THE UNUSUAL LIFE HISTORY OF *ALSEIS BLACKIANA*: A SHADE-PERSISTENT PIONEER TREE?

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Abstract. Classifications of tree species into regeneration guilds or functional groups are often based on a limited number of life history characteristics indicative of requirements for early establishment, with the assumption that these traits are correlated with growth requirements of larger individuals. We tested the validity of this assumption for *Alseis blackiana,* a common canopy tree in central Panama, by examining its seed germination, seedling growth, and sapling distribution, growth, and mortality. We found that the early life history of *Alseis* is characteristic of pioneer species: the seed germination rate was much higher in forest gaps than in the forest understory, small seedlings were absent from the understory, and seedlings showed strong plastic responses to variation in light. Seedling relative growth rate, leaf area production rate, and maximum carbon assimilation rates of *Alseis* are much more similar to those of the pioneer tree *Miconia argentea* than to those of the non-pioneer tree *Tetragastris panamensis.* However, in contrast to *Miconia,* established seedlings of *Alseis* are capable of remarkable persistence in the understory; in a 1-ha plot on Barro Colorado Island, the mortality rate for 722 saplings <1 cm dbh was <4% per year between 1986 and 1998. We suspect that shade tolerance in *Alseis* is achieved by both physiological and morphological adaptations, e.g., efficient light interception by thin, nonoverlapping leaves, tolerance to litterfall damage, and a high resprouting capacity. These results show that existing functional group classifications do not account for the full range of seedling trait combinations found in tropical trees and indicate that a gap requirement for seedling establishment need not limit the abundance of adult individuals in a stand.

Key words: Alseis blackiana; *functional group;* Miconia argentea; *ontogeny; pioneer; regeneration guild; seed germination; seedling growth; shade tolerance;* Tetragastris panamensis.

INTRODUCTION

One of the most enduring paradigms in forest ecology has been the classification of species into "pioneer" and "non-pioneer" regeneration guilds or functional groups based on their light or gap requirements for seed germination, seedling establishment, or subsequent growth (e.g., Heyer 1852, Baker 1950, van Steenis 1958, Swaine and Whitmore 1988, Whitmore 1989, Oldeman and Dijk 1991). This framework has been used for predicting plant and animal community responses to disturbance and forest management (e.g., Verner 1984, Bayer and Porter 1988, Reader 1988, Hawthorne 1993) and is becoming the focus of predictive models of environmental change (Severinghaus 1981, Steffen et al. 1992). While recent analyses of plant communities have recognized that demographic responses to the light environment tend to be continuous rather than discrete (Alvarez-Buylla and Martínez-Ramos 1992, Clark and Clark 1992, Condit et al. 1996)

a broad-scale classification of species into functional types remains valid if it is assumed that seedling traits among pioneer and non-pioneer species are strongly correlated, and that species responses to light vary little through ontogeny.

Both plastic and ontogenetic responses to variation in environmental conditions are probably limited by the energetic costs associated with altering physiological and morphological characteristics, and by constraints imposed by trade-offs among life history traits. Over tree life-spans, however, some "ontogenetic niche shifts" may occur. Clark and Clark (1992) found evidence for size-dependent shifts in the relative growth performance of a group of canopy and emergent tree species across sapling to adult size classes. At juvenile life history stages, however, dramatic shifts appear to be rare, and it is probable that few species are capable of both sustained rapid growth in gaps and prolonged survival in the shade (e.g., Kitajima 1994, Kobe et al. 1995, Pacala et al. 1996, Kobe 1999).

In this study, we examine the regeneration ecology of the small-seeded tree *Alseis blackiana* Hemsl. (Rubiaceae), one of the most abundant canopy species in seasonally moist tropical forest in central Panama. Initial observations indicated that whereas small saplings

TABLE 1. Demographic and life history characteristics of *Alseis,* the pioneer tree species *Miconia,* and the shade-tolerant tree *Tetragastris panamensis.*

Characteristic	*Alseis blackiana*	*Miconia agentea*	*Tetragastris panamensis*
Reproductive dbh (cm)†	18	11	30
Maximum dbh (cm)‡	92	39	86
Density (no./ha)§	11.3	1.2	2.2
Seed size (mg)‖	0.18	0.08	587
Seed per fruit†	1–6	1–80	6
Dispersal agent¶	wind	bird, monkey, coati	bird, monkey
Fruit type	capsule	berry	drupe
Fruiting period#	Feb–May	Mar–Jul	Apr–Jun
Seed bank density (seeds/m^2)††	190	430	...

Note: The abbreviation ''dbh'' refers to diameter at breast height.

† J. W. Dalling, *personal observation.*

‡ Largest individual recorded in the 1995 census of the 50-ha plot (R. Condit, S. Hubbell, and R. Foster, *unpublished data*).

§ Density of reproductive-size individuals averaged over the 50-ha plot in 1995 (R. Condit, S. Hubbell, and R. Foster, *unpublished data*).

‖ Mass of air-dried seeds, excluding dispersal structures.

¶ Hladik and Hladik (1969).

Foster (1982).

†† Measured in the 50-ha Forest Dynamics Plot in August 1993 (Dalling et al. 1997).

of this species are abundant in the understory, small seedlings are restricted to gaps. To determine how seedling traits of *Alseis* compare to pioneer and non-pioneer species, we compare the morphology and physiology of *Alseis* seedlings to those of a similarly small-seeded pioneer tree, *Miconia argentea* (Sw.) DC (Melastomataceae), and a large-seeded non-pioneer tree, *Tetragastris panamensis* (Engl.) Kunze. (Burseraceae). Using long-term seedling census data, we present evidence that *Alseis* has the attributes both of a pioneer (sensu Swaine and Whitmore 1988), recruiting from seed exclusively in canopy gaps, and also of a non-pioneer species, with one of the lowest juvenile mortality rates in the tree community (Condit et al. 1995).

METHODS

Study area and species

The field study was carried out in seasonally moist tropical forest on Barro Colorado Island (BCI), Panamá. Rainfall on BCI averages 2700 mm per year, with a pronounced dry season from January through April (Rand and Rand 1982). The flora is described by Croat (1978) and by Foster and Brokaw (1982); in this paper, species nomenclature follows Croat (1978). Investigations of seed and seedling distribution patterns were carried out within the Forest Dynamics Project 50-ha plot located on the central plateau of BCI. The plot was established in 1982, and all trees and shrubs >1 cm dbh censused in 1985, 1990, and 1995. The plot is described in detail by Hubbell and Foster (1983). An additional pot experiment designed to simulate gap environments was carried out in an open field at the Summit Botanic Gardens, ~20 km south of BCI (described in detail in Dalling et al. 1999).

Alseis blackiana is a canopy tree reaching at least 30 m, and is recorded from tropical moist forests of Costa Rica, Panama, and Colombia. It is possibly synonymous with other *Alseis* species growing from Mexico to Honduras and in northern South America (Croat 1978). During the dry season and early wet season it disperses numerous, tiny, wind-dispersed seeds from small, dehiscent capsules borne in dense clusters along terminal fruit spikes (Table 1). Seeds are apparently capable of some persistence in a dormant state in the soil; seedlings can be germinated from the soil throughout the year, and it is the third most common species in the seed bank, present in >50% of 192 samples of 250 cm^3 of soil collected in the 50-ha forest dynamics plot on BCI (Dalling et al. 1997). Seeds store well for one year in an air-conditioned laboratory (J. Dalling, *personal observation*). Small seedlings (<5 cm height) are apparently restricted to recent (<2-yr-old) canopy openings (Dalling et al. 1998a), although larger seedlings (>20 cm height) and saplings are widespread and abundant throughout the forest. *Alseis* is the second most abundant canopy tree species >1 cm dbh in the 50-ha plot (Condit et al. 1995).

We compared *Alseis* seedling growth, resource allocation patterns, and photosynthetic rates with those of a pioneer species, *Miconia argentea*, and with a non-pioneer species, *Tetragastris panamensis* (henceforth referred to by their generic names only). *Miconia* is the most abundant species in the soil seed bank, and its seeds are of similar size to those of *Alseis* (Table 1). Unlike *Alseis, Miconia* is not represented by seedlings or saplings in the shaded understory (Brokaw 1987, Dalling et al. 1997, 1998b). *Miconia* ranges from southern Mexico to Panama and occurs from lowland dry forests to pre-montane wet forest (Croat 1978). During the late dry season–early wet season, *Miconia*

produces numerous berries mainly dispersed by birds (Table 1). *Tetragastris panamensis* is a relatively large-seeded non-pioneer canopy tree of tropical moist forests ranging from Belize to Peru and Brazil. Fruits are fleshy-walled multiseeded capsules ripening in the early–mid wet seasons. Seeds are monkey and bird dispersed, and germinate rapidly to produce seedling carpets that persist for several months or years in the forest understory.

METHODS

Seed germination

Using seeds collected from fallen infructescences from three *Alseis* trees on BCI, we asked if seeds show microsite preferences for germination in the understory or in canopy gaps. We placed seeds in three replicate Petri dishes in the center of each of four small treefall gaps (~20 m²), and in four adjacent paired understory sites. Each Petri dish contained 20 seeds placed on moist tissue paper. Petri dishes were sealed with parafilm to avoid desiccation, and were remoistened as necessary through the experiment. Seedlings were counted and removed from Petri dishes each three days until no further germination occurred (after 10 wk). We tested germinability in Petri dishes rather than by sowing seeds on to the natural soil because small seeds exposed on the soil surface are rapidly removed by litter ants on BCI (Dalling et al. 1998*b*). To estimate the viability of the seed lot used, we dissected an additional 60 seeds under the microscope and scored as viable those seeds with an intact endosperm.

Seedling growth and allocation patterns in simulated gaps

To examine how growth and allocation patterns of seedlings of *Alseis* might compare with those of the pioneer species *Miconia,* and non-pioneer species *Tetragastris* in gaps, we grew eight seedlings of each species under each of six different light regimes. Light conditions simulated canopy openings ranging from 25 m² to 800 m², the full range of gap sizes successfully colonized by pioneer species on BCI (Brokaw 1985, 1987, Hubbell et al. 1999). Although these species may vary markedly in their growth response to understory light conditions, we did not simulate complete shade conditions in this experiment. Instead, our objective was to determine whether *Alseis* is capable of the morphological and physiological plasticity reported for pioneer species when grown under varied light conditions (reviewed in Veneklaas and Poorter 1998). To ensure that seedlings of *Alseis* and *Miconia* were of sufficient size to survive transplantation, we initially germinated seeds and raised seedlings in a growing house on BCI. Light conditions within the growing house (40% of total daily photosynthetically active radiation [PAR]) were within the range of light conditions in the simulated gaps, but may have affected subsequent growth

and survival for seedlings transplanted into the smallest simulated gaps. Seedlings of *Alseis* were transferred to Summit Gardens and transplanted into 8-L plant pots containing a 2:1 mixture of forest soil and sand 35 d after germination, in May 1997, and seedlings of *Miconia,* 80 d later in August 1997. Seedlings of both species were transplanted when they had four true leaves, 10 mm mean seedling height, and an estimated mean seedling dry mass of 0.01 g (*n* = 5 harvested seedlings). Seedlings of *Tetragastris* were transferred to Summit Gardens in June 1998, 21 d after seedling emergence, when they had one pair of true leaves and a mean seedling dry mass of 0.24 g (*n* = 5 harvested seedlings).

Each of the six light treatments was created by suspending the tree pots within steel mesh frames. Each frame was draped with one layer of black mesh 70% shade cloth, and one layer of a dye-impregnated energy film (Gold Point ST7 SLT-60, Panama City, Panama; R:FR transmittance = 0.15) used to simulate the total radiation and red:far red (R:FR) light ratio found in forest gaps (R:FR defined as the ratio of quanta at 655–665 nm to quanta at 725–735 nm). Different light treatments were obtained by varying the width of a central open aperture in the roof of the frame, which exposed seedlings to direct sunlight for varying periods, and to differing amounts of diffuse light, and light quality (range 30–195 min direct sun). The environmental conditions within these treatments are described in detail elsewhere (Dalling et al. 1999).

Four replicate benches, with two seedlings of each species grown in each bench, were used for each of the six treatments (4.8, 8.2, 11.8, 14.9, 19.4 and 26.2 mol·m⁻²·d⁻¹ total PAR). Assuming a circular gap, and a 30 m tall canopy, these aperture widths would represent gap sizes of 25, 50, 100, 200, 400, and 800 m², respectively. As seedlings grew they were progressively lowered beneath the bench roof so that newly expanded seedling leaves were always maintained in the same light environment. Although species with higher rates of height growth might experience greater whole-canopy shading in this experiment, differences in mean seedling height at harvest time between the faster growing species *Alseis* (61 ± 19 cm; mean ± 1 SD), and *Miconia* (69 ± 20 cm) remained quite small. Seedlings were grown under these conditions for 110 d (*Tetragastris*), 112 d (*Alseis*), and 117 d (*Miconia*) before harvesting, when seedlings of *Alseis* and *Miconia* in the highest light treatments had mean total leaf areas of ~200 cm².

In the morning of the day that seedlings were harvested (0900–1130), seedlings were removed from the benches and exposed to full natural light (>800 μmol·m⁻²·s⁻¹) for ~10 min before maximum rates of photosynthesis 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 Incorporated, Lincoln, Nebraska, USA). The environ-

ment within the leaf cuvette was controlled to be similar to ambient conditions. Leaf temperatures during the measurements were between 28°C and 35°C. The leaf area of harvested seedlings was measured using an automated LI-COR leaf area meter (LI-3000A, attached to a transparent belt conveyer LI-3050A), and the mass of foliar, stem and root fractions was measured after drying for 72 h at 70°C.

Relative growth rate (RGR) was calculated as the slope of the relationship between the natural log of total biomass and time between transplantation and harvest for each species in each gap treatment. Net assimilation rate (NAR) was calculated according to the following equation:

$$NAR = ((W_f - W_i) \times (t))/((A_f - A_i)/(\ln A_f - \ln A_i))$$

where W_f and W_i are the final and initial dry mass (in grams), respectively, A_f and A_i are the final and initial leaf area (in square meters), respectively, and t is the duration of the experiment (in days). Leaf mass ratio (LMR; leaf mass per unit whole-plant mass), root mass ratio (RMR; root mass per unit whole-plant mass), leaf area ratio (LAR; leaf area per unit whole-plant mass), and specific leaf area (SLA; leaf area per unit leaf mass), were calculated from the harvest data.

To determine whether the three species differ in dark respiration rates, six additional 10–20 cm tall seedlings were collected from understory and gap-edge (*Miconia*) sites on BCI, transplanted into pots, and acclimated to shade conditions (10–60 μmol·m^{-2}·s^{-1}) for one month in a growing house (PAR). Respiration measurements were made using a portable open gas exchange system (LI-COR 6400, LI-COR Incorporated, Lincoln, Nebraska, USA).

Alseis *distribution, survival, and growth in the understory*

To examine patterns of *Alseis* recruitment in gaps and in the understory, we analyzed data from a complete census of all *Alseis* individuals in 1 ha within the 50-ha plot (D. A. Murawski, *unpublished data*). The census was carried out in December 1986 and January 1987. All individuals were mapped to the nearest 10 cm within 5 × 5 m subplots, and the basal diameter and height of seedlings and saplings <1 cm dbh was measured. For individuals >1 cm dbh only basal diameter was measured. In 1998 the 1-ha plot was completely recensused, and new *Alseis* seedlings were mapped, tagged, and heights remeasured.

To determine whether the original seedlings (mapped in 1986–1987) and new seedlings (mapped in 1998) had recruited in sites with a history of canopy disturbance, we examined seedling abundance surrounding a grid of 400 canopy height measurement points extending across the 1-ha area. Within the 50-ha plot, canopy height has been measured each year since 1983 (except 1994 and 1997) at each corner point of each 5 × 5 m subplot (see Hubbell and Foster 1986, and Wel-

den et al. 1991 for more details). Canopy height is classified into six height classes (0–2 m, 2–5 m, 5–10 m, 10–20 m, 20–30 m, and >30 m). For individuals censused in 1986–1987, we identified as ''disturbed'' sites having a canopy height of <10 m in any year 1983–1986. For new recruits censused in 1998, we classified ''disturbed'' sites as having a canopy height of >10 m in 1983–1986 and <10 m in any year 1987–1996. As *Alseis* can establish even in small gaps (Dalling et al. 1998a), we considered the four 25-m^2 subplots surrounding each low canopy point as the area potentially influenced by disturbance, and compared *Alseis* abundance in these sites to sites unaffected by canopy disturbance over the same periods.

Data analysis

The comparison of total seed germination in gaps vs. paired understory sites was made using the Mantel-Haenszel chi-square test (Tables procedure, SYSTAT, Wilkinson et al. 1992). This statistic tests for the association between two binary variables (germination and habitat type) while controlling for a stratifying variable (site). Effects of gap size and species on seedling size, allocational patterns, growth, and photosynthesis were analyzed using a split-plot analysis of ANOVA with ''species'' effect nested within the plot term (Multivariate General Linear Hypothesis procedure, SYSTAT 5.2). Analyses were performed on the means of the two seedlings of each species grown in each simulated gap. Significant regressions of mean values for each seedling attribute vs. log (gap size) are also plotted on figures.

Dispersion patterns of *Alseis* individuals within the 1-ha plot were examined using a nearest neighbor analysis. We tested the null hypothesis that the distribution of nearest neighbor distances of the 1986–1987 *Alseis* population was identical to that of a population of randomly distributed individuals of the same size. Although limited seed dispersal results in a clumped seedling distribution for most species, we found little evidence in an earlier study that proximity to adults affects recruitment probabilities for *Alseis* in natural gaps in the 50-ha forest dynamics plot. The cumulative distributions of nearest neighbor distances for the two seedling populations were compared using the two-sample Kolmogorov-Smirnov test. Significance testing is determined from the maximum difference in cumulative frequency for any nearest neighbor distance (D_{max}), and from the sample sizes of the seedling populations (n_1, n_2), using the expression:

$$P = 2e^{-[(2(n_1 n_2)(D_{max})^2)/(n_1 + n_2)]}$$

where P is the smallest level of significance at which the null hypothesis is rejected (Pacheco and Henderson 1996). Seedlings that were closer to the edge of the 1-ha plot than to the nearest neighbor were excluded from the analysis.

As a partial test of whether density-dependent thin-

TABLE 2. *F* values from split-plot analyses of variance for seedling growth patterns.

Attribute	Species	Gap	Species × gap
Leaf area (cm^2)	6.1**	0.6	1.1
Whole plant mass (g)	1.3	2.9	1.2
Leaf mass ratio	7.2**	0.6	3.5**
Root mass ratio	13.1***	2.6	1.7
Specific leaf area (cm^2/g)	361.7***	26.7***	2.7*
Leaf area ratio (cm^2/g)	258.0***	14.5***	5.1***
Net assimilation rate ($g \cdot m^{-2} \cdot d^{-1}$)	55.0***	7.6**	1.8
Relative growth rate ($g \cdot g^{-1} \cdot d^{-1}$)	47.5***	21.2***	4.0*
Photosynthesis ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	41.4***	2.5	3.4*
Photosynthesis ($\mu mol\ CO_2 \cdot g^{-1} \cdot d^{-1}$)	35.0**	1.1	1.8

Notes: *F* tests were conducted on the mean values from two seedlings of each of three species grown within each simulated gap. *Alseis, Miconia,* and *Tetragastris* seedlings were grown for 112, 110, and 117 days, respectively, under six simulated gap sizes. Degrees of freedom for growth and morphology measurements: species = 2, 26; gap = 5, 13; species × gap = 10, 26. For light-saturated photosynthesis measurements the degrees of freedom are smaller, as plants with small leaves were excluded: species, df = 2, 12; gap, df = 5, 6; species × gap, df = 10, 12.
 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ning of the *Alseis* seedling population occurred between 1987 and 1998, we also compared the nearest neighbor distribution of surviving seedlings in 1998 with the 1986–1987 population after random thinning had removed the same number of individuals as died during the census interval. An important caveat to interpreting this analysis is that 274 individuals occurring in tight seedling clumps had to be excluded from both the 1986–1987 and 1998 datasets (see *Results*: *Seedling distribution, survival and growth in the understory*). These individuals were excluded, as their identity as either survivors or new recruits could not be determined. A failure to detect density dependence in this analysis therefore only implies that it does not operate at the seedling densities for which we have reliable mortality data.

Results

Seed germination

Seeds of *Alseis* began germinating 14 d after being placed in Petri dishes, and had mostly completed germinating after 30 d. Germination in gaps (40 ± 9%; mean ± 1 SE) was significantly higher than in the understory (8 ± 2%; Mantel-Haenzel $\chi^2 = 68.2$, df = 1, $P < 0.001$). Dissection of an additional sample of 60 seeds under the microscope revealed that many seeds (40%) were colonized by fungi and were inviable; germination in gaps may therefore represent almost complete germination of the viable fraction of the seeds used in the experiment.

Seedling growth and allocation patterns in simulated gaps

Total seedling mass at the end of the experiment was not significantly different between the three species (Table 2; Fig. 1a), and leaf area was not significantly different between *Miconia* and *Alseis*, but was significantly higher than that of *Tetragastris* (Fig. 1b; post

hoc contrast $P > 0.01$). In general, the seedling growth and allocation patterns of *Alseis* were more similar to those of the pioneer *Miconia,* than those of the non-pioneer species *Tetragastris* (Fig. 1).

Biomass allocation to leaves or to roots was not significantly different between *Miconia* and *Alseis,* but was significantly higher than for *Tetragastris* (Table 2; Fig. 1c, d; post hoc contrast $P < 0.01$), and did not vary significantly with gap size for any species (Table 2). Instead, most variation between species in allocation patterns resulted from differences in leaf thickness or density reflected in the specific leaf area (SLA; Fig. 1e). The SLA of *Alseis* paralleled that of *Miconia,* but was consistently 40% higher across all gap treatments (Fig. 1e). The SLA of *Tetragastris* also varied with gap size, but showed lower plasticity than the other two species. Differences in SLA between species account for the higher leaf area ratio (LAR) values for *Alseis* (Fig. 1f), and, in part, for its lower net assimilation rates (NAR, Fig. 1g). Whereas both *Alseis* and *Miconia* show strong plastic response of NAR to gap size, *Tetragastris* is unable to respond to increased duration of direct sunlight, so that neither NAR nor relative growth rate (RGR) increase in larger gaps (Fig. 1g, h). RGR was not signficantly different between *Miconia* and *Alseis* (post hoc contrast $P > 0.05$), but only *Miconia* showed a significant, but small effect of gap size on RGR ($F = 3.1$; $P < 0.05$).

Net photosynthetic rates measured on a per unit area basis increased significantly with gap size for both *Miconia* and *Alseis,* but not for *Tetragastris* (post hoc contrast $P < 0.05$; Fig. 2a). The higher photosynthesis rate for *Miconia* is entirely attributable to its lower SLA; photosynthetic rate on a per mass basis did not differ between *Miconia* and *Alseis* (post hoc contrast $P > 0.05$; Fig. 2b), and did not vary significantly across the range of gap sizes, indicating that higher irradiance in the large gaps was balanced by the construction of thicker or denser leaves.
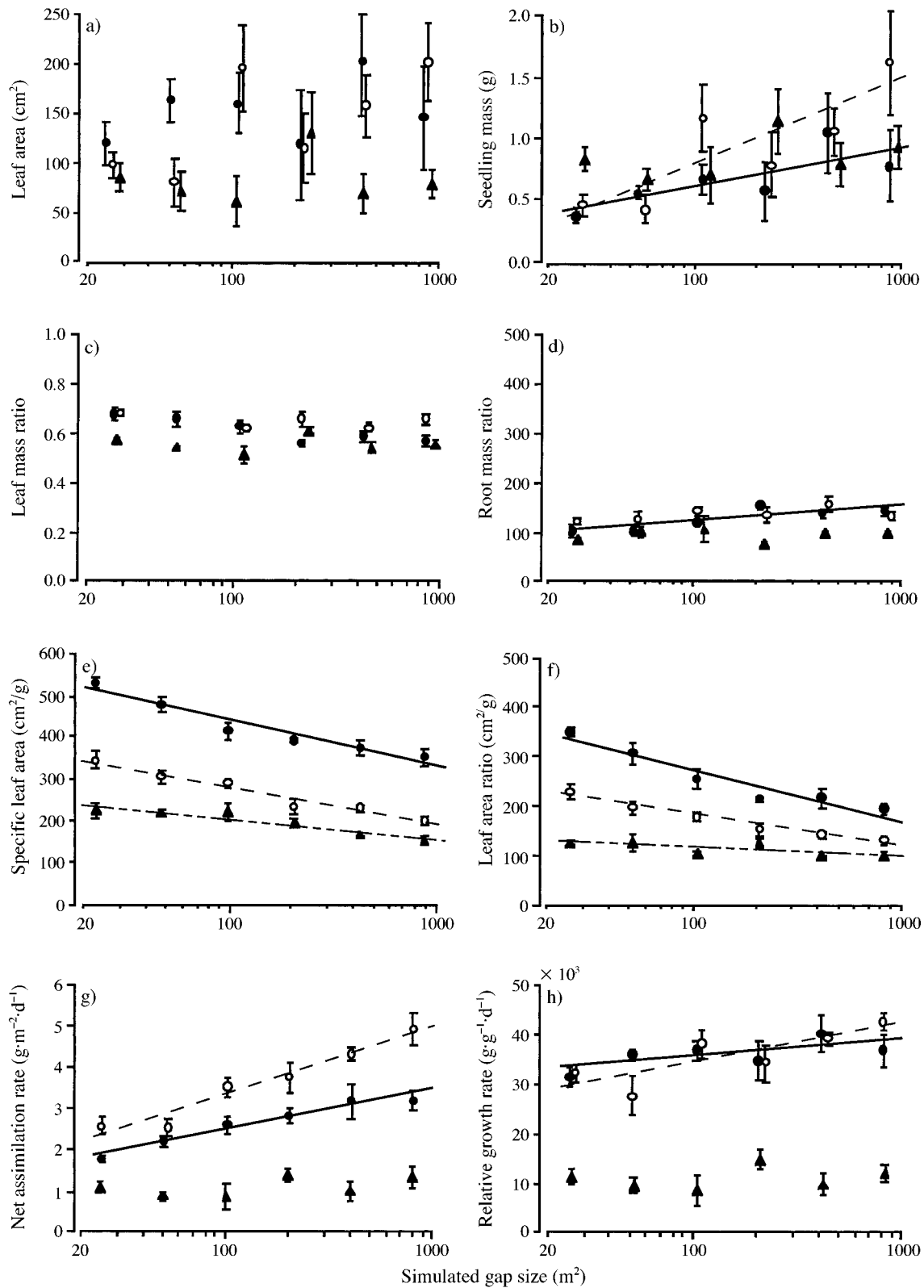
FIG. 1. Mean values (± 1 SE) of (a) leaf area, (b) total seedling dry mass, (c) leaf mass ratio (LMR), (d) root mass ratio (RMR), (e) specific leaf area (SLA), (f) leaf area ratio (LAR), (g) net assimilation rate (NAR), and (h) relative growth rate (RGR) for seedlings of *Alseis* (solid circles), *Miconia* (open circles), and *Tetragastris* (triangles) grown under six light regimes simulating gaps of different sizes. Solid lines (*Miconia*), dashed lines (*Alseis*), and double-dashed lines (*Tetragastris*) indicate significant regressions of seedling attributes with gap size.
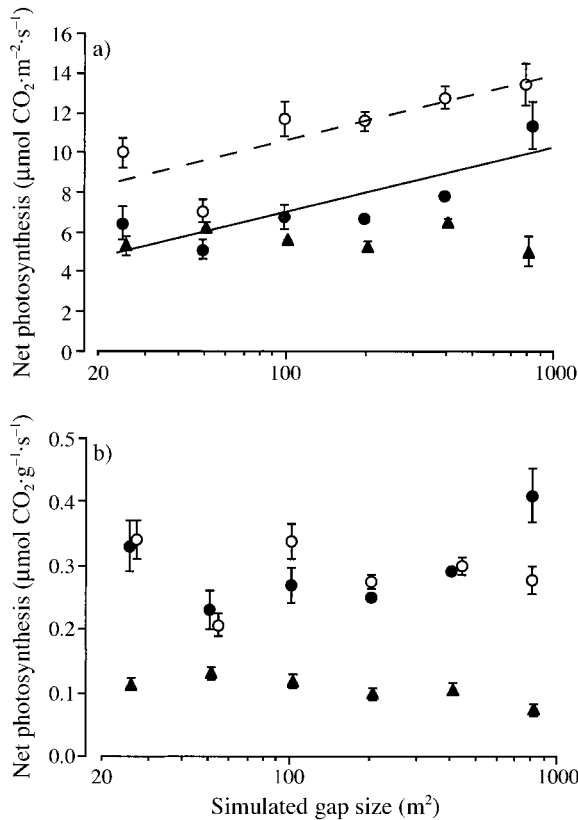
FIG. 2. Mean values (± 1 SE) of (a) light-saturated photosynthetic rate on a per-area basis, and (b) on a per-leaf-mass basis for seedlings of *Alseis, Miconia*, and *Tetragastris.* Symbols are as for Fig. 1.

Seedling distribution, survival, and growth in the understory

In total, 996 *Alseis* individuals were found in the hectare censused in 1986–1987. All except 90 individuals were smaller than the 1 cm dbh size class at which plants enter the main census of the 50-ha forest dynamics plot. The seedlings mapped in 1986 (Fig. 3a) were highly clumped at the scale of 1 ha (median nearest neighbor distance = 0.5 m; expected median distance for a random population = 1.6 m; K-S test, D_{max} = 0.44, $P < 0.001$), and were present in only 249 of the 400 25-m^2 subplots in the hectare.

The clumped distribution of juveniles does not reflect localized seed dispersal around reproductive adults since genetic analysis of the seedlings revealed that they were not generally the progeny of the reproductive-sized trees present in the 1 ha in 1986–1987 (J. D. Nason et al., *unpublished manuscript*). Instead, seedling and sapling distribution patterns in 1986–1987 probably reflect the past disturbance history of the plot. More of the 25-m^2 subplots that surrounded a low canopy point between 1983 and 1986 contained at least one *Alseis* individual than subplots surrounding continuously high canopy points over the same period (χ^2

= 15.4, $P < 0.001$), and seedling densities were higher in the occupied plots surrounding a low canopy point than in the occupied plots surrounding a high canopy point (Mann-Whitney U test = 5617, $P < 0.001$).

Alseis individuals censused in 1986–1987 were mapped at the scale of the 25-m^2 subplots. Since most of these subplots contained few *Alseis* individuals (more than half the subplots contained ≤5 individuals), and because little recruitment occurred after 1986 (Fig. 3b), we were able to determine whether juveniles had survived or had died for 722 of the original 996 individuals. The remaining 274 individuals were omitted from mortality analyses because they occurred in tight
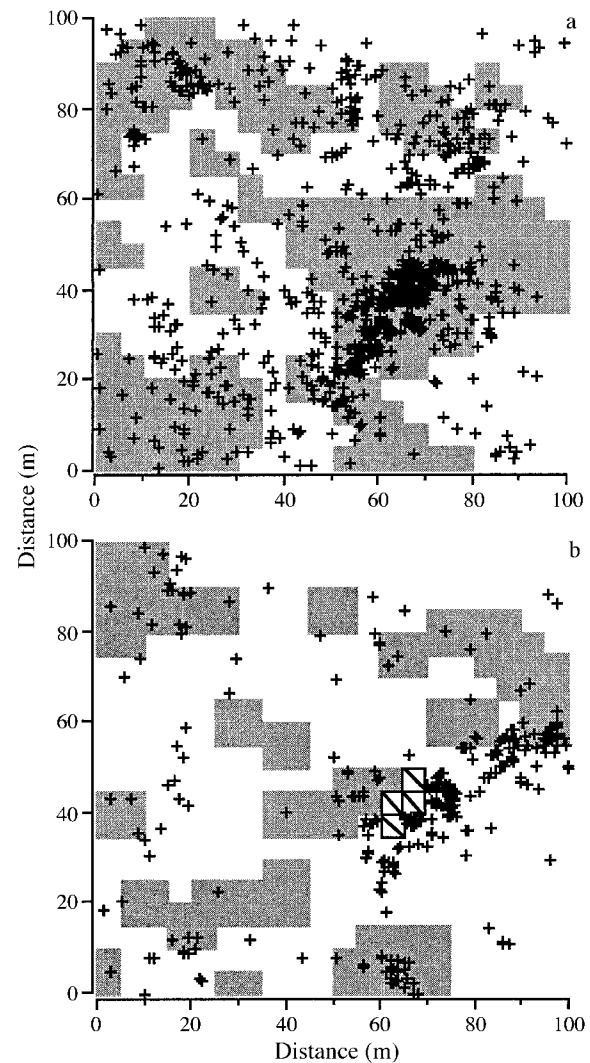

FIG. 3. Distribution of (a) *Alseis* individuals (+) in a 1-ha plot in 1986, and (b) new *Alseis* recruits in 1998. Shaded patches are the 100 m^2 surrounding any point that had a canopy height <10 m between 1983 and 1986 (a) or between 1987 and 1996 (b). Four of the 25-m^2 plots in 1998 (marked by a crossed box) were excluded from the 1998 analysis because very high *Alseis* sapling densities made it impossible to distinguish new recruits from the survivors.

TABLE 3. Population size distribution, mortality rate (1986–1998), and recruitment in 1998 for *Alseis* within 1 ha in the 50-ha forest dynamics plot on BCI.

Size class†	Individuals 1996 (n)‡	Mortality $(\%/\text{yr})$§	Recruits 1998 $(n)\|$
<5 mm	151	3.7	104
5–9.5 mm	327	4.0	176
10–14.5 mm	181	2.7	47
15–19.5 mm	125	3.3	16
20–29.5 mm	98	5.6	11
>30 mm	76	4.3	0
All size classes	996	3.8	354
1–10 cm dbh¶	...	1.2	...

† Basal diameter.

‡ Data are missing for 38 individuals.

§ Mortality rates are calculated for 722 individuals (excludes individuals for which recensus identification was uncertain).

‖ Excludes four 25-m² subplots in which *Alseis* seedling densities were too high to distinguish individuals in the original census from new recruits.

¶ Mortality rate calculated between 1990 and 1995 for the entire 50-ha forest dynamics plot.

clumps where the identity of any individual was difficult to determine. The four 25-m² subplots with the highest *Alseis* densities (total 162 individuals) were omitted in their entirety (marked on Fig. 3b).

Of the 722 individuals recovered in the recensus, 465 had survived since 1986. The remaining 257 were considered dead, although the remains of only 36 individuals could still be found. Somewhat surprisingly, mortality varied little with size, although annual mortality was higher for individuals in this census (3.8%) than for the mostly much larger individuals in the 1–10 cm dbh class in the 50-ha plot as a whole (1.2%; Table 3). Comparing only the 722 individuals recovered in the recensus, we found no evidence of density-dependent mortality between censuses. The nearest neighbor distribution of the surviving seedlings in 1998 was not significantly different from that of the randomly thinned 1986–1987 population (median nearest neighbor distance = 0.88 m; randomly thinned median = 0.95 m; D_{max} = 0.03, NS). Importantly though, we could not determine if higher rates of mortality had occurred in the highest density seedling patches excluded from this analysis.

Surviving individuals mostly persisted rather than grew. Considering only individuals alive in 1986 and 1998, and excluding 90 individuals >1 cm dbh in 1986 (for which no height data are available), mean height declined (mean ± 1 SD) from 73 ± 64 cm to 64 ± 61 cm and median height from 49 to 43 cm (n = 370 individuals). Mean relative height growth was also negative (-0.19 mm·cm^{-1}·yr^{-1}), although median relative height growth was positive (0.06 mm·cm^{-1}·yr^{-1}). Declines in seedling and sapling size between censuses are mostly attributable to stem breakage or dieback; 210 out of the 370 individuals had conspicuous stem scars and had regrown from resprouts. Some individ-

uals, however, did grow significantly over the 11-year period, and 13 individuals recruited into the 1 cm dbh size class.

Many 25-m² subplots contained no new *Alseis* recruits in 1998, reflecting a general absence of canopy disturbance in this hectare. However, the *Alseis* population did increase, with 354 new recruits, compared with 257 individuals recorded as dead. In the four subplots in which the *Alseis* density was too high to confidently relocate survivors from the 1986 census there was a net total increase of 40 individuals.

The distribution of 1998 recruits was also highly clumped (Fig. 3b). Nonetheless, seedling distributions for new recruits did not as closely match sites with a history of canopy disturbance as did individuals in the original census. Although subplots adjacent to sample points at which the canopy dropped to <10 m between 1987 and 1996 were more likely to be occupied by a new *Alseis* recruit than subplots unaffected by canopy disturbance (χ^2 = 8.6, P < 0.01), the highest densities of new recruits occurred in the same subplots that had the highest densities in 1986 (Fig. 3). Either *Alseis* continued to recruit into these sites as a result of elevated light levels that persisted after 1986, or some new recruits are in fact older individuals that were missed in the original census, perhaps because they were leafless during the census or grew back from basal resprouts. Many of the new recruits were quite large in 1998; 18% were >50 cm tall, and 46% had resprouted. Consistent with the absence of any very recent canopy disturbance in the plot (no new low canopy sites since 1994) was the failure to find any very young seedlings (<10 cm height without resprouts).

DISCUSSION

Alseis *regeneration requirements*

Alseis blackiana essentially fits the description of a pioneer species (sensu Whitmore 1998) in its seedling establishment requirements, seedling growth and allocation patterns, and life history traits associated with reproduction (Table 4). Higher seed germination success in gaps than in the understory in *Alseis* is also consistent with a pioneer habit, and contrasts very-small-seeded non-pioneers reported for some paleotropical sites (e.g., *Pternandra* and *Urophyllum*; Raich and Gong 1990, Grubb 1996). In an earlier study, Dalling et al. (1998b) found evidence of seedling establishment of *Alseis* in gaps, with young seedlings <10 cm in height present in 21 out of 36 treefall gaps <2 yr old. In contrast, in March 1998, no similarly small seedlings were found in a 1-ha plot that lacked treefall gaps <2 yr old.

The seedling growth and allocation patterns of *Alseis* are also similar to those of pioneer species grown under a range of light conditions (e.g., Popma and Bongers 1988, Osunkoya et al. 1994, Veenendaal et al. 1996, Poorter 1999). In our pot experiment in which seedlings

TABLE 4.   Characteristics recognized as typical of pioneer and shade-tolerant species, modified from Swaine and Whitmore (1988).

Characteristic	Pioneer	Shade-tolerant	*Alseis*
Germination only in gaps?	++	−	yes
Seedlings survive in shade?	−	+++	yes
Seed dormancy?	++	−	yes
Small seeds, early reproduction?	++	+	yes
High photosynthetic rates	++	+	yes
High herbivory rates	++	+	yes†‡
Wide ecological range	++	+	no?
Short lived	++	+	no
Poorly chemically defended	++	+	no§
Low leaf toughness (high SLA)	++	+	yes†
High leaf N concentration	++	+	yes†
High leaf turnover rate	++	+	yes‡

Note: +++ = always, ++ = commonly, + = rarely, − = never.
   † Coley (1983).
   ‡ Barone (1996).
   § *Alseis* is intermediate in its defense allocation between pioneers and shade-tolerant species, but was classified as a shade-tolerant species using a discrimination analysis based on defense factors listed by Coley (1993).

were grown in light treatments simulating six different gap sizes, we found no differences in relative growth rate, leaf area production, and maximum carbon assimilation rate between *Alseis* and *Miconia argentea*, a well-studied pioneer tree species incapable of prolonged survival in understory shade (Brokaw 1987, Dalling et al. 1998*a, b*). Although the maximum relative growth rates of both *Alseis* and *Miconia* were relatively low in comparison to the large gap specialist pioneers *Ochroma pyramidale* (Cav. ex Lam.) Urban and *Trema micrantha* (L.) Blume, they are similar to those of other pioneer tree species *Alchornea costaricensis* Pax and Hoffm. (Euphorbiaceae), *Luehea seemannii* Tr and Planch. (Tiliaceae) and *Apeiba membranacea* Spruce ex Benth. (Tiliaceae) grown under the same conditions (Dalling et al. 1999; J. Dalling, *unpublished data*).

Nonetheless, previous classifications of the BCI flora do not recognize *Alseis* as a pioneer (Coley 1983, Welden et al. 1991, Condit 1996, Guariguata 1998) because its saplings are abundant in the understory. A 1-ha plot censused in 1986 recorded 906 *Alseis* individuals <1 cm dbh, while the abundance of individuals >1 cm dbh in the 50-ha forest dynamics plot as a whole (*n* = 8424 in 1990) is the second highest of any canopy tree species (Condit et al. 1995). Clearly, the simple requirement for gaps for seedling establishment does not alone limit abundance in larger size classes in the BCI forest. Gap dependency for early establishment does, however, affect the distribution pattern of individuals. *Alseis* individuals were found to be strongly clumped, reflecting sites of canopy disturbance rather than local seed dispersal.

Given limits to recruitment for *Alseis* dictated by the frequency of canopy disturbance, its abundance in the sapling layer must be attributable to very low mortality rates of individuals persisting in the shade after canopy closure. Indeed, annual mortality rates for *Alseis* seedlings 25–50 cm tall were 4%/yr, markedly lower than the 10–20%/yr of similar-sized non-pioneer species *Trichilia tuberculata* (Tr. and Pl.) C. DC. (Meliaceae), *Tetragastris panamensis* (Engl.) Kunze (Burseraceae), and *Quararibea astrolepis* Pitt. (Bombacaceae) that had established in the forest understory (De Steven 1994 and *personal communication*). The low mortality rate for *Alseis* may reflect persistently higher light conditions in old gaps or, perhaps, use of carbohydrate reserves stored under high light conditions. However, the mortality rate for *Alseis* is also remarkably low for larger individuals. Comparing tree species with >500 individuals in the 1–10 cm dbh size class in the 50-ha plot (*n* = 22 species), *Alseis* had the fourth lowest mortality rate (1.2%/yr; Condit et al. 1995). In general, pioneer species had mean mortality rates of 7–10%/yr in this size class (Condit et al. 1995).

The high survival of *Alseis* in the shade may be at the cost of growth, since growth in the shade of individuals >1 cm dbh is relatively poor compared with other non-pioneer and pioneer species (Welden et al. 1991). In the understory, *Alseis* drops and flushes new leaves every year (Lovelock et al. 1998), leaving conspicuous leaf scars. In most individuals, leaf scars were tightly aggregated along the stem, with periodic internodes several centimeters to tens of centimeters long, indicating prolonged periods with little or no net growth, interspersed with short periods of release from suppression (J. W. Dalling, *personal observation*). Many individuals in the 1-ha plot actually decreased in height over the 11-year intercensus period, reflecting damage and resprouting lower on the stem, presumably inflicted by litterfall and herbivores. Overall the mean relative height growth for all individuals <1 cm dbh was negative over the 11-year census period.

What factors permit *Alseis* survival in the understory?

Many of the morphological and physiological characteristics of *Alseis* are unusual, if not unique, among

understory plants. These include thin, short-lived, nitrogen-rich leaves, low wood density, and a lack of seed reserves (Table 4). Relatively thin, nitrogen-rich leaves have been found in understory plants in many tropical forests, and in aseasonal forests, species with tiny seeds establish in the shade on rock or root substrates free of litter (Metcalfe et al. 1998; P. J. Grubb, *personal communication*). We suspect that the combination of these characters permits survival in the understory for several reasons: leaf morphology and physiology allows efficient light capture and use of sunflecks, rapid growth during the early high-light establishment phase allows the development of a shade-persistent architecture, and plant morphology affords a high tolerance to physical damage.

Most plants in the understory have thick, tough, long-lived leaves (average 2–4 yr, with an extreme of 14 yr; Coley and Barone 1996), as is to be expected given the need to maximize carbon gain per unit investment in a resource-limited environment (Reich et al. 1991, 1992). *Alseis* and a few other understory shrubs on BCI, however, have thin leaves with a lifespan of only one year (Kursar and Coley 1993, Lovelock et al. 1999). Thin leaves increase the area per unit leaf mass (SLA) available to intercept patchily distributed sunflecks that occur in the spatially heterogeneous light environments of the forest understory (Chazdon and Fetcher 1984), and have faster photosynthetic induction times in sunflecks and greater plasticity in photosynthetic rates than thick leaves (Mulkey et al. 1991, Kursar and Coley 1993). High SLA (and consequently LAR) can therefore explain why pioneer species can grow faster than non-pioneers both in high- and low-light conditions (Veneklaas and Poorter 1998).

The greater shade tolerance of *Alseis,* compared with *Miconia*, may be directly related to this high SLA. King (1994) reported that 1–2 m *Miconia* and *Alseis* saplings had similar leaf life-spans in the forest (11–12 months), but that the shade SLA for *Alseis* was twice that of *Miconia* (see King 1994: Table 5). This difference in SLA largely accounts for the difference in the estimated whole-plant light compensation point found between the species (see King 1994: Table 6). SLA is so high in *Alseis* that light use efficiency, in terms of total carbon fixed per unit investment in leaf mass, may approach that of species with long-lived leaves. Leaves of *Garcinia edulis* (Seem.) Planch. and Tr., and *Aspidospermum cruenta* Woods., for example, have an SLA in the understory six times lower than those of *Alseis* (T. Kursar, *unpublished data*).

Despite the advantage of high SLA to carbon gain in the shade, non-pioneer plants typically have tough low-SLA leaves. This results from the higher herbivory of tender, high-SLA leaves (Coley 1983, Lowman and Box 1983). Herbivory losses are particularly significant in the understory, where the rate of photosynthetic carbon gain is low and lost biomass cannot readily be replaced. Unsurprisingly, therefore, mature leaves of *Alseis* suffer high rates of herbivory compared with other non-pioneer species (Coley 1983: Appendix). Nonetheless, *Alseis* falls along the regression line on a plot of herbivory rate against leaf toughness when data for both non-pioneer and pioneer species are included (data plotted from Appendix in Coley [1983]; $r^2 = 0.45$; $n = 46$), indicating that *Alseis* does not suffer particularly high rates of herbivory despite its high abundance in the understory.

Greater persistence of *Alseis* in the understory may also be achieved by maintaining lower rates of respiration in the shade than pioneer species (Hutchinson 1967, Loach 1967). Fredeen and Field (1991) measured respiration of six *Piper* species with different habitat requirements and showed that species normally found in gaps and clearings had twice the dark respiration per unit leaf area or dry mass as species found predominantly in shaded understory sites. Respiration rates of shade-acclimated seedlings of *Alseis, Miconia*, and *Tetragastris* were similar (range of 0.14 and 0.26 $\mu mol \cdot m^{-2} \cdot s^{-1}$; K. Winter, *unpublished data*). However the infrared gas analyzer used may be insufficiently sensitive to detect differences among species, and further comparisons should be made using an oxygen electrode. Walters et al. (1993) have also pointed out that low respiration of shade-tolerant plants in low light does not necessarily equate with a more efficient carbon economy if plants with high respiration also have higher photosynthetic rates or faster induction times and therefore accumulate more dry mass per unit CO_2.

Alseis whole-plant architecture also minimizes investment in support tissue, and may also minimize damage from falling litter. *Alseis* seedlings <50 cm in height in the understory are typically monopodial with a single crown layer of 4–6 large leaves arrayed in a rosette. The development of this monopodial architecture occurs during the initial gap phase of seedling recruitment. Subsequent exposure to sunflecks permits rapid height growth into higher light strata. The absence of lateral branching may also reduce the probability that saplings are hit by falling litter.

Guariguata (1998) also found that artificially damaged *Alseis* saplings (1.0–2.5 m tall) suffered significantly lower mortality following simulated litterfall damage (stems cut or pegged to the ground) than three other common non-pioneer tree species, *Protium panamense* (Rose) I. M. Johnston, *P. tenuifolium* (Rose) Porter, and *Tetragastris panamensis. Alseis* suffered no mortality at all in either controls, or in the treatment in which individuals were cut in half, and <5% mortality in the treatment where stems were pegged to the ground, compared to 25–40% mortality for *Protium* spp. *Alseis*'s resilience was attributable to both its resprouting capacity, and its ability to produce adventitious roots (Guariguata 1998). Prone individuals of *Alseis* were even observed to generate several new sprouts, which subsequently grew independently (Guariguata 1992). The explanation for the superior

damage tolerance of *Alseis* in comparison with other non-pioneer species remains unclear. Guariguata (1998) suggested that it was linked to its inherently slow growth rate, but he found no evidence of a trade-off between growth and carbohydrate storage (sensu Kobe 1996), since *Alseis* had concentrations of non-structural carbohydrate in the taproot similar to the other three species in his study (Guariguata 1993).

Implications for understanding of forest dynamics

Canopy trees that require gaps for establishment and are shade tolerant appear to be rare in tropical forests, and we know of no other canopy tree species that shares the life history of *Alseis.* In central Panama, *Alseis* is very abundant only locally in the forests surrounding BCI; it is rare or absent from the wetter forests of the Atlantic coast and drier forests of the Pacific coast of central Panama. Other species of *Alseis* occur from Mexico to Peru but we know nothing of their ecology. In contrast, small-seeded shrubs and treelets may more frequently shift from gap recruitment to understory persistence (e.g., *Clidemia discolor* and *Miconia gracilis* at La Selva, Costa Rica; [Ellison et al. 1993], and ''cryptic pioneers,'' e.g., *Mareya micrantha* in Ghana; [Hawthorne 1993]), but these species have received less attention than canopy trees.

Variation in light requirements for establishment, and for growth and survival through ontogeny, is probably quite common (Parrish and Bazzaz 1985, Clark and Clark 1992, Bazzaz 1996). This is to be expected given the diversity of plant architectures, and consequently in allometric relationships between size and growth rate (King 1994, Davies et al. 1998), and in allocation to structural and chemical defenses. Guild or functional group classifications of plants should therefore encompass as much life history as possible. Classifications that consider only seedling establishment requirements (Swaine and Whitmore 1988), or conversely, consider only growth and mortality of well-established plants (Condit et al. 1996), may otherwise misrepresent community responses to environmental change.

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