COMMUNITY ECOLOGY - ORIGINAL PAPER

Habitat partitioning among neotropical pioneers: a consequence of differential susceptibility to browsing herbivores?

**James W. Dalling · T. R. H. Pearson · J. Ballesteros ·
E. Sanchez · D. F. R. P. Burslem**

Abstract Four species of fast-growing pioneer tree species in the genus *Cecropia* exist in the forests in central Panama. *Cecropia insignis* is dominant in old-growth forests but absent from nearby secondary forests; *C. obtusifolia*, and *C. peltata* are abundant in secondary forests but rare in old-growth forest, and *C. longipes* is uncommon in both. To determine whether *Cecropia* habitat associations are a consequence of local dispersal or differences in recruitment success, we grew seedlings of these species in common gardens in large treefall gaps in secondary and old-growth forest. In contrast to the observed adult distribution, only *C. insignis* grew significantly over 16 months in secondary forests; remaining species were heavily browsed by herbivores. *C. insignis* also grew and survived best in old-growth forest. Differences in susceptibility to herbivory did not result from an ant defence mutualism; none of the plants were colonised by ants during the experiment. To test whether *C. insignis*, the species least susceptible to herbivory, trades off investment in growth in favour of defence, we also grew the four *Cecropia* species in a screened growing house under light conditions comparable to large forest gaps. Contrary to expectation, species growth rates were similar; only *C. peltata* grew significantly faster than *C. insignis*. These results suggest that (1) conditions in ~40-year-old secondary forests no longer support the recruitment of *Cecropia* species, which are canopy dominants there; and (2) among congeners, differences in plant traits with little apparent cost to growth can have large impacts on recruitment by affecting palatability to herbivores.

Keywords Herbivory · Growth · *Cecropia* · Browsing · Ant–plant

J. W. Dalling (✉)
Department of Plant Biology,
University of Illinois Champaign-Urbana, 265 Morrill Hall,
505 South Goodwin Avenue, Urbana, IL 61801, USA
e-mail: dallingj@life.uiuc.edu

J. W. Dalling · J. Ballesteros · E. Sanchez
Smithsonian Tropical Research Institute,
Apartado, 0843-03092 Balboa, Panama

T. R. H. Pearson · D. F. R. P. Burslem
School of Biological Sciences,
University of Aberdeen, Aberdeen AB24 3UU, UK

Introduction

Several mechanisms have been proposed that promote high tree diversity in tropical forests. According to Hubbell's (1979, 2001) community drift model, species within broadly defined functional groups are assumed to be ecologically equivalent, with similar per-capita probabilities of recruitment success. The assumption of ecological equivalence arises as a consequence of predicted convergent responses among species to long-term mean environmental conditions and biotic neighbourhoods. This, in turn, results from limited seed dispersal and seedling recruitment success, leading to unpredictability in the physical and biotic characteristics of recruitment sites that are ultimately occupied (Hubbell 2005, 2006). In contrast, deterministic models of community organisation have emphasised the importance of limiting similarity in determining the trait composition of tree communities, with species differentiated according to their resource requirements (e.g. Engelbrecht and Kursar 2003; John et al. 2007), or through

interactions with mutualists, herbivores and predators (Fine et al. 2004). When communities contain closely related species, then potential niche overlap might be expected to be especially high, and divergent responses to habitat conditions may be necessary to prevent competitive exclusion.

Phylogenetic analyses of tree communities provide some evidence for habitat divergence among closely related species. For example, local communities of oak species occurring in the same habitat type are more likely to contain distantly related species than species from within the same section of the genus (Cavender-Bares et al. 2004). In tropical forests, where phylogenetic information is often incomplete, congeneric species pairs also often exhibit significant differentiation in local distribution. For shade-tolerant species these are often reflected in soil or topographic preferences that seem unlikely to be maintained by local dispersal (e.g. *Shorea*, *Polyalthia* and *Aporosa* in S.E. Asia, Ashton 1988; Rogstad 1990; Debski et al. 2002; *Entandrophragma* in the Central African Republic, Hall et al. 2004; *Rinorea* in Ecuador, Valencia et al. 2004).

For closely related pioneer species that require high-light conditions for seedling recruitment, coexistence may depend on differential responses to gap size or disturbance regime (Brokaw 1987). In Peru and Ecuador, pairs of *Cecropia* species inferred to be close relatives based on morphology show differential distributions across habitat types (i.e. habitat partitioning), where habitats consist of either stream-edges and landslides, or treefall gaps in old-growth forest (Folgarait and Davidson 1994). This habitat partitioning has been attributed to a trade-off between growth and defence against herbivores (Folgarait and Davidson 1994). This arises because gaps in mature forest tend to be smaller and more shaded disturbances than landslides and river meanders. According to the resource availability hypothesis (Coley et al. 1985), lower intrinsic growth rates associated with lower light availability should select for a higher investment in defence due to a higher replacement cost if tissue is lost to herbivores. As a consequence, forest gap species may be unable to compete in more open habitats dominated by faster growing pioneers, whereas faster growing species suffer higher mortality associated with herbivore damage in more shady environments.

Our previous work at the Barro Colorado Nature Monument (BCNM) in central Panama, provides support for a growth-defence trade-off among pioneers, as growth rate and mortality rate are positively correlated across a taxonomically diverse species group (Dalling et al. 1998). Species with the highest seedling height growth in similar-sized gaps had the highest mortality rates, due to a higher incidence of attack from browsing herbivores and stem-boring insects (Dalling and Hubbell 2002). However, it is unclear whether this trade-off between growth and mortality can be extended to groups of closely related species.

In this study we explored an example of apparent habitat partitioning among four *Cecropia* species on BCNM. Our goal was to determine whether habitat preferences of species are a consequence of colonisation history, or whether they arise from an allocation trade-off between growth and defence, as proposed by Folgarait and Davidson (1994). If *Cecropia* species are strongly dispersal limited, and colonisation history plays a dominant role, then adaptations to particular habitat conditions are unlikely to arise (Hubbell 2005), and species should have similar growth and mortality rates. Alternatively, *Cecropia* species now common in secondary forest may have evolved to colonise open habitat types resulting from natural disturbances. These species may have been under selection for increased growth at the expense of investment in defence. However, as secondary forest stands age, and pioneer stem densities decline, herbivore communities may come to resemble those of old growth forest, creating conditions that favour the survivorship *Cecropia* found in old-growth forest.

We tested these hypotheses by growing seedlings of the four species in common gardens in tree fall gaps in ~40-year-old secondary forest, where *C. obtusifolia* and *C. peltata* dominate, and in old growth forest, where *C. insignis* dominates. A fourth species, *C. longipes*, is uncommon in both forest types. We tracked growth, mortality and herbivory on these plants until the sapling stage. In addition, we examined whether growth rates, allocation patterns and a subset of plant defence traits varied among these species when grown in the absence of herbivores in a screened growing house.

Materials and methods

Study site and species

The study was conducted in seasonally moist semi-deciduous forest at BCNM (9°05′N, 79°45′W) in lake Gatun, central Panama. BCNM encompasses the 1,600 ha Barro Colorado Island (BCI), covered primarily with old growth forest, and 2,400 ha of surrounding mainland peninsulas of second growth forest <1 km from BCI, recovering from agricultural abandonment 40–100 years ago (see Leigh et al. 1982; Denslow and Guzman 2000 for a full site description). The four *Cecropia* species that occur on BCNM (Croat 1978, Table 1) are dioecious canopy trees that colonise high-light microsites from seed rain and the soil seed bank. All species form associations with ants (primarily *Azteca*) that defend plants against insect herbivores (Schupp 1986). Plants become colonised as large saplings (Coley 1986; Del Val and Dirzo 2003).

Cecropia insignis Liebm. is the most abundant *Cecropia* in old-growth forest on BCNM, with 443 individuals in the

Table 1 Air-dry seed mass, growth period, and mean (SE) of growth, allocation and physiological parameters for seedlings ($n = 8$) of four *Cecropia* species grown in pots

Parameter	C. insignis	C. longipes	C. obtusifolia	C. peltata
Seed mass (mg)	0.42	0.83	0.57	0.55
Growth (days)	72	86	78	71
Leaf area (cm^2)	243.5 (37.9)	224.0 (39.7)	280.2 (36.3)	287.1 (43.5)
RGR (mg g^{-1} day^{-1})	72.7 (2.8) a	56.5 (2.7) b	73.5 (2.0) a	84.9 (2.9) c
SLA (cm^2 g^{-1})	361.9 (7.4) a	550.0 (30.0) b	435.5 (16.3) c	475.2 (13.4) c
NAR (g m^{-2} day^{-1})	2.87 (0.1) a	1.74 (0.2) b	2.14 (0.1) b	2.46 (0.2) a
LAR (cm^2 g^{-1})	254.9 (4.5) a	361.6 (29.8) b	328.2 (11.4) b	331.2 (12.5) b
LMR	0.70 (0.01) a	0.65 (0.03) a,b	0.75 (0.01) a,c	0.70 (0.01) a,b
RMR	0.17 (0.01) a	0.25 (0.02) b	0.15 (0.01) a	0.18 (0.01) a
N (%)	3.69 (0.06) a	4.60 (0.05) b	4.06 (0.18) a,c	4.20 (0.03) b,c
Amax (area)	15.27 (0.74) a	11.47 (0.54) b	14.47 (0.60) a	14.94 (0.33) a
Amax (mass)	0.56 (0.03) a	0.62 (0.02) a	0.64 (0.05) a,b	0.71 (0.02) b
PPNUE	213.3 (10.8) a,b	190.1 (5.2) a	220.7 (13.7) a,b	236.5 (6.9) b

Main effects were significant for all parameters after leaf area. Different letters reflect significant differences among species for each parameter (Bonferroni-adjusted $P < 0.05$). *RGR* Relative growth rate, *SLA* specific leaf area, *NAR* net assimilation rate, *LAR* leaf area ratio, *LMR* leaf mass ratio, *RMR* root mass ratio, *Amax* maximum rate of net carbon assimilation, *PPNUE* photosynthetic potential nitrogen use efficiency

50 ha forest dynamics plot (Condit et al. 1995), but it is rare or absent from young secondary forest (<60 years old) on nearby islands and peninsulas (Adler 2000; Dalling and Hubbell 2002; J. Dalling, personal observation), and from more seasonal secondary forest 30 km to the south east at Parque Metropolitano (1 ha plot data; http://www.stri.org/english/research/facilities/terrestrial/cranes/research_info.php) and Cocoli, where *Cecropia* congeners are abundant (4 ha plot data; http://www.ctfs.si.edu/site/Cocoli). *C. obtusifolia* Bertol. occurs at much lower density in the 50 ha plot (37 individuals), while *C. peltata* L. is entirely absent from old growth forest. Both species are common in young secondary forest at BCNM, and also occur in a large clearing surrounding laboratory buildings on Barro Colorado Island. *C. longipes* Pittier is rare in old-growth forest (1 individual in the 50 ha plot) and also uncommon in young forest.

Cecropia insignis is also abundant in old-growth forest at the La Selva Biological Station in Costa Rica, 500 km N of BCNM, whereas *C. obtusifolia* is more abundant in young forest at the same site (Gallery et al. 2007). At the regional scale, *C. peltata* appears restricted to Pacific slopes and lowlands of Costa Rica, while *C. obtusifolia* is more abundant on the wetter Atlantic side of the continental divide (Longino 1989). *C. longipes* is restricted to central, eastern and drier Pacific coastal Panama and northwestern Colombia (Franco-Rosselli and Berg 1997).

Seedling growth experiments

In June 2001, seeds of three individuals of each *Cecropia* species were collected from old growth and secondary

forest on BCI and germinated in Petri dishes in a growing house on BCNM. Emergent seedlings were transplanted to flats containing forest soil and allowed to grow up in a screened growing house (30% full sun) until August 2001, when eight seedlings of each of *C. insignis*, *C. obtusifolia* and *C. peltata*, and five seedlings of *C. longipes* were transplanted into each of four 15 × 15 m treefall gaps. Gap size was sufficient to allow successful recruitment of *C. insignis* to the canopy on BCI (Brokaw 1987) and Buena Vista (Pearson et al. 2003), and for establishment of *Cecropia obtusifolia* and *C. peltata* seedlings from the seed bank (Dalling and Hubbell 2002). The gaps were created for a separate study in April 2000 by felling canopy trees in 40-year-old secondary forest on the Buena Vista Peninsula on BCNM (described by Pearson et al. 2003). Seedlings were transplanted at random with one in each 1 m^2 grid square in a central portion of each gap cleared of all understorey vegetation. Gap light conditions, expressed as canopy openness, were characterised in October 2001 using a single hemispherical photograph taken 1 m above the ground with a Nikon Coolpix 950 camera and an 8 mm fish-eye lens (Nikon, New York, NY). Canopy openness for the four gaps ranged from 12.7 to 17.7% (mean 15.9%).

At the time of transplant, heights of *C. insignis* (1.9 cm, SE = 0.2 cm) and *C. peltata* (1.6 cm, SE = 0.2 cm) seedlings were significantly lower than those of *C. obtusifolia* (11.6 cm, SE = 1.1 cm) and *C. longipes* (12.4 cm, SE = 2.0 cm; Tukey post hoc comparison after two-way ANOVA, $P < 0.05$). Within species, seedlings did not differ significantly in height and leaf area among gaps. Seedling height, leaf area, and presence of ants were re-censussed after 3 and

5 months, and monthly thereafter until 16 months. At this time, the largest *C. insignis* plants were >2 m height and cast substantial shade within the common gardens. At each census the percent leaf area missing, and any damage to apical meristems was also recorded. *Cecropia* seedlings and saplings <3 m tall are typically monopodial with leaf tissue arrayed close to the apical meristem. We frequently observed that the entire leaf area of seedlings and saplings was removed. An earlier study indicated that this damage could be attributable to stem-boring insects (Dalling and Hubbell 2002), as excised seedling shoots were observed on the ground. However, in this study, damaged parts of the seedling were not observed during censuses; seedling apices may therefore have been consumed by browsing herbivores rather than stem-boring insects.

In November 2004, we established a similar study in old growth forest on BCI. The same maternal seed sources were used as the transplant experiment at BCNM. Six seedlings of each species were transplanted into four large natural gaps chosen to have similar dimensions to those used at Buena Vista. Canopy openness, measured in July 2007, a year after the experiment was completed, and after removing planted *Cecropia* individuals, varied from 9.4 to 17.5% (mean 12.6%). Seedling height did not differ among species at the time of transplant (*df* 3,92, *F* = 45.7, *P* = 0.051). Censuses of seedling growth and damage were conducted as before every 2 months for 1 year.

Cecropia growth analysis

Growth rate and allocation patterns of *Cecropia* were determined from eight seedlings of each species raised in a screened growing house (30% full sun) in pots containing 3 L of a 50:50 mixture of BCI forest soil and sand (to improve drainage). The same maternal seed sources were used as the field experiments. Seedlings were planted when they had 0.5 cm^2 of true-leaf area, and when species' initial dry mass ranged from 1.9 to 4.5 mg (*n* = 5 seedlings per species). Species were harvested when mean leaf area approximated 250 cm^2 after 71 (*C. peltata*) to 86 (*C. longipes*) days of growth. Differences in leaf area among species at the time of harvest were not significant (*F* = 0.52; *P* = 0.67; *df* 3,26).

On the morning of the day of harvest (0900–1130 hours), seedlings were exposed to saturating light conditions (>800 µmol m^{-2} s^{-1}) for approximately 10 min before maximum rates of net carbon assimilation (Amax) were measured. Rates of net CO_2 uptake of one leaf per plant were measured using a portable open gas exchange system (LI-COR 6400, LI-COR, Lincoln, NE). The environment within the leaf cuvette was controlled to be similar to ambient conditions. Leaf temperatures during the measurements were between 28 and 35°C. The leaf area of

harvested seedlings was measured using an automated leaf area meter (LI-3000A, LI-COR). The mass of foliar, stem and root fractions was measured after drying for 72 h at 70°C. Foliar nitrogen concentrations were determined using an elemental analyser (Costech Analytical, Valencia, CA).

Relative growth rate (RGR, units mg g^{-1} day^{-1}) was calculated as the slope of the relationship between ln total biomass and time between transplantation and harvest for each species in each gap treatment. Net assimilation rate (NAR; biomass increment per unit leaf area, units g m^{-2} day^{-1}) was calculated according to Dalling et al. (1994). Leaf mass fraction (LMF; leaf mass per unit whole plant mass, units g g^{-1}), stem mass fraction (SMF; stem and petiole mass per unit whole plant mass, units g g^{-1}), root mass fraction (RMF; root mass per unit whole plant mass, units g g^{-1}), leaf area ratio (LAR; leaf area per unit whole plant mass, units cm^{-2} g^{-1}) and specific leaf area (SLA; leaf area per unit leaf mass, units cm^{-2} g^{-1}), were calculated from the final harvest data. Photosynthetic potential nitrogen use efficiency (PPNUE; net carbon assimilation per unit leaf nitrogen, units µmol CO_2 mmol N^{-1} s^{-1}) was calculated from maximum net assimilation rate and foliar nitrogen concentration measured on the same leaves.

Defensive traits

In January 2005, single mature leaves were collected from two or three individuals of each of three maternal genotypes of each *Cecropia* species grown in pots in a shaded growing house (30% full sun). Phenolics in the leaf tissue were assayed using the Folin–Ciocalteau method (Waterman and Mole 1994), where phenolic content is expressed as tannic acid equivalents per unit leaf dry mass. *Cecropia* species have noticeably different leaf textures. We therefore also counted the number of trichomes present in a 16 mm^2 field of view using a dissecting microscope. Trichomes were counted at three sample points in the centre of the adaxial surface of three fully expanded leaves from three maternal genotypes for each species.

Statistical analyses

Comparisons of growth and survivorship for field-grown seedlings were made separately for Buena Vista and BCI, using the program R version 2.1.1 (http://www.r-project.org). Height growth over time was analysed using linear mixed effects analysis of variance on seedlings that survived to the end of the experiment. Both species and gap were coded as fixed effects, as gaps were not selected at random. As growth was approximately exponential over the course of the experiment at both sites, both height and time

were log-transformed to equalise variance. Additionally, at Buena Vista, the variance function 'varIdent' was used (Crawley 2002), to account for the greater variance in growth observed in *C. insignis*. The significance of main and interaction effects were assessed through model simplification. Maximum likelihood was used to compare fixed effects in models with different fixed effect structures. Parametric survival analysis was used to compare the timing of seedling browsing and seedling mortality across species and gaps, and to allow predictions of the mean time of death or browsing for each species. Analyses were performed using the function 'survReg' in the program R (Crawley 2002). Survival analysis models were fit using an exponential error distribution (implying the risk of seedling death or browsing is independent of seedling age), with the exception of the analysis of the timing of seedling browsing at Buena Vista, where a logistic error distribution provided a better fit of the data. Kruskall–Wallis non-parametric analysis of variance was used to compare foliar damage rates among species at each site. Species differences in tannin levels and in trichome densities were assessed using analysis of variance with individual nested within maternal genotype.

Results

Seedling growth performance in the field

There was strong interspecific variation in seedling growth over 16 months at the secondary forest site of Buena Vista (Fig. 1). Only seedlings of *C. insignis* showed sustained growth over the period, with mean seedling height reaching 1 m, and with the largest individual 2.3 m tall. In contrast, apical damage from herbivores entirely suppressed growth of the other three *Cecropia* species, with mean height <0.3 m after 16 months and with no individual >0.6 m. Repeated measures analysis of height growth for individuals that survived to 16 months showed that growth did not vary significantly among gaps ($df = 3$, likelihood ratio = 5.38, $P = 0.14$), but did vary among species (df 3,62, $F = 13.1$, $P < 0.001$), and among species over time (species x time interaction; df 3,854, $F = 55.32$, $P < 0.001$). Species differences in growth could be attributed to significantly higher growth of *C. insignis*, compared to the other species ($df = 4$, likelihood ratio = 43.9, $P < 0.001$).

Similar growth patterns were observed in old-growth forest at BCI, although variance in growth was much greater at this site. After 12 months, mean seedling height for *C. insignis* was 0.5 m, compared to 0.3 m for the remaining species. Nonetheless, species effects on growth were not significant ($df = 1,43$, $F = 0.70$, $P = 0.41$), whereas there was a strong effect of gap on growth
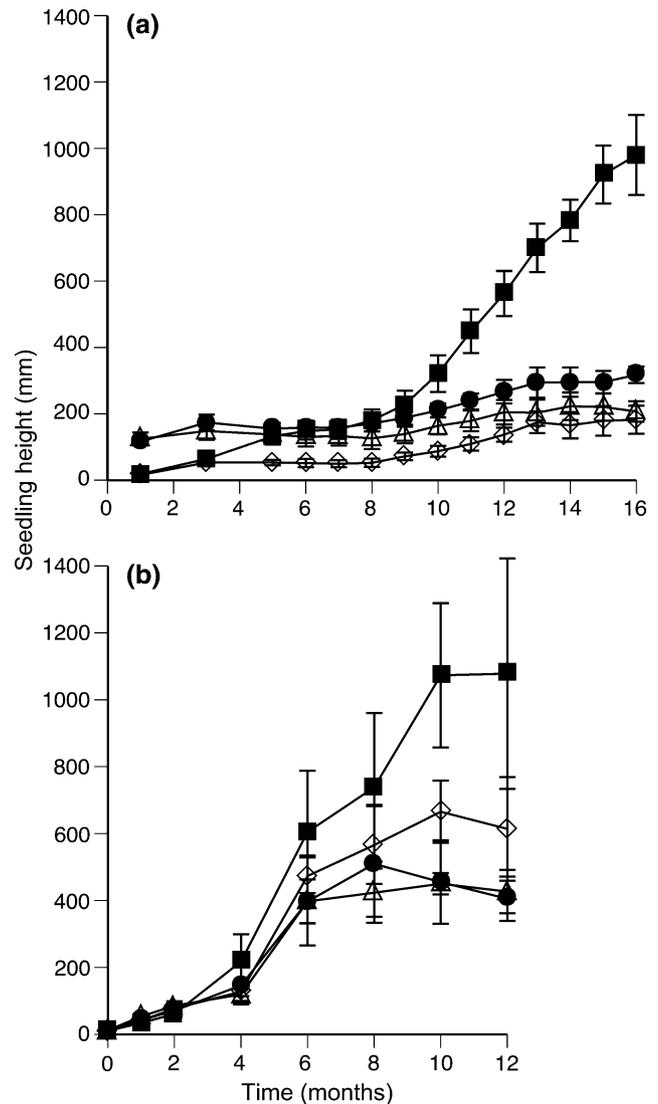

Fig. 1 Mean height growth (+1 SE) of seedlings **a** transplanted into four artificially created canopy gaps in secondary forest on the Buena Vista (BV), and **b** transplanted into four natural canopy gaps in old growth forest on Barro Colorado Island (BCI). *Filled squares Cecropia insignis, open triangles C. longipes, filled circles C. obtusifolia, open diamonds C. peltata*

($df = 3,43$, $F = 7.75$, $P < 0.001$). All two-way and three-way interactions between species, gap and time were significant at BCI, reflecting differences in species performance among gaps, and higher growth of *C. insignis* later during the experiment (Fig. 1).

Apical and foliar damage

On Buena Vista, browsing, and possibly stem-boring herbivores, strongly discriminated between *C. insignis* and other *Cecropia* species. After 16 months, 20% of *C. insignis* plants received apical damage, whereas all seedlings of the remaining species were damaged (Fig. 2). The predicted
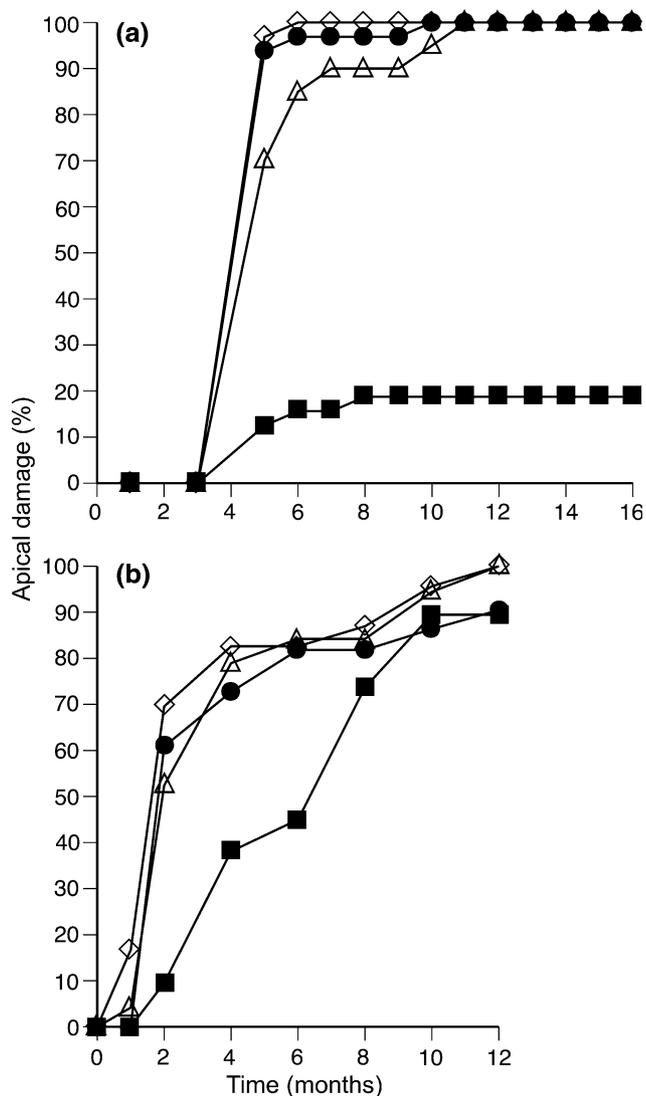
Fig. 2 Percent of individuals that received apical damage (loss of growing shoot and leaf area) **a** in four Buena Vista gaps and **b** in four BCI gaps. Symbols as in Fig. 1

mean time to apical damage was significantly longer for *C. insignis* (17 months) than for the remaining species (5.1–5.6 months; $df = 3,114$, deviance = 164.5, $P < 0.001$). Time to apical damage for species other than *C. insignis* did not differ ($df = 2,113$, deviance = 0.91, $P = 0.63$). Time to apical damage also did not differ significantly among gaps ($df = 3$, deviance = 0.87, $P = 0.87$), and there was no interaction between gap and species ($df = 9,109$, deviance = 5.45, $P = 0.79$).

Similar patterns of apical damage were observed on BCI, although *C. insignis* individuals escaped damage less frequently on the island (Fig. 2). Species also differed in the predicted mean time to damage ($df = 3,92$, deviance = 13.78, $P = 0.003$), with a longer predicted time for *C. insignis* (12.5 months) compared with the remaining

species (4.0–6.3 months), which did not differ significantly ($df = 2,91$, deviance = 2.09, $P = 0.35$). On BCI, however, there was a larger effect of gap than species on time to apical damage ($df = 3$, deviance = 29.2, $P < 0.0001$).

Foliar damage rates after 12 months growth were quite low at both Buena Vista and BCI. At Buena Vista, 2.6% ($\pm$SD 5.3), and at BCI 7.3% ($\pm$SD 13.1) of leaf area was eaten. Foliar herbivory rates did not differ significantly among species at either site (Buena Vista: Kruskall–Wallis $\chi^2 = 2.4$, $df = 3$, $P = 0.5$; BCI: $\chi^2 = 1.7$, $df = 3$, $P = 0.7$).

Seedling mortality

Despite repeated apical damage, seedling survivorship remained high for most species (Fig. 3). At Buena Vista there was no significant effect of gap ($df = 3,112$, deviance = 7.67, $P = 0.053$), or any gap x species interaction ($df = 9,109$, deviance = 9.75, $P = 0.37$). Model simplification showed that the only significant difference in survivorship was between *C. peltata*, with mean predicted survival of 16.5 months, and the remaining species combined, with mean predicted survival of 80.8 months ($df = 1,115$, deviance = 20.40, $P < 0.001$). At BCI, there was a significant effect of gap on seedling survival ($df = 3,92$, deviance = 16.33, $P < 0.001$), but no gap x species interaction ($df = 9,89$, deviance = 12.26, $P = 0.20$). Model simplification showed a significant species difference in survivorship between *C. insignis*, with mean predicted survival of 73.1 months, and the remaining species combined, with mean predicted survival of 29.1 months ($df = 1,92$, deviance = 5.38, $P = 0.02$).

Cecropia growth analysis

In the growing house, species differed significantly in all growth, allocation, and physiological parameters measured (Table 1). However, variation in these parameters for the most part failed to distinguish the old-growth forest species, *C. insignis*, from the three secondary forest species (Table 1). Contrary to the prediction of low-relative growth in *C. insignis*, we found that the RGR of *C. insignis* was slower only than that of *C. peltata*, was not significantly different from *C. obtusifolia* and was faster than that of *C. longipes* (Table 1). The relatively high RGR of *C. insignis* was maintained through a high-NAR reflecting a high-carbon assimilation rate per unit leaf area and a low SLA. This was achieved despite maintaining the lowest foliar nitrogen concentration among the species tested (Table 1). PPNUE was similar for *C. insignis* and *obtusifolia*. In contrast, the relatively low growth rate of *C. longipes* occurred despite maintaining the highest foliar nitrogen concentration (but lowest Amax$_{area}$ and PPNUE), and was attributable largely to a significantly higher proportional investment in root
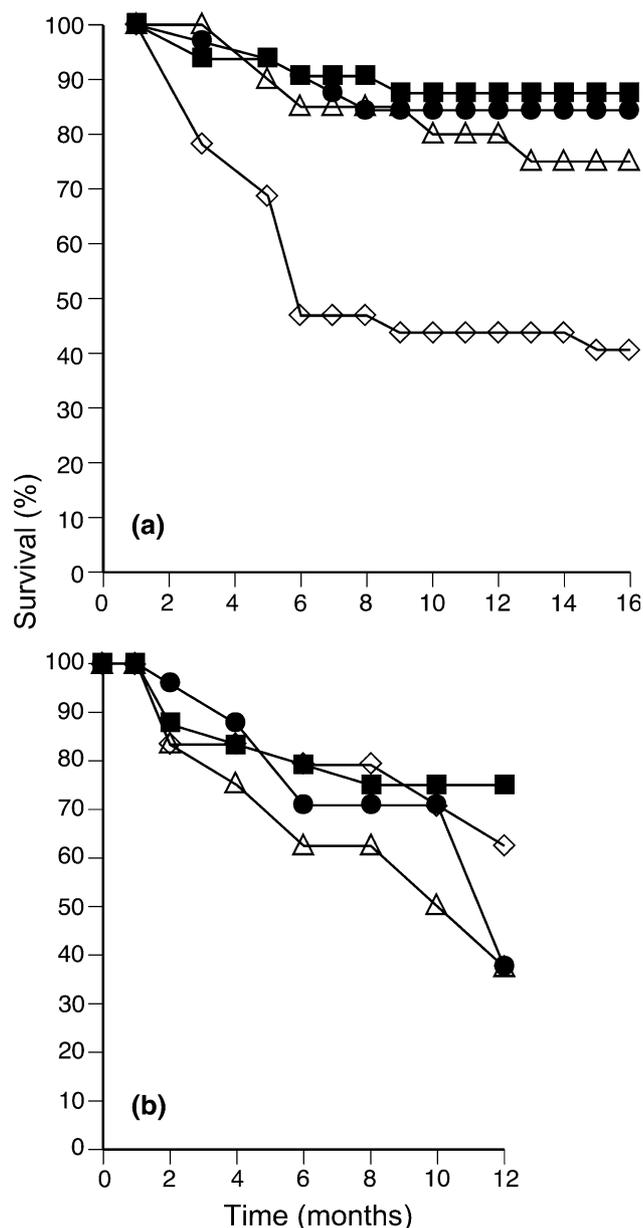
Fig. 3 Percent survival of individuals in **a** four Buena Vista gaps and **b** four BCI gaps. *Symbols as in Fig.* 1

among species ($df = 2,9$, $F = 10.9$, $P < 0.004$), with the lowest concentration in *C. insignis* (4.2 mg/g dry mass tannic acid equivalents, ±3.6 SD), followed by *C. longipes*, 13.9 (±1.7), *C. peltata*, 20.9 (±9.4), and *C. obtusifolia* 34.7 (±12.3). Differences among species were significant ($P < 0.05$), except between *C. longipes* and *C. peltata* (df 1,9, $F = 1.2$, $P = 0.31$). Trichome densities also differed significantly among species (df 3,28, $F = 28.7$, $P < 0.001$); densities were significantly higher for *C. insignis* (91.9/cm^2 ± 1.2 standard error of genotype means), than *C. longipes* (30.1/cm^2 ± 4.4; $t = 2.87$, $P < 0.01$) and *C. peltata* (54.9/cm^2 ± 2.2; $t = 2.47$, $P < 0.05$), but not *C. obtusifolia* (69.7/cm^2 ± 2.9; $t = 1.84$, $P = 0.08$).

Discussion

Growth and survival differences among *Cecropia* species

Growth trajectories of the four *Cecropia* species in secondary forest at Buena Vista were dramatically different. Whereas *C. insignis* grew rapidly, reaching an average height of >1 m over 16 months, all individuals of the other three species were continually browsed and, on average, seedlings remained <0.3 m tall. Browsing, however, strongly affected the survivorship of only one species, *C. peltata*, which was unable to resprout after apical damage. Mortality of *C. peltata* in the common gardens was consistent with earlier observations at Buena Vista; *C. peltata* dominates natural recruitment from the soil seed bank at this site, but herbivores eliminate it from the seedling community a year after emergence (Dalling and Hubbell 2002). Growth and survival patterns in old-growth forest at BCI largely paralleled those observed at Buena Vista. While there were significant differences in growth and survival rates among gaps at BCI, potentially reflecting wider variation in gap size, and spatial heterogeneity in herbivore communities, *C. insignis* still had the fastest overall height growth, escaped apical damage from browsers more frequently than the other species, and had higher overall survivorship over 1 year. In contrast to apical damage, foliar damage to expanded leaves was low at both sites, did not differ among species, and is therefore less likely to account for habitat partitioning.

The large interspecific differences in growth and survival rates observed here are likely to have a significant impact on recruitment success. We therefore reject the null hypothesis of ecological equivalence of *Cecropia*, at least when comparing the old-growth and secondary forest species. The superior performance of *C. insignis* is consistent with its high-relative abundance in old-growth forest at BCI, but contrasts with the local and regional rarity of this species in second-growth stands. A possible explanation is that regeneration conditions have changed at the Buena Vista

biomass. The remaining species did not differ in biomass allocation across the whole plant.

Plant defence traits of *Cecropia*

Ant defences did not contribute to species differences in damage and survival rate in the field. None of the field-grown plants were colonised by ants over 16 months at Buena Vista. On BCI, one individual of *C. obtusifolia* was colonised by *Azteca* ants after 8 months; however, colonisation was transient and ants were not observed in following censuses. Tannin concentrations differed significantly

site over the ~40-year period since agricultural abandonment. *C. obtusifolia* and *C. peltata* individuals that now occupy the forest canopy are likely to be several decades old (Alvarez-Buylla and Martínez-Ramos 1992), and may therefore have recruited under more open conditions associated with low-canopy height, and possibly in a forest stand that supported a different herbivore community.

The fourth species, *C. longipes*, was as susceptible as *C. obtusifolia* and *C. peltata* to browsing damage. The rarity of this species in both forest types may reflect its low growth rate and relatively high investment in root biomass, as was apparent from the pot experiment. *C. longipes* may be adapted to edaphically dry microsites, and the drier climate zone along the Pacific coast of Panama.

Recruitment success and the growth–mortality trade-off

Measures of relative growth rate in the growing house can be used to test whether the lower frequency of browsing damage of *C. insignis* can be attributed to a growth–defence trade-off. This would arise if resources that could be allocated to the production of leaf tissue are instead invested into physical or chemical defences (Kitajima 1994; Fine et al. 2004). If additional investment in defence underlies the superior performance of *C. insignis* in the field, then we would predict that, in the absence of herbivores, the growth rate of *C. insignis* should be slower than that of its congeners.

Measures of growth in the greenhouse, however, provide only partial support for a growth–defence trade-off. While *C. peltata*, which had the highest mortality at Buena Vista, had significantly higher growth than the remaining species in the pot experiment, *C. obtusifolia* grew no faster than *C. insignis*, and *C. longipes* had the slowest growth rate. Analyses of growth and defence characters of other groups of related species have not always found support for a trade-off. Among temperate herbs in the Asteraceae, growth rate is not related to the toxicity of their chemical defences (Almeida-Cortez et al. 1999). Likewise, for different geographic populations of sagebrush (*Artemisia tridentata*), there is little evidence for a trade-off between inherent growth rate and either tolerance or resistance to herbivory (Messina et al. 2002).

In our study, differences in growth performance among *Cecropia* species may have become more apparent if seedlings were grown for longer periods, or under different conditions of resource supply. Nonetheless, evidence for substantial shifts of rank performance of species across a gradient of light availability is limited; RGR of 14 pioneer species from BCI, including *C. insignis*, were strongly positively correlated under conditions simulating gap sizes ranging from 25 to 800 m² (Dalling et al. 2004).

Defence traits of BCNM *Cecropia*

What might account for the lower incidence of apical damage to *C. insignis* relative to its congeners? Analysis of the traits measured on plants in the growing house fail to reveal a clear answer. *C. insignis* had lower SLA than its congeners, which is likely to also correspond to greater leaf toughness, the single most important predictor of foliar herbivory damage for plants on BCNM (Coley 1983); indeed leaf toughness of field-collected mature leaves of *C. insignis* is twice that of *C. obtusifolia* (Coley 1983). However, *Cecropia* leaf toughness is generally low compared to other pioneer species (see Appendix in Coley 1983), so toughness alone may not be much of a deterrent, particularly if apical damage is caused by large browsing herbivores such as deer. Foliar nitrogen concentration was also significantly lower in *C. insignis* compared to congeners, potentially influencing insect feeding preferences (McNeill and Southwood 1978; Athey and Connor 1989); however, nitrogen concentration in *C. insignis* is still high relative to non-pioneers (Coley 1983).

Foliar tannin concentrations are a strong predictor of within-species variation in growth and herbivory rate in *C. peltata* (Coley 1986). In this study, however, tannin concentrations (measured as tannic acid equivalents), were lower in *C. insignis* than its congeners. Nonetheless, the bioactivity of tannins present in plant tissue may vary among species and independently of the concentration assayed using the Folin-Ciocalteau method (Appel et al. 2001). *Cecropia* species may also contain an array of other defensive compounds, including alkaloids, glycosides, and flavonoids that were not measured in this study (Morton 1981). *Cecropia* species also differ in foliar trichome density. *C. insignis* leaves have the highest trichome density and are noticeably more asperous than those of its congeners. Although trichomes are an effective defence against phytophagous insects (Levin 1973), it is unclear whether they deter browsing herbivores.

Previous studies have emphasised the importance of *Azteca* ants in defending *Cecropia* from herbivores (Schupp 1986; Folgarait and Davidson 1994, but see Fáveri and Vasconcelos 2004). Clearly, there are species differences in the size at which plants become colonised by ants; Davidson et al. (1991) reported that two *Cecropia* species that colonised gaps in old-growth forest in southeast Peru had high probabilities of ant colonisation when individuals were <1 m tall. For *Cecropia* in central Panama, however, ant defences may have a more limited role in mediating recruitment success; none of the plants in this study were permanently colonised by ants over a period when large interspecific differences in growth and survival emerged.

Habitat partitioning among pioneer species

Local and regional distributional differences among *Cecropia* species are a striking example of habitat differentiation in closely related species. Other congeneric pairs of pioneer species in central Panama also show associations with either old-growth or secondary forest (*Luehea seemannii* and *Luehea speciosa*, and *Apeiba aspera* and *Apeiba tibourbou*, J. Dalling, personal observation). Additionally, two species of *Trema*, distinguishable only based on seed morphological traits and internal transcribed spacer (ITS) nuclear ribosomal sequence data, show associations with either treefall gaps or landslides along the edge of BCI (Silvera et al. 2003; Yesson et al. 2004). In *Trema*, habitat partitioning also appears to be driven by differences in susceptibility to browsing damage, as well as species-specific responses to gap and landslide soils (C. Pizano, unpublished data).

Collectively, these results argue against the ecological equivalency (i.e. demographic similarity) of species assumed at the community level by the neutral theory (Hubbell 2005), and implicit to the assignment of species to functional groups. Field and growing house experiments indicate that, at least comparing *Cecropia insignis* with its congeners, large differences in recruitment potential can arise from traits that have little apparent effect on realized growth. The close proximity of secondary forest at Buena Vista and old growth forest at BCI, and the apparent restriction of *C. peltata* to the BCI laboratory clearing, suggests that the habitat associations of *Cecropia* at BCNM have not arisen from local dispersal limitation. Our results, however, also suggest that the habitat associations we observe may be transient. If the distribution of pioneer species at BCNM is a legacy of altered herbivore communities early during succession then we can expect significant turnover of pioneer species composition in the coming decades.

References

Adler GH (2000) Tropical tree diversity, forest structure and the demography of a frugivorous rodent, the spiny rat (*Proechimys semispinosus*). J Zool 250:57–74

Almeida-Cortez JS, Shipley B, Arnason JT (1999) Do plant species with high relative growth rate have poorer chemical defences? Funct Ecol 13:819–827

Alvarez-Buylla ER, Martínez-Ramos M (1992) Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree—an evaluation of the climax-pioneer paradigm for tropical rain forests. J Ecol 80:275–290

Appel HM, Govenor HL, D Ascenzo M, Siska E, Schultz JC (2001) Limitations of folin assays of foliar phenolics in ecological studies. J Chem Ecol 27:761–778

Ashton PS (1988) Dipterocarp biology as a window to the understanding of tropical forest structure. Annu Rev Ecol Syst 19:347–370

Athey LA, Connor EF (1989) The relationship between foliar nitrogen content and feeding by *Odonta dorsalis* Thun. on *Robinia pseudoacacia* (L.). Oecologia 79:390–394

Brokaw NVL (1987) Gap phase regeneration of three pioneer tree species in a tropical forest. J Ecol 75:9–19

Cavender-Bares J, Ackerley DD, Baum DA, Bazzaz FA (2004) Phylogenetic overdispersion in Floridian oak communities. Am Nat 163:823–843

Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol Monogr 53:209–233

Coley PD (1986) Costs and benefits of defense by tannins in a neotropical tree. Oecologia 70:238–241

Coley PD, Bryant JP, Chapin FS III (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol Monogr 65:419–439

Crawley MJ (2002) Statistical computing: an introduction to data analysis using S-Plus. Wiley, Chichester

Croat TB (1978) Flora of Barro Colorado Island. Stanford University Press, Stanford

Dalling JW, Hubbell SP (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. J Ecol 90:557–568

Dalling JW, Swaine MD, Garwood NC (1994) Effect of soil depth on seedling emergence in tropical soil seed-bank investigations. Funct Ecol 9:119–121

Dalling JW, Hubbell SP, Silvera K (1998) Seed dispersal, seedling emergence and gap partitioning in gap-dependent tropical tree species. J Ecol 86:674–689

Dalling JW, Winter K, Hubbell SP (2004) Variation in growth responses of neotropical pioneer species to simulated gaps. Funct Ecol 18:725–736

Davidson DW, Foster RB, Snelling RR, Lozada PW (1991) Variable composition of some tropical ant-plant symbioses. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds) Plant–animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, Chichester, pp 145–162

Debski I, Burslem DFRP, Palmiotto PA, Lafrankie JV, Lee HS, Manokaran N (2002) Habitat preferences of *Aporosa* in two Malaysian forests: implications for abundance and coexistence. Ecology 83:2005–2018

Del Val E, Dirzo R (2003) Does ontogeny cause changes in the defensive strategies of the myrmecophyte *Cecropia peltata*? Plant Ecol 169:35–41

Denslow JS, Guzman S (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. J Veg Sci 11:201–212

Engelbrecht BMJ, Kursar TA (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136:383–393

Fáveri SB, Vasconcelos HL (2004) The *Azteca–Cecropia* association: are ants always necessary for their host plants? Biotropica 36:641–646

Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. Science 305:663–665

Folgarait PJ, Davidson DW (1994) Antiherbivore defenses of myrecophytic *Cecropia* under different light regimes. Oikos 71:305–320

Franco-Rosselli P, Berg CC (1997) Distributional patterns of *Cecropia* (Cecropiaceae): a panbiogeographic analysis. Caldasia 19:285–296

Gallery R, Dalling JW, Arnold AE (2007) Diversity, host affinity and distribution of seed-infecting fungi: a case-study with neotropical *Cecropia*. Ecology 88:582–588

Hall JS, McKenna JJ, Ashton PMS, Gregoire TG (2004) Habitat characterizations underestimate the role of edaphic factors controlling the distribution of *Entandrophragma*. Ecology 85:2171–2183

Hubbell SP (1979) Tree dispersion, abundance and diversity in a tropical dry forest. Science 203:1299–1309

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Hubbell SP (2005) Neutral theory in ecology and the hypothesis of functional equivalence. Funct Ecol 19:166–172

Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. Ecology 87:1387–1389

John RC, Dalling JW, Harms KE, Yavitt JB, Stallard RF, Mirabello M, Hubbell SP, Valencia R, Navarrete H, Vallejo M, Foster RB (2007) Soil nutrients influence spatial distributions of tropical tree species. Proc Natl Acad Sci USA 104:864–869

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428

Leigh EG Jr, Rand AS, Windsor DM (1982) The ecology of a tropical forest. Smithsonian Institution, Washington, DC

Levin DA (1973) The role of trichomes in plant defense. Q Rev Biol 48:3–15

Longino JT (1989) Geographic variation and community structure in an ant–plant mutualism. Biotropica 21:126–132

McNeill S, Southwood TRE (1978) The role of nitrogen in the development of insect/plant relationships. In: Harborne JB (ed) Biochemical aspects of plant and animal coevolution. Academic, London, pp 77–98

Messina FJ, Durham SL, Richards JH, McArthur ED (2002) Trade off between plant growth and defense? A comparison of sagebrush populations. Oecologia 131:43–51

Morton JF (1981) Medicinal plants of Middle America: Bahamas to Yucatan. Thomas, Springfield

Pearson TRH, Burslem DFRP, Goeriz RE, Dalling JW (2003) Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer trees. J Ecol 91:785–796

Rogstad SH (1990) The biosystematics and evolution of the *Polyalthia hypoleuca* species complex (Annonaceae) of Malesia. II. Comparative distributional ecology. J Trop Ecol 6:387–408

Schupp EW (1986) *Azteca* protection of *Cecropia*: ant occupation benefits juvenile trees. Oecologia 70:379–385

Silvera K, Skillman JB, Dalling JW (2003) Seed germination, seedling growth and habitat partitioning in two morphotypes of the tropical pioneer tree *Trema micrantha* in a seasonal forest in Panama. J Trop Ecol 19:27–34

Valencia R, Foster RB, Villa G, Condit R, Svenning JC, Hernandez C, Romoleroux K, Losos E, Magard E, Balslev H (2004) Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. J Ecol 92:214–229

Waterman P, Mole S (1994) Analysis of phenolic plant metabolites. Blackwell, London

Yesson C, Russell SJ, Parrish T, Dalling JW, Garwood NC (2004) A phylogenetic framework for *Trema* (Celtidaceae). Plant Syst Evol 248:85–109