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Growth dynamics and leaf quality of the stinging trees *Dendrocnide moroides* and *Dendrocnide cordifolia* (Family Urticaceae) in Australian tropical rainforest: implications for herbivores

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Abstract. Leaf growth dynamics and leaf quality of *Dendrocnide moroides* (Wedd.) and *Dendrocnide cordifolia* (L.S.Sm.) Jackes and Hurley varied widely with age, season, plant height and habitat. Although leaves were produced continuously, growth rates varied seasonally. Leaf moisture and nitrogen content increased in spring and summer and decreased with age, while toughness increased with age. All leaf growth attributes varied with height, with the majority of activity occurring on mid-sized plants. Leaf growth rates and proportions of different leaf age classes were similar for both species. Leaves were larger and lived longer in shade. Size and longevity responded rapidly to changing light conditions, reflecting their ability to survive in small rainforest gaps. Leaves of all ages were highly nutritious and the exceptionally nutritious young leaves were abundant throughout the year making them susceptible to herbivore attack. However, immature stinging tree leaves were densely covered with painful stinging hairs and hair density decreased with age. Further to causing pain, stinging hairs of *D. moroides* and *D. cordifolia* are shed continuously and may deter mammalian herbivores by causing allergic reactions. However, the leaves of stinging trees appeared better suited to the rapid colonisation of rainforest gaps, than in fending off or avoiding herbivore damage.

Introduction

Leaves are a resource for herbivores that vary in quality and quantity both temporally and spatially. The leaf quality and growth dynamics of the host plant can directly influence insect herbivore population abundance and herbivore damage. A high proportion of damage occurs during leaf expansion (Coley and Aide 1991). A leaf that matures quickly and can rapidly employ the defenses of leaf toughness and decreased nutrient content, should receive less damage than a slowly expanding leaf (Mooney and Gulmon 1982; Aide and Londono 1989). Rapid and synchronous leaf expansion has been suggested as a mechanism to minimise damage either by satiating herbivores (Coley 1983; Aide 1988) or by minimising the time young leaves are available to herbivores (Crawley 1983). Herbivore damage varies with height (Lowman 1992) and is inversely related to leaf longevity (Nunez-Farfan and Dirzo 1989), probably due to a decline in concentration of nitrogen with leaf age (Mooney and Gulmon 1982). The amount of young foliage was the best predictor of herbivore distribution in an Australian subtropical rainforest tree (Basset 1991*a*). The size of leaves may affect feeding rates of herbivorous insects (Heinrich 1979) and is involved in host–plant selection (Brown and Lawton 1991). Variations in stinging hair density influences the degree of herbivory in *Urtica* species, Family Urticaceae (Levin 1973; Pollard and Briggs 1984; Pullin and Gilbert 1989) and variations in leaf nutrient content (Mattson 1980), leaf moisture and toughness (Scriber and Slansky 1981; Berish 1986) also influence levels of herbivore damage.

The stinging tree shrubs *Dendrocnide moroides* (Wedd.) and *Dendrocnide cordifolia* (L.S.Sm.) Jackes and Hurley are early colonisers in rainforest gaps, germinating in full sunlight after soil disturbance. Slight contact with human skin produces an extremely painful, burning sensation, caused by toxins injected via silicon hairs that densely cover the leaf surface. Severe contact causes excruciating pain often requiring urgent medical attention and can cause death in humans (Winkler 1922) and dogs and horses (Robertson and MacFarlane 1957). Do stinging hairs then prevent herbivore damage? How important are growth dynamics and leaf quality of stinging trees important in influencing herbivore feeding? Leaf quality and growth dynamics of *D. moroides* and *D. cordifolia* were measured, and the pattern of food availability for herbivores was investigated. Permanent labelling allowed continuous measurements of growth rates, size, phenology, longevity and age proportions of stinging tree

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leaves. This was the first quantitative study of the ecology of the notorious North Queensland stinging trees and part of a wider investigation of stinging tree herbivory (Hurley 1995).

Materials and methods

Study sites

Two study sites were selected at Wongabel State Forest Reserve 191:11C, Atherton Tablelands, North Queensland (17°19′S, 145°30′E, altitude 760 m). The reserve consisted of *Araucaria cunninghamii* Ait. ex D.Don plantations surrounded by Complex Mesophyll Vineforest (Webb 1959). One study site was situated within a block of *A. cunninghamii* plantation. The understorey was dominated by rainforest pioneer species, particularly *Dendrocnide* species, and received full sunlight for most of the day due to poor conifer foliage production. The second study site was situated within an adjacent rainforest gap, 80 m in diameter and receiving full sunlight from about 1000 to 1400 hours.

The soils at both sites were typical Krasnozems (type Gn 3.11 of Northcote (1971); cited in Brasell *et al.* (1980)). The climate of the Atherton Tablelands is defined as tropical with summer rains (Walter 1971). Rainfall and temperature data were obtained from the nearest long-term climate recording station at CSIRO. Atherton. Site temperatures were recorded periodically at Wongabel State Forest and regressed against temperatures recorded at Atherton, adequately predicting site temperatures at Wongabel State Forest for the 18 month sampling period. The plantation experienced higher maximum and lower minimum temperatures than the rainforest recording differences of up to ± 1.5°C (Hurley 1995).

Plant and leaf populations

Measurements were conducted monthly in two habitats contrasting in light intensity from May 1988 to December 1989. Leaf nitrogen and moisture content, toughness and stinging hair density were measured on smaller spatial and temporal scales. A total of 20 *D. moroides* plants and 42 *D. cordifolia* plants were chosen from both sites, ranging from 0.1 to 1.5 m in height. Plant height was measured from the base of the main stem to the growing tip of the highest branch. All leaves from one branch of each plant were permanently labelled by loosely wrapping marked plastic tags around the leaf petiole. New leaves were labelled at each measuring occasion.

Leaf area measurements

Many stinging tree leaves were too large to be measured using a portable leaf area meter so an indirect method of determining area was developed. Linear leaf measurements were tested as indicators of leaf area on 70 harvested *D. moroides* and 90 *D. cordifolia* leaves by using a computer digitiser (Delta-T Devices). Separate linear regressions were performed on leaf width and length to leaf area. For both species width and length were satisfactory indicators of area ($r^2 > 0.96$) and width was a marginally better predictor of area than length (Hurley 1995). Width was used as the indicator of leaf area in the field. Length was used when the lateral margins of leaves were damaged. All leaves were measured from time of emergence to full expansion. Full expansion was determined when three successive width measurements were about equal according to this test: an analysis of variance was performed to evaluate the magnitude of the measurement error upon the final three width measurements of 30 fully mature leaves. The residual mean square of these measures was 0.76 (Table 1). The measurement error was then calculated at 0.876 cm (root MSE) × 2 s.e. = ± 1.75 cm, with 95% confidence limits (MSE = Mean Square Error). If three consecutive width measurements fell within ± 1.75 cm of the mean, the leaf was considered to be fully expanded at the date of the first of the three prescribed measures.

Table 1. ANOVA results: measurement error of leaf width values (cm)
MSE = Mean Square Error, C.V. = coefficient of variation

Source of variation	d.f.	Sum of squares	Mean square
Between leaves	29	7655.6	232.90
Within leaves	60	46.0	0.76
Total	89	6801.5	
$r^2 = 0.993$	Root MSE = 0.876*		$Pr = 0.0001$
C.V. = 3.28	$F = 303.85$		

*The measurement error is 0.876 cm (root MSE) × 2 s.e. = ± 1.75 cm.

Leaf age determination

Due to monthly sampling, the exact date of leaf emergence or abscission was not known. When establishing leaf age, the mid-point between sampling intervals (2 weeks) was added to the age of leaves that had emerged and subtracted from the age of the leaves that had abscissed between sampling intervals. Leaf age was expressed as weeks.

Leaf quality measurements

Leaf toughness, nitrogen, water content and hair density were measured from leaves harvested *in situ*. Toughness was measured using a leaf penetrometer *Chatillon* Model AG50: capacity 50 g/cm^2 (Sands and Brancatini 1991). Leaf age classes were estimated in the field as *immature*, *mature* or *senescent*. *Juvenile* leaves, classified as newly emerged and less than 2 cm in width, were analysed as a separate class to immature leaves. Stinging hair density was very high on newly emerged leaves and expected to interfere with measures of toughness. The sampling probe was inserted through the upper leaf surface, five times at points randomly selected across the leaf blade, avoiding major veins.

Leaf moisture and nitrogen content were measured from leaves harvested from non-experimental plants in February (summer), July (winter) and October (spring). Immediately following harvesting, all leaves were weighed, dried at 40°C, then weighed for dry weights. Moisture content was calculated as the percentage of water relative to total fresh leaf weight. All dried leaves were then crushed individually for analysis of nitrogen content. The minimum dry weight necessary for the analysis was 0.5 g. When individual dry leaf weights were less than 0.5 g, samples were pooled, within age classes and if necessary within age classes between individuals of the same species. Leaf nitrogen content (percentage of dry weight) was determined by Modified Kjeldahl procedure.

The upper leaf surfaces of *D. cordifolia* were photographed with a scanning electron microscope to assess density of stinging hairs. Samples of juvenile, immature, mature and senescent leaves were cut into 0.5-cm^2 sections, dehydrated in Pildry solution to reduce shrinking of plant tissue, placed on aluminium stubs, critical point dried and coated with a fine layer of gold. The scanning electron microscope was operated at 10 KeV accelerating potential, 40× magnification.

Data classification

Leaves were separated into classes according to their stage of growth. Once a leaf had reached its maximum size, the proportion of its expansion during its development was determined retrospectively. For example, at any point in the development of leaf 'X', i.e. at measuring interval *T*, the proportion of expansion was calculated by dividing the width of leaf 'X', at measuring interval *T*, by the maximum width of leaf 'X'

$$\% \text{ expansion X} = (\text{width } T/\text{maximum width}) \times 100$$

Preliminary analysis showed growth rates did not differ between species (Hurley 1995), so age classification for all leaves was based on stage of growth and age in weeks. Data reduction into class boundaries was also necessary for season and plant height categories to simply data analysis and interpretation (Table 2).

Data analysis

All data analyses were performed with SAS statistical package. Where necessary data were $\log_{10}$ transformed. Trends are discussed only in cases of statistical significant effects. Significant main or interaction effects are ignored if the sum of square (SS) values were lower than that of a higher-order interaction effect in which they are embedded. Due to the extent of the data, in some instances significant interaction effects are not discussed. However, further detail of analyses is available (see Hurley 1995). Data on leaf production, longevity and size were analysed by using ANOVA models, investigating variables according to species, site, plant height and season. Preliminary analysis showed leaf size varied widely according to plant height with many significant interactions with all treatments (Hurley 1995). Therefore, separate ANOVAs examined leaf size within each plant height class. Data on growth rates and leaf quality measurements were analysed by ANOVA models, investigating species, site, leaf age and season, except for toughness which was measured once. Leaf growth rates were analysed by estimating the geometric increase of leaf size (GINC). GINC is the geometric increase in leaf size, per week, between one sampling occasion *A* and the next sampling occasion *B*. WK'S is the number of weeks between *A* and *B*.

$$\text{GINC} = (\text{leaf width at } B/\text{leaf width at } A)^{(1/\text{WK'S})}$$

When analysing the proportions of leaf age classes, data were collated on the total number of leaves within each age class. Multiple preliminary chi-square tests showed minimal differences between species but site, plant height and season differences were significant (Hurley 1995). Variations in proportions of leaf age classes, comparisons of leaf production to climate data and stinging hair density are investigated qualitatively.

Table 2. Classification boundaries for plant* and climate data
(Wks = weeks)

Class description	class boundaries	Attributes
	Leaf age	
Early immature	<6 wks	<60% expansion
Late immature	>5 wks to <10 wks	60–90% expansion
Early mature	>9 wks to <13 wks	100% expansion
Late mature	>12 wks	100% expansion
Senescent	>12 wks (yellowing)	100% expansion
	Plant height	
Small	<60 cm tall	
Medium	>60 cm to <120 cm tall	
Tall	>120 cm tall	
	Season	
Winter	Jun.–Aug. 1988, 1989	Lowest °C and rainfall
Spring	Sep.–Nov. 1988, 1989	High °C and rainfall
Summer	Dec. 1988–Feb. 1989, Dec. 1989	Highest °C, high rainfall
Autumn	May 1988, Mar.–May 1989	High °C and highest rainfall

*Data analysis shows classification suitable for both *Dendrocnide cordifolia* and *D. moroides* (Hurley 1995).

Results

Units of measurements, means, standard errors and sample sizes of foliage data of both species are presented in Table 3. A list of the significant main and interaction effects of all foliage attributes are given in Table 4. More details of data and analysis are available elsewhere (Hurley 1995).

Leaf production

Leaf production varied with plant height (most young leaves produced on mid-sized plants and fewest on small plants ($F_{2,29} = 13.86$; $P < 0.0001$)) and with season (least produced in winter, increasing in abundance through to summer and decreasing again in autumn ($F_{2,29} = 4.06$; $P < 0.001$)). Production generally increased with height for both species in the plantation (interaction of species × site × height: $F_{2,29} = 7.38$; $P < 0.001$), whereas in the rainforest, *D. cordifolia* produced less leaves with an increase in height, while mid-sized *D. moroides* produced leaves much faster than small or tall plants. Monthly variation in leaf production was compared to climate data (Fig. 1). Leaves were produced continuously, with rates lowest in winter and highest in summer. No clear month to month association of leaf production with patterns of rainfall or with maximum and minimum temperature were evident.

Leaf longevity

Once a leaf had begun to turn yellow it usually senesced in <4 weeks and many branches lacked senescent leaves. Leaf longevity differed significantly between species (*D. cordifolia* leaves lived 2.6 weeks longer than *D. moroides* leaves: $F_{4,88} = 10.6$; $P < 0.005$) and between sites (rainforest leaves lived 5.9 weeks longer than plantation leaves: $F_{4,88} = 14.31$; $P < 0.001$). As interaction effects, longevity differed with height in both species. *Dendrocnide moroides*, but not *D. cordifolia*, longevity increased with height ($F_{4,88} = 3.04$; $P < 0.05$). Longevity increased with height in the rainforest but not in the plantation ($F_{4,88} = 3.6$; $P < 0.05$). Leaf lifetime was longest on tall plants, where rainforest leaves lived eight weeks longer than plantation leaves.

Proportions of leaf age classes

Late mature leaves were the most abundant leaf age class, followed by early immature leaves, late immature leaves, early mature and senescent leaves (Fig. 2). The proportion of late mature leaves and early immature leaves varied markedly with plant height, site and season, while proportions of late immature and early mature varied less. The proportion of late mature leaves increased with height while the proportion of early immature leaves decreased, and this was more pronounced in the rainforest site. This was consistent with the leaf longevity analysis, in that leaves on tall rainforest plants tended to live longer than leaves on smaller plants. Overall, rainforest stinging trees generally had a larger proportion of late mature leaves and a smaller proportion of early immature leaves than the plantation stinging

Table 3. Units of measurement, means, standard errors and sample sizes of *Dendrocnide cordifolia* and *D. moroides* foliage attributes

Foliage attribute	Unit	*D. cordifolia*			*D. moroides*		
		mean	s.e.	*n*	mean	s.e.	*n*
Leaf production	per plant per week	0.35	0.02	76	0.38	0.03	70
Longevity	weeks	24.89	0.44	236	22.27	0.52	102
Geometric Increase	cm week^{-1}	1.29	0.01	844	1.32	0.01	947
Maximum width							
Small plants	cm	18.84	0.59	126	13.33	0.95	28
Mid-sized plants	cm	25.71	0.54	220	30.77	0.87	109
Tall plants	cm	25.75	0.62	116	26.21	0.89	60
Toughness	g cm^{-2}	15.52	0.32	181	13.76	0.26	267
Moisture	% wet weight	87.56	0.21	131	88.65	0.21	271
Nitrogen	% dry weight	2.56	0.12	35	2.94	0.08	132

trees. This was also consistent with the earlier observation of overall greater longevity of rainforest leaves. The differences between seasons were more pronounced in the rainforest site, with generally more late mature leaves in summer and autumn and fewer in winter and spring.

Leaf growth rates

Early immature leaves grew faster than late immature leaves ($F_{9,18} = 245.45$; $P < 0.0001$) and leaves grew at a reasonably constant rate for most of the year, except for spring when they grew twice as fast ($F_{9,18} = 12.4$; $P < 0.0001$). Leaf growth was similar on small and tall plants but faster on mid-sized plants ($F_{9,18} = 5.01$; $P < 0.001$). Overall the rate of leaf growth of stinging tree leaves was rapid. New leaves completed the majority of their development within 6 weeks of emergence, roughly one-quarter of their life span

Leaf size

Small plants

Leaf size differed between species and sites. *Dendrocnide cordifolia* leaves were larger than *D. moroides* leaves ($F_{5,02} = 8.51$; $P < 0.005$) and rainforest leaves were larger than plantation leaves ($F_{5,02} = 12.61$; $P < 0.005$).

Mid-sized plants

Leaf size differed between species and sites. *Dendrocnide cordifolia* leaves were smaller than *D. moroides* leaves ($F_{6,39} = 29.11$; $P < 0.0001$) and rainforest leaves were larger than plantation leaves ($F_{6,39} = 17.91$; $P < 0.0001$).

Tall plants

Leaf size varied significantly between species across seasons. *Dendrocnide moroides* leaf size increased during the year, while *D. cordifolia* leaf size was small in autumn ($F_{4,42} = 9.17$; $P < 0.0001$).

Leaf quality

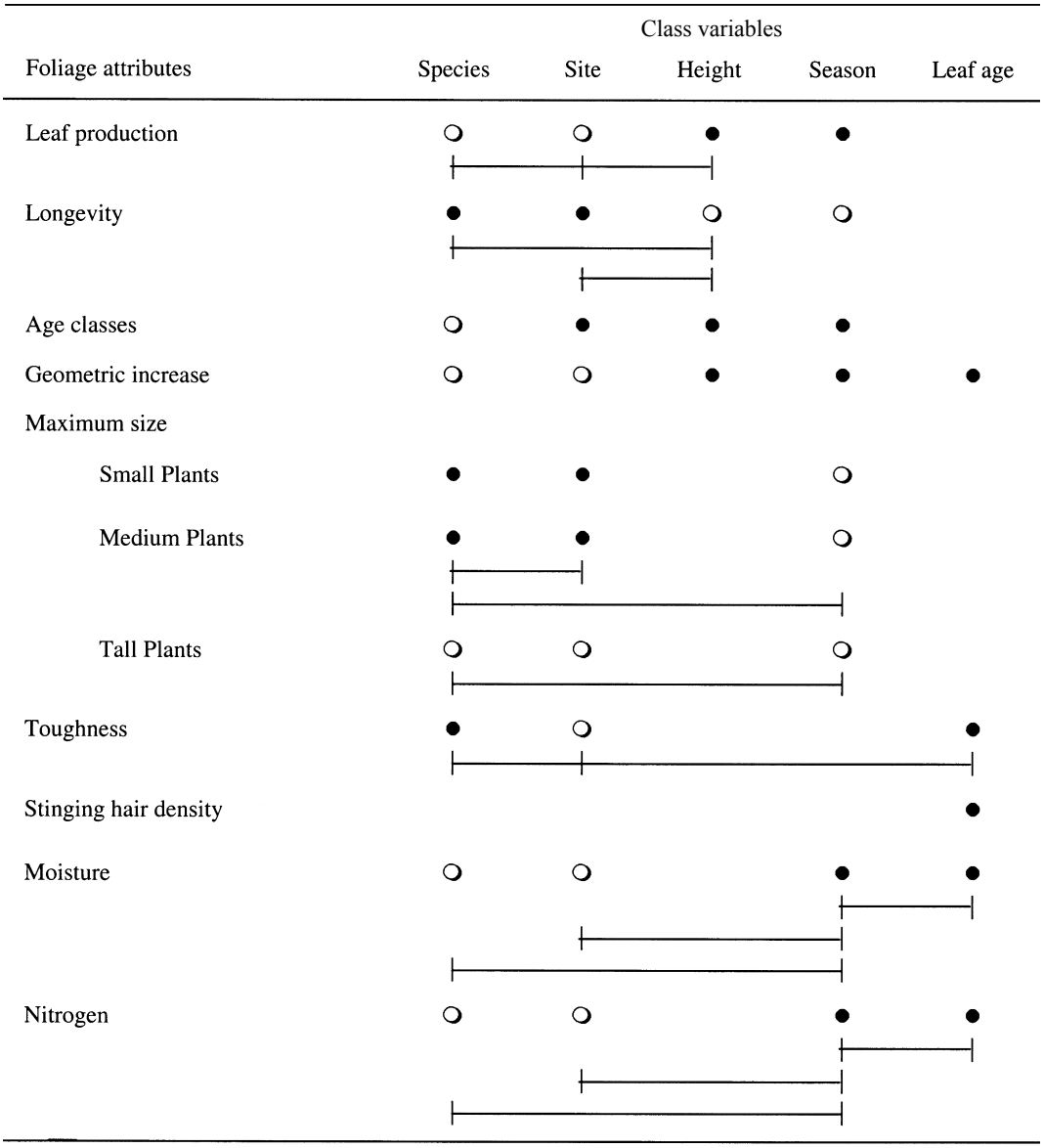
Stinging hair density

The density of stinging hairs on *D. cordifolia* leaves decreased dramatically with leaf age (Fig. 3*A–D*). The juvenile leaf samples were so dense with stinging hairs that the leaf surface was difficult to see, while few hairs were visible on the senescent samples. Newly emerged leaves were so dense with stinging hairs that it was not possible to see the epidermis until the leaves were about 3–4 cm wide. Over time, stinging tree leaves shed their hairs. Air-borne hairs could be seen when looking above the leaf surface, through rays of sunlight. Every person spending more than 1 h in the vicinity suffered from harsh, continuous bouts of sneezing, presumably a reaction to the air-borne stinging hairs. This phenomenon was prevented by wearing particle masks, providing they were replaced regularly.

Leaf toughness

Leaf toughness differed between species and age classes. *Dendrocnide cordifolia* leaves were tougher than *D. moroides* ($F_{8,80} = 19.13$; $P < 0.0001$). Toughness was highest in juvenile leaves, lowest for immature leaves and increased with leaf age ($F_{8,80} = 29.06$; $P < 0.0001$).

Table 4. Summary of ANOVA results testing significance of class variables of stinging tree foliage attributes
Data of foliage attributes were tested by separate models of multi-factor analysis of variance, except for stinging hair density. ● indicates main effect significant at 5% level. ○ indicates main effect not significant at 5% level. ⊣| indicates a two-way significant interaction. ⊣⊣| indicates a three-way significant interaction



Leaf moisture content

Leaf moisture content varied with season and leaf age. It was lowest in winter and highest in spring ($F_{21,89}$ = 48.86; $P < 0.0001$), highest in immature leaves and decreased with age ($F_{21,89}$ = 82.71; $P < 0.0001$). Several interactions were significant. Moisture content varied seasonally with leaf age ($F_{21,89}$ = 4.12; $P < 0.0028$) and between sites. Rainforest leaves were seasonally moister than plantation leaves ($F_{21,89}$ = 3.68; $P < 0.0261$). The main seasonal effect was evident in *D. moroides* leaves while *D. cordifolia* leaves remained at ≥ 88% all year ($F_{27,01}$ = 12.15; $P < 0.0001$).

Nitrogen content

Nitrogen content varied with season and leaf age. It was lowest in winter and highest in spring ($F_{29,62}$ = 135.01; $P < 0.0001$), highest in immature leaves and decreased with age ($F_{29,62}$ = 44.66; $P < 0.0001$). Nitrogen content varied seasonally with leaf age, and immature leaves had an unusually

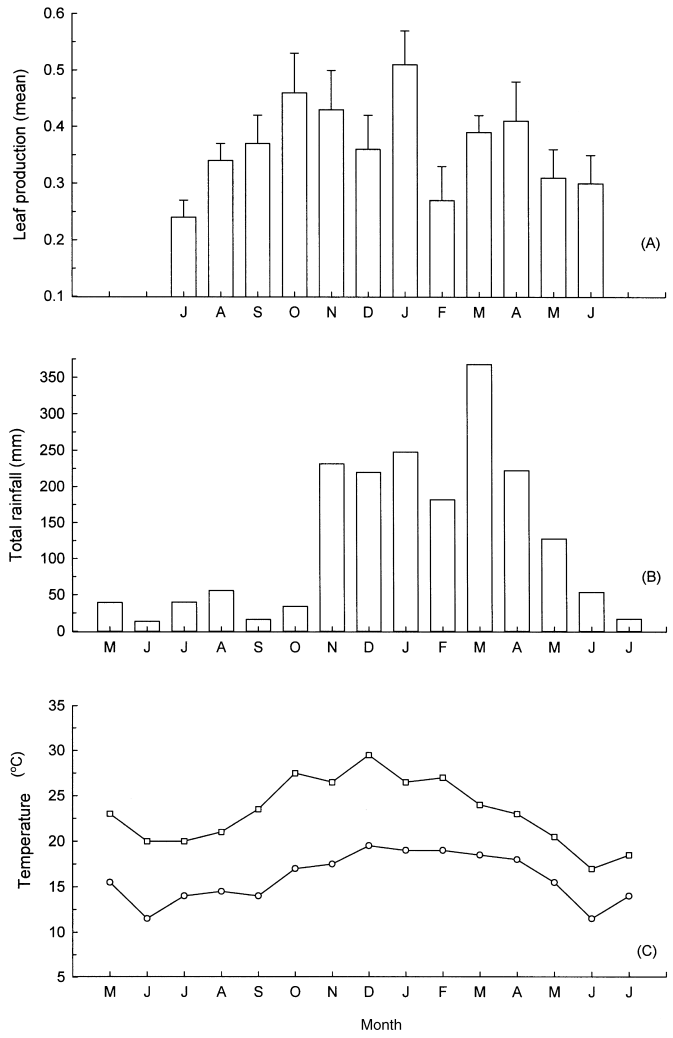


Fig. 1. The monthly variation of (*A*) mean *Dendrocnide* species leaf production (per plant, per week), (*B*) total rainfall (mm) and (*C*) mean temperatures (°C) (□ maximum, ○ minimum) at Wongabel State forest.

high nitrogen content in summer ($F_{29,62} = 2.63$; $P < 0.0367$). Rainforest leaves were richer in nitrogen than plantation leaves, except in winter ($F_{29,62} = 6.41$; $P < 0.0021$).

Summary

Season had a strong influence on leaf production, growth rates and moisture and nitrogen content, with increased activity in spring and summer months. Leaf quality and growth rates decreased with age. Foliage attributes varied with plant height often as a positive or negative continuum, but with the majority of growth activity occurring on mid-sized plants. Only with leaf growth rates and proportions of leaf age classes were there no significant differences in foliage attributes between species.

Discussion

Spatial considerations

Leaf responses to variations in solar radiation were expected to be evident with respect to site, with plantation leaves growing in direct sunlight and rainforest leaves growing in shade for most of the day. It was expected that variations with respect to height would also influence the proportion of sun and shade leaves in both sites. Stinging tree leaves were large (*D. moroides* >50 cm wide on some plants) and leaf density increased with plant size; thus, self shading of leaves within individual plants was common. As most leaves grew at the apex of the stem, older leaves were continually being shaded by new growth.

Leaf production, longevity and age class distribution

Stinging trees produced leaves all year round with a significant peak in production in late spring and summer. Although leaf production did not coincide with monthly fluctuations of either temperature or rainfall, almost twice as many leaves were produced in the warmer, wetter months than in the cooler, drier months. This pattern of new leaf production has been observed in individual Australian subtropical rainforest tree species *Dendrocnide excelsa* (Lowman 1992), *Argyrodendron actinophyllum* (Basset 1991*a*), and in different rainforest formations (Hopkins and Graham 1989; Lowman 1992). It would be expected that the larger the plant, the greater reserves and subsequently the more leaves produced. Yet mid-sized plants produced more leaves than either small or tall plants, especially *D. moroides* in the rainforest. These differences may also be due to plant age. Small plants would not have the resources to produce large numbers of new leaves and tall plants might produce less due to aging.

Leaves in the rainforest site lived 6 weeks longer and were more variable in longevity with respect to height than plantation leaves. This may be a shade effect. Leaf longevity is influenced by differences in sunlight, as leaf abscission of plants growing in high light environments is often faster than in low light (Bentley 1979). Leaf lifespan may also be shorter under high light because of an increased likelihood of damage caused by photodestruction of pigments, desiccation and overheating (Bongers and Popma 1990). In addition, as a leaf's light environment affects its rate of energy capture and carbon gain (Nunez-Farfan and Dirzo 1989), a leaf growing in shade would have a reduced photosynthetic capacity (Mooney and Gulmon 1982) and would be expected to increase its longevity in order to increase its overall carbon gain. Higher maximum temperatures recorded in the plantation could also have contributed to reduced leaf life, as water and heat stress accelerate senescence (Reich and Borchet 1984) and once initiated, the rate of senescence is positively related to temperature (Thomas and Stoddart 1980).

Leaves of small *D. moroides* plants abscissed 5 weeks earlier than those of taller plants. For both *D. moroides* and *D. cordifolia* longevity increased with height in the rainforest. If low light intensity increases longevity on a macro-habitat

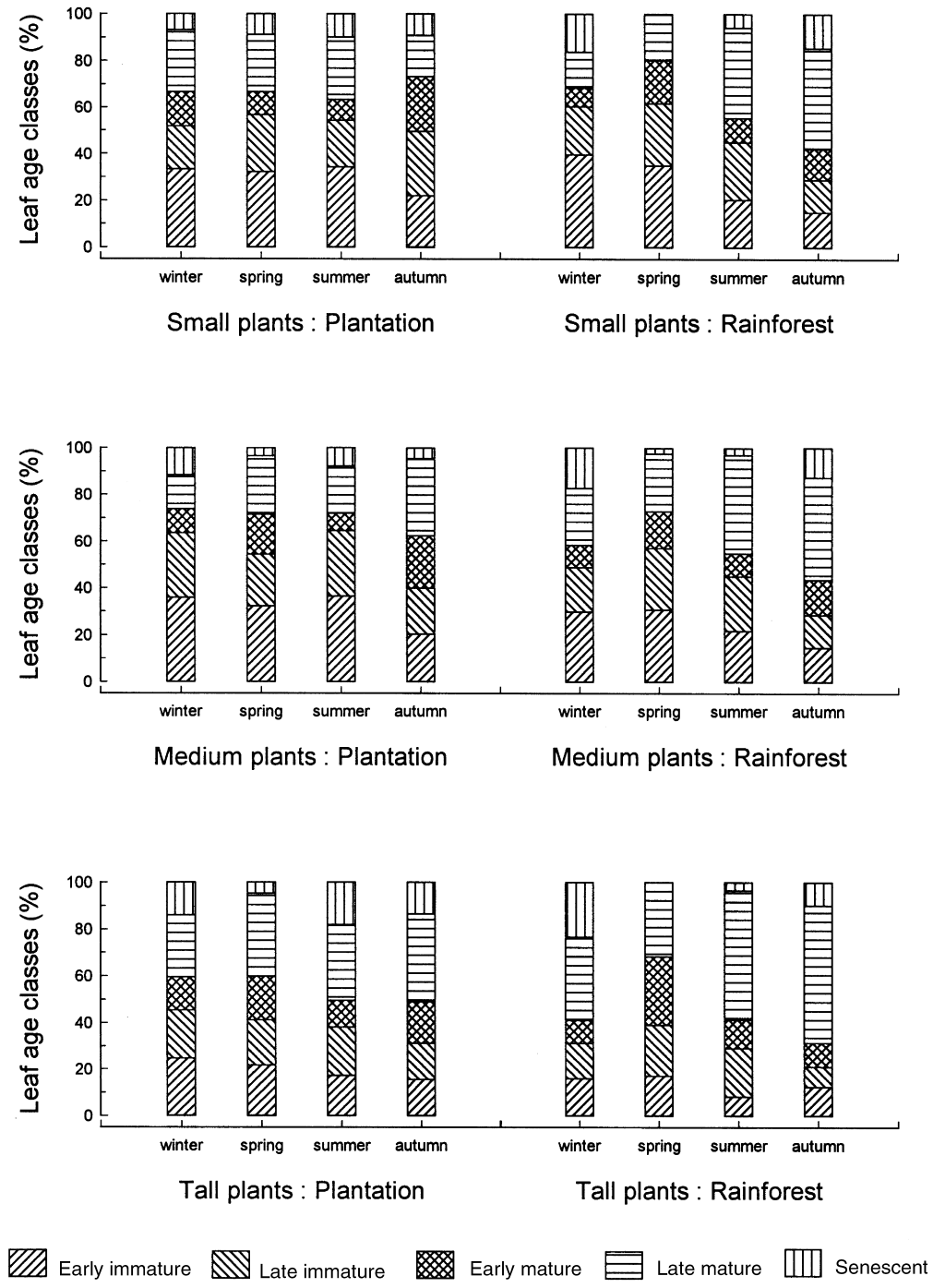


Fig. 2. Seasonal variations in the proportions of leaf age classes between sites and plant height classes.

scale, reflecting the differences in longevity between sites, then it could be argued to increase longevity on a micro-habitat scale, with self-shaded leaves living longer than sun leaves. Stinging trees need full sunlight to germinate and grow and small plants were usually only growing in direct sunlight in either the rainforest or plantation. Taller (older) rainforest stinging trees were more likely to be found in later stages of gap regrowth and often shaded by surrounding gap specialists and by canopy trees. This was not the case for tall plantation trees, which all grew in virtually full sunlight (due to very poor conifer foliage production) and their leaves did not show a height-longevity effect.

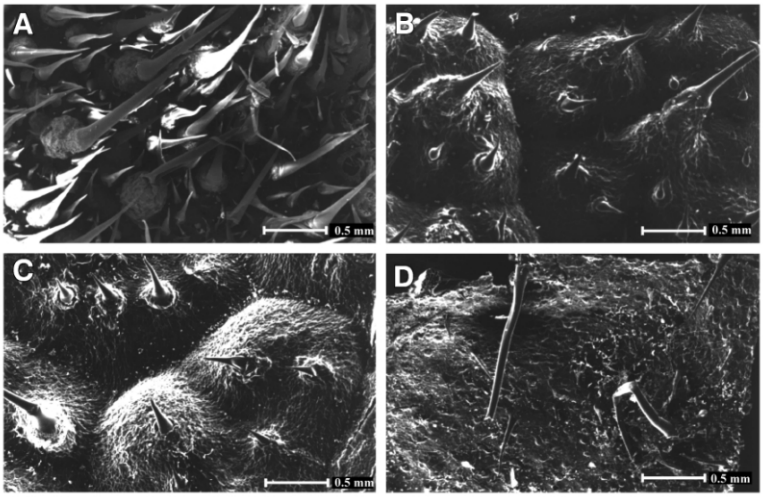


Fig. 3. *Dendrocnide cordifolia* stinging hair density of (*A*) a juvenile leaf, (*B*) an immature leaf, (*C*) a mature leaf and (*D*) a senescent leaf.

Dendrocnide cordifolia leaves lived 3 weeks longer and were less variable in longevity than *D. moroides* leaves. Stinging tree leaves were relatively short-lived: *D. moroides* 22 weeks, *D. cordifolia* 27 weeks and *D. excelsa* roughly equivalent at 7 months (see Lowman 1992), compared with the leaves of most evergreens which usually live for at least one year (Opler 1978). Within this short period longevity was highly variable. Absolute changes in leaf lifespan have been shown to be greatest amongst species with short leaf lifetimes and small absolute differences in leaf duration for species with a short leaf lifetime may have important physiological and ecological ramifications (Reich *et al.* 1991). Stinging tree leaf lifetimes exhibited a high degree of flexibility and such a trait may enhance their survival in rainforest gaps.

Few studies have analysed the relative abundance of leaves of different age classes. However, one study attributed high proportions of young leaves to increased levels of radiation. Plants in neotropical forest gaps had a higher proportion of young leaves (39%) than those in the primary forest understorey and pioneer vegetation (13%) (Newbery and de Foresta 1985). Higher light levels in the plantation site could have contributed to the high proportion of young leaves observed in this study, with plants taking advantage of high light conditions by increasing leaf production. The small and mid-sized stinging trees also had a larger proportion of immature leaves than tall plants. The larger proportion of late mature leaves in the rainforest site was consistent with longevity results, in that rainforest leaves lived longer than plantation leaves. It is likely that shade increased longevity in this site and thus increased the proportion of late mature leaves. The increase in proportions of early immatures increasing in spring is consistent with findings of increased leaf production in spring.

Young leaves were abundant throughout the year and on small and mid-sized plants half of the leaves were still expanding. For some plants, the timing of leaf production may be a defence tactic, to synchronise leaf flush during high herbivore abundance to satiate herbivores or to produce leaves when herbivores are scarce (Aide 1988). About twice as many new leaves were produced during spring and summer compared with other times. Similarly, the subtropical *Dendrocnide excelsa* produced leaves continuously throughout the year, with production peaking in summer (Lowman 1992). It unlikely that these plants were utilising the timing of leaf production as a defence tactic against herbivores, as herbivory was consistent all year round. Rapid leaf growth is considered a mechanism to escape herbivore attack (Crawley 1983); early immature leaves grew faster than late mature leaves and yet they were more abundant, nutritious and less tough than late immature leaves.

Growth rates and leaf size

Faster growth rates of very young leaves are expected. Leaf expansion rate decreases with age due to an increase in leaf toughness that occurs as leaves reach maturity (Berish 1986). Young leaves on mid-sized plants grew fastest and this was surprising as more young leaves were also produced on mid-sized plants. This indicates that a major proportion of the plant's resources were used both to produce and rapidly expand a high concentration of young leaf tissue. In view of the ontogeny of a stinging tree, it appears that mid-sized plants were at their most productive stage. Small plants struggled to become established and would have had less resources than mid-sized plants, while tall plants were older, perhaps approaching the end of their lifespan and more affected by the shade of neighbouring plants, which would reduce leaf growth.

Spring leaves grew faster than leaves produced at other times of the year and this coincided with increased rates of leaf production in spring. Leaf production was higher in

summer but growth was slower, perhaps indicating that plants were increasing leaf production at the expense of leaf growth rate. However, high temperature causes water stress and inhibition of leaf growth can occur (Cornelissen 1992).

The stinging tree *D. moroides* is one of the largest-leaved tropical plants in Australian rainforest, with leaves exceeding 50 cm in width. Leaf size was highly variable. The largest leaves were recorded on mid-sized *D. moroides* in the rainforest and for both species, leaves were larger in the rainforest. Shade leaves are often larger than sun leaves (Crawley 1986; Cornelissen 1992) as increased leaf area maximises carbon gain by photosynthesis and a seedling will decrease its relative investment in leaf area in response to a high light regime (Chabot and Hicks 1982). As with leaf longevity, the stinging trees growing in the shadier rainforest sites would have larger leaves to maximise photosynthetic capacity. Cornelissen (1993) found variation in leaf morphology of *Castanopsis fargessii* partly due to overall plant size and partly as a direct effect of sunlight. Moisture availability also influences leaf size. Mature leaves were often smaller during dry periods, which is a predictable response to minimise water loss (Bunce *et al*. 1977). Leaf size was shown to vary seasonally. Low rainfall during winter may have been responsible for the smaller size of winter leaves. However, when analysing the effect of seasonal rainfall on maximum leaf size, it must be remembered that it takes an average of 9 weeks for a leaf to mature and fluctuating rainfall could have influenced dynamics at any point from emergence to maturity.

The consequences of differences in leaf size for herbivores of stinging trees are difficult to interpret. In theory, the larger the leaf, the more 'apparent' it may be to a herbivore, making it more vulnerable to attack than a smaller leaf (Rhoades and Cates 1976). Leaf size and shape are important in host–plant recognition (Heinrich 1979; Crawley 1986) and may influence the number of species attacking plants and alter herbivore abundance (Brown and Lawton 1991). However, Basset (1991*b*) found that leaf size had little, or no apparent effect, on herbivore distribution and abundance on a subtropical rainforest tree.

Leaf quality

Leaves of *D. cordifolia* were tougher than leaves of *D. moroides* and toughness increased with leaf age. The increase in toughness with leaf age is reported elsewhere (Scriber and Slansky 1981; Lowman and Box 1983; Coley *et al.* 1985; Aide and Londono 1989). Separating juvenile from immature leaves was useful in this analysis, as the effects of leaf hair density could be separated from the effects of leaf toughening *per se*. The high toughness of juvenile leaves was probably due to very high leaf hair density and not to the thickening of cell walls. Lowman and Box (1983) also found that leaf toughness was high in young *D. excelsa* leaves and attributed the high measure to leaf hair density. Leaf toughness was marginally higher in rainforest mature leaves compared with plantation mature leaves. The physical attributes of leaf toughness are expected to reduce insects' chewing capacity (Lowman and Box 1983), thereby reducing leaf palatability, and leaf toughness of mature neotropical rainforest leaves has been shown to be the strongest negative effect against leaf damage (Coley 1983).

High stinging hair density is considered to be a defense tactic against herbivores (Levin 1973) and reduction with leaf age has been observed for other species of Urticaceae (Lowman 1982). New stinging hairs were not produced during the life of the leaf, so the reduction of stinging hair density from the juvenile to the mature stage would be attributed to the increase in leaf area as the leaf grows. The reduction of leaf hair density from the mature to the senescent stage was probably due to 'hair senescence'. This characteristic may be an adaptation that deters herbivorous mammals. The prolonged presence of humans in the proximity of stinging trees induces violent fits of sneezing and bleeding of the nasal passages as the stinging hairs are inhaled and lodged in the nasal passages (MacFarlane 1963). The stinging hairs may be inhaled with deleterious effects by other vertebrates which keep them away. This phenomenon of stinging hair senescence has not been noted previously, but Pullin and Gilbert (1989) found that stinging hair density of *U. dioica* remained constant throughout leaf expansion and that hairs were lost due to abrasion.

The leaf moisture content of most trees averaged between 45 and 75% (Soo Hoo and Fraenkel 1966: cited in Scriber and Slansky 1981; Scriber and Feeny 1979). Leaf moisture of stinging trees was very high, not usually less than 84% and up to 90% and decreased with leaf age. High moisture content in young leaves is common (Scriber and Slansky 1981; Lowman and Box 1983; Reich *et al*. 1991) and is an important factor in leaf choice by herbivores (Scriber and Slansky 1981; Berish 1986). Older leaves may be lower in moisture content as they are less able to prevent water loss (Reich and Borchet 1984). Generally, leaf moisture was lower in winter (dry season) than in spring and summer (wet season) and this pattern was more pronounced for *D. moroides* leaves than for *D. cordifolia*. That the rainforest site was cooler could account for moister leaves, but the average difference in leaf moisture between sites, although statistically significant, was only about 1% and is probably not biologically significant.

Total nitrogen content of leaves can vary from 0.03 to 7% (Mattson 1980; Crawley 1983), with highest concentrations occurring in younger tissues (3–7%) and lowest concentrations in senescent leaves (0.5–1.5%) (Mattson 1980). For most plant species, nitrogen concentration falls in the region of 1–2% (Bentley and Johnson 1991). In comparison, stinging tree leaves were high in nitrogen content, ranging from 1.4 to 5.78%, and as high as 4.12% total nitrogen was recorded for some individual senescent leaves. However, nitrogen content was generally highest in younger leaves and

decreased with age. Nitrogen content averaged at 2.83% in summer, 2.38% in winter and was very high in spring, 3.94%. High nitrogen levels in spring would reflect the increase in leaf growth rates (Mattson 1980) that were observed in spring and could indicate that resources were being mobilised for the observed increase in leaf production in summer. Conversely, leaf growth and production were minimal in winter and nitrogen levels were lowest at this time of the year. Total nitrogen content only gives a rough indication of the amount of nitrogen available to herbivores, as a proportion of nitrogen within leaves is tied up in complexes that are not easily metabolised (Bentley and Johnson 1991), e.g. tannins (Feeny 1969). Even so, herbivores prefer nitrogen-rich leaves (Mattson 1980; Crawley 1983) and young leaves are commonly highest in protein (Mattson 1980; Scriber and Slansky 1981). Variations in leaf moisture may influence leaf choice but the degree of influence of either nitrogen or moisture cannot be predicted as the pattern of variability of leaf moisture was similar to that of total nitrogen and both are said to have similar effects on herbivore leaf choice. The seasonal changes in leaf moisture may affect leaf palatability (Mattson 1980; Scriber and Slansky 1981), but perhaps only when water is limiting as Basset (1991*b*) found that leaf water content had little influence over herbivore distribution and attributed this to excess water in the rainforest during the wet season.

Conclusions: implications for herbivores

The growth dynamics of stinging trees appeared well suited to a fluctuating light environment. All foliage attributes showed considerable variability between species and sites through the 18-month measuring period, approximately one-third of the plants' lifespan. Pioneer rainforest plants need to be responsive to an environment that rapidly changes in light availability. This study demonstrates the that the foliage attributes of stinging trees are dynamic and responsive to changing light conditions. When a gap in the rainforest canopy forms stinging tree seeds germinate, producing a single stem, and grow rapidly. After they reach about 1 m in height they develop secondary branches and produce large numbers of rapidly expanding leaves, quickly shedding senescent leaves. As they age and the canopy closes, leaf production drops, leaf lifetime and leaf size increase to compensate for the reduction in light intensity. The proportion of mature leaves increases. The high moisture and nitrogen contents of these plants are a reflection of the high resource (light) environment. Other studies have shown that leaves of tropical gap species are high in nitrogen (Choong *et al*. 1992) and short-lived (Coley *et al*. 1985). Ogawa *et al*. (1995) suggested that plants exhibiting rapid leaf growth and low longevity were maximising high photosynthetic production and that a fast turnover of leaf area was important for rainforest species in canopy gaps.

There is little evidence to suggest that these plants are avoiding herbivores by reducing quality and quantity of immature foliage. They have large, moist leaves that are high in nitrogen and support a large proportion of young leaf tissue all year round. But the stinging hairs that densely cover the nutritious immature leaves may be considered to present a strong line of defense, particularly as they are well known to inflict considerable harm to humans and are thought to protect leaves from herbivore damage (Pollard and Briggs 1984; Pullin and Gilbert 1989). However, these plants did receive very high levels of herbivore damage (Hurley 1995). Plants growing in high-resource environments may sustain high levels of herbivore damage due to the rapid turnover of leaf material, which maximises energy acquisition, and the loss of nutrients and carbon associated with this rapid turnover are not considered a strong selective influence, because nutrients and light are readily available (Coley *et al.* 1985). The growth dynamics and leaf quality of stinging trees appear suited to the rapid colonisation of rainforest gaps, rather than responding to pressure from herbivores or to defending leaves against herbivores.

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