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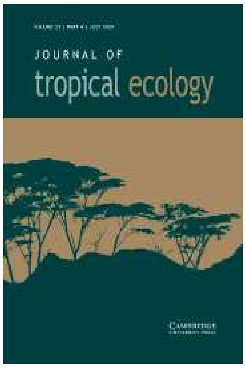

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Responses of seedling transplants to environmental variations in contrasting habitats of Central Amazonia

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Abstract: In the Central Amazon we investigated whether seedling performance (survival, and relative growth rates in height and leaf numbers) was affected by initial seedling size (height and leaf numbers) in habitats that varied in their degree of human disturbance: cattle pasture, young secondary forest, 1-ha forest fragment and old-growth forest. Additionally, effects of photosynthetically active radiation (PAR), litter standing crop (LSC) and insect herbivory were evaluated 12 mo after transplantation in seedlings from the native canopy trees *Chrysophyllum pomiferum*, *Micropholis venulosa* and *Pouteria caimito*. Seedling performance changed rank across the understorey environment depending on species. Seedlings of *Chrysophyllum* thrived in all conditions but under high PAR, *Micropholis* thrived only in intermediate light conditions, whereas *Pouteria* thrived under high PAR. Effects of initial seedling size, PAR and herbivory after 1 y were specific to species, whereas LSC had no effect on performance. Initially larger seedlings resulted in lower survival for *Chrysophyllum* and *Pouteria*. Herbivory affected seedling performance in all species. Negative effects of herbivory were intensified under low PAR. Overall, our results showed that, as seedlings, species of the same family and characteristic of old-growth forests respond differently to the environmental constraints present in contrasting human-disturbed conditions. Larger seedlings may not always present greater tolerance to physical and biotic mortality risks.

Key Words: Amazonia, *Chrysophyllum pomiferum*, fragmentation, herbivory, light environment, *Micropholis venulosa*, *Pouteria caimito*, Sapotaceae, seedlings, succession

INTRODUCTION

Deforestation has led to the replacement of rain forests by crop fields, pastures, second-growth forests and old-growth forest remnants scattered in the landscape (Aide & Cavellier 1994, Benítez-Malvido *et al.* 2001, Mesquita *et al.* 2001). Generally, the community of advanced regeneration (seedlings and saplings in the understorey) disappears or is strongly reduced in both places where slash-and-burn practices have been applied and in the remaining forest fragments (Benítez-Malvido 1998, Benítez-Malvido & Martínez-Ramos 2003). Factors such as low nutrient availability, soil compaction, increased plant litter, competition with other plants (e.g. pasture grasses), drought, reduced seed rain and increased seedling herbivory, make seedling regeneration extremely difficult in these altered areas (Aide & Cavelier 1994, Benítez-Malvido & Martínez-Ramos 2003, Buschbacher *et al.* 1988, Holl 1999, Nepstad *et al.* 1996, Sizer *et al.* 2000, Uhl *et al.* 1988). Some of the physical and biological barriers to seedling establishment in altered tropical systems are present in the old-growth forest, although their relative importance as regeneration facilitators or inhibitors may differ according to the species involved (Benítez-Malvido *et al.* 2001, Ganade & Brown 2002, Lewis & Tanner 2001).

For most cases, the vegetation structure of cattle pastures, secondary forests and old-growth forest fragments is simpler than that of continuous old-growth forest (Brown & Lugo 1990, Guevara & Laborde 1993, Laurance *et al.* 1998, Reiners *et al.* 1994). Changes in vegetation structure across altered tropical habitats may differently affect the understorey environment in terms of light incidence, soil moisture and micro-organisms, temperature, the fall and accumulation of litter, and

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the abundance and diversity of herbivores (Camargo & Kapos 1995, Facelli & Pickett 1991, Janos 1980, Klein 1989, Nepstad *et al.* 1996, Sizer *et al.* 2000). Such environmental changes may affect seedling performance according to species ecological attributes, such as: seed and seedling size, tolerance to shade, susceptibility to herbivory damage, etc. (Benítez-Malvido & Kossmann-Ferraz 1999, Gray & Spies 1997, Gross 1984, Molofsky & Augspurger 1993, Sarukhán *et al.* 1984).

It is expected that land-use history may interact differently with the natural forces to influence the performance of seedling species (Chazdon 2003). Many studies assessing barriers to seedling establishment on altered tropical systems have not considered the range of major habitats in the landscape, concentrating research efforts on no more than two contrasting habitats (mainly old-growth forest and pasture), or secondary forest of different types and successional stages (Aide & Cavelier 1994, Mesquita *et al.* 2001, Nepstad *et al.* 1996, Peña-Claros & de Boo 2002). Few have considered more than two contrasting tropical altered habitats (Camargo *et al.* 2002), and there are virtually no studies exploring simultaneously the relative effects of physical and biotic factors on the performance of trees in early developmental stages across a range of habitats. This paper explores the relative importance of light, litter, insect herbivory and initial seedling size on the performance of three native seedling species (Sapotaceae) transplanted into habitats that differ in their degree of disturbance, encompassing a recent abandoned pasture, a young secondary forest, a 1-ha forest fragment and an old-growth (non-human-disturbed) forest in Central Amazonia. We approached the next questions: (1) Is size a good predictor of seedling performance after transplantation? (2) Do differences in light, litter, and herbivory across the understorey affect seedling performance according to species? (3) Do seedling species differ in their abilities to cope with habitat alteration?

METHODS

Study sites and study species

The study was conducted in the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, Brazil (Bierregaard & Gascon 2001). Annual rainfall varies between 1900–3500 mm (Laurance 2001) and the mean annual temperature is 27 °C; on rare occasions the temperature can drop to 17 °C (Lovejoy & Bierregaard 1990). The soils are mostly nutrient-poor yellow latosols of high clay content (Chauvel *et al.* 1987). The vegetation of the area is mature *terra firme* tropical rain forest. The primary forest (old-growth) canopy averages 35 m in height, with occasional emergents up to 55 m (Rankin de Merona *et al.* 1990). The forest is characterized by a high density of small-diameter trees with few individuals ≥ 60 cm (dbh) and by remarkably high species richness coupled with low population densities for most species (Oliveira & Mori 1999). The understorey is dominated by stemless palms (Klein 1989) and there is an extremely low density of herbs and shrubs (Gentry & Emmons 1987). Lianas are sparsely distributed (Laurance *et al.* 2001).

The forest fragments were isolated in the early 1980s by creating cattle pastures. In some areas the pasture vegetation has developed into secondary forests of two kinds: those rich in plant species dominated by *Cecropia* spp. (clear-cut areas) and those poor in plant species dominated by *Vismia* spp. (clear-cut and recurrent fires, Mesquita *et al.* 2001). The BDFFP area adjoins vast areas of old-growth undisturbed forest. We took advantage of this mosaic of vegetation and selected four habitats that differed in their degree of alteration and hence in their understorey environment: (1) old-growth forest (control, in reserve no. 1501); (2) 1-ha forest fragment (isolated in 1984, reserve no. 1207, Lovejoy *et al.* 1986); (3) secondary forest dominated by *Vismia* spp. previously used as cattle pasture and abandoned in 1985; and (4) a cattle pasture created in 1980 dominated by the grass *Brachiaria humidicola* (J. Benítez-Malvido, pers. obs.). The old-growth forest and the pasture were located at the Esteio ranch; whereas the 1-ha forest fragment and the secondary forest were at the Dimona ranch (Bierregaard & Gascon 2001). Sites were selected following different criteria: firstly, on a logistical basis (i.e. accessibility to transport the seedlings, permission by the owners to wire fence the pasture and secondary forest, etc.); secondly, because the 1-ha fragment selected was surrounded by pasture in its four sides when the study was initiated which ensured complete isolation; thirdly, because secondary forests dominated by *Vismia* spp. appear to limit seedling establishment (Mesquita *et al.* 2001); and finally, because reserve no. 1501 is considered as the control (undisturbed) forest area in the BDFFP. Distances among study sites varied between 0.3 and 40 km (Benítez-Malvido & Martínez-Ramos 2003).

Three species of seedlings from the Sapotaceae were used in the experiment: *Pouteria caimito* (Ruiz & Pavón) Radlkofer, *Chrysophyllum pomiferum* (Eyma) T. D. Pennington, and *Micropholis venulosa* (Martius & Eichler) Pierre (Pennington 1990). The species were selected on the basis of seed availability at the time of the study and because the Sapotaceae are the family with the most species and individuals in the study region (Rankin de Merona *et al.* 1990, T. D. Pennington, pers. comm.). The species are native to the study area and are considered as large-seeded (> 0.1 g dry mass, Foster 1982, Garwood 1983), recalcitrant, long-lived, old-growth forest canopy tree species (Benítez-Malvido 1995, Benítez-Malvido &

Table 1. Mean values (± SE) of environmental factors and their (range) at four contrasting tropical habitats. Herbivory levels on percentage of leaf area removed are given for each seedling species, CP = *Chrysophyllum pomiferum*; MV = *Micropholis venulosa*; and PC = *Pouteria caimito*; whereas PAR = Photosynthetic active radiation and LSC = litter standing crop for each habitat. Temperature indicates the maximum and minimum values recorded in each habitat in a 6-mo period (Benítez-Malvido, unpubl. data).

				Herbivory (%)		
Habitat	Temperature (°C)	PAR (%)	LSC (kg m^{-2})	CP	MV	PC
Old-growth forest	28.8–23.6	3.8 ± 1.2 (0.37–19.9)	1.8 ± 0.2 (4.2–39.2)	7.1 ± 1.4 (1.5–26.8)	21.4 ± 4.6 (0.0–64.5)	31.8 ± 4.3 (12.5–75.0)
1-ha fragment	31.2–20.5	2.0 ± 0.4 (0.7–6.9)	1.8 ± 0.1 (2.4–32.6)	5.8 ± 0.9 (0.0–16.2)	4.4 ± 1.6 (0.0–25.6)	15.9 ± 2.5 (10.6–45.2)
Secondary forest	34.2–23.3	15.5 ± 3.4 (1.2–54.9)	1.8 ± 0.1 (2.9–36.8)	10.1 ± 4.1 (1.9–75.0)	2.8 ± 0.9 (0.0–17.1)	11.0 ± 1.5 (0.4–22.4)
Pasture	46.3–20.3	75.6 ± 2.8 (53.1–94.1)	1.0 ± 0.04 (1.2–13.2)	3.1 ± 1.2 (0.0–20.3)	0.9 ± 0.3 (0.36–2.9)	2.3 ± 0.3 (0.6–5.5)

Kossmann-Ferraz 1999, Pennington 1990, Ribeiro *et al.* 1999). Mean seed length and dry mass weight declined from *Pouteria* (4.0 cm, 2.3 g), to *Chrysophyllum* (1.8 cm, 0.5 g), to *Micropholis* (1.7 cm, 0.4 g). Details on seed collection and sowing are given in Benítez-Malvido & Kossmann-Ferraz (1999).

Experimental design

In each habitat we placed 20, 1-m^2 plots arranged in a stratified random manner; with four plots located along each of five 100-m-long parallel transects. To assess seedling performance, in each habitat we planted the seedlings of the three species at random positions within the 1-m^2 plots (20 cm apart). Randomization was introduced by construction of a grid with 20-cm subdivisions; location of each seedling was chosen by random draw. To prevent above-ground interference with the transplanted seedlings and to have the same number of replicates per plot, all the naturally occurring seedlings present on each plot were removed by hand before transplantation.

A total of 13 seedlings per plot were planted at each habitat as follows: *Chrysophyllum*, $n = 3$; *Micropholis*, $n = 5$; and *Pouteria*, $n = 5$. This gave a total of 1040 seedling transplants, at a density of 260 per habitat. Sample sizes changed as time elapsed and seedlings died. Dead seedlings were not replaced. Because of differences in the fruiting phenology of the study species, seeds of these species were not available simultaneously. Hence seedling species were transplanted at different times. Seedlings of *Pouteria* were planted in January 1992, those of *Chrysophyllum* during March 1992, whereas those of *Micropholis* in May 1992. All species were planted during the rainy season. Apparently, habitat type rather than transplantation affected seedling performance because 2 mo after transplanting seedlings from the three species had ≥ 90% survival in all habitats except for *C. pomiferum* (70%) and *M. venulosa* (57%) in pasture (J. Benítez-Malvido, unpubl. data). All seedlings were measured for height to the nearest mm (length from the ground to the stem apex) and the number of leaves counted previous to transplantation. Initial seedling mean height (± SE) and leaf number (± SE) per species were *Chrysophyllum*, 7.4 (± 0.6) cm and 2.7 (± 0.5) leaves; *Micropholis* 14.7 (± 1.9) cm and 15.2 (± 6.3) leaves; and *Pouteria*, 15.3 (± 2.3) cm and 7.9 (± 1.8) leaves, respectively.

Environmental variables

One year after transplantation, we collected information on several environmental variables that are known to affect seedling performance in tropical rain forests and that are strongly modify with habitat disturbance: insect herbivory, photosynthetic active radiation (% PAR), litter standing crop (LSC) and temperature at the soil level (Table 1). Estimates of the standing levels of herbivory were determined visually. Leaves of all seedlings were assigned to one of the following categories of damage: 0 = intact; 1 = 1–6%; 2 = 6–12%; 3 = 12–25%; 4 = 25–50%; 5 = 50–100%. Living seedlings that were completely defoliated were assigned to category 5. The score for each leaf was used to define an index of damage (*ID*) per plant as:

$$ID = \sum_{i=1}^{5} n_i(C_i)/N$$

Where i is the category of damage, n_i is the number of leaves in the ith category of damage, C_i is the midpoint of each category (i.e. $C_1 = 3.5\%$, $C_2 = 9.0\%$, $C_3 = 18.5\%$, $C_4 = 37.5\%$, $C_5 = 75.0\%$), and N is the total number of leaves on the plant (Benítez-Malvido & Kossmann-Ferraz 1999, García-Guzmán & Dirzo 2001, Morrow 1984). Values are expressed as a weighted average of the percentage of leaf area damaged per seedling. Photosynthetic active radiation was measured

0.5 m above each plot where the seedlings were planted. Measurements were taken using a Sunfleck Ceptometer (Decagon Devices Inc. 1989). Fine-litter standing crop (LSC) consisting of leaves, branches (< 2 cm diameter) small woody material, unidentifiable organic matter and reproductive structures, lying on the forest floor, was measured per plot in the four habitats. Maximum and minimum temperature values were recorded per habitat type over a 6-mo period (Table 1). Detailed information of the methods used to collect data on PAR and LSC can be found in Benítez-Malvido (1995).

Seedling performance

One year after transplantation (January 1993 for *P. caimito*, March 1993 for *C. pomiferum* and May 1993 for *M. venulosa*) we recorded seedling performance in terms of survival, relative growth rates in height (RGR_H) and number of leaves (RGR_L) following Hunt (1990). RGR_H was calculated as: $RGR_H = (\log H_{t2} - \log H_{t1})/(t_2 - t_1)$, where: H_{t1} = height at t_1; H_{t2} = height at t_2; t_1 = time of the first height measurement and t_2 = time of the second height measurement (1 y). RGR_L was obtained as $RGR_L = (L_{t2} - L_{t1})/L_t\ (t_2 - t_1)$, where: L_{t1} = number of leaves at t_1; L_{t2} = number of leaves at t_2; t_1 = time of the first leaf count and t_2 = time of the second leaf count (1 y).

Statistical analysis

Because seedlings of the three species were not transplanted at the same time, leading to potential different responses, each species was analysed separately. To test for the effects of initial seedling size (in terms of height and leaf number) and the influence of environmental variability across habitats (LSC, PAR and herbivory) on performance we used a multiple regression analysis. We used survival and relative growth rates (RGR_H, RGR_L) as response variables, and initial seedling size and environmental variables as regression factors.

We used a logistic link function for the case of survival, analysed as a binary response variable (Crawley 1993). For relative growth rates we used a normal error. The proportion of leaf area damaged by herbivores and PAR were arcsine-square-root transformed; leaf-numbers and LSC values were log $(x + 1)$-transformed, prior to analysis (Sokal & Rohlf 1998). Following a parsimonious criterion, in those cases in which a term was found to be insignificant it was removed from the model. All data were analysed through generalized linear models using the Data Desk statistical program. To handle pseudoreplication (*sensu* Hurlbert 1984), we treated each 1-m^2 plot as a replicate by averaging initial height and leaf number, and the resulting RGR_H, RGR_L and levels of seedling herbivory (Crawley 1993). Significance was set at the 0.05 level.

RESULTS

Patterns of species performance and herbivory

Each species showed a different response to the environmental variability present within and among habitats. Seedling performance of *Chrysophyllum* was enhanced in shaded conditions, seedlings of *Micropholis* performed better in intermediate light regimes; whereas those of *Pouteria* performed better in brighter conditions. Herbivory was highest in old-growth forest for *Micropholis* and *Pouteria*, whereas for *Chrysophyllum* herbivory was higher in the secondary forest than in any other habitat. Differences in herbivory levels among habitats, however, were much lower (three times difference among extremes) in *Chrysophyllum* than in the other species (two to three orders of magnitude difference, cf. Table 1).

Survival across habitats in *Chrysophyllum* ranged between 25–90%; in *Micropholis* between 17–81%; and in *Pouteria* between 45–73%. Species showed a positive RGR_H under all conditions except for *Pouteria* in the old-growth forest with no RGR_H after 1 y. For all species RGR_H was greater under high PAR. The range across habitats of absolute increases (mean) in height was: *Chrysophyllum*, 2.7–5.0 cm; *Micropholis*, 0.7–6.9 cm; and *Pouteria*, 0.25–8.4 cm. Seedlings of *Chrysophyllum* showed a positive RGR_L under all conditions; whereas those of *Micropholis* and *Pouteria* lost leaves under shade. The range across habitats of absolute (mean) increases in leaf numbers was: *Chrysophyllum*, 2.8–10.6 leaves; *Micropholis*, −4.8–58.5 leaves; and *Pouteria*, −4–14.4 leaves. Under very high PAR, seedlings from all species replaced their leaves with numerous tiny leaves. Seedlings of *Pouteria* gained leaves only under very high PAR.

Initial seedling size, environmental variability and performance

Overall, initial seedling size, PAR and levels of herbivory differently affected seedling performance; whereas no effect of LSC was observed for any species. The magnitude of the effects varied according to species and the environmental variable considered.

Seedling survival

For *Chrysophyllum*, larger seedlings growing under high PAR resulted in significantly lower proportion of survivors (Table 2). Seedlings of *Chrysophyllum* survived better at incident PAR values under *c.* 20% (Figure 1), whereas for *Pouteria* larger seedlings also resulted

Table 2. *F* values from multiple regression analysis for the effects of initial seedling size and environmental variability on seedling performance after 1 y for three seedlings species transplanted into contrasting habitats north of Manaus, Brazil. Data were analysed with generalized linear models.

	Chrysophyllum pomiferum	*Micropholis venulosa*	*Pouteria caimito*
Survival			
Constant	14.8***	4.4*	9.9**
	(1, 71)	(1, 62)	(1, 74)
Initial height	5.0*	NS	5.4*
Herbivory	NS	5.9*	NS
PAR	15.7***	4.6*	NS
Relative growth rate in height			
Constant	419.2***	85.9***	28.6***
	(1, 71)	(1, 62)	(1, 74)
Initial height	12.2**	10.7**	8.8**
Herbivory	NS	14.1**	NS
PAR	4.9*	5.0*	17.8***
Relative growth rate in number of leaves			
Constant	63.0***	26.5***	NS
	(1,71)	(1,62)	(1, 74)
Initial leaf number	NS	4.8*	NS
Initial height	NS	NS	4.8*
Herbivory	5.8*	5.6*	17.5***
PAR	40.0***	NS	14.6**

Numbers in parentheses are degrees of freedom (same for all variables) $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, NS = non-significant. Interaction effects were non-significant in all cases.

in a lower proportion of survivors but no effect of PAR or herbivory was observed (Table 2, Figure 1). In *Micropholis*, increasing herbivory and high PAR resulted in lower proportion of survivors (Table 2), and no seedling survived at *c.* 50% defoliation regardless of PAR availability (Figure 1).

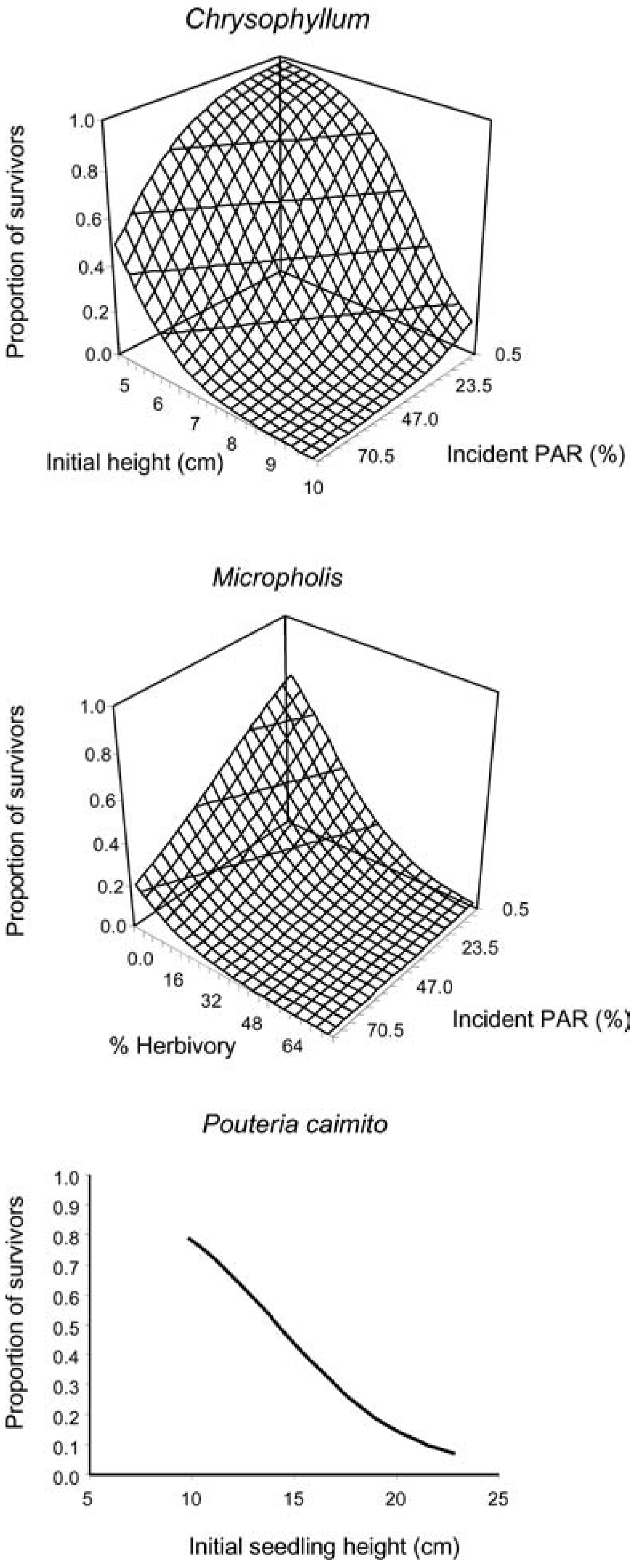

Figure 1. Logistic regressions for the effects of initial seedling height, percentage of leaf area damaged by herbivory and photosynthetic active radiation (% PAR) on seedling survival 1 y after being transplanted into contrasting tropical habitats north of Manaus, Brazil. Survival in *Pouteria* was only affected by initial height, whereas survival for *Chrysophyllum* and *Micropholis* was affected by different factors.

Seedling growth

For seedlings of *Chrysophyllum* and *Pouteria* initial height and PAR significantly affected RGR_H (Table 2). Small seedlings under high PAR had greater RGR_H than larger seedlings. The effect of initial height and PAR on RGR_H was greater for *Pouteria* (Figure 2). In contrast, for *Micropholis* taller seedlings under high PAR resulted in slightly greater RGR_H than small seedlings (Table 2). Furthermore, greater herbivory in *Micropholis* seedlings growing under low PAR resulted in lower RGR_H (Figure 2).

Initial number of leaves and herbivory affected RGR_L for *Micropholis* and *Pouteria* (Table 2). For both species, seedlings with initial greater number of leaves and greater herbivory showed lower RGR_L (Figure 3). For *Pouteria* RGR_L was also affected by initial height. Large seedlings growing under low PAR showed lower RGR_L than

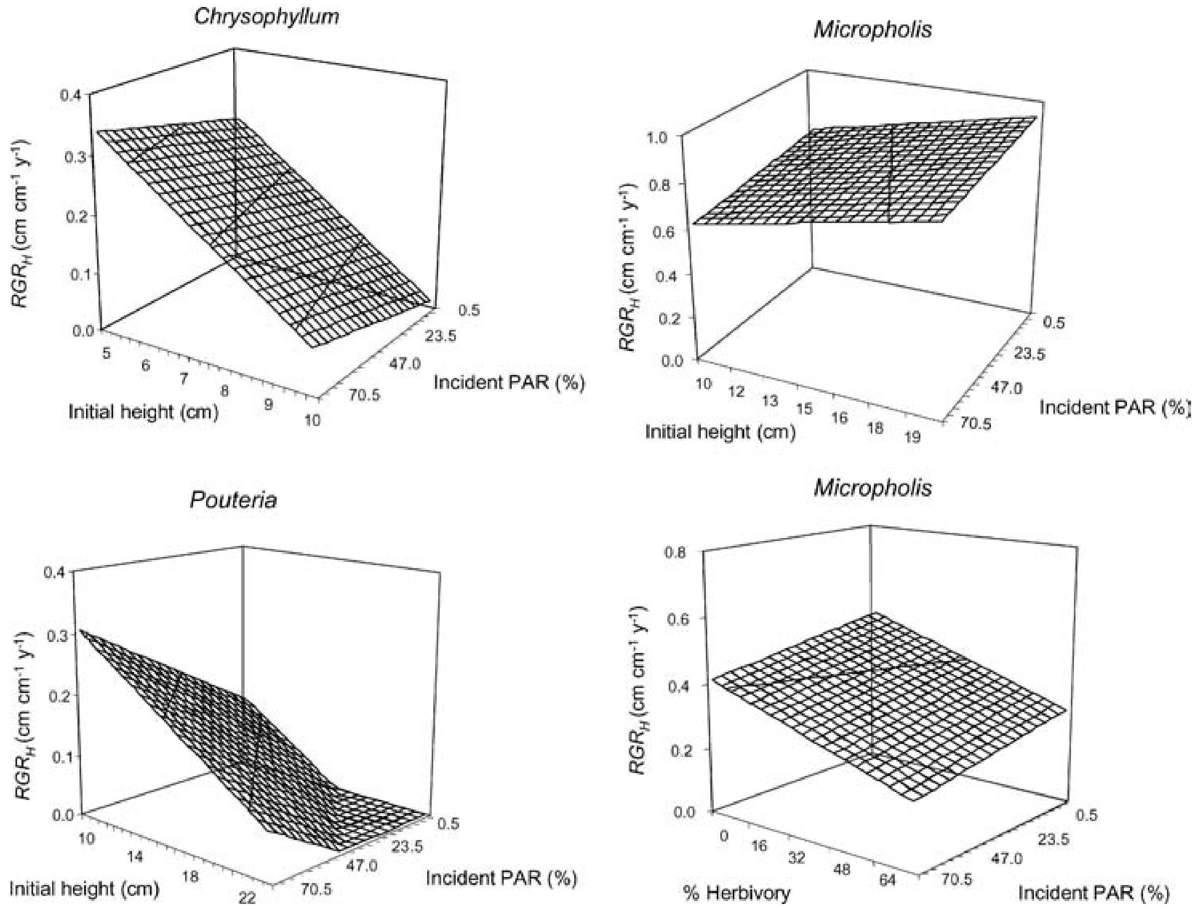

Figure 2. Best-fit linear regressions for the effects of initial seedling size, percentage of leaf area damaged by herbivory and photosynthetic active radiation (% PAR) on relative growth rate in height (RGR_H) after 1 y. Seedling species were transplanted into contrasting tropical habitats north of Manaus, Brazil, that differed in PAR and herbivory levels. Only significant relationships between different factors and RGR_H are shown.

small seedlings under high PAR (Figure 3). Herbivory and PAR significantly affected seedling performance according to species (Table 2). In *Chrysophyllum* and *Pouteria* greater herbivory and low PAR resulted in lower RGR_L (Figure 4). Seedlings of *Chrysophyllum* were very sensitive to defoliation, as at *c.* 25% of leaf area damaged by herbivores under low PAR no new leaves were produced (Figure 4).

DISCUSSION

Overall, our data showed that being a large seedling does not necessarily confer an advantage over smaller seedlings for successful establishment. Furthermore, the variability in the understorey environment (PAR and herbivory) strongly affected the performance of the seedling transplants. The effects of PAR and herbivory on seedling performance were species specific, which indicates that seedlings with similar ecological attributes (large seeds and shade tolerance) cope differently with the constraints imposed by the environment.

Initial seedling size and performance

Studies in naturally occurring seedling populations show that size plays an important role in differential survivorship from very early in the life cycle of plants (Paz & Martínez-Ramos 2003, Paz *et al.* 1999, Sarukhán *et al.* 1984). Larger seedlings may have greater vigour and hence tolerance for physical and biotic mortality risks (Gross 1984, Sarukhán *et al.* 1984), and are able to tolerate extreme conditions for longer periods than small seedlings (Gray & Spies 1997). Generally larger seed/seedlings confer survival advantages to seedlings in light-limited environments but less often in habitats that are not light limited (Kobe 1999, Paz & Martínez-Ramos 2003, Paz *et al.* 1999). Larger seedlings of *Chrysophyllum* and *Pouteria* transplanted from the nursery to the different habitats sustained greater mortality. Mortality risks of large seedlings in *Chrysophyllum* were exacerbated under high PAR. Seedlings of *Chrysophyllum* have been shown to thrive under the shaded conditions for more than 10 years (J. Benítez-Malvido, unpubl. data), and over saturation by

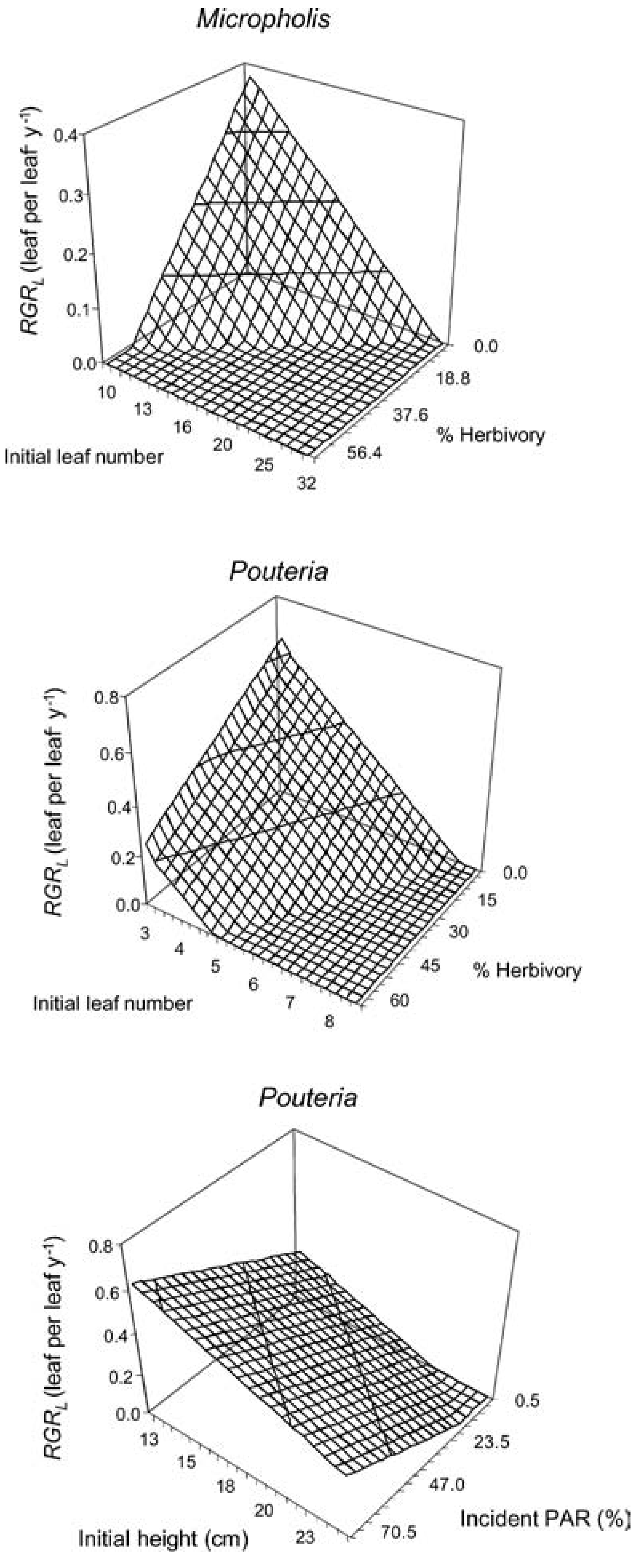

Figure 3. Best-fit linear regressions for the effects of initial seedling size, percentage of leaf area damaged by herbivory and photosynthetically active radiation (% PAR) on relative growth rate in leaf number (RGR_L) after 1 y. Seedling species were transplanted into contrasting tropical habitats north of Manaus, Brazil. Only significant relationships between different factors and RGR_L are shown.

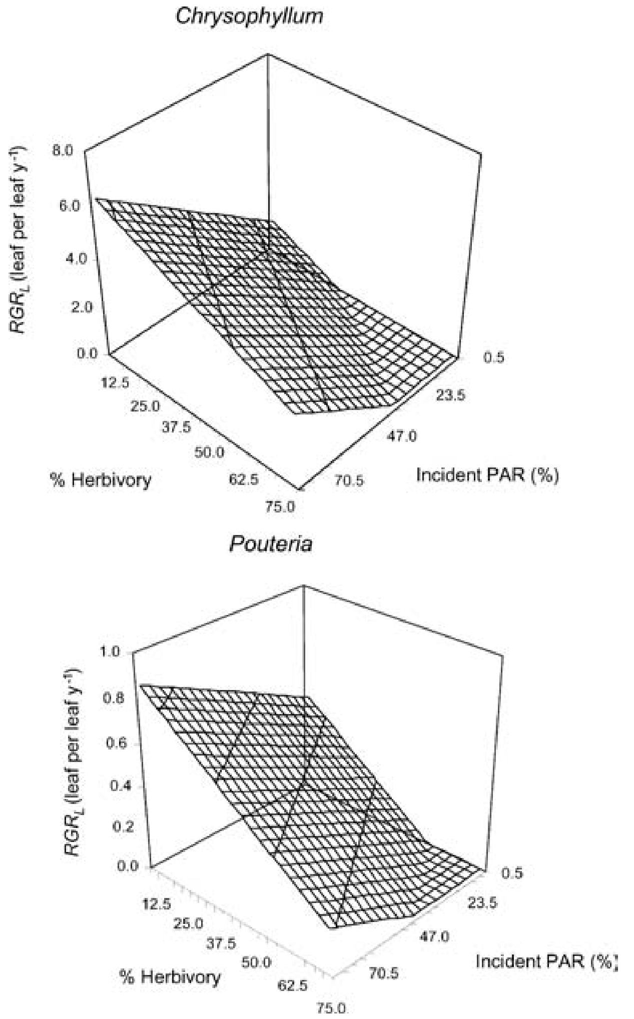

Figure 4. Best-fit linear regressions for the effects of percentage of leaf area damaged by herbivory and photosynthetic active radiation (% PAR) on relative growth rate in leaf number (RGR_L) after 1 y. Seedling species were transplanted into contrasting tropical habitats north of Manaus, Brazil. Only significant relationships between different factors and RGR_L are shown.

light and its interaction with high temperatures and imbalanced water relations may be lethal.

Seedlings growing in low-light environments tend to gain less biomass and to invest less in roots than seedlings growing in high-light conditions (Popma & Bongers 1988). For example, seedlings in large canopy gaps of the canopy tree species *Cordia megalantha* grew larger and invested about 40% in roots while others of the same cohort in the shaded understorey attained smaller sizes and invested half as much biomass in roots (Bongers *et al.* 1988). We do not know whether or not, and to what extent, the planting process (transplant shock) affected seedling performance according to the size-dependent root/shoot ratios (Bloor 2003, Khan & Tripathi 1989) or other aspects of plant physiology. Larger seedlings may be more susceptible to damage during transplanting – notably in the root systems. Larger seedlings under shaded conditions also showed decreased RGR_L in *Pouteria*. Leaves are energy-gaining organs (Kikuzawa 1995) hence leaf-loss could have resulted in seedlings unable to cope with the constraints imposed by limited environmental conditions (e.g. extreme shade) causing high mortality.

Our results for *Chrysophyllum* and *Pouteria* support the concept of a negative relationship between seedling size and RGR_H (Marañon & Grubb 1993, Paz & Martínez-Ramos 2003). Such relationship can be partially explained by large seedlings having relatively low light capture area per unit mass of phostosynthetic tissue (Kitajima 1994, Paz & Martínez-Ramos 2003, Paz *et al.* 1999). There was evidence that larger seedlings had higher RGR_H for *Micropholis*, which probably resulted from etiolation (H. Paz, pers. comm.).

Environmental variability and seedling performance

All species had to acclimate to the new environment to which they were transplanted. Seedlings were grown under the same conditions (intermediate light (*c.* 15% PAR), soil type, moisture and temperature) in the nursery and they were at the same developmental stage (3–4 mo old) when transplanted. These two features are important for comparisons among species (Kitajima 1994). Nevertheless, seedlings required physiological adaptations to the stresses imposed by the environmental conditions of the different habitats.

The extreme high temperature, low atmospheric humidity and low soil moisture in pasture fell outside the range of conditions that occurred in the natural forest (Table 1). These conditions in pasture might cause limitations for acclimation of *Chrysophyllum* and *Micropholis*, which was expressed in greater mortality levels than in the other habitats (Ashton & Berlyn 1992, Robinchaux *et al.* 1984, Strauss-Debenedetti & Bazzaz 1991). Nevertheless, *Chrysophyllum* showed acclimation to a wider range of environmental conditions which resulted in greater overall survival. Conversely, *Pouteria* thrived in the high light environment of the pasture, independently of initial seedling size. Seedling species with larger seeds, such as *Pouteria*, have been shown to better tolerate the extreme conditions in pastures and open areas. It has been suggested that large-seeded species should be sown directly into degraded areas for rehabilitation purposes in the central Amazon (Camargo *et al.* 2002). What is interesting, however, is the relative low survival exhibited by *Pouteria* in the forested habitats. It is likely that large seedling species with cotyledons functioning as storage organs, rich in resources, as is the case of *Pouteria* but not of the other two study species (Benítez-Malvido & Kossmann-Ferraz 1999), are under higher risk of being damaged by animals that eat roots, the stem base or the cotyledons. Whether such herbivory risk was lower for *Pouteria* in pasture than in the other habitats is an open question.

For all species, herbivory had a negative effect on performance, whereas PAR had a positive, negative or neutral role on seedling performance. The results suggest that canopy tree species at the seedling stage differed in their light demands, and that there can be excessive light levels for forest seedlings of some species (*Pouteria*). The variation we observed among species in their relationships with light and herbivory might have resulted from the interactions with other ecological factors. Factors such as physical damage (Clark & Clark 1989), pathogens (Gilbert 2002), competition and interference with other plants (Ganade & Brown 2002), soil fertility (Vitousek & Sanford 1986), cotyledon, root and stem damage by animals, and mycorrhizas (Janos 1980) have been mentioned as important ecological forces. The nature and magnitude of such factors may be habitat and species specific. For example in pasture, secondary forest and in the forest fragment mycorrhizal associations might be affected; in pasture and secondary forest, seedlings may struggle with strong competitors such as grasses and clonal *Vismia* individuals; whereas in old-growth forest lower survival within plots with greater PAR might have resulted from canopy openings that killed all seedlings (J. Benítez-Malvido, pers. obs.), and from seedlings being exposed to a more diverse and abundant number of predators (herbivores and pathogens) than in the other habitats (Benítez-Malvido 2001).

Overall, our study showed that species characteristics such as seed size, seedling size and initial seedling morphology might not provide complete information to predict the performance of planted species into different habitat types. Each species presented specific requirements for successful establishment and showed specific responses to the constraints imposed by the physical and biological environment. Finally, understanding the responses of several native tree species to disturbances caused by human activities is an important component of the efforts to manage and restore tropical forests.

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