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Acclimation of seedlings of three Mexican tropical rain forest tree species to a change in light availability*

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ABSTRACT. A comparison is made of the light acclimation potential of seedlings of three canopy species of the tropical rain forest of Los Tuxtlas, Mexico: *Cordia megalantha*, *Lonchocarpus guatemalensis*, and *Omphalea oleifera*. These species showed similar growth rates in a range of microhabitats. Gap dynamics were simulated by transferring plants between three environments: beneath a closed canopy, a small gap, and a large gap. Plants of all three species were able to adjust their morphology and growth rates in response to changes in light availability. Growth rates increased when plants were moved to a (larger) gap, and decreased when plants were moved to a more shaded environment. Shade-grown plants were able to acclimate faster to increasing light availability than sun-grown plants to decreasing light availability. Also, plants moved from shady to sunny conditions showed higher relative growth rates than sun control plants, whereas sun-grown plants when moved to the shade showed lower relative growth rates than shade control plants. Species differed in their response to gap dynamics. *Omphalea* could not acclimate morphologically to shading, but reacted faster than the other species in response to the occurrence of a large gap. Acclimation potential seemed to be related to plasticity in physiological rather than in morphological traits. Suppressed seedlings of all three species performed well in the shade, and were able to acclimate rapidly to gap-conditions.

KEY WORDS: acclimation, biomass allocation, *Cordia megalantha*, growth, *Lonchocarpus guatemalensis*, Los Tuxtlas, Mexico, morphology, *Omphalea oleifera*, treefall gaps, tree seedlings, tropical rain forest.

INTRODUCTION

It has been hypothesized frequently that tropical rain forest tree species are differentiated ecologically in their growth response to environmental conditions associated with canopy gaps of different sizes (Bazzaz 1984, Bazzaz & Pickett 1980, Brokaw 1985, Denslow 1980, Hartshorn 1980, Pickett 1983, Whitmore

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1982, 1984). Treefall gaps cause environmental heterogeneity on a time scale which is small in comparison to the potential life span of a tropical rain forest tree (cf. Brokaw 1985, Lieberman *et al.* 1985). This makes the potential to acclimate to a continually varying environment a necessity. The effect of a canopy gap on micro-environment will be most pronounced in the shaded forest understorey (Chazdon & Fetcher 1984). If a differentiation in growth response to gap conditions exists among species, it is expected to be most pronounced during early stages of their life cycle (i.e. germination, seedling establishment and growth).

Early successional (pioneer) species only occur in gaps. These species often *have dormant seeds which germinate in large gaps only, as a result of high* temperature, high light intensity, or high red/far-red ratio of incident light (Vázquez-Yanes & Orozco-Segovia 1984). Most species, however, are shade-tolerant to some extent (i.e. non-pioneers), as they grow or survive below a closed canopy as well (85% of the species in a 1 ha plot of mature rain forest in Los Tuxtlas are non-pioneer and 15% pioneer, Bongers *et al.* 1988a). Their seeds show either a short dormancy till the next rainy season, or no dormancy at all, resulting in rapid germination after dispersal (Garwood 1983, Ng 1978, Whitmore 1984). Depending on the efficiency of dispersal and the amount of seeds produced, more or less well-developed seedling banks are formed (Schulz 1960, Whitmore 1984). For these species, growth response to different levels of light availability may be an important factor determining establishment and survival probabilities.

In an earlier paper Popma & Bongers (1988) demonstrated that seedling growth of 10 species, covering a range from large gap pioneers to shade tolerant understorey species, was enhanced even in very small gaps, in comparison with shaded forest understorey. Also, it was found that the pioneer species *Cecropia obtusifolia* Bertol. maintained a high relative growth rate at high light availability because of its relatively high leaf area ratio. Shade tolerant species on the other hand were able to grow well in all conditions because they possessed a higher unit leaf rate in the shade as well as in gaps of different sizes. However, 6 out of 10 species investigated did not show a clear shade tolerant or pioneer species type of response. In the three environments studied, these species had intermediate growth rates.

Acclimation to a change in light availability (either increase or decrease) will be directed towards maximizing the total plant carbon gain in the changed environment. This may be achieved in two ways, which can operate simultaneously: (a) a change in carbon exchange properties of leaves, which involves physiological as well as morphological adjustments in newly formed and possibly also in existing leaves, and (b) a change in overall plant architecture leading to an adjustment of the ratio of photosynthesizing v. non-photosynthesizing tissues, which involves changing biomass allocation patterns.

In this paper the acclimation of seedlings of three tropical rain forest canopy species to experimentally simulated gap dynamics will be evaluated. Our hypothesis is that the three species are differentiated in their acclimation potential

to gap-associated environmental heterogeneity rather than in their growth response to different environments. The question is whether these species with similar biomass growth rates differ in the relative importance of both acclimation processes, in the magnitude of adjustments effected and in the rate at which adjustments take place. Another question is whether acclimation differs in relation to both the magnitude of change in light availability (i.e. to gap size), and in relation to the sign of this change (i.e. increasing or decreasing light availability).

STUDY SITE AND SPECIES

This study was carried out at the biological station 'Los Tuxtlas', Mexico (18° 35′ N, 95° 07′ W). The station is situated in a tropical rain forest reserve on volcanic soil. Mean annual rainfall is 4639 mm, and mean annual temperature is 24.6°C (data from Coyame, 35 km from the station). The structure, dynamics, and floristic composition of the forest have been described elsewhere (Bongers *et al.* 1988a, Popma *et al.* 1988). The species studied are *Cordia megalantha* Blake (Boraginaceae), *Lonchocarpus guatemalensis* Benth. (Leguminosae), and *Omphalea oleifera* Hemsl. (Euphorbiaceae). These are canopy tree species, and when mature reach a height of 30–35 m. Adult densities are low (around 1–3 ha^{-1}, Bongers *et al.* 1988a). All three species show a rapid germination of their seeds after dispersal, and often dense carpets of seedlings can be found under mature trees after seed release. Seedlings of these species were found to be able to grow below a closed canopy, although very slowly. Gaps enhanced growth, and all three species were able to grow well in a large gap. Growth rates were intermediate when compared with a range of species in all three conditions (i.e. forest understorey, small gap and large gap) studied by Popma & Bongers (1988). The study species were remarkably similar in their growth response (in terms of biomass growth rate) to gaps of different sizes.

METHODS

In June 1983, recently emerged *Cordia* seedlings were collected below a parent tree isolated from conspecifics. They were transplanted to plastic bags filled with c. 2 l of homogenized forest soil and kept in a moderately shaded greenhouse until the start of the experiment. The 'start' sample was taken when plants were large enough (when at least two leaves developed above the cotyledons) and the remains of attached seeds had fallen off. The same was done for *Lonchocarpus* and *Omphalea*, except that plants were raised from fresh seeds from the same parent tree.

In December 1983, 300 individuals of both *Cordia* and *Lonchocarpus*, and 200 of *Omphalea* were randomly divided between three mosquito cloth greenhouses which were constructed at different sites: in the mature forest understorey, below a closed canopy (FU), in a small (50 m²) gap with c. one hour of direct insolation daily (SG), and in a large gap with nearly seven hours of insolation daily (LG).

The large gap was actually a roadside clearing, similar to a gap of c. 500 m². Relative Daily Photosynthetic Photon Flux (DPPF) received in the three conditions ranged from 0.9% to 2.3% of the above canopy total in FU, from 2.1% to 6.1% in SG, and from 38.6% to 53.4% in LG (Bongers *et al.* 1988b). No clear change in light level over the season occurred. During the dry season (March–May) plants were watered every other day. No extra nutrients were added. The mosquito cloth served well in excluding most insect herbivores. However when signs of herbivory were detected, plants were immediately sprayed with insecticide. Damaged plants (due to either herbivore action or to manipulations) were excluded from further analyses. The greenhouse mosquito cloth hardly affected the light quality. Red/far-red ratio inside and outside the greenhouse was the same in FU and LG and slightly lowered in SG (cf. Bongers *et al.* 1988b).

Plants were harvested at t = 0, 81, 162, 237, and 345 days (except for *Omphalea*, no harvest at t = 345 days). At t = 162 days one-third of the individuals from each greenhouse was transferred to each of the two other greenhouses. Plants which remained in the same environment are hereafter called controls. After transfer, the environment from which plants were transferred is called the previous environment, whereas the environment to which plants were transferred is called the present environment. In these terms present and previous environments are the same for control plants, while for transferred plants they are different. The whole experiment involved 66 experimental groups of usually 9 plants (range 7–12). In the case of *Omphalea* only one harvest after transfer could be taken, because not enough seedlings could be raised for two harvests. All plants were relocated regularly within each treatment to avoid possible effects of location within the greenhouse.

Harvested plants were washed free of soil. Every plant was divided into a root, stem plus petioles, and leaf fraction. Leaf area was determined with a leaf area meter (LiCor, Lincoln, Nebraska) or by drawing the leaf circumference on paper and tracing it later on a computer digitizer. Both methods for leaf area determination gave the same results. All three fractions were oven dried (24 hours at 105°C) and weighed.

From the primary dry weight and leaf area data the following parameters were derived: leaf area ratio (LAR, leaf area/total plant dry weight, $m^2 g^{-1}$), root-shoot ratio (R/S, root dry weight/stem + leaf dry weight, $g g^{-1}$) and specific leaf weight (SLW, leaf dry weight/leaf area, $g m^{-2}$). Relative biomass growth rate (RGR_w) and unit leaf rate (E) were calculated as: (Evans 1972)

$$RGR_w = \frac{\ln W(t_2) - \ln W(t_1)}{t_2 - t_1} \ in \ g g^{-1} day^{-1}$$

$$E(t_1 - t_2) = \frac{W(t_2) - W(t_1)}{t_2 - t_1} \cdot \frac{\ln A(t_2) - \ln A(t_1)}{A(t_2) - A(t_1)} \ in \ g m^{-2} day^{-1}$$

where W is plant dry weight (g), A is plant leaf area (m²) and t is time (in days).

RESULTS

Plant morphology

The development of specific patterns in plant architecture and morphology is described in Figures 1, 2 and 3. Although the species differed quantitatively in their response to the three environments, their qualitative response is the same. Differences between FU and SG control groups were small and mostly insignificant, plants in both environments showed a typical shade plant morphology with high LAR, low R/S and low SLW. Plants of the control groups growing in LG showed a different architecture and morphology: these were typical sun plants with low LAR, high R/S and high SLW.

After transfer, plant architecture and morphology changed. A change in environment had predictable effects. After 75 days the transferred groups took intermediate positions between the control group from their previous environment
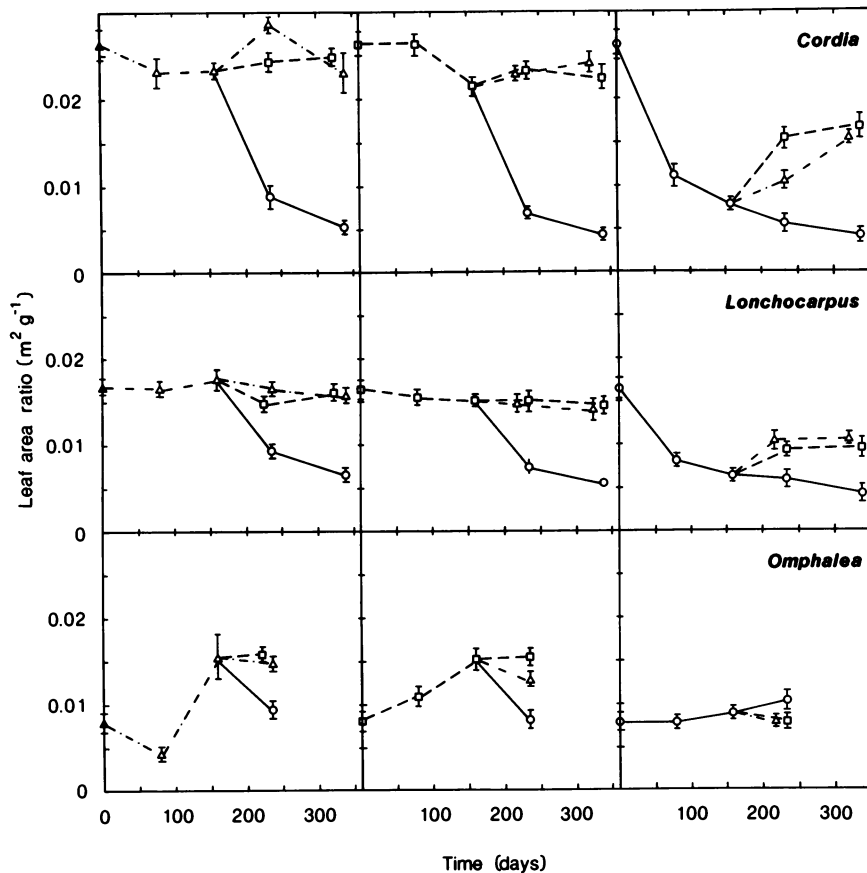
Figure 1. The effect of change in environment on leaf area ratio, LAR, of seedlings of *Cordia megalantha*, *Lonchocarpus guatemalensis* and *Omphalea oleifera*. Values are means for 7–12 plants ± SE. Line style indicates environment: –·–·– = plants growing in forest understorey (FU); – – – – = plants growing in small gap (SG); ——— = plants growing in large gap (LG). Initial growing conditions are thus: forest understorey (left panel), small gap (middle panel), large gap (right panel).

Figure 2.   The effect of change in environment on root/shoot ratio, R/S. Linestyles as in Figure 1.
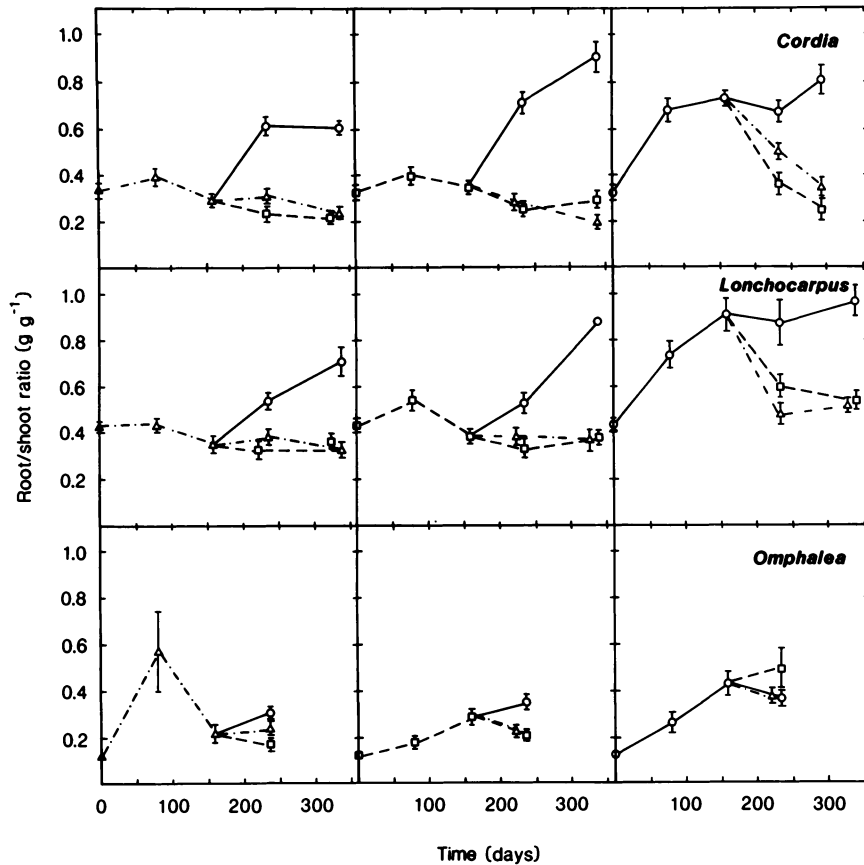
and that from their present environment. Table 1 shows that this effect was significant, i.e. in all but one case (*Omphalea* previously in LG) effects of present environment on plant morphology were highly significant at 75 days after transfer. In *Cordia* and *Lonchocarpus*, the effect of present environment remained highly significant at 183 days after the change. After 183 days the transferred groups were usually close to the control groups of the present environment. In Table 2 the significance of differences in plant morphology as a result of previous environment is presented qualitatively. The statistical significance of effects of previous environment was larger and lasted longer in present shade (FU and SG) environments than in the present sun (LG) environment. In both *Cordia* and *Lonchocarpus*, effects due to previous environment were still highly significant in the present FU and SG environments 183 days after transfer. In present LG, however, both species did not show differences in plant morphology after 183 days (except for R/S in *Cordia*). In *Omphalea* the significance of the difference between plants growing in present LG decreased more rapidly than in both other species, as 75 days after transfer only R/S showed a significant difference at the 5% level.
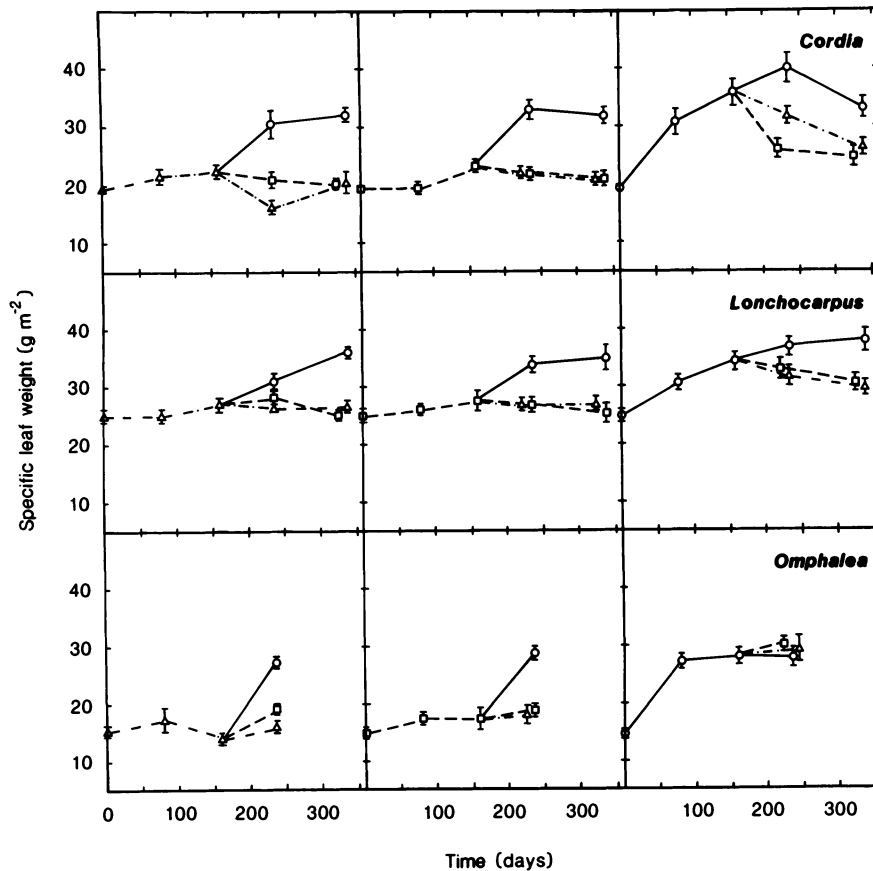
Figure 3. The effect of change in environment on specific leaf weight, SLW. Linestyles as in Figure 1.

Growth

Differences in biomass growth rate between species in SG, and also in LG, were small (Figure 4). In SG *Lonchocarpus* had the highest RGR_w and *Omphalea* the lowest. In LG *Omphalea* had the highest RGR_w, and *Lonchocarpus* the lowest. In FU differences between species were larger. *Omphalea* had the highest RGR_w, and *Cordia* had the lowest, negative, rate.

Relative growth rates (Figure 4) show consistent differences among control groups. In all species RGR_w was higher when light availability was higher. RGR_w was highest in the LG, and lowest in FU.

When plants were transferred to a more shaded environment RGR_w decreased, and increased when they were moved to a lighter condition. It is remarkable that the RGR_w of FU and SG plants moved to LG was higher than the RGR_w of the LG controls. Sun plants (LG), when transferred to FU or SG, showed a lower RGR_w than the FU and SG controls (in 4 out of 6 cases).

In Figure 4 unit leaf rate (E) and leaf area ratios (LAR) are also presented. Instantaneous RGR_w is equal to the product of instantaneous E and LAR, but when calculated over longer periods this relationship does not hold exactly

Table 1. Effects of present environment on plant morphology 75 and 183 days after a change in environment[1].

	time	t = 75 days				t = 183 days			
	present	FU	SG	LG	P	FU	SG	LG	P
Cordia previous									
	LAR m²g⁻¹	a	b	c	****	a	a	b	****
FU	R/Sg g⁻¹	b	c	a	****	b	b	a	****
	SLW g m⁻²	b	b	a	****	b	b	a	****
	LAR m²g⁻¹	a	a	b	****	a	a	b	****
SG	R/Sg g⁻¹	b	b	a	****	b	b	a	****
	SLW g m⁻²	b	b	a	****	b	b	a	****
	LAR m²g⁻¹	b	a	c	****	a	a	b	****
LG	R/Sg g⁻¹	b	c	a	****	b	b	a	****
	SLW g m⁻²	b	c	a	****	b	b	a	****
Lonchocarpus previous									
	LAR m²g⁻¹	a	a	b	****	a	a	b	****
FU	R/Sg g⁻¹	b	b	a	****	b	b	a	****
	SLW g m⁻²	b	b	a	*	b	b	a	****
	LAR m²g⁻¹	a	a	b	****	a	a	b	****
SG	R/Sg g⁻¹	b	b	a	***	b	b	a	****
	SLW g m⁻²	b	b	a	****	b	b	a	****
	LAR m²g⁻¹	a	a	b	***	a	a	b	****
LG	R/Sg g⁻¹	b	b	a	***	a	b	b	****
	SLW g m⁻²	b	b	a	*	b	b	a	***
Omphalea previous									
	LAR m²g⁻¹	a	a	b	****	–	–	–	–
FU	R/Sg g⁻¹	b	c	a	****	–	–	–	–
	SLW g m⁻²	c	b	a	****	–	–	–	–
	LAR m²g⁻¹	b	a	c	****	–	–	–	–
SG	R/Sg g⁻¹	b	b	a	****	–	–	–	–
	SLW g m⁻²	b	b	a	****	–	–	–	–
	LAR m²g⁻¹	b	b	a	*	–	–	–	–
LG	R/Sg g⁻¹	a	a	a	NS	–	–	–	–
	SLW g m⁻¹	a	a	a	NS	–	–	–	–

[1] The number of * indicates the level of significance of the effect of present environment among plants coming from the same environment (F-test, * = P < 0.05, ** = P < 0.01, *** = P < 0.001, **** = P < 0.0001, NS = not significant). Letters qualitatively indicate significant differences (a > b > c) according to Duncan's multiple range test (alpha = 0.05).

(Evans 1972). Within the pooled growth data over the first 75 days after transfer (i.e. all treatments, all species) RGR_w is highly correlated with E (r = 0.944, P < 0.0001) and weak and negatively to LAR (r = −0.48, P < 0.05). *Cordia* had the highest LAR in the shade (FU and SG), while it did not have higher growth rates than both other species in these conditions, due to the low E values. In LG, LAR of *Cordia* seedlings was similar to or lower than that of both other species.

The fact that the growth rates reported here are slightly different from those reported earlier for the same species (Popma & Bongers 1988) may be due to

Table 2. Effects of previous environment on plant morphology 75 and 183 days after a change in environment[1].

time previous		t = 75 days				t = 183 days			
		FU	SG	LG	P	FU	SG	LG	P
Cordia present									
	LAR m²g⁻¹	a	b	c	****	a	a	b	**
FU	R/S g g⁻¹	b	b	a	****	b	b	a	**
	SLW g m⁻²	c	b	a	****	b	b	a	**
	LAR m²g⁻¹	a	a	b	****	a	a	b	**
SG	R/S g g⁻¹	b	b	a	***	b	a	a	**
	SLW g m⁻²	b	b	a	**	b	b	a	**
	LAR m²g⁻¹	a	a/b	b	*	a	a	a	ns
LG	R/S g g⁻¹	a	a	a	ns	b	a	a	**
	SLW g m⁻²	b	b	a	*	a	a	a	ns
Lonchocarpus present									
	LAR m²g⁻¹	a	a	b	****	a	a	b	****
FU	R/S g g⁻¹	b	b	a	****	b	b	a	****
	SLW g m⁻²	b	b	a	****	b	b	a	****
	LAR m²g⁻¹	a	a	b	****	a	a	b	****
SG	R/S g g⁻¹	b	b	a	****	b	b	a	****
	SLW g m⁻²	b	b	a	****	b	b	a	****
	LAR m²g⁻¹	a	b	b	**	a	a	a	ns
LG	R/S g g⁻¹	b	b	a	**	a	a	a	ns
	SLW g m⁻²	b	a/b	a	**	a	a	a	ns
Omphalea present									
	LAR m²g⁻¹	a	b	c	****	–	–	–	–
FU	R/S g g⁻¹	b	b	a	****	–	–	–	–
	SLW g m⁻²	b	b	a	****	–	–	–	–
	LAR m²g⁻¹	a	a	b	****	–	–	–	–
SG	R/S g g⁻¹	b	b	a	***	–	–	–	–
	SLW g m⁻²	b	b	a	****	–	–	–	–
	LAR m²g⁻¹	a	a	a	NS	–	–	–	–
LG	R/S g g⁻¹	b	a	a	*	–	–	–	–
	SLW g m⁻¹	a	a	a	NS	–	–	–	–

[1] The number of * indicates the level of significance of the effect of previous environment among plants presently growing in the same environment (F-test, * = P < 0.05, ** = P < 0.01, *** = P < 0.001, **** = P < 0.0001, NS = not significant). Letters qualitatively indicate significant differences (a > b > c) according to Duncan's multiple range test (alpha = 0.05).

the fact that growth rates are calculated here over a shorter period, and for older plants. RGR_w may be expected to decrease with age and/or size (Evans 1972).

DISCUSSION

Plant morphology

A significant acclimation occurred in all three species in terms of plant architecture and morphology, as demonstrated by the ANOVA with present environment as main effect (Table 1). In both *Cordia* and *Lonchocarpus* plants from any one of the three treatments showed significant differences in LAR, R/S,
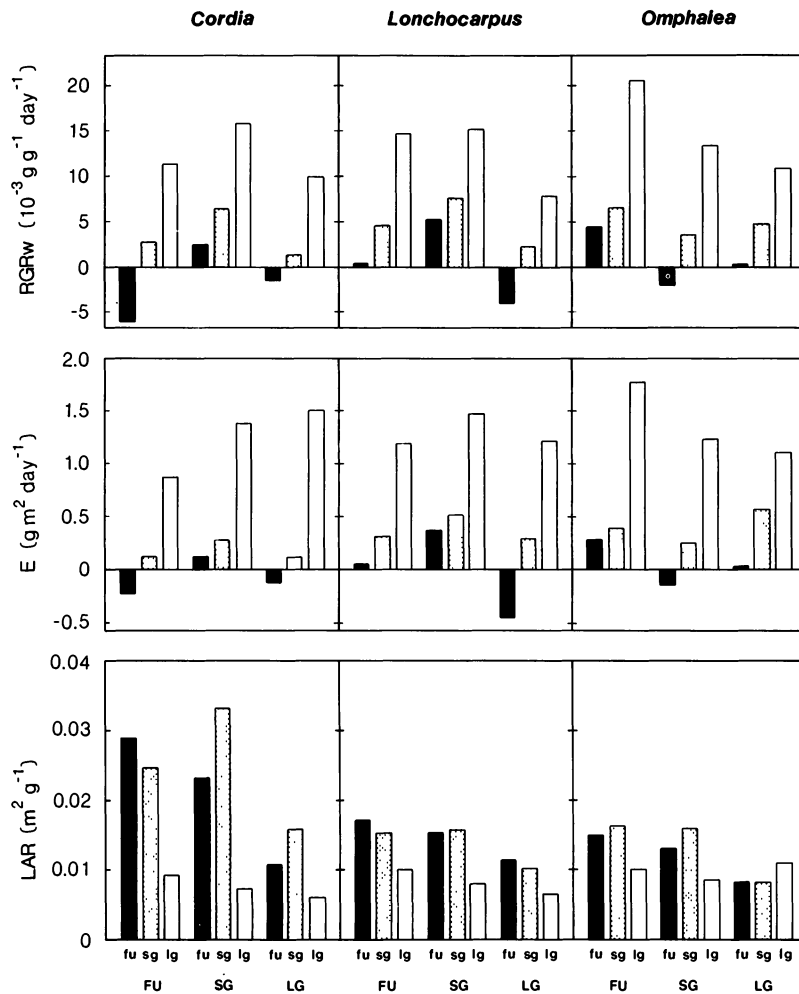
Figure 4. Effect of change in environment on growth parameters: (a) Relative growth rate, RGR_w, (b) Unit leaf rate, E, and (c) Leaf area ratio, LAR. Values are calculated over the first 75 days after transfer of the seedlings. The order of experimental treatments is indicated below the figure; upper row represents present environment, lower row previous environment. Dark bars represent plants harvested in FU, grey bars plants harvested in SG, and open bars plants harvested in LG.

and SLW due to effects of the present environment. Plants responded to either increasing and decreasing light availability by changing their architecture and morphology. The change was always directed from the morphology of previous environment controls towards that of the present environment controls. In *Omphalea*, on the other hand, morphological acclimation only occurred in response to a large increase, and not to a decrease, in light availability.

Acclimation to an increase in light availability was faster than acclimation to a decrease. Plants transferred from FU or from SG to LG acclimated rapidly to their new environment, as was shown by the ANOVA with previous environment as main effect. At 183 days after a change no or only weakly significant effects

due to previous environment could be detected among plants in LG, as far as architecture and morphology were concerned. Plants transferred from LG to SG or FU on the other hand were still architecturally and morphologically different from SG and FU controls respectively.

Thus, shade grown plants were able to acclimate rapidly to sun conditions, while in the reverse case (shading) acclimation was only slow (*Cordia, Lonchocarpus*) or possibly even absent (*Omphalea*). Availability of assimilates may be insufficient to change morphology due to low productivity in the more shaded environment. This relatively low productivity could be due to several reasons, e.g. inadequate leaves or a large proportion of non-photosynthesizing but respiring tissues. This suggests that acclimation potential is related directly to net production of assimilates after a change in environment has occurred, and to biomass allocation pattern at the time of change.

The type of morphological response to changing light availability found in these three species is similar to that described for Costa Rican rain forest species (Fetcher *et al.* 1983, Oberbauer & Strain 1985). Morphological variation was not as large as described for the pioneer species *Heliocarpus appendiculatus* Turcz. (Fetcher *et al.* 1983). However a high plasticity in a trait (the change in that trait in response to a change in environment) is not necessarily of larger adaptive value than a small plasticity: without a proper evaluation against some independent measure of success (growth, survival), little insight is gained concerning the adaptive value of plasticity.

Growth

Considering growth rate as a relative measure of success it is possible to compare the acclimation of the three species here. It has been shown (Figure 4) that growth rate was largely a function of the environment. Plants of the same species growing in the same environment but with a different history (i.e. coming from different environments) exhibited rather different growth rates. FU or SG plants moved to LG had (in some cases considerably) higher relative growth rates than LG plants which stayed in the same environment. LG plants moved to either SG or FU in general had smaller RGR_w values than FU controls or SG controls. This again indicates that plants growing in the shade possess a higher potential of acclimation to increased light availability than plants growing in sun to decreased light availability.

These results are largely consistent with the results found by Oberbauer & Strain (1985) with *Pentaclethra macroloba* (Willd.) Kuntze. They also found higher RGR_w in full shade plants (1% DPPF) moved to partial shade (25% DPPF) than in partial shade controls. Also, they reported lower RGR_w values in plants transferred from partial shade to full shade in comparison with full shade controls. Burton & Müller-Dombois (1984) report a different type of response in *Metrosideros polymorpha* Gaud. in Hawaiian rain forest, where sun-born seedlings had higher growth rates than shade-born seedlings above which the canopy had been removed.

RGR_w was shown to be strongly correlated with E, while less strongly and negatively correlated with LAR, pooling species and treatments. In FU and SG *Cordia* had a higher LAR, but did not have higher growth rates in these environments than either *Omphalea* or *Lonchocarpus*, which both had much lower LAR there. It seems that the value of LAR has no effect on RGR_w when E is low; differences in RGR_w are determined by differences in E. In LG, in contrast to FU and SG, E is relatively high and differences in LAR are much smaller. Differences in RGR_w in LG may be attributed to differences in E and to a lesser extent also in LAR. *Cordia* may have an advantage (higher RGR_w) over both the other species due to its ability to maintain a relatively high LAR at light levels intermediate between LG and FU/SG (cf. Blackman & Wilson 1951). Based on our results, acclimation potential in terms of relative growth rate thus seems to be largely determined by plasticity in the unit leaf rate.

Species differentiation

The three species described here were shown previously (Popma & Bongers 1988) to possess similar growth rates in the three environments used here. In this paper, it has been shown that their potential to acclimate to changing light availability is similar too. The hypothesis that these species are differentiated in their acclimation potential to gap-associated environmental heterogeneity rather than in their growth response to different environments is only in part supported by the results of this study. If a differentiation in regenerative characteristics of these species exists, this probably will be the result of a combination of differences in dispersion, germination, growth and defence aspects, rather than of differences in their growth response alone (cf. Augspurger 1984, Clark & Clark 1985). The growth response and acclimation potential itself are probably necessary attributes to survive as a seedling-bank forming species in a temporally and spatially variable environment.

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