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Tree Growth Rates in North Australian Savanna Habitats: Seasonal Patterns and Correlations with Leaf Attributes

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Short Title: Tree growth in Australian savanna habitats

Abstract

We demonstrate a significant relationship between leaf attributes and growth rates of mature trees under natural conditions in northern Australia, a pattern that has not been widely reported before in the literature. Increase in diameter at breast height (DBH) was measured every 3 months for 2 years for 21 tree species from four habitats near Darwin: *Eucalyptus* open forest, mixed eucalypt woodland, *Melaleuca* swamp and dry monsoon rainforest. Assimilation rates and foliar chlorophyll, nitrogen and phosphorus concentrations were positively correlated with growth rate and negatively correlated with leaf mass per area. For most species, increases in DBH were confined to the wet season (summer) period between November and May. Average annual increases in DBH were larger in the dry monsoon rainforest (0.87 cm) and the *Melaleuca* swamp (0.65 cm) than in the woodland (0.20 cm) and the open forest (0.16 cm), and were larger in non-Myrtaceous species (0.53 cm) than in Myrtaceous species (0.25 cm). These results are discussed in relation to the frequent fire regime prevailing over much of northern Australia that cause the marked contrast between the small pockets of fire tender closed monsoon rainforest embedded within large expanses of fire-tolerant savanna.

Introduction

Eucalypt open forests and woodlands dominate the landscapes of monsoon tropics in northern Australia. These tropical savannas occupy 25% of the Australian continent, and play a major role in the continent's carbon and water cycles (Eamus and Prior 2001) Rainfall in Australian savannas is strongly seasonal, and 97% of Darwin's annual average rain falls between the summer months of October and April, while June, July and August are virtually rainless (Commonwealth Bureau of Meteorology, Australia 2001). Consequently patterns of leaf production and leaf fall are strongly seasonal, and many species are deciduous or semi-deciduous during the dry season (Williams *et al.* 1997). There are also large seasonal variations in photosynthesis per unit leaf area (Eamus and Cole 1997; Prior *et al.* 1997*a*,1997*b*; Eamus *et al.* 1999), suggesting that stem growth is also likely to be seasonal in most species, a notion that is supported by a few studies of individual tree species. For example, Mucha (1979) found that stem growth of mature *Eucalyptus tetrodonta* trees in savanna near Darwin was confined to the wet season, as was growth of *E. tetrodonta* (Prior *et al.* 1997*a*) and *Terminalia ferdinandiana* saplings (Prior *et al.* 1997*b*). However, there have been virtually no comparisons of tree growth rates in different habitats within or between regions, or between different plant families.

Australian savannas vary structurally and floristically with rainfall and soil type (Williams *et al.* 1996). Within the eucalypt savanna there is fine-scale patterning of different habitat types such as small patches of wet and dry monsoon rainforests and *Melaleuca* swamp forests embedded within the matrix of woodland or open forest. Wet monsoon rainforests are associated with sites of perennial moisture availability such as along streamlines or in seepage areas, while dry monsoon rainforests occur in areas that are topographically protected from fire, and *Melaleuca* swamps are found in seasonally-inundated or poorly-drained areas (Bowman and Minchin 1987; Russell-Smith 1991; Brock 1993). The native flora in the area contains species from Gondwanic groups such as the eucalypts, and from numerous Pan-tropic, Old World Tropic, Indomalaysian and Cosmopolitan families (Bowman *et al.* 1988), thereby allowing useful phylogenetic comparisons.

Our previous work has shown that leaf attributes differed among habitats within the Darwin region (Prior *et al.* 2003). The largest differences were between tree species in a dry monsoon rainforest, and those in the other 3 habitats studied (*Melaleuca* swamp, and two

savanna types, *Eucalyptus* open forest and mixed woodland). Species from the dry monsoon rainforest had on average larger A_{mass} and foliar chlorophyll (Chl_{mass}), nitrogen (N_{mass}) and phosphorus (P_{mass}) content, and smaller LMA than those from other habitats (Prior et al. 2003). However, it is unclear if these differences are reflected in faster growth rates.
While there are many studies showing growth rates of woody seedlings are correlated with leaf attributes such as photosynthesis per unit mass (A_{mass}) and leaf mass per area (LMA) (King 1991; Reich *et al* 1992; Huante *et al.* 1995; Cornelissen *et al.* 1996; Wright and Westoby 1999), there are few reports of such correlations in mature trees. Reich *et al.* (1997) demonstrated a relationship between growth and LMA in natural forests, using data from temperate deciduous and coniferous forests in the USA. Additional studies are needed, especially in other biomes, to establish whether leaf attributes such as LMA or A_{mass} can be used to predict growth rates of mature trees under natural conditions. The wet-dry tropics provide a useful contrast to the warm-cold temperate systems that have been more intensively studied. In this paper, we report relationships among leaf attributes and growth rates of 21 tree species from four contrasting habitats in the wet-dry tropics near Darwin, in northern Australia.

This study addressed the following questions: (1) how do growth rates differ between four contrasting habitats within the Darwin region? (2) can leaf attributes in be used to predict growth rates of trees in these habitats? (3) how much does tree growth vary between the wet and dry seasons in the various habitats? and (4) are there differences in tree growth rates between the characteristically Australian (Myrtaceous) and other (non-Myrtaceous) species in this region?

Materials and methods

Study sites

The study sites were located near Darwin, in four distinct habitats common in the north of the Northern Territory, Australia, and are described by Prior *et al.* (2003). Temperatures in this region are high year round, with monthly means for Darwin ranging from 24.9°C in July to 29.2°C in November. Rainfall is extremely seasonal. Ninety-seven percent of Darwin's average 1710 mm rain falls between October and April inclusive; June, July and August are virtually rainless (Commonwealth Bureau of Meteorology, Australia 2001).

Records of temperature at Darwin Airport and rainfall for both Leanyer and Berry Springs during the study period were obtained from the Bureau of Meteorology (Fig. 1).

The dry monsoon rainforest site was at Leanyer (12.4°S., 130.9°E.), 7 km north of Darwin Airport, while the other habitats were located at Berry Springs Wildlife Park and the adjacent Berry Springs Nature Park (12.7°S., 131.0°E), about 40 km south-east of Darwin Airport. The Leanyer monsoon rainforest contracted from 20 ha to 1.5 ha between 1945 and 1990 (W.J. Panton, unpublished) due largely to the interaction of cyclone damage, weed invasions and wildfire (Panton 1993). Since 1990, active rehabilitation has increased the area of monsoon rainforest to 14 ha in 2001. This has involved fire protection, weed control, replanting using seed from remnant trees, and irrigation during only the first few years following replanting. The forest forms a closed canopy during the wet season, and there is virtually no herbaceous ground strata. Study trees were between 2 and 6 m high and included remnant individuals from the original forest and planted trees that were 4-5 years old and had not been irrigated for at least 2 years. Soils were alluvial loam.

The vegetation, soils and landforms of the Berry Springs locations have been described by Sivertsen *et al.* (1980) and by Bowman and Minchin (1987). Soils here have developed on highly weathered parent material and have undergone intensive leaching (Sivertsen *et al.* 1980). The open forest was located on deep red sandy loam, and was dominated by *Eucalyptus tetrodonta*, with a well developed understorey. The woodland was located on shallow earthy sands that contained extensive surface gravel (Sivertsen *et al.* 1980). The vegetation was dominated by *Corymbia foelscheana*, with well-developed secondary tree, shrub and grass layers. The woodland habitat also included two species at the nearby Berry Springs Nature Park - a stand of the conifer *Callitris intratropica* growing on a low ridge of shallow earthy sand, and *Melaleuca viridiflora* growing on a sandy drainage floor at the base of the ridge. The *Melaleuca* swamp was in a seasonally-inundated section of a poorly-drained depression (Sivertsen *et al.* 1980). Soils were organic loam over light clay. *Melaleuca viridiflora* was the only tree species found in the lower part of this habitat, but *Lophostemon lactifluus* and *Acacia auriculiformis* occurred in the more elevated zone between the swamp and adjacent woodland. Each study site comprised an area of about 0.5 - 1 ha.

Study species

In each habitat, all tree species with 6 or more representatives at least 2 m tall and with accessible leaves (i.e. lower than about 2 m from the ground) were included in the study, giving a total of 21 species from the four habitats described above. Three species (*M. viridiflora, T. ferdinandiana* and *P. careya*) were each found in two habitats. A full set of measurements was made at both sites for these species. Nomenclature follows that of the Northern Territory Herbarium (2003). The study species included evergreen, semi-deciduous and deciduous trees from 12 families (Table 1). The eight Myrtaceous and one coniferous species are from characteristically Australian genera; all other families are widely distributed in the tropics outside Australia (Thiele and Adams 1999).

Tree measurements

In each habitat measurements of leaf attributes and increase in diameter at breast height (1.3 m) (DBH) were made for six individual of each species that had leaves accessible from the ground, and most were therefore of quite small stature. As individuals of eight of the study species have the potential to become large canopy trees, the growth of an additional six larger individuals of these eight species was also determined, thereby enabling an investigation of the effect of tree size on DBH increment. These 6-12 trees from each species were all tagged and marked at 1.3 m height with permanent marker pen to allow repeat measurements. Some species (*M. nesophilus, W. pubescens* and *F. scobina*) in the dry monsoon rainforest were either multi-stemmed or the main stem branched low to the ground; the largest stem or branch of each tree was then marked. Diameter at breast height was measured with a fibreglass tape every 3 months between May 2000 and May 2002. In addition, over-bark band dendrometers (Agricultural Electronics Corporation, Tuscon, Arizona, USA) were installed on four individuals from each of 10 species (listed in Fig. 2), and circumference change was measured monthly. There was good agreement between dendrometer readings and those made with the tape ($r = 0.97$, $n = 40$).

A range of leaf attributes was measured in the dry season (July 2000) and again in the wet season (December 2000/January 2001/April 2001) as described by Prior *et al.* (2003). Briefly, light-saturated assimilation rates per unit area (A_{area}) and per unit mass (A_{mass}), leaf mass per area, thickness, density, saturated water content, Chl_{mass}, N_{mass} and P_{mass} were measured on 3 leaves from each of 6 trees per species. All measured leaves were mature and healthy, from different shoots and exposed to full sun for at least part of the day. Additional leaves from these trees (60–190 leaves per species) were tagged for assessment of median lifespan. General canopy appearance and presence of new leaf flush on all study trees were also noted each month.

Tree basal area and stem density were measured on all trees in 2-6 quadrats per habitat in July and August 2001. Diameter at breast height was measured for all stems higher than 1.5 m. Quadrats were between 10 m by 10 m to 20 m by 20 m depending on stem density thus a total of 300 to 1200 m^2 ground area was sampled in each habitat.

Percentage canopy was measured at 8-10 random locations within each habitat with a densiometer (Model A, Forest Densiometers, Oklahoma, USA) in March 2002, when leaf area was at its yearly maximum.

Data analyses

Three measures of tree growth were considered: (i) DBH increment; (ii) increment of stem cross-sectional area at breast height (CSA); and (iii) relative growth rate based on CSA. Diameter at breast height is useful because it is easily measured and can be largely self-scaling; any given DBH increment represents more biomass in large than in small trees, and since large trees generally grow more biomass, these two factors tend to compensate for each other. CSA increment is important ecologically as it can be summed for individual trees to give species or stand basal area. It is easily calculated from DBH and, unlike biomass estimates, does not involve use of allometric equations. We compared CSA increment and DBH increment as dependent variables in developing general linear models to describe relationships between growth and habitat, tree size, maximum photosynthetic rates and leaf lifespan.

Relative growth rate (RGR) for each tree was calculated using CSA as

$$\mathrm{RGR} = (\mathit{ln}\ \mathrm{CSA}_{\mathrm{MAY02}} - \mathit{ln}\ \mathrm{CSA}_{\mathrm{MAY00}})/\ 2\ \text{years}.$$

Correlation matrices were calculated for annual growth and wet season leaf attributes to investigate relationships between stem growth and leaf attributes. Additional correlation matrices were calculated separately for both the wet season (Nov to May DBH increments) and dry season (May to November DBH increments) to determine whether growth in a particular season was most closely related to leaf attributes in that season. Correlations were calculated for the three measures and initial DBH were calculated with data from all trees in the study.

Differences among habitats in basal area, stem density and average stem DBH were tested using analysis of variance (ANOVA). ANOVA was also used to test for differences among habitats and family in the three measures of mean annual growth between May 2000 and May 2002. DBH increment was found not to be significantly correlated with tree size and was therefore used as the dependent variable in repeated measures ANOVAs to test significance of differences between (i) species, (ii) habitat and (iii) family, during the four quarters of both years. Data were log-transformed as required so that standard deviations were independent of means. Statistica v. 6 (StatSoft Inc., OK, USA) was used for all statistical analyses. Tukey HSD test was used to determine significance of differences between individual means. Differences are termed 'significant' where $P < 0.05$, 'highly significant' for $P < 0.01$. Unless otherwise specified, species means are of the six trees for which leaf attributes were studied. We report DBH increments for *Callitris intratropica*, the only coniferous species in the region. However, it is difficult to meaningfully compare growth rates in this conifer with those of the broadleaved angiosperms, given the differences in foliage morphology and xylem water conducting elements (e.g. Reich *et al*. 1998; Niinemets 1999; Kloeppel *et al.* 2000), so we excluded *C. intratropica* from most analyses.

Results

Differences in stem growth rate among species

Tape measurements showed there were large, highly significant differences in DBH increment among species (Fig. 3). The largest annual DBH increments were 1.6 cm for *F. racemosa* and 1.5 cm for *A. auriculiformis*, and the smallest increments were 0.04 cm for *L. lactifluus* and *M. viridiflora* in the woodland. The dendrometers also showed largest DBH increments occurred in *F. racemosa, A. auriculiformis* and *T. microcarpa* (Fig. 2).

Myrtaceous versus non-Myrtaceous species

Differences between Myrtaceous and non-Myrtaceous species were highly significant, as were interactions with time of year. Annual average DBH increment of non-Myrtaceous species was double that of Myrtaceous species (Fig. 4), with the difference between the two groups most pronounced during the November to February period (Fig. 5). Stem CSA increments and RGRs were also larger in non-Myrtaceous than in Myrtaceous trees (Fig. 4).

Differences in stem growth rate among habitats

Total basal area was significantly lower in the woodland than in the open forest or dry monsoon rainforest, while stem density was significantly lower in the open forest than in the dry monsoon rainforest (Table 2). Small stems predominated in all habitats; median stem size was 3.2 cm DBH over all habitats, but ranged from 2.5 cm in the swamp to 4.0 cm in the dry monsoon rainforest. There were many more stems in the 5-10 cm DBH class in the monsoon rainforest than in the other habitats. The dry monsoon rainforest had the largest, and the woodland the smallest, % canopy (Table 2).

Differences in growth rates among habitats were significant, with all of DBH increment, CSA increment, and RGR being larger in the dry monsoon rainforest and swamp than they were in the open forest or woodland (Figs 4 and 6).

There were significant differences between habitats for two of the three species common to more than one habitat. DBH increment for *Melaleuca viridiflora* was nearly 12 times larger in the swamp than the woodland (Fig. 3), while *T. ferdinandiana* grew more in the woodland than in the open forest.

Relationship between tree growth and size

Linear correlations between DBH increment and initial DBH were not significant, either for all species combined (r = 0.15) or within individual habitats. However, there was a weak dependence (R^2 = 0.14) of DBH increment on tree size, with maximum growth occurring in intermediate-sized trees with DBH of 5-10 cm (not presented). Of the eight species represented by 12 individuals, there was a significant linear relationship between growth and DBH only for *C. foelscheana* (r = -0.75). In this species, there was significant growth only in those individuals with DBH less than 6 cm. By contrast, six species showed a non-significant positive relationship. The multi-stemmed species (*M. nesophilus, F. scobina* and *W. pubescens*) recorded smaller absolute DBH increments than did the single-stemmed species in the dry monsoon rainforest.

Initial DBH was positively correlated with both CSA increment ($r = 0.52$) and negatively correlated with RGR ($r = -0.36$).

Stem growth rate in relation to leaf attributes

There were significant positive correlations between annual DBH increment and wet season assimilation on both a leaf mass and a leaf area basis as well as with foliar chlorophyll, nitrogen and phosphorus content (Table 3). Annual DBH increment was negatively correlated with leaf mass per area ($P < 0.05$). Results were almost identical for wet season as for annual DBH increment, because annual DBH increment was dominated by wet season DBH increment. Dry season DBH increment was not significantly correlated with any dry season leaf attributes, but it was significantly correlated with wet season DBH increment.

Correlations between relative growth rates and leaf attributes were generally similar to or stronger than those for DBH increment, while those between CSA increment and leaf attributes were generally weaker (Table 3).

Modelled stem cross-sectional area increment

We compared CSA increment and DBH increment as dependent variables in developing general linear models to describe relationships between growth and habitat, tree size, maximum photosynthetic rates and leaf lifespan. Models using CSA increment accounted for more total variance than those using DBH increment, and while the effect of leaf lifespan was sometimes significant, including it improved the fit of the model by only about 1%. The model we present here therefore describes the relationship between CSA increment, A_{mass}, initial CSA and habitat, and omits leaf lifespan. For any given A_{mass}, stem CSA increment was largest in the swamp and dry monsoon rainforest, and smallest in the open forest and woodland. CSA increment increased significantly with increasing initial tree size and A_{mass} (Fig. 6). Adjusted R^2 for the model describing the relationship between CSA increment, A_{mass}, initial DBH and habitat was 0.625.

Timing of stem growth

Time of year had a highly significant effect on DBH increment, which was maximal in the November-February quarter. Virtually all stem diameter increases occurred in this and the February-May quarters (Figs 5, 7). This finding was supported by dendrometer measurements for species other than *M. leucadendra* in the monsoon rainforest and *M. viridiflora* and *A. auriculiformis* in the swamp (Fig. 2). In these three species, although stem diameter increased through most of the year, there was still a seasonal minimum in the late dry season. In most other species, slight stem shrinkage often occurred during the dry season (Figs 2, 7).

Growth increments were on average 49% larger in the first than the second year of measurement ($P < 0.001$).

Leaf phenology

Leaf flush was maximal in October and November (early wet season), especially in deciduous species (Fig. 8), and sometimes occurred before the first rain. Leaf production in the semi-deciduous species *Erythrophleum chlorostachys*, *B. obovata* and *S. eucalyptoides* was also concentrated in this period, whereas other semi-deciduous and evergreen species tended to produce some new leaves through much of the year.

Leaf loss was most pronounced between April and August (dry season), although there was also substantial leaf drop during the wet season in some species, most notably *C. fraseri*. In this deciduous species, median leaf lifespan was very short (3 months) and leaf exchange occurred throughout the wet season.

Discussion

Relationship between stem growth and leaf function

Annual DBH increment was positively correlated with wet season A_{mass}, A_{area}, Chl_{mass}, N_{mass} and P_{mass}, and negatively correlated with LMA. The attributes A_{mass} and A_{area} are estimates of maximum instantaneous carbon gain and thus potential biomass increase, while LMA is a measure of carbon invested per unit leaf area in capturing light energy. Similar findings have been reported for woody seedlings and young plants (King 1991;

Huante *et al.* 1995; Cornelissen *et al.* 1996; Wright and Westoby 1999), but we are not aware of many other extensive study relating leaf attributes to growth in mature trees under natural conditions. Reich *et al.* (1997) combined a number of data sets to show that ecosystem production efficiency (kg kg^{-1} $year^{-1}$) of 48 temperate forest stands was negatively correlated with LMA, and that this relationship applied to both natural systems and to plantations. Our study provides further support for the importance of LMA as an indicator of plant and ecosystem function. However, the relationship was not sufficient for LMA to be a reliable predictor of growth.

For all species leaf production and stem growth were both maximal during the early wet season. Stem growth was confined to the wet season despite the fact that rapid photosynthesis by evergreen and semi-deciduous trees occurs well into the dry season (Prior *et al*. 1997*a;* Eamus *et. al*. 1999). By contrast, Schöngart *et al.* (2002) reported that in a Venezuelan semi-deciduous forest, diameter growth occurred during 9-10 months of the year, and this may reflect the shorter, less severe dry season experienced in Venezuela.

The woodland and open forest contained a number of species (e.g. *E. tetrodonta, Erythrophleum chlorostachys, S. eucalyptoides, X. paradoxus*), that maintained a photosynthetically active canopy for all or most of the dry season. There is some evidence that this is achieved because such evergreen and very briefly deciduous savanna trees have a larger root system than deciduous ones; for example Eamus *et al*. (2002) estimated that there was 2-3 times more root mass in evergreen than deciduous trees of the same DBH in savanna near Darwin. As well as enabling more efficient extraction of soil water, a larger root system would enhance tree recovery after the frequent fires that regularly occur in the savannas. One would therefore expect a greater proportion of photosynthate being allocated below ground in evergreen trees, and those in the most fire-prone habitats - the woodland and open forest. This hypothesis is consistent with the finding that above-ground growth rates predicted from A_{mass} and tree size were lower in savanna and woodland trees than in dry monsoon rainforest trees.

Fire, habitat and tree stem growth

Stem density in the open forest was much higher (2881 cf. 753 stems ha^{-1}) than that reported by O'Grady *et al.* (2000) in similar forest subject to frequent fires. O'Grady *et al.* (2000) found the largest number of stems in the 5-15 cm DBH size range, with relatively few stems in the 0-5 cm class. In our study, the overwhelming majority of stems was less than 5 cm in DBH, and this difference in stand structure was presumably due to the decade-long absence of fire and hence frequent recruitment to the smallest size class. In sites burnt every 1-2 years, many lignotuberous resprouts would be burnt before attaining a height of 1.5 m.

DBH increments for *E. tetrodonta* (0.09 cm/year) in our study were lower than the average 0.39 cm annual increase in DBH reported by Mucha (1979), and the 0.48 cm/year reported by Chen (2002) for several open forest species. The high basal area (17 m^2 ha^{-1}) at our study site associated with fire protection compared with the more typical 8-12 m^2 ha^{-1} in comparable forest subject to frequent fire (Bowman 1992; Bowman *et al.* 1993; O'Grady *et al.* 1999) may be responsible for these differences in growth rates. Consistent with this, Werner (unpubl. data) found that tree growth rates were lower in unburnt savanna than in that subject to early dry season burning. While growth rates in the open forest were lower than expected, the DBH increase for *A. auriculiformis* in the swamp was very similar to the 1.5 cm $year^{-1}$ reported by Cole (1994) for the NT provenance of this species.

We found some significant intra-specific differences between habitats, for example the growth rate of *M. viridiflora* between the swamp and woodland habitats. This is not surprising since the swamp is inundated for several months each year, and the soil has a high organic content with high moisture availability throughout the dry season (L. Prior, unpublished data). By contrast, woodland soils are gravelly, dry out early in the dry season but also have poor sub-surface drainage. More surprising was the faster growth of *T. ferdinandiana* in the woodland than the open forest, which has deep, well-drained soils free of gravel and with a relatively high nutrient status (Prior *et al.* 2003).

Myrtaceous species had lower average growth rates than other species, yet they usually contribute the largest component of woody biomass in north Australian savannas; eucalypts comprised 87% of above-ground tree biomass in typical savanna near Darwin (O'Grady *et al.* 2000), and 56-64% of total basal area at 20 savanna sites in Kakadu National Park (Bowman *et al.* 1993). As biomass of an individual tree is a function of both growth rate and longevity this suggests the Myrtaceae dominants are long-lived trees. However, there is very little information on average tree longevity in northern Australia, and whether there are systematic differences among plant families. Inherent differences in longevity may be modified by different responses to factors such as fire, drought and termite attack. Extensive, frequent fires are a feature of Australian savannas (Russell-Smith *et al.* 1997), and Williams *et al.* (1999) found that deciduous non-eucalypt species comprised the group most susceptible to fire in savanna similar to the open forest and woodland in this study. Based on their data, Myrtaceous and non-Myrtaceous species had similar *plant* survival rates after a single, high-intensity fire (86 *cf* 82%), but *stem* survival was higher in the Myrtaceous species (43% *cf* 15%). Werner (unpubl. data), in an 8-year study, also found that Myrtaceous individuals lived longer on average than non-Myrtaceous ones, even in the absence of fire.

The dry monsoon rainforest had a significantly larger growth increment compared to the other habitats. While it is true that the monsoon rainforest site was characterised by a high density of small stems, most less than 10 years old, it is unlikely this is the cause of the higher growth rate given the observed a poor relationship between tree size and DBH increment, either within or between species. Furthermore, competition between individuals would have been greater in this habitat at the high density of stems (Prior *et al.* 2003). It is possible that the higher growth rate in the monsoon rainforest reflects more favourable edaphic conditions. For example, although surface soil dried out at a similar rate in all of the dry monsoon rainforest, open forest and woodland habitats, it is possible there was more soil water available at depth in the dry monsoon rainforest. Equally, it is possible that the growth was greater due to the higher total Kjeldahl N and P content of soil in the dry monsoon rainforest compared with that in the other habitats. However, it is striking that most dry monsoon rainforest species had leaf attributes generally associated with fast relative growth rates (e.g. Reich *et al.* 1997; Wright and Westoby 1999) — thin leaves with low LMA, high N_{mass}, P_{mass} and chlorophyll content — and canopy density was also larger (Prior *et al.* 2003). Consequently, we would thus expect these species to grow faster than many woodland or open forest species, even under the same growing conditions, and that this growth rate advantage is amplified more fertile soil characteristic of infrequently burnt monsoon rainforest sites. Unfortunately there were no study species common to the dry monsoon rainforest and another habitat to help distinguish the 'species effect' from the effect of growing conditions to evaluate this hypothesis.

Given the very fast potential growth rates of dry monsoon species, and their apparent ability to survive seasonal drought, why are these species restricted to a few relatively small areas of the landscape? Bowman (1992) argued that edaphic factors cannot explain dry rainforest boundaries, and that such forests are typically restricted to sites topographically protected from fire. It is possible that, in the absence of fire, these dry monsoon rainforest species would have a competitive advantage over woodland and open forest species and gradually invade these habitats.

Conclusion

We have demonstrated significant correlations amongst a range of leaf attributes and between these attributes and growth rates (whether expressed as DBH increment, CSA increment or RGR). However, unlike many pot-based seedling studies, these correlations from mature trees growing *in situ* were insufficiently robust to satisfactorily predict growth rates. Tree growth was highly seasonal in all habitats and confined predominantly to the wet season, when water availability was largest, evaporative demand was lowest and leaf canopy cover maximal. Trees in the dry monsoon rainforest and the paperbark swamp grew more quickly than those in the woodland and open forest. This was partly because Myrtaceous species grew more slowly than non-Myrtaceous species. However, despite their lower growth rates, Myrtaceous species account for 60-80% of standing biomass in this region, perhaps because they are more fire-tolerant than non-Myrtaceous species. Myrtaceous species are generally sclerophyllous, with long-lived leaves having a low A_{mass} and low foliar N content. By contrast, non-Myrtaceous species appear to conform to the 'live fast, die young' strategy (Eamus and Prichard 1998).

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Table 1. Study species listed by habitat with details of family and leaf phenological guild

Nomenclature is according to Northern Territory Herbarium (2003)

Species	Family	Leaf Phenology
Dry Monsoon Forest		
Ficus scobina L. f.	Moraceae	semi-deciduous
Ficus racemosa Benth.	Moraceae	semi-deciduous
Mallotus nesophilus Mull. Arg	Euphorbiaceae	semi-deciduous
Melaleuca leucadendra (L.) L.	Myrtaceae	evergreen
Terminalia microcarpa (formerly *T. sericocarpa*) Decne.	Combretaceae	deciduous
Wrightia pubescens R. Br.	Apocynaceae	deciduous
Open Forest		
Brachychiton megaphyllus Guymer	Sterculiaceae	deciduous
Buchanania obovata Engl.	Anacardiaceae	semi-deciduous
Erythrophleum chlorostachys (F. Muell.) Baill.	Caesalpiniaceae	semi-deciduous
Eucalyptus tetrodonta F. Muell.	Myrtaceae	evergreen
Planchonia careya (F. Muell.) Kunth	Lecythidaceae	deciduous
Syzygium suborbiculare (Benth.) T.G. Hartley & L.M. Perry	Myrtaceae	semi-deciduous
Terminalia ferdinandiana Exell	Combretaceae	deciduous
Woodland		
Callitris intratropica R.T. Baker & H.G. Sm.	Cupressaceae	evergreen
Cochlospermum fraseri Planch.	Bixaceae	deciduous
Corymbia foelscheana (formerly *Eucalyptus foelscheana*) (F. Muell.) K.D.Hill & L.A.S. Johnson	Myrtaceae	semi-deciduous
Melaleuca viridiflora Sol. ex Gaertn.	Myrtaceae	evergreen
Planchonia careya (F. Muell.) Kunth	Lecythidaceae	deciduous
Syzygium eucalyptoides ssp. *bleeseri* (O.Schwarz) B.Hyland	Myrtaceae	semi-deciduous
Terminalia ferdinandiana Exell	Combretaceae	deciduous
Xanthostemon paradoxus F. Muell.	Myrtaceae	semi-deciduous
Swamp		
Acacia auriculiformis A. Cunn. ex Benth.	Mimosaceae	evergreen
Lophostemon lactifluus (F. Muell.) Peter Wilson & J. T. Waterh.	Myrtaceae	semi-deciduous
Melaleuca viridiflora Sol. ex Gaertn.	Myrtaceae	evergreen

Table 2. Characteristics of the four study habitats

Soil attributes at 0.2 m depth are from Prior *et al.* (2003). Total Kjeldahl nitrogen was determined on the soil fraction that passed through a 1 mm sieve, thus the available N per volume of soil was reduced in proportion to the amount of gravel present. Canopy cover was measured at the end of the wet season, and is thus the annual maximum

Habitat	Soil texture	gravel (%)	Soil Nitrogen ($mg\ g^{-1}$)	Basal area ($m^2\ ha^{-1}$)	Stem density (ha^{-1})	canopy cover (%)
Dry monsoon forest	loam	36 ± 6	1.25 ± 0.29	22 ± 1	6883 ± 812	75 ± 3
Open forest	sandy loam	0.18 ± 0.05	0.69 ± 0.14	17 ± 2	2881 ± 204	47 ± 3
Woodland	loamy sand	47 ± 9	0.24 ± 0.03	10 ± 2	4165 ± 946	30 ± 3
Swamp	sandy loam	2.5 ± 1.9	0.22 ± 0.03	16 ± 3	2625 ± 75	42 ± 2

Table 3. Correlation coefficients between and leaf attributes and increments in DBH (diameter at breast height), biomass increments and relative growth rates, using species means

Correlation coefficients were calculated separately for the wet season ($n = 23$) and dry season ($n = 14$) for DBH increment and leaf attributes. The leaf attributes A_{area} and A_{mass} are assimilation rates on an area and a mass basis respectively, H_2O is saturated water content, LMA is leaf mass per area, 'Thick' is leaf thickness, Chl_{mass}, N_{mass} and P_{mass} are leaf chlorophyll, nitrogen and phosphorus content respectively, all per unit mass, and lifespan is median leaf lifespan. Significant correlations are shown in bold. Rows (i) to (v) respectively indicate correlation coefficients between (i) wet season DBH increment *v.* wet season leaf attributes; (ii) dry season DBH increment *v.* dry season leaf attributes; (iii) annual DBH increment *v.* wet season leaf attributes; (iv) annual cross-sectional area increment *v.* wet season leaf attributes; (v) relative growth rate *v.* wet season leaf attributes. Significant correlations are shown in bold. The correlation coefficient between wet and dry season DBH increments was 0.49 ($P < 0.05$)

	A_{area}	A_{mass}	H_2O	LMA	Thick	Density	Chl_{mass}	N_{mass}	P_{mass}	Lifespan
(i) wet DBH incr	**0.64**	**0.75**	0.33	**-0.45**	-0.41	-0.27	**0.65**	**0.50**	**0.59**	-0.28
(ii) dry DBH incr	0.44	0.43	0.21	-0.09	-0.03	-0.15	0.39	0.21	0.36	0.04
(iii) Annual DBH incr	**0.64**	**0.74**	0.33	**-0.44**	-0.41	-0.25	**0.62**	**0.47**	**0.55**	-0.29
(iv) CSA incr	**0.63**	**0.70**	0.26	-0.38	-0.33	-0.27	**0.56**	**0.53**	**0.57**	-0.19
(v) RGR	**0.46**	**0.75**	0.38	**-0.54**	**-0.48**	-0.33	**0.67**	**0.54**	**0.62**	-0.38

Captions for Figures

Fig. 1. Mean monthly maximum (closed circles) and minimum (open circles) temperatures for Darwin, and total monthly rainfall at Leanyer (black bar) and Berry Springs (grey bar) during the study period. Data were obtained from the Bureau of Meteorology.

Fig. 2. Mean monthly circumference increment, from the previous month to the month shown, as indicated by band dendrometers, for four individuals each of 10 species in the four habitats. Black horizontal bars indicate the wet season, and symbols represent the species as follows: *E. tetrodonta* (solid triangle up), *S. suborbiculare*, (open diamond) *M. viridiflora* (woodland and swamp) (solid circle), *C. foelscheana* (open square), *X. paradoxus* (solid triangle down), *A. auriculiformis* (open triangle up), *F. racemosa* (open circle), *M. leucadendra* (solid diamond) and *T. microcarpa* (open triangle down).

Fig. 3. Mean annual DBH increment for individual species in the four habitats. Species names are listed in full in Table 1.

Fig. 4. Differences among habitats and between Myrtaceous and non-Myrtaceous species in DBH increment, CSA increment and relative growth rate based on CSA (RGR). Abbreviations are as follows: DMF is dry monsoon forest, Sw is swamp, OF is open forest, W is woodland, non-M is non-Myrtaceous and M is Myrtaceous. Lines indicate standard errors.

Fig. 5. Mean DBH increments were higher in non-Myrtaceous than in Myrtaceous species, especially during November to February.

Fig. 6. Actual CSA increment in dry monsoon forest (closed circle), swamp (open triangle), open forest (open square) and woodland (open diamond) as a function of (a) maximum assimilation rate per unit mass (A_{mass}) and (b) initial CSA. CSA increment was modelled as a function of initial DBH, A_{mass} and habitat. Modelled relationships, assuming (Fig. 6*a*) the overall average CSA and (Fig. 6*b*) the overall average $A_{mass,}$ are indicated by a solid line (dry monsoon forest), long dashed line (swamp), medium dashed line (open forest) and short dashed line (woodland).

Fig. 7. Mean DBH increment for each quarter during the first (black bars) and second (grey bars) years of measurement in the four habitats. M-A indicates May to August; A-N indicates August to November; N-F indicates November to February; and F-M indicates February to May. Increases in DBH were virtually confined to the two wet season quarters between November and May, except in the swamp. By contrast, light-saturated assimilation rates (A_{mass}), indicated by the open circles, were positive during the dry season for species that retained leaves.

Fig. 8. Periods of major (solid black horizontal bars) and minor (hatched horizontal bars) leaf flush in deciduous, semi-deciduous and evergreen species, as well as periods of substantial leaf drop, as indicated by downward arrows, for July through June. '0' indicates when most individuals were leafless. Full species names are listed in Table 1.