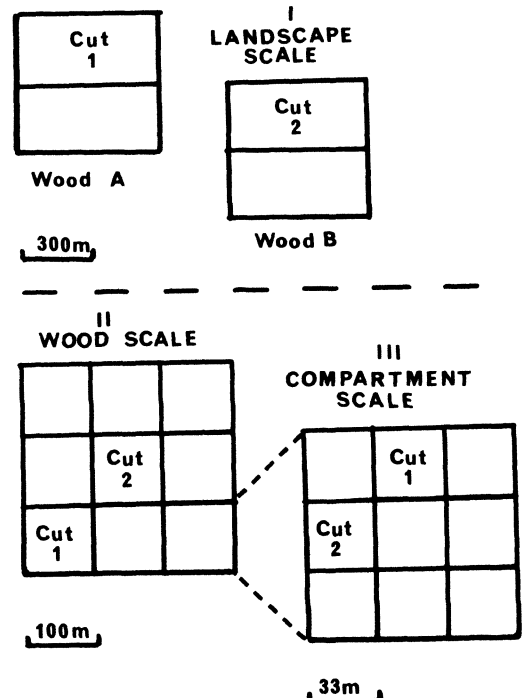


Figure 1.4

Pattern and scale of woodland structure.

Woodland structure may be at different scales. Whether it is suitable for a particular species depends on their mobility (4.1.2). At the landscape scale (I) only the most mobile species may be able to move from the area cut in year 1 (wood C) to that cut in year 2 (wood B). There is more scope for movement at the wood scale (II), but the least mobile species may require diversity on the compartment scale (III). Some species may be able to use all of the open ground created by the large fellings of I and II, others may be confined to the edge of such areas. Some species may find the areas cut in III too small to meet their requirements.



1.3.4 Silvicultural systems and woodland structure

Selection and group selection systems are small-scale, operating

with patches (miniature stands) of around 0.01 to 0.25 ha. Shelterwood systems and even-aged clear felling are on a medium to large scale, say, 0.5 ha upwards. Assuming a normal forest (see glossary for definition) is the aim the actual scale is often determined by the total area to be managed by a particular system.

The pattern can be irregular, as in many selection systems, or regular. Regular arrangements occur in the young regenerating stands marching across the wood in the strip shelterwood or the spaced-out groups with concentric annuli of successively younger regeneration in the group shelterwood. The clear felling system can be regular, but seldom is in existing woods, because the crops present are not uniform. A regular woodland structure has high contiguity, i.e. stands adjacent in the sequence of stages are also adjacent on the ground, but it also has less edge (here used in the sense of a boundary between two stands at different stages; Figure 1.5). This is because the early stages are shorter than the later ones: two stands which differ in age by less than about 20 years differ in stage only when young and spend many years together at the later stages. Therefore where edges are important for particular nature conservation reasons, the occurrence, height and duration of the stages associated with different silvicultural systems and the actual layout of stands in the wood must be carefully considered (Figures 4.2, 4.4). The length of edge per unit area depends on the scale as well as the pattern. Contiguity is low in the selection systems but here the small scale ensures that all stages are close together (Figure 1.5b).

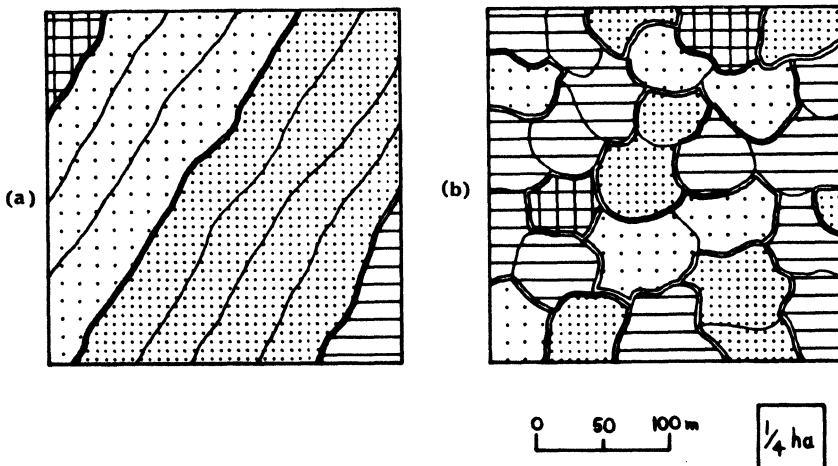
The even-aged clear felling system of upland afforestation tends to be regular and large-scale, although windthrow and consequent regeneration earlier than planned disrupt the original pattern and may reduce its scale. The Bradford-plan (Figure 1.6; 3.4.2) is a geometrical selection system which is regular and has high contiguity since one boundary is always with a stand at an adjacent stage. (This regularity is the main advantage over the traditional selection system for the control of yields and the tending and harvesting operations.) Most managed ancient woods have patterns that fall between these two extremes.

Figure 1.5 Regular and irregular forest structures.

(a) Successive strips of regeneration created at 5 year intervals.

(b) Irregular structure in a group selection system.

() young trees 0-15 yrs, () thicket 15-35 yrs, () pole 35-70 yrs, () mature over 70 yrs. () boundaries between different stages.



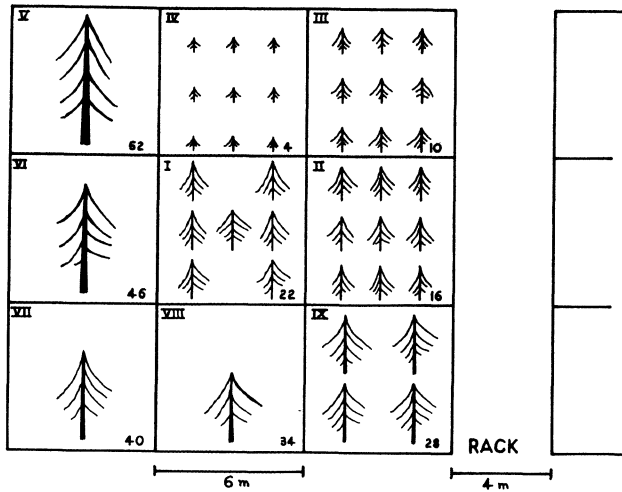


Figure 1.6 One unit of the Bradford-plan selection system. Each unit is 18m square and is subdivided into nine subunits of 6m square. Roman numerals = subunit number. Arabic numerals = age of trees. On each subunit the stand consists initially of nine planted trees (or natural regeneration if present), then a decreasing number of trees as thinning takes place between 18 and 30 years and then a single tree up to the age of felling at 54 years. The young trees are tended annually as required but otherwise working is on a six year cycle. In two years time, for the unit shown, subunit V will be felled and replanted and subunits II, I and IX will be thinned. For access 4m wide permanent racks are left between every other file of units (Hutt 1974) or every file (Harris & Kent 1987a); this means that 9% or 18% of the stand area, i.e. excluding roads and rides, is occupied by racks (cf. the notional 15% for unproductive areas (roads, rides) and for understocking in the stands allowed in the Forestry Commission yield tables between gross and net areas (Hamilton & Christie 1971). The small size of the subunits and the proximity of tall trees in adjacent subunits limits the choice of species to at least moderate shade-bearers: *Nothofagus*, Douglas fir, western hemlock and western red cedar have been used.

1.3.5 Comparing effects of forestry practices between stands and woods

1.3.5.1 Allowing for rotational effects

Stands change during the rotation so that the datum against which to set the effects of forestry practices is not constant. How should the progress through the rotation be measured so that fair comparisons can be made? The age of the stand is not as helpful as might be supposed. For instance the transition from incomplete to complete canopy is an important one but it can take place at a wide range of ages depending on the initial spacing, the number of trees lost after establishment, the rate of growth and the form of growth (spreading or compact). No other

quantitative measure such as top height or basal area is totally satisfactory. A general system of growth stages (Figure 1.2) as used by Moss (1979) or Rose (1979) is more useful. From a nature conservation point of view the critical periods are likely to be the lengths of the open, thicket and overmature stages. The transition from thicket to pole stage is one where foresters have considerable scope to influence events to benefit nature conservation.

If any quantitative measure of nature conservation value (number of species, cover or density of species, etc.) is plotted against a measure of progress through the rotation (stages, time, height) the result is likely to be not a horizontal line but some sort of curve (see Figure 2.2). There will be different curves for groups or individual species within the flora and fauna. Moreover, at later stages in the rotation differences in the stocking of the stand also have an effect so that there is a family of possible curves for any species or group of species. To assess the effect of a change in forestry practice over the whole wood the curves for all the individual stands have to be combined or considered together.

1.3.5.2 Allowing for site differences

Apart from stage of the rotation the other problem with comparing different forestry practices is to find comparable sites. The occurrence of soil types, plants and animals varies on a regional scale according to climate, geology and biogeography. In any one wood the occurrence of plants and to a lesser extent animals depends on the soil characteristics. A further source of variation is the history of the site: whether ancient or recent woodland, and what the previous management was. For a fair comparison all these factors must be taken into account, i.e. different practices should be compared on sites within a uniform region, on a uniform soil and having the same site history. Multivariate analysis may overcome some of the problems and Bibby, Philips & Seddon (1985) provide an example of its use with bird surveys. However to date it has not been applied critically to a wide enough range of data in Great Britain to separate out the different influences of site, species, treatment and age of crop.

Thus, fair comparisons of the effects of tree species or different treatment are difficult to make. The results from any one study are often specific to the region, the soil type or the particular site used. Conflicting evidence can often be produced to counter almost any statement made. Poore & Fries (1985) had the same difficulty in their review on the ecological effects of eucalypts: "Generally speaking the most useful literature was that which illuminated the general processes in the systems under review". So we must proceed cautiously, be aware of the complicating factors and seek to understand the underlying ecological processes. In this way common patterns may emerge.

1.4 Structure of this review

1.4.1 General approach

We have adopted an analytical approach to the changes resulting from forestry practices to emphasize changes in structure and the distinction between the stand and the wood. This separates the more drastic changes that occur in modern forestry practice from the routine forestry operations of thinning and felling (coppicing) that also occurred to some extent under most traditional management. It does not answer

directly questions such as what are the effects of different silvicultural systems or of converting broadleaved coppice to coniferous high forest, but from a more fundamental breakdown of the problem it should be possible to assemble answers to such questions. The alternative approach based on silvicultural systems is adopted by Helliwell (1982; revised edition in preparation).

In theory each type of change caused by forestry (1.2.2; Table 1.2) affects each ecological group (1.2.1; Table 1.1), forming a large matrix of possibilities. In practice not every combination occurs and for some nothing useful can be said. Soils are little affected by any changes of structure. For the flora, changes of species, stand structure and on the site are the most important. The fauna is less affected by changes on the site than the other types. The actual coverage is shown in Table 1.3. Chapters 2, 3 and 4 have a similar layout. The first section sets out the background including the changes due to stage and stocking, and the last is a discussion. In between the effects of the four types of change are considered in turn, except for the fauna where it was more convenient to take each group separately.

1.4.2 Bias and gaps in the coverage

We have tried to be comprehensive, but there are gaps and there is a lowland bias. This in part reflects the nature of the available material, but is also justified because most semi-natural woodland is in the lowlands and it is here that changing forestry practices are most likely to pose a threat to nature conservation interests. In the uplands, commercial forestry is concentrated in large conifer plantations and the semi-natural woods are under more pressure from grazing. This last topic is the subject of a separate study by the Macaulay Land Use Research Institute.

1.4.3 How to use this review

In the subsequent chapters on soil, flora and fauna the reader may pick out a particular type of change and follow its influence through the range of features and species groups considered. Alternatively the effects of a whole range of possible changes may be examined for one particular group of species. Another mode of entry is through the reference list which gives the numbers of the sections in which references are cited. The final discussion (5.3.6) includes an illustration of how the effects of a particular proposal might be assessed. Throughout cross-referencing is indicated by a section number.

Table 1.3 Coverage of soils, flora and fauna (by section number, N.I. = no information)

<u>Type of change caused by forestry</u>				
<u>Change of species</u>		<u>Change in stand structure</u>	<u>Change in woodland structure</u>	<u>Changes on the site</u>
<u>Soil property</u>				
Organic matter	2.2.2	- 2.3	- 2.4	N.I.
pH	2.2.3			N.I.
Nutrients & fertility	2.2.4			2.5.3
General changes	2.2.5			2.5.4
Water relations	2.2.6			2.5.1
Soil flora and fauna	2.2.7			2.5.2
				N.I.
<u>Flora</u>				
Trees & shrubs	3.2.1	3.3.1	3.4	3.5.2
Ground flora	3.2.2	3.3.2	3.4	3.5.3
Bryophytes	3.2.3	3.3.3	3.4	N.I.
Epiphytes	3.2.4	3.3.3	3.4	N.I.
<u>Fauna</u>				
Invertebrates	4.2.2	4.2.3	4.2.4	4.2.5
Lepidoptera	4.3.2	4.3.3	4.3.4	4.3.5
Molluscs	<----- 4.4 ----->			
Amphibians & reptiles	<----- 4.5 ----->			
Birds	4.6.2	4.6.3	4.6.4	4.6.5
Mammals	4.7.2	4.7.3	4.7.4	4.7.5

2 SOILS

2.1 Background

2.1.1 Soil and trees

Trees have major effects on the soil, especially through the nutrient cycles. Large amounts of organic matter arrive at the soil as leaf litter, or in the soil through the death of fine roots and as root exudates. The death of fine roots and mycorrhizas can contribute more than two-thirds of the total input of organic matter (Miles 1986). The annual turnover of roots less than 2mm in diameter in stands of Douglas fir 40 years old was 33% of total organic matter input on a good site and 75% on a poor site (Keyes & Grier 1981).

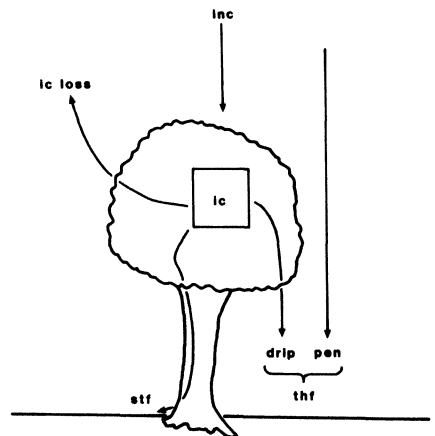
The uptake of nutrients from the various soil horizons and their ultimate return, partly at the soil surface, redistribute the nutrients. The incident precipitation is also redistributed as stemflow and throughfall (Figure 2.1) and altered in chemical composition by its contact with the leaves and the bark of the branches and trunk. Gersper & Holowaychuk (1971) thought this important enough to be defined as the "biohydrologic" soil-forming factor.

Figure 2.1 The redistribution of precipitation by a tree canopy.
(based on Parker (1983) and Reynolds & Henderson (1967))

inc Incident or gross precipitation
ic Interception
pen Penetration without throughfall
drip Drips from the canopy
thf Throughfall
stf Stem flow

$stf + thf = \text{net precipitation}$
or total forest water

csc = canopy storage capacity (not shown),
the maximum retained in the canopy.



2.1.2 Historical perspective

Much has been written on the different soils which develop under broadleaves and conifers, usually in connection with afforestation or the conversion of broadleaved stands to coniferous ones, e.g. Rennie (1962), Noirfalise & Vanesse (1975) and Miles (1978). Soil changes have been described as degradation, impoverishment, deterioration or improvement but these terms are rarely properly defined. Will & Ballard (1976) defined deterioration as any alteration of soil properties which

reduced the productive potential of the site; but this depends on the crop or species. Soil degradation and improvement look very different from the points of view of a cabbage or a rhododendron (Miles 1978).

As knowledge and understanding of soils has increased so ideas have changed. Fitter (1985) shows how many and complex are interactions of plants, microbes and animals in the soil. Only in the last ten years or so has it been appreciated that mycorrhizal association is the norm, not just a special case in coniferous forest or ericaceous vegetation.

Although nutrient cycling is an active process the earlier view of nutrient stocks and cycles tended to be a static one. The removal of wood as a crop was equated with an irreplaceable depletion of the nutrient stock of the site. However measurements of the nutrient stock of the soil and vegetation at one time are little help in assessing the long-term consequences of forestry practices or the adequacy of nutrient levels for current growth. Coleman (1985) has emphasized that "the turnover rate of a relatively small pool ... is far more important than pool size". It is significant that a new method of assessing soil nutrient status measures not total or available nutrients, but the rate of nutrient supply in a way that can be replicated and repeated cheaply to explore the variation in space and time (Gibson, Colquhoun & Grieg-Smith 1985).

This dynamic view places more emphasis on the long-term nutrient balances and the importance of the atmospheric input (Nys, Ranger & Ranger 1983; Sykes & Barr 1973). The large, aerodynamically rough canopy of trees is good at intercepting air-borne nutrients and it is present on the site for a long time.

2.1.3 Variations in soil characteristics in space

Horizontal variation can occur in soils under a uniform stand of trees on a uniform site. Usher (1970) studied small scale (centimetre to decimetre) variation and recommended that sample cores should be at least 13cm in diameter to integrate this variation. The causes on this scale could be ant or earthworm activity (Scheu 1987; Troedsson & Lyford 1973) or animal droppings, random accumulations of litter or concentrations of soil organisms, variations in the ground vegetation and so on.

On a larger scale, radial variation around trees in a stand was postulated by Zinke (1962) and has been described by Crampton (1982), Gersper & Holowaychuk (1971), Mina (1967) and Riha, Senesac & Pallant (1986). This arises from the patterns of stemflow and throughfall (Ford & Deans 1978) and the accumulation of bark litter around the trunk, but the soil patterns are strongly developed only in favourable circumstances.

Another cause of horizontal variation is the pit and mound topography of natural forests where windthrow is common (Beatty & Stone 1986; Falinski 1978; Stephens 1956; Stone 1975a). Pits and mounds locally disrupt the continuous processes of profile development and by bringing lower horizons to the surface partly reverse the trends of leaching and lessivage.

Definite soil patterns of these last two types are unlikely to develop on any scale in most British woodland where harvesting takes place before windthrow and trees rarely reach the age that they would in natural forests. However, these processes do occur, for example in the native pinewoods where windthrow of individual trees is not uncommon. There is also considerable potential for the development of pits and mounds following exceptional windthrows such as that in south-east

England on 16th October 1987 (Whitbread 1988). Grieve (1977) claimed that the greater variability in soil properties under 170 year old oak than in a 50 year old conifer plantation was evidence for the stronger development of a pattern in the older and more irregular oak stand.

Other types of pattern may be created through litter fall and redistribution, the effects of soil compaction along access routes, or nutrient enrichment from piles of brushings, lop and top or fallen trunks, and on fire sites. In a beech/chestnut coppice Boddy & Swift (1983) found high spatial heterogeneity in woody litter fall. Under gaps the contribution of the trees to the litter is reduced with increasing gap size (Shure & Phillips 1987). Leaf litter is also redistributed so that local accumulations occur (Merriam, Dwyer & Wegner 1982), for example at the foot of slopes or in the lee of ridge tops. Increased concentrations of nitrogen, calcium and magnesium can occur in the mineral soil associated with such accumulations (Welbourn, Stone & Lassoie 1981). There is considerable nutrient displacement if stumps and lop and top are bulldozed into rows to clear the ground for replanting. Morris, Pritchett & Swindel (1983) found that most of the nutrients were in displaced soil, but the woody material in such windrows (which covered only 6.2% of the stand area) contained as much nitrogen and 20-40% of the phosphorus, calcium and potassium as was removed in the wood of the trunks (2.5.4). Sites where logs disintegrate may still show nutrient differences 5-10 years after their complete disappearance and this is suggested as a reason why Allium ursinum does not invade such zones in the Bialowieza Forest, Poland (Falinski 1986).

The possibility of spatial variation and of radial patterns should be borne in mind in work on forest soils. Despite intensive sampling, Frankland, Ovington & MacRae (1963) found that large spatial variability obscured possible monthly differences in soil properties. A nature conservation aim with respect to soils should be the protection of examples of soil pattern development in British woodland.

2.1.4 Variations in soil characteristics through time

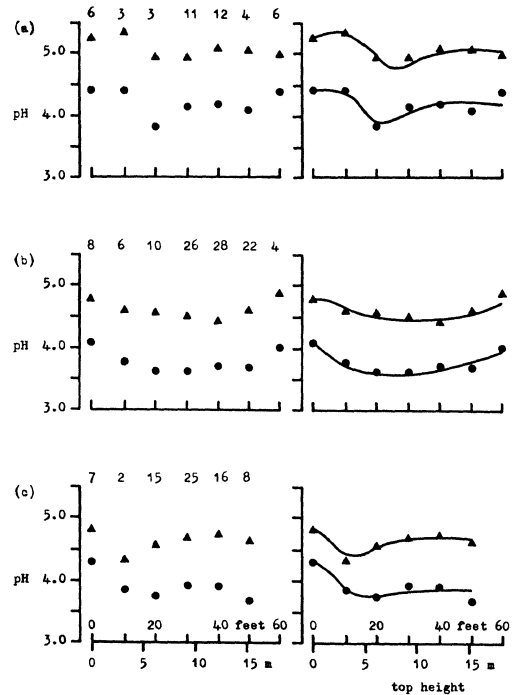
Some of the conflicting results about the effects of different tree species on the soil can be explained by changes in soil properties during a rotation. Page (1968, 1971, 1974) obtained data from stands at all stages of the rotation and constructed a time sequence. Most changes were cyclical, going through a peak or trough in the middle of the rotation and returning to near the initial value at the end (Figure 2.2). Clear felling, whenever it took place, reset many of the soil properties to the initial values. The curves were clearer when top height rather than age was used to trace progress through the rotation. Page (1974) suggested that the changes were a consequence of the different rates of accumulation and decomposition of organic matter as conditions changed during the rotation. Evidence for a similar cyclical pattern of pH change during a rotation under Norway spruce was found by Hallbäcken & Tamm (1986).

Some of the changes measured by Page (1968) were not cyclical: the depth of the A2 horizon (the bleached layer in podzolic soils) continued to increase throughout the rotation, at least under Sitka spruce. Similarly Miles (1986) pointed out that although the rate of podzolization by conifers on susceptible soils was probably cyclical during the rotation the results were cumulative and stable. However, even podzolization can be reversed by mixing the soil horizons, which occurs through the activities of animals and in natural forests by pit

and mound formation from windthrow. It is quite normal during regeneration after disturbance in natural forests for conifers to follow broadleaves (e.g. north-western North America) or vice versa (eastern North America), presumably with corresponding alterations in soil development. Soil changes, even where not cyclical, do not therefore proceed ineluctably in one direction either in managed or unmanaged forests.

Figure 2.2

Soil pH changes through the rotation at depths of 2.5cm (circles) and 30cm (triangles) for (a) balsam fir on brunisols, (b) balsam fir on podzols (c) black spruce on gleysols; without (left) and with (right) the curves drawn by Page (1974). The number of stands in each class of top height (10 feet (3m) interval) is shown above the left hand graph.



Clear felling produces the most dramatic changes on the site at whatever point it occurs in the cycle of change in soil properties (Page 1974). After felling or coppicing there is usually an initial decrease in the weight of the surface organic matter resulting from more rapid decay brought about by higher temperatures, higher nutrient levels, higher moisture content and usually an input of readily degradable herbaceous litter. In many cases there are increased losses of nutrients from fertile soils to stream and ground water, particularly of nitrates. Later there is a rise in the weight of the organic matter as the stand grows and nutrients may become less available (Covington 1981; Vitousek 1985).

Hill *et al.* (1984) set out a table of twenty effects of clear felling with their immediate causes, and gave some early results of a multi-disciplinary study. The effects vary with the site making it difficult to generalize. The decomposition of organic matter may be accelerated by more favourable temperature and moisture conditions in the open, or may be little changed in a cool, wet, cloudy climate where the conditions are similar to those under the mature tree canopy. The loss of nutrients by leaching or their retention in the soil varies with the particular element, with the climate and with the speed of establishment of ground vegetation and the next rotation of trees. Clear felling greatly increases the rate of erosion on susceptible sites

(steep slopes, poorly structured soil with little protection by ground vegetation or a layer of organic matter, slow infiltration of water, high intensity rainfall).

The initial stage in traditional coppice management is broadly equivalent to a clear fell, but the subsequent development on clear-felled or coppiced areas is often different. The presence of the stools in a coppice area may permit greater retention of litter and there is probably a much smaller rise in the water-table because the established root system and rapid shoot regrowth leads to greater transpiration than from young trees.

Changes through the rotation probably take place in the communities of the soil flora and fauna, but little work has been done on this (Usher & Parr 1977). Dighton, Poskitt & Howard (1986) surveyed the fungal fruit bodies in stands of lodgepole pine and Sitka spruce ranging from 11 to 27 years in age, that is from before canopy closure to the thicket stage. The dominant species of fungi changed with age or height of the stand. For the mycorrhizal species this would be expected from other work showing how these fungi change with time as a young tree grows. The changes in saprophytic species were related to the amount and quality of the accumulated tree litter. Declines, with age of stands of Douglas fir, have been found in the density and diversity of fungal fruit bodies and mycorrhizas in the Netherlands, possibly connected with air pollution (Jansen & de Nie 1988). However these are afforestation sites and such changes may not occur on old woodland sites where there is an established fungal flora.

2.1.5 Variations in soil characteristics due to stocking

2.1.5.1 Variations under a Norway spruce thinning trial

Wright (1957) studied the soil of even-aged Norway spruce plots maintained at different levels of stocking by different grades of thinning (the Bowmont plots). Thinning started at age 20 on a five year cycle. The experimental plots were all 45 years old and of similar top height (General Yield Class 10) and differed only in stocking. Thinning grades B, C and D (low thinning) formed a series with increasing numbers and size of tree removed, from only small, badly suppressed, dead and dying trees in B to all but the best trees removed in D where space was allowed for full crown development. At age 45 D had half the basal area and only one-sixth of the trees of B (Table 2.1).

Grade LC, the light crown thinning, was similar to D in favouring the crown development of the best dominants but suppressed trees and sub-dominants were left to fill the spaces in between. In terms of basal area and number of trees it was intermediate between C and D but the size distribution of trees was different from either. No results were given for the LC plots because the soil properties were so variable under the more irregular canopy: similar to B grade under a group of sub-dominants casting heavy shade, and to D grade on more open ground under dominants (Wright 1957).

Out of the sixteen physical and chemical soil properties measured only seven showed statistically significant differences between treatments, mainly where the B grade differed particularly from C and D. The nutrients (N, P, K, Ca, Mg) returned in the litter varied little except that treatment B tended to have slightly higher amounts in line with the greater amount of litter. However, there were up to four-fold differences (between B and D) in the amount per tree (rather than unit area) because of the vastly different numbers of trees per hectare.

Table 2.1 Tree crop and soil organic matter in Norway spruce stands (from Wright 1957). Each value is the mean of four replicate plots.

Thinning grade	B	C	D	LC
Trees per hectare	3052	1712	512	1334
Basal area (m ² /ha)	52.9	40.5	25.8	31.3
Quadratic mean dbh (cm)	15	17	25	17
Forest floor (L and F layers), dry weight (t/ha)	49.3	26.3	16.7	29.5
Litter fall in one year, dry weight (t/ha)	5.72	4.32	3.73	4.21
Ratio of forest floor to annual litter fall	8.6	6.1	4.5	7.0

Stand details are for the main crop after the 1955 thinning.

Thinning grades.

- B - light low thinning - only badly suppressed, dead and dying trees removed.
- C - moderate low thinning - intermediate between B and D.
- D - heavy low thinning - only the best trees retained, with space for full crown development.
- LC - light crown thinning (see text).

Although the litter fall was recorded for one year only, the ratio of the weight of the forest floor (L and F layers; H was very poorly developed) to annual litter fall gives an indication of the average number of years accumulation of litter. This figure (Table 2.1) emphasizes the difference between the treatments by combining the differences in forest floor weight and in litter fall; it suggests much faster decomposition in the more heavily thinned D grade than the B grade plots, with the other treatments intermediate. Wright attributed this to different microclimates in the plots, in particular the heavy shade in the B grade plots.

Thus the more heavily thinned stands with lower stocking levels had a slightly reduced litter fall but a faster rate of decomposition. A similar amount of nutrients was cycling up to twice as fast on an area basis (D grade compared with B) and through fewer trees. In contrast the differences in static soil properties were smaller: the slower cycling plots with more organic matter in the forest floor had slightly higher amounts of nutrients in the soil.

2.1.5.2 Other work

Scohy, André & Lebrun (1984) sampled the soil fauna in a Norway spruce thinning experiment in Belgium. Thinning had started at age 19 and continued on a three year cycle. At age 29 the number of trees per hectare were: treatment A, 1960; B, 1420; C, 1060; D, 840; and E, 660. No consistent differences were found between the stands in the numbers of enchytraeid worms, spiders or myriapods (mainly centipedes), but this could have been due to inadequate sampling for these organisms which tend to be aggregated. However, lumbricid earthworms increased from 26/m² in treatment A to 54 in C and 61 in E. This was associated with the faster decomposition of organic matter and nutrient cycling in the least stocked plots (consistent with Wright's work described above), resulting from the changed environment (higher solar radiation and rainfall, presence of ground vegetation).

2.1.6 Effects of shrubs and ground vegetation on soil conditions

In some circumstances the ground vegetation and shrub layer can play an important rôle in nutrient cycling in the stand through its rapid growth and uptake of nutrients, its (usually) easily decomposed litter compared with tree leaves (Dwyer & Merriam 1984) and, in some cases, its interaction with rainfall. The amount of such vegetation, and hence its effect on the soil, varies in space, in time (seasonally and through the rotation) and with stocking (chapter 3).

There was a more rapid turnover of litter under pine where a hazel shrub layer was present than under a pure pine stand (Tappeiner & Alm 1975). Carlisle, Brown & White (1967) found that bracken in an oakwood contributed 31% of the total annual return of potassium to the soil, by throughfall from the fronds in the growing season and through its litter. In northern hardwood forests (USA) Erythronium americanum flourishes between snowmelt and full development of the tree canopy. The plants mop up nitrogen from the spring flush of mineralization which then passes back to the soil after the plants die down in the summer when the tree roots are active in nutrient uptake (Bormann & Likens 1979).

The mosses in an oakwood in north Wales contained appreciable amounts of nutrients and took up the same amount of potassium and magnesium each year as the trees (Rieley, Richards & Bebbington 1979). Continual harvest of the moss, for floristry, could reduce the amounts of nutrients in the system and increase the risk of soil erosion in some places.

Vigorous ground vegetation can modify the influence of a tree species on a soil. Miles (1986) suggested that the ground vegetation under oak is influential in tipping the balance to mull (herbaceous swards) or to mor (Vaccinium, with Calluna under light canopies (2.2.2)).

2.1.7 Effects of grazing and trampling

Grazing in woodlands affects the species composition and structure of the ground vegetation (Putman 1986) and increases the rate of nutrient cycling; it could cause either a net loss or gain of soil nutrients depending on animal behaviour and husbandry. Nutrients would be gained by supplementary feeding in the wood but lost if animals grazed in the wood and dunged outside, in addition to nutrients lost when animals grazing in a wood are slaughtered elsewhere. The former practice of gathering litter for animal bedding from woodland also eventually leads to significant nutrient losses particularly on naturally acid soils (Ellenberg 1988).

Localized erosion, compaction or poaching of the soil will occur in areas where animals congregate, particularly in wet conditions. The same effects can be seen in woods heavily used for recreation, especially along paths or around viewpoints and famous trees (e.g. Surprise View, Borrowdale or the Major Oak, Sherwood Forest).

2.2 The effects on the soil of changing tree species

2.2.1 Other reviews

Reviews of all or part of this topic include Jones (1965), Hornung

(1985), Noirfalise & Vanesse (1975), Miles (1978, 1986) and Stone (1975b). P.J.A. Howard and D.M. Howard at Merlewood Research Station are compiling a review on the role of forest vegetation in soil formation. A detailed study of trial plots of different tree species is described in Ovington (1953 *et seq.*), Ovington & Heitkamp (1960) and Ovington & Madgewick (1955).

Much early European work failed to take into account the effects of agricultural use of the study sites such as litter collection for animal bedding, grazing of domestic stock or even a few years arable cropping between rotations (Jones 1965). Sites were not always strictly comparable and there was some unjustified extrapolation of results by analogy.

Stone (1975b) emphasized the lack of detailed knowledge of forest nutrient cycles in some of the earlier work and the importance of taking a long-term view; for example, considering the effects of the rate of supply of nutrients over the whole rotation rather than reading too much into the nutrient levels in the soil at a given time. The changes attributable to species were in general much smaller or more limited than those resulting from forestry management: site preparation, fertilization, thinning and felling, especially with modern machinery. Hornung (1985) similarly felt that the site characteristics and management practices were as important as the tree species as far as the acidification of soil was concerned.

We have drawn very heavily on Noirfalise & Vanesse (1975), a splendid paper with good coverage on the European literature, which concentrates on the comparison between Norway spruce and beech or oak in the context of the afforestation of abandoned agricultural land in Belgium. Miles (1978, 1986) independently came to similar conclusions: that conifer stands tend to accumulate organic matter on the soil surface, with a lower pH and immobilization of nutrients (a reservoir rather than a loss), which can lead to podzolization on certain sites; that irrespective of tree species there are changes during the rotation and because of management; and that there is no evidence for a decline in the productivity of the site under conifers.

2.2.2 Organic matter

2.2.2.1 Differences in the amounts of surface litter produced

Most conifer stands contain more organic matter on the soil surface (the L, F and H layers) than most broadleaved stands, despite the variation due to stage in the rotation, stocking, site and management. (Recollect, for instance, the three-fold difference between heavily and lightly stocked stands of the same species found by Wright (1957); 2.1.5.1) Accumulations of organic matter up to 97 tonnes per hectare do occur but more typical figures are 10-35 for conifers and 4-10 for broadleaves (Noirfalise & Vanesse 1975; Reichle 1981).

On the plots at Abbotswood and Bedgebury (Ovington 1954a) litter as a proportion of the total soil surface organic matter varied from 5% (46 year old pedunculate oak) to 33% (22 year old western hemlock) (Figure 2.3). The contrast between European larch and hybrid larch is striking. Amongst the broadleaves, beech stands out with over twice as much organic matter as most of the others. There is no general relationship between weight and thickness of organic matter: Nihlgård (1971) found that Norway spruce litter packed more tightly than beech so that there was three times as much weight for equal thickness.

Abbreviations for tree species.

SP Scots pine
 CP Corsican pine
 NS Norway spruce
 OMS Serbian spruce
 EL European larch
 HL hybrid larch
 DF Douglas fir
 WH western hemlock
 RC western red cedar
 LC Lawson cypress
 GF grand fir
 OK oak
 POK pedunculate oak
 SOK sessile oak
 ROK red oak
 BE beech
 SC sweet chestnut
 OBN roble (*Nothofagus obliqua*).

Locations:

A Abbotswood
 B Bedgebury

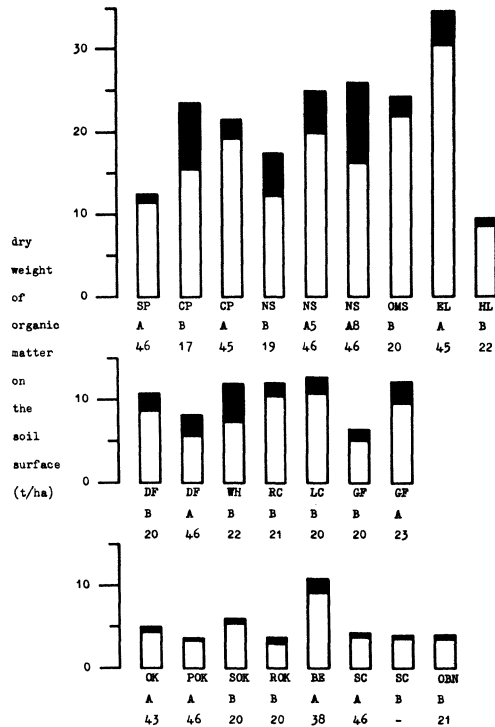


Figure 2.3 Dry weight of surface organic matter (L, upper box; F+H, lower box) on Ovington's plots, June-August 1951 (from Ovington 1954a). The figure is the age in years in 1951. There were two plots, numbers 5 and 8, of Norway spruce at Abbotswood. The sweet chestnut at Bedgebury was the shelterbelt: oak standards, about 135 years old, over chestnut coppice, age unknown.

2.2.2.2 Differences in litter type and breakdown

Species differ in the rate at which their leaves break down (Howard & Howard 1980). Scheffer and Ulrich (in Ellenberg 1988) considered that most leaves of elm, ash and alder disappeared within a year, those of hornbeam, lime, sycamore and sweet chestnut lasted for two years while oak, birch and beech might last three years. Similarly the greater accumulation of surface litter under conifers than broadleaves does not arise from much heavier inputs of litter by conifers, but from the slower rate of decomposition and lack of mixing with the mineral soil. Although the physical environment under conifers may be less favourable for decomposition than under broadleaves, it is the different properties of conifer litter that are more important.

The conifers commonly used in British forestry have needles with a low ratio of surface area to weight which limits the initial area of attack by microbes and microfauna. More importantly, conifer needles are generally tougher, contain less protein and more lignin, have a higher carbon to nitrogen ratio, are more acid and contain more secondary compounds than the leaves of broadleaved trees. (This is simply a consequence of their being gymnosperms and hence constrained by evolution to have needles and gymnosperm biochemistry. A similar point was made by Satchell (1983) in contrasting grass and tree litter generally: trees pass on a "legacy of herbivore chemical repellents" in

their leaf litter.) Most conifers are evergreen with the needles having to withstand several years of weather and insect attack so that tougher leaves and abundant secondary compounds may be an advantage. (Note that larch, although deciduous still has litter which is slow to decompose.)

Conifer litter is thus a different, and in general less hospitable, resource for decomposers. Fungi, particularly Basidiomycetes and Fungi Imperfecti, are favoured but bacteria are much reduced in number and activity, including those involved in the mineralization of nitrogen from the organic matter and those that fix atmospheric nitrogen. The different kind of litter and the different microflora and paths of decomposition influence the soil fauna. Groups such as isopods, millipedes and molluscs, which are frequent under broadleaves, decrease under conifers, but mites and springtails increase. Lumbricid earthworms are much reduced in biomass, particularly under spruce, but enchytraeid worms increase, possibly influenced by soil pH changes (2.2.3).

The different resource and sequence of decomposition produce the mor type of organic matter, contrasting with the mull from broadleaved litter. Mor stays in a layer on top of the mineral soil whereas the activities of earthworms usually incorporate mull into the mineral soil. Among conifers the tendency towards well developed mor is greater under spruce and pine than under fir (*Abies*) or Douglas fir.

2.2.2.3 Influence of soil conditions and treatment on litter type

The association of conifers, a particular soil flora and fauna, and type of organic matter is not rigid but can vary with the type of soil and the management (thinning, liming and fertilizing, soil cultivation) (Noirfalise & Vanesse 1975). The presence of some broadleaved trees in a conifer stand can produce an intermediate system of decomposition or even mull organic matter. Conversely, on certain sites mor can develop under beech or oak (Mackney 1961). In a comparison of the disappearance of chestnut and beech litter Anderson (1973) illustrated the effects of both species and site. On one site abiotic influences (wind, rain, etc.) were more important in breaking up leaves, on the other earthworms played a major role. The chestnut litter was both more likely to be broken up (at the first site) and was more readily selected by earthworms (at the second) than was beech.

2.2.3 Soil pH

The pH of the soil is generally lower in conifer than in broadleaved stands. In eleven comparisons of Norway spruce or Scots pine and the previous beech or oak the pH decrease ranged from 0.1 to 1.0 unit (Miles 1978). The eight examples of Noirfalise & Vanesse (1975) (all except one on soils of pH 5 or less) ranged from 0.3 to 0.8 units decrease. Conversely adding broadleaf litter to spruce stands may lead to a rise in the soil pH (Leibundgut in Ellenberg 1988).

These changes result from the chemistry of conifer foliage which produces a more acid throughfall than broadleaved foliage and a more acid litter with acid decomposition products. The accumulation of organic matter also increases the cation exchange capacity but, without more bases the extra capacity is occupied by hydrogen ions (Miles 1978). All these changes take place at the top of the soil so it is in the organic layers and the upper mineral horizon that the decrease in pH is most marked.

The plots recorded by Ovington (1954a) provide the most detailed set

of pH measurements from three sites, many tree species, from the surface to 65cm depth, and from both 1951 and 1974 (Howard & Howard 1984a,b). For example, at the Bedgebury site pH curves with depth are strikingly uniform; the organic matter layers generally have a pH of 5 or more, there is a minimum around pH 4 at between 5 and 20cm, then a slight rise with depth to pH 4.3-4.5 at 65cm. Statistically significant differences between 1951 and 1974 tended to occur between 5 and 20cm depths but they were small (less than one pH unit) and there was no clear pattern of change.

Just as for organic matter (2.2.2), there is no exact and absolute relationship between species and soil pH or the size of any pH change when the tree species is changed. Beech can decrease the pH on soils low in bases (Pigott 1989) but did not do so on nutrient-rich soils (Hornung 1985).

Most differences in pH between species are about the same size as the seasonal variation found by Howson & Brown (1980). In winter the pH of the top layer of mineral soil was one unit less, and was more variable, than it was in summer. Nevertheless a small but consistent difference between the pH produced under different trees is significant if it crosses a biological threshold. The threshold for lumbricid earthworms may be particularly important because they are responsible for much of the incorporation of organic matter into the mineral soil (and hence determine litter type). If they become reduced in numbers because the pH decreases across their threshold of tolerance (about pH 5.5) then the type of organic matter may start to switch from mull to mor (M. Anderson personal communication).

2.2.4 Nutrients and fertility

The greater accumulation of organic matter in conifer than in broadleaved stands immobilizes nutrients and could conceivably give rise to a short-term deficiency in young, fast-growing stands. Liming or fertilizing could alleviate this but would be undesirable in nature conservation terms, because they cause even greater changes to the nature of the soil and in the flora. In the long term the nutrients in the organic matter are a slowly cycling pool, a reservoir and not a permanent loss from the site.

A study in the Ardennes compared the biomass and nutrient contents of rowan/birch/mixed broadleaf coppice under oak standards (J. Ranger, Nys & Ranger 1981) and a Norway spruce plantation (D. Ranger, Nys & Ranger 1981). Allowing for inputs in precipitation (measured) and from rock weathering (unknown) a nutrient model was calculated for 150 years, i.e. five rotations of coppice with one rotation of the standards and two rotations of spruce (Nys, Ranger & Ranger 1983). Despite the much higher productivity of the spruce the input of nutrients in precipitation and from weathering would balance the removal of nutrients in the harvest. On poor soils harvesting branches in addition to trunks would lead to a net export from the site unless the extra nutrients were replaced using fertilizers (2.5.4).

Duvigneaud & Denaeyer (1984) reviewed the nutrient relations of eleven types of plantation and semi-natural woodland in Belgium. Comparisons are difficult because the stands were at different stages in the rotation, but they gave a detailed analysis of the compartments and flows of nutrients, and good mensurational details of the stands used. It is apparent that tree species do differ in their annual nutrient uptake and in the amount stored in the above ground biomass. Changing species would alter the distribution of nutrients, but no species could

be said to decrease the fertility of the site.

This is supported by the work at Bedgebury and Abbotswood (Ovington 1956a, 1958a, b). Differences in nutrient stocks in the soil under different tree species were found, but Anderson (1987b) concluded that these did not increase during the second half of the rotation. In some cases the nutrient stock was greater beneath conifers than broadleaves.

2.2.5 General changes in the soil

Physical changes (for example bulk density and porosity) in soils under conifers arise from the different amount and distribution of organic matter and the lack of (lumbricid) earthworm activity compared to most broadleaves, although this may be reversible (Noirfalise & Vanesse 1975).

Increased gleying in the soil has sometimes been attributed to a previous conifer crop (Noirfalise & Vanesse 1975). However gleyed soils are on sites which tend to be intrinsically difficult to manage for productive forestry, being prone to a rise in the water-table after clear felling with vigorous growth of ground vegetation. A similar rise in the water-table would be expected after clear felling broadleaves, so that poor establishment of the next crop is due to the type of felling and restocking rather than species. Smaller coupes or allowing coppice regrowth would alleviate the problem.

2.2.5.1 Podzolization

As soil processes go, podzolization is dramatic and podzols with their well differentiated horizons are conspicuous soils that have been thought of as inherently low in fertility. The process depends on acid leaching. Mor organic matter is closely associated with the process even if not causing it. Podzols develop more quickly and to their fullest extent on acid, free-draining, sandy soils, whereas clay soils never show signs of podzolization even after 10,000 years (Miles 1986). In suitable conditions podzols may develop or be maintained under almost any vegetation - conifers, beech (Noirfalise & Vanesse 1975; Pigott 1989), heathland vegetation or oak (Mackney 1961).

Grieve (1975, 1978) studied the soils under 50-60 year old conifers and adjacent 170 year old oak stands, similar to those replaced by the conifers (Table 2.2). He noted some evidence of micro-podzolization under oak on the Neath soil. There was, under thicker accumulations of leaf litter in slight hollows, a thin (less than 1cm), discontinuous bleached layer, with occasional traces of an ironpan beneath.

The lack of signs of podzolization on the Radyr soil could have been because Douglas fir had less effect than Norway spruce and because of slower internal drainage and a higher cation exchange capacity due to a higher clay content than the Neath soil (Grieve 1975). Only the most susceptible soils showed slight evidence of podzolization, and the conifer effect was one of degree not of kind.

Podzolization may be reversible under the influence of vegetation. Nielsen, Nørnberg & Dalsgaard (1987) reported that the soil under oak scrub invading a Danish heathland, formerly under extensive agricultural use, was changing from the heath podzol towards an acid brown forest soil. Birch invasion may likewise lead to a reversal of the surface acidification found under heather or conifers (Miles 1986).

Noirfalise & Vanesse (1975) concluded that signs of podzolization in a soil should not necessarily be equated with a loss of fertility. Reductions in productivity of stands on sandy podzolized soils were

attributable to a net export of nutrients from the site. Similarly Nys (1981) examined the soils under a first rotation, 45 year old Norway spruce plantation and a comparable site carrying coppice with standards. Differences in the soils were thought to be the start of podzolization under the spruce. After an elaborate and careful analysis of the reserves of nutrients and an attempt to quantify the rates of weathering in the soils he concluded that spruce did not reduce the fertility of the soil, at least in the short and medium term.

Table 2.2 Grieve's (1975) sites in the Forest of Dean.

Soil series	Soil type	Drainage	Tree species	Signs of podsolisation
Neath	acid brown earth pH 4-5	free	NS P25, EL P31, DF P16	yes*
Eardiston	brown earth pH 5-6	free	NS P17	yes*
Radyr	brown earth	free	DF P23	none
Miskin	slightly gleyed brown earth	imperfect	NS P25	none
Pendolyn	surface-water gley	poor	NS P15, P25, P32	none
Hirwaun	surface-water gley	very poor	NS P15	none

The tree species were NS, Norway spruce; EL, European larch; DF, Douglas fir (with date of planting) compared with oak planted early to mid-19th century.

* but not yet reached the brown podzolic stage (sol ocre podzolique) of Duchaufour (1965).

Concern about a decrease in site productivity caused by podzolization under conifers (Grieve 1978 for example), does not seem to be justified as far as commercial forestry is concerned. Given the much higher physical and financial productivity of conifers than broadleaves on the same site, there would have to be a massive drop in fertility before the slower growing broadleaves on the original brown earth became financially attractive compared with conifers on the new podzol. At the very worst, podzolization might reduce species choice in the distant future, especially if foresters were not prepared or able to alter site conditions by fertilization or other treatments.

The implications for nature conservation of even slight decreases in productivity, and particularly of any ground preparation treatments taken to correct them, are more serious (2.6.4). At the least there will be a change in the soil flora and fauna, as well as possibly in the ground flora.

2.2.6 Hydrology and water relations (see also 2.5.2)

Most work on forest hydrology in the British Isles has been in relation to the planting of peat bogs or other open catchment areas (Miller 1984, 1985; Nature Conservancy Council 1986; Savill & Weatherup 1974). Forested catchment areas affect the water yield (less yield than from grassland because more water evaporates as interception loss from trees, but usually a more regular flow) and water quality (particulate

loads may increase with badly laid out drains or careless soil management on steep slopes; acidity may rise with conifers on certain soils or where the trees are more effective at trapping air-borne pollutants). Such issues are however not the concern of this review. Less is known about the effect of changing forestry practices within existing woodland.

Tree species vary in the way their canopies interact with incident precipitation and in the amount of water transpired, with conifers tending both to intercept more and to transpire more than broadleaves. These processes are also influenced by site conditions, by the stage of growth and the management of the stand. In the Ardennes Norway spruce stands reduced the yield of water from a catchment area compared with beech (Noirfalise & Vanesse 1975). Swank & Douglas (1974) reported a lower water yield from a 15 year old pine stand than a comparable catchment with mature oak/hickory, although more than just the tree species had changed in this example. Nihlgård (1971) measured the availability of water (pF values) for a year under a beech and a spruce stand in southern Sweden. There was less water available under the Norway spruce at most depths and at most times of year but the availability of water on both sites was sufficient for plant growth. Redistribution of rainfall into throughfall and stemflow under different tree species also affects the pattern of soil moisture (Ovington 1954b).

The changes in soil moisture patterns that follow a change of tree species are probably less important than the changes to the water table following thinning or felling where the transpiration rate of the whole stand is altered (2.1.3, 2.2.5, 2.4.1.2, 3.6.3.3).

2.2.7 Soil flora and fauna

The soil flora and fauna range from widespread generalist species to restricted specialists. Apart from species feeding on or parasitic on the roots and mycorrhizas of trees, shrubs and ground vegetation, the soil flora and fauna depend on the organic matter input to the soil. Even predators in the soil fauna are influenced directly by the properties of the litter in the physical environment that it provides and indirectly through the occurrence and abundance of their prey species.

Only the leaf litter has been much studied but the input of dead fine roots and root exudates are also significant food sources. The properties of the litter largely determine the pathways of decomposition and the type of organic matter which develops, whether mor (associated with low pH and low base status) or mull (higher pH and base status). The third kind of organic matter, moder, is intermediate in some ways and the decomposition is dominated by mites and springtails. These differences arise from the different organisms which are suited to a particular kind of litter as a food source.

2.2.7.1 Variations in fungi under different tree species

There are long lists of fungi that are associated with particular trees, e.g. Orton (1986), Watling (1974), but relatively little work linking such lists to the broader ecology and management of woods. It is unclear how far distinct fungal communities on different sites may be recognized that are comparable to higher plant communities (Jansen 1984; Wilkins, Ellis & Harley 1937). Unless "site" differences can be allowed for, the identification of treatment or species effects will be difficult.

After leaf fall, ash, birch, hazel and oak leaves each have a characteristic flora of Hymenomycetes and Fungi Imperfecti which is replaced by a common flora after one year (Hering 1965). The rate of decomposition of test cotton strips and the fungal populations as indicated by number of fruit bodies can vary with the tree species (Brown 1978; Howson & Brown 1980). Decomposition was fastest under alder and slowest under Norway spruce, with oak and Scots pine in between. There were more litter-decomposing fungi under the conifers than the broadleaved species, a difference emphasized by Noirfalise & Vanesse (1975) (2.2.2.2). Litter type was also found to be important for fungi by Hansen (1988).

2.2.7.2 The soil fauna associated with different tree species

Ponge & Prat (1982) performed a multivariate analysis on the numbers of 44 species of collembolid collected from eleven sites which varied in the proportion of conifers in the stand. The second axis (the only readily interpretable one) spread out the sites from the broadleaved through the mixed to the conifer stands in a sequence paralleled by the type of organic matter and, less closely, by the pH. A few collembolid species were common in almost every site sampled while others were characteristic either of only broadleaved or of only coniferous stands.

Similar results were obtained in a survey of soil invertebrates in Lake District woodland (Nature Conservancy 1956) where the species fell into one group mainly in very acid soils, another predominantly in mull soils, and a third equally represented in both soil types. Mull and mor have different earthworm communities and, other things being equal, mor tends to have fewer species, a lower population density and a lower biomass than mull (Satchell 1983). Page (1983) found variations in the soil fauna under different tree species in Ovington's plots at Bedgebury, but her results are inconclusive. Roble (*Nothofagus obliqua*) seemed particularly different from the rest: high in mites, collembolids and beetle larvae and in the total number of animals.

The earthworm fauna under beech with mull or mor humus is affected by the site, independent of tree species, in terms of its number of species, population density and biomass (Satchell 1983; Staaf 1987). Since the soil type can affect the chemical composition of the litter some of the site difference was probably through effects on the beech litter. Nicolai (1988), for example, found a higher nutrient content, lower phenolic level and more rapid breakdown of beech leaves on a calcareous than on an acid sandy soil.

The development of mor or moder may depend on the occurrence of drought in the summer (Jones 1965). The fauna of moder which is dominated by mites and springtails needs uniformly moist conditions throughout the year and is slow to recover after a drought. The fungi characteristic of mor survive droughts as spores and quickly re-establish themselves when suitable conditions return. With litter that could go either way, sites with regular summer droughts tend to develop mor.

Overall there does not appear to be a close link between any one tree species and particular members of the soil flora and fauna (except for root parasites and mycorrhizal species). Rather, the populations of these species are tied to the litter type, which is also affected by site and treatment.

2.2.8 The effects on soils of mixtures of tree species

Noirfalise & Vanesse (1975) and Ponge & Prat (1982) found that mixed conifer/broadleaved stands were intermediate between pure stands in their soil characteristics and soil fauna. However, some afforestation mixtures have interactive rather than intermediate effects.

Taylor (1985) described the beneficial effect of nurse crops of lodgepole pine (on upland peat), Japanese larch or Scots pine (on dry heathland) for the growth of Sitka spruce on sites where the spruce suffered nitrogen deficiency which was not remedied by removing heather. The nurse effect was the same as repeated applications of nitrogen fertilizer provided that there was adequate phosphate and potassium. This suggested that the nurse species, presumably through its litter, was speeding up nitrogen cycling.

A similar effect of pine has been found in the Gisburn experiment. This consists of pure plots and mixed plots of Scots pine, Norway spruce, oak and alder planted in 1955 (Brown 1978, 1982; Howson & Brown 1980). The mixture is by groups of sixteen trees. There was a two-fold increase in fresh biomass of earthworms in spruce/alder plots and a six-fold increase in spruce/pine plots compared with pure spruce (Brown & Harrison 1983). This was correlated with better spruce height growth in the mixed plots. Mineralization of the organic matter may have been faster in the mixed plots but it was not known whether the increase in worm biomass was a cause or an effect. (Miles (1986) suggested it was probably the result of increased availability of nitrogen and phosphate.) Alder litter is more palatable to earthworms than are conifer needles but the mixture effect was more marked with the pine, suggesting that the root growth of the pine could be involved.

Similar effects might be found, if searched for, in mixtures of broadleaved species in semi-natural woods on poor soils, given the observed effects of shrubs and the ground flora in promoting tree litter breakdown (2.1.6) and the effect of birch in reversing podzolization (2.2.5.1).

2.3 The effects on soils of changes in stand structure

Coppice stools have an established root system so that after cutting there may be fewer changes in the soil such as a rise in water-table (Payne & Backhouse 1967) or nutrient loss (2.5.1.1) than in high forest where there is a lag before the young trees are established. Thus a difference in soil conditions early in the rotation might occur but there is no reason to expect that generally a change of stand structure has much effect on the soil. Albert & Barnes (1987) for example found no significant differences between an old-growth sugar maple stand and natural regrowth 50 years after clear-felling in soil pH, texture or soil horizons, although there was a decrease in potassium in the upper soil in the young stand.

Bonneau & Ranger (1984) compared the soils under oak high forest and oak, birch and hornbeam mixed coppice with oak standards. They gave brief details of measurements to show the losses of potassium, calcium and magnesium under the high forest which had been converted from coppice with standards, this undesirable change in the soil being linked with the change in silvicultural treatment of the one species. The soils (sol lessivé à pseudogley = (?) a brown earth with clay leaching and a tendency to surface-water gleying) had a pH less than 4.5 and were low in calcium at the surface, but with a slightly higher pH and more calcium in the B horizon which had a higher clay content. The coppice

with standards had mull or mull-moder organic matter, associated with faster litter decomposition because of the comparatively short rotation for the coppice (25-30 years) and its less regular canopy compared to the high forest. The organic matter was moder under the high forest where the canopy was more continuous, less frequently interrupted by felling and had only one tree species contributing to the litter. No details were given of the stands examined, no account was taken of the possibility of change during the rotation and the change in stand structure was confounded by the changes in species composition; but this seems to be preliminary work and suggestions are made for further research.

In the long term, differences between coppice and high forest systems (especially low-input high forest) may develop because of variations in the dead wood input. Even in managed high forest some trees may die and these and large dead branches end up on the ground. In a coppice the dead wood input is in smaller pieces: in a beech/chestnut coppice in south-east England 60% of the woody litter was less than 10cm long and less than 15% more than 2cm in diameter (Boddy & Swift 1983).

2.4 The effects on soils of a change in woodland structure

2.4.1 The effect of silvicultural systems on soil conditions

Silvicultural systems vary in the size of the felled areas, from extensive clear fellings through group selection to true selection forest. The effects of felling decrease as the coupe size is reduced because the influence of the surrounding trees increasingly dominates the felled area. In selection forest where individual trees are removed the effects of felling are probably similar to those of thinning in managed even-aged stands: a gap is created in the canopy which is filled by growth of the remaining trees. A gap may not be formed in the root system of the stand since the roots of neighbouring trees are intermingled and may be connected by natural root grafts.

Silvicultural systems which use small coupes reduce the extent of the changes at felling, hence they are favoured on sites where the aim is to try to maintain mature closed canopy conditions over much of the site. They are also used in sites vulnerable to erosion or in catchments where a consistently high water quality is essential.

2.4.1.1 Coupe size and soil disturbance

An indirect effect of the use of small coupes may be that the frequency and extent of disturbance along extraction routes is increased. On difficult sites this increases the risk that access will be required at times when, on nature conservation grounds, it would be better to stay out. On the other hand less material is removed on each occasion, so that the machines involved may be smaller and the severity of the disturbance on each occasion is less (2.5.1). Reader (1987) found that disturbance from tree skidding in a stand increased as the percentage of trees felled rose.

2.4.1.2 Strip felling to control water yield

Changes in woodland structure have been used to control the effects of clear felling on water yield from a catchment. Hornbeck *et al.* (1986) compared the run-off from catchment areas completely clear felled

or felled in strips, against an unfelled area. The strip felling was of three successive 25m wide strips cut parallel to the contours at two year intervals. Both treatments increased run-off for seven years from the initial felling, especially during the growing season because of the reduced transpiration from the catchments. The strip felled area produced much smaller increases in run-off in the first two years, in line with the smaller area which had been cut by that time.

2.4.2 The effects of road or ride creation

Changes to woodland structure through the creation and maintenance of roads, glades and ponds affect the soil mainly through the effects of altered drainage (2.5.2). An incidental effect of road construction can be the addition of dust and roadstone to the adjacent soil. Roadstone is often calcareous and so could raise the soil pH. The effect of bringing in nutrient-rich material from outside may be long-lasting. Parts of a wood which were formerly a habitation or a rubbish dump often have a richer soil especially in phosphate, indicated by a rank growth of nettles (Pigott & Taylor 1964; Rackham 1976).

Hill (1979) mentioned the rich flora on the verges of forest roads surfaced with limestone in Dalby Forest, Yorkshire. In the Forêt d'Orléans Ponge & Prat (1982) suggested that the higher pH of one site (5.7 compared to 3.6-4.6 for the others) was due to calcareous contamination from an old Roman road nearby. In Fontainebleau a strip of calcareous grassland has been created on limestone rubble alongside a 19th century aqueduct through an otherwise acid woodland. The consequent species enrichment may be a nature conservation benefit in some sites, but is unwelcome on a site where the rides are valuable as examples of acid grassland or where the base-rich material is washed off into naturally acid streams.

2.5 The effects on soils of changes on the site

2.5.1 Soil disturbance

Disturbance of the soil can occur during site preparation, site amelioration and from the extraction of timber. A major concern is that modern machines produce larger or longer-lasting effects.

2.5.1.1 Nutrient loss

Disturbance to the soil usually takes place in the interval between tree crops under open conditions and mixes the layers of organic matter with the mineral soil; all this is likely to increase the rate of decomposition (Noirfalise & Vanesse 1975). The resulting mineralized nutrients are either taken up by plants, remain in the soil, or are leached. The fate of individual elements varies depending on the conditions of the particular site. A herb layer, dominated by Chamaenerion angustifolium, developed by the third year after felling a Norway spruce stand and contained about 50% of the amount of nutrients in the felled spruce (Klimo 1984), but the herbs die down and nutrients may be lost from the soil each year in this fast-cycling system.

2.5.1.2 Extent of soil disturbance during harvesting

Soil is disturbed during harvesting through compaction, displacement

(rutting, scraping or erosion) and disruption of surface drainage (Moehring 1970). The extent of ground disturbed by operations such as thinning or felling depends on the methods adopted and the type of machinery. Any rise in the water-table associated with thinning or felling will exacerbate risks of subsequent compaction or rutting by machinery, particularly on clay soils.

Bockheim, Ballard & Willington (1975), who looked at clear felling in south-western British Columbia, gave figures for ground disturbance of 5% (helicopter extraction), 29% (high lead system), 69% (tractor extraction). The severity of damage is related to the transported volume (number of machine passes multiplied by volume of load) but the first few passes have the greatest effect (Wingate-Hill & Jakobsen 1982). Reisinger, Simmons & Pope (1988) give values of 21-34% of ground disturbed in various studies with 5-14% serious compaction. Damage is reduced if only stems rather than whole trees are extracted and by organized felling systems where vehicles run on lop and top (although the lop and top has other effects on the soil and ground flora).

Thinning operations have less effect than felling because a lower volume is removed. In an American study, thinning led to some compaction and soil disturbance on 20-40% of the extraction routes (racks) through the stand, or about 7-10% of the total area of the thinned unit. Heavy compaction and disturbance was, however, limited to 2-10% of the racks, 0.5-3% of the whole unit (Sidle & Laurent 1986). This is similar to the general figures reported by Wingate-Hill & Jakobsen (1982) of 1-3% of the total area heavily disturbed (mainly on or around log dumps); 3-20% moderately disturbed (primary tracks); and 8-45% of the ground showing low levels of disturbance through use as secondary tracks.

2.5.1.3 Recovery of soil conditions after harvesting

There is natural recovery from compaction through the forces of freeze/thaw and shrink/swell cycles in clays but it is slow, taking for example up to 18 years after severe disturbance, or 40 years on a badly compacted track (Moehring 1970). Klimo (1984) measured the bulk density of the soil before and after harvesting and estimated that recovery after compression by machines would take 8-10 years. Even longer-lasting effects have been reported - 17-21 years (Corns 1988) and up to 100 years (Munns in Wingate-Hill & Jakobsen 1982).

In the USA, especially the south-east, there seems to be much more emphasis on repairing damage than avoiding it (Moehring 1970). Ploughing or discing relieve compaction immediately. Disruption of drainage and extensive rutting or scraping require restoration of the land surface by machines such as bulldozers.

In nature conservation terms there is more benefit from practices aimed at decreasing the level of disturbance by minimizing the load on the soil (use of tracked vehicles or ones with many wide wheels) and by not working on wet soils. On some sites extraction of winter-felled material should be left until the summer; 15% more ground was exposed by winter logging when wet than in the summer (Reisinger, Simmons & Pope 1988). Minimizing the disturbance also reduces the effects on the ground flora and in the long term is as much in the interest of good growth of the young trees (Corns 1988) as of the soil and ground flora. Even so there is likely to be some compaction in almost any managed stand, so that minimum intervention areas are needed to assess this effect (1.1.3).

2.5.2 Fertilization, drainage and woodland streams

Fertilization and drainage are likely to increase the rate of decomposition of the organic matter. On wet sites decomposition is slow because of anaerobic conditions. On most sites decomposition is increased through stimulation of the activities of the decomposer organisms by the readily available nutrients in fertilizer (Noirfalise & Vanesse 1975). Fertilizers, particularly nitrogenous ones, may also affect soil acidity. Any consequent lowering of the pH can affect both soil fauna diversity and biomass (Huhta *et al* 1986).

Heavy fertilizer use is not a common practice in lowland woods, but is suggested for areas of willow or poplar coppice for biomass production. If the measures are effective in promoting tree growth, and alter the composition and vigour of the ground vegetation, then the different amounts and types of litter returned to the soil will lead to further changes in the soil properties. These would be undesirable in nature conservation terms (see also 2.4.2 on the introduction of extra nutrients through roadstone).

2.5.2.1 Woodland streams

The treatment of woodland streams is often linked to more general drainage proposals (2.2.6). Guidelines for the management of streams in upland conifer plantations are well known (Forestry Commission 1988; Mills 1980). However, some of the issues are different in lowland woods. Unlike much surrounding farmland the drainage pattern in ancient woods (streams, springs, small ponds) is often relatively natural (Rackham 1980). Intricate meanders may survive as at Wormley Wood, Hertfordshire (Peterken 1981). Straightening or canalization destroys these features.

Streams may get blocked by logs or lop and top during thinning or felling, which is more likely to happen during the large-scale operations usually associated with modern forestry practice. An interesting contrast is provided with old-growth conifer forests in north-western USA. There, foresters are asked not to remove logs that have fallen naturally into the streams and rivers, because the pools that develop behind such obstructions are important for fish, particularly salmonids.

The opening up of the canopy above woodland streams which run next to or through clear fells may lead to changes in light, temperature (Holtby 1988), nutrients, sediment particle size or invertebrate food in the stream. The sediment load may go up after forestry operations where lowland streams cut through free-draining strata with loosely consolidated soils, e.g. Triassic pebble beds. However increased light and temperature as well as the effects of felling debris entering the stream are probably the most significant effects in lowland woods. For example after clear felling next to streams through broadleaved and coniferous forests in New England, green algae (Chlorophyceae) increased whereas diatoms (Bacillariophyceae) dominated the reference streams in the unfelled area (Noel, Martin & Federer 1986). Unfelled buffer strips were recommended to reduce the effect of the clear felling on stream biology, but strips 9m wide on each side of the stream were too narrow to be effective.

2.5.3 The effects of weed control on soil properties

The shrubs and ground vegetation contribute to soil properties

through their litter and involvement in nutrient cycling (2.1.6). Elimination of the ground vegetation by weeding increases the likely loss of nutrients through leaching during periods when the tree roots are inactive or not well-developed as in young stands. This could contribute to a long-term decline in site fertility. However the effects of such weed control on the ground flora would be much more important in nature conservation terms (3.5.3).

2.5.4 Increased intensity of harvesting (see also 2.2.4)

2.5.4.1 Nutrient balances under modern forestry practice

Normally only the required woody material is removed from the site during harvesting. The lop and top is trimmed off in the stand and left there. This reduces nutrient loss from the site, but there is a redistribution of nutrients through piles of small branches, tops, trimmed bark, etc (2.1.3). Depending on how long these take to rot down and how much nutrient enrichment they cause, the local effects on soil fertility and hence on flora and fauna could be important in nature conservation terms.

Increased intensity of harvesting includes removing more of the tree biomass and taking it more often through shorter rotations. Since the nutrient content of leaves and branches is higher than the trunk, and leaves and branches are a larger proportion of the total early in the rotation, more frequent harvests and harvesting more of the tree increase the export of nutrients from the site. Whole-tree harvesting sometimes occurs incidentally when felled trees are extracted to the road to be trimmed in safer working conditions.

For Sitka spruce on upland sites, phosphate is the element most likely to be critical because a much larger proportion of the total available is removed in whole-tree harvesting and many sites are low in phosphate (Anderson 1985; Miller 1984). However elsewhere other nutrients might be the most depleted, for example calcium in central hardwood stands in the USA (Tritton *et al* 1987).

In an analysis of the effect of increased intensity of harvesting Ranger & Bonneau (1984, 1986) reviewed the data available on the mineral content of trees, by species, components (wood, bark, leaves, etc.) and age. The long-term nutrient balance for a site is the sum of atmospheric inputs, weathering and nitrogen fixation less the export of nutrients in the harvest and drainage losses. (Apart from the harvest, all of the nutrient flows are low rates, not necessarily constant, and they are therefore difficult to estimate accurately.) A net export of nutrients cannot be continued indefinitely without decreasing the productivity of later crops. Therefore the rotation must be long enough and the harvest sufficiently less than the total biomass for the exports and inputs to balance. For a given species and proportion of tree harvested there is a minimum rotation length (the "révolution écologique") during which the accumulated inputs match the export at harvest. To apply this to forest management would require figures for the inputs from the atmosphere and weathering for each site and tables of nutrient content, parallel to yield tables, for each species.

The long rotations used in forestry mean that the comparatively small amounts of nutrients usually removed are often balanced by natural inputs to the site. However this does not mean that forest management must always arrange for this to be so. Poore & Fries (1985) and Will & Ballard (1976) note the double standards that are sometimes applied to productive agricultural and forest crops. If a high physical yield is

required then nutrients may have to be replaced on the site using fertilizers or other means, and the more productive the crop or the poorer the site the more likely this is to be necessary. While there may be no objection on the grounds of soil conservation to maintaining forest site productivity through fertilizers on some sites, it may be very damaging in nature conservation terms because of the effects on the ground flora, or on the characteristics of the soil itself.

2.5.4.2 The nutrient balance under long-sustained coppice regimes

The same considerations of inputs and outputs apply to traditionally managed coppice which included rotations as short as 3-7 years in the Middle Ages. Short rotations could lead to a net loss of nutrients from the site and Rackham (1980) suggested this a reason for the gradual lengthening of rotations on some sites. Sykes & Barr (1973) estimated that the nutrients removed in a 15 year rotation of oak/ash/hazel coppice on a calcareous site were balanced by the aerial input, but the positive balance was small for phosphate. In Romania the interposition of a high forest rotation every five or six coppice rotations was thought necessary to conserve soil nutrients as well as to provide maiden stems to recruit into the population of coppice stools (G. Bumbu & A. Alexe, personal communication).

Whole-tree harvesting, or the Mediaeval equivalent of removing even small twigs for kindling in coppices, does overcome what is sometimes perceived as a problem in nature conservation terms: the localized soil enrichment from piles of lop and top, or fire sites.

2.5.4.3 Whole-tree harvesting and the soil fauna

Bird & Chatarpaul (1986) compared the densities of soil micro-arthropods under conventional and whole-tree harvesting. The numbers of mites (Oribatei, Prostigmata and Mesostigmata) and of total micro-arthropods were lower (56-68%) in the harvested than the unfelled areas, and higher in the conventionally harvested areas than under whole-tree harvests. At this stage it is not possible to determine whether such changes would have a significant effect in the long term on the rates of litter breakdown and nutrient turnover.

2.5.4.4 Indirect effects of whole-tree harvesting

The indirect consequences of increased intensity of harvesting are likely to be more soil compaction by machinery, and more disturbance to the organic matter on the soil and alteration of the litter inputs (Anderson 1985; Ranger & Bonneau 1986). Shortening the rotation with no change in coupe size increases the proportion of the rotation without a complete canopy and would probably lead to faster decomposition and less accumulation of organic matter. Anderson (1987c) reports an increased risk of waterlogging leading to shallower root development in the next crop after whole-tree harvesting because there is less interception and re-evaporation of rainfall from branchwood left on site. Such indirect effects are likely to be of more immediate nature conservation concern than the extra nutrient loss.

2.6 Discussion

2.6.1 Soil as a woodland feature of nature conservation value

Woodland soils are worth conserving because they are as much a component of the natural woodland system as the above-ground vegetation. They are not simply the medium for plant growth. Therefore to assess the significance for nature conservation of changes under modern forestry practice we must include effects on the structure of the soil, its type and profile, its surface features (including historical ones such as banks and ditches) as well as those on the soil flora and fauna.

2.6.2 Tree species and litter type

Many changes can be connected directly or indirectly with the amount and properties of litter arriving on the soil surface. Since the characteristics of the litter depend on the species in the vegetation, which is dominated by the trees, the concentration of research on the effects of tree species is justified. Provenances and genotypes within a species could also vary in their effects (D.J. Mabberley, personal communication; Miles 1986) but this question is still untouched.

The tree species is a distinct qualitative character, but when trees are present as a crop it is overlain by the quantitative differences in the size and number of trees and how these vary with time, i.e. the problems of changes during the rotation and of different levels of stocking. Any one tree species may occur on a range of possible sites. The three factors, species, site and treatment, interact so that prediction is difficult from study of only a limited number of the possibilities.

Of the species studied by Ovington (Figure 2.3; 2.2.2) three groups can be distinguished: pines and spruces, other conifers, broadleaves. This is based on the accumulation of organic matter which reflects the ease of decomposition of the litter. Change of species within any of the three groups is likely to have smaller effects than changes between the groups. As stocking increases or soil acidity decreases so more litter is likely to accumulate and so species differences may increase. The effects of site and management are most significant for the larches and beech which are to some extent intermediate between groups in their litter characteristics and so may go either way according to conditions.

The soil flora and fauna at any point is sensitive to changes in the litter type and quantity. The abundance of individual species on a particular spot at a particular time is thus likely to vary considerably. On a larger scale in space and time and in terms of genera or families the soil flora and fauna is probably robust, fluctuating around a long-term average composition and abundance. Any change in forestry practice, especially change of species, affects the soil flora and fauna in detail but probably only the more drastic changes alter its overall character and composition.

Where the nature conservation aim is to maintain the character of the particular soil conditions on a site then the best way to do this is to keep the native tree and shrub communities under which it has developed. If this is not possible then a change of species within the groups indicated above will lead to least disruption of existing soil conditions and processes, particularly if the effects of site are taken into account. Management should be adjusted to minimize the tree-species effect.

2.6.3 Soil disturbance

From a timber production point of view the effects of soil disturbance within the stand can often be remedied by subsequent cultivation. However, the extra costs right at the beginning of the rotation encourage good management on the site to minimize soil disturbance.

Often there is a choice between slight disturbance to the whole coupe by minimizing the number of passes over any one route or concentrating inevitable damage on tracks which can later be restored or converted to permanent rides or roads. The same principle applies to the use of the rides themselves. If most of the damage is done in the first few passes (Wingate-Hill & Jakobsen 1982) then concentration of use is the best strategy. Concentration of access to limited specified routes also becomes especially desirable as the frequency or the probable severity of disturbance increases.

In nature conservation terms reduction of the initial disturbance is always preferable to re-instatement. We suggest that at least ten years are likely to be needed for a ride to recover from major disturbance and that not more than 20% of the ride length should be subject to damage or recovering from major disturbance at any time.

2.6.4 Soil conservation

Concern over the maintenance of soil fertility is not primarily a matter of nature conservation but of conservation, i.e. the sustained productive use of the soil as a resource (Peterken 1981). The physical loss of soil by erosion is thought to be of limited importance in lowland woods (though important in surrounding farmland). Occasionally, however, major landslips do occur within or through semi-natural woods, as happened in autumn 1985 on the east side of Loch Lomond.

Provided there is adequate nutrition of the crop during the whole rotation, the maintenance of long-term site fertility depends on the balance between inputs and outputs. Ranger & Bonneau (1986) introduced the valuable idea of a balanced rotation (so-called "révolution écologique"), a minimum rotation during which the accumulated continuous inputs less losses balance the ultimate removal of nutrients in the harvest. In whole-tree harvesting, we suggest that the main issue from the point of view of nature conservation in lowland woods is not the extra nutrients that may be removed but the higher ground disturbance or remedial action that is associated with the practice.

There is no soil conservation reason why fertilizers should not be used in forestry as far as financial constraints allow, but this could involve conflict where one of the other stated objectives for a wood is nature conservation. The more the site, its soil and associated species are modified by fertilizers the more its value for nature conservation declines because it departs further and further from the natural or semi-natural state.

2.7 Implications for nature conservation (soils)

(a) Modern forestry practices can lead to a number of changes to woodland soils of which the most important are probably in the amount and type of organic matter, in pH, drainage, compaction and soil surface disturbance.

(b) Ball & Stevens (1981) point out the great value of the undisturbed soils in ancient woodlands. On the most valuable sites the soil profile characteristics should be preserved with as little alteration as possible, because they are part of the natural woodland system. This can only be achieved reliably by minimum intervention or by continuing or re-introducing traditional management.

(c) Natural surface features, often related to soil drainage patterns, are similarly irreplaceable and should be preserved on the best sites, independently of (b). Disturbance to banks in woodland should be avoided, because these have great historical value and may cast light on past conditions through analysis of the buried soil surfaces beneath them. On most sites such natural and man-made features can be maintained under traditional or modern management provided care is taken over harvesting, especially with large machines.

(d) Periodic soil disturbance is a natural part of woodland systems and certainly occurs under traditional as well as modern forestry practices. It is the frequency and increased intensity of such disturbance under modern practices that causes concern from a nature conservation viewpoint. Re-instatement following soil disturbance may be sufficient to restore conditions for good tree growth, but modifications of practice to reduce disturbance in the first place is the preferred option for nature conservation. Heavy timber extraction should be avoided during wet conditions on peat and clay soils.

(e) On sites where nature conservation is less important, forestry practices will certainly cause soil changes, but not to the point that a soil flora and fauna of a general woodland character is completely eliminated. It is in the foresters' own interests to ensure that the long-term fertility of sites is maintained.

(f) Changes and remedies of little importance from the point of view of the soil have large effects on the woodland flora and thence on the fauna. In particular, changes in soil pH and the type of organic matter that result from a change of tree species cause changes in the species composition and vigour of the shrub and ground vegetation (chapter 3).

3 FLORA

3.1 Background

3.1.1 Flora and vegetation

In this chapter the flora means simply the plant species present, irrespective of their relative abundance or spatial distribution. We use the term vegetation when the way in which the species (flora) are distributed or grouped is also important. Vegetation thus embodies the ideas of woodland plant communities and their relation to environment. Detailed descriptions of British woodland vegetation are given by Peterken (1981), Ratcliffe (1977) and Rodwell (1986).

The potential flora at any place is determined primarily by the region, climate and soil. In particular, woodland vegetation in Great Britain shows a south-east to north-west trend which is mainly climatic (temperature and rainfall) and, cutting across that, a trend from base-rich to base-poor soils (Rodwell 1986). The flora actually present in any wood depends also on the woodland history and present management. In addition, at any one time, the flora in a stand depends on the stage of the rotation and the level of stocking (3.1.3, 3.1.4, 3.1.5).

In most cases the flora or vegetation used as the baseline for comparison with that under modern forestry practice is not the flora of natural woodland, although the development of a more natural vegetation may be a valid nature conservation aim (1.1.3). Rather it is the vegetation of established woodland under its traditional management. In the lowlands this generally meant coppices from which domestic stock were excluded for at least the early part of the rotation and wood pasture where grazing was normal. In the uplands the distinction between woods with and without regular grazing was probably less rigid. Many woods were coppiced but there were also substantial areas of Scots pine and birch high forest which regenerated from seed.

3.1.2 Groups within the woodland flora and their relationships

We have divided the woodland flora into four groups: trees and shrubs, vascular ground flora, bryophytes and epiphytes, although this chapter deals mainly with the vascular ground flora, on which most work has been done (Table 1.3). Trees which are not part of the main crop are joined with the shrubs since from the commercial forestry point of view they are all woody weeds. More detailed sub-division of these layers is possible e.g. Falinski (1986).

In terms of species composition the groups or layers tend to be independent of or only weakly correlated with each other (Kirby 1984b). They vary at different scales and in response to different environmental pressures. This is not just a consequence of the long history of management of woodlands in Great Britain (Peterken 1981; Rackham 1975) but seems to be a general phenomenon shown also in unmanaged North American forests (Dunn & Stearns 1987; Gagnon & Bradfield 1986; McCune & Antos 1981; Rogers 1981). The flora of a wood is thus not so much a single community as several loosely associated ones.

Rackham (1980) suggests that only alder and elm have strong associations with particular species in the ground flora. In the case of valley alder-woods the species have similar requirements for a moist spring-fed soil. The species found with elm seem to be a real plant to plant association, perhaps because the rooting habit of elm and the high

mineral content in its leaf litter create an area generally richer in soil nutrients. However, even the existence of a distinct elm flora is questioned by Rodwell (1986) and Ellenberg (1988) states that in central Europe no single ground flora species can be said to be absolutely associated with a particular tree species.

3.1.2.1 Competition between and within the layers or groups

The layers or groups interact functionally since they grow in the same soil and the larger plants substantially alter the aerial environment of the smaller ones. In old-growth areas in the Bialowieza National Park 12-15% of the forest floor was occupied by uprooted trees and 4% by the living tree bases, so that over a sixth of the soil surface might be unavailable to the herb layer at any one time (Falinski 1986). A shrub layer also influences the distribution of the ground flora (Wilson 1988). Even within the ground flora layer there are interactions between the larger, strongly-growing species such as brambles and bracken, the smaller herbs such as violets and bluebells and any ground-living bryophytes. For instance the cover of bramble and bracken was inversely related to the number of other species in the ground flora under eight tree species (Page 1981; 3.1.3.3). Dense stands of ramsons (Allium ursinum) may reduce the local diversity of the spring flora (Ernst 1979). Removal of Mercurialis perennis shade without altering the tree canopy was followed by a marked increase in bluebell (Endymion non-scriptus), primrose (Primula vulgaris) and other species (Pigott 1977). Collins & Good (1987) also concluded that interactions within the ground layer could be as important in determining the distribution of species as variations in canopy type.

As a general rule only two or three well-developed layers can occur at any one point: trees plus shrubs, with very little ground vegetation if both the taller layers are complete, as in coppice with standards; shrubs plus ground vegetation in coppice; and trees plus ground vegetation in high forest. (Taking a general figure of 10% transmission of photosynthetically active radiation (PAR) by any leaf canopy then the fourth layer is down to 0.1% of incident PAR which is not enough to support a green plant in the long term.) However, four or five layers can occur on an area because of patchiness, for example of standard trees above coppice, or in the ground vegetation. Coexistence of layers is easier if there is at least some separation phenologically, for example bluebell growing in the spring before the trees are in leaf and before bracken fronds reach their full size in June.

3.1.2.2 The influence of grazing

Grazing alters the species composition of vegetation in all layers (Putman 1986; 2.1.7). Low levels of grazing and browsing may reduce the vigour of some species and allow greater overall diversity. Roe deer, for example, may reduce the amount of bramble in the ground vegetation so allowing smaller species to survive. At very high levels of grazing the ground vegetation may become dominated by a few unpalatable species such as bracken and those tolerant of grazing, especially grasses. Reduction in the cover of vascular plants favours ground-living bryophytes.

Palatable shrubs can be eliminated and in the long term the composition of the tree layer may be changed. Pigott (1983) found that sheep grazing allowed birch to form a large part of the canopy of an oakwood: when grazing ceased the change in ground vegetation and lack of sheep enabled oak to regenerate but prevented further regeneration of

birch. At Coed Corswen sycamore was more susceptible to grazing than ash or hawthorn and was eliminated from the regeneration in grazed areas (Linhart & Whelan 1980). The fallow deer in Hayley Wood have definite preferences among the coppice species so that heavy grazing would eventually eliminate ash and willow and favour the less palatable field maple and aspen (Rackham 1975, p112).

3.1.2.3 Other sources of variation in the flora

Further causes of variation in the flora include the vagaries of the weather, the effects of different speeds of response of the layers (carry-over effects and lags), and the heterogeneity of sites. Survey work in woodland commonly uses 5x5m, 10x10m, 14x14m or larger quadrats, but there is considerable heterogeneity in the ground flora at smaller scales than this, related to micro-topography, canopy variations, vegetative spread of species to form dense patches, etc. (Christy & Mack 1984; Maguire & Forman 1983; Rogers 1982; Smith & Cottam 1967; 3.2.3). Our casual observations suggest that small-scale patterning also exists in British woods. As it is a fundamental element of the woodland vegetation it would be desirable to know how far patterns in coppice, managed high forest and those of long-neglected high forest stands differ.

The species composition at any one point may vary over time. In Canada, Holland (1978) found 14-20% turnover in the species found in metre-square permanent quadrats in beech/maple forests during an eight year period even though the stand composition remained the same. Falinski (1986) also reports changes from year to year in the species composition of permanent plots in undisturbed woodland.

Thus interpreting the presence and abundance of species in the woodland flora on any one site is difficult, and prediction of the detailed consequences of management such as re-introduction of coppicing is impossible (Rackham 1975).

3.1.3 Changes during the rotation in worked coppice

The classical early work on changes during a coppice rotation was done by Wilson (1911), Adamson (1912) and Salisbury (1916a, 1918 and summarized 1924). They were mainly concerned with the vegetation on different soil types and Wilson and Adamson mentioned the changes through the rotation almost incidentally. Rackham (1975) has given a full account for Hayley Wood, while Ash & Barkham (1976) concentrated on the floristics and Ford & Newbould (1970, 1977) on the biomass production of particular coppices. Brown (1979a, 1979b, 1981), Brown & Oosterhuis (1981), Brown, Pearce & Robertson (1979) surveyed the flora and seed banks in a number of worked and neglected coppices.

The essential features of the coppice system are that the rotation is short, usually less than 20 years, and apart from occasional deaths or establishments the stools remain at a constant density. An additional feature, following from the short rotation and small areas (one to a few hectares) cut each year, is that stands of all ages are usually present close together in a wood. Standards over the coppice add complexity, where present, but unless very many or very large their influence on the ground vegetation is much less than that of the coppice. (During the late nineteenth century the number of standards in many coppices was greatly increased and the structure of some woods is now closer to that of high forest.)

After the coppice is cut the existing, perennial, shade tolerant

plants grow more vigorously and they are joined by other species (annuals, biennials and perennials) from buried seed, from seed dispersed in by wind or other means and by vegetative spread from the edges or from permanent gaps in the stand. The ground vegetation flourishes for a few years but gradually decreases as the coppice regrows. Salisbury (1916a, 1918) coined the term marginal species for those which are present all the time along rides and edges but grow in the stands only after coppicing. There is a considerable seed bank in the soil under coppice from which most of these marginal species can re-appear (Brown & Oosterhuis 1981). The increase in vegetative growth and especially in flowering is usually much greater in the second season after coppicing than the first. For some species the growth in the first year after coppicing is particularly important. Pons & During (1987) found that marsh thistle (Cirsium palustre) rosettes formed in the second or third year were very much less likely to flower subsequently and hence contribute to the soil seed bank.

3.1.3.1 Changes in biomass and species number during the rotation

In a chestnut coppice the number of species reached a maximum in the fifth year, not long before canopy closure (Figure 3.1b). However, in a floristically very rich wood in mixed coppice, probably with a lower stocking, the number of species was highest immediately after coppicing and declined from then on, well before canopy closure (Figure 3.1b). In the chestnut coppice the changes in above-ground dry weight were remarkably similar for total ground vegetation and for two species abundant on the site: the shade tolerant Anemone nemorosa and the light demanding Chamaenerion angustifolium (Figure 3.1a). Anemone persisted throughout the rotation; Chamaenerion was absent from the ninth year and presumably re-invaded at the beginning of the next rotation.

As the coppice shoots grew the seasonal peak of ground vegetation dry weight became earlier, from July in the second year to early May in the ninth year (Ford & Newbould 1977). Similarly the seasonal peak in number of species present became earlier and flatter from a sharp peak of 33 in August at 0-1 year to a plateau of 10 in April to June at 17-33 years (Ash & Barkham 1976). The spectrum of life forms also changed: the number of annual species declined exponentially almost to zero; the biennials peaked at 2-3 years and declined steeply to zero; the open-habitat perennials also peaked at 2-3 years and declined steadily; the shade perennials rose from about 10 to 22 species at 11-16 years and then declined slightly (Ash & Barkham 1976). The vegetation changes from one dominated by marginal species and a few flourishing shade species to increasing dominance by shade species. These are geared to spring activity which can use the peak in solar radiation before leafing of the coppice canopy in May and June (Anderson 1964; 3.6.3.1).

Brown, Pearce & Robertson (1979) recorded cover and the number of species in different categories in coppice in four age-classes (Figure 3.2). Shade and marginal species were defined after Salisbury (1916a, 1918). Similar trends can be seen, except for the unexplained increase in cover with age in coppice with standards. (Possibly the coppice was suppressed in the vicinity of the standards. If the competition from the standards was less (for the ground flora) than dense coppice, an increase in the ground flora could then occur.)

3.1.3.2 Spatial patterns in the ground flora

Spatial patterns develop in coppice as the ground vegetation, particularly the marginal species, become increasingly restricted to the

areas between the stools. With canopy closure the marginal species are eliminated and the shade species remain at a low level of activity (Salisbury 1916a; Pons 1976). An analogous pattern was found by Gustafsson (1988) in willow coppices cut annually for biomass production in Sweden. Shade species were found close to the stools, whereas more light-demanding species occurred in the intervening zone.

Figure 3.1 Changes in the ground vegetation during a coppice rotation. The arrows indicate the time of canopy closure.

(a) The above-ground dry weight (maximum during the year) of all the ground vegetation and of *Anemone nemorosa* and *Chamaenerion angustifolium* in sweet chestnut coppice with oak standards, Ham Street Kent (from Ford & Newbould 1977).

(b) The number of vascular plant species in hazel, ash and maple coppice with oak and ash standards in Foxley Wood, Norfolk (from Ash & Barkham 1976) and at Ham Street (details above). For Foxley Wood the number of species is shown separately for the total and for the sample plots only (7.5 x 6.5m, average of nine for each age-class), and they are plotted at the middle of the age ranges (0-1, 2-3, 4-10, 11-16, 17-33 years) given for the regrowth. The results for Ham Street are for the sample plots (15 x 30m, one at each age).

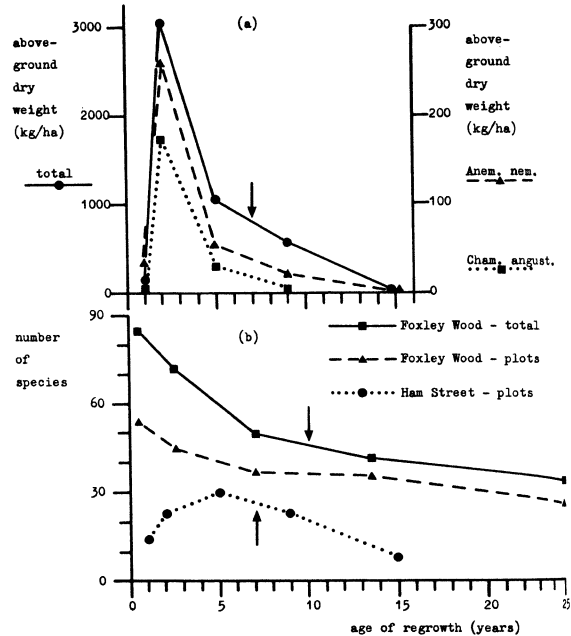
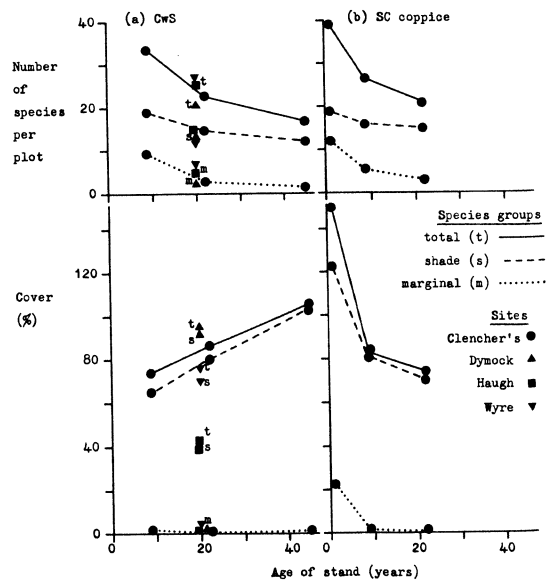


Figure 3.2

Changes in the ground flora during the rotation for (a) mixed coppice with standards, (b) chestnut coppice, on four sites in the south-western Midlands (drawn from data in Brown, Pearce & Robertson 1979). The number of species and cover were averages for eight plots of 200 square metres, recorded in May and June. See text for definitions of shade and marginal species.

The results were recorded for very young (1-2 years), young (3-15), middle-aged (15-30) and old (30-60) age-classes and are plotted at the mid-point of the range. The control coppices are plotted at 20 years in (a).



The time of canopy closure depends on the spacing of the stools and the vigour of growth. In vigorous chestnut coppice at around 2,000 stools per hectare the canopy closed after three years (Mitchell 1984) but at 600 stools per hectare canopy closure was after seven years (Ford & Newbould 1970). In a hazel/ash/maple coppice the canopy did not close until the tenth year (Ash & Barkham 1976).

3.1.3.3 The effect of vigorous species such as brambles

On some sites a tall rank vegetation of brambles, large grasses and living and dead flowering stems of biennials develops from the third year onwards which tends to shade out smaller species (Mason & Long 1987; 3.1.2.1) and itself persists until shaded out by the coppice regrowth. If the period of dense shade under the closed coppice canopy is absent or short because of wide spacing of stools or a short rotation then these strongly growing species may persist through the rotation, merely reduced in vigour during the later stages.

Ash & Barkham (1976) noted that in contrast to the newly coppiced areas, permanent glades were often dominated by these vigorous species. If coppice regrowth is delayed, for example by browsing of rabbits or deer, then even the regrowth may even be suppressed (Salisbury 1918, p29: brambles replaced hornbeam browsed by rabbits). Natural regeneration from seed may also be inhibited in such areas (Koop & Hilgren 1987).

3.1.4 Changes during the rotation in high forest

There are relatively few old semi-natural high forest stands in Great Britain so that most of the work on fluctuations in the ground vegetation within a rotation is based on plantations. Brown, Pearce & Robertson (1979), Hill (1979) and Ovington (1955a) pieced together the changes using sites of different ages and Hill & Jones (1978) used one site revisited 32 years after an initial survey which had been before most stands reached the thicket stage.

3.1.4.1 Post-felling changes

After felling, the vegetation consists of plants already present, those germinating from buried seed and a few species germinating from seed dispersed in by wind (Hill & Stevens 1981); there is often much bare ground. The early stages are similar to coppice: a flourishing and species-rich ground vegetation when the trees are small which becomes increasingly restricted to shade tolerant or competitive species as the canopy closes, or as the more vigorous ground flora species assume dominance (Hebb 1971).

In high forest naturally regenerated under shelterwood systems the rotations are overlapped (1.3.2.2). The vital point of these methods, in classical European practice, is the careful manipulation of the tree canopy during the extended period of harvesting to obtain good establishment and growth of the seedlings whilst minimizing the increase in the herbaceous ground vegetation (Everard 1987). In other words, the usual period of flourishing ground vegetation at the beginning of the rotation is evaded.

3.1.4.2 The thicket stage

During the thicket stage with its closed and low tree canopy the

ground vegetation is at a minimum, the absolute amount depending on the degree of shade, the smothering effect of the litter and the water and nutrient demand of the trees. Under western hemlock, spruces and firs ground vegetation is often eliminated but under other conifers and broadleaves some usually remains. During the thicket stage side light from rides and small canopy gaps where occasional trees fail can be particularly important in allowing some species to survive in patches in the stand.

3.1.4.3 The pole stage

Less is known about the slower changes during and after the pole stage. As the tree canopy moves upwards and the stand is thinned the ground vegetation increases, often greatly under most broadleaves, pines and Douglas fir, but only slightly under spruce (Figure 3.3). At this stage, on afforestation sites some woodland species may invade (Doyle & Moore 1982).

Anderson (1979) found that the composition of the ground flora under a range of tree species became more similar at the later stages in a rotation, largely because most stands on neutral to acid soils contain some of about a score of widespread woodland herbs and grasses (3.2.2.1; Table 3.1). In sugar maple forests Albert & Barnes (1987) found few differences in species number, but differences in the cover of individual species under 50 year-old natural regrowth after clear felling and the undisturbed stand. The thinning pattern and the level of stocking also influence the ground vegetation at these stages (3.1.5).

Ellenberg (1988) illustrates the changing and increasingly patchy light climate with increasing age under an even-aged beech stand. Mitscherlich (in Geiger 1965) used photographic exposure meters to measure the light as a percentage of that in the open in stands of Norway spruce (*Fichte* mistranslated as fir in Geiger 1965) from 16 to 130 years old. After canopy closure around 17 years and light down to 10% or less there was a steady rise to about 30% (range 19% to 38%) at 120 years. Although there was considerable variation, the higher yield classes with fewer, larger trees tended to transmit more light. The increase in light permitted the ground vegetation to increase after the thicket stage: at 17% (40-60 years) the first mosses appeared, at 24% (55-100 years) "berry plants" grew, and at 30% (90-120 years) seedling spruces appeared.

Figure 3.3

Changes in the ground flora during a high forest rotation.
(a) Norway spruce
(b) Douglas fir
on four sites in the south-western Midlands (drawn from data in Brown, Pearce & Robertson 1979).
Details as for Figure 3.2

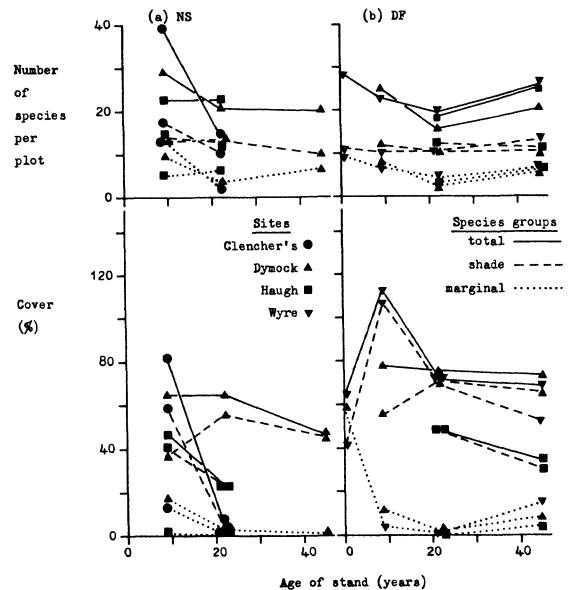


Table 3.1 The twenty widespread species in the ground flora, as recorded in the Ovington plots in Gloucestershire, Kent and Norfolk (22 plots, 17 tree species aged 40-69 years): "widely-encountered species.....in more than 50% of the forest plots" (Anderson 1979, p.97).

<u>Agrostis tenuis</u>	<u>Pteridium aquilinum</u>
<u>Chamaenerion angustifolium</u>	<u>Rubus fruticosus</u>
<u>Deschampsia caespitosa</u>	<u>Rubus idaeus</u>
<u>Dryopteris dilatata</u>	<u>Solidago virgaurea</u>
<u>Dryopteris filix-mas</u>	<u>Teucrium scorodonia</u>
<u>Endymion non-scriptus</u>	
<u>Hedera helix</u>	<u>Ilex aquifolium</u>
<u>Holcus mollis</u>	<u>Quercus spp</u>
<u>Juncus effusus</u>	<u>Sambucus nigra</u>
<u>Lonicera periclymenum</u>	
<u>Luzula campestris</u>	
<u>Oxalis acetosella</u>	

3.1.4.4 Changes in old unmanaged stands (the over-mature stage)

Mitscherlich's spruce stands were probably thinned but, even in unmanaged stands, changes occur in the later stages of the rotation. In a "mature oak forest" over a 30 year period the number of shrub species doubled. The cover of ground vegetation increased seven-fold through the increased cover of the dominant species, although rare species decreased. Davison & Forman (1982) attributed these changes to the decrease in shade following windthrow of trees and the fall of large branches. In contrast, Malmer, Lindgren & Persson (1978) and Persson (1980) working in mixed broadleaved stands 150-250 years old with vegetation records spanning 40 years thought that the changes (loss of ground vegetation species, and increases or decreases in cover for several individual species) were linked to an increase in shading and litter fall, as wych elm and ash increased in the canopy and oak decreased. Occasional heavy insect defoliation may open up the canopy (and increase available nutrients through frass) and lead to ground vegetation increases (Zlotin & Khodashova 1980).

These changes through a high forest rotation are a general phenomenon. Alaback (1982) studied the shrubs and ground vegetation in 60 near-natural stands of Sitka spruce/western hemlock/western red cedar in Alaska, of various site classes and on several soil types, up to 550 years old. In young stands the above-ground dry weight of the ground vegetation and shrubs (mainly shrubs) increased to a maximum at the time of canopy closure at 20-30 years and then dropped steeply to a very low level maintained for 150 years. Self-thinning and irregularities in the stand presumably caused the very slight decrease of canopy closure from 100% and were associated with the increase in shrubs and ground vegetation from 150 to 300 years. In terms of annual production shrubs dominated up to about 50 years, then ferns and mosses to 150 years, then shrubs and herbs for the rest of the rotation (Alaback 1982).

The current commercial rotation in south-east Alaska is 100 years, so that many stands never reach the later stages with the return of herbs and shrubs. Thinning would perhaps advance this stage but this has not been investigated (Alaback 1982). Herbs and shrubs also invade windthrow gaps. Much the same is true in British conditions where the rotations are shorter. The expansion of the ground flora in older commercial plantations can be brought forward by thinning, but the shrub layer generally remains sparse (Kirby 1988) and is unlikely to develop much before the time of felling.

3.1.5 The effects on the flora of changes in stocking

Work on range management in the USA and Australia has shown that the stocking of trees is a major element in determining the biomass of the ground vegetation. Both inverse linear and negative exponential relationships have been reported, according to tree species, for tree densities between 0 and 640 trees per hectare (basal area 0-25 m²/ha; all trees around 18m tall and 22cm dbh) (Walker *et al* 1986). Such results are generally from dryer climates where competition for water between the trees and the other vegetation is correspondingly more intense, but they illustrate the relationship between factors such as stocking, grazing and fire.

In the early growth stages more densely stocked stands simply progress through the stages more quickly. For example, the open phase vegetation persists for much longer in a lightly stocked stand, particularly between the rows (3.1.3.2). Initial levels of stocking may however have indirect consequences, for example in terms of how much ground is affected by weeding (3.6.4). At later stages, when regular thinnings take place, stands at the same stage can differ in stocking and hence in ground vegetation.

3.1.5.1 Effects on the number of species and their flowering

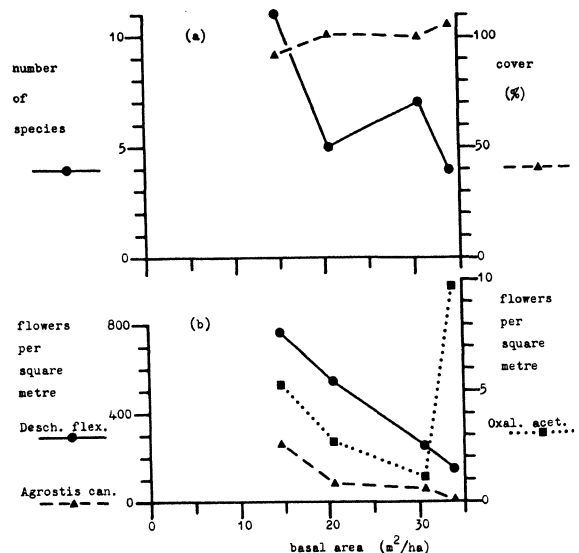
When the basal area on two woodland sites was reduced by about 30% and 70% there were small increases in the number of species (McComb & Noble 1982a). On the more heavily thinned site the cover of ground vegetation and shrub layer (less than 1.8m tall) increased by about 40%. There were also changes in the relative abundance of many species, i.e. community re-organization.

Nihlgård (1970) recorded the ground vegetation in three adjacent stands of Norway spruce in southern Sweden containing 1400, 600-500 and 400-300 trees per hectare and with 80%, 70% and 50% canopy cover. The dominant species was Oxalis acetosella in the densest stand but Deschampsia flexuosa in the least dense; the other stand was intermediate. Other species occurred with medium to high frequency in all three stands, but with low cover. Thus, as in McComb and Noble (1982a), the vegetation clearly varied with stocking but the flora changed less.

Figure 3.4

Effects of stocking (basal area/ha) on ground vegetation in stands of Japanese larch 46 years old in Kincardineshire (from Sakura, Gimingham & Millar 1985).

(a) Number of vascular plant species and total percentage cover (estimated from Domin scale values for individual species).



(b) Flowering of Deschampsia flexuosa, Agrostis canina and Oxalis acetosella.

Sakura, Gimingham & Millar (1985) compared 46 year old, first rotation Japanese larch stands on heathland in Kincardineshire, yield class 10, thinned to basal areas of 15 to 34 m²/ha (250 to 1,500 stems/ha) and a thicket stage, 17 year old stand, at 33 m²/ha (3,900 stems/ha). The surrounding heath was mainly Calluna vulgaris, Deschampsia flexuosa and Vaccinium myrtillus. In the thicket-stage larch Deschampsia flexuosa and Oxalis acetosella were the commonest species but with very low cover. In the older dense stand there was a high cover of Deschampsia and in the old, but lightly stocked, stand other grasses appeared (Anthoxanthum odoratum, Festuca ovina and Holcus mollis). The overall trend was to more species in the ground flora with lower stocking but little difference in cover (Figure 3.4). Flowering showed the largest and clearest response: there were many more flowers in the lowest stocked stand, except for Oxalis which flowered prolifically in the most densely stocked stand, perhaps because there was least interference from other ground vegetation there.

In 20-30 year old, even-aged stands of mixed beech and larch in Saltridge Plantations, Gloucestershire (unpublished results) which have been line thinned more species and greater cover can be seen along the rows where trees had been removed.

The general pattern that emerges is that small reductions in stocking lead first to increased cover and flowering of the species already present; larger ones to an increase in species number as well.

3.1.5.2 Effects on the radiation regime of the stand

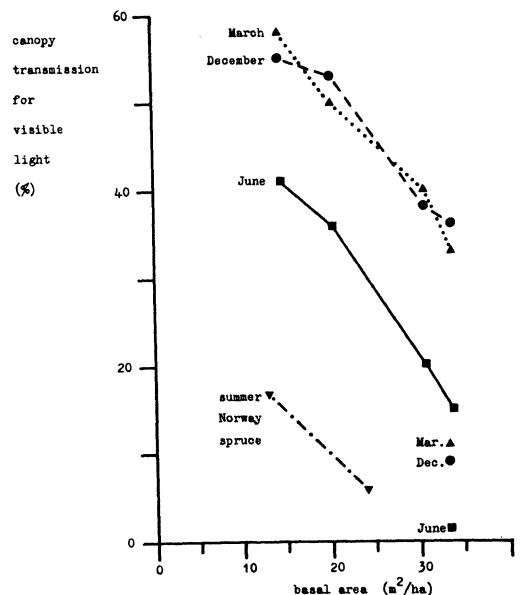
The percentage of visible light transmitted by the thinned stands of Japanese larch varied linearly with basal area (Figure 3.5). The difference between the least and most densely stocked stands (25 percentage points) was larger than the seasonal difference between full leaf and leafless canopies (15-20 percentage points). The thicket stage stand transmitted much less light (10% when leafless, 1% in leaf) even though it had the same basal area as the most densely stocked thinned stand.

Figure 3.5

Effect of stocking, (basal area/ha) on transmission of visible light in stands of Japanese larch 46 years old in Kincardineshire (from Sakura, Gimingham & Millar 1985). Transmission, as a percentage of the light in the open, was measured under overcast skies with a selenium cell light-meter 50cm above the ground.

The isolated points are for a 17 year old, unthinned stand of Japanese larch.

The Norway spruce points are stands 29 years old one year after the first thinning and are the weighted means for sunflecks and shade on the ground as a percentage of the light incident, measured in lux on three summer days (from François, André & Devillez 1985).



François, André & Devillez (1985) measured light in a different way in two stands of Norway spruce heavily and selectively thinned to 13 and 24 m²/ha. The slope of the line is similar to that for Japanese larch but much lower down the y-axis, indicating the heavier shade cast by a spruce canopy.

The pattern of the thinning is as important as the intensity of thinning in determining how the radiation regime changes. A herring-bone system is likely to allow a greater if more localized opening up of the canopy than simple line thinning of similar intensity (Anderson 1979).

The large differences in radiation regime, as indicated by these measurements of light transmission probably have a lot to do with the observed differences in ground vegetation between stands of different stocking levels. However, other environmental differences, e.g. organic matter decomposition, nutrient turnover, decreased competition for water, activities of grazing animals, could also be involved. Barker (1985) reported substantial die-back of Impatiens noli-tangere following thinning of a wood. This species is sensitive to moisture stress and showed severe wilting after the canopy was opened up.

3.2 The effects on the flora of a change of tree species

3.2.1 Trees and shrubs

To change the tree species on a site the existing trees and shrubs are usually felled and regrowth from the stumps is controlled thereafter. This destroys the tree and shrub communities present. If regrowth of the original crop is so vigorous, and survival and tending of the young plantation so poor, that the planted trees form only a small proportion of the subsequent thicket a stand similar to the previous one may emerge, but then the plantation has failed. This not infrequently happens on fertile lowland sites. Coppice regrowth and any seedlings which survive the disturbance of felling have established root systems and so are at an advantage to the planted trees. Where the change in species is accomplished by selective felling or thinning of coppice stems the effect on the trees and shrubs is usually less drastic (3.3.1).

Both broadleaved and conifer plantations can eliminate the previous tree and shrub species during the thicket stage. However the former tend to be less effective competitors and the longer rotations used for many broadleaves allow more time for shrub invasion towards the end of the rotation. The shrubs that reappear may arise from seed brought in by mammals and birds (Malmberg & Willson 1988). However it is unlikely that all the previous shrub and secondary tree species will return because some such as wild service tree have only limited ability to spread to new sites under present conditions (Peterken 1974).

3.2.2 Ground flora

It is easy to demonstrate differences in ground flora between semi-natural stands of broadleaves and various conifer plantations (e.g. Bamford 1987). However the question to be answered here is: given identical sites, and subtracting the effects of stage of growth and level of stocking, what consistent differences occur in the ground flora simply because of the effect of the different tree species?

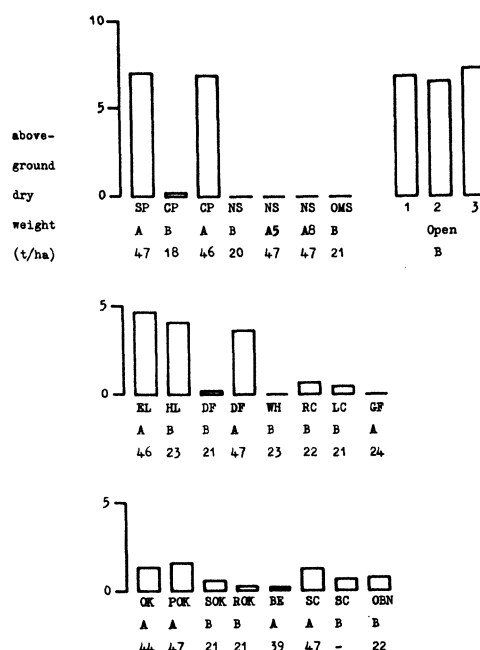
Figure 3.6

Above-ground dry weight of the ground vegetation in Ovington's plots in July-August 1952 (Ovington 1955a). Species abbreviations as in Figure 2.3 and Appendix 2.

Locations:

A, Abbotswood; B, Bedgebury.

The figure is the age in years in 1952. The sweet chestnut at Bedgebury was the shelterbelt: oak standards, about 135 years old, over chestnut coppice, age unknown. Ovington recorded in two plots of Norway spruce (5 and 8) at Abbotswood. There was no measurable dry weight under the spruces, western hemlock or grand fir.



3.2.2.1 The Ovington Plots (see also 2.2.2.1)

The most wide-ranging examination (17 tree species) of the ground flora has been based on Ovington's plots (Ovington 1955a, Anderson 1979, Page 1981, 1983), established in 1951 at Abbotswood (Forest of Dean), Bedgebury (Kent) and West Tofts (Thetford Forest). Abbotswood and Bedgebury were woodland sites; West Tofts was afforested heathland.

In 1952 the most frequent species were Endymion non-scriptus, Pteridium aquilinum, Rubus fruticosus (but completely absent under Douglas fir and Corsican pine at Bedgebury), Teucrium scorodonia at Bedgebury (only one occurrence at Abbotswood) and Oxalis acetosella at Abbotswood (very infrequent at Bedgebury). The plots differed more in the amount of ground vegetation (Figure 3.6) than in the species composition. Judging from the frequency of their occurrence the large dry weights were composed mainly of brambles (larch at Bedgebury), brambles and bracken (pines and larch at Abbotswood) or brambles and grasses (Douglas fir at Abbotswood, the open plots at Bedgebury). In 1981 the Bedgebury vegetation was dominated by brambles, bracken and Rhododendron ponticum (Page 1983).

There were marked differences in the distribution of vegetation in a plot. At Bedgebury it varied from uniform and thin under Corsican pine, sessile oak and roble (Nothofagus obliqua) to very patchy under red cedar and Lawson cypress (Ovington 1955a). The establishment of the red cedar and Lawson cypress had been irregular and the ground vegetation was vigorous in the gaps but absent under the complete canopy. At Abbotswood there was little or no vegetation under Norway spruce except where the canopy was patchy and in a narrow plot where vegetation had spread in from the edges (Ovington 1955a).

Anderson (1979) interpreted the changes in species numbers (Figure 3.7) between 1952 and 1974 at the three Ovington sites as a convergence to about 20 species (Table 3.1) as the crops progressed to the middle and late stages of the rotation. Species of scrub and grassland were replaced by woodland species. For each plot at Abbotswood the percentage of species in common with the oak plot was calculated. The average for the six plots was an increase from 37% in 1952 to 62% of species in common in 1974. However the changes ranged from a decrease

of 7% (larch) to an increase of 81% (grand fir).

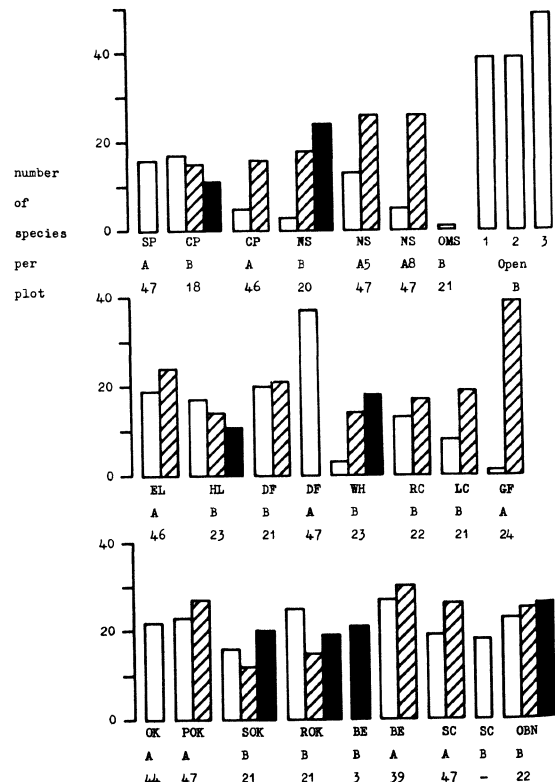
Once site heterogeneity and differences in growth stage and stocking are allowed for, no ground flora species or vegetation type can definitely be closely associated with any one tree species, or even with just conifers or broadleaves. There are undoubted differences between the plots, primarily in the amount of vegetation, but also in the number of species which is lower under trees that cast deeper shade. However in some plots with less shade, species number is lower apparently because of rampant bramble and bracken growth (3.1.2.1). Apart from the 20 widespread species (Table 3.1) additional species occurred in some stands associated with particular features of the aerial or soil environment imposed by certain tree species. However, the site, by defining the climatic and soil variables, fixed the range within which the flora under any particular tree crop on the site lay. The over-riding influence of site differences was also noted by Kirby (1988).

Nihlgård (1970) similarly showed that whilst the thicket stage in planted Norway spruce normally eliminated all ground vegetation, the vegetation that developed in later stages with regular thinnings, increasingly separated into types which reflected the soil conditions.

This suggests that differences between tree species may be greatest at the thicket stage when a dense and low closed canopy with heavy litter fall exerts maximum influence on the site. The dry weight of ground vegetation was zero in Norway spruce, Serbian spruce, western hemlock and grand fir and very low in Corsican pine, Douglas fir and red oak at or just after the thicket stage (Figure 3.6); the number of species was also low in the spruces, western hemlock and grand fir but increased later (Figure 3.7). Ovington (1955a) thought that at Abbotswood, where his results were for stands mostly 47 years old, the ground vegetation had "remained abundant" under the broadleaves in the thicket stage but "had been completely destroyed" under all the conifers, including European larch, except in a gappy plot of Norway spruce.

Figure 3.7

Number of species in the ground flora of Ovington's plots in 1952 (open columns; Ovington 1955a), 1974 (hatched columns; Anderson 1979) and 1981 (filled columns; Page 1981). Details of the plots as in Figure 3.6. The figure is the age in years in 1952; add 22 for age in 1974 and 29 for 1981.



3.2.2.2 Other British studies

Brown (1979b) and Brown, Pearce & Robertson (1979) found more species under coppice than on coppice sites planted with conifers although the reduction under conifers in the Midlands was sometimes less than in East Anglia. As an example of their results, in Dymock Forest (south-west Midlands) larch stands had 81% of the species number found in the coppice flora, Scots pine 82%, Douglas fir 76%, Norway spruce 73%. Beech caused a similar reduction in the ground flora to that of the conifers (see also Pigott 1989).

In plantations on ancient woodland sites in lowland England post-thicket stands of pine and larch were usually richer than those of spruce, Lawson cypress or beech on the same site (Kirby 1988). Differences in species number or ground vegetation cover between the pine or larch stands and remnant semi-natural oak stands on some sites were small.

In the Lake District coniferous and beech stands had fewer species under them than semi-natural oak stands on the same site. Barker (1985) found an inverse relationship between estimated percentage canopy cover for the different stands and their percentage ground flora cover.

In a survey of managed southern beech stands (Wigston 1983) the ground flora under the deciduous species was similar in number of species and cover to that of oak and richer than that of beech. Coppiced rauli (*Nothofagus procera*) was vigorous and suppressed the ground flora after five years. Evergreen species suppressed the ground vegetation, presumably by the heavy continuous shade and slowly decomposing litter.

Hill (1979) reviewed the ground flora in upland afforested conifer stands. Thicket stage spruces, firs, and western hemlock generally eliminated vascular plants and little vegetation reappeared before the age of clear felling. In pine and larch stands the cover of ground vegetation reached a minimum of 20-30% in the thicket stage but then increased, to almost 100% in some cases, towards the end of the rotation. Similar results were obtained by Hill & Jones (1978) who compared the ground vegetation under pre-thicket and thicket stage stands (mostly new afforestation) in 1944 and the same stands in 1976. In this case vigorous Japanese larch also eliminated the vegetation in the thicket stage, but there was a large increase in vegetation again at later stages in the rotation. The use of closely spaced larch for fire-belts (Hibberd 1986) is based on its reputation for rapid establishment and growth and the reliable suppression of at least the larger and more inflammable species in the ground vegetation.

Other comparisons that have been made between different crop species on the same site, e.g. Brewster (1974) appear to be consistent with the results above when allowance is made for pre-existing variation on the site or the effects of crop age.

3.2.2.3 Some other European work

Nihlgård (1970) in Sweden compared old stands of Norway spruce and beech (tree height 20-30m but age not given) on adjacent sites where the spruce had been planted on former beech ground. *Oxalis acetosella* was present with high frequency and cover under both beech and spruce, *Milium effusum* increased slightly, *Anemone nemorosa* and *Mercurialis perennis* decreased, and *Galeobdolon luteum* was eliminated under spruce. Nihlgård viewed the changes under spruce as a swing towards the vegetation found in "heath beech forests" with podzols and mor. However no information was given about the thicket stage in beech.

Rogister (1975) compared the ground vegetation in 68 year old planted stands of beech, pedunculate oak and ash/sycamore in Belgium, which were heavily stocked and very lightly thinned by British standards. The boundaries between the plots were sharp on the ground (just as Ovington (1955a) noted). Under beech the vegetation type was Milium effusum - Athyrium filix-femina with 38% cover and an average of 7.7 species; under oak, Holcus mollis - Rubus sp. (bramble presumably) with 92% cover and 9.0 species; and under ash-sycamore, Milium effusum - Galeobdolon luteum with 76% cover and 10.5 species. The differences seem to be mainly in the vegetation (the frequency and performance of the species) rather than in the flora; the species lists were similar apart from occasional absences, e.g. Stellaria holostea under beech, Hedera helix under oak, Pteridium aquilinum under ash-sycamore. The ash/sycamore group was actually one stand of ash/pedunculate oak/sycamore and two of sycamore/Norway maple. That stands dominated by ash or sycamore should have similar vegetation is puzzling given that sycamore comes into leaf about four weeks before ash (Salisbury 1921) and casts denser shade.

3.2.2.4 Grouping tree species by their thicket stage characteristics

The classification of tree species by their effects on the ground vegetation is probably best based on the characteristics of the thicket. Broadleaved species tend not to eliminate the ground vegetation (except perhaps beech or hornbeam) although the less shade tolerant species that flourish in the early stages die out as part of the normal fluctuation during the rotation. Larch may behave similarly but in some cases the ground vegetation can be eliminated. The spruces, firs and western hemlock normally have bare ground in the thicket stage but pines may not. Red cedar and Lawson cypress have such compact crowns, at least when young, that any gaps from the loss of individual trees are long-lasting and are more likely to carry some ground vegetation even though it is absent directly beneath the crowns. Douglas fir has been less studied: it strongly suppresses the ground flora but may not always eliminate it. (In a comparison of natural stands in Oregon there was a richer ground flora under Douglas fir than under hemlock (Stewart 1988)).

After the thicket stage the ground vegetation usually increases, notably under broadleaves, pine, larch and Douglas fir, but even, in terms of number of species, under Norway spruce and grand fir (Figure 3.7; Anderson 1979; Kirby 1988). However the crucial point is whether the vegetation is completely eliminated at the thicket stage. This determines the subsequent composition of the ground flora and hence its "quality" from the nature conservation point of view.

3.2.2.5 Behaviour of ground flora species

Many of the species that occur in the stands at some part of the rotation either have a seed bank in the soil or are vagrants, relying on long-distance seed dispersal. Most of these species occur in other habitats as well. They avoid the problem of the thicket stage by persisting in the seed bank or by their ability to re-invade post-thicket stands from elsewhere.

In contrast the woodland species of most interest to nature conservation tend to be those rarely abundant in other habitats and which are characteristic plants of the later stages of the rotation. These shade tolerant, "true" woodland species are the persisters. (See 5.4.3 for further details of this way of classifying the ground flora,

Bierzzychudek (1982) for a general review of life histories and demography of some shade-tolerant temperate forest herbs, Grime, Hodgson & Hunt (1988) for a discussion of life-strategies in plants generally and Reader (1989) for problems with the approach.)

The characteristics of the persisters are that they all appear as green plants for at least part of each year of the rotation; most do not have a seed bank (but a few do, e.g. bramble); and most are poor at colonizing suitable areas. There is a weak link or links somewhere in the chain of seed production, seed dispersal, germination, and establishment of the seedling, especially among existing vegetation.

The persisters survive in semi-natural woodland which largely consists of deciduous broadleaves. (Holly and box are only important locally while the only extensive semi-natural conifer woods of Scots pine are characteristically very open.) They are less likely to be present on rides because they survive competition best in the shade of a shrub or tree canopy. In some species individual plants are potentially as long-lived as the trees above them (Inghe & Tamm 1985). Although they can survive several rotations of trees, the thicket stage of densely shading species such as spruce may go beyond their shade or moisture tolerance. Hence they are eliminated.

Unlike the species of more open conditions that are regularly eliminated even under broadleaved thickets they cannot return easily afterwards. There is no seed bank and they appear to be poor at colonizing.

Much of the work on the apparent colonizing ability of species is inferred from comparisons of the flora of ancient and recent woodland. While lists of possible ancient woodland indicator species have been compiled, less has been done on the mechanisms behind the differences in observed distributions (Rackham 1980; Peterken 1981). Not all persisters are ancient woodland indicators and not all ancient woodland indicators are persisters. Species that are normally poor colonists may spread under the right conditions (Rackham 1975; Webster & Kirby 1988).

Sanicula europaea, which rarely colonized woods in central Lincolnshire (Peterken 1974), is abundant along the path through the recent woodland of the Triangle of Hayley Wood, where it was probably spread by the hooked fruits adhering to botanists' clothing (D.E. Coombe, personal communication). There are regional differences in the behaviour of the persisters, even within eastern England (Rackham 1980) and certainly within the British Isles (Gibson 1988). Oxalis acetosella is strongly associated with ancient woodland in central Lincolnshire (Peterken 1974) and East Anglia (Rackham 1980) but occurs in the north and west in suitably moist or shaded habitats outside woodland (Packham 1978). It was found under Japanese larch by Sakura, Gimingham & Millar (1985) but not in the adjacent heathland. Oxalis sets seed freely but is not known to form a seed bank in Great Britain. (In Scandinavia its seeds have been found in the soil on some sites (Staaf, Jonsson & Olsen 1987).) The seeds are discharged explosively from the capsule and travel up to one metre away from the parent, but are sticky and could be further dispersed attached to dead leaves or perhaps to an animal; and seedlings are commonly found (Packham 1978). Would Oxalis be permanently lost from a stand after one inimical thicket stand? Perhaps in eastern England, but not necessarily elsewhere.

3.2.3 The ground flora under mixtures of tree species

3.2.3.1 Under mixed plantations

Most work in the U.K. on the effects of planted tree species on the ground flora has been done in pure stands, but Brown (1982) gave brief results for the 25 year old mixed stands at Gisburn (an afforestation site). Scots pine, Norway spruce, sessile oak and alder were planted, pure and in all two-species combinations. The mixtures consisted of groups of 18 trees alternating in each direction with groups of the other species. The ground flora was recorded within an 18-tree group of each of the canopy species in stands pure or mixed with each of the other tree species.

In general the pine, spruce and oak canopies had similar ground vegetation with increasing cover and number of species from spruce to pine to oak. Agrostis tenuis and Deschampsia cespitosa were associated with the alder canopy as were increased frequencies for the bryophytes Eurhynchium praelongum, Lophocolea species and Rhytidiadelphus squarrosus, presumably connected with the nitrogen-fixing ability of the alder. There were some interactive effects of the mixtures, mostly with pine: the presence of pine as the admixed species was associated with the occurrence of Agrostis tenuis and Deschampsia cespitosa under oak and an increase in the frequency of these species under alder. Pine was also the species which produced marked interaction in tree growth with spruce, probably through its litter and nitrogen cycling (2.2.8).

There is no information as to whether such interactive effects would apply in plantations on existing woodland sites.

In mixed 32 - 38 year-old stands consisting of alternating bands of oak and Norway spruce in Salcey Forest, Northamptonshire, there was much higher cover and number of species in the ground flora under the oak than the spruce (Figure 3.8; Kirby 1988). Casual observations in British mixed plantations suggest that the influence of the conifers is much greater than the proportion by number of stems because the conifers, especially Norway spruce when mixed with oak, grow more vigorously and have a greater lateral spread. Vigorously growing conifers also produce more litter than the slower-growing broadleaves.

3.2.3.2 Under natural stands

In near-natural forest there is much heterogeneity at the microsite level (pits and mounds after windthrow, logs, tree bases, boulders, soil disturbed by animals) which allows more opportunities for ground flora species of differing requirements to survive in a stand (Beatty 1984; Bratton 1976; Hicks 1980). Subject to effects of the scale of the mixture, a range of tree species adds to this heterogeneity in the stand and may allow more species to flourish in the ground flora, because tree species differ in their shade and litter, especially a conifer among broadleaves (Beatty 1984); in stemflow (Crozier & Boerner 1984); and in phenology of leafing (Brewer 1980). (See also 5.2.1.3). Trees also vary in their life span: birch or aspen in mixture with oak will die first and so gaps occur earlier than in a pure oak crop.

In North America stands containing hemlock (Tsuga canadensis) generally had fewer species of herbs than mixed stands without hemlock (Glenn-Lewin 1975). On the other hand, in a similar forest type, Beatty (1984) showed that, while pits and mounds from windthrown trees produced a fine-scale variation in the soil properties and vegetation, this pattern was obscured if hemlock was in the canopy. Sites with hemlock had notably altered soil properties.

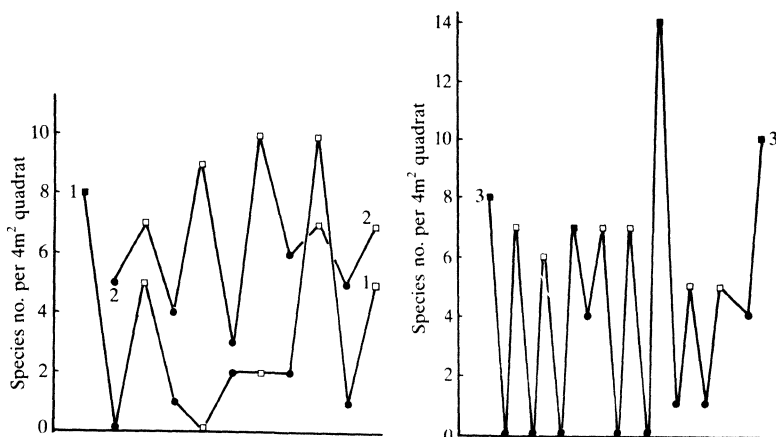


Figure 3.8 The ground flora under alternating bands of oak and spruce. Variations in species number per 2x2m quadrat along transects through alternating bands of 135 yr old oak (■), young spruce (●) and young oak (□) at Salcey Forest (Northants.). In transect one the spruce/oak mixture is 38 years old, in transect two 36 years old, in transect three 32 years old.

Crozier & Boerner (1984) examined the soil and vegetation in 1m radius plots around the bases of the seven most abundant trees and in control plots at least 2m from a tree trunk but not in a canopy gap, in mixed broadleaved forest in Ohio, undisturbed by Man since 1900. The main differences were associated with white oak and American beech. Of the seven species sampled the stemflow of white oak was the highest in calcium and sulphate and the lowest in hydrogen ions and the soil at the base of the tree was consequently higher in calcium and sulphate and with a pH up to two units higher than the control areas. The vegetation was noticeably different around the base of the white oaks. Geranium maculatum was more abundant and closely correlated with the concentration of calcium in the soil. Around the bases of the American beech the soil pH was lower and there was a slight change in the vegetation.

A local concentration of more acidophilous species (Deschampsia flexuosa, Luzula albidula, Maianthemum bifolium, Mnium hornum) was found around the bases of beech trees in the limestone districts of Germany and there was a close correlation between the direction of water flow off the trunk, soil pH and species distribution (Ellenberg 1988; Wittig & Neite 1985). The localized occurrence of Mnium hornum and Polytrichum formosum around the base of beech in Great Britain could similarly be due to acid stemflow although these mosses may benefit from reduced competition from higher plants and more moisture in such situations.

In mixed broadleaved forest studied by Brewer (1980) American beech and sugar maple increased their dominance over a 50 year period at the expense of less shade-tolerant trees, some of which came into leaf up to one month later than sugar maple. Accompanying this was a shift in the ground flora towards spring ephemerals and away from species whose life histories were such that they could not evade the effects of the increased spring shade.

3.2.4 Bryophytes

Tree species probably influence the ground-living bryophytes through their shade and litter with the thicket stage being the crucial one for any poorly-dispersed species. The effects on bryophytes of grazing and the shading by the vascular ground vegetation, and how that depends on the shading by trees and shrubs, are complicating factors.

3.2.4.1 Effects on common ground-living species

Ground-living bryophytes tend to be tolerant of deeper shade than vascular plants, but are more restricted to or thrive only in sites with a damp substrate and high relative humidity. They are less affected by the properties of the mineral soil because they often grow on litter, rocks and stumps (Hill 1979). In some old North American conifer stands the moss layer makes a significant contribution both to the ground layer biomass and nutrient cycling (Binkley & Graham 1981; Long & Turner 1975). This is true also for some western oakwoods in Great Britain (Rieley, Richards & Bebbington 1979; 2.1.6).

The number of species and cover are often inversely related to those of vascular plants so that bryophytes reach their maximum cover in the thicket and early pole stages, but decrease if vascular plant cover increases at later stages (Hill 1979). The greater number and cover of bryophyte species under old Norway spruce compared to beech stands (Nihlgård 1970) may arise as much from the differences in the ground vegetation of vascular plants as from the direct effects of shade and litter from the trees.

Hill (1979), Hill & Jones (1978), Nihlgård (1970) and Ovington (1955a) found no obvious close associations of bryophyte species with particular tree species. Bryophytes occurred wherever conditions were suitable, because of the stage of the rotation, the stocking or the presence and vigour of the ground vegetation.

Large accumulations of litter may inhibit growth of some Dicranum species (Briggs 1965). Johnsen (1959) found a marked increase in bryophytes and lichens (from four mosses and two lichens with 1% cover to seven mosses, two liverworts and seven lichens with 19% cover) in 60 year old stands of loblolly pine where the litter had been raked off every other year for 20 years. In these pine stands with no vascular ground vegetation the low abundance of bryophytes and lichens is probably because of the thick litter. Spruce litter may be less smothering than broadleaved litter (Hill & Jones 1978) because the needles are smaller and fall over a longer season, and members of the Plagiotheciaceae may be particularly favoured by coniferous litter. The physical properties of the litter are probably as important as the chemical composition which parallels work on the vascular ground flora (3.6.3.2; Anderson 1979; Sydes & Grime 1981a,b).

3.2.4.2 Bryophytes as ancient woodland indicators?

In the above studies most of the species found tended to be common ones with good dispersal powers. In the study by Nihlgård (1970) most of the species (16 species with high frequency, and 18 others) must have arrived and established late in the rotation since only Lophocolea heterophylla and Plagiothecium species were found in the densest thickets of Norway spruce. There are however bryophyte species which have a much more restricted distribution, both regionally and in terms of their habitat requirements, particularly the "Atlantic" species found mainly in western Britain.

Ratcliffe (1968) suggested that some of these species only survived in woods never completely felled, i.e. that they could not persist in the open conditions in the early states of the rotation. Such primaeval conditions can exist in Great Britain only in gorges and so Edwards (1986) proposed that if the bryophyte habitat was good enough (moist, with suitable substrates such as logs, tree bases, coarse-grained sandstone) then even these species might persist provided regeneration was fast and not delayed by grazing. In sites marginal for these bryophytes a continuous tree canopy became essential for their survival. It is very unlikely, however, that such species can survive under a conifer stand with the greater levels of habitat disturbance and canopy opening usually associated with modern forestry practice. A Swedish study found that the bryophytes of specialized habitats were the ones missing from managed, compared to primaeval, forests (Gustafsson & Hallingback 1988). Preliminary work in Argyll suggests that, as in North Wales, ancient woodland is richer in Atlantic bryophyte species than those woods of more recent origin (B. Averis personal communication).

In Cambridgeshire ancient woods tend to have more bryophyte species than recent woods, and the bryophytes in recent woods tend to be the undemanding, widespread species found in other habitats besides woodland (Birkinshaw 1985). The limitations of Birkinshaw's survey prevented the identification of indicator species. Birkinshaw also recorded bryophytes in transects across the ancient-recent boundary in Hayley Wood. Only a few species seemed to be invading the recent woodland, but this was not necessarily because they were poorly dispersed since the recent woodland contained more leaf litter and so was less favourable for bryophytes.

3.2.5 Epiphytes

Rose (1974) stated that "no bryophyte epiphytes appear to be strictly host-specific". However epiphytic bryophytes and lichens have strong associations with particular tree species through the differing physical properties (texture and water-holding capacity) and chemical characteristics (especially pH) of the bark (Barkman 1958; Table 3.2). Bates & Brown (1981), for example, found considerable differentiation in the epiphytes of oak and ash. The variation was best correlated with bark pH, which was on average higher for ash than for oak, but the ranges overlapped. These bark properties themselves vary on the tree from twigs to trunk, so that zonation of lichens occurs on a tree (Coppins 1984; Harris 1971), and they may change with time. Some lichen species, more or less confined to one tree species in the New Forest, are known to occur on a wider range of trees in other regions with a climate more favourable to epiphytes (Rose & James 1974).

The 43 species of epiphytic bryophytes (4.5% of the total bryophytes for the British Isles) and 303 species of lichens (22%) for oak (Table 3.2) reflect its favourable bark texture, the general prevalence of oak and its occurrence as large, old trees (Rose 1974).

Introduced tree species such as sycamore can be good lichen hosts when present as large trees and the mature beech in Great Wood, Borrowdale, (well outside the native range of the tree) is noted for its unusual lichen assemblage. Wigston (1983) found considerable variation in the southern beeches (*Nothofagus* spp.), varying from poor to very rich epiphyte cover. In general roble had more species and cover than rauli. Conifers, particularly in the south, have poor epiphytic floras presumably because of the more acid bark, usually more heavily shaded

trunks and branches (Rose 1974; Rose & James 1974) and their shorter life spans in managed stands.

Table 3.2 No. of species of lichens found on different tree species (Harding & Rose 1986; updating the list in Rose 1974).

Tree species or genus	Number of species of epiphytic lichens
oak (2 species)	326
ash	265
beech	213
elm	200
sycamore	194
willows	160
hazel	162
birch (2 species)	134
maple	101
alder	116
holly	96
lime	83
hornbeam	44

Large old trees which have always had a suitable aerial environment (the correct degree of shade and humidity) are likely to have the highest cover and number of species of epiphytes. Even some species of epiphytic moss such as *Orthotrichum* spp. and *Leucodon* spp. may require quite high levels of light. There is also a specialised lichen flora associated with the lignin of standing dead trees and dying timber (particularly in the native pine stands) - "bleached bones" habitat. However, more than any other group, the distribution of lichens over much of the country is affected by aerial pollution (Fry & Cooke 1984). Acidic precipitation may limit some species now to trees such as ash or elm with an inherently better buffered bark than oaks of similar age (R.G. Woods, personal communication).

3.2.6 Effects of tree species on the ride flora

Brown (1979b) sampled the rides separately in coppiced areas and areas planted with conifers in southern East Anglia, but presented the results reclassified into managed (metalled, concreted or mown) and unmanaged rides (3.4.1). The implication was that the managed/unmanaged division was much more important in explaining the differences in the ride flora than the character of the neighbouring stands provided that the rides are wide enough not to be shaded by the adjacent crop.

3.3 The effects on the flora of a change in stand structure

3.3.1 Trees and shrubs

When stand structure is changed from coppice or coppice with standards to high forest there is a slow sorting out of the existing species by speed of growth and stature, so that for example ash poles in a coppice are likely to self-thin and contribute to a tree canopy whereas hazel tends to be shaded out by larger trees (Peterken 1981). The early stages of this process can produce the two-size coppice

described by Rackham (1975). Species not favoured by coppicing, such as beech, may ultimately increase in importance. (This is also true for beech in oak/hornbeam woods in central Europe (Ellenberg 1988).)

The pecking order of tree and shrub species in the change from coppice to high forest varies from site to site. It depends on the initial composition and whether other species have a chance to invade. Rackham (1980) has remarked on the great increase in birch in the last century in East Anglian woods because of its high seeding capacity. Watt (1934) discussed differential species regeneration in the Chilterns and Pigott (1985) the effects of voles on lime regeneration. Exceptional events that act selectively against particular species, for example the effects of the 1976 drought on beech (Peterken & Jones 1987) or Dutch elm disease, also shift the balance.

Silvicultural treatments normally favour species with good timber potential (oak, beech, ash, chestnut) over others (maple, hornbeam, lime) even though these latter species are capable of forming trees. Shrubs such as elder, blackthorn, hawthorn and Ribes species are tolerated provided they do not interfere with the growth of the crop species or with operations in the stand.

Both these effects were involved, but cannot be separated, in a comparison of coppice with standards and high forest in Lorraine, France, (Becker 1978, 1979). In the tree layer, pedunculate oak and hornbeam were more abundant in the coppice with standards area, whereas beech was more important in the high forest. In the understorey and shrub layers, pedunculate oak, small-leaved lime, hornbeam, wild service tree, hazel and Cornus mas were found in the coppice with standards, while Norway maple, sycamore, wych elm, ash, Daphne mezereum and beech were the main species in the high forest. Beech coppiced poorly (and apparently was not often selected as a standard) so was not favoured by coppice with standards treatment, but was preferred in the conversion of the stands to high forest.

Further selection stages occur each time a high forest crop is felled and regenerated. In worked coppice the composition is more or less fixed by the population of stools on the site (plus occasional recruitment from maiden stems, minus occasional stool deaths) whereas the composition in high forest is potentially much more dynamic, even if only natural regeneration is considered. The size of the gaps, seed supply, competition from the ground vegetation and the effects of grazing or browsing all influence which species grow up in any one place.

In the USA Hix & Barnes (1984) found that hemlock was virtually absent after clear felling whereas it dominated adjacent unfelled stands. In cove hardwoods in West Virginia clear felling produced stands with a high percentage of shade-intolerant species; selection felling favoured shade-tolerant species such as sugar maple (Trimble 1965). Similarly group selection (average gap-size 2000 square metres, about 50m across) in New Hampshire hardwood forests allowed intermediate and shade-intolerant trees to maintain their place in the stand at about 25-35%, but single tree selection led to shade-tolerant species coming to hold 92% of the canopy individuals (Leak & Filip 1977). Areas which are clear felled can therefore sometimes hold a greater range of woody species than selectively felled areas (Smith & Miller 1987). To mimic the original species composition of the northern hardwoods region a mixture of felling systems from single tree selection to clear fells would be needed (Runkle 1985). Regeneration in natural gaps in North American forests has long been studied, e.g. Bray (1956) and the principles involved could be extended to British woods.

In Great Britain the minor species components of the tree and shrub

layer (e.g. lime) are most at risk from these fluctuations in a high forest system. They are often of high nature conservation interest, because they are characteristic of particular tree and shrub communities, but of low interest to foresters because their timber properties are poor, their growth rates slow, or they occur in too small quantities to be worth marketing. Some shrubs may have been more species of the woodland edge in natural forests.

3.3.2 Ground flora

Comparisons of the effects of different high forest systems on the ground flora within the stand are difficult to find, but in part may be deduced from the response to gaps of varying sizes, or intensities of felling (3.4; 5.4.1).

3.3.2.1 Observed differences between coppice and high forest stands

Coppices are frequently associated with a richer and more abundant ground flora than is found in high forest. At the scale of a whole wood, coppices tend to have stands at all stages of the rotation and are usually of mixed species so producing a diversity of conditions in which many ground flora species can thrive (Rackham 1976). Species that rely for their survival in a wood on spread from one suitable stand to the next are more likely to always be able to find areas at the right stage in the rotation.

However, even in individual stands there may be a difference between high forest and coppice. Salisbury (1924), concluded that, in Hertfordshire, on the same soil and under the same tree species the ground vegetation was usually more abundant under coppice than high forest. Coppice with standards was intermediate: closer to coppice if there were few standards and closer to high forest if there were many standards over scanty coppice. If the coppice rotation was long the ground vegetation tended to become sparse, more like that under high forest (Salisbury 1916a, p.97).

Barker (1985) compared neglected oak coppice on acid soils with oak high forest in the Lake District. The high forest plots were the less shaded and the coppice plots had fewer species (a reversal of the usual pattern). There was a higher proportion of shade-tolerant species in the coppice, more bryophyte cover (37% compared to 17% in the high forest) and higher litter cover. Brown (1979b) and Brown, Pearce & Robertson (1979) also found fewer species under neglected than worked coppice. Both shade and woodland margin species were affected.

Differences in the ground flora between coppice with standards and high forest were found in a large continuous block of forest in Lorraine (Becker 1979) although many species were apparently indifferent to silvicultural treatment. The coppice (oak, hornbeam, small-leaved lime) was cut on a 30 year rotation and was densely stocked with about 2,500 stools/ha and 120-140 standards/ha (oak, hornbeam) of a range of ages and sizes (M. Becker, personal communication). The high forest was predominantly of beech, converted from previous coppice with standards. Hence the ground flora was probably also responding to the different species forming the tree and coppice canopies. For example three of the species associated more with high forest in Lorraine flourish under coppice in the U.K.: Anemone nemorosa, Galeobdolon luteum, Primula elatior.

3.3.2.2 The differing light regimes in coppice and high forest

When leafless the horizontal branches of trees may cast more shade than the near-vertical stems of coppice, thus increasing the shade at the critical time in the spring when the ground flora makes most growth (Salisbury 1924; Figure 3.9). More significant is probably the "periodic impetus" (Salisbury 1916a) given to the ground flora by coppicing. The shorter rotation means that the ground flora has to survive many fewer years under a closed canopy between the periods of open conditions after cutting.

For the shade-tolerant species which persist, usually with reduced flowering, as green plants throughout the rotation the open conditions after harvesting allow increased growth, flowering and opportunities for the establishment of more individuals. Perhaps these shade-tolerant plants are really at their limit under a closed canopy and live off their reserves which slowly decline, over decades rather than years.

Barkham & Hance (1982) constructed a computer model of a population of Narcissus pseudonarcissus using figures based on field observations. Alternate five years of open conditions and five years of shade, roughly simulating a coppice cycle, allowed this species to be more abundant than either constant shade or constant open conditions. Other characteristic plants of coppices might show similar population dynamics.

3.3.2.3 The importance of the seed bank for marginal species

Many of the species of woodland margins and glades are present as a seed bank which can survive at least 30 years (Brown & Oosterhuis 1981). This seed bank is renewed by the burst of growth and flowering of these species that follows felling or coppicing. Thus there are two populations, the plants growing in the site and the seeds in the soil (Livingston & Allesio 1968; Solbrig, Newell & Kincaid 1980), and each contributes to the other. Considerable differences may exist between the two (Anderson & Carter 1988; Kramer & Johnsson 1987). (By contrast Granstrom (1982) found that a persistent seed bank was not a common survival strategy among the ground flora species in boreal forests.)

Chancellor (1986) and Hill & Stevens (1981) suggested that seeds have a definite life span (a slow decline in numbers followed by a steep decline at the end of the life span) which for woodland species may be generally between 50 and 100 years. The topping up effect of a coppice rotation of 10-20 years is probably significantly greater than that of a high forest rotation of 80 years or more (Harris & Kent 1987b; 3.4.2.3).

3.3.2.4 Trampling and ground disturbance

The effect of increased light, temperature or throughfall is often assumed to be the major factor in the greater richness of coppice woods compared to high forest. However there is also more regular ground disturbance and trampling which affects different sites and communities in different ways. Damage may occur at quite low levels of trampling (Leonard, Conkling & McMahon 1985). The dominance of species such as Allium ursinum (Ernst 1979), Endymion non-scriptus (Peace & Gilmour 1949) or Mercurialis perennis may be temporarily reduced and so allow other woodland species to establish.

In natural forests a similar effect may occur through tree falls: Thompson (1980) noted that a linear transect of more diverse herbs developed along the line of a tree fall through an otherwise monospecific patch of Asarum canadense. However there could also have

been some nutrient enrichment from the rotting log at this point (2.1.3). Disturbance of the soil from animals such as wild boar certainly does lead to changes in the ground flora (Falinski 1986).

3.3.3 Bryophytes and epiphytes

3.3.3.1 Bryophytes

Many bryophytes are sensitive to desiccation. The more regular opening up of the canopy under a coppice regime compared to high forest may discourage their spread, although large coppice stools provide suitable microsites for some species. Rackham (1975) noted two mosses and four liverworts as occurring on stool bases.

Birkinshaw (1985) sampled the bryophytes in Hayley Wood on the lowest one metre of standards in each of seven plots, last coppiced 1, 3, 8, 10, 12, 15 and about 100 years ago respectively. Significantly fewer species (6 against 11), occurred to a lower maximum height (31 against 115cm) and with less cover in the recently coppiced plots compared with the 100 year old plot. No significant recovery over the 15 year age-range of the coppiced plots was detected, probably because recovery was irregular and varied with the particular plot and the weather during the first few years. The exposure of the trunks of the standards for several years after coppicing may discourage bryophyte growth, as would the selection of standards of good form with fewer of the irregularities that produce uneven stemflow and moisture-retentive hollows.

Within high forest stands the retention of dead fallen logs is particularly important for bryophytes. Fifty-five species have been recorded from such sites in the Bialowieza National Park (a fifth of the total from the area) (Falinski 1986). Large fallen logs are much more valuable as habitats than small ones because they are less readily overgrown by the ground flora and retain more water which enables drought sensitive species to survive (Soderstrom 1988). Rare liverworts growing on logs were the main feature distinguishing the bryophytes of virgin from managed stands (Gustafsson & Hallingback 1988; 3.2.4.2).

3.3.3.2 Lichens

Lichens tend to be favoured by open, long-rotation high forest and wood pasture (where regular pollarding prolonged the life of the individual trees) rather than by coppice or short-rotation high forest. Coppice woods in particular have very reduced lichen floras (Rose 1974). Generally only widespread lichen species occur in coppice with standards; the species characteristic of old broadleaved woods tend to be absent. Coppicing leads to large fluctuations in shade and humidity on the bark of the standards and, in addition, most standards would traditionally have been felled while still quite young, so that there has not been a continuity of large old boles in many of these woods.

In the oceanic and pollution-free conditions of western Scotland it might be expected that epiphytes would depend less on undisturbed stand structures. However, Gilbert (1984) attributed large differences between patches of hazel scrub to some having been more disturbed in the past. Long continuity of woodland cover may still be essential because some species depend on the nutrient content of runoff from the leaves. This combined with a poor dispersal capacity, would explain why they might be lost and not return following disturbance.

3.4 The effects on the flora of a change in woodland structure

3.4.1 Roads and rides

Creating roads and rides in woods previously lacking open spaces introduces a new set of species to the woodland flora, just as failure to maintain such habitats may lead to their loss. In Bedford Purlieus only about 200 of the 432 vascular plant species might be present if the site were completely occupied by closed canopy stands (Rixon & Peterken 1975). Brown (1979b) and Brown, Pearce & Robertson (1979) found that the rides on acidic sites were as rich as, and on base-rich ones markedly richer than, the richest, young coppice stands. Managed rides were richer than unmanaged ones, with the loss of one or two shade species more than balanced by acquisition of more marginal or ride species. Part of the richness of the ride flora was probably because of the higher soil pH, almost always about one unit higher than in the adjacent stands. Similar results were found by Hill (1979) especially where the roads were surfaced with limestone (2.4.2). Roads and verges may also serve as routes for the spread of invasive species into large forest blocks (Falinski 1986).

Management is the key to maintaining the nature conservation interest of rides and managing existing rides is preferable to creating new ones (Peterken 1981). This is particularly important where the rides contain unimproved grassland or heath that is now rare in the surrounding countryside. Ride management to maintain both shrub and ground flora is discussed by Anderson & Carter (1988) and is generally linked to the conservation of invertebrates, especially butterflies (4.2.4; 4.3.4.2).

3.4.2 The effects of selection systems: the Bradford plan

Harris (1986, and some results published in Harris & Kent 1987a,b) compared the floras of the clear felling system and a type of selection forest - the Bradford-plan stands on the Tavistock Woodlands Estate in Devon. The Bradford-plan (B-plan) or continuous-cover forestry was designed by the late 6th Earl of Bradford and his estate forester P.A. Hutt as a geometrically controlled selection forest (Harris & Kent 1987a; Hutt 1974; Figure 1.6) although Pryor & Savill (1986) classify it as a group-felling system (1.3.3).

3.4.2.1 Effects on shrubs

There were more species of shrubs and more individuals with B-plan management compared to clear felling (Harris 1986). They occurred mainly on the edges - of which there were plenty in the B-plan system - of subunits, racks and rides. However most shrubs were cut back during tending operations and cut out altogether at some stage if they interfered with the crop.

3.4.2.2 Effects on the ground flora

The ground flora was sampled with 100 x 50 cm quadrats in B-plan subunits of known age. The number of species per quadrat decreased slightly from 6-7 in the first year to 5 at 20 years. Results from even-aged stands of different ages in the same woods showed similar trends which suggests that the individual sub-units did behave like larger even-aged stands (Harris & Kent 1987a). (Low numbers of species

in individual quadrats tended to occur where one species such as bramble was very abundant and dominated the quadrat (3.1.3.3.) Both mean and total abundance increased sharply from year 1 to year 2 and then decreased steadily to year 20 (Harris 1986).

The marginal, light-demanding or disturbance-requiring species such as Digitalis purpurea or Holcus lanatus occurred only in B-plan subunits 1-2 years old. Hypericum pulchrum and Teucrium scorodonia occurred in subunits up to 8 years old. The more shade-tolerant species such as bramble and honeysuckle were found throughout the B-plan unit. A few species, including the ferns Athyrium filix-femina and Blechnum spicant, tended to occur more in subunits older than 5 years (Harris & Kent 1987a).

3.4.2.3 Changes in the seed bank

The seed bank in B-plan subunits of different ages contained seeds of species which had flourished earlier in the rotation on that particular spot (3.3.2.3) and with age the number of species in common with the current ground flora declined (Harris & Kent 1987b). A comparison was made between seed banks in neglected oak coppice last cut 66 years ago and in Douglas fir planted in 1950 (probably replacing coppice) and subsequently partly replanted with B-plan subunits created in 1961, 1967, 1973 and 1980. The seed bank in the neglected coppice had declined drastically, as expected if the life span of many seeds is between 50 and 100 years (Hill & Stevens 1981), but there was a larger and more diverse seed bank in the Douglas fir stand, parts of which had been disturbed by the establishment of the B-plan subunits. This periodic disturbance had allowed the seed bank to be topped up over a wider area of the stand than just that felled and replanted, even though at the thicket stage of the rotation Douglas fir was less favourable for the survival of the ground vegetation than oak coppice.

3.4.2.4 Conclusions on the Bradford plan

The changes in the ground flora and seed bank in B-plan subunits of different ages were similar to those on a clear felled area with time (Harris & Kent 1987a,b). Under the B-plan the different stages, as 6 x 6m patches, are brought close together in space. However the young subunits are partly surrounded by much larger trees so are not as "open" as a clear-felled area would be. "After B-plan clearing the ground flora does not appear to respond with as abundant growth as after a clear-fell" (Harris 1986, p.265) perhaps because there was less soil disturbance and more shading. Honeysuckle and ivy which do not flower under a complete tree canopy also did not flower in young subunits, which suggests that they need a larger, open area than 6 x 6m (Harris 1986, p.275, p.277). A benefit of the small areas treated each time may be that more sidelight can reach the centre of stands. With only nine trees on a 6 x 6m subunit, thicket conditions may be limited to the central few square metres, assuming that all the trees survive.

The claimed similarity of the ground flora under the B-plan system and under coppice is because, in both, all the stages of the rotation are present close together: in the B-plan all the stages of high forest occur on one 18 x 18m unit. In addition both traditional coppice and B-plan management provide a large amount of edge in a given area. The same would be probably be true of a more irregular selection system. However selection systems and coppice differ in that the open conditions produced after coppicing are more extensive.

3.4.3 Other silvicultural systems

Metzger & Schultz (1981) examined the spring ground flora and shrub layer (from 15cm tall to 2.5cm dbh) in four stands of northern hardwood forest in Michigan 50 years after the start of different silvicultural treatments (Table 3.3). Stands A and B contained large amounts of even-aged regeneration as a result of the single harvest and stands C and D contained trees of all sizes after the periodic harvests every 10 to 35 years.

Table 3.3 Details of four silvicultural treatments in Michigan, USA, and their effect on the ground flora (Metzger & Schultz 1981).

Stand :	A	B	C	D
	all trees over 12 cm dbh clear-felled	all trees over 30 cm dbh clear-felled	Group-selection	Single tree selection
Stand	A	B	C	D
Initial basal area (m ² /ha)				
in trees >24 cm dbh	30	25	32	24
Basal area removed initially	30	21	14	14
Year felled	1927	1927	1929	1927
			3 rectangular groups	Over-mature and defective trees
Basal area removed later				
Year felled 1944			6	
			Groups enlarged	
1955			5	
			Selected trees felled	
1962				3
				Further trees felled
1966			6	
			Selected trees felled	
Basal area in 1966	7	19	14	17
Number of ground flora species	22	22	29	23

Seven species, including sugar maple seedlings, formed the consistent major component of the ground vegetation in all the stands. Stands A and B were the most similar with 22 species each, stand D had 23 species and stand C 29 species, five of which were found only in that stand. Only two species of the spring ground vegetation were not woodland species and these occurred, infrequently, in stand C. The recurrent disturbance in stand C allowed more chance for invading species to establish (or perhaps they came from a soil seed bank; 3.3.2.3). Stands A and B had more spring plants per square metre with more cover than C and D, but C and D had more shrub layer plants and cover.

Metzger & Schultz concluded that the differences in spring ground vegetation were minor and more quantitative than qualitative. There was a clearer difference in the structure of the shrub layer and ground vegetation: there was a restricted shrub layer under the clear felled

stands which now had a lower, denser and more uniform tree canopy, whereas the gaps from the periodic harvests in stands C and D encouraged the growth of shrubs and tree seedlings at the expense of the spring ground vegetation. Metzger & Schultz cautioned against extrapolation to the summer vegetation or to stands on different soil types.

In broadleaved forest in southern Ontario, Canada, Reader (1987) compared the loss of shrub and ground flora species in circular plots of 0.01, 0.05 and 0.20 ha either with no felling or with selective felling of 33% or 66% of tree basal area. There were small losses of species as felling intensity increased (statistically significant for shrubs, not significant for herbs). These tended to be the infrequent species. Plot size had no effect, but the number of shrub species lost was correlated significantly with the amount of disturbed mineral soil in the plot. Reader concluded that the most effective way of reducing losses during selective felling was by minimizing the soil disturbance caused by tree extraction. These results were only for the first year after harvesting and monitoring of the plots continues.

In Californian pine forests differences in vegetation structure, though not in frequency, of occurrence of species were found 40 years after a series of treatments of increasing intensity of cut, from no felling to complete clear fell. However Vora (1988) points out that disturbance to this type of forests were not uncommon prior to the treatments so that the flora may already have lost any sensitive species.

There appears to be no directly comparable work from Great Britain. At Sheephouse Wood (Buckinghamshire) preliminary data suggest that greater invasion of ruderal and grassland species occurred in a clear felled area in the first three years after the felling than in nearby group fells. However overall there was only a small difference in ground flora response between the centres of felled groups of 0.25 ha and a clear-felled area of about 3 ha.

3.4.4 The effects of coupe and stand size on plant diversity

Silvicultural systems vary in the range of gap sizes provided: large in clear felling, intermediate in group shelterwood or group selection systems and small (the area of the final size of harvested tree) in the selection systems (1.3.4; Figure 5.6). The size of the felling coupe usually sets the stand size for all subsequent stages.

By analogy with studies on whole woods (Game & Peterken 1984) and by sampling theory more plant species are likely to survive in a particular stage if it is dispersed as small patches through the wood than if, say, all the open ground is in one block. A series of small patches are more likely to span the range of soil variation within the wood and there is probably less risk that the whole of one stage will become dominated by a single ground flora species (3.1.3.3). However, this does not appear to have been tested in the field, either in worked coppice or high forest. (This principle of dispersion of age classes does not necessarily follow for animal groups which need minimum sizes of habitat patches and easy access between them; nor may it apply when considering areas for minimal intervention which should be as large and self-contained as possible.)

There is a limit to how far such sub-division of stands may be taken, as far as benefits to the ground flora are concerned. This limit occurs when there is no increase under the gap in the number of species and no increase in flowering or spread of the species already present.

Collins & Pickett (1987) created six gaps from 33 to 151 m² in area

in a stand 25-30m tall. The trees were felled and left in the stand so that there was minimal soil disturbance. They found little change in the ground vegetation over three years apart from a small increase in the number of species in the centres of the gaps, and no significant correlation between gap size and the environmental factors measured (PAR, air temperature, soil moisture, soil temperature, nitrogen mineralization). They concluded that these gaps were not large enough to produce marked responses in the ground vegetation.

Moore & Vankat (1986) recorded environmental factors and cover of ground vegetation in 15 gaps ranging in age from 0 (created that growing season) to 15 years and from 22 to 256 m² in current area. Their results suggested that two annual, spring and summer leafing species had increased in cover in young gaps (1-2 years) and then decreased. Spring leafing plants decreased in gaps or were unaffected. The young and middle-aged gaps (5-7 years) received markedly higher amounts of PAR in the summer, when the trees were in full leaf, and had higher soil moisture levels during the summer drought, than the old gaps (12-15 years) or the control areas under the intact tree canopy.

Thus if all the gaps are very small, as in a selection system, some of the open phase flora is likely to be eliminated more or less permanently from the stands. Similarly any change in the woodland structure that leads, albeit temporarily, to the loss of other growth stages from the site depletes the populations of those species that are relatively most abundant at that stage. Birch (1979), for example, found that some ground flora species were less frequent in a series of samples from native pinewoods than in nearby young pine plantations. The appropriate growth stages for these "missing" species were absent from the native pine stands because of past suppression of regeneration. Hence the distribution of growth stages in a normal forest (in the forestry sense) provides most opportunities for retaining the widest range of species on a site.

These examples show some of the complexity of plant responses to gaps and the conflicting, or site-specific, results that can be obtained. The selection and measurement of the environmental factors relevant to plant growth in gaps is conceptually and technically difficult. The area of ground not vertically covered by tree canopy provides a repeatable and comparable method of measuring the size of gaps but this is rarely directly relevant to plant responses. The area of increased illumination for example includes a zone to the north of the gap (in the northern hemisphere) which receives increased side-light. Gaps are an active topic in ecological research in forests in North America and the tropics (Pickett & White 1985) and results should become available that can be applied to assessing the effects of the gaps created by silvicultural systems (5.4.1).

3.5 The effects on the flora of changes on the site

The forestry literature contains numerous papers on site preparation and the control of weeds (both herbaceous and woody) but almost always from the point of view of the tree crop. For example Stewart, Gross & Honkala (1984) summarize 260 American papers on the effects of weeds on trees. By contrast there appear to be no comparisons of the flora in naturally regenerated and otherwise similar planted stands in the British Isles.

3.5.1 Treatments to achieve natural regeneration

Natural regeneration means only the restocking of a stand without planting trees, in the case of high forest from the natural seed fall in the stand. However, the term carries with it a host of associations so there is much scope for misunderstanding between those involved primarily with commercial forestry or with nature conservation.

From the forestry point of view natural regeneration is not necessarily an easy or cheap option, but often requires a large investment in management time and skilled operations to obtain adequate stocking of the wanted species within a reasonable time. These operations include fellings, usually in two or three stages several years apart; soil cultivation and control of ground vegetation if necessary, e.g. by disc harrows; cutting racks for access once the regeneration has come; and careful cleaning to encourage the growth of the wanted species. The French often go at this hammer and tongs in order to obtain oak stands, with beech and hornbeam tolerated as an understorey to keep the oak free of epicormics (Everard 1987; Lanier 1981).

The disturbance to the soil, flora and fauna by these operations to obtain satisfactory natural regeneration can be similar to that of plantation management. While there is always the benefit of maintaining a local genetic stock, how much ancillary activity is acceptable? Unless owners and managers are prepared to wait the extra time for adequate regeneration to occur without preparation, which on some sites could be decades, a balance must be struck between extensive ground preparation for regeneration and possibly less disturbance if low density planting is used.

There is a need for better guidance on how to get good regeneration of native species in Great Britain (Evans 1988).

3.5.2 Effects of site preparation on the existing trees and shrubs

The native tree and shrub community on a site is part of the value of the site in nature conservation terms. Coppicing is frequently promoted because it effectively maintains this community more or less as it was when coppicing began. Coppicing is relatively unnatural in that ground disturbance is minimal and the bulk of the regeneration comes from existing stools, although vegetative reproduction of trees under natural conditions does occur (Koop 1987). Greater fluctuation in the composition of the tree and shrub composition might be accepted for nature conservation purposes as long as it was fluctuation about the existing mean and not slow reduction and elimination of some species from the site (3.3.1).

Any thorough site preparation clears away non-crop trees and shrubs. Established trees or coppice regrowth interfere strongly with planted trees - they have a head start with established root systems - so that if not removed during site preparation they will have to be dealt with by later cleaning if timber production is a high priority.

The more the crop is favoured, the less scope there is for other native woody species except perhaps as an understorey or as a minor part of the canopy. It would not solve the problem but might make solutions easier to find if broad figures were set as to what are the acceptable limits for different objectives. For example, the minimum level for the nature conservation objective might be set at 80% of the canopy comprised of the native species for the site, of which 20% must be minor (poor timber) species; the minimum level for the commercial timber

production objective might be, for the same site, 80% canopy trees of timber species etc. These hypothetical figures illustrate one approach to the problem of identifying the extent to which objectives conflict.

3.5.2.1 Control of non-crop species

There are many papers about the methods, results and degree of success (in crop tree growth) of controlling unwanted trees and shrubs by hand, machine or chemicals in North America and Europe. MacLean & Morgan (1983) is a good example, atypical only in the 30 year span of results. Cleaning unwanted species from naturally-regenerated balsam fir/spruce stands in New Brunswick gave substantial increases in the volume of balsam fir, the main commercial species. Manual cutting of unwanted species in a one-metre radius around the conifers resulted in better growth of the balsam fir; the increases in height and volume increments of trees in the treated stand lasted for over 20 years. The spraying of 2,4-D/2,4,5-T herbicide produced a better species composition (many fewer broadleaved trees; balsam fir increased from 42% to 84% of stand basal area) but had only small effects on conifer growth. Lanteigne (1985), working in similar stands, concluded that cleaning by 2,4-D/2,4,5-T did not alter the direction of stand development but only accelerated it, with little effect on the ground vegetation. (These stands would in time develop naturally to balsam fir so that the best analogy in Great Britain might be elimination of birch in a birch-oak stand, not suppression of broadleaved regrowth in a conifer plantation.)

3.5.3 Site preparation and the ground flora

Ground disturbance, often by windthrow creating pits and mounds or by large mammals such as wild boar (Falinski 1986), is important in the regeneration of natural woods. Current forestry practice in Great Britain which uses planting to achieve adequate stocking of young maiden stems probably involves greater, in some cases very much greater, levels of disturbance than would occur naturally (in the absence of natural woods and wild boar this cannot be shown absolutely).

Site preparation usually adds to the disturbance of the soil and vegetation caused by harvesting (Reader 1987; 3.3.2.4). The relative abundances of species change, but the effects of site preparation are mixed with the changes resulting simply from the progress from the late stage of one rotation to the early stages of the next and are difficult to distinguish.

However, the effects of extraction, ground preparation and weeding are likely to be cumulative so that individual disturbances must not be seen in isolation. Forest herbs are now less abundant on felled areas in the Bialowieza Forest because of timber extraction and mechanization of soil cultivation (Falinski 1986). Gustafsson (1987) considered that the depleted floras in some energy coppices in Sweden was related to the intense cultivation and herbicide use. Serious long-term damage to the woodland flora can occur even from small-scale disturbance if small colonies of an uncommon plant, such as Paris quadrifolia, are disturbed or destroyed.

Various studies have compared different ground preparation techniques in plantations (particularly of pines) in the USA (Conde, Swindel & Smith 1986; Stransky, Huntley & Risner 1986; Ohmann 1984). The preparation methods used are frequently more severe (often including fire) than are currently practised in lowland British broadleaved woods

and a different suite of ground flora species are involved. The studies illustrate however that the effects of ground preparation treatments do differ according to the ground flora species considered (some treatments favour some species or groups of species, for instance grasses over shrubs if fires are too frequent) and that differences between treatments may be apparent for several years after initial establishment, in some cases up to canopy closure and establishment of the thicket stage (Hendry & Gholz 1986).

3.5.3.1 Soil disturbance

Increased disturbance to the site occurs if harvests (and subsequent restockings) are more frequent (i.e. short rotations), are more intensive or involve the use of larger machines (2.5.1). The disturbance may be locally severe, but unless it involves complete cultivation or large-scale windrowing of stumps, the ground vegetation is not likely to be completely or permanently destroyed.

More frequent or heavier disturbance favours the marginal, seed-bank species over the shade-tolerant ones because the open conditions in which the marginal species flourish recur more often; and the greater soil disturbance from machinery encourages more germination of seeds in the soil. The shade species, the persisters, which rely more on vegetative propagation are likely to be damaged more by increased disturbance.

For a given level of disturbance the disruption to the ground vegetation is worse, other things being equal, on wet than dry areas and in summer than in winter (when more of the plant is below ground). Luxuriant vegetation may suffer more, but probably also has the greater capacity to recover (Falinski 1986; 3.3.2.4).

3.5.3.2 Drainage

There is a delicate balance between the ground vegetation communities and soil moisture in an ancient, poorly drained woodland (Martin 1968; Rackham 1975). Several of the more interesting communities would be lost if drainage were improved. Rackham (1975, p.133) suggested that maintaining the existing drainage regime is a general principle for woodland nature conservation (2.5.2).

3.5.3.3 Fertilization

Applying fertilizers without weed control can increase the growth of the ground vegetation even more than the trees (Davies 1985). Usually the more vigorous species (grasses and bramble) benefit at the expense of many smaller species.

Grabherr in Ellenberg (1988) showed that the effects of a single fertilizer treatment including lime on an acid soil were still visible after thirteen years. Acidophilous species were reduced because of the increased competition from species more typical of base-rich or disturbed ground. The fertilizers, once applied are locked into the system because the timber harvesting removes few nutrients.

Liming stands of Norway spruce raised the pH by 3 units and changed the organic matter from mor to mull (Nihlgård 1970). The cover of ground vegetation doubled, with loss of a few species and gain of several others, and a large increase in the cover of the main shrub, Sambucus racemosa.

The whole character of the ground vegetation may be changed. From a mainly lichen flora, increasing levels of nitrogen fertilizer resulted

in the appearance in sequence of Agrostis tenuis, Rumex acetosella, Chamaenerion angustifolium, and Holcus lanatus (Miller *et al.* 1977) in a trial within the forest on Culbin Sands.

Few long-established woodland soils are likely to be as deficient in nutrients as Culbin, but phosphate enrichment often leads to rank growth of nettles and a few other species (Pigott & Taylor 1964; Rackham 1975). The corollary may be true: that the richest ground flora depends on a lower level of fertility especially of phosphate, or potassium (M.A. Anderson, personal communication).

3.5.3.4 Weeding

Weeding must eliminate competition for water and soil nutrients to be effective. This can be achieved by soil cultivation, herbicide application or mulching, but not by cutting off the above-ground parts of the weeds; indeed regular mowing of a grass sward around trees was worse than one cut in a season (Davies 1985; Potter 1988). It is not clear whether below-ground competition from broadleaved weeds is as important in long-established woods.

Any weeding practised for more than a year is likely to lead to a shift in the relative abundances of species in the vegetation, towards those able to recover quickly (e.g. grasses after cutting; seed-bank or wind-dispersed species on ground made bare by herbicides) or to plants resistant to the herbicide.

Dreyfus (1984) gave examples of the changes in vegetation after herbicide application on four soil types in France. The usual site preparation on these sites involved the removal of stumps and cultivation, and grasses were the main weed problem. About 50% of the total area was treated, with bands 1-1.5m wide (implying 2-3m spacing (5.6.4)). On untreated bands there was 100% cover of ground vegetation by the end of the first growing season after site preparation. On the treated bands the vegetation averaged only 40% cover, but was up to 80% in places. Rapid invasion of the bared soil occurred from the vegetation in the untreated band, which also accounted for the floristic similarity, although the proportions of the species were different (i.e. a change of vegetation rather than flora). Minko (1981) similarly found no long-term differences in the number of ground vegetation species in plantations of Monterey pine in New Zealand after herbicide application in bands along the rows.

Initial results from a herbicide trial in Bagley Wood (near Oxford) showed no significant decline in number of species per square metre two months after the plots were treated with glyphosate, but there were declines in overall species cover and invasion of treated areas by the annual Senecio sylvaticus (Watt, Kirby & Savill 1988). A similar invasion of herbicide-treated plots by Senecio vulgaris was noted by Christensen (1988).

More major changes to the ground flora may occur however: Frochot (1979) reported the replacement of Carex brizoides by Rubus species following two annual applications of dalapon (10 kg/ha) on a clear felled area in France.

3.6 Discussion

The immediate effects of forestry practices on the survival of the flora and vegetation of the stand and wood are the main concern of this chapter, but reduced abundance of plant species may mean also less food for invertebrates or less cover for small mammals. Reduced flowering,

even without a change in abundance may mean less seed being contributed to the seed bank.

3.6.1 Summary of effects by groups of flora

3.6.1.1 Trees and shrubs

Trees and shrubs which are not part of the crop are tolerated only if they do not interfere with the crop or operations in the stand. Even if eliminated from the centre of the stand they may persist on the edges, particularly if there are lots of edges, because the stands are small (3.4.2.1) and the rides are sympathetically managed.

The trees of semi-natural stands are valuable as vegetation, i.e. as the communities that have developed over the centuries (since the last glaciation in primary woodland) and which vary with soil, slope, aspect and so on. Traditional management or minimal intervention are the most certain ways to perpetuate them. It may be possible to devise alternative treatments based on high forest that are as satisfactory, but we cannot be certain yet about these and must proceed cautiously. (The variety and value of the tree and shrub communities in ancient woodland, and the realization that traditional management perpetuated them, but most modern forestry did not, is a product of the 1970's, primarily of Rackham and Peterken. Not surprisingly it is taking time for this to become fully known and accepted in forestry circles.)

3.6.1.2 Ground flora

Once the trees are established forestry management takes little interest in the ground vegetation. It generally recovers from site preparation and weeding, which rarely treat 100% of the area or last more than a few years. Shifts in species abundances occur and persist until the thicket develops. Small populations of localized species such as Paris quadrifolia might be permanently destroyed. The more intensive or widely applied the disturbance during the establishment phase the longer the vegetation takes to recover.

The most damaging effect of changing tree species is likely to be the permanent loss of the persisters during an inimical thicket stage (3.2.2.5), particularly in the east of the country. The occurrence of some of these species under post-thicket conifers in the west (e.g. Anemone nemorosa, Galeobdolon luteum, Mercurialis perennis, Brown, Pearce & Robertson 1979; E.H.M. Harris, personal communication) suggests that there some may behave differently. The mechanism for greater persistence or colonizing ability in the west is unclear. Chance factors may be important in determining which of a particular set of species establish or survive in young stands but the effect of such factors diminishes with age (Christensen & Peet 1984).

Old well-thinned plantations may have much of the flora and a broadly similar ground vegetation to closed canopy semi-natural stands on that site. The differences are likely to be in the presence or absence or levels of abundance of particular species. Even if bluebell survives as isolated plants through a spruce thicket stage it is unlikely to reform the extensive carpets that characterized the former broadleaved stand, whereas for bramble the reduction in the thicket stage is no more than a temporary set-back. The significance of such differences depend on which species are involved.

3.6.1.3 Ground-living bryophytes

The abundance of this group tends to be inversely related to the cover of ground vegetation. Poorly-dispersed species may be eliminated by an inimical thicket stage, or a treatment, such as fertilization without adequate weed control that greatly favours the ground vegetation. Since the nature conservation value of sites for bryophytes is currently determined largely by the presence of the more restricted, generally poorly-dispersed species even traditional woodland management should be viewed with caution in such sites.

3.6.1.4 Epiphytes

This group generally requires old substrates in the right, continuous climatic conditions maintained either because the climate is generally suitable (the west) or because the stand maintains a suitable microclimate. Exceptionally, e.g. Borrowdale in the Lake District, old forest species of lichens have spread to non-native trees such as beech planted in the early nineteenth century. Epiphytes are favoured by wood pasture or long-rotation high forest, not by modern forestry or by coppicing. Any management which involves removing old trees for timber prevents the development and survival of rich epiphyte communities. Lichens are also particularly sensitive to sulphur dioxide pollution so many species may be absent from lowland areas for that reason (Rose 1974).

3.6.1.5 Vegetation versus flora

The vegetation is more susceptible to change than the flora, i.e. the species list for the stand or the wood may be the same but the relative abundances and performances of the species vary producing differences in the communities (3.1.1). Peterken & Game (1984) found that the species lists for woods containing conifer stands were not significantly shorter than those from woods that were entirely semi-natural. If the flora can be maintained largely unchanged then there is scope in theory for managing the vegetation in the future to restore the former community: thinning more heavily, changing tree species or stand structure again, or simply waiting for the appropriate stage to develop.

However the maintenance of the range of semi-natural vegetation within woodland, now and in the future is the concern of nature conservation as much as the mere retention of the full range of species, the flora. At present neither ecologists nor foresters can predict precisely how, when and with what success woodland communities disrupted by forestry operations may be fully restored. If the nature conservationist is to be asked to allow disruption of the present vegetation as part of the long-term management for the wood (in which that vegetation will eventually re-appear) the commercial forester should be able to give the guarantee that the necessary future management will take place and will achieve the restoration proposed.

3.6.2 Relative importance of the four types of change

In general change of tree species has the most important effect on the flora, followed by changes on the site and then by changes in stand and woodland structure. The background changes due to stage and stocking are often of similar magnitude to the effects of a change in

tree species or change on the site.

The effects vary with the plant group: few practices are consistently good or bad for all groups. In any stand and in the wood as a whole choices have to be made as to which group to favour. The choice usually depends on past treatment: the trees and lichens in a wood pasture, shrubs and ground flora in a coppice. Even when the tree species or stand structure has been changed there is often scope for management to modify the effect.

There are limits: management can have little effect on the characteristics of the thicket stage. This stage is associated with the development of the stand microclimate and a period of accelerating tree growth (Ford 1979). Even natural thicket stands of spruce/fir forests in North America "may present a bare aspect of needles and twigs" (Crandall 1958). However, the start of the thicket stage can be delayed by planting at wider spacing; the end can be hastened by early thinnings; and stand size can be reduced so that there is proportionately more edge per unit area. At the edges there is side light and more opportunities for shrubs and ground flora plants to survive.

3.6.2.1 Identifying the main source of change

The four types of change are conceptually independent, but in practice they occur together and often work in the same direction. The decrease in shrubs and ground vegetation as a result of site preparation and weeding to ensure good establishment of Norway spruce would be reinforced by the dense thicket stage and little decrease in shade at later stages of the rotation. Nevertheless, it is important to be able to think of the practices separately to see their contributions to the overall change, as in the following example.

McComb & Noble (1982b) compared the shrubs and ground vegetation in an old stand of mixed broadleaves with those under eleven-year-old poplar (Populus deltoides), planted at 6 x 6m spacing after intensive site preparation using bulldozers to clear and level the site, and disc ploughing. The plantation contained a higher cover of shrubs and a slightly higher cover of ground vegetation, dominated by species with persistent root systems and early successional species, which had survived or had established after site preparation respectively. Many species found in the old broadleaved stand were absent from the plantation.

The differences were probably due to site preparation first, then differences in stage and stocking and then the change of tree species. If conservation of the ground flora combined with timber production was the objective then the best single change of management would be to use less intensive site preparation, not to use one of the less productive, naturally occurring tree species. Or, looking at it another way, if the same site preparation had been used with native tree species the vegetation would probably have been altered just as much.

3.6.3 Change of tree species

The relationship between the lower layers of vegetation and the tree species is not a close, chemically-mediated link as with a monophagous herbivore, but works through the environment, most importantly solar radiation (e.g. Blackman & Rutter 1946) and litter (e.g. Sydes & Grime 1981a). Management can modify these factors for a given tree species through control of stocking: more heavily thinned stands cast less shade

and have faster decomposition of soil organic matter and thinner layers of litter (2.1.5).

3.6.3.1 Differences in the transmitted radiation regime

Photosynthetically active radiation (PAR, the wavelengths between 400 and 700nm) under a dense tree canopy is reduced up to 100-fold. For green plants PAR is the only source of energy and the amount intercepted by the plant is coupled quantitatively to the amount of growth (Kumar & Monteith 1981). Water relations and soil nutrients influence growth but their modification of the relationship between intercepted PAR and growth is more important than their direct effects (Cannell *et al.* 1987).

For the ground vegetation it is the absolute PAR that matters and this is the product of the amount incident at the top of the tree canopy and the proportion transmitted by the canopy (consisting of radiation penetrating, i.e. not touching a leaf or branch, and scattered, i.e. transmitted through or reflected from a leaf). The incident PAR follows a sine-wave curve after the solar march through the year. An evergreen canopy transmits a more or less constant amount between 1% and 5% depending on the species (Ovington & Madgwick 1955). The peak in absolute PAR is therefore in midsummer and is symmetrical. The deciduous canopy also transmits 1-5% PAR from June to September, but much more, commonly 30-60%, between December and April. The peak in absolute PAR is in April or May and is asymmetrical with a gradual build up in late winter and early spring and a sharp cut-off when the tree canopy develops. The exact shape and position of the cut-off depends on the phenology of leafing of the tree species. In autumn there can be a second peak in absolute PAR, but always much lower and broader than the spring peak because of the much lower incident PAR, and again its position and shape, and whether it occurs, depend on the phenology of leaf fall (Figure 3.9; Anderson 1964; Mitchell 1984; Salisbury 1916a).

The highest levels of PAR occur in the spring in deciduous stands and this is reflected in the phenology of British woodland plants (Salisbury 1921). Most woodland species flower early. There is a range of vegetative growth patterns from strictly confined to spring for the vernal flora, through spring and summer, or winter and spring, to evergreen. Wintergreen and evergreen plants are able to photosynthesize whenever the temperature and PAR are high enough in the leafless half-year. Under an evergreen tree canopy spring ephemerals are not at an advantage and successful plants are likely to be summergreen or evergreen. In mixed broadleaved stands with or without hemlock this was indeed found (Beatty 1984): spring ephemerals occurred only in stands without hemlock, and in stands with hemlock many of the ground flora species made most growth in summer and autumn. A European example is Oxalis acetosella, which thrived under Norway spruce in Sweden (Nihlgård 1970) and increased under conifers on former coppice sites (Brown, Pearce & Robertson 1979); it is evergreen and particularly shade tolerant. In fact growth is so much worse at 100% PAR that this species is one of rather few that could be called shade demanding (Packham & Willis 1977).

3.6.3.2 Litter effects

The amount and quality of litter varies between tree species. It affects the ground vegetation physically by smothering the foliage or hindering the growth of stolons, rhizomes and roots, and chemically by its initial composition and then by its decomposition and influence on

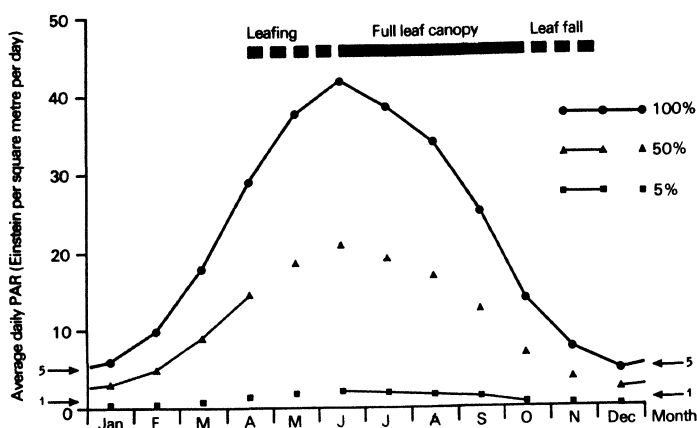


Figure 3.9. Seasonal change in photosynthetically active radiation in southern England, based on the monthly averages of solar radiation for ten years at Bracknell. (Photosynthetically active radiation (PAR) is here measured in quantum terms where one einstein is Avogadro's number (6×10^{23} or one mole) of photons.) The points for 50% (leafless canopy) and 5% (full leaf canopy) are joined for the appropriate periods of the year, but not during leafing and leaf fall when the shape of the curve depends on the precise timing which varies with tree species and the weather. Generalized canopy phenology for deciduous trees is shown at the top. The arrows at the sides indicate suggested thresholds for plant growth: at 5 E/sq. m./day most species can grow and flower; at 1 E/sq. m./day shade-tolerant species can grow but few can flower (Mitchell & Woodward 1988).

soil properties.

Certain morphological features of woodland plants suit emergence through coverings of litter (spear leaves or shoots, e.g. *Primula vulgaris*, *Ranunculus ficaria*; or recurved stems or petioles with leaves which unfold after emergence, e.g. *Mercurialis perennis*) (Salisbury 1916b). The American species, *Floerkea proserpinacoides*, establishes better where seedlings are dense because the growth of a mass of seedlings is more effective at pushing through the litter than one or two alone (Smith 1983).

The growth of *Holcus mollis* and *Poa trivialis* was reduced by persistent deciduous leaf litter or artificial plastic litter whereas that of *Endymion non-scriptus*, *Galeobdolon luteum* and *Viola riviana* was not (Sydes & Grime 1981b). Differences in the persistence of litter between tree species may allow *Anemone nemorosa* and *Galeobdolon luteum* to persist in competition with *Anemone ranunculoides* and *Mercurialis perennis* (Persson, Malmer & Wallén 1987).

Differences in the packing of litter influence the ground flora: Anderson (1979) listed nine species including *Geranium robertianum*, *Milium effusum* and *Poa trivialis* which tended not to occur under Corsican pine or chestnut that have long leaves forming a loose litter layer which readily dries out. Another physical effect could be the timing of litter fall. Litterfall from evergreen conifers occurs throughout the year with only small seasonal peaks which vary with the species, site and year (Owen 1954). Litterfall in deciduous trees is concentrated in a few weeks in the autumn and this could account for the unexpectedly large reduction in ground flora species under larch compared with other conifers (Brown, Pearce & Robertson 1979). Briggs

(1965) noted that carpets of Dicranum mosses were never found where heavy accumulations of fallen leaves occurred.

The chemical effects of litter merge into the long-term changes in the soil under different species (2.2.2). Conifer litter in general is more acid and more prone to form mor than broadleaved litter and this may contribute to the vegetation change (Nihlgård 1970; 3.2.2.3).

The concentration of water-soluble phenolic acids in the soil beneath eighty-year-old Norway spruce was almost twice that in a twelve-year-old clearing in the same stand (Kuiters, Lakeman & Middelkoop 1987). In water culture experiments growth of Senecio sylvaticus and Chamaenerion angustifolium, which occur in these clearings, was significantly reduced in the presence of phenolic acids. (However, the authors did not relate the concentration measured in the soil, in micrograms per gram of dry soil, to the concentrations used in the experiments, 10^{-3} , 10^{-4} or 10^{-5} molar solutions, so that it is not immediately obvious that any reduction in growth of these plants can be attributed to the phenolic acids in the soil.)

Brown (1979b) and Brown, Pearce & Robertson (1979) suggested that the change in ground vegetation under first-rotation conifers could be associated with the lower soil pH, either directly or through the interaction between pH (or soil fertility) and shade tolerance (Corre 1983; Peace & Grubb 1982). In general the minimum light requirement for woodland herbs rises with increasing soil acidity (Ellenberg 1988).

3.6.3.3 Below-ground competition

Surprisingly little has been done on the significance of below-ground competition between trees and the ground flora (apart from the effect of herbs and grasses on seedlings). Work with trenched plots (McCune 1986; Slavikova in Ellenberg 1988; Toumey 1929) suggests that it may be important. Throughfall patterns and hence soil moisture are altered by the trees (Ovington 1950) and even under gaps the improved ground flora growth may be better correlated with increased throughfall than light (Anderson, Loucks & Swain 1969). If below-ground competition is generally important an important difference between clear felling and coppicing is that coppicing reduces root competition for a shorter time.

3.6.4 Changes on the site

The object of operations on the site is to establish the crop quickly and cheaply, so the consequent changes are usually restricted in space and time. The exception is intensive site preparation where economies of scale encourage the full use of large machines to completely clear the site. This destroys the tree and shrub layers and epiphytes on the trees, but the ground vegetation may recover. It is in the interests of good tree establishment as well as the recovery of the ground vegetation that there should be minimum soil compaction by the machinery.

Weeding is usually restricted to bands along rows or spots around trees. There may be some invasion by ruderal plants such as Rumex species (J.R. Heap, personal communication) but the woodland vegetation remains on the untreated parts and can later re-invade the treated areas. It may be more cost effective to treat larger areas around each tree, but only once a year, accepting the less complete weed control Davies (1985), but what percentage of the ground is it acceptable to treat (on nature conservation grounds) without diminishing unduly the effectiveness of the herbicide? Figure 3.10 shows the relation between

width of strip or size of spot and the spacing of trees, and how these affect the percentage of ground treated. Herbicide treatment is a disturbance additional to that of extraction and ground preparation. To keep the cumulative effect of these to a minimum the present nature conservation recommendation is to restrict the area treated with herbicide to less than 10% of any restocked area.

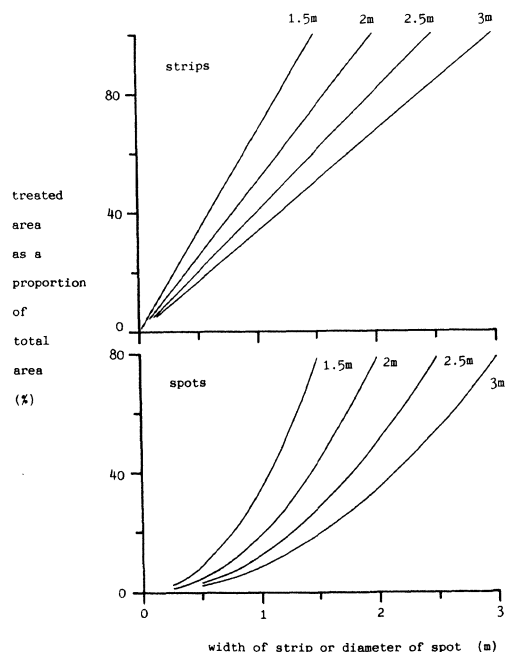
3.6.5 Rides and their flora

Rides often contain most of the flora of a wood (e.g. 80-90% of the total species list (Brown 1979b)) and in eastern England may have vegetation types (unimproved or marshy grassland) which are rare in that district outside woods (Peterken 1981). Their value depends on their being only lightly shaded or unshaded and on periodic light use and cutting to control shrub growth. In a wood more intensively managed for forestry they may be abandoned if a new road system is constructed or be over-used and altered by drainage and partial surfacing.

Although Brown (1979b; 3.2.6) found no differences in the floras of rides between coppice and conifer stands, a change of stand structure or tree species, especially to taller, more densely and continuously shading conifers, could lead to more shaded rides. Because conifers tend to be taller than broadleaves of similar age, and high forest stands are taller than coppice, the width of rides to retain the full range of open ground flora has to be greater. The growth form of trees is important: species with spreading limbs such as Norway spruce or larch cast more shade on the ride than those with compact crowns such as Lawson cypress.

With appropriate management (4.3.4.2; 4.8.4.3; Steele & Welch 1973) the flora of the rides can probably be maintained irrespective of changes in the stands. However this does not mean that the vegetation of the wood can be maintained just on the rides: the communities within the stands are quite distinct even if some of the species are held in common.

Figure 3.10 Assessing the total area treated by herbicide for different widths of strips or diameters of spots for four tree spacings. The trees are assumed to be at square spacing and the strips run either along the rows or between the rows.



3.7 Implications for nature conservation (flora)

(a) The conservation of the semi-natural tree and shrub communities especially in ancient woodland is important in its own right, but poses the greatest economic problem because they are seldom worth treating as a crop. To maintain the existing tree and shrub community in managed woods the options appear to be limited to traditional systems such as coppice, or restricted high forest, using small-scale felling, mainly natural regeneration and the minimum of ground preparation (Steele & Peterken 1982).

(b) The ground flora as a whole, that is the species list for a wood, is robust. Unless a particular operation takes place on the only spot of a localized species, broad shifts in tree species, silvicultural system, method or scale of working are unlikely to cause the complete loss of any species. Most can be found in association with or on rides and open areas and lack of maintenance of such areas is the single factor most likely to lead to loss of species from the wood.

(c) The flora within the stands is subject to periodic fluctuations in composition and abundance, from high levels immediately after felling to a low point in the thicket stage followed by gradual increases as the stands thin out naturally or are thinned. Three main mechanisms exist whereby species cope with changing conditions: by having a large seed bank in the soil; by high seed dispersal powers; or by persisting as vegetative plants during periods of dense shade. The species that rely on persistence as vegetative plants through the rotation are most at risk from changes in management, followed by those that depend on a seed bank (since the seeds have a limited life span).

(d) The ground vegetation, i.e. the communities present in the stand, is more susceptible than the flora to disruption by changes in forestry practice. Site conditions (environment and soils) set the broad limits for the community within which factors such as tree species operate to cause local variations. Differences between tree species are generally most apparent at the thicket stage. In older, well-thinned stands the differences may show in the presence or absence and abundance of individual species in those communities.

(e) Changes in forestry practices reduce the composition and abundance of the stand flora (and hence the vegetation) if the density of shade at the thicket stage is increased; the length of the thicket stage is increased or the extent of stands at the thicket stage is increased; the frequency or length of the open phase is reduced, so that there is less opportunity for plants to flower and set seed; or stands at a given growth stage are concentrated at one point and time, rather than being dispersed in time and space which would allow more opportunities for colonization from similar nearby stands. Such changes may come from changing the silvicultural system, from changing the scale of working, or from changing the main crop species.

(f) Small stands scattered throughout the site are most likely to retain the full range of the flora and vegetation within the wood than the same area concentrated into a single stand.

(g) Bryophyte cover is generally inversely related to the ground flora abundance, but may also be restricted by the tree litter. There is limited information on the long-term effects of forestry practices on

common species, but the rarer species of nature conservation importance appear to be sensitive to any form of management including traditional forms such as coppicing.

(h) Lichens and other epiphytes are usually associated with specific large old trees in a site. In most of the lowlands rates of colonization of new trees are low. Therefore any felling of such trees is undesirable even if they are standards in a coppice, which would normally be felled eventually. The main conservation requirements for lichens and bryophytes are best met by identifying the important bryophyte areas or lichen trees and ensuring that they are not affected by management - either by traditional or modern forestry practice.

4 FAUNA

4.1 Background

4.1.1 Approach and limitations

4.1.1.1 Bewildered by diversity

A temperate botanist feels overwhelmed by the sheer numbers of species comprising the woodland fauna: thousands of invertebrates, scores of birds and several dozen mammals. Given the numbers of animal species and the wide variation in numbers of individuals of each species in a community, zoologists more often than botanists resort to various measures of diversity (Southwood 1978). These summarize the frequency distribution of species in the community, but may conceal numbers of species and the total number of individuals, both of which are important in nature conservation terms (Nilsson 1979).

Some of the different diversity measures are mathematically related and form a series, with the position of each index of diversity determined by the relative emphasis given to the rarer species (Hill 1973). Swindel, Conde & Smith (1987) examined whether all measures of diversity agreed in the ranking of sites. For nature conservation the number of species is usually the best measure of diversity. The value of each species depends not on how large the population is, so long as it is sustainable, but on which species it is since nature conservation can and does value species differently.

4.1.1.2 The need for ecological studies

Elton (1966) attempted to synthesize the mass of observations available on Wytham Woods. However, comparatively little work has been carried out in Great Britain on how the fauna changes during the forest rotation or in relation to forestry management, except for birds and pest species. Harding & Rose (1986) commented on the lack of autecological studies, especially on the fauna of dead wood, even though the invertebrate fauna of the British Isles is comparatively well known. At the beginning of a new survey of Canadian insects McLeod (1980) called for a more ecological approach, taking account of the rôles of disturbance and patch size in forest regeneration, rather than a more diffuse, collect-and-name type of survey.

The quantitative, ecological approach is hindered by the need for specialists to identify species in most invertebrate groups and the difficulty of sampling small animals from a heterogeneous environment. These problems can be overcome sometimes by using signs left by the animals, such as spider webs and leaf mines, rather than the animals themselves (Sterling & Hambler 1988).

4.1.1.3 The stand-wood distinction

Ornithologists tend to divide structure into vertical and horizontal components which correspond to our stand and woodland structure. A similar horizontal and vertical division is made by Rochelle & Bunnell (1979). They describe a general framework for looking at how plantation management alters, in time and space, the resources required (food, shelter, escape cover, etc.) for any particular species.

An important difference between plants and animals is that the latter may be able to use or require more than one stand at any one time

or during different stages in their life cycle. Consequently in much research on birds, e.g. French, Jenkins & Conroy (1986), the study area includes a number of different stands. Relating the occurrence of birds to particular stands is neither possible nor particularly useful since the birds do not restrict themselves.

4.1.2 Mobility of species and habitat patch distribution

Apart from a few insect species where the cohort of pupae of one year produces adults in several successive years (Schowalter 1985) animals are not dispersed in time, unlike plants with a seed bank. The continuous presence of an animal species in a wood thus depends on its ability to use either permanent features such as the rides and glades, or all the stages in the rotation, or to move to suitable stages as they occur.

Species that use the early open stages in a rotation have proved particularly vulnerable to local extinctions where woods have been neglected and the habitat that they require has been temporarily unavailable. The permanent open habitats (rides and glades) can act as a refuge for the field vole (Gurnell 1985) from which stands at a suitable stage can be colonized. For other species, permanent open glades may not be a substitute for temporary clearings (such as follow coppicing), because the flora or vegetation structure differs.

The mobility of animals varies enormously from sedentary molluscs, through insects which can move but may be reluctant to cross unsuitable habitat (Mader 1984), to migratory butterflies and birds. The more mobile species may spread easily from wood to wood especially if they are linked by hedgerows or strips of woodland (Wegner & Merriam 1979). However Boone and Tinklin (1988) found that there was little interchange between hedgerow and wood populations of small mammals.

The least mobile may hardly spread from stand to stand unless these are contiguous. Some of these species were formerly widespread but are now isolated in islands of suitable habitat, e.g. the heath fritillary butterfly or some dead wood beetles (Girling 1982; Hammond 1974; Harding & Rose 1986). Their limited mobility makes it unlikely that they will colonize new areas or return to a former site from which they have been lost as a result of changed management. Even within apparently mobile groups such as birds there may be a high degree of site fidelity which limits movement (Knopf & Sedgewick 1987).

For species that depend on one particular stage the wood must be large enough and managed so that this stage is always present (Pickett & Thompson 1978) and within the effective mobility range of that species. If mobility is small the different stages need to be well mixed, i.e. a small-scale patchwork (Figure 1.4). A patchwork of stages close together may also be needed for species that use more than one stage and are strongly territorial. For example Leclercq (1987) suggests that good capercaillie habitat is a small-scale mixture of open ground, tall shrubby stages and trees. Invertebrates often need two markedly different sets of conditions close together because those needed for the larvae differ from those for the adults.

4.1.3 The effects on the fauna of changes in stocking

Trees grown at wide spacing, such as the standards in coppice, grow faster and have a higher proportion of their wood in the branches than in the main stem (Bisch & Auclair 1988). They may reach more quickly

the stage where they have large dead branches and holes suitable for breeding birds such as tawny owls or nuthatches. On the whole, however, the influence of levels of tree stocking on animals is through altering other characteristics of the stand. Lower stocking usually allows more ground vegetation and shrubs to grow and this may be associated with more bird species, more spiders (Lavery 1980) or the occurrence of insects associated with particular shrubs or ground flora. There is an extensive American literature on thinning to improve "browse" available for game animals (e.g. Crawford 1971; Halls 1973).

Stands of 30-40 year and 70 year old neglected lime/ash coppice held more bird species (but not higher total numbers) where they had been thinned once in the previous decade (Fuller & Taylor 1983). The number of species was significantly negatively correlated with canopy cover: from around 30 species at 85% canopy cover to 20 species at 100%.

4.2 Effects of forestry practices on invertebrates (general)

4.2.1 Changes during the rotation

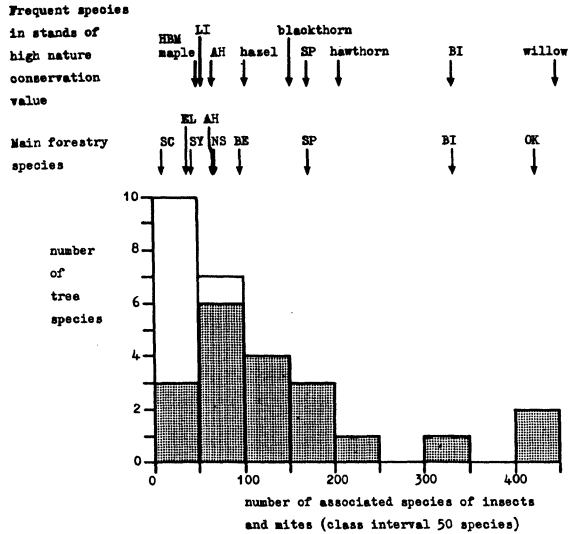
Less is known of the fluctuations of invertebrates through the rotation than for some other groups (Steel & Mills 1988). Molluscs may survive throughout the rotation: Paul (1978a) found that no species had been lost in stands coppiced 0 to 8 years previously compared with the rest of Hayley Wood. Phytophages that depend on particular species in a certain condition have to recolonize areas, as they become suitable, from other stands, and then they die out as those areas grow out of that stage. Several butterfly species thrive only during the young stages, particularly of coppice, when their food plant flourishes (e.g. violets for the pearl-bordered and small pearl-bordered fritillaries; Melampyrum pratense for the heath fritillary in Kent (Warren, Thomas & Thomas 1984)). For several groups of different organisms the highest diversity and species number occurred in the first few years after a coppice cut (Steel & Mills 1988).

In contrast the white admiral only occurs at later stages, not reached in worked coppice, in which honeysuckle grows in a suitably shaded condition (Pollard 1979). Similarly the populations, if not the species composition, of forest floor groups such as carabid beetles may be expected to change between the closed canopy and open (post-felling) stages (Jennings, Houseweart & Dunn 1986). The number of web-spinning spiders and Lepidopteran leaf-miners on the lowest 2m of hazel increased with the age of coppice regrowth from 0 to 8 years, and at 8 years the numbers were slightly higher than in 40 year old neglected coppice (although the lowest 2m is a smaller fraction of the whole canopy in 40 year old than 8 year old coppice, so the total canopy population could be much higher in the neglected coppice) (Sterling & Hambler 1988).

Thus coppicing or felling, while benefitting some species, reduces the populations of others to very low levels which may take up to a decade to recover. Species which depend on dead wood, mainly beetles and flies, flourish only the over-mature stage which is usually not attained in stands managed primarily for a timber crop whether as coppice or high forest.

Figure 4.1.

No. of species of insects and mites associated with 28 tree species (Kennedy & Southwood 1984). The shaded part of the bar represents native species of tree. The arrows indicate the position of individual tree species important in forestry and nature conservation (abbreviations as in Figure 2.2 and Appendix 2). Willow includes five species; oak, birch and lime include two species each.



4.2.2 The effects on invertebrates of a change of tree species

4.2.2.1 Natives versus introductions

The number of species of insect associated with different species of tree varies greatly. Fewer species may be present where a species is introduced than in its native country (Ashbourne & Putman 1987). The much-quoted paper by Southwood (1961) has been updated (Kennedy & Southwood 1984) by the inclusion of mites and more groups of insects as well as new discoveries. Associated insects are those "typically" or "normally" found on a tree species, as recorded by taxonomic experts for each group of insects and mites. Widely polyphagous species tended to be excluded from the lists of associated species. Tree "species" includes small groups in the same genus: two species each of oak, birch, lime and elm; four species of poplar; and five of willow. The number of associated species has been increased by about 65% from 1961 to 1984, fairly consistently for all trees.

What stands out from this work is the sheer variability of the tree species: many with fewer than 50 insects and only a few with more than 250 (Figure 4.1). It is not that all native trees support more insects than all introductions, but that willows, oaks and birches are outstandingly rich and put all the others in the shade. Some of the trees that characterise particular stand types of coppiced ancient woodland (field maple, hornbeam, lime) are poor in insects, and the native and widespread ash has only as many as the introduced Norway spruce.

In general conifers have fewer associated species than broadleaves (Kennedy & Southwood 1984, Welch 1986) so that a change from a broadleaved to a conifer stand is likely to produce a smaller and markedly different list of associated insects. The difference probably arises because most conifers have tough, evergreen leaves high in secondary compounds which deter generalist herbivores.

4.2.2.2 Other factors

Regional differences are important. Birch is much more important as a host plant for insects in Scotland than in southern England or Wales (Shaw 1984). A survey of birch in Norway showed changes with altitude, with generally low numbers of species above 500m (Hagvar 1976). In

addition, Rackham (1986, p.151) has pointed out that much of the value of oak for wildlife depends on old oak.

The number of phytophagous insects associated with introduced trees increases with time (Winter 1974) not least because of the gradual introduction of species that feed on them. For example 67 species of Lepidoptera are known from roble and rauli (the two main species of Nothofagus introduced as forest trees in 1930 and more widely planted from 1955) as well as 11 Homoptera, 8 weevils and 7 wood-boring beetles (Welch 1981). Most species had oak or beech as their usual host and none were monophagous on Nothofagus so the list of associated species by the criteria of Kennedy & Southwood (1984) would be much shorter.

4.2.2.3 Differences between groups of invertebrates

The bark beetles inhabiting weakened, dying or recently dead trees tend to be specific to one or two tree species but as decay proceeds the other insects taking part are increasingly polyphagous (Elton 1966). Species associated with dead wood tend to appear on newly introduced species much more slowly than those consuming other parts of the plant (Welch 1986).

Herbivorous insects range from strictly monophagous to polyphagous, but even the polyphages may have preferences for groups of tree species. New (1970) found nine species of foliage-inhabiting Psocoptera on twelve tree species. Two species were widespread on all the trees and one was almost confined to conifers. Others were more or less confined to broadleaves but were most common on oak and hawthorn. These insects feed on the leaf microflora and debris, and oak leaves in June were rich in these sources, especially algae, probably because of the greater amounts of honeydew.

Predators are rarely restricted to one prey species in one situation but nevertheless may have preferences for groups of tree species. Curtis & Morton (1974) found that numbers of spiders (individuals) was related to the degree of cracking of the bark, but the relationship varied with tree species. Pine yielded comparatively few spiders considering the very broken texture of its bark. The canopy-inhabiting lacewings which feed on aphids and bugs also illustrate this: some Chrysopa species are found on both broadleaves and conifers, but Hemerobius species range over many species of either broadleaves or conifers (Elton 1966).

Even with polyphagous species the genetic structure of the population may depend on the particular mix of host plants available at the time (Thompson 1985).

4.2.2.4 Changes in insect populations

Insects closely associated with a particular tree species are likely to be lost from a stand if that species is replaced by another with its own set of insects. If oak is replaced by European larch then the number of associated insects decreases; but if ash/maple/hazel coppice is replaced by oak and Norway spruce it could increase (ignoring any effects on the ground flora and its associated fauna (4.2.2.5)). Insects only loosely, or not attached to one particular tree, such as most predators and parasites, are less affected by changes in tree species. If the tendency to be wide-ranging over tree species, but only within the broadleaved or conifer groups, is common then changing group makes more difference than changes within the group.

The details of exactly which insect species increase or decline are also significant. The loss of a few specialist species may be more

important in nature conservation terms than the gain of a greater number of generalist widespread species. The quality as well as the quantity of the species list must be considered. Waring (1988) concluded that when neglected coppices were replanted the quality of the species showing declines was greater than that of those that increased.

Insects are food for other animals, especially birds, so that the total biomass on a tree becomes important. For example sycamore makes up in amount (mainly aphids) what it lacks in number of species, when compared with ash (Elton 1966). Trees with more foliage tend to support a higher biomass of insects.

There is also the assumption that there are no bars to colonization. In practice the gains of species may be less than predicted from Figure 4.1. Not all species associated with a particular tree will reach and survive on every site to which that tree is introduced (Figure 5.2).

4.2.2.5 Indirect effects of changing tree species

A consequence of changing the tree species is often that the stand structure changes because there are effects both on the composition and abundance of the shrub or ground flora layers (chapter 3). Since many more plant species are involved than are present in the canopy the indirect effects of changing tree species on the invertebrates of the lower layers may be at least as great as the direct effect on canopy invertebrates. This aspect seems to have been little studied.

4.2.3 The effects on invertebrates of a change in stand structure

4.2.3.1 Relative length of the open phase

Much of the greater richness in invertebrates associated with worked coppice compared to high forest systems can probably be attributed to the relatively longer open phase at the start of the rotation. Although the time to canopy closure may be less in coppice, because coppice regrowth is quicker than sapling growth, this is offset in coppice by the more frequent harvesting of the stand. Conversely species of the closed canopy phases may be less well-developed in coppice.

4.2.3.2 Over-mature trees and dead wood

Whatever forestry system is used, any felling of all the mature trees in a stand (including standards in a coppice with standards) reduces the potential invertebrate fauna in that stand because the range of species that can exist on old trees is greater than that on young trees. The older the trees the greater the potential loss. A change from coppice to coppice with standards or to high forest, but leaving four or five old trees per hectare not harvested, could provide suitable habitat for these species, although long-term continuity of dead wood resources is as important as the amount present at a given time. Heliövaara & Vaisanen (1984) noted that species associated with decayed wood and wood-rotting fungi were particularly affected by modern forestry. Similarly in Finland although most species of carabid beetle (generalized above ground predators) were not thought to be threatened by intensive modern forestry, some species did require primaeval forest conditions (Niemela *et al* 1988).

Steele & Welch (1973) pointed out that large old trees with dead branches and hollow centres are an important micro-habitat for rare spiders. More generally Elton (1966) considered that about 1,000

species, one fifth of the total woodland fauna, depend on dead, dying or over-mature wood, or the large fruit bodies of the wood-rotting fungi (Crowson 1962; Hammond 1974; Maser & Trappe 1984; Stubbs 1972).

4.2.3.3 Neglected coppice as a habitat

Neglected coppice and hence, presumably, high forest with a shrub layer of similar composition hold larger populations of some invertebrates than occur in worked coppice (Sterling & Hambler 1988; 4.2.1).

Leaf litter accumulates among the stem bases of hazel coppice stools, up to 45cm deep, and this provides a larger and more permanent micro-habitat than the thin layer of rapidly decaying litter on the ground. The numbers of the pseudoscorpion *Chthonius ischnocheles* were 3-4 times higher at all times of year in the stool litter than in litter on the ground, probably because the thicker layer provided more shelter and more prey (saprophytic springtails and mites) (Jones 1970). Coppicing both helps and hinders conservation of these litter-inhabiting species. In the coppice stand, stools with their many stems provide good sites for litter accumulation but ideally they should last for decades without disturbance; actually cutting the coppice sets the system back to zero. Such species might be favoured by conversion to high forest if there were greater opportunities for the build up of litter deposits. Thickness of litter layer and to a lesser extent its structural complexity also influences the abundance and diversity of spiders (Bultman & Uelz 1982) and molluscs (Phillipson 1983).

4.2.4 The effects on invertebrates of a change in woodland structure

The adults of many woodland insects need sheltered and sunny areas which are provided by rides, glades and the edges of the wood. The rides and glades in managed high forest are likely to be as suitable as those in traditionally-managed woods and better, because less shaded, than in neglected coppice (3.6.5).

The effect of a different pattern of stands depends on the mobility of the insect. Those which rely on finding widely-dispersed food plants and are generally mobile are likely to be indifferent to an alteration of the pattern and enlargement of its scale provided the relevant stage is still present. Species which are good at finding hosts locally, but do not cross unsuitable habitat, may be at a disadvantage.

Wormell (1977) noted that the woodland on Rhum held a disappointing range of woodland beetles considering the amount of dead wood present. The dead wood beetles, unlike many other insects, appeared not to have spread as easily from the mainland or from the small relict stands of trees left when the island was deforested. The dead wood beetles are prone to restriction to isolated suitable woods and are poor at colonizing newly suitable woods (Hammond 1974; Hunter 1977). For these species it will be necessary to arrange that in a large wood the structure of the woodland always provides suitable stands close together in space as well as overlapping in time.

4.2.5 The effects on invertebrates of changes on the site

Any insect control programme (whether by chemicals or by biological means) in long-established woods has the potential to affect more than just the target species, although in lowland woods such schemes have

been very limited so far.

Suppression or removal of weeds reduces or eliminates for a time the associated populations of insects (Santillo, Leslie & Brown 1989). Control of the ground vegetation rarely covers the whole ground area (3.6.4) or lasts for more than a few years so the effect on insects ought to be small and short-lived. However, if the first two years after felling are normally the best time for, say, the flowering of violets, weed control and ground preparation at this time could have a disproportionate effect on associated invertebrates. Thorough cleaning completely removes shrubs and weed trees from the stand so that shrubs and trees along rides and in odd corners become even more important in maintaining insects dependent on them (Waring 1988).

4.3 Effects of forestry practices on Lepidoptera

4.3.1 Introduction

This group, especially butterflies, has been comparatively well studied. The rare species tend to have precise and restrictive needs for larval food plants, e.g. black hairstreak (Steele & Welch 1973) or are colonial and reluctant to cross unsuitable habitat, e.g. heath fritillary (Warren 1987b). Butterfly populations fluctuate widely from year to year, probably because of the weather but not always in a simple way. Warm, sunny summers are good for adult activity and may be good for rapid larval and pupal development, which reduces the period of vulnerability to predators. For a few species wet springs may suit the food plant and therefore produce a larger adult population in the following year (Pollard, Hall & Bibby 1986). Long-term trends resulting from habitat changes, climate change or chance can only be detected against a long run of the background fluctuations.

4.3.2 The effects on Lepidoptera of a change of tree species

A few species of butterfly and many moths have trees as the larval food plant. If they are not polyphagous then they will be lost from stands without the appropriate tree species, and from the wood if the tree is absent from all stands and does not occur along the edges or in the rides.

Waring (1988) compared three stands in Bernwood Forest: Norway spruce with broadleaved, weed trees, mainly birch; a semi-natural broadleaved stand of oak, aspen, hazel and hawthorn (neglected coppice with standards); and a similar stand recently coppiced. Over two years of light-trapping the number of species occurring was very similar (181, 183, 177) but the relative number of individuals varied (66%, 100%, 44%). Increases and decreases in numbers of moths were in line with the changes in the abundance of their larval food plants. Moths dependent on oak declined in the conifer stands but not in the recently coppiced stands where the oak standards were left. Some species with larvae feeding on aspen, hazel and hawthorn declined on the recently coppiced site.

Other Lepidoptera have larval food plants in the shrub and ground vegetation layers, or in the ride vegetation. These species are affected indirectly by changes in tree species through changes in the other layers, for instance by eliminating ground vegetation during the thicket stage. Hadley (1982) reported a decline in the number of macro-Lepidoptera from Abbots Wood (east Sussex) since 1945 when the

wood was felled and replanted although both a change of tree species and to stand structure were involved.

4.3.3 The effects on Lepidoptera of changes in stand structure

Several butterflies do well in coppiced woods because their food plants flourish in newly cut areas (violets for fritillaries, Melampyrum pratense for the heath fritillary in Kent (Warren 1987a)). A warm micro-climate may be increasingly important for species at the edge of their range so that a scatter of flowers with some bare soil between (greater heat absorbance) may be more valuable than the same number of flowers in denser vegetation. The fritillaries can also thrive in the early stages of high forest or in some cases in glades or rides if the food plant is abundant.

The violets in newly-cut areas are not out-competed by vigorous marginal species because the latter are eliminated by the deep shade of the complete coppice canopy which the violets can survive. Melampyrum pratense is an annual with rapid population growth in the early stages of the rotation, but is absent or sparse in later stages except in canopy gaps (Warren, Thomas & Thomas 1984). It may be present in the seed bank, but it was not found by Brown & Oosterhuis (1981) or Harris (1986). The coppice system also provides a favourable woodland structure for these and other butterflies.

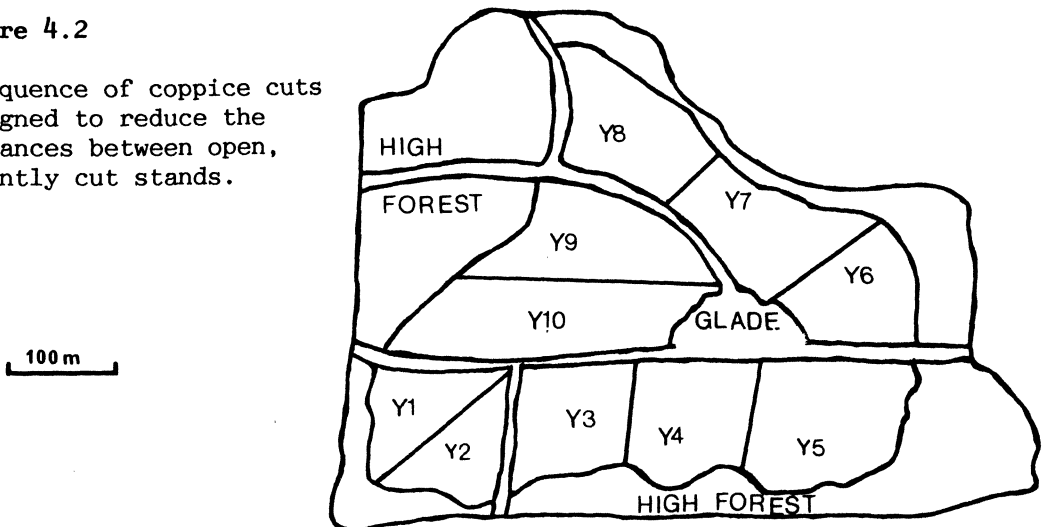
4.3.4 The effects on Lepidoptera of changes in woodland structure

4.3.4.1 The value of a worked coppice structure

A worked coppice stand provides a short period of good conditions for open glade species particularly butterflies and hoverflies, e.g. 4-5 years for the heath fritillary in Kent (Warren 1987c). This period recurs every 10-15 years and the stands are often less than one hectare in size, so that suitable areas are never far apart. Heath fritillaries are notoriously reluctant to cross unsuitable habitat so that continuous provision of suitable areas close together is vital for the survival of the colony (most colonies occupied less than one hectare). Figure 4.2 shows a design for coppice cutting proposed by M. Warren and R. Fuller (personal communication), to minimize the distances that species must travel to find suitable habitat.

Figure 4.2

A sequence of coppice cuts designed to reduce the distances between open, recently cut stands.



Traditional chestnut coppice in Kent provided such conditions, but the recent trend to twenty-year rotations and a 10-20 ha scale of working does not; nor does high forest (Warren 1985b; Warren, Thomas & Thomas 1984). Failure to maintain sufficient worked coppice and open rides in the 1950s and 1960s contributed to the loss of other species from Monks Wood (Pollard 1982). Even if particular species of butterfly will move to adjacent stands when at a suitable stage the abundance of these species in a wood will be reduced by a shift from worked coppice to high forest because open conditions occur less frequently or over a smaller area at any one time in the latter. Some species may be eliminated altogether from the stands in single tree selection systems.

Robertson, Woodburn & Hill (1987, 1988) found that many species of butterfly increased in abundance in neglected coppice treated by "skylighting" primarily to favour pheasants, i.e. cutting a few stools, where not shaded by standards, in scattered patches so as to allow growth of the ground vegetation. Butterflies were also favoured by the wide rides and a more open canopy. Similarly good butterfly populations may survive along the rides in intensively managed conifer plantations (Peachey 1980) even though the closed canopy conditions in conifer stands are an extremely poor habitat.

4.3.4.2 Rides as a habitat for Lepidoptera

A number of species find all their needs catered for in the rides and are thus unaffected by the characteristics of the stands, e.g. the moth *Semiothisa brunneata* in the Highlands occurs in rides of commercial woods where *Vaccinium myrtillus* is allowed to grow (Young 1986), the wood white butterfly in rides containing its leguminous food plants (Warren 1984). Rides provide grasses for the larvae of the speckled wood and dappled shade for the adults. Warren (1985a) showed that the adult butterflies found in rides varied in their shade preferences. The open habitat species preferred the least-shaded rides and only a few species the moderately-shaded ones. Providing a range of shade but especially minimally-shaded rides is likely to encourage the most diverse butterfly community.

Warren (1985a) modelled the direct solar radiation reaching the ground at latitude 52°N in June in rides of different orientations, widths and height of bordering trees. There is more direct radiation in wider rides and much more in east-west rides than north-south ones, especially when the trees are below 15m. East-west rides at least 20m wide provide from 30% to 50% direct radiation even with trees 20-30m tall when in north-south rides the radiation is down to 25%. Therefore, for a given management effort, the best results will be obtained by removing trees along the south side of east-west rides.

Steele & Welch (1973) give a scheme of ride management for insects, designed to produce a sequence of short to tall vegetation from the centre of the ride outward. This has been further developed by M.S. Warren & R. Fuller (unpublished), Anderson & Carter (1988) and Hall & Greated-Davies (1989). At Monks Wood some species have increased in response to improved ride management, although none of the species previously lost have reappeared (Pollard 1982).

4.3.5 The effects on Lepidoptera of changes on the site

The remarks in section 4.2.5 about invertebrates in general apply equally here. Some butterflies are affected by intensive cleaning more than others. The white admiral, which depends on partly shaded

honeysuckle near the edge of stands or in shady rides (Pollard 1979), is more likely to be lost from a particular stand than the black hairstreak which feeds in thickets of blackthorn (usually on wood edges) rather than on isolated plants in the stand (Steele & Welch 1973). On the other hand because the black hairstreak colonies are often in just a few bushes they are more likely to be lost completely from a wood if the wrong area is treated.

4.4 Effects of forestry practices on molluscs

Terrestrial molluscs do not form associations or communities, although species vary in their ecological amplitude (Boycott 1934). Food is rarely limiting and the other requirements are shelter (damp atmosphere and substrate) and lime (especially for snails). Beech and ash woods tend to be rich in molluscs probably because they are often on calcareous soils.

Beyer & Saari (1977) trapped slugs in plots of ten tree species in New York (stands about 35 years old). They found only six species and no clear associations with tree species. A few slugs were not found under spruce or pine because of the lack of ground vegetation. Phillipson (1983) found highest numbers of slugs (individuals) in areas of deep litter and with ground vegetation. Thus molluscs seem to be unaffected by tree species as long as the structure of the stand includes low cover for food and shelter.

Paul's (1978b) survey of different types of woodland showed that ancient semi-natural woodland held the most species (24.7, average of six sites). Recent woodland adjacent to ancient woodland held 23.0 species (two sites) but detached recent woodland only 15.5 species (two sites). These lower numbers were related to the limited mobility of molluscs: some species can move 60-90 cm in a night but the colonizers of the recent woodland in Hayley Wood, the Triangle, had moved only up to 1.3 m per year (Paul 1978a). Ancient woods recently planted with conifers appeared to have lost species (18.0, two sites). From a survey of hedgerow mollusc faunas Cameron & Down (1980) also concluded that there was only limited colonization of new sites.

Within Hayley Wood, Paul (1978a) found more species and larger populations where the soil was better drained and less acid. Drainage and fertilization would probably not reduce the mollusc fauna unless it caused the loss of the ground vegetation; liming might even increase the mollusc fauna. The effect of weeding would be limited to the area actually weeded and the few years early in the rotation when weeding is necessary (3.6.4).

4.5 Effects of forestry practices on amphibians and reptiles

The endangered species of reptiles and amphibians in Great Britain are mainly associated with heathland or dunes, where the spread of plantations can threaten their survival. Woodland can provide food (invertebrates, small mammals) and suitable sheltered and sunny areas for basking (Spellerberg 1982, 1988) for several of the twelve native species, but it is not an important habitat for these animals (Steele 1975). Rides, glades and unplanted areas (Dent & Spellerberg 1988) around ponds and along streams can act as permanent habitats from which these animals can spread to suitable stands, mainly at the early stages of the rotation, as and where they occur. Amphibians also use forest ponds for breeding.

Pough et al found that the depth of shrub and ground vegetation and litter gave the best positive correlation with salamander numbers in woodland, which were much fewer in recently disturbed (felled) than in adjacent old growth forests. Some small-scale disturbance could however be tolerated. Differences between tree species are probably mediated through their effects on the ground flora. Bennett, Gibbons & Glanville (1980) trapped amphibians in summer in three contiguous stands of second-growth mixed broadleaves and 25 year old planted stands of slash pine and loblolly pine around a lake in South Carolina. There were no differences in the number of species but there were 50% more individuals in the broadleaves than in either pine stand.

Reptiles and amphibians are likely to decrease under forestry practices which reduce or eliminate ground vegetation (tree species with inimical thicket stages, drastic weeding) since their own shelter and the food and shelter of their prey depend on this. Arranging the woodland structure so that stands at the early stages of the rotation are contiguous with the habitat reservoirs such as rides and with each other may encourage their spread (if they are present in the first place) into other suitable areas. As with other groups the long-term maintenance of suitable open conditions is crucial, particularly in fast-growing plantations where shade conditions on rides can change very rapidly.

4.6 Effects of forestry practices on birds

4.6.1 Introduction

4.6.1.1 Other reviews

There is a huge literature on birds and forestry, especially in relation to upland afforestation. Newton (1986) outlined the principles of woodland bird ecology, while Fuller (1982) discussed regional differences in breeding bird populations, their relation to site size and broad woodland type. Moss, Taylor & Easterbee (1979) surveyed the song-birds in afforested conifer stands and discussed the results in terms of tree species, stand and woodland structure. French, Jenkins & Conroy (1986) recorded the birds and habitat characteristics in some Deeside woods and derived recommendations for management. Harris (1983) collated information from numerous studies to provide details for individual bird species in three comparisons: afforestation and moorland, upland conifer and broadleaves, and lowland conifers and broadleaves. Much recent European work is in Blondel & Frochot (1987).

4.6.1.2 Survey methods used

Much quantitative work on woodland birds has been done with song-birds because these hold well-defined territories of up to a few hectares and can be reasonably accurately censused. In the mapping method all sightings and activity seen during several visits are mapped and then interpreted using standard rules to establish the number of territories (= pairs; International Bird Census Committee (1969)). The results are sometimes given as pairs per square kilometre, but it is easier to appreciate them as the number per 5 ha or 10 ha which is more closely related to the sizes of the study areas and the scale of pattern of woodland (Nilsson 1979; French, Jenkins & Conroy 1986).

Another method used is the point count whereby birds seen or heard at a sample point during a specified length of time are recorded (e.g.

Bibby, Phillips & Seddon 1985). In general this provides estimates of relative abundance rather than absolute densities of birds, although the ratio of "near" to "far" (> 25m) registrations of a bird seen or heard can be used to calculate a density figure. The bird records can also be related to vegetation data collected at the sample points.

The knowledge of non-passerines tends to be more qualitative. Petty (1988) provides some information on raptors in upland conifer forests. Newton (1986) gives 30 non-passerines (compared to 38 song-birds) in his list of breeding birds in Scottish woods. Most require open land in glades or outside the wood although some species often considered to be birds of open country in Great Britain e.g. buzzard, make more use of forests elsewhere (Jedrzejewski, Jedrzejewska & Keller 1988). Non-passerines are more difficult to census because they tend to occur at lower densities and hold larger territories than song-birds and not give overt territory signs.

4.6.1.3 Changes during the rotation and the importance of structure

The different stages of the rotation have different bird communities. In plantations established on bare ground Moss, Taylor & Easterbee (1979) described the change in song-bird species composition from before planting to the pole stage. Rose (1979) identified six stages in pine stands and showed a general increase in number of species from 5-10 at the very young stage (1-5 years) to 15-20 at the late pole stage (over 60 years). Sykes, Lowe & Briggs (1985) monitored for 12 years the changes following afforestation on one site and found a similar pattern. Moss (1979) observed parallel changes in non-passerines: open habitat species (e.g. lapwing, red grouse) were replaced by species of shrubby vegetation (e.g. black grouse, short-eared owl) and these in turn by species of older stands (e.g. woodpigeon, tawny owl).

Similar changes (fluctuations) take place at restocking (Hansson 1978; Leslie 1981) except that the species typical of the former open habitat may not return if the felled area contains shrub growth, advance tree regeneration and rampant growth of brambles (Currie & Bamford 1981), or if the restocked stand is too small. The amounts of lop and top, open ground, herbaceous growth and stump regrowth were also found to influence the bird populations in clear-felled areas in North American forests (Titterton, Crawford & Burgason 1979).

In older stands Currie & Bamford (1982) found twice as many song-bird species breeding at twice the total density in 1.5-2 ha stands of 100 year old Norway spruce, European larch or Douglas fir compared with 53 year-old Norway spruce, 26 year-old Japanese larch and 53 year-old Douglas fir respectively. Breeding pairs of non-passerines occurred in ones and twos with a tendency to favour the old stands. These differences were related to the greater canopy depth and the presence of shrub layers and wind-snapped trees in the old stands, rather than to tree species differences.

In long-established woods Hope-Jones (1972) and Massey (1974) carried out studies in different stages in coppiced oakwoods in Wales; Smith, Averis & Martin (1987) looked at a range of oak plantations in the Forest of Dean; Muller (1987) compared the changes in bird population of a mixed pine and a beech stand; Thompson & Capen (1988) studied the changes in American hardwood forests; while Helle and Fuller (1988) summarise a variety of studies on migrant passerine birds. They show much the same pattern. Different sets of species occupy the open and low shrubby stages and are replaced as the canopy grows. The trans-Saharan migrants such as warblers for example, tend to be greatest in

vegetation 1-2m high. Species number and abundance usually increase with age (there may be a dip at the thicket stage) with more specialist species (hole-nesters) appearing in the oldest stands.

In worked chestnut coppice in Kent one group of birds including tree pipits occurred in the early stage; another group around canopy closure at seven years was dominated by willow warblers, while there was a third group at the closed canopy stage including thrushes. The early stages were preferred by summer migrants, the last one by residents (Fuller & Moreton 1987).

These fluctuations during the rotation are related to the changing structure of the habitat, which has often been considered to be more important than tree species itself for birds, with MacArthur & MacArthur (1961) much cited in this context. They showed that the diversity of bird species and diversity of foliage height, both measured as the Shannon-Weaver index, were linearly related. The Shannon-Weaver index has been criticized by Nilsson (1979) and James & Wamer (1982): for any site it obscures in one figure the separate and interesting values of the number of species (richness) and the total density of birds, and the different types of vertical and horizontal structures that may produce any given foliage height diversity value.

James & Wamer (1982) concluded from their analysis of North American bird census results that both number of tree species and stand structure affected birds: the lowest density and number of species occurred in areas with few tree species, low canopy height and high density of small trees.

4.6.2 The effects on birds of a change of tree species

There are regional differences in breeding bird densities (Fuller 1982) and it can be difficult to separate the effects of tree species and stand structure in a general survey of woods. Tree species do differ in their suitability as nesting sites or the supply of food (fruits, seeds, invertebrates) associated with them. Differences in branching patterns between species and type of foliage affect the structure of the habitat for foraging birds (Holmes & Robinson 1981; Holmes, Bonney & Pacala 1979). Clear preferences for different trees between bird species and within a year for the same bird species have been shown at Hammersley Forest (Durham) (Peck 1989 & personal communication). Morrison *et al.* (1985) provide an American example of how the use by birds of one particular tree, incense cedar, increased during the winter.

Even after trees die some differences may persist. Smith (1987) found that dead ash, beech and hornbeam were preferred by great spotted woodpeckers to oak or chestnut. There are also large indirect tree species effects through their influence on the ground flora or shrub layer development (chapter 3), or the length of the rotation on which they are normally grown.

A few birds are confined to broadleaves (e.g. hawfinch, pied flycatcher) or to conifers (e.g. crested tit, capercaillie) (Newton 1986), but most can be found in either category although usually at higher densities in the broadleaves. Broadleaves (especially if not intensively managed) generally allow the development of understorey, shrub and ground vegetation layers more readily than many conifers, although Muller (1987) found that the pattern of change for most birds through a rotation was similar in a mixed pine and a beech stand. Moss, Taylor & Easterbee (1979) and Newton (1986), working mainly in upland woods, concluded that in general the richest bird fauna was in

broadleaved, then spruce, then pine woods. French, Jenkins & Conroy (1986), in contrast, did not find pine poor for birds and their order was oak, conifers, birch. In Ireland spruce stands were found to have a less diverse bird community than the native yew woodland (Batten 1976).

Only the Scottish crossbill among British bird species has a specific requirement for one particular tree species (Scots pine). Other woodland types, e.g. western sessile oakwoods do have distinctive bird communities, but this reflects more than just the presence or absence of a particular tree species (Bibby 1988).

French, Jenkins & Conroy (1986) found that in general mixed broadleaf/conifer woods where the minor component formed at least 20% of the total held more birds and more species than less-mixed woods. A mixture in clumps was better than a uniform, intimate mixture. In contrast, Bibby (1987, 1988), who looked specifically at the effects of having different areas of broadleaved species distributed through a coniferous stand, concluded that dispersing the trees as small groups or even as individual trees would produce the greatest gains in bird species or populations for a given total area of broadleaves.

4.6.3 The effects on birds of a change in stand structure

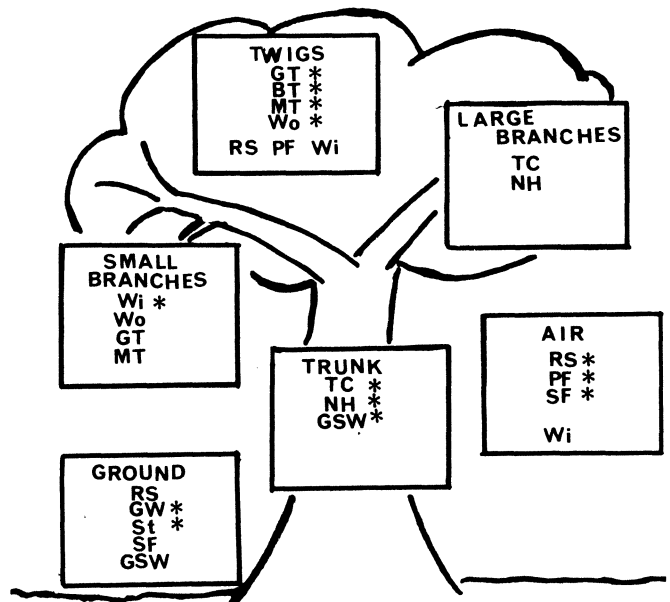
4.6.3.1 Variations in the density of different layers

Birds vary in their preferences for canopy height in which to feed and nest (4.6.1.3). Edington & Edington (1972) illustrate for one particular wood in Wales the way in which different species use the different habitat elements present.

High forest with an understorey, shrubs and ground vegetation, i.e. with a wide range of canopy height, supports more species and individuals than high forest with a uniform high canopy (French, Jenkins & Conroy 1986; Newton 1986). Smith, Averis & Martin (1987) in the Forest of Dean similarly found species that were associated with relatively dense shrub cover (although the mean cover was only 15%), but others that were associated with low shrub volume (tree pipit and to a lesser extent redstart and pied flycatcher). Levels of competition between species may be influenced by the degree of shrub cover (Stowe 1987). As shrub cover increases so does the ratio of blue tits to flycatchers.

Figure 4.3 Differentiation in habitat use by birds in a Welsh alder wood (after Edington and Edington 1972).

GT great tit
BT blue tit
MT marsh tit
Wo wood warbler
Wi willow warbler
Tc tree creeper
NH nuthatch
RS redstart
PF pied flycatcher
SF spotted flycatcher
GW green woodpecker
GSW great spotted woodpecker
St starling
* most popular feeding zone



Retaining clumps of trees and bushes of about 0.5 ha when the rest of a broadleaved wood is felled helps to maintain the breeding bird population (Williamson 1972). In relatively open park-like situations clumping of shrub layer can be important (Hooper, Crawford & Harlow 1973).

The presence of berry-bearing shrubs may influence bird populations (Snow & Snow 1988). Sorensen (1981) compared species feeding patterns in Wytham Woods, near Oxford, from late August to May. Tits fed largely on white and black bryony, honeysuckle, woody nightshade, elder and bramble, and mainly in the early part of the study period. Thrushes also used the last two species, but took more haws, sloes and rose hips, and more in the middle and end periods. Such shrubs are more likely to occur in coppice, or long-rotation broadleaved high forest stands than other types of system.

Broome (1980) compared the birds recorded by the point count method in June and August in three differently managed beechwoods (Table 4.1). Only plot F contained dead wood and holes in the oldest, dying trees. The bird community consisted of a common core of species with more added in Q and F and a further set in F. All comparisons of the bird community showed that F and Q were most similar, F and S most dissimilar. The differences in bird communities were related to the vertical structure (hence F and Q richer than S) and the presence of dead wood (hence F richer, because of the hole-nesters, than Q and S) although there were differences in horizontal (woodland) structure as well.

Table 4.1 Stand characteristics and no. of species of birds recorded in differently managed beechwoods (Broome 1980).

Plot	F	Q	S
Location	Frithsden Beeches	Queen Wood	Shotridge Wood
Size (ha)	22	33	30
Management	Minimal; old trees and natural regeneration in gaps; occasional removal of dangerous trees	Group selection; contained no very old trees	Even-aged, about 130-150 years; thinned at intervals
Cover profile:			
canopy 15-30m	most	most	all
canopy 1-15m	some	some	none
ground vegetation	about 40%	about 40%	70%, mainly bramble
No. of bird species	34	23	15
Total no. of species recorded:		34	
No. of species common to all three plots:		14	
No. of species found only in F and Q:		9	
No. of species found only in F:		10	

4.6.3.2 Dead trees and nest-boxes

Dead standing trees or dead branches on trees are vital for hole-nesters. The total number of hole-nesting birds (nine species, ranging from willow tit to tawny owl) was directly related to the number of trees with dead branches in neglected lime/ash coppice going to high forest (Fuller & Taylor 1983). The proportion of stand basal area that was dead was the best predictor of the number of species and of total

density in a wide range of stand types in southern Sweden (Nilsson 1979).

Lack of nest sites in stands without suitable dead wood limits the density of hole-nesting song-birds but they take readily to nest-boxes (East & Perrins 1988; Newton 1986). Non-passerine hole-nesters also depend on suitable dead wood for their, usually larger, holes, although the tawny owl for example may use other sites if holes are not available (Petty 1988), so that provision of nest-boxes does not always raise the population.

Nest-boxes cannot replace over-mature, dying and dead trees where they are important as feeding sites. The size and shape of the territories of great spotted woodpeckers vary according to the quality and quantity of the dead wood available (Smith 1987). Standing dead trees used for foraging were in an earlier state of decay than those used as nest cavities (Swallow, Howard & Gutierrez 1988).

The significance of standing dead trees (snags) for birds (and some mammals) has been extensively investigated in the USA. Scott (1979) for example found a decline in species (mostly tree cavity users) in pine stands from which dead trees were removed experimentally. The characteristics and population dynamics of standing dead trees, and their use by birds, in Douglas fir stands are described by Cline, Berg & Wright (1980) and Mannan, Meslow & Wright (1980). Recommendations for maintaining this type of habitat include leaving some very old stands (over 200 years) unfelled and leaving some large dead trees when an area is felled. Large snags are may be preferred for foraging and nest sites and last longer than small ones (Raphael & Morrison 1987; Rosenberg, Fraser & Stauffer 1988). McComb & Muller (1983) suggest retaining in a stand some tree species known to be prone to dying on their feet (birch might be the British equivalent) and deliberately killing a few trees. Recommendations on the number and size of dead trees to leave vary but in mixed forests Zarnowitz & Manuwal (1985) suggested six broadleaves and three conifers per hectare with most greater than 50cm diameter.

4.6.4 The effects on birds of a change in woodland structure

A bird remains abundant in a stand only as long as that stand remains at a suitable structural stage. For some species the most suitable growth stage (and hence highest use by the bird) may vary according to time of year and sex of bird (Rolstad, Wegge & Larsen 1988). Structure changes rapidly during the early part of a rotation (whether coppice or high forest) so that to keep the open phase birds a sequence of recently-cut stands must be maintained in a wood. Similarly for nightingales a sequence of fairly young dense stands are required (Bayes & Henderson 1988; Studdart & Williamson 1971) which were regularly provided by a 12-25 year coppice cycle. During the latter part of a rotation the structure is more stable and remains suitable for the species that use the old stands for longer.

The richest bird community for the wood is maintained by a patchwork including all stages assuming that the birds are mobile enough to move from one stand to another as they change in suitability. In afforestation sites Moss, Taylor & Easterbee (1979) found a maximum of twelve song-bird species in any one stage in the rotation, but the list for the forest as a whole was around twenty-five species. However what scale of patchwork would be best: should individual stands be of 1, 2, 5, or 10 ha?

4.6.4.1 Scales of woodland structure for song-birds

On Deeside intimate mixtures were less good than clumped ones (French, Jenkins & Conroy 1986). Clumps of 0.2 to 0.8 ha (50-100m diameter) were needed to allow for a bird with a preference for the minor tree species to maintain its territory entirely in the clump. Most quantitative measures of the bird community were higher with four or more distinct profile types in 10 ha. Profile types were mapped down to 0.2 ha.

Glades (gaps) counted as a distinct profile type, as did a 15 year age difference, or presence of a shrub layer. The best woods for birds contained around 20% glades by area, of average width 20-35m (about 0.03-0.10 ha). Glades were defined as at least 15m diameter, i.e. excluding the ubiquitous small gaps resulting from thinning or loss of one or two trees during establishment, and ranged from 0.02 to 1.0 ha with many small glades and a few large ones.

French, Jenkins & Conroy (1986) recommended that even-aged stands over 5 ha should be avoided, so that the best woodland structure for birds is a patchwork of stands 0.5 to 3 or at the most 5 ha, with clumps of minor tree species down to 0.2 ha and glades down to 0.03 ha. Rides were no substitute for glades, but restocking areas count as glades for a time. These areas would provide the large glades of one hectare per 10 ha suggested, but unless they remain suitable for many years or the rotation is very short restocking areas could not account for the 20% total area of glades. The remainder would have to be a rather high level of "blank" throughout the older stands.

These figures provide a starting point but they may not apply to other woodland types or other regions. In North Wales even single broadleaf trees in a conifer plantation could add to the overall bird diversity, whereas size of restock areas was not important (Bibby, Phillips & Seddon 1985).

4.6.4.2 Edges

Fuller (1988) and Fuller & Whittington (1987) found higher densities for some bird species at the edge of woods but not at internal edges, e.g. rides. This was attributed to better development of shrub layers near woodland edges and consequently the "edge effect" may be more pronounced in stands whose interior lacked a shrub layer (overstood coppice or thicket stage plantations) than where the shrub layer was well developed throughout.

Song-birds in two Buckinghamshire woods differed in their use of the edge and the interior of a wood (Fuller 1988). The willow warbler was an extreme edge species and did not occur in the interior; the chaffinch occurred in both areas but seemed to prefer edges (nests at higher density); the robin occurred on the edges and in the interior; and tree creeper and nuthatch were definite interior species and avoided edges. Research continues, including the question of whether the edge of a clear felled area within the wood produces the same effect.

4.6.5 The effects on birds of changes on the site

4.6.5.1 Herbicides and pesticides

Few studies explicitly examine the effects on birds of work on the site, but the reduction or loss of ground vegetation or shrubs during weeding and cleaning reduces the vertical diversity of structure (loss

of feeding and nest sites) until or unless these layers redevelop later in the rotation.

Moss, Taylor & Easterbee (1979) state that using herbicides on ground vegetation reduces the habitat for song-birds. Morrison & Meslow (1984) found some shifts in the use bird species made of shrubs, ground vegetation and small deciduous trees in a 5 year-old Douglas fir plantation sprayed with glyphosate to reduce shrub growth. These changes were short-lived, however, because the vegetation recovered within a few years. In contrast Cayford (1988) found greater use of herbicide-treated areas by black grouse in N. Wales. The reduction of Calluna vulgaris by the herbicide may have increased the amount of the lower growing Vaccinium myrtillus berries that were accessible to the birds.

Pesticides are not widely used in lowland broadleaved forests. Monitoring of the pine beauty moth control programme using fenitrothion in northern Scotland has shown no short-term effects on bird populations although they have been reported from Canada (Crick & Spray 1987; Spray, Crick & Hart 1987). Stribling & Smith (1987), working in oak/maple forests in North America concluded that the spraying for gypsy moth had not affected the avian fauna. However the potential effects of any new programme of pesticide application are very great and need careful study beforehand.

4.6.5.2 Site preparation

Sites of higher fertility generally support more birds though not necessarily more species (Newton 1986). The use of fertilizer to raise the productivity of sites might in the long run lead to denser bird populations although the consequences for the ground flora would be undesirable (3.5.3.3).

Birds are affected by the general intensity of management. If every piece of marketable wood is harvested, if site preparation produces almost bare soil and weeding and cleaning are ruthlessly efficient then the bird community will decrease in total size and contain fewer species. Currie & Bamford (1981) showed how different from afforestation of grassy or heathery sites was restocking on a site where there was dead wood, patches of shrubs and brambles and birch regeneration among the spruce. The restocked plot surveyed held much richer and different bird communities, without the meadow pipits or whinchats which were abundant on the afforestation plot. Disturbance, particularly during the breeding season must also be considered, particularly for large or scarce species with a few traditional nesting sites (Petty 1988).

4.7 Effects of forestry practices on mammals

4.7.1 Introduction

Mammals need food, shelter and breeding sites, but the larger species can survive when these needs are met by separate areas in the wood (Staines 1983). Some species are only likely to flourish at particular stages in the rotation (e.g. field vole just after felling, squirrels from the pole stage on) and must move from stand to stand or from reservoir habitats such as rides and glades. Deer and predators use all stage of the rotation, tending to favour early stages for food and later stages for cover. The larger predators (fox, badger) breed in woods, but may use open ground outside the wood for feeding. Several

mammals are more common or at least more conspicuous outside woods, e.g. mole, hedgehog, red deer. Most however can live in a variety of woodland types. Like birds, mammals depend on the stand and woodland structure as much as on the tree species composition.

Because of their mobility many mammals may be able to tolerate or use seasonally sub-optimal habitat within their range provided there is enough of the preferred stages. For example, in an American study martens made most use of unfelled or partially-felled stands, but did forage in clear-felled areas for raspberries when these were available (Steventon & Major 1982).

4.7.1.1 Changes during the rotation

Field voles are often very abundant in the early stages following afforestation, but soon disappear and bank voles and woodmice become more common (Ferns 1979). There have been few British studies, however, of changes in the later stages of an established woodland rotation. The dense bramble growth common on many felled or coppiced areas might be expected to favour the bank vole: Pigott (1985) reported that bank voles were found inside an ungrazed enclosure at Grizedale that had a bramble layer, but absent from the surrounding much lower, grazed woodland vegetation. Preliminary results from worked coppice at Bradfield Woods (Suffolk) (Hicks 1986) show that one-year old coppice was dominated by wood mice (Apodemus sylvaticus); common shrews (Sorex araneus) and bank voles (Clethrionomys glareolus) appeared by the second summer when there was more ground cover and increased dramatically in the third year.

Wolk & Wolk (1982) noted the change in species and increases in numbers following clear felling in parts of Bialowieza Forest, but the open phase species had disappeared between years 15 and 20 after which the community structure was similar to that in the old growth. In North America increases in small mammal density following clear felling of spruce/fir forests are common, paralleling the increase in ground cover and food availability (Gunther, Horn & Babb 1983). However, some studies of the sequence of species through a rotation show highest numbers in stands more than 80 years old (Scrivener & Smith 1984) and declines in some species following clear felling (Gashwiler 1970; Halvorson 1982).

Maser, Trappe & Nussbaum (1978) showed that the vole species typical of the old-growth forests in Oregon, Clethrionomys californicus, depended on fungi which were much reduced in the clear-felled area and hence declined, whereas another species, Microtus oregoni, could take advantage of the greater herbage growth and increased. There does not seem to be such a high degree of specialization in the British and central European small mammal faunas, although as in old-growth forests in the USA (Thomas 1988) British bats may depend on old trees locally as roost sites.

The populations of red deer found at different stages in upland plantations have been modelled by Ratcliffe, Hall & Allen (1986), but there appears to be no comparable study for muntjac or fallow in lowland woods. Bitter experience shows, however, that these species move into recently felled or coppiced areas to feed, while sheltering in nearby older stands.

4.7.2 The effects on mammals of a change of tree species

Few mammals depend on broadleaves but many occur at lower densities in other habitats (Staines 1983). Broadleaved trees can provide more

food than conifers because of the large fruits (acorns, chestnuts, haws, hazelnuts) and the greater biomass of invertebrates (4.2.2). Berry-bearing trees may be particularly important for dormice (P. Bright personal communication). Also most broadleaved stands have some ground vegetation during the whole of the rotation (beech and hornbeam being the main exceptions) and are more likely to contain shrubs; both layers provide food and shelter for mammals. High annual fluctuations in seed and fruit production mean that in some years the tree layer may be important, in other years the shrub layer (Smal & Fairley 1980). In Great Britain old broadleaved trees (rather than conifers) are more likely to have large hollows within them which are suitable for bats. Ash and alder tend to be better than oak, since the larger holes in oak may allow squirrels in (J. S. Messenger personal communication).

Encouraging the development of ground vegetation and shrub layers and allowing shrub growth along rides and in odd corners could reduce the generally deleterious effect of converting broadleaved stands to conifers.

The red squirrel is an exception to this general rule that broadleaves are better for our native mammals than conifer stands. Both red and grey can use either broadleaves or conifers but the red has a stronger preference for conifers and conservation of the red is promoted by large contiguous stands of conifers at the pole stage and later (aged 25-80 years for Scots pine) (Corbet & Southern 1977; Gurnell 1988).

4.7.3 The effects on mammals of a change in stand structure

Generally, small mammal populations are related to the diversity and amount of low cover for shelter and food (Geier & Best 1980). Species requiring ground vegetation (e.g. bank vole) or shrubs with high branch overlap (e.g. dormouse) are sparse or absent without these layers in a stand. Coppice provides both ground vegetation and a shrub layer with only short absences (scanty ground vegetation at late stages if the coppice is dense or cut on a long rotation; a low, scattered shrub layer in the first few years of the rotation). Thus worked coppice may be an unusually good habitat for small mammals.

A key feature for dormice appears to be a continuous and dense shrub and tree canopy in which the animals spend most of their lives. This could perhaps be provided in high forest with a well developed shrub layer although the latter tends to occur, if at all, only in very old high forest stands. Dormice densities may also be limited by suitable nest holes and higher levels have been found in woods with nest-boxes (Bright 1987).

4.7.4 The effects on mammals of a change in woodland structure

Shortening the rotation produces a rapid increase in the proportion of a normal forest occupied by stands under 20 years old preferred by deer (Staines 1983). This would generally encourage species thriving in early stages at the expense of those dependent on later stages and large trees. Several bat species roost or hibernate in hollow trees (Steele 1975) which are liable to be removed under commercial management for wood production. Reducing the size of the felling coupes creates a smaller scale woodland structure which provides more edges. This should benefit bats that hunt along rides or margins of stands (Steele 1975).

Small-scale structure is essential for dormice which are reluctant to cross open space. Patch sizes of not more than 0.2 - 0.5 ha have

been suggested (P. Bright personal communication).

Woodland structure is particularly relevant to large mammals, especially deer which may use different stands for different purposes. Thicket stands may provide more cover while adjacent older, more open stands are used for feeding. Deer are mobile enough to use the large-scale woodland structure of upland forests and to find isolated small areas of suitable habitat (König & Gossow 1979). Woodland structure may be deliberately designed to help monitor deer numbers and their control by shooting. Two to five glades, of 0.2-1.0 ha, per 100 ha are recommended by Ratcliffe (1985) and these can include existing glades or strips along streams with grassy vegetation.

In North America increased food (ground vegetation) after clear felling often increases the population of game (deer, grouse) over the previous mature stand (and probably over an alternative selection forest). Pengelly (1972) however pointed out that clear felling was not always followed by a rise in deer numbers partly because of their behaviour: deer need cover and may not move far from it for food. Movement in hilly country may be hindered by new roads with steep unstable sides and by much deeper-lying snow in clear fells which in one case was 90cm compared to 20cm in the adjacent mature stand. (Deer movement is hindered by snow over 50cm deep).

Clear felling is under the control of management and can come in different sizes, shapes and patterns (Resler 1972). Some studies have suggested guidelines for clear felling to maximize the increase in deer, e.g. areas under 8 ha or strips less than 320m wide were advised for deer and elk in spruce/fir forest in Arizona. In Great Britain increases in deer numbers are not favoured either by nature conservationists or foresters so that such research may be most valuable in illustrating practices to avoid.

In lowland areas a return to small-scale coppicing is restricted by the effects of deer on regrowth: large areas felled or cut are less damaged because total browse availability is greater in relation to deer numbers. Rabbits may similarly nibble back or bark seedlings and saplings and there is also increasing evidence for the rôle of small mammals in determining the balance of species in regeneration (Pigott 1985). In this way changes in mammal populations may determine the changes in forestry practice that are possible rather than being an effect of them.

4.7.5 The effects on mammals of changes on the site

Control programmes against mammal pests such as the grey squirrel using poison bait (Warfarin) have to be limited in areas where this poses a risk to other mammals or birds of high conservation value.

Weeding and cleaning mean the temporary or permanent removal of sources of food, shelter and breeding sites for some species; any intensification is likely to reduce dependent mammal populations. Sullivan & Sullivan (1982) did not find any change in small mammal populations following an aerial application of herbicide to a 20 year-old Douglas fir plantation, but here the herbicide was aimed at broadleaved trees and shrubs and it is not clear how much of the ground vegetation was actually killed; the changes in ground cover may not have been as great as expected. Ritchie, Harestad & Archibald (1985) and Santillo, Leslie & Brown (1989) did find reductions in small mammal populations in glyphosate-treated clear fells, almost certainly because of the indirect effects of reducing the vegetation cover and invertebrate populations (4.2.5).

4.8 Discussion

4.8.1 General points

The huge variety in size and life-cycle of animals makes it difficult to generalize about the effects of the changes caused by forestry. There are different responses even in small groups. Among the butterflies, the speckled wood can thrive in grassy rides irrespective of the neighbouring stands; others such as the fritillaries are best catered for by the early stages of the rotation; and the white admiral requires the later stages. These last two examples also show the chains of cause and effect that link animals to their habitat: it is not the stage itself which matters but the response of the ground vegetation at these stages (violets and honeysuckle respectively).

The types of change that favour particular species or groups may well disadvantage others and this conflict is inevitable. Management for high diversity could be detrimental for rare species (Stauffer & Best 1980). The specialist species tended to be lost in managed rather than primeval pine forests in Finland, even though the total bird densities in the two areas were not different (Virkkala 1987). Thus for a particular site and time it is necessary to choose the groups to favour. McIlroy (1978) pointed this out for Australian birds and mammals in the debate on timber felling and multiple land use. Outside large reserve areas with minimum intervention, other areas would have to be managed differently and solely for particular desired species (or group of species) of wildlife. No single management would benefit them all.

In Great Britain there are sites of high value for certain groups or for rare species where directed management is necessary. This is particularly true for species in ancient woods since most sites are small and the options for combining different requirements correspondingly less.

For animals overall, change of tree species can have the largest effects, especially for small or less mobile animals at a low trophic level. Changes in the structure of the stands or of the woodland are second in importance, particularly for larger, mobile animals at higher trophic levels. Where the effect of a change of tree species is indirect (e.g. through the ground flora) there is often scope for management of structure to offset the deleterious changes.

4.8.2 Change of tree species

Elton (1966) proposed the principle of the Inverse Pyramid of Habitats where there is a greater habitat range the higher the trophic level (but fewer animals, the Pyramid of Numbers). The preferences of small herbivores for their host species, ranging from monophagous to polyphagous, mean that their pattern of occurrence is closely related to the pattern of plant species. The pattern of predators and parasites becomes more diffuse and top predators (birds) show even less relation to the pattern of plants, becoming more influenced by the structure of the habitat. Large herbivores such as birds and mammals do not fit into this scheme well because they range more widely and need several habitats to provide food, shelter and breeding sites.

The effects of changing tree species depend on the group or species considered. There are direct effects, and indirect effects through the shrub and ground vegetation layers. If the essential tree, shrub or ground vegetation species is eliminated or replaced then strictly

dependent species, mainly herbivores, will be lost. Less closely-associated species (polyphagous herbivores, predators and parasites) may decrease in numbers, or be lost if they cannot find a suitable replacement plant species. Least affected are top predators especially if the stand structure is not altered.

The detailed changes also depend on which particular tree species are involved. Some generalizations on groups of tree species are possible. Within a group the changes between species will be less than those between species from different groups. The first distinction is between broadleaves and conifers. Among the broadleaves oak, birch and willow stand out as exceptionally rich in numbers of associated insect species. Oak, hazel and beech are important as fruit producers. Ash though poor in associated insects itself usually has a rich ground flora whereas beech because of its heavy shade often has poor shrub and ground vegetation layers in managed high forest.

The insect fauna of conifers is much less well known (Welch 1986) and likely to be of lesser interest in nature conservation terms because the insects are usually introductions or widespread polyphages. Division on the basis of the indirect effects through the ground vegetation may be the most useful approach. Pines often have good shrub and ground vegetation layers which may not be eliminated at the thicket stage and some of the fauna of the native Scots pine may transfer to others. Heavy shade-casters (spruces, firs, western hemlock, western red cedar, Lawson cypress) eliminate ground vegetation as thickets and little returns later. Larches and Douglas fir are somewhat intermediate: Douglas fir does and larches can eliminate the ground vegetation but at later stages it returns, as often do some shrubs (3.2.1; 3.2.2).

Given the difficulty of establishing the effects of one tree species it is not surprising that the effect of the infinite variety of mixtures is unknown. For invertebrates a mixture could support more species in unit area by the addition of another set or sets of dependent species and the same is often true for birds (5.2.1.3). The relative merits of different arrangements of mixtures need further study.

4.8.3 Change in stand structure

Stand structure is particularly important for birds and mammals and if the structure is suitable they may be largely indifferent to the tree species within broad groups. The change from coppice to high forest may involve the loss of animal species typical of the shrub layer and the gain of upper canopy species. High forest with a shrub layer could retain at least some of the shrub species. However, those animals affected by stand structure are probably more affected by the structure of the woodland.

4.8.4 Change in woodland structure

In general the two sets of species which by their nature are most likely to suffer from changes in the woodland structure are those at either end of the rotation (open ground species and those associated with over-mature timber or rotting wood). These are the stages most easily lost completely from a site either by management or, for open ground, by neglect. Both groups contain species known to be poor colonizers. Hence the value of maintaining in all managed woods both open ground, e.g. wide rides, and some minimal intervention areas.

Ratcliffe, Hall & Allen (1986) used growth stages defined by top height to predict the changing proportions of the stages in two upland forests. Knowing the preferences of red deer for the stages as sources of food and shelter they could forecast the changes in populations and the probability of deer damage. This approach can probably be extended to other groups or species. However there is little evidence on what the minimum distances between stands of similar or adjoining stages should be for most species so that only general points can be made.

4.8.4.1 Scales of pattern

The scale of the pattern of stands is important. A small scale with patches in the range of a half to five hectares seems likely to benefit animals most as it produces horizontal heterogeneity on the scale of song-bird and mammal territories and within the flying capabilities of many insects. For some, e.g. dormice, the scale may need to be smaller. For animals that depend on particular stages of the rotation it reduces the distances to move to the next suitable stand, and increases the chances that all stages can be present in small woods. (The exceptions to this generalization are open habitat birds which might use early stages if of large enough area, but this is a problem of extensive upland afforestation not of forestry in long-established woodland.) For a given area of felling, the distribution of coupes, and therefore of the stands which follow, becomes important. There is probably more benefit from five 1 ha patches scattered through a wood than from one 5 ha patch (3.4.4).

4.8.4.2 Edges and ecotones

The concept of ecotones and the edge effect is well known (Odum 1971): the boundary between two habitats is richer in species and numbers because species from the interior of each habitat are present as well as species which need both habitat types or the distinct conditions created at the edge. The edge effect is most striking between woodland and open habitat. It is invoked for example to help explain why small woods often have denser bird populations than comparable larger woods (Newton 1986; 4.6.4.2).

For the most edge the stands should be small and irregularly shaped (tending to be long and thin rather than circular or square). However there are also species that avoid edges (e.g. the interior birds of Fuller (1988), (4.6.4.2)) which sets limits on how small stands should be. Edges between stands are most marked and last longest if the stands are at well separated stages, e.g. restocking and an old stand. But if the old stand is the next to be regenerated that edge now against a stand of young trees or thicket will become less conspicuous and will effectively disappear in time. Arranging the pattern of stands so that widely separated stages are adjoining, both at present and in the future as the trees grow, is difficult but could be useful if the maximum edge effect is to be obtained (Figure 4.4). It does, however, conflict with the idea of contiguity of adjacent stages for the least mobile animals (Figure 4.2). The need for clear wildlife objectives in planning the felling pattern is again emphasized.

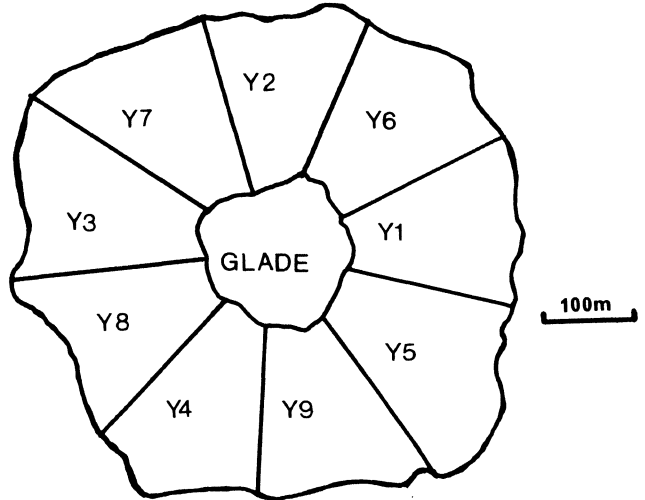
4.8.4.3 Rides and glades

Elton's (1966) concept of edge included rides and glades within the wood as well as the wood edge. Rides and glades are important for some species which spend their entire life-cycle there (speckled wood) or use

them at certain times (deer). They should remain unshaded as far as possible so they must either be wide to start with or be enlarged as the surrounding trees grow. Solar geometry dictates that in temperate latitudes east-west rides are the least shaded (4.3.4.2). Details of ride and glade management have been worked out (Steele & Welch 1973; Ratcliffe 1985; 4.3.4.2).

Figure 4.4

Arrangement of stands to give maximum edge and separation of stages (after Harris 1984).



4.8.5 Changes on the site

There are many studies on the direct control of animals by spraying, shooting, fencing etc., but less work has been done on the effects of other types of change on the site. Operations on the site often appear dramatic and damaging, but may have only limited long-term effects. Periodic disturbance by wind, fire, landslip, disease or pest outbreak must have caused major changes in conditions in natural temperate forests and the animals survived under such conditions. However, such naturally disturbed areas were generally small in relation to the total woodland cover and were surrounded at that time by undisturbed forest from which animals could recolonize, slowly or swiftly depending on the species.

With only isolated blocks of woodland now left the effects of changes on the site depend on the proportion of the stand or wood that is affected at any one time. There is little information on how quickly animals, but invertebrates in particular, can spread out from undisturbed areas and what constitutes a significant boundary to such spread. Tarmac roads may limit the movement of small mammals and beetles (Mader 1984). Even metalled or earth forest roads are a partial barrier. Dormice in particular may be unwilling to cross wide open extraction tracks (J. S. Messenger personal communication). The combination of deep ditches either side of a bare central strip seems a formidable barrier for small ground-living animals, at least in the short term.

4.9 Implications for nature conservation (fauna)

(a) The richest animal communities occur where there is a diverse woodland structure, but this diversity must be continually maintained if

the faunal richness in not to be a temporary phenomenon. In the small woodland patches now left a diverse structure can more reliably be achieved by management than by neglect. With a suitable scale of felling and associated treatments a high forest system could produce as diverse a structure as traditional coppice.

(b) Some groups, especially dead wood beetles, are not favoured by either managed high forest or traditional coppice. Senescent trees, large rotting logs and small areas with minimal intervention should be left to accommodate such species in managed woods.

(c) Species of the open phase, before canopy closure, are most likely to be lost by neglect. They can usually be accommodated through ride management and adjusted felling patterns even in intensively managed high forest, but this does not provide as much open habitat for these species as would be maintained in a worked coppice.

(d) Changing tree species has two effects on the invertebrate fauna: a direct one for those using the species as a host and an indirect one through consequent effects on the ground vegetation and shrub layers. A few native tree species are very rich in associated invertebrates, but others less so. More attention should be paid to which individual species are lost or gained by a change of tree species and to the indirect effects on the invertebrates of the lower vegetation layers.

(e) Birds depend more on the structure of the stand or the wood than the tree species in itself, but the variety of invertebrate food is usually higher in most broadleaved than conifer stands of a given age and structure. Within stands, developing patches with a good shrub layer (particularly favoured by summer migrants) and with some over-mature trees left (four or five per hectare) for hole-nesters provide most benefits. This type of structure can be achieved either in broadleaved high forest or in coppice with standards. Within the wood a pattern of open, dense scrubby and tall tree areas is desirable to provide conditions for the birds of different stages. This can be provided by any system (if standards are present in the coppice) if the area is large enough to develop a normal age structure.

(f) Individual mammal species, e.g. dormouse, red squirrel, have specific requirements, but most are favoured by well-developed ground flora and shrub layers. Most mammals are relatively mobile at least between stands within a wood and in many cases between woods. Hence provision of areas of dense ground or shrub cover can be rotated round the site through a normal forestry rotation. Tree species that provide good fruit crops or that permit good growth of shrub or ground layers should encourage the mammal populations. Leaving over-mature and fallen trees is also beneficial by providing shelter and increased food.

(g) Site preparation or tree protection treatments such as screefing or herbicide application that reduce or eliminate ground flora are likely to have corresponding effects on the fauna, but these may be shortlived according to the availability of alternative food supplies and the mobility of the animal species.

(h) Direct pest control programmes may have adverse effects on other species.

5 DISCUSSION

5.1 Introduction

The previous chapters have followed an analytical approach, in order to try to understand each item in isolation. Our aim in this discussion is to generalize about the four types of change identified. We suggest how the previously described research can be applied to the real questions that arise in trying to assess the effect of particular forestry proposals. It must be repeated that this review is not a set of prescriptions for nature reserve management, but an attempt to explore how far modern forestry practices and nature conservation are likely to be compatible, where there are both timber production and conservation objectives for a particular site.

Finally we consider possible future research lines. There is a dearth of British data that can be used to make quantitative (or even in some cases qualitative) predictions as to the effects of particular changes in either tree species or treatment.

5.2 Generalizations about types of change.

5.2.1 Change of tree species

5.2.1.1 The role of trees

Tree species have three rôles in nature conservation (Peterken 1981). They are part of the semi-natural community of trees and shrubs; they provide a suitable environment for many organisms; and they are hosts (used in a general sense), i.e. substrates for epiphytes, food for herbivores, and complete habitat for the larvae of wood-boring insects. The species matters much more in the first and third rôles than the second. The importance of a change of tree species varies therefore according to why the site is valuable for nature conservation. If because of the tree and shrub community or the closely associated insects then a change is much more damaging than if the value is only in the ground flora or the song-bird community which may survive under a range of other species if appropriately managed.

5.2.1.2 Grouping tree species by their relative effects

When the tree species is altered some change is inevitable because each tree species exerts its particular influence on the soil, the other plants around it and on the fauna of the stand. It is not practical to detail all combinations of possible species changes but the species may be grouped so that within-group differences are much less than those between groups (Figure 5.1). For their effects on the soil (2.6.2) broadleaves, pine and spruce, and other conifers are the main groups. Beech and larch stand out from these as the species whose effects are most influenced by differences of site and management. For the ground flora (3.2.2.4) the main groups are broadleaves, pine, and spruce and other (heavy shade-casting) conifers. Here larch and Douglas fir are the main coniferous exceptions with marked changes in their ground vegetation through the rotation, again to some extent mediated by site or management. Among the broadleaves beech and hornbeam stand out because of the dense shade that they cast. For the fauna (4.8.2) the groups follow those for the ground flora except that pine, larch and

Douglas fir are lumped together (all can be diverse in vertical structure with good ground vegetation and shrub layers for part of the rotation) and the broadleaves are divided. Oak, birch and willow are especially rich in associated insect species; beech and hornbeam can often have poor shrub and ground flora layers.

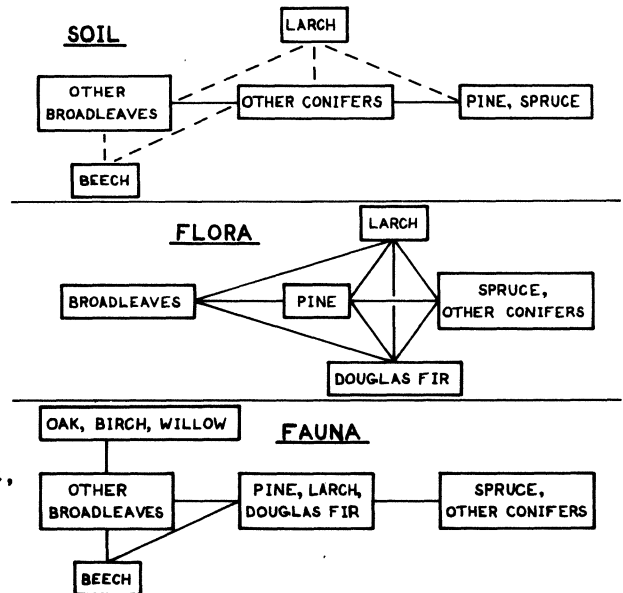
The most extreme changes are likely to take place between broadleaves and spruce. This does not mean that there will be no effects of changes of tree species within a group, merely that they are much less than between groups.

5.2.1.3 Effects of tree mixtures

Tree species vary in the environmental conditions they provide and so a mixture produces greater heterogeneity within a stand. This should enable a wider range of species to survive (3.2.3; 4.6.2), but it does not always occur in practice. Consider an existing wood composed entirely of one tree species A compared to similar stands with increasing amounts of a second species B. Assuming there are no barriers to colonization by any associated plant or animal species and that the pattern of the mixture is irrelevant, then the species content of a mixture may be represented by Figure 5.2a. However if there is no chance of colonization by species associated with the new tree then the species content of the mixture depends on which pure crop was the starting point (Figure 5.2b,c). Figure 5.2d illustrates what happens where some species require a minimum amount of tree B before they can colonize the mixed stand. Finally if some species are of higher nature conservation value than others then the value of the mixed stand may be as in Figure 5.2e. The more dissimilar the species in the mixture (e.g. Japanese larch/Douglas fir or ash/sycamore compared with Sitka spruce/western hemlock or beech/sycamore) the more heterogeneous the conditions in the stand and hence the greater the potential change in the mixture.

Figure 5.1

Tree species grouped according to their generalized effects on soil, ground flora and fauna. The differences between species within a group are less than those between groups. The number of links indicates the degree of difference, e.g. for the ground flora spruce is one step from pine, larch or Douglas fir but two steps from broadleaves. Pine is not intermediate between spruce and broadleaves but only one step from either. For soil, beech and larch are outliers because their effects show interactions with site and silvicultural treatment, hence the pecked lines.



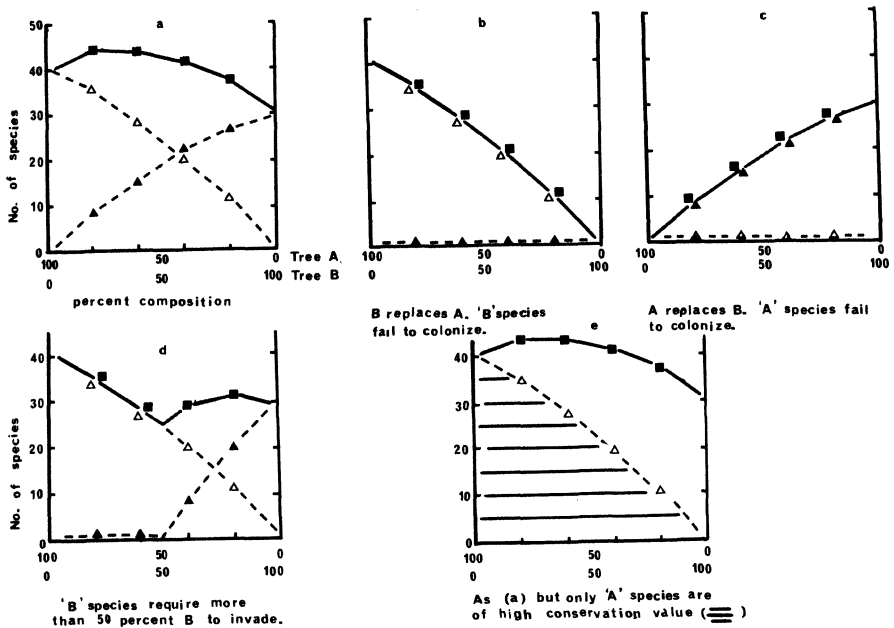


Figure 5.2 The effects of species mixtures on the species content of a stand. (Δ) no. of "A" species; ($\blacktriangle$) no. of "B" species; ($\blacksquare$) no. of species under the mixture of trees A and B as the proportion of each varies.

Two further points should be made about this model of the mixture effect. First, if there are interactions between the trees in the mixture e.g. in the breakdown of litter or in the flora (2.2.8; 3.2.3.1) or because a butterfly such as the purple emperor requires two tree species, then the species total of the mixture may be greater than predicted from a study of single species stands. Secondly casual observation suggests that the influence of conifers in mixed conifer-broadleaved stands is determined by their share of the canopy or basal area, rather than their proportion of stems.

5.2.2 Change in stand structure

For nature conservation, as a general rule, the more layers of vegetation and the more diverse the stand structure the better. A major difference in an individual stand between coppice and high forest are in the different lengths of the later stages of the rotation. High forest with shrubs should be almost as good as coppice with standards for conserving the shrub flora and the associated fauna, e.g. many birds, dormouse. This could be achieved by planting final crop trees at wide spacing with tree shelters and accepting coppice regrowth or regeneration from seed of other native species on the site as a matrix which might provide some useful thinnings (depending on species and local markets) (Kirby 1984a). However, productive crops of conifers or heavy shade-casting broadleaves, such as beech or sycamore, are rarely compatible with a good shrub layer.

The woodland structure must also be adjusted to compensate for the less frequent opening out of individual stands in high forest compared to worked coppice. If this is not done, then, as in neglected coppice, the change to high forest leads to long-term reductions in the early stage species such as the heath fritillary butterfly.

5.2.3 Change in woodland structure

5.2.3.1 Value of small-scale patterns

A small-scale pattern of woodland structure is likely to have most benefits for nature conservation (3.4.2; 3.4.4; 4.3.4.1). Slowly mobile animals have the least distance to move to suitable stands, there are more edges and stands of all stages are more likely to be present in a wood of any given area.

The four silvicultural treatments compared by Metzger & Schultz (1981; 3.4.3) produced differences in the shrubs and spring ground flora in stands of 0.5 ha. Just as for the Bradford-plan selection system (Harris & Kent 1987a; 3.4.2) much of the diversity of ground flora resulted from different stages of an even-aged stand being brought close together as small patches in one stand at the same time. However, there may be some drawbacks in going to the limit of single tree selection unless the open phase conditions can be maintained separately, e.g. along rides. In addition because the true selection system must use shade-tolerant trees it is difficult to practise with native species in Great Britain.

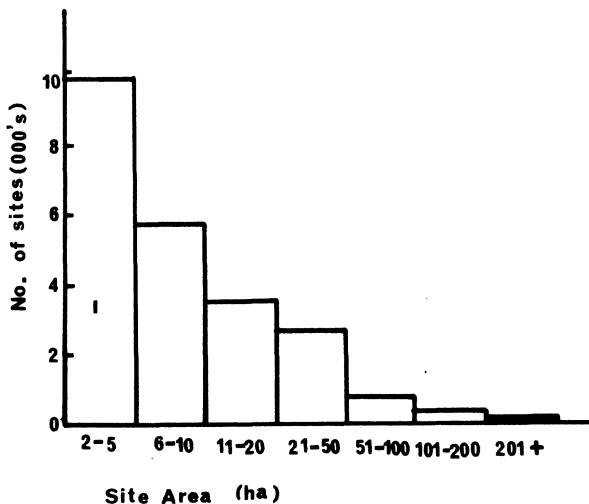
Clearly a similar variety can be maintained with clear felling if all stages are present in a wood (rather than in the same stand), as in the normal forest. However, diversity is likely to be less because each stage is more uniform the larger the block in which it is present (3.4.4). Also, the possibility of even achieving a normal forest structure with clear felling may be limited by the size of the woods, since the longer the rotation, the smaller must be the clear-fell if all growth stages are always to be present.

5.2.3.2 Achieving a stable woodland structure in small woods

Most ancient woods are small (Figure 5.3). A stable woodland structure can be maintained in such sites by coppicing because the coppice rotation is short. To achieve a stable high forest structure with the consequent much longer rotation constrains the manager to adopt group selection or selection systems. These are, however, just the sites where the extra complexity of selection systems and the small size and difficulty of extraction of each harvest may prevent their adoption. Thus the most desirable woodland structure may be difficult to achieve for practical and economic reasons.

Figure 5.3

Size distribution for ancient woods based on 80% of counties in England and Wales.



A further complication may be that the desirable woodland structure is unattainable from the present starting point without losing some of the current nature conservation value. For example a neglected broadleaved wood may have a high nature conservation value because of the rich fauna of dead wood insects, hole-nesting birds, etc. It is almost impossible to organize the regeneration of such a wood to achieve a structure with all stages always present, and still maintain some old stands until the new structure is complete (Kirby 1984a), without severe economic penalties.

This intractable problem is the result of the fragmented state of lowland woodlands, the practical limits and difficulties of small-scale working, and the arithmetic of long rotations and small areas. On such sites compromise between nature conservation and timber production objectives may not satisfy either. Alternative forms of income from the wood might be sought; the nature conservation value may have to decline in the short term; or efforts should be made to expand the woodland so that multiple objectives do become possible.

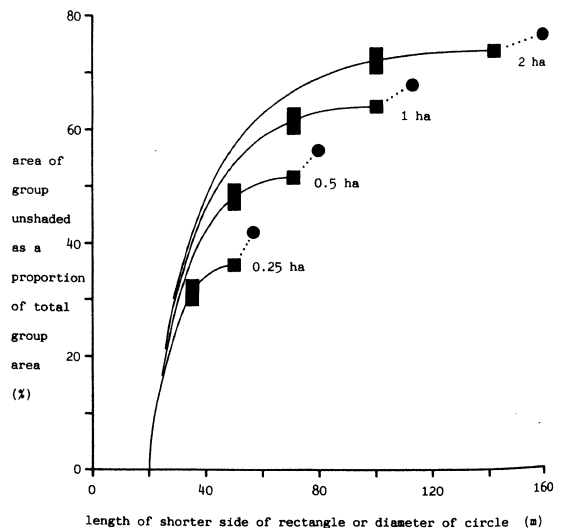
5.2.3.3 Size and shape of felling coupes

To obtain a small-scale pattern of woodland structure the regeneration of stands in groups of around 0.25 ha (56m diameter) is often advocated. However, the smaller the group, the more shaded it is by surrounding trees (especially at the start when the groups are made in an old stand), therefore the greater the restriction to the use of shade-bearing species in restocking (and few native trees are shade bearers). Stern (1985) considered that 0.5 ha (80m diameter) was the minimum successful size for oak. At the 6 x 6m group extreme in the Bradford-plan only moderate to good shade-bearers can be used (1.3.4).

Secondly, if group size is small then the shape is severely constrained to a circle (Figure 5.4). Circles maximize the area which is more than a set distance from the edge. For example if the heavily shaded strip around the edge of a coupe is judged to be 10m wide, then the "unshaded" portion rises as the groups get larger: from 42% to 76% for 0.25 to 2 ha circles respectively. For 0.25 ha groups no rectangle, only a circle, has an unshaded area over 40%, but if the groups can be 0.5 ha any rectangle squarer than 38 x 132m has over 40% unshaded area. Similarly only a square or circle of 0.5 ha has over 50% unshaded area but for 1 ha any rectangle squarer than 45 x 222m has.

Figure 5.4

The effect of size and shape of coupe on the proportion of its area which is unshaded. Here "unshaded" is defined as the area within the 10m wide, heavily shaded, strip around the edge of the group. The symbols represent a circle, a square and a rectangle with the longer side twice the shorter. For a given size of group the square, and even more the circle, maximizes the area unshaded.



Thus a larger group size is more flexible in shape and could still minimize the distance in one direction that a slow colonizer has to travel. The same considerations hold as for rides (Warren 1985a; 4.3.4.2), so that rectangular groups with the long axis east-west are less shaded than those north-south.

Varying the shape of clear felled areas has been explored in North America with particular reference to integrating good deer habitat with timber needs (McComb 1982; Marcot & Meretsky 1983), but it may be worth further study here to take account of our rather different requirements for nature conservation. The size and shape of coupes are also important for landscaping and ease of working so that in any wood the final solution may be a compromise between these three considerations.

Overall, changing the structure of the wood probably involves less loss of production or profit for a given level of nature conservation benefit than changing the tree species or stand structure.

5.2.4 Changes on the site

There is a huge range in the intensity of site preparation and amelioration used in modern forestry practice: from the inevitable disturbance of felling and extraction, minimal weeding and no use of fertilizers of much forestry to the agricultural style of complete soil cultivation, complete weed control and heavy use of fertilizers envisaged for high productivity biomass coppices of poplar or willow. At the lower end of this range it is difficult to see much long-term effect but there is almost no work which would help to establish a limit of intensity beyond which the damage in nature conservation terms becomes unacceptable. We have, however, tried to suggest provisional guidelines, for example for soil compaction, herbicide use and the retention of dead trees (2.6.3; 3.6.4; 4.6.3.2).

The rides are probably more vulnerable than the stands to an increase in intensity of forestry because they can be easily subjected to over-use, improvement for vehicles or replacement by roads (3.6.5). Sympathetic management could avoid some of this. Rotational cutting of the edges would be best concentrated on the rides running east-west (4.3.4.2). If it is not possible to avoid all ride damage, least conflict with nature conservation interests is likely to arise if heavy use is concentrated on the intrinsically more shaded north-south rides.

5.3 Concepts and approaches

Management of coppice in the Middle Ages seems to have been delightfully casual (although the woodman may not have viewed it that way). Underwood was taken when it was ready and as required for immediate local use, and timber when needed for particular works. We can hardly expect to return to this except on the small-scale of outdoor museums, and as yet the markets for coppice are still sluggish.

There is a need in modern forestry, as in commerce and industry, for prediction, control and accountability. More information is available (other opportunities for resources, the ability to compare investments and yields) and society is organized such that a manager must account for the decisions taken to others (owners, trustees, accountants, the Inland Revenue, even to Parliament in the case of the Forestry Commission). Simple, predictable and controllable silvicultural systems are preferred and the options have to be evaluated using the best tools that forest economics can offer.

Rackham (1980, p.169) points out that the medievals would not have believed a mathematical calculation designed to compare the value of the underwood and the timber in coppice with standards, and that the calculation is very sensitive to assumptions about the interest rate. However this is no argument for abandoning such imperfect tools as exist. They must be used carefully, being aware of the assumptions and limitations of the method, and in the end the results should be over-ridden if necessary, taking what the economist calls a non-rational decision. It is still worth knowing what the economist's rational decision would have been however. The manager probably has to account for the difference, which represents the cost of non-monetary benefits such as landscape and conservation, to someone else. Such accounting may be easier if nature conservation has been incorporated right at the start of the planning process (Boyd 1987; Leslie 1981).

5.3.1 Nature conservation as an objective not a constraint

For any wood the ranking of the objectives differs according to the owner's wishes, the condition of the wood, the physical setting, legal restrictions, social pressures and so on. An important part of a management plan is the statement of priorities. For woodland nature reserves nature conservation should be the main objective, but on many other sites timber production has a high priority; and in areas such as the Chilterns landscaping and amenity are important factors. However, nature conservation should always be seen as one of the potential values of a wood alongside production, landscape, amenity, recreation or sport. The nature conservation objectives for a site can be either general, or be made more specific in relation to a particular feature of the wood such as a rich ground flora, bats in hollow trees, butterflies, or a rare bird (1.1.4).

Transferring nature conservation from a constraint to an objective may appear to be a sleight of hand deceiving nobody, but it puts the problems of reconciling nature conservation and wood production into an altogether more positive light. (Shaw (1983) and Thomas *et al* (1988) come to similar conclusions for forestry in Australia and the USA respectively.) Discussion can involve then the priority of nature conservation as an objective and how conflicts in achieving that objective are to be resolved, instead of trying to define standard allocations of money or land to be given up for nature conservation or the placing of equally arbitrary restrictions on some types of management. Ride maintenance, for example, becomes not an unnecessary cost to the woodland enterprise, but a way of achieving the nature conservation objective of the site without conflicting with wood production or other objectives. The cost of the operation is not reduced but it may make it easier to identify the benefits.

Moves along these lines are occurring. Under the Broadleaves Policy, for the first time within Forestry Commission grant-aided schemes, nature conservation can be the major objective of woodland management. Similarly the Forestry Commission now have a statutory duty to seek a reasonable balance between timber production and wildlife conservation (Forestry Commission 1986).

5.3.2. Nature conservation objectives must be defined

Traditional management such as coppicing has itself contributed to major changes in the woodland flora and fauna compared to the original

wildwood (1.1.2). No single group of species is favoured by all treatments; nor does any treatment favour all groups. Therefore those concerned with nature conservation must make clear their objectives and priorities in terms of groups of species, natural features or processes on any site (or nationally), before sensible debate can take place about the effects of a particular proposal or treatment. On most sites different prescriptions are needed for different areas (1.1.4, 3.6.2, 4.8.1).

Woodland owners and managers should contribute their particular conservation objectives for a site, but in general its value is judged in a wider, county, regional or national context, by how it contributes to maintaining natural or semi-natural communities or features, to maintaining or enhancing a diversity of woodland species and to the protection of rare species (1.1.4). If the treatments proposed fail to take account of these wider aspects the manager has failed to meet the nature conservation objectives: i.e. if the priority is defined as the lichens and ground flora, management to benefit the birds is inappropriate.

5.3.3. What is the level of acceptable change?

We have tried to indicate parallels between the changes in natural forests and in forests under traditional management or modern forest practice. Some modern practices may have no clear parallel (the use of chemicals or the introduction of non-native species) but the effects they bring about may be similar to some other agent acting under traditional management. Consequently the differences in the effects of modern forestry are frequently quantitative rather than qualitative: it is not that ground is disturbed during restocking, but that more ground is disturbed; it is not the reduction of species at the thicket stage in modern forestry that is distinctive, it is the greater reduction found in most plantations that is important. Qualitative changes (complete elimination, sudden introduction of a species or feature) do also exist but the significance of these is fairly easy to debate; more work is needed to determine the consequences of different degrees of change. Where does the acceptable limit of change lie if the objectives of nature conservation are to be met?

The more that nature conservation objectives at the site level can be expressed in quantifiable terms the more likely a forest manager is to be willing and able to meet them. To do this is a challenge that must not be shirked; indeed it is the logical development of the ideas expressed by Steele & Peterken (1982) on nature conservation objectives at the national level. Initially such quantification must be done empirically, but gradually these ideas should be tested by survey and experiment. Possible areas for quantification include the percentage area of soil disturbance (2.6.3); the response of ground vegetation to the size and distribution of gaps (3.4.4); the percentage area of disturbed vegetation during site preparation or weeding (3.5.3, 3.6.4); and the scale of woodland structure for animals (4.8.4).

5.3.4. The long-term maintenance of habitat conditions

Continuity of habitat conditions on site is essential for the long-term survival of many species; maintaining such conditions to retain the species is thus a common nature conservation objective. However, stands whether in managed or unmanaged woodland change during

the rotation and allowing some population fluctuations may be acceptable if in the longer term the current or an improved state can be achieved.

Two difficulties arise. First, with many groups of species or communities there is insufficient knowledge to define precisely what are the critical habitat requirements if their present and future survival is to be guaranteed. Secondly, there is almost no instance where the modern forest manager can point to a mature native broadleaved crop that has been grown under the same conditions as will prevail during the life of a crop starting now. So, while we can be sure that almost any change of tree species, of stand or woodland structure is going to have a wide variety of ecological effects, we do not have the knowledge to be sure we can return the wood to its present condition and composition at some future date. Faced with this uncertainty conservationists tend to be conservative.

Ideas borrowed from risk analysis and discounted revenue may be helpful in appreciating this attitude to what is an acceptable change: the longer the time before the nature conservation benefits of a change appear the more those benefits are discounted. Leaving the site unaltered is thus likely to be valued more. The uncertainty as to whether the benefit can even be achieved has the effect of raising the effective discount rate so that future benefits have less present value.

Responsibility for improving our knowledge and understanding of the managed forest ecosystem rests with those in the forestry industry, as well as those in the nature conservation movement. It is the former who are usually promoting change.

5.3.5. Inter-relations of site, treatment and tree species effects

The separate effects of changes to the tree species, stand and woodland structure or to the site generally have been described. However, most forestry proposals involve several changes either together or in sequence. The combined effect then depends on whether the individual effects are simply additive, whether they counterbalance one another or whether the effect of one change multiplies the significance of the next proposed change.

For example, the effects on the ground flora of felling, extraction, site preparation and herbicide treatment around planted trees are broadly additive - each operation disturbs a given percentage of ground. Later operations partly affect areas already disturbed, but it would be possible theoretically to calculate the degree of disturbance for the whole sequence. The nature conservation significance is different from that for each operation separately: a little disturbance may be a good thing, but the combined effect may be beyond the limits of acceptability. The use of early thinning to reduce the length of a dark thicket stage was noted earlier (3.6.2). Equally a treatment designed to benefit the ground flora through a series of small coppice cuts, might be wrecked by use of heavy machinery to extract during wet conditions (2.5.1; 2.6.3; 3.6.5).

The effects of treatment and of tree species vary in their relative importance during the rotation and according to site conditions. For example, for the ground flora tree species is relatively unimportant in the early stages, but becomes critical in the thicket; treatment (thinning) is important in the mid-rotation; site conditions predominate in determining the ground flora in the oldest stages when the canopy is relatively open. For birds treatment is relatively more important throughout the rotation.

The effects of site, treatment and tree species over the rotation as

a whole may or may not be evenly matched. Some sites are on such poor soils that the ground flora is extremely limited whatever treatment or tree species are used. For example the ground flora of mature oak stands at Orlestone Forest (Kent) is little richer than forty year-old conifer stands, suggesting that "site" is the major limitation here (Kirby 1988). Elsewhere the complete elimination of ground flora species under beech or spruce thickets may prevent the recolonization of these stands in the later stages of the rotation after they are thinned; some ground preparation treatments could have a similar effect.

Recognition that site, treatment and tree species effects are limiting at different points in the rotation helps us to identify where research on one or other of these would most profitably be done, i.e. at the stage where their effects are strongest. It may also make the forest manager or nature conservationist more aware of the longer-term consequences of a decision to use a particular tree species or treatment.

In the following section we illustrate both short and long-term effects of a specific proposal.

5.3.6 A practical example of changes that may occur

Consider the wood whose broad characteristics are outlined in Table 5.1 and Figure 5.5 and the forestry proposals given below (based on those for a real site). We are deliberately using a case where it may not be immediately obvious whether the changes will produce a large reduction in nature conservation values on the site because we believe that it is these types of case where a clear understanding of what changes are or may be involved is essential. The issues with more dramatic or intensive forestry practices tend to be clear cut.

The first stage is to consider which of the four types of change are involved in this proposal.

(a) Is the system proposed inherently unlikely to maintain the nature conservation value of the site? No.

High forest of predominantly native species is potentially compatible with retaining the nature conservation value and may be viewed as a more natural state (1.1.2). Complete clearance to agriculture or conversion to Norway spruce would be ruled out at this stage however.

(b) Will the tree species change? Yes.

Although oak and ash already occur on the site, the character of the site is largely determined by the range of other woody species present and these will decline in abundance through the promotion of oak and ash and the introduction of sycamore which is not native to the site.

(c) Will the stand structure change? Yes.

The present structure is a dense understorey of neglected coppice poles with scattered large standards. Felling eliminates the present stand structure (as would coppicing), but the structure that subsequently develops will consist of more but smaller diameter trees in the overstorey and less of a shrub layer in consequence.

(d) Will the structure of the woodland change? Yes.

The present structure is fairly uniform in that there is little difference between the various stands of neglected coppice and the rides are overgrown. The felling proposals will create a more varied woodland at least in the short term (as would re-introduction of coppicing) both

by creating young open stands and by the necessary opening up of the rides. After forty years when all of the wood has been felled (at one hectare each year) the woodland structure will start to become uniform again since more and more stands will move into the young-mature stage where differences of 5-20 years in age are not very important (4.8.4; 5.2.3).

(e) Will other changes on the site occur? Yes.

Disturbance to the ground will occur during felling and extraction; work needs to be done on the rides; the planting and tending will also cause changes.

Table 5.1 The initial state of the wood and the forestry proposals

Initial state

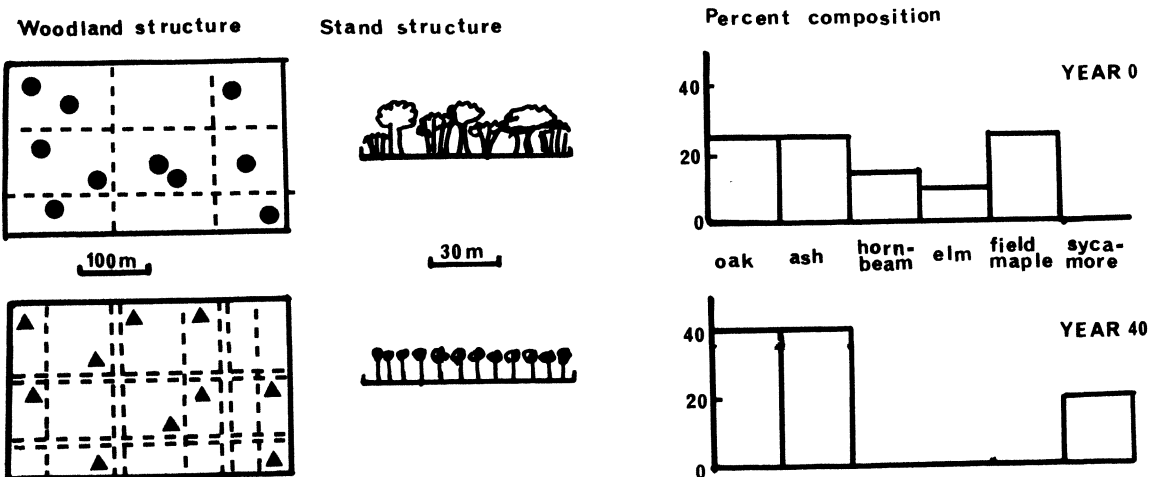
Ancient woodland (40ha) on heavy clay soil.
Neglected coppice with standards structure.
Semi-natural tree and shrub composition, characteristic of the soils and region.
Some large (more than 70cm dbh) standards with dead branches.
Reasonably rich ground flora in the stands.
No glades; rides shaded but containing some species not found in the stand.

No invertebrate records available.	Effects must be inferred from changes in the structure
No bird records available.	

Forestry proposals

To convert the wood to a high forest of oak (40%), ash (40%) and sycamore (20%) over a 40 year period, by a series of fellings of one hectare followed by replanting (but accepting natural regeneration of ash as part of the new crop).

Figure 5.5 The initial state of a wood and the effect of proposed changes. (●) mature oaks, (▲) stands under 10 years, (---) shaded rides, (==) open rides.



The consequences of each of these changes are shown below (Table 5.2). We suggest a sequence of effects that need to be considered, their probable "sign" in nature conservation terms, ways in which they may be offset if necessary and references back to relevant sections in earlier chapters. It is intended only as a guide to assessing the effects of a proposal: there are for example more cross-linkages than it is practicable to indicate.

Table 5.2. The changes resulting from a particular forestry proposal.

Significance for nature conservation: desirable + ; undesirable - ; undetermined or neutral u. Potential changes in brackets.

A. Changes in tree species composition.

- (1) -- Loss/reduction of the semi-natural tree and shrub layer (3.2.1, 3.3.1).

This is difficult to offset, since it is fundamental to the forestry proposals that the tree and shrub species change. Some of the minor species might be deliberately selected for so that they remain within the stand; shrub species could be encouraged by heavy thinning. Alternatively the basic proposal must be reviewed.

- (2) - Reduction in insects associated with tree species that decline (4.2.2, 4.3.2)

Loss of insect species (but not the reduced populations) might be offset by retaining some of the original tree species along ride and stand edges. (This does not satisfy (1).)

- (3) u - Increases in oak and ash, introduction of sycamore (1.1.4)

The increase in oak and ash in itself is neutral. The introduction of sycamore means a reduction in naturalness (especially if it is likely to spread) regardless of any effects on other groups (3.7).

- (4) u (+) Increases in invertebrates associated with oak, ash and sycamore (4.2.2).

It is unlikely that the range of oak or ash associates will increase, nor is there likely to be a high conservation value attached to any species that come in with the sycamore. It is possible that there might be a higher biomass of invertebrates which could be useful as food for larger animals since none of the tree species being replaced are as rich as oak.

- (5) u - Change in the abundance of ground flora species and communities through altered light, moisture and litter (3.2.2, 3.6.3). Some reduction in the naturalness of ground flora patterns because of the effects of sycamore are to be expected, otherwise changes due to tree species alone are likely to be small in this instance. The wood is already partly dominated by heavy shade casters and the amounts of sycamore being introduced are relatively small. Most effects could be offset by treatment.

- (6) u Change in the abundance of associated animal communities (4.2.2, 4.3.2, 4.4, 4.6.2, 4.7.2).

This is almost impossible to predict. It is unlikely to be major. For some groups such as birds other changes are far more significant.

B. Changes in the structure of the stands.

(7) ++ Creation of a series of open areas by felling over the next 40 years (3.3, 3.4, 4.2.3, 4.3.3, 4.6.3, 4.7.3).

This will increase the range of ground flora species. There should be invertebrate gains as well depending on whether species have been able to survive on rides and wood edges or in nearby sites. A different suite of birds may be introduced.

(8) - Longer term development of high forest structure, with less shrub layer than at present (4.6.3).

The reduced shrub layer in the high forest is likely to mean fewer birds than at present. After 40 years the open phase stands will have virtually disappeared. These effects could be offset by treatments such as heavy thinning and management of the ride edges. Species of mature timber phase would remain low.

(9) -- Loss of current mature and over-mature standards (3.2.3, 3.2.4, 4.2.2, 4.6.5.2).

Associated invertebrates and birds will be lost. A local tree/ground flora/soil pattern developed over 100-150 years will be destroyed. Some effects could be offset by leaving a proportion of old timber both in current and all future fellings.

(10) - Creation of uniform plantation areas, rather than irregular patterns determined by stool regrowth or natural regeneration (3.3.3.1; 4.2.2.4).

Loss of stools may itself be important where these are old and large, both in themselves and in the associated invertebrates and bryophytes. Inclusion of natural regeneration within the plantation offsets some of these effects (4.3.2).

C. Changes in the structure of woodland.

(11) ++ Creation of a more varied woodland structure in the first 40 years (see 7).

The value of this will depend on the size distribution and shape of the coupes. The relatively small sizes proposed are a good feature of the scheme (3.4, 4.2.4, 4.3.4, 4.6.4, 4.7.4; 5.2.3.1).

(12) (+) Opening up of rides (see 16, 17).

(13) (+) Potential for developing uneven-aged high forest.

Likely to be beneficial in the long run, but depends on how it is achieved.

D. Changes on the site.

(14) (+) (-) Disturbance during felling and extraction (2.5.1, 3.5).

Some periodic disturbance is often beneficial, but as the scale of operations increases so disturbance may become damaging.

(15) u (-) Fires, windrows, etc. to dispose of lop and top (3.5.3.1). It depends on the scale, but the more there are the more likely the effects are to become damaging. As the site already has good dead wood habitat, piles of lop and top left to rot would not be an improvement over leaving the existing over-mature trees.

(16) + Opening up of ride system.

This generally benefits both plants and invertebrates, especially on east-west rides (3.6.5, 4.3.4.2, 4.8.4.3).

(17) - Drainage of rides and surfacing of rides.

These two changes are undesirable but may be unavoidable if extraction is to take place. They may be offset by careful selection of rides to be improved for vehicles and creation of new extraction routes.

(18) (+ -) Site preparation for natural regeneration.

Depends on the scale and method (3.5.1).

(19) - Ground preparation for planting.

Planting is generally undesirable (reduction in naturalness), so that any associated work is also likely to be a negative change.

(20) - Weeding to ensure growth of the young trees.

Effects of weeding may be limited at the scale usually used (3.5.3.4; 3.6.4; 4.2.5; 4.6.5.1).

The above analysis of the effects of a particular proposal is not complete (no mention of soil changes for instance) but it is a guide to the many and various ways in which forestry practices alter the conditions on a site. We have presented only the nature conservation side of the case and that only in a qualitative manner. To come to a conclusion as to whether or not the proposal should go ahead requires two things. First, the assigning of values to the various changes identified; how important on this site is it to maintain the semi-natural tree and shrub layer; do the benefits of creating a more varied woodland structure outweigh the loss of over-mature timber? Secondly the other objectives for the wood must be considered: how will they be affected if changes to the proposals are made to favour nature conservation? These are beyond the scope of this account - not least because they must usually be decided on the ground for each particular case.

5.4 Further research

5.4.1 Long-term trials and short-term experiments

We sympathize with the plea by Helliwell (1985) for experimental comparisons of silvicultural systems. The trouble with long-term experiments such as the plots set up by Ovington (1953 et seq.; Anderson 1979, 1987; Page 1983) is that after a long wait the results may answer only yesterday's questions which are no longer interesting (rather like military academies training officers to fight the last war better). Inevitably a long-term experiment is overtaken by policy changes or developments in science - better methods, new knowledge and new understanding. Information and understanding on basic processes are accumulating all the time and they can make a 30 year old experiment appear naive and not very useful. Consider for example the conclusions of Payne & Backhouse (1967) about the future for forestry on the boulder clay of eastern England: a series of trials on growing conifers might have been proposed (since broadleaved planting was expected to decline over the next 20 years) which would have yielded results just in time for the Broadleaves Policy in 1985!

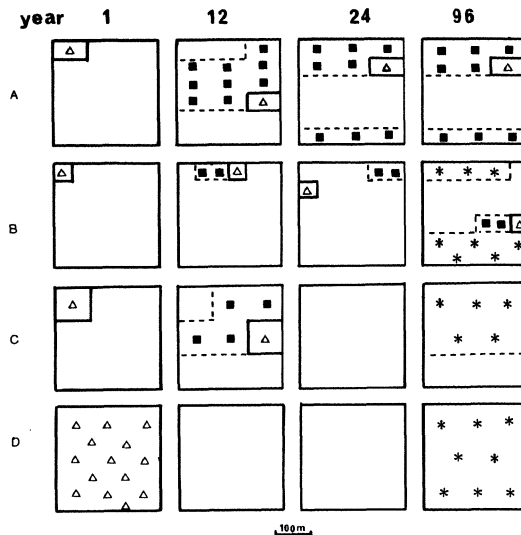


Figure 5.6 The differentiation of forestry systems by their gap dynamics. (Δ) recently cut stands; ($\blacksquare$) stands under 10 years old; (*) stands over 80 years old at year 1, 12, 24, and 96. All stands originate as 18 year old coppice in year 0. The subsequent treatments are: A - continue with 18 yr coppice cycle with 0.5 ha cut each year; B, C & D are conversions to high forest. B - Group selection with 0.25 ha felled every 4 years. C - Clear fell 1 ha every 2 years. D - Clear fell the whole 9 ha at outset.

Long-term monitoring, on the other hand, is worthwhile but it has to be done in a disinterested manner, as far as possible not restricting the questions that could be asked of the results, e.g. Dawkins & Field (1978), Dawkins, Hockin & Power (1985), Horsfall & Kirby (1985), Peterken & Jones (1987), Peterken & Stace (1987).

There is also scope for shorter experimental investigations directed more at the processes in woodland ecology and at the critical stages or operations within the different systems that distinguish them. Hester (1988a, 1988b), for example, provides an excellent example of how experiments can be used to distinguish the separate effects of nutrients, shading and competition associated with the observed shift from Calluna vulgaris dominance to Vaccinium myrtillus, to Deschampsia flexuosa, to Agrostis tenuis in developing birchwoods. Such a programme can be flexible and take account of new developments as they occur. If the basics are understood then models of the system can be constructed and tested, to explore the infinite combinations of site types, species and treatments.

One way of combining short and long-term interests would be to design experiments to obtain the main results in three to five years but to continue with less intensive monitoring afterwards. As a specific example, several silvicultural systems differ mainly in the size and pattern of the gaps that are created during harvesting and regeneration (Figure 5.6) and the amounts of mature timber. A study of the response of species to gaps could thus be developed as part of the model for different systems. In the case of the ground flora this could be linked to a study of patterning on the forest floor (3.1.2.3) which would be relevant to the significance of extraction disturbance for example.

5.4.2 Research on the mechanisms of change

5.4.2.1 Growth stage and stocking

The basic changes due to stage in the rotation and to stocking still need investigation. The changes with stage are fundamental but they are little known or appreciated for some groups especially invertebrates. The changes with different levels of stocking are a lower priority but important because they are easily influenced by management. Small alterations in stocking might have large benefits, e.g. heavier thinning early in the rotation to allow better development of ground vegetation and shrub layers.

5.4.2.2 Tree species effects

Most work in the past has been done on the differences between tree species. The broad characteristics of the main forestry species are now known and more detailed investigations would become further complicated by interactions with sites and treatments. If any more work on species is needed it should concentrate on the thicket stage which is the critical one for the ground flora.

Little has been done on mixtures. Considering the controversy over conifer nurses and the availability of many conifer/broadleaved stands planted in the 1950s a survey and then monitoring the results of thinning or conifer removal could be useful. The recovery of the ground flora on some sites from which conifers have been removed is being investigated by the NCC while the Forestry Commission now have a more general research project in this field.

5.4.2.3 Structure

More effort should be put into investigating the effects of changes in the structure of stands and in the structure of woodland. These are again features that are closely controlled by management. It would be useful to know more about the variations within a stand and how the scale of the pattern of stands themselves affects different groups. What is the right balance between contiguity and maximum edge (1.3.4; 4.8.4.2; Figures 4.2, 4.4)?

5.4.2.4 Margins and edges

The edge effect is known as a general ecological concept (Elton 1966; Odum 1971; 4.8.4.2) but detailed research which uses this concept is lacking, apart from that on birds and, to a lesser extent, butterflies. Margins of stands and woods, the narrow areas along the boundaries between stands, between stands and rides and glades, and at the boundary of the wood (Peterken 1981) should receive more attention. The margin could for instance be defined quantitatively as extending to half the tree height inside the stand. Management of the margins could be very cost effective for nature conservation (Anderson 1987a; Carter & Anderson 1987).

5.4.2.5 Ground disturbance and site preparation

The disturbance associated with site preparation in modern forestry practice is largely a difference of degree compared to that in natural or traditionally managed stands. How far can you go before it becomes unacceptable in nature conservation terms? In most cases the intensity

of site preparation is limited by the cost of operations and it may be that on light and free-draining soils little or no permanent harm is caused. On clay soils, particularly where there is a rich ground flora, the risks are much greater. However there is almost no British research to allay or confirm the fears of nature conservationists on this point. Comparing different intensities of site preparation would need a survey or a large experiment, but the effects of weeding at least could be investigated by small experiments (Watt, Kirby & Savill 1988).

5.4.3 Research on ecological groups

The attention which has been given to the groups varies, depending on their attractiveness, ease of finding and identification and so on. Most work has been done on the ground flora, butterflies and birds and least on the soil flora and fauna. Other invertebrates, bryophytes and lichens tend to be the province of specialists. The relevance of their research could be increased by taking on board the forestry concepts of stages of the rotation and stocking, and considering the effects of woodland structure on their organisms. In the immediate future further work on invertebrates and the ground flora may produce the most useful results in terms of predicting forestry effects.

For invertebrates the questions which deserve investigation turn on how species survive the unfavourable stages of the rotation, i.e. the mobility of these species in relation to woodland structure. Do populations move elsewhere and then move back later? Do populations plummet and recover slowly from very low numbers? If species become extinct in the unfavourable stage how do they recolonize: local movement back from other stands which are still suitable, or by chance long-distance colonization? How far do the requirements of the different stages in an invertebrate's life cycle depend on different components within a stand or wood?

For the ground flora, ancient woodland indicator species have their uses in the survey and comparison of woods in a region, but are less helpful in research on the effects of changes caused by forestry. Classifying the ground flora by their long-term phenology may be more useful in suggesting research topics.

Group 1. Persisters: present as green plants at some time each year of the rotation.

These are mostly shade-tolerant perennials whose performance varies with the stage of the rotation. If there is an unfavourable stage they will eventually be lost and may not re-establish when suitable conditions return (3.2.2.5). Subdivision of this group could be by phenology of leafing: evergreen, spring and summer, summergreen (probably few), winter and spring. The general research topics which might produce most benefits include the mechanisms of shade tolerance or evasion and how performance varies with environmental factors. Collins, Dunne & Pickett (1985) for example split species into light-flexible herbs and shade plants and discussed the probable response of each group to gaps in the canopy. More specifically, seed production and dispersal, and seedling establishment including the influence of other species, deserve investigation, especially in the west and north of Great Britain where these species appear to behave differently from the south and east.

Group 2. Seed bank species: present only as buried seed for part of the rotation.

These are the marginal species, mainly annuals and biennials, which

flourish at the beginning of the rotation and sometimes towards the end but are absent as green plants in between. Re-establishment is from buried seed, so the important questions are: do the pattern and intensity of flowering differ in a group fell, clear fell or coppice cut; how long is the life of buried seeds; does this vary with soil conditions; and (less immediately relevant) how is dormancy broken and germination triggered?

Group 3. Vagrants: not present at all for part of the rotation. These genuine immigrant species are casual weeds and marginal species without a seed bank. They are confined to suitable stands or rides and glades and at times may not be present in the wood at all. What are their seed dispersal patterns and how large and dependable is the influx of seeds? This group contains plants with the weakest attachment to woodland so research is lower priority than for the other two.

Some species straddle these groups. Bramble for instance is in Group 1 but has a sizeable seed bank so could behave as a Group 2 species if completely eliminated by a thicket stage. Cirsium palustre has a small seed bank but probably also spreads from other stands where it is fruiting.

The effects of the changes caused by forestry on the ground flora are mediated by the changes in environmental factors. Of these solar radiation and litter are probably the most important (3.6.3). There is considerable scope for experiments on the physical and chemical effects of litter on ground flora plants using the whole range of size, shape and packing ability of conifer and broadleaved litter, and plastic imitation litter to separate the chemical effects. We would also suggest that on some sites below-ground competition between tree species and ground flora could be important but has received less attention.

5.5 Woodland management, preservation and conservation

Preservation and conservation have been distinguished as preservation from loss or change and conservation for future use (Poore 1982). Conservation has become the preferred term for dynamic systems which need management to maintain their value and preservation was relegated to works of art. The distinction was useful to emphasize the need for management but now that this is accepted the word preservation should be welcomed back from exile. The traditional management perpetuated so as to prevent the system from losing its value can reasonably be called preservation, as in the case of Bradfield Woods, Suffolk. ("The Bradfield Woods have been managed uninterruptedly for at least 700 years, and there is no obvious reason why they should not last a further 700; total preservation in their present state is a perfectly reasonable conservation objective" (Rackham 1976).) Other, less valuable sites can be conserved where a balance is struck between the need to maintain and improve the nature conservation interest and the other objectives of wood production, landscape and amenity, and game.

The level of concern for the detail of the nature conservation interest determines where a site should be on the preservation - conservation spectrum. At the preservation end few changes caused by forestry could be allowed, e.g. to keep the woodland soil with its flora and fauna unchanged in every detail means no change of tree species, natural regeneration with minimal work on the site and if possible no change in stand structure. Further along the spectrum, to maintain most of the ground flora but not necessarily in the existing communities then

a wider range of treatments would be acceptable: change of species within limits, change of stand structure and work on the site. At the conservation end, in a wood initially of low nature conservation interest management could increase the number of tree species, encourage shrubs below the high forest canopy and along edges, maintain a small-scale woodland structure and widen and maintain the rides with rotational cutting, and decrease the intensity of harvesting to leave a few old stands and some scattered old trees. All of this would improve the site for birds, many plants and some insects even if it did not create in detail the most diverse or most natural flora and fauna.

Steele & Peterken (1982) proposed four treatment classes for the 660,000 ha of broadleaved woodland in Great Britain (Table 5.3). The minimum intervention class (I, 3%) is a special case in that change within such areas is almost inevitable but their value and use is for nature conservation and research - an extreme end of the preservation spectrum.

Class I Minimum intervention. Mimimise human activity; some control of exotic species or grazing may be required.	22 kha
Class II Coppice or coppice with standards. Maintain or restore these systems in ancient semi-natural woods	167 kha
Class III Restricted high forest. Manage as high forest with uneven aged or small scale working using native species.	197 kha
Class IV Unrestricted high forest. More intensive methods and a wider choice of broadleaf species are acceptable.	274 kha

Table 5.3 Treatment classes for broadleaved woods (Steele & Peterken 1982).

For the coppice class (II, 25% of the area) the treatment recommended is largely preservation: the re-instatement of the traditional management of coppice with standards as far as possible, with minimal planting. Management for the restricted high forest class (III, 30%) is a mixture of preservation and conservation, with a restriction to species native to the site and encouragement of very small-scale woodland structure, if possible by silvicultural systems other than even-aged clear felling. The unrestricted high forest class (IV, 42%) has the minimum of preservation elements in the recommendation and recognizes the importance of wood production; it allows a wider choice of species and more intensive practices.

Any change caused by forestry has ecological effects, certainly in the details of soil properties and plant and animal communities. On sites of high nature conservation value (all Sites of Special Scientific Interest and most ancient semi-natural woods) preservation as used in this final section is the right course of action and the case for this is made by Rackham (1980) and Peterken (1981). However there is also considerable scope for nature conservation on other sites, especially the class IV unrestricted high forest of Steele & Peterken (1982), where reconciliation with other objectives and the use of modern forestry practices are possible. Changes will occur in these latter woods and new patterns of species occurrence and abundance will develop. Perhaps we can produce something that people in the twenty-first century will think worthy of preservation, as we now value our surviving coppices.

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APPENDIX 1

GLOSSARY

The main sources are Ford-Robertson (1983), Peterken (1981) and Rackham (1976).

AFFORESTATION The conversion of ground from some other land use to forest; not the same as regenerating or restocking land which is already forest.

ANCIENT WOODLAND Woodland known to have existed continuously from some date (e.g. 1600 A.D.) until the present including ancient secondary woodland.

BASAL AREA The cross-sectional area at breast height of a tree (cm^2 or m^2) or of all the trees in a stand (m^2/ha).

CLEANING The removal of unwanted trees and shrubs from a stand, usually done before the first thinning.

CLEAR FELLING Felling all of the trees in a stand to leave the ground clear for regeneration. This is not deforestation unless the intention is to convert to some other land use.

COPPICE A method of regeneration which relies on regrowth from a cut stump, mainly from broadleaved trees. As a silvicultural system it can be worked as simple coppice or as coppice with standards where scattered trees are grown over the coppice and felled at intervals much longer than the coppice cycle.

DBH Diameter at breast height; in day-to-day mensuration taken over bark. Breast height in the U.K. and Europe is 1.3m (4ft. 3in.), but in North America 1.4m (4ft. 6in.).

DEFORESTATION The conversion of forest to some other land use; not to be confused with clear felling.

ECOTONE The boundary zone between two types of habitat.

F LAYER The middle layer of soil surface organic matter: undergoing decomposition (fermentation) but still recognizable as leaves, twigs, etc.

GLADE An area in a wood without trees for at least most of one rotation. This differs from gaps which occur temporarily in stands.

GRUBBING Removal of stumps after felling.

H LAYER The bottom layer of soil surface organic matter: fully decomposed (so-called humus) and no longer traceable to the original plant parts.

HIGH FOREST Trees grown to their full height and usually single-stemmed, in contrast to coppice.

L LAYER The top layer of soil surface organic matter: litter more or less as it fell.

LEACHING The washing of soluble substances down the soil profile and ultimately into the groundwater and drainage.

LESSIVAGE The washing of insoluble clay particles down the soil profile.

LOP AND TOP Branches and tree-tops trimmed from the harvested stems.

MARGINAL SPECIES Ground flora plants which are found at the margins of stands and in rides but only occur in the stand for a few years after coppicing or felling (Salisbury 1916a, 1918).

MEAN ANNUAL INCREMENT The total increment in timber volume divided by the age taken to reach it.

MODER A type of soil organic matter intermediate in some ways between mor and mull, with decomposition dominated by mites and springtails.

MOR A type of soil organic matter which remains on the surface and in which L, F and H layers can often be easily distinguished.

MULL A type of soil organic matter which is well incorporated by

earthworms into the mineral soil, except for a layer of litter which may be present for only part of the year.

NORMAL FOREST A forest in which all age-classes are represented so as to provide a sustained yield and an even flow of work. Ford-Robertson (1983) gives a wider definition: "That forest which has reached and maintains a practically attainable degree of perfection in all its parts, for the full and continued satisfaction of the objects of management". The more restricted sense given above is usually part of this.

PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR) The wavelengths of solar radiation that are active in photosynthesis, with conventional limits of 400 and 700nm. The rest of solar radiation (700-3000nm, about half in terms of energy) is the infra-red band.

PODZOL A soil with a profile of mor, a leached A horizon and a B horizon with accumulated organic matter or iron compounds or both.

PRIMARY WOODLAND Woodland which has existed continuously since its return after the last glaciation. Like the population mean in statistics it is unknowable and ancient woodland is the usable analogue of the sample mean. For full discussion of primary, secondary, ancient and recent woodland see Peterken (1977, 1981).

RECENT WOODLAND Secondary woodland which has arisen since 1600 A.D..

RIDE A track running through woodland wide enough for a vehicle. (On Forestry Commission maps only rides usable by a light van in good weather are recorded.)

ROAD A surfaced and drained road, usable by heavy vehicles in all weathers.

ROTATION The number of years between establishment and removal of a stand. In managed forest this is a planned length of time; in extension to natural forest it is unpredictable and depends on when the next disturbance leading to regeneration happens to occur.

SCARIFICATION Disturbance of the ground vegetation and surface soil to encourage the germination and establishment of tree seeds for natural regeneration.

SELECTION SYSTEM A silvicultural system in which thinning and felling are done on a tree-by-tree basis in a stand containing trees of all ages and sizes. The aim is to produce an intimate mixture of trees of all ages such that a uniform sustained yield is possible. The French term "jardinage" indicates the high level of intervention needed. The **GROUP SELECTION SYSTEM** is similar but operates with small groups instead of individual trees.

SEMI-NATURAL Woodland which has a high degree of similarity and continuity with natural woodland of the site, especially in the species composition of trees and shrubs. Old plantations of species native to the site may have many of the characteristics of semi-natural stands.

SHADE SPECIES Ground flora plants which are present in the stands throughout the rotation, although varying in vigour depending on the stage (Salisbury 1916a, 1918).

SHELTERWOOD SYSTEM Silvicultural systems in which the old trees of one rotation are often the source of seed and provide some protection and control of the ground vegetation for the young trees of the next. There are uniform, group and strip variants, depending on the arrangements of the old trees and the regeneration.

SILVICULTURAL SYSTEMS The system of treatment of stands during the rotation. Good summaries are available in Peterken (1981), Kirby (1984) and Helliwell (1982).

STEMFLOW Precipitation intercepted by the tree canopy which runs down the trunk to the ground - see Figure 2.1.

STOCKING A general term for the quantity of trees in a stand, measured

by density (i.e. the number of trees per unit area), basal area, canopy closure and so on. (Our usage differs slightly from that of many foresters for whom stand density as volume, basal area or number of trees per unit area is a measure of stocking (Ford-Robertson 1983).)

THROUGHFALL Precipitation which drips from the tree canopy or falls through without touching - see Figure 2.1.

TIMBER Wood large enough to use as beams or to saw into planks, so from tree trunks and the largest branches; not underwood.

TOP HEIGHT A standard measure of the height of a stand: the average of the heights of the 100 trees of largest dbh per hectare.

UNDERSTOREY A lower storey of trees beneath a taller and generally older tree canopy. N.B. In North America the word understory is used for all the vegetation under the trees, i.e. the ground vegetation and shrubs together.

UNDERWOOD Small-sized roundwood produced by coppicing; not suitable for sawtimber.

YIELD CLASS A system of classifying the growth of stands by the maximum mean annual increment in stem volume over the rotation under a set type of management. The system was established empirically by measurement of many permanent sample plots. General yield class is measured from age and top height of the crop and is given in steps of 2 m³/ha/year. Local yield class is a refinement of GYC taking into account local variation in stem form and is given in steps of 1 m³/ha/year.

APPENDIX 2 SCIENTIFIC NAMES OF TREES, SHRUBS AND OTHER PLANTS for which names in English were used in the text

Trees and shrubs (using Mitchell (1978) where possible; standard Forestry Commission abbreviations)

CAR	alder	<u>Alnus glutinosa</u> (L.) Gaertn. (unless otherwise specified)
	American beech	<u>Fagus grandifolia</u> Ehrh. (synonym <u>Fagus americana</u> Sweet)
AH	ash	<u>Fraxinus excelsior</u> L.
	aspen	<u>Populus tremula</u> L.
	balsam fir	<u>Abies balsamea</u> (L.) Mill.
BE	beech	<u>Fagus sylvatica</u> L.
BI	birch	<u>Betula pendula</u> Roth and <u>Betula pubescens</u> Ehrh.
	black spruce	<u>Picea mariana</u> (Mill.) B.S.P.
	blackthorn	<u>Prunus spinosa</u> L.
	box	<u>Buxus sempervirens</u> L.
	cherry	<u>Prunus avium</u> L. (wild cherry)
	chestnut	see sweet chestnut
CP	Corsican pine	<u>Pinus nigra</u> var. <u>maritima</u> (Aiton) Melville
DF	Douglas fir	<u>Pseudotsuga menziesii</u> (Mirb.) Franco
	elder	<u>Sambucus nigra</u> L.
	elm	<u>Ulmus procera</u> Salis. (English elm) and <u>Ulmus carpinifolia</u> Gleditsch (smooth-leaved elm)
EL	European larch	<u>Larix decidua</u> Miller
	fir	used for true firs, i.e. <u>Abies</u> species; not including Douglas fir
GF	grand fir	<u>Abies grandis</u> Lindl.
	hawthorn	<u>Crataegus monogyna</u> Jacq.
	hazel	<u>Corylus avellana</u> L.

hemlock	<u>Tsuga canadensis</u> (L.) Carr.	
holly	<u>Ilex aquifolium</u> L.	
HBM hornbeam	<u>Carpinus betulus</u> L.	
HL hybrid larch	<u>Larix x eurolepis</u> Henry	
JL Japanese larch	<u>Larix kaempferi</u> (Lamb.) Carr.	
LC Lawson cypress	<u>Chamaecyparis lawsoniana</u> (Murr.) Parlatore	
LI lime	in British semi-natural woods small-leaved lime or large-leaved lime (<u>Tilia platyphyllos</u> Scop.)	
loblolly pine	<u>Pinus taeda</u> L.	
LP lodgepole pine	<u>Pinus contorta</u> Dougl.	
maple	<u>Acer campestre</u> L. (field maple)	
Monterey pine	<u>Pinus radiata</u> D. Don	
NOM Norway maple	<u>Acer platanoides</u> L.	
NS Norway spruce	<u>Picea abies</u> (L.) Karst.	
OK oak	unless otherwise specified usually pedunculate or sessile oak	
POK pedunculate oak	<u>Quercus robur</u> L.	
PO poplar	<u>Populus</u> species	
PRN rauli	<u>Nothofagus procera</u> (Poepp. & Endl.) Oerst	red
cedar	see western red cedar	
ROK red oak	<u>Quercus borealis</u> Michx. f. (synonym <u>Quercus rubra</u> du Roi)	
OBN roble	<u>Nothofagus obliqua</u> (Mirb.) Bl.	
rowan	<u>Sorbus aucuparia</u> L.	
sallow	<u>Salix caprea</u> L.	
SP Scots pine	<u>Pinus sylvestris</u> L.	
OMS Serbian spruce	<u>Picea omorika</u> (Pancic) Purkyne	
SOK sessile oak	<u>Quercus petraea</u> (Mattuschka) Lieblein	
SS Sitka spruce	<u>Picea sitchensis</u> (Bong.) Carr.	
slash pine	<u>Pinus elliottii</u> Engelm.	
SLI small-leaved lime	<u>Tilia cordata</u> Mill.	
southern beech	<u>Nothofagus</u> species - see rauli and roble	
sugar maple	<u>Acer saccharum</u> Marsh.	
SC sweet chestnut	<u>Castanea sativa</u> Mill.	
SY sycamore	<u>Acer pseudoplatanus</u> L.	
WH western hemlock	<u>Tsuga heterophylla</u> (Raf.) Sarg.	
RC western red cedar	<u>Thuja plicata</u> D. Don	
white oak	<u>Quercus alba</u> L.	
wild service	<u>Sorbus torminalis</u> (L.) Crantz	
willow	<u>Salix</u> species	
WEM wych elm	<u>Ulmus glabra</u> Huds.	
Other plants (using Clapham, Tutin & Warburg (1962))		
bluebell	<u>Endymion non-scriptus</u> (L.) Garcke	
bracken	<u>Pteridium aquilinum</u> (L.) Kuhn	
bramble	<u>Rubus fruticosus</u> agg.	
gorse	<u>Ulex europaeus</u> L.	
heather	<u>Calluna vulgaris</u> (L.) Hull	
honeysuckle	<u>Lonicera periclymenum</u> L.	
ivy	<u>Hedera helix</u> L.	
nettle	<u>Urtica dioica</u> L.	
violets	<u>Viola reichenbachiana</u> Jord. ex Bor. and <u>Viola riviniana</u> Rchb. (the commonest species in woodland)	

INDEX

This should be used in conjunction with the contents list.

- access** 1.2.2.1, 1.2.2.2, 2.4.1.1
- acidification** 2.2.1, 2.2.6
- afforestation** 1.2.2-3, 1.3.2, 1.3.4
 - amphibians and reptiles 4.5
 - birds 4.6.1.1, 4.6.1.3, 4.6.4, 4.6.5.2
 - fungi 2.1.4
 - ground flora 3.1.4.3, 3.2.2.2
 - hydrology 2.2.6
 - soil 2.1.2, 2.2.1, 2.2.8
 - streams 2.5.2.1
- air pollution, lichens** 3.2.5
- amphibians and reptiles** 4.5
- ancient woodland** 1.1.1, 1.1.4, 1.2.2, 1.2.3, 5.5
 - area 1.1.1, 1.1.2, 5.2.3.2
 - drainage 2.5.2.1
 - indicators 3.2.2.5, 3.2.4.2
 - molluscs 4.4
 - soils 1.2.1, 2.7
 - stand scales and pattern 1.3.4
- Atlantic bryophytes** 3.2.4.2
- banks and ditches** 2.6.1, 2.7
- biomass coppice** 2.5.2, 3.5.3
- birds** 4.6
 - afforestation 4.6.1.1, 4.6.1.3, 4.6.4, 4.6.5.2
 - dead trees 4.6.2, 4.6.3.1-2
 - disturbance 1.2.2.1, 4.6.5.2
 - edges 1.3.3, 4.6.3.2, 4.6.4.2
 - fragmentation effects 1.2.3
 - growth stages 4.6.1.3, 4.6.4
 - herbicides and pesticides 4.6.5.1
 - lop and top 4.6.1.3
 - neglected coppice 4.1.3
 - open stage species 4.6.1.3, 4.6.4
 - over-mature stage 4.6.1.3, 4.6.3.1
 - regional differences 4.6.2, 4.6.4.1
 - rides and gaps (glades) 4.6.4.1
 - rotational change 1.3.2, 4.6.1.3
 - scales of pattern 4.6.4.1
 - seasonal variation 4.6.2, 4.6.3.1
 - shrub layer 4.6.1.3, 4.6.3.1
 - soil disturbance 4.6.5.2
 - structure 4.6.1.3, 4.6.3, 4.6.4
 - thicket 4.6.1.3, 4.6.3.2, 4.6.4
 - thinning 4.1.3
 - tree mixtures 4.6.2, 4.6.4.1
 - tree species effects 4.6.1.3, 4.6.2
 - weeding 4.6.5.1
- Bradford plan** 1.3.4, 3.4.2, 3.4.2.3
 - comparison with coppice 3.4.2.3
 - ground flora 3.4.2.2, 5.2.3.1
 - seed banks 3.4.2.3
 - shrubs 3.4.2.1
- broadleaf litter, pH** 2.2.3, 2.2.5.1
- broadleaves** see conifer-broadleaves
- bryophytes** 3.7
 - ancient woodland indicators 3.2.4.2
 - Atlantic species 3.2.4.2
 - coppice stools 3.3.3.1
 - dead wood 3.3.3.1
 - effects of collecting 2.1.6
 - grazing 3.1.2.2, 3.2.4
 - ground flora 3.2.4.1
 - litter 3.2.4, 3.2.4.1
 - nutrient cycling 2.1.6, 3.2.4.1
 - shade 3.2.4, 3.2.4.1
 - soil erosion 2.1.6
 - stand structure 3.3.3.1
 - tree species effects 3.2.4
 - unmanaged woods 3.2.4.2, 3.3.3.1, 3.6.1.3
- butterflies** see Lepidoptera
- clear felling** 1.3.4, 5.2.3.1
 - effect on soil 2.1.4
 - effect on streams 2.4.1.2, 2.5.2.1
 - erosion after 2.1.4
 - nutrients 2.1.4, 2.5.4.1
 - organic matter 2.1.4
 - soil fauna 2.5.4.3
 - trees favoured by 3.3.1
 - water table 2.2.5
- compaction (soil)** 2.1.3, 2.1.7
 - see also soil disturbance
- competition, plant groups** 3.1.2.1, 3.1.3.3
- conifer-broadleaf mixtures** 2.2.2.3, 3.2.3.1, 5.2.1.2
- conifer-broadleaves differences**
 - alternation of species 2.1.4
 - birds 4.6.2
 - fauna 4.8.2
 - fungi 2.2.7.1
 - ground flora 3.1.4.2, 3.2.2.2, 3.6.3.1
 - invertebrates 4.2.2.1, 4.2.2.3
 - Lepidoptera 4.3.2
 - mammals 4.7.2
 - nutrient stocks 2.2.1, 2.2.4
 - organic matter 2.2.1, 2.2.2.1
 - pH 2.2.1, 2.2.3
 - soil fauna 2.2.7.2
 - soils 2.1.2, 2.2.5
 - water yield 2.2.6
- conifer litter** 2.2.2.2
- conifers** podzolization 2.1.4
- coppice**
 - disturbance in 1.2.2.1
 - extent 5.5
 - faunal diversity 4.2.1

- flora 3.1.3
- ground flora and seed bank 3.1.3
- ground flora patterns 3.1.3.2
- growth stages, birds 4.6.1.3
- over-mature trees 1.1.2, 4.2.1, 4.2.3.1
- Lepidoptera 4.3.2, 4.3.4.1
- mammal changes in 4.7.1.1, 4.7.3
- nutrient balance 2.5.4.2
- open stage 1.1.4, 3.1.3, 4.3.4.1
- regrowth, grazing 3.1.2.2, 3.1.3.3
- regrowth and ground flora 3.1.3.3
- rotational changes 1.3.2.1, 3.1.3, 4.6.1.3, 4.7.1.1
- scarcity of dead wood species 4.2.1
- structure 1.3.1, 4.3.4.1
- trees in 1.2.2.1, 3.3.1, 3.6.1.1
- coupe shape** 4.8.4.2, 5.2.3.3
- coupe size** 1.1.5, 1.3.4, 5.2.3.1-3
- extraction disturbance 2.4.1.1
- fauna 4.1.2, 4.7.4
- flora 3.4.4, 3.7
- soil erosion 2.4.1
- dead trees**
- birds 4.6.2, 4.6.3.1, 4.6.3.2
- extent & number 2.3, 3.1.2.1, 4.2.1
- recommendations to leave 4.6.3.2
- dead wood** 1.1.2-3, 2.3, 4.2.1
- bryophytes 3.3.3.1
- fauna 4.1.1.2, 4.9
- input 2.3
- invertebrates 1.1.4, 4.2.4, 4.2.2.3
- minimum intervention areas 1.1.3
- soil nutrients 2.1.3
- disturbance**, natural forests 1.3.2, 4.1.1.2, 4.8.5
- drainage** 1.2.2.3, 2.4.2, 2.5.2, 3.5.3.2, 5.3.6
- patterns, value of 2.5.2.1, 2.7
- earthworms** 2.1.3, 2.2.2.2, 2.2.7.2, 2.2.3, 2.2.8
- ecological effects** 1.2.1
- edges** 1.3.3, 1.3.4, 5.2.3.1, 5.4.2.4
- bats 4.7.4
- birds 1.3.3, 4.6.4.2
- fauna 4.8.4.2
- flora 1.1.4
- in small woods 4.8.4.2
- invertebrates 4.2.4
- shrubs 3.4.2.1, 3.6.1.1 4.6.4.2
- epiphytes** 3.2.5 (see also lichens)
- erosion** 1.2.1, 2.1.4, 2.1.6, 2.4.1, 2.6.4
- experiments**, value of 5.4.1
- extinction of species** 1.1.2-3, 4.1.2, 4.3.5
- extraction damage** (see also soil disturbance) 1.1.3, 2.4.1.1, 2.5.1.2, 3.4.3, 3.5.3
- fauna** see also individual groups
- barriers to movement 4.8.5
- dead wood 4.1.1.2
- edges 4.8.4.2
- effect of stocking 4.1.3
- effects of ground flora 4.8.1
- importance of habitat stability 4.9
- minimum intervention 4.8.1
- natural disturbance 4.1.1.2, 4.8.5
- open stages 4.2.1, 4.8.1
- over-mature stage 4.8.1, 4.9
- poor colonizers 4.1.2, 4.8.4
- rides 4.8.4.3
- scale 4.1.2, 4.1.1.2, 4.8.4.1
- site differences 1.3.5.2
- site preparation 4.9
- structure 4.1.1.3, 4.8.3-4, 4.9
- tree mixtures 4.8.2
- tree species effects 4.8.2, 4.9, 5.2.1.2
- fertilization**
- ground flora 3.5.3.3
- soil 2.5.2, 2.5.4.1, 2.6.4
- fires**, nutrient enrichment 2.5.4.2
- flora** 3.1.1, 3.6.5, 3.7
- see also specific groups
- coupe size 3.4.4
- disturbance in coppice 1.2.2.1
- extraction damage 3.4.3
- grazing 3.1.2.2
- groups within 3.1.2, 3.1.2.1
- natural forests 3.1.1
- natural regeneration 3.5.1
- open stage 3.1.3.1
- poor colonizers 1.3.3
- regional differences 3.1.1
- roads and rides 3.4.1
- rotational change 1.3.2, 3.4.4
- silvicultural systems 3.1.1, 3.4.3, 5.2.3.1
- site differences 1.3.5.2, 3.1.1
- site preparation 3.6.4
- soil type 3.1.1
- stand structure 3.3
- thinning effects on 5.4.2.1
- tree species effects 3.2, 5.2.1.2
- woodland structure 3.4
- flowering** 3.1.3, 3.1.5.1, 3.3.2.2
- forestry practices** 1.2.2
- fungi**
- afforestation sites 2.1.4
- air pollution 2.1.4
- conifers 2.2.7.1
- invertebrates 4.2.3.1
- litter breakdown 2.2.2.2
- tree species effects 2.2.7.1
- gaps** 5.4.1

- birds 4.6.4.1
- ground flora 3.1.4.2, 3.2.2.1, 3.2.2.4, 3.4.4
- insect defoliation 3.1.4.4
- regeneration in 3.3.1
- soil effects 2.1.3, 2.4.1
- solar radiation regime 3.4.4
- genetic conservation** 1.2.1, 4.2.2.3
- Gisburn plots** 2.2.8, 3.2.3.1
- grazing** 1.2.1, 1.4.1
 - bryophytes 3.1.2.2, 3.2.4
 - effect on small mammals 4.7.1.1
 - plant diversity 3.1.2.2
 - soils 2.1.7, 2.2.1
 - thinning for browse 4.1.3
 - trees and shrubs 3.1.2.2
- ground flora** (see also flora) 1.1.4
- amphibians and reptiles 4.5
- below-ground competition 3.6.3.3, 5.4.3
- changes in coppice 3.1.3
 - in high forest 3.1.4
 - in natural forests 3.1.2.3
- convergence 3.1.4.3, 3.6.1.2
- drainage 3.5.3.2
- dry weight 3.1.3.1, 3.2.2.1
- effect of pH change 3.6.3.2
- effect on soils 2.1.3, 2.1.4, 2.5.1.1, 2.1.6
- effects of litter 3.6.3.1, 3.6.3.2
- extraction damage 3.5.3
- fauna 4.8.1
- fertilization 3.5.3.3
- gaps 3.1.4.2, 3.2.2.1, 3.2.2.4
- herbicides 3.5.3.4, 3.6.4
- high forest pole stage 3.1.4.3
- invertebrates 4.2.2.4, 4.3.3
- machinery 3.5.3.1
- mammals 4.7.1.1, 4.7.3
- molluscs 4.4
- neglected coppice 3.3.2.1
- nutrients 2.1.4, 2.1.6, 2.5.1.1
- open stage 3.1.3, 3.1.4.1
- over-mature stage 3.1.4.4
- relation to bryophytes 3.2.4.1
- relation to tree layer 3.1.2
- rides 3.2.6, 3.4.1, 3.6.5
- rotational changes 3.1.3, 3.1.4
- seed bank 3.1.3, 3.2.2.5, 3.3.2.3
- selection system 3.4.2, 3.4.2.2
- shelter wood regeneration 3.1.4.1
- site preparation 3.5.3
- site effects 3.2.2.1, 3.6.2.1, 3.7
- soil disturbance 3.5.3.1
- solar radiation 3.1.4.3
- spatial variation 2.1.3, 3.1.2.3, 3.1.3.2, 3.2.2.1
- stand structure 3.3.2
- stemflow 3.2.3.2
- suppressed by brambles 3.1.3.3
- regeneration and regrowth 3.1.3.3
- thicket 3.1.4.2, 3.1.4.4, 3.2.2.1-2, 3.2.2.4
- thinning 1.1.4, 3.1.4.3, 3.1.4.4, 3.1.5.1, 3.1.5.2
- throughfall 3.6.3.3
- trampling effects 3.3.2.4
- tree bases 3.2.3.2
- tree mixtures 3.2.3.1
- tree species 3.2.2
- value of small coupes 3.7
- weeding 3.5.3.4, 3.6.4
- group selection** see selection
- growth stages** 1.3.2-4, 1.3.5.1, 5.4.2.1
 - birds 4.6.1.3, 4.6.4
 - coppice-high forest 5.2.2
 - flora 3.4.4
 - interaction with stocking 3.1.5
 - light transmission 3.1.4.3
 - mammals 4.7.1
 - patch dynamics 4.1.2
 - selection system 1.3.2.2
 - transitions between 1.3.5.1
 - use to predict change 4.8.4
- habitat stability** 4.5, 4.9, 5.3.4
- herbicides** 3.5.3.4, 3.6.4, 4.6.5.1, 4.7.5
- high forest**, 1.3.1-2, 3.1.4
 - birds 4.6.1.3, 4.6.3.1
 - bryophytes 3.3.3.1
 - extent 5.5
 - ground flora 3.1.4
 - over-mature stage 3.1.4.4, 4.2.3.1
 - seed bank in 3.3.2.3
 - shrub layer 3.1.4.4, 4.6.3.1, 5.2.2
 - trees favoured by 3.3.1
- high forest-coppice differences**
 - dead wood input 2.3
 - fauna changes 4.8.3
 - ground flora 3.3.2.1, 3.3.2.2
 - length of stages 4.2.3.1, 4.3.4.1, 5.2.2, 5.3.6
 - lichens 3.3.3.2
 - litter type 2.3
 - nutrient stocks 2.3
 - solar radiation 3.3.2.2
 - trees and shrubs 3.3.1
 - water table rise 2.3
- hole-nesting birds** 4.1.3, 4.6.1.3, 4.6.3.2
- hydrology** 2.2.6
- integration of objectives** 1.1.3, 5.2.3.2, 5.3.1, 5.5
- introduced trees** 1.1.2-3, 1.2.2, 3.2.5, 4.2.2.1

- invertebrates** (see also fauna, Lepidoptera, molluscs) 5.3.6, 5.4.3
- biomass 4.2.2.4
- dead wood 1.1.2, 1.1.4, 4.2.3.1
- edges 4.2.4
- ground flora 4.2.2.4, 4.3.3
- introduced trees 4.2.2.1
- litter 4.2.3.2
- neglected coppice 4.2.1, 4.2.3.2
- open stage species 1.1.4, 4.2.3.1
- over-mature trees 1.1.4, 4.2.3.1
- pest control 4.2.5
- population changes 4.2.2.3, 4.2.2.4
- regional differences 4.2.2.2
- rides 4.2.4, 4.2.5, 4.3.2, 4.3.4.2
- rideside shrubs 4.2.5, 4.3.4.2
- rotational changes 4.2.1
- stand structure 4.2.3
- tree species effects 4.2.2, 4.2.2.3, 4.2.2.4,
- weeding 4.2.5
- woodland structure 4.2.4
- Lepidoptera**, 4.3
- neglected coppice 4.2.1, 4.3.2, 4.3.4.1
- open stage 4.2.1, 4.3.3
- rides 4.3.3, 4.3.4.1, 4.3.4.2
- rotation changes 4.2.1
- scale of working 4.3.4.1
- stand structure 4.3.3
- tree species effects 4.3.2
- weeding 4.3.5
- woodland structure 4.3.4
- lichens** 3.7
- air pollution 3.2.5
- bark properties 3.2.5
- high forest 3.3.3.2
- introduced trees 3.2.5
- loss following felling 3.6.1.4
- over-mature trees 1.1.4, 3.2.5, 3.3.3.2, 3.6.1.4
- regional differences 3.2.5
- stand structure 3.3.3.2
- tree species effects 3.2.5
- litter** 5.4.3
- amphibians and reptiles 4.5
- bryophytes 3.2.4, 3.2.4.1
- ground flora 3.6.3.1, 3.6.3.2
- invertebrates 4.2.3.2
- molluscs 4.2.3.2
- neglected coppice 4.2.3.2
- removal 2.1.7, 2.2.1
- rotational changes 2.1.4
- site type effects 2.2.2.3, 2.2.7.2
- spatial variation 2.1.3
- thinning effects 2.1.5
- tree species effects 2.2.2.2-3
- litter breakdown** 2.1.3, 2.2.2.2, 2.2.7
- litter type** 2.2.2.3, 2.3
- long-established woodland** 1.2, 1.2.3
- lop & top** 2.1.3, 2.5.4.1, 4.6.1.3, 5.3.6
- machinery** 1.2.2.2, 1.2.2.3, 3.5.3.1
- mammals**
- coppice 4.7.1.1, 4.7.3
- coupe size 4.7.4
- edges 4.7.4
- grazing effects on 4.7.1.1
- ground flora 4.7.1.1, 4.7.3
- growth stages 4.7.1, 4.7.4
- herbicides 4.7.5
- open stage 4.7.1.1
- over-mature stands 4.7.1.1, 4.7.2, 4.7.4
- pest control 4.7.5
- regeneration 4.7.4
- rides 4.7.2
- rotational changes 4.7.1.1, 4.7.4
- stand structure 4.7.3
- tree species effects 4.7.2
- weeding 4.7.5
- woodland structure 4.7.4
- marginal flora** 3.1.3, 3.1.3.1, 3.3.2.3, 3.4.2.2
- margins of stands** 1.3.3, 5.4.2.4
- minimum intervention** 1.1.3, 2.5.1.3, 3.6.1.1, 4.8.1, 4.9, 5.5
- modern forestry** 1.1.2, 1.2.2, 1.2.2.2-3, 1.3.2.2, 5.3.5.3.3
- molluscs** 4.4
- ancient woods 4.4
- ground flora 4.4
- litter thickness 4.2.3.2
- rotation changes 4.2.1
- soil type 4.4
- stand structure 4.4
- tree species effects 4.4
- weeding 4.4
- monitoring** 5.4.1
- moths**, see Lepidoptera
- mull/mor humus** 2.1.6, 2.2.2.2, 2.2.2.3, 2.2.7.2, 2.2.3
- native trees and shrubs** 2.6.2, 3.5.3, 4.2.2.1, 5.3.6
- natural disturbance** 1.3.2, 4.8.5
- natural forests** 1.1.1, 1.1.2, 1.1.3
- bryophytes 3.2.4.2, 3.3.3.1
- dead trees 3.1.2.1
- flora 3.1.1, 3.1.2, 3.1.2.3, 3.5.3
- rotational changes 1.3.2, 3.1.4.4
- scale of stands 1.3.2
- soils 1.2.1, 2.1.3, 2.7, 3.5.3
- specialist species of 4.2.3.1, 4.8.1
- nature conservation values** 2.6.1,

- 4.1.1.1, 4.2.2.4, 5.2.1.1, 5.2.3.2
- neglected coppice** 1.2.2.1, 5.2.3.2
- birds 4.1.3
- ground flora 3.3.2.1
- invertebrates 4.2.1, 4.2.3.2
- Lepidoptera 4.2.1, 4.3.2, 4.3.4.1
- litter accumulation 4.2.3.2
- open stage species 4.8.4, 5.2.2
- rides 4.2.4
- seed bank 3.4.2.3
- normal forest** 1.3.3, 1.3.4, 5.2.3.1, 5.2.3.2
- nutrient**
 - balance 2.5.4.1, 2.5.4.2, 2.6.4
 - cycles 2.1.1-2, 2.1.5-6, 2.2.1, 2.5.1.1, 2.2.8, 3.2.4.1
 - displacement 2.1.1, 2.1.3, 2.5.4.1
 - enrichment 2.4.2, 2.5.4.1, 2.5.4.2
 - input 2.2.4, 2.5.4.1
 - loss after felling 2.1.4, 2.3, 2.5.1.1
- nutrient stocks** 2.1.2
- branchwood harvesting 2.2.4
- coppice & high forest 2.3
- organic matter 2.2.4
- podzols 2.2.5.1
- whole-tree harvesting 2.5.4.1
- tree species effects 2.2.4
- old trees** see over-mature trees
- open stage** 1.3.2, 1.3.5.1, 4.2.3.1, 4.3.4.1
- amphibians and reptiles 4.5
- beetles 4.2.1
- birds 4.6.1.3, 4.6.4
- fauna 4.2.1, 4.8.1
- ground flora 3.1.3, 3.1.4.1, 3.3.2.2, 3.4.4
- invertebrates 1.1.4, 4.2.3.1
- Lepidoptera 4.2.1, 4.3.3, 4.3.4.1
- mammals 4.7.1.1
- neglected coppice 5.2.2
- seed bank species 3.3.2.3
- selection systems 3.4.4, 4.3.4.1, 5.2.3.1
- species loss 4.1.2, 4.3.4.1, 4.8.4, 4.9
- species on rides 5.2.3.1
- organic matter** 2.1.1
- accumulation 2.2.1, 2.2.2.1, 2.2.3
- breakdown 2.1.4, 2.1.5.2, 2.2.8, 2.5.2, 2.5.4.4
- immobilization of nutrients 2.2.4
- soil flora and fauna 2.2.7
- tree species effects 2.2.2.1
- over-mature stands and trees** 1.1.2, 1.3.2, 1.3.5.1
- birds 4.6.1.3, 4.6.3.1-2
- fauna 4.8.1
- flora 3.1.4.4
- invertebrates 1.1.4, 4.2.3.1
- Lepidoptera 4.2.1
- lichens 1.1.4, 3.2.5, 3.3.3.2, 3.6.1.4
- mammals 4.7.1.1, 4.7.2, 4.7.4
- retention 4.2.3.1, 4.6.3.2, 4.9
- species loss 4.8.4
- Ovington plots** 5.4.1
- ground flora 3.2.2.1
- nutrients 2.2.4
- plots organic matter 2.2.2.1
- pH 2.2.3
- soil flora and fauna 2.2.7.2
- patterns**
 - in British woodland soils 2.1.3
 - in ground flora 3.1.2.3, 3.1.3.2
 - of stands 1.3.3, 1.3.4, 4.2.4
- persisters** 3.2.2.5, 3.6.1.2, 5.4.3
- pest control** 4.2.5, 4.6.5.1, 4.7.5
- pH**
 - earthworms 2.2.3
 - fertilization 2.5.2
 - ground flora 3.6.3.2
 - mull-mor switch 2.2.3
 - organic matter accumulation 2.2.3
 - roads and rides 2.4.2
 - rotation changes 2.1.4
 - seasonal variation 2.2.3
 - site type 2.2.3
 - soil fauna 2.5.2
 - tree species effects 2.2.1, 2.2.3
- pit and mounds** 2.1.3, 2.1.4, 3.2.3.2
- podzolization** 2.1.4, 2.2.5.1
- poor colonizers** 4.3.1, 5.2.3.3, 5.4.3
- dead wood species 4.2.2.3, 4.2.4
- fauna 4.1.2, 4.8.4, 4.8.4.2
- flora 1.3.3, 3.2.2.5, 3.2.4.5, 3.6.1.3
- invertebrates 4.2.4, 4.3.1, 4.4
- lichens 3.3.3.2
- molluscs 4.4
- rare species 4.3.1
- spread in tree mixtures 5.2.1.2
- value of small stands 5.2.3.1
- preservation** 5.5
- primeval forests** see natural forests
- rare species** 1.1.4, 1.2.1, 4.1.1.1, 4.3.1, 4.8.1
- regeneration** 3.1.2.2, 3.1.3.3, 3.5.1, 4.7.4
- regional differences** 3.1.1, 3.2.2.5, 3.2.5, 4.2.2.2, 4.6.2, 4.6.4.1
- research** 1.2, 5.4
- edges 5.4.2.4
- ground flora 5.4.3
- growth stages 5.4.2.1

- invertebrates 5.4.3
- litter effects 5.4.3
- poor colonizers 5.4.3
- priorities 5.4.1
- soil disturbance 5.4.2.5
- solar radiation 5.4.3
- stand structure 5.4.2.3
- stocking 5.4.2.1
- thicket stage 5.4.2.2
- tree mixtures 5.4.2.2
- weeding 5.4.2.5
- woodland structure 5.4.2.4
- rides** 1.2.2.1, 1.2.2.3, 1.3.3
 - altered drainage 2.4.2
 - barriers to movement 4.8.5
 - effects on soils 2.4.2
 - management 3.2.6, 3.4.1, 3.6.5, 4.3.4.2, 5.3.6
 - minimizing damage to 2.6.3
 - neglected coppice 3.4.1, 4.2.4
 - orientation and shade 4.3.4.2
 - source of marginal flora 3.1.3
 - value for birds 4.6.4.1
 - value for fauna 4.1.2, 4.8.4.3
 - value for grassland 2.4.2, 3.4.1
 - value for invertebrates 4.2.4, 4.2.5, 4.3.2
 - value for Lepidoptera 4.3.3, 4.3.4.1, 4.3.4.2
 - value for mammals 4.7.2
 - value for open stage species 5.2.3.1
 - value for reptiles & amphibians 4.5
 - vulnerability to damage 5.2.4
 - value for shrubs 4.2.5, 4.3.2
- roads** see rides
- root competition** 3.6.3.3, 5.4.3
- rotation**, changes through 1.3.2, 1.3.5.1
 - birds 1.3.2, 4.6.1.3
 - coppice 1.3.2.1, 3.1.3
 - flora 1.3.2, 3.1.3, 3.1.4
 - invertebrates 4.2.1
 - litter 2.1.4
 - mammals 4.7.1.1, 4.7.4
 - modern forestry 1.3.2.2
 - molluscs 4.2.1
 - natural stands 3.1.4.4
 - pH 2.1.4
 - soil 2.1.4
- rutting of soil**, see disturbance
- scales of pattern** 1.3.3, 5.2.3.1
 - birds 4.6.2, 4.6.4.2
 - clear felling 1.3.4
 - fauna 4.8.4.1
 - Lepidoptera 4.3.4.1
 - natural forests 1.3.2
 - selection systems 1.3.4
- seasonal variations**
 - birds 4.6.2, 4.6.3.1
 - ground flora dry weight 3.1.3.1
 - mammal use of open stage 4.7.1
 - nutrient cycling 2.1.6
 - pH 2.2.3
 - soils 2.1.3
 - solar radiation 3.1.5.2, 3.6.3.1
- sediment in streams** 2.2.6, 2.5.2.1
- seed bank** 3.1.3, 3.2.2.5, 3.3.2.3, 3.4.2.3, 5.4.3
- selection system** 1.3.4
 - Bradford plan 1.3.4, 3.4.2
 - ground flora 3.4.2, 3.4.2.2, 3.4.4
 - open stage species 3.4.4, 4.3.4.1, 5.2.3.1
 - stand structure 1.3.1, 1.3.2.2
 - trees favoured by 1.3.4, 3.3.1, 5.2.3.1
- shade species in coppice** 3.1.3.1
- shape of coupe** 4.7.4, 5.2.3.3
- shelterwood** 1.3.2.2, 1.3.4, 3.1.4.1
- shrub layer** 3.1.2, 3.1.4.4, 3.2.1, 3.3.1, 3.4.2.1, 5.2.2
 - birds 1.1.4, 4.6.1.3, 4.6.3.1, 4.6.4.2
 - mammals 4.7.2
 - soils 2.1.6
- silvicultural system** 1.1.5, 1.2.2.3, 1.3.2.2, 1.4.1, 5.3, 5.3.6, 5.4.1
 - flora 3.4.3, 5.2.3.1
 - soils 2.4.1
 - structure 1.3.1, 1.3.3, 1.3.4
 - tree and shrub differences 3.3.1
- site preparation** 3.5.2, 3.5.3, 3.6.4, 4.9
- site type** 2.2.2.3, 2.6.2, 3.6.2.1, 5.2.1.2, 5.3.5
 - birds 4.6.5.2
 - earthworms 2.2.7.2
 - ground flora 1.3.5.2, 3.2.2.1, 3.7
 - soil 2.2.1, 2.2.2.3, 2.2.3, 2.2.7.2
- small coupes** 1.3.4, 5.2.3.2-3
 - fauna 4.1.2, 4.7.4
 - flora 3.4.4, 3.7
 - more edges 5.2.3.1
 - poor colonizers 5.2.3.1
 - soils 2.4.1.1
- small woods** 4.8.4.2, 5.2.3.1-2
- snags** see dead trees
- soil**
 - afforestation 2.1.2, 2.2.1
 - clear felling 2.1.4
 - cyclical changes 2.1.4
 - features 2.6.1, 2.6.2, 2.7
 - gaps 2.4.1
 - grazing and trampling 2.1.7, 2.2.1
 - litter removal 2.1.7, 2.2.1

- nature conservation 2.1.3, 2.7
- seasonal variation 2.1.3
- silvicultural system 2.4.1
- small coupes 2.4.1
- spatial variation 2.1.2, 2.1.3, 2.1.6
- stand structure 2.3
- thinning 2.1.5
- tree species effects 2.6.2, 5.2.1.2
- tree species mixtures 2.2.8
- type 2.2.2.3, 2.2.5.1, 2.5.1.2, 3.1.1, 4.4
- soil disturbance** 1.2.2.3, 2.7
 - birds 4.6.5.2
 - extraction 1.1.3, 2.4.1.1, 2.5.1.2
 - ground flora 3.3.2.4, 3.5.3.1
 - harvesting 2.5.1.2, 3.5.3
 - minimizing adverse effects 2.6.3
 - minimum intervention areas 2.5.1.3
 - natural regeneration 3.5.1
 - nutrient loss 2.5.1.1
 - recovery times 2.5.1.3
 - species invasion 3.4.3
 - thinning 2.5.1.2
 - wet soils 2.5.1.2
 - whole-tree harvesting 2.5.1.2, 2.5.4.4, 2.6.4
- soil flora and fauna** 2.6.2
 - clear felling 2.5.4.3
 - litter type 2.2.2.2, 2.2.7
 - organic matter 2.2.7
 - pH 2.5.2
 - rotation changes 2.1.4
 - thinning 2.1.5.2
 - tree species effects 2.2.7
- solar radiation** 3.1.2.1, 3.1.4.3, 3.1.5.2, 3.3.2.2, 3.4.4, 3.6.3.1, 5.4.3
- spiders** 2.1.5.2, 4.1.3, 4.2.1, 4.2.3.1, 4.2.3.2
- stand structure** 1.2.2.3, 1.3.1, 5.2.2, 5.3.6, 5.4.2.3
- birds 4.6.1.3, 4.6.3
- bryophytes 3.3.3.1
- fauna 4.8.3
- ground flora 3.3.2
- invertebrates 4.2.2.4
- Lepidoptera 4.3.3
- lichens 3.3.3.2
- mammals 4.7.3
- molluscs 4.4
- soils 2.3
- trees and shrubs 3.3.1
- stem flow** 2.1.1, 2.1.3, 3.2.3.2
- stocking** 1.3.5.1, 5.4.2.1
 - fauna 4.1.3
 - ground flora 3.1.5, 3.6.4
 - growth stages 3.1.5
 - soils 2.1.5
 - time of canopy closure 3.1.3.2
 - tree size 4.1.3
- streams** 2.2.6, 2.4.2, 2.5.2.1
- thicket** 1.3.2, 1.3.2.2, 1.3.5.1, 5.4.2.2
- birds 4.6.1.3, 4.6.4
- deer 4.7.4
- ground flora 3.1.4.2, 3.2.2.4
- length and thinning 3.6.2
- loss of species 3.1.4.2, 3.2.1, 3.2.2.1-2, 3.2.2.5
- natural stands 3.1.4.4, 3.6.2
- selection system 3.4.2.3
- tree species differences 3.2.2.4
- thinning** 1.3.2, 1.3.2.2
 - birds 4.1.3
 - browse 4.1.3
 - ground flora 1.1.4, 3.1.4.3, 3.1.4.4, 3.1.5.1, 3.1.5.2, 5.4.2.1
 - litter 2.1.5
 - nutrient cycling 2.1.5
 - organic matter 2.1.5.2
 - soil disturbance 2.5.1.2
 - soil fauna 2.1.5.2
 - solar radiation 3.1.5.2
- throughfall** 2.1.1, 2.1.3, 3.6.3.3
- traditional management** 1.1.3, 1.2.2.1, 1.3.2.1, 3.1.1, 5.3.2, 5.3.3
- trampling** 2.1.7, 3.3.2.4
- tree bases** 2.1.3, 3.2.3.2
- tree mixtures** 5.2.1.2, 5.4.2.2
 - birds 4.6.2, 4.6.4.1
 - earthworms 2.2.8
 - fauna 4.8.2
 - ground flora 3.2.3.1
 - soils 2.2.8
- tree species effects** 1.2.2.3, 5.3.6
 - amphibians and reptiles 4.5
 - bats 4.7.2
 - birds 4.6.1.3, 4.6.2
 - bryophytes 3.2.4
 - epiphytes 3.2.5
 - fauna 4.8.2, 4.9, 5.2.1.2
 - flora 3.2, 5.2.1.2
 - fungi 2.2.7.1
 - ground flora 3.1.4.3, 3.2.2
 - hydrology 2.2.6
 - invertebrates 4.2.2
 - Lepidoptera 4.3.2
 - lichens 3.2.5
 - litter 2.2.2.2, 2.2.2.3
 - mammals 4.7.2
 - molluscs 4.4
 - nutrients 2.2.4
 - organic matter 2.2.2.1
 - pH 2.2.3

- podzolization 2.2.5.1
- ride flora 3.2.6
- soil flora and fauna 2.2.7
- soils 2.2.1, 5.2.1.2
- solar radiation 3.6.3.1
- thicket characteristics 3.2.2.4
- trees and shrubs 3.2.1
- trees and shrubs** 3.2.1, 3.7
 - coppice to maintain 3.6.1.1
 - grazing 3.1.2.2
 - minimum intervention 3.6.1.1
 - silvicultural systems 3.3.1
 - site preparation 3.5.2
 - stand structure 3.3.1
 - survival on edges 3.6.1.1
 - weed control 3.5.2.1
- undisturbed soils** 2.7
- unmanaged woods**, see natural forests and neglected coppices
- virgin forests** see natural forests
- water table rise** 2.3, 2.2.5, 2.5.4.4
- water yield** 2.2.6, 2.4.1.2
- weeding** 1.3.2.2, 5.3.6, 5.4.2.5
 - amphibians and reptiles 4.5
 - area affected 3.1.5, 3.6.4
 - birds 4.6.5.1
 - ground flora 3.5.3.4
 - invertebrates 4.2.5
 - Lepidoptera 4.3.5
 - mammals 4.7.5
 - molluscs 4.4
 - trees and shrubs 3.5.2.1
- whole-tree harvesting** 2.5.4, 2.6.4
- wildwood** 1.1.1, 1.1.2, 1.2.2.1, 5.3.2
- woodland communities** 3.1.1
- woodland structure** 1.2.2.3, 1.3.3, 5.3.6, 5.4.2.4
 - birds 4.6.4
 - coppice 3.1.3
 - fauna 4.8.4
 - flora 3.4
 - invertebrates 4.2.4
 - Lepidoptera 4.3.4
 - mammals 4.7.4
 - silvicultural systems 1.3.3, 1.3.4
 - soils 2.4
- woodmanship** 1.2.2, 1.2.2.1

