

Drought and root herbivory in understory *Parashorea* Kurz (Dipterocarpaceae) seedlings in Borneo

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ABSTRACT. The influence of herbivory on dipterocarp seedling growth and survival in Bornean primary lowland forest understory during and after the 1997–8 El Niño–Southern Oscillation was investigated. During the drought, a coleopteran (Scolytidae) root borer attacked dipterocarp seedlings, primarily of the genus *Parashorea*. Infestation was spatially heterogeneous on a large (*c.* 100 m) scale. Attack rate decreased with plant vigour within infested areas. Experiments showed that root damage was fatal under drought conditions, but not after rain. Defoliation and apical meristem removal did not increase mortality. The spatio-temporal heterogeneity of herbivore outbreaks and difficulties involved in experimenting with root herbivores limit the power of such short-term investigations. However, the study shows that herbivores can cause differential mortality between species, and can therefore influence dipterocarp regeneration dynamics. The effect of herbivory depends on the plant organ attacked and interactions with other stresses such as drought. El Niño-related droughts are increasing in frequency in South-East Asian rain forests, which may lead to increased numbers of herbivore outbreaks and greater seedling mortality due to these factors.

KEY WORDS: dipterocarp seedlings, drought, El Niño, *Parashorea*, root herbivory, Scolytidae, *Xyleborus*

INTRODUCTION

The recent 1997–8 El Niño event caused widespread drought and fire across South-East Asia (Walsh & Newbery 1999). Huge plumes of smoke from thousands of fires on Borneo and Sumatra drifted across the region for several

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months (Davies & Unam 1999). In East Kalimantan an estimated 5.2 million ha burned, of which 2.3 million ha was natural-forest concession (Hoffman *et al.* 1999). Dipterocarp tree mortality rates due to drought were up to 30 times higher than normal in a lowland forest in Sarawak (Nakagawa *et al.* 2000).

The increasing frequency of El Niño events (Walsh & Newbery 1999) could have wide-ranging consequences for tropical forest dynamics (Markham 1998, and references therein). Forest regeneration is one important process that may be affected (Whitmore 1998), both directly through effects on plant growth and reproduction, and indirectly through factors that impact regeneration, such as herbivory (Coley 1998).

Drought stress affects almost all aspects of plant physiology, many changes leading to increased susceptibility to attack and suitability of the plant as a food source (Mattson & Haack 1987). Increased herbivory on stressed plants has been dubbed the plant stress hypothesis (White 1974), and there are many examples of insect outbreaks in temperate forests related to drought (reviewed in Mattson & Haack 1987), and several in the tropics (reviewed in Coley 1998). However, there are also examples of insect outbreaks unrelated to drought (Anderson 1961), and of experimental studies showing insect preference for well-watered plants (Price 1991). These apparently contradictory observations have to some extent been reconciled, since insect performance depends both on the origin of stress (natural vs. experimental) and on insect feeding guild (Koricheva *et al.* 1998, Schowalter *et al.* 1999, Waring & Cobb 1992). Though there is considerable idiosyncrasy in the behaviour of different species, boring and sucking insects generally perform best on stressed plants, whilst chewers and gallers prefer healthy plants.

The extent to which El Niño-related drought influences plant–herbivore interactions in lowland dipterocarp forest is currently unknown. In order to address this question, the relationship between drought, herbivory, and dipterocarp seedlings growing in lowland forest in Sabah was investigated during the 1997–8 El Niño.

STUDY SITE

The study was conducted in lowland dipterocarp forest of the Danum Valley Conservation Area, Sabah, East Malaysia, 5°N, 117°E. The Conservation Area is 438 km² in size and is surrounded by a mosaic of secondary forest at various stages of regeneration after logging. The forest lies 70 km inland of the east coast of Borneo, at around 200 m asl. The geology and soils of the region are complex and variable, and the topography is undulating with differences of 30–50 m in elevation (Marsh & Greer 1992).

Climate

The climate of the Danum Valley is documented exhaustively by Walsh & Newbery (1999). Mean annual rainfall between 1985 and 1998 was 2669 mm,

and mean annual temperature was 26.7 °C. The highest recorded annual rainfall was 3294 mm in 1995, and the lowest was 1918 mm recorded in the El Niño year of 1997. Mean monthly temperatures range only 1.9 °C around the annual mean, and exceed 34 °C only rarely, usually during long dry spells. Relative humidity is close to saturation at 08h00, dropping to an average of 72% at 14h00.

The study was conducted in 1997 and 1998, during which time one of the strongest recorded El Niño events developed (Wolter & Timlin 1998). In each month from June to December 1997 record-high sea surface temperatures were recorded in the eastern equatorial Pacific. Negative Southern Oscillation Index (SOI) values were recorded from March 1997 to April 1998, with the greatest anomalies in early 1998. Sea surface temperatures remained anomalously high until May 1998, when the SOI became positive (McPhaden 1999). Severe droughts affected many areas of northern Borneo during this time (Walsh & Newbery 1999). At Danum, rainfall was below the long-term (15 y) monthly mean 95% confidence interval for most of March 1997 to April 1998, after which it increased (Figure 1). Several months had rainfall below 100 mm, the estimated transpirational threshold (Walsh 1996), with April 1998 having the lowest rainfall ever recorded at Danum (11.3 mm). Rainless or near-rainless spells totalled 139 d between March 1997 and May 1998, or 33% of the time.

MATERIALS AND METHODS

Monitoring of wild seedlings

As part of a study on the influence of herbivory on dipterocarp seedling mortality in the forest understorey, dead seedlings were periodically harvested from several seedling populations, separated by a maximum distance of around 2 km. Surveys were conducted over three periods: February–May 1998, August–October 1998 and March–May 1999. Surveying involved searching for seedlings with wilted leaves, or the brown stems of dead seedlings that had lost their leaves. Dead seedlings were investigated for signs of herbivore damage, and dissected to discover evidence of root and stem boring.

One site ('Site 4') was further investigated to determine the relationship between attack and seedling vigour at a smaller spatial scale. A 10-m × 10-m plot was marked out in an area of high seedling mortality, and all seedlings, alive and dead, within the plot were pulled out and investigated for evidence of insect attack. A smaller 5-m × 5-m plot, at a distance of 20 m from the large plot, was also investigated. Seedlings were classified as healthy (no sign of wilting), partially wilted (some leaves wilted and stem alive), totally wilted (all leaves wilted and stem alive), or dead. The number of beetle bore-holes in the stem and root were counted.

Experimental investigation of drought–herbivore interactions

An experiment was conducted to determine whether seedlings were more susceptible to insect damage under drought conditions. Four suitable areas

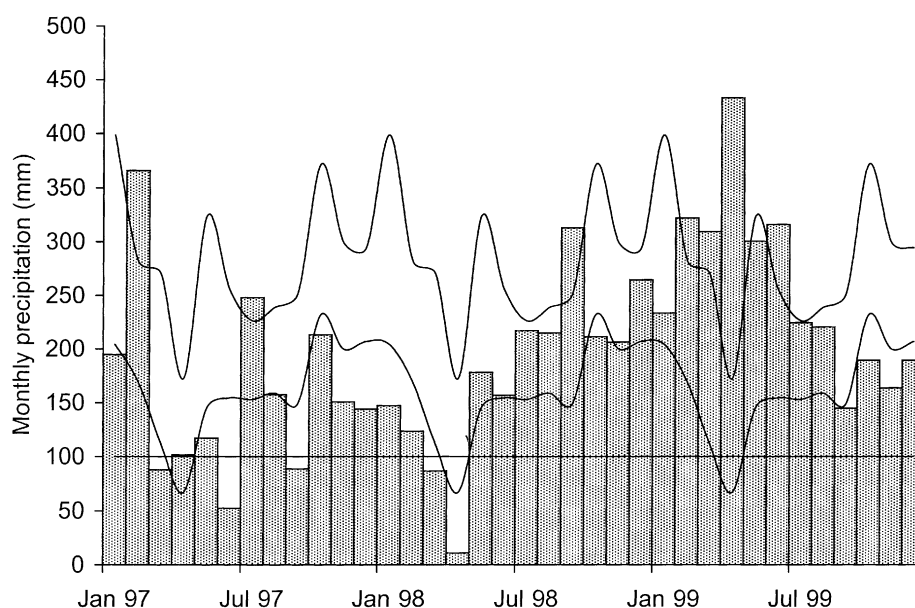


Figure 1. Danum Valley rainfall during the 1997–8 El Niño event (shaded bars), showing 95% confidence interval of the long-term monthly means taken over 15 y (smoothed lines). Horizontal line at 100 mm indicates transpirational threshold. Data are from Danum Valley Field Centre records.

(blocks) were located in the forest. These areas contained high densities of *Parashorea* seedlings (> 15 seedlings m^{-2}), were under intact canopy, and were separated from one another by at least 100 m. Two common species of *Parashorea*, *P. malaanonan* (Blanco) Merr. and *P. tomentella* (Symington) W. Meijer, cannot be reliably distinguished as seedlings (Meijer & Wood 1964) and so no distinction was attempted.

Within each block, two experimental plots were demarcated, separated by *c.* 5 m. One plot was randomly assigned as the dry plot, the other as the wet plot. Each plot contained 32 seedlings, and was approximately 1 m \times 2 m in size. Only seedlings with less than 10% leaf damage were included in the study. Each seedling was tagged and numbered, and each leaf marked on the underside with a fine-tipped black indelible marker. Seedling height and leaf number were noted.

A shelter, consisting of a clear plastic corrugated roof 1 m \times 2 m in size, which sloped from a height of 1.5 m to 1.3 m, was erected over each dry plot. The shelter roofs were swept of fallen litter weekly during the experiment to maintain light transmittance. The seedlings within each plot were randomly assigned one of three treatments or an untreated control, giving eight seedlings per treatment per plot. Leaf damage was simulated by removing the lamina on the right-hand side of the midrib with scissors. Apical damage was simulated by removing the apical meristem with scissors. The defoliation and apical damage treatments were similar to Becker (1983). Root damage was simulated

by grasping the seedling at the base of the stem, pulling the seedling slowly out of the soil by 1 cm then pushing it slowly back again. The root damage treatment is unprecedented but was hypothesized to damage fine roots, since examination of uprooted seedlings showed that the tap root and major lateral roots remained intact.

Natural variation in rainfall was employed to alter soil moisture between the experimental periods for dry and wet treatments. The dry plot seedlings were first measured and treated in May 1998, and re-measured in September 1998. No shelters were erected over the wet plots, and treatments were applied in September 1998. The wet plots were re-measured in March 1999. Rainfall was very low for 2 mo prior to the first census period (Figure 1), and this was taken as the experimental period for the dry plots. Rainfall was high prior to and during the experimental period for the wet plots. Such an approach has been used previously (Coley 1998), and allows for a community-wide response as opposed to a limited experiment-scale response.

Analysis

Results from the large and small sampling plots were pooled, and differences in rates of infestation between seedling vigour categories sought using the loglinear analysis procedure of SPSS (SPSS 1999).

Relative monthly height increment (RMHI) was calculated by the difference between the \log_{10} of starting and finishing height over the time between censuses. Relative monthly leaf loss (RMLL) and gain (RMLG) were calculated as the number of leaves gained and lost over the starting leaf number, divided by the time between censuses. Differences in growth were investigated using analysis of variance in a split-plot design using S-Plus (Mathsoft 2000). Differences in mortality rates between treatments were found using logit loglinear analysis (SPSS 1999).

RESULTS

Monitoring of wild seedlings

Altogether 215 dead seedlings were examined from various sites in the forest from February to May 1998 (Table 1). The seedlings were of the genus *Parashorea* and species *Shorea johorensis* Foxw. (Dipterocarpaceae). Small (approximately 1 mm diameter) pinholes were found in the stem or roots of 44% of the dead *Parashorea* seedlings, and of those with pin-holes 70% contained one or more adult beetles of the genus *Xyleborus* Eichhoff (Coleoptera: Scolytidae). Almost a third of the attacked seedlings also contained one or more beetle larvae. Between 0 and 19 (median = 1) beetles and between 0 and 22 (median = 0) larvae were found in attacked seedlings. A further census of the same sites from August to October 1998 and March to May 1999 revealed no evidence of root borer attack, and only a few tens of dead seedlings were found. In some areas soil disturbance by emerging cicada larvae caused some seedling death.

Intensive sampling plots were set up on Site 4, where the highest incidence of root-borer attack had been found. Altogether 1173 *Parashorea* seedlings were removed from the large plot, and 554 from the small plot, giving 1727 seedlings in total. More than three-quarters of all seedlings were either dead or showed signs of wilting (Table 2). Almost half of all seedlings were found to be attacked, though this varied significantly with the health of the seedling (logistic regression, $P < 0.0001$). The proportion of seedlings attacked decreased with seedling vigour (Table 2).

Experimental investigation of drought–herbivore interactions

There was far greater mortality due to root damage in the dry plots than in any other treatment combination (Figure 2). The interaction between water availability and treatment was significant (loglinear analysis, $P = 0.02$). Survival after root damage in the dry plots was only 8%, whereas other treatments showed more than 80% survival. Dead seedlings that remained intact were examined for signs of herbivore damage. In the first census period 6 of 19 dead seedlings examined showed evidence of attack by root borers. These were found in two of the four blocks. In the second census, none of four seedlings examined showed evidence of attack. No data could be obtained from Site 4 wet plot on the third census because a fallen branch had crushed it.

Some seedling growth occurred during the experiment, though the mean growth rate was very low (Table 3). No significant differences were found between treatments (analysis of variance, $P > 0.05$), and only the wet Control seedlings showed RMHI significantly greater than zero (t-test, $P < 0.01$). RMLL and RMLG distributions were highly skewed, with most seedlings neither flushing nor losing leaves (Table 3). Leaf gain was significantly greater in

Table 1. Results of dead seedling censuses conducted in February–May 1998 (C1), August–October 1998 (C2) and March–May 1999 (C3).

Site	Species	Dead seedlings found			% Attacked		
		C1	C2	C3	C1	C2	C3
East Trail	<i>Parashorea</i> spp.	20	0	0	30	0	0
Nature Trail	<i>Parashorea</i> spp.	23	0	0	9	0	0
Site 4	<i>Parashorea</i> spp.	37	16	0	86	0	0
Site 1	<i>Parashorea</i> spp.	102	11	0	34	0	0
West Trail	<i>Parashorea</i> spp.	5	0	0	40	0	0
Tembaling Trail	<i>S. johorensis</i>	25	0	0	24	0	0

Table 2. Incidence of root borer attack by seedling vigour. Pooled data from large and small sampling plots.

Status	Number	% Attacked
Healthy	386	31
Partly wilted	371	35
Fully wilted	415	47
Dead	555	67

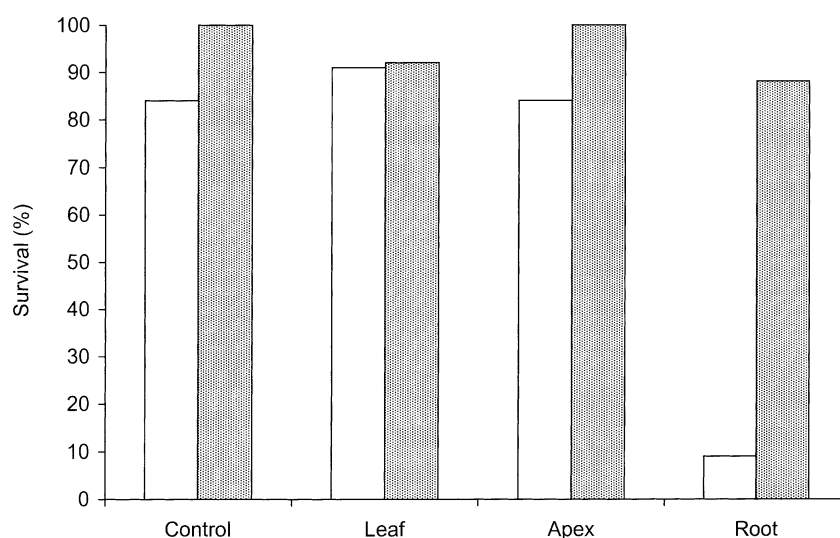


Figure 2. Percentage survival by damage treatment for dry (open bars) and wet (shaded bars) plots. Pooled data for four blocks. Damage was artificially imposed.

dry plot seedlings for all treatments except root damage (Mann–Whitney tests, $P < 0.05$). Regrowth from secondary meristems was significantly more common in those seedlings that had their apical meristems removed than in control seedlings (Table 3, logistic regression, $P < 0.05$).

DISCUSSION

The root-borer outbreak provides some support for the plant stress hypothesis, since it was observed at the end of a strong El Niño-induced drought, attack was related to seedling vigour, the highest level of infestation was found in a site where many seedlings were wilting under drought stress, and no root borers were found in seedlings surveyed after the drought had passed. Infestation of apparently healthy seedlings should not be taken as evidence for the plant vigour hypothesis, since seedlings may have been stressed without showing obvious symptoms. Furthermore, healthy seedlings may not have been spatially independent of nearby infested seedlings, and so could have been attacked despite their greater resistance or lower suitability to the beetles. Scolytid beetles are known preferentially to attack drought-stressed trees (examples in Berryman 1988). South-East Asian scolytids have life cycles of only a few weeks (Chey 1996), allowing very rapid population growth and the potential for outbreaks. The genus *Xyleborus* has a worldwide distribution, and is a common timber pest in South-East Asia (Anon. 1950, Schedl 1958, Thapa 1970).

The beetle showed a high degree of preference for *Parashorea* despite the presence of other seedling species, though a small number of dead *Shorea johorensis* seedlings were found with evidence of root boring. In another study of

Table 3. Growth and leaf turnover.

	Treatment	N	RMHI ($\times 10^{-3}$) mean \pm SE	RMLG ($\times 10^{-3}$) median (IQR)	RMLL ($\times 10^{-3}$) median (IQR)	Shoot regrowth
Dry	Control	27	2.0 \pm 1.2	83 (51–125)	0 (0–0)	19%
	Leaf	29	0.0 \pm 1.4	63 (26–115)	0 (0–0)	7%
	Apex	27	0.0 \pm 1.2	83 (6–125)	0 (0–0)	44%
	Root	3	1.7 \pm 2.8	12 (na)	12 (na)	33%
Wet	Control	24	2.2 \pm 0.8*	39 (0–56)	0 (0–17)	17%
	Leaf	22	1.0 \pm 0.6	33 (22–56)	0 (0–12)	23%
	Apex	24	1.2 \pm 1.1	42 (8–56)	0 (0–22)	33%
	Root	21	1.4 \pm 0.9	27 (0–42)	29 (24–79)	24%

* Significantly greater than 0 at $P < 0.05$. RMHI, relative monthly height increment; RMLG, relative monthly leaf gain; RMLL, relative monthly leaf loss. Interquartile range (IQR) is given for RMLG and RMLL since the data have a strong right skew.

dipterocarp seedling growth in the Danum Valley, *Parashorea* was preferentially attacked by a grasshopper (Orthoptera) (Whitmore & Brown 1996). The forest at Danum Valley has been described as *Parashorea malaanonan* type due to the prominence of this species among the large dipterocarps (Fox 1972), and it could be that some density-dependent mortality mechanism (*sensu* Connell 1978, Janzen 1970) is in operation.

The observed outbreak occurred over a large area of forest, the furthest affected sites being separated by over 2 km. The outbreak was very patchily distributed, with some seedling populations apparently untouched, whilst others showed high levels of infestation. This patchy distribution has been noted in many soil herbivores (Brown & Gange 1990), and may be due to the distribution of dry soils or infested adult trees harbouring beetle populations. Emigration from stressed ‘focus’ trees to nearby ‘recipient’ trees has been described in the spruce beetle *Dendroctonus frontalis* (Hard 1989). Since only one outbreak in one area of forest was observed, further examples and experimental manipulations are required to draw firm conclusions concerning the relationship between drought and root borer outbreaks. To detect future outbreaks, large-scale seedling surveys spanning several droughts are required. Studies of tree recruitment are many, but they emphasize a large number of samples within a small area and for a short time (Clark *et al.* 1999). At Danum, a relatively large-scale survey of seedling growth and survival was undertaken by Still (1992), though this only lasted for 2 y and did not investigate herbivory. Perhaps the increasing frequency of droughts and associated pest outbreaks will provide ample opportunities for such studies in the future.

Root herbivory was shown to be more detrimental to seedlings than either

defoliation or apical meristem damage, but further experiments are necessary to prove that drought-stressed seedlings are more susceptible to attack by herbivores. Root herbivory is difficult to investigate and is often ignored, leading to a false conclusion that absence of evidence equals evidence of absence (Brown & Gange 1990). Manipulative field experiments using soil insecticides (Brown & Gange 1989*a, b*) may be used to exclude herbivores if the scale of heterogeneity of herbivore distribution is less than that of the experiment, otherwise the areas treated may be without herbivores anyway. Experimental manipulation of water availability and exposure to beetles (Dunn & Lorio 1993) could be employed to determine unequivocally whether beetles preferentially attack stressed seedlings.

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