

## Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees

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**Abstract.** An experiment was conducted with *Heliocarpus appendiculatus*, a pioneer or large gap species of tropical moist forest in Costa Rica, and *Dipteryx panamensis*, a small gap species. Seedlings were grown in full sun, partial (80%) shade, and full (98%) shade. After one month of growth they were switched between environments and grown for two more months.

Growth in height of *Heliocarpus* was greatly affected by irradiance, being increased in response to full shade and decreased in full sun. Height of *Dipteryx* was unaffected by irradiance level. Survival of *Heliocarpus* seedlings was only 49% in full shade, whereas *Dipteryx* had 100% survival. Biomass of *Heliocarpus* was not significantly greater in full sun than in partial shade whereas it was for *Dipteryx*. The response of root:shoot ratio was similar for both species. They were lowest in full shade and highest in full sun. *Heliocarpus* exhibited greater changes in leaf thickness, specific leaf weight, and stomatal density than did *Dipteryx*. Stomatal conductance of both species was lower in full shade and full sun than in partial shade.

The results of the experiment indicate that growth of *Heliocarpus* is more plastic than that of *Dipteryx* in response to changes in irradiance. Previous environment did not affect the response to the present environment in either species. Both species responded positively to increases in irradiance.

### Introduction

The role of gaps of various sizes in the regeneration of tropical moist forest has received considerable discussion (Hartshorn 1978, 1980; Whitmore 1975, 1978; Oldeman 1978). Whitmore (1982) proposed gap formation and replacement as a general process in temperate and boreal forests as well as tropical forests. He distinguished between pioneer trees that colonize large gaps or clearings and those that use small holes in the canopy or single tree falls for regeneration. Autecological characteristics of species belonging to both of these groups have been studied for many temperate zone species (Bourdeau and Laverick 1958; Loach 1967, 1970; Wallace and Dunn 1980) and were recently summarized by Bazzaz (1979). Comparatively little is known about the autecology of tropical tree species (Bazzaz and Pickett 1980; Mooney et al. 1980; Whitmore

1982). In this paper we report on a comparison of seedlings of a pioneer species and a small gap species of tropical moist forest in the Atlantic lowlands of Costa Rica.

The process of gap formation is characterized by a sudden increase in irradiance, temperature, and atmospheric humidity deficits. We hypothesized that species that depend on gaps for regeneration must adjust quickly and successfully to such changes. Hence the ability of seedlings to acclimatize to sudden changes in microenvironment may be an important factor in their survival.

We compared growth characteristics, leaf morphology, and water relations of *Heliocarpus appendiculatus* Turcz. and *Dipteryx panamensis* (Pitt.) Record & Mell. *Heliocarpus* is found primarily in open clearings where it attains a height of 20 m. *Dipteryx* is one of the more common canopy trees, attaining a height of 50 m. It requires a gap to reach the canopy. Because *Heliocarpus* is found in the comparatively homogeneous environment of the clearing throughout its life cycle, we hypothesized that it would be able to acclimate less to shade than *Dipteryx*, which may encounter the heavily shaded forest floor as a seedling, a partially shaded gap as a sapling, and the sunlit canopy as an adult tree.

### Materials and methods

This study was performed at the La Selva Biological Station owned and operated by the Organization for Tropical Studies. La Selva is located in premontane wet forest in the Province of Heredia, Costa Rica, near the confluence of the Rio Puerto Viejo and Rio Sarapiquí (84° 02' W, 10° 26' N).

Seedlings were germinated in trays or taken from the field and transplanted into plastic pots filled with a 50:50 mixture of river sand and old alluvial soil from La Selva. The addition of river sand improved drainage and aeration of the heavy soil from La Selva. Plants were grown for a month in a partially shaded environment. At the end of the month they were randomly assigned to one of three treatments; full sun (FSU), partial shade (PSH), and full shade (FSH). The FSU treatment was provided by benches in the open. The FSH and PSH treatments were obtained by placing the plants in shade houses made with neutral density shade cloth at 98% and 80% shade. While the shade houses were under construction, the FSH and PSH treatments were initially provided by placing the seedlings in an abandoned cocoa grove and a palm grove, respectively. Measurements with the light integrators designed by Wood-

**Table 1.** Mean total daily photosynthetic photon flux densities (PPFD) ( $\text{mol m}^{-2} \text{d}^{-1}$ ) for different microenvironments at Finca La Selva, Costa Rica during the period January 27, 1982 – February 1, 1982

|                     | Open | Gap  | Under-story | Partial shade | Full shade |
|---------------------|------|------|-------------|---------------|------------|
| PPFD                | 27.6 | 6.87 | 0.27        | 7.05          | 0.38       |
| Percent of full sun | 100  | 24.9 | 1.0         | 25.5          | 1.4        |

ward and Yaqub (1979) showed that the same daily totals of PPFD were obtained in the groves as in the corresponding shade houses. After an additional 4 weeks, we re-assigned the plants in FSH to either FSH, PSH, or FSU and did the same for the plants grown in PSH and FSU. The plants were grown for eight more weeks in the new environments and then harvested.

Table 1 summarizes the various light environments and the mean daily total photosynthetic photon flux density (PPFD) received in each. Values were obtained with the light integrators and with a data logger using sensors designed by Biggs et al. (1971). Mean values are also given for a light gap ( $400 \text{ m}^2$ ) and understory at the forest at La Selva. In terms of total daily PPFD, the partial shade treatment corresponds to a light gap, while the full shade treatment corresponds to the understory.

At the end of the experiment, the height of seedlings was measured and they were divided into leaves, stem, and roots, dried for 48 h at  $65^\circ \text{C}$ , and weighed. Leaf area at the final harvest was measured with a leaf area meter (LiCor Instruments, Lincoln, Nebraska).

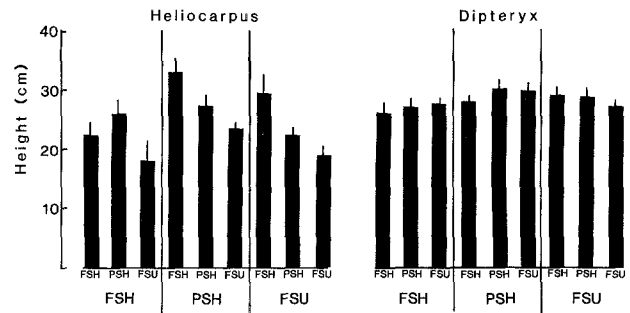
Leaf anatomy and morphology were measured for fully expanded leaves produced in FSH, PSH, and FSU environments. Specific leaf weight was determined from leaf disks dried for 48 h at  $65^\circ \text{C}$ . Stomatal density and pore length were determined using peels of model cement. Leaf thickness was measured using a light microscope from free hand sections of tissue fixed in FAA.

Leaf conductance was measured with a diffusion porometer (Kanemasu et al. 1969) shortly after each move. At the time of the conductance readings, measurements were made of air temperature, atmospheric humidity, and xylem pressure potential. Leaf temperature was measured with a thermocouple on a clamping device and PPFD was measured with a quantum sensor (LiCor Instruments, Lincoln, Nebraska). To evaluate the effects of present versus previous environment on leaf conductance, we selected five plants from each environment and transferred them to full shade, where leaf conductance was measured. We did the same in the partial shade and full sun environments. Thus we measured leaf conductance in every combination of present and previous environment. The results were analyzed using two-way analysis of variance with present and previous environment as factors. We performed a similar type of analysis for leaf angle.

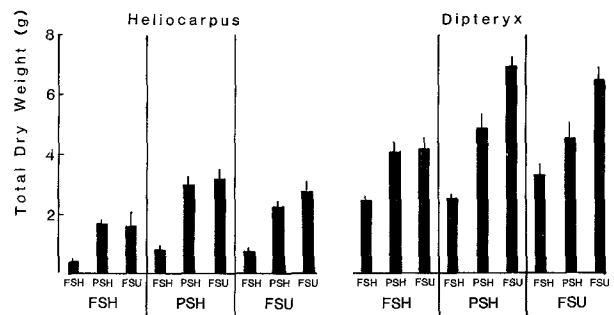
## Results

### Height, biomass, and survival

Growth in height is often a useful indicator of fitness because it is usually correlated with increases in biomass and



**Fig. 1.** Mean  $\pm$  SE for height of seedlings of *Dipteryx panamensis* and *Heliocarpus appendiculatus* grown in FSH, PSH, and FSU for one month and transferred to FSH, PSH, and FSU for two more months. Treatments for the first month are designated by the large letters and treatments for the second two months are designated by the small letters



**Fig. 2.** Mean  $\pm$  SE for total dry weight in the experiment described in Fig. 1

because it measures seedling response to competition for light. Height of *Heliocarpus* after three months of growth was significantly affected by both the first and the second set of shade treatments ( $P < 0.01$ ) (Fig. 1). Height was greatest in the PSH treatment and least in the FSH treatment. In contrast, height of *Dipteryx* was not altered significantly by the treatments.

Biomass of both species at the end of the experiment was significantly affected by the experimental treatments. Biomass of *Heliocarpus* and *Dipteryx* was lowest in the FSH treatment (Fig. 2). Response to the FSU treatment differed for the two species. Biomass of *Heliocarpus* in FSU was not significantly different from biomass in PSH (Duncan's test,  $P > 0.05$ ). *Dipteryx*, however, significantly ( $P < 0.05$ ) increased in biomass in response to the FSU treatment when compared to the PSH treatment (Fig. 2).

Survival of *Heliocarpus* was greatly reduced in full shade. Only 49% of the seedlings initially moved to full shade survived the first month. Most appeared to succumb to a fungal infection. In contrast there was no mortality for *Dipteryx* seedlings in any of the environments.

### Root: shoot and leaf area ratios

Allocation of biomass to roots and shoots was similar for both species, with highest root:shoot ratios in FSU and lowest in FSH (Fig. 3). Leaf area ratios, defined as the leaf area divided by total plant weight, differed significantly ( $P < 0.05$ ) between treatments for both species, being greatest in FSH and least in FSU. Leaf area ratio of *Heliocarpus*

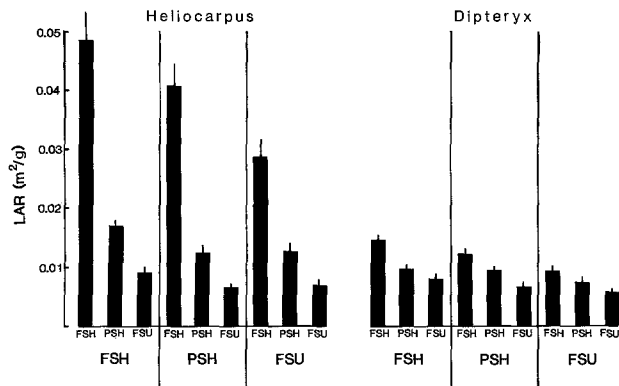


Fig. 3. Mean  $\pm$  SE for root:shoot ratios for the experiment described in Fig. 1

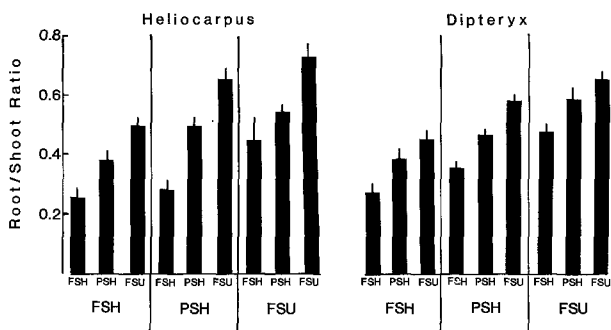


Fig. 4. Mean  $\pm$  SE for leaf area ratio in the experiment described in Fig. 1

decreased from FSH to FSU much more than did leaf area ratio of *Dipteryx* (Fig. 4). Plants grown in PSH had intermediate values for leaf area ratio.

#### Leaf morphology

The greater change in leaf area ratio of *Heliocarpus* is largely explained by the greater change observed in specific leaf weight (SLW) (Table 2). *Heliocarpus* experienced a 5-fold increase in SLW, whereas *Dipteryx* had only a 2-fold increase in SLW.

Changes in leaf thickness paralleled the changes in SLW. *Heliocarpus* seedlings grown in FSH had significantly thinner leaves than did plants grown in PSH, which in turn had significantly thinner leaves than those from seedlings grown in FSU. *Dipteryx* seedlings grown in FSH also had

significantly thinner leaves than those grown in PSH and FSU. Leaves from PSH seedlings and FSU seedlings were not significantly different. *Heliocarpus* had a 1.9-fold difference in leaf thickness from FSH to FSU, while *Dipteryx* had a 1.2-fold difference.

Stomatal density was also more plastic in *Heliocarpus* than in *Dipteryx* (Table 2). Mean abaxial stomatal density increased 2.3 times from FSH to FSU. Adaxial stomatal density increased from 0/mm<sup>2</sup> to 28/mm<sup>2</sup> to 55/mm<sup>2</sup>. In *Dipteryx*, abaxial stomatal density increased 1.6-fold from FSH and PSH to FSU. Thus *Heliocarpus* is considerably more plastic in the response of leaf morphology than is *Dipteryx*.

#### Effect of changing environment

The response of seedlings to sudden changes in microenvironment was assayed by switching them from one microenvironment to another after one month of growth. The switch from FSH to PSH or to FSU would simulate the effect of light gap formation on the seedlings growing in or near a new gap, for example. In the forest, sudden changes from a higher light regime to a lower one are less likely, but they may occur as in the unfolding of a palm over a small light gap. Two-way analysis of variance was used to separate the effects of present environment, in which the seedlings had been growing for two months, from the effects of previous environment, in which the seedlings were grown for one month. Growth characteristics analyzed were: height, total dry weight, leaf, stem, and root dry weight, root:shoot ratio, leaf area ratio, and leaf weight ratio at the final harvest in August. In most of the analyses for both *Heliocarpus* and *Dipteryx*, both previous environment and present environment had a significant effect on the response variable. Significant interactions between previous environment and present environment were found only for total dry weight and dry weight of leaves and roots of *Dipteryx* and for leaf area ratio of *Heliocarpus*.

#### Stomatal conductance and xylem pressure potential

At the end of the growing period in August, leaf conductances for plants that had been grown in FSH, PSH, and FSU environments were measured in each of the three environments (Table 3). Two-way analysis of variance was used to separate the effects of previous environment, in which the plants had been growing for one month, and present environment, into which the plants were transferred at least two hours before the beginning of the measurements. The analysis showed significant ( $P < 0.05$ ) interaction between

Table 2. Leaf characteristics of *Heliocarpus appendiculatus* and *Dipteryx panamensis* seedlings grown in full sun, partial shade, and full shade. Values in parentheses represent standard errors. Values with same letter for superscript are not significantly different ( $P < 0.05$ )

|  | <i>Heliocarpus appendiculatus</i> |                          |                          | <i>Dipteryx panamensis</i> |                          |                          |
|--|-----------------------------------|--------------------------|--------------------------|----------------------------|--------------------------|--------------------------|
|  | Full shade                        | Partial shade            | Full sun                 | Full shade                 | Partial shade            | Full sun                 |
| Specific leaf weight (g m <sup>-2</sup> )      | 11.8 <sup>a</sup> (0.86)          | 24.4 <sup>b</sup> (1.57) | 51.9 <sup>c</sup> (3.30) | 22.8 <sup>a</sup> (0.80)   | 33.6 <sup>b</sup> (1.20) | 46.5 <sup>c</sup> (3.30) |
| Stomatal density (abaxial) (mm <sup>-2</sup> ) | 164 <sup>a</sup> (5.3)            | 255 <sup>b</sup> (15.9)  | 383 <sup>c</sup> (15.8)  | 110 <sup>a</sup> (4.9)     | 88 <sup>a</sup> (5.1)    | 158 <sup>b</sup> (6.2)   |
| Stomatal density (adaxial) (mm <sup>-2</sup> ) | 0                                 | 28 <sup>a</sup> (4.4)    | 55 <sup>b</sup> (3.4)    | 0                          | 0                        | 0                        |
| Stomatal length (adaxial)                      | 15.4 <sup>a</sup> (0.56)          | 18.0 <sup>a</sup> (0.54) | 17.0 <sup>a</sup> (0.48) | 15.1 <sup>a</sup> (0.34)   | 14.1 <sup>a</sup> (0.51) | 14.0 <sup>a</sup> (0.46) |
| Stomatal length (adaxial) (μm)                 | 0                                 | 21.4 <sup>a</sup> (0.51) | 21.8 <sup>a</sup> (0.32) | —                          | —                        | —                        |
| Leaf thickness (μm)                            | 86 <sup>a</sup> (1.9)             | 130 <sup>b</sup> (1.6)   | 166 <sup>c</sup> (4.4)   | 129 <sup>a</sup> (1.5)     | 153 <sup>b</sup> (2.4)   | 155 <sup>b</sup> (3.1)   |

**Table 3.** Mean conductances (mm/s) (n=5) and results of fitting an additive model (see text) for seedlings of *Heliocarpus appendiculatus* and *Dipteryx panamensis* that were grown in full shade (FSH), partial shade (PSH), and full sun (FSU) and measured in all three environments

|                             |     |      | Mean conductance |      |             | Typical value | Effect of present environment | Effect of previous environment | Table of residuals |       |       |
|-----------------------------|-----|------|------------------|------|-------------|---------------|-------------------------------|--------------------------------|--------------------|-------|-------|
|                             |     |      | Previous         |      | Environment |               |                               |                                | FSH                | PSH   | FSU   |
|                             |     |      | FSH              | PSH  | FSU         |               |                               |                                |                    |       |       |
| <i>Heliocarpus</i><br>AM    | P   | FSH  | 0.74             | 0.77 | 1.02        | 2.49          | -1.72                         | -0.03                          | 0                  | 0     | 0     |
|                             | R   | PSH  | 2.83             | 4.75 | 2.41        |               | 0.37                          | 0                              | 0                  | 1.89  | -0.70 |
|                             | E   | FSU  | 2.17             | 2.49 | 3.48        |               | 0                             | 0.25                           | -0.29              | 0     | 0.74  |
| PM                          | S   |      |                  |      |             |               |                               |                                |                    |       |       |
|                             | E   |      |                  |      |             |               |                               |                                |                    |       |       |
|                             | N   | FSH  | 0.69             | 0.60 | 1.01        | 2.06          | -1.05                         | -0.79                          | 0.47               | -0.89 | 0     |
| T                           | PSH | 1.27 | 4.34             | 2.06 | 0           |               | 0.48                          | 0                              | 1.80               | 0     |       |
|                             | FSU | 1.12 | 2.99             | 2.51 | 0.45        |               | 0                             | -0.60                          | 0                  | 0     |       |
| <i>Dipteryx</i><br>Early AM | E   | FSH  | 0.77             | 1.73 | 0.85        | 1.57          | -0.72                         | -0.08                          | 0                  | 0     | 0     |
|                             | N   | PSH  | 1.49             | 2.49 | 1.40        |               | 0                             | 0.88                           | 0                  | 0.04  | -0.17 |
|                             | V   | FSU  | 0.68             | 2.95 | 3.89        |               | 0.50                          | 0                              | -1.31              | 0     | 1.82  |
| Late AM                     | I   |      |                  |      |             |               |                               |                                |                    |       |       |
|                             | R   |      |                  |      |             |               |                               |                                |                    |       |       |
|                             | O   | FSH  | 0.65             | 1.03 | 0.48        | 0.65          | 0                             | 0                              | 0                  | 0     | 0     |
| N                           | PSH | 1.23 | 1.79             | 0.98 | 0.58        |               | 0.38                          | 0                              | 0.18               | -0.08 |       |
| M                           | FSU | 0.98 | 0.62             | 0.65 | 0           |               | -0.17                         | 0.33                           | -0.41              | 0.17  |       |
| PM                          | E   |      |                  |      |             |               |                               |                                |                    |       |       |
|                             | N   |      |                  |      |             |               |                               |                                |                    |       |       |
|                             | T   | FSH  | 0.58             | 0.77 | 0.36        | 1.71          | -1.13                         | 0                              | 0                  | -0.37 | 0     |
|                             | PSH | 1.93 | 2.62             | 0.93 | 0.22        |               | 0.56                          | 0                              | 0.13               | -0.78 |       |
|                             | FSU | 0.87 | 2.27             | 1.71 | 0           |               | -0.22                         | -0.84                          | 0                  | 0.22  |       |

**Table 4.** Mean leaf angles (from horizontal plane) and results of fitting an additive model for seedlings of *Heliocarpus appendiculatus* and *Dipteryx panamensis* that were grown in full shade (FSH), partial shade (PSH), and full sun (FSU) and measured in all three environments

|                    |     |     | Mean leaf angle (°) |     |             | Typical Value | Effect of present environment | Effect of previous environment | Table of residuals |     |     |
|--------------------|-----|-----|---------------------|-----|-------------|---------------|-------------------------------|--------------------------------|--------------------|-----|-----|
|                    |     |     | Previous            |     | Environment |               |                               |                                | FSH                | PSH | FSU |
|                    |     |     | FSH                 | PSH | FSU         |               |                               |                                |                    |     |     |
| <i>Heliocarpus</i> | P   | FSH | 36                  | 30  | 33          | 33            | 0                             | 5                              | -2                 | 0   | 0   |
|                    | R   | PSH | 31                  | 14  | 26          |               | -7                            | -3                             | 0                  | -9  | 0   |
|                    | E   | FSU | 78                  | 73  | 50          |               | 40                            | 0                              | 0                  | 3   | -23 |
| <i>Dipteryx</i>    | N   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | T   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | E   | FSH | 22                  | 26  | 40          | 26            | 0                             | -3                             | -1                 | 0   | 0   |
| N                  | PSH | 27  | 20                  | 39  | 1           |               | 0                             | 3                              | -7                 | -2  |     |
| V                  | FSU | 18  | 21                  | 38  | -5          |               | 14                            | 0                              | 0                  | 3   |     |
| PM                 | I   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | R   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | O   |     |                     |     |             |               |                               |                                |                    |     |     |
| Late AM            | N   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | M   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | E   |     |                     |     |             |               |                               |                                |                    |     |     |
| PM                 | N   |     |                     |     |             |               |                               |                                |                    |     |     |
|                    | T   |     |                     |     |             |               |                               |                                |                    |     |     |

previous environment and present environment for all sets of readings except those taken on *Dipteryx* in the late morning.

To better understand the effects of previous environ-

ment and present environment on leaf conductance, an additive model was fitted to the mean conductances using the median polish procedure (Tukey 1977; McNeil 1977). The model had the form:

Conductance = Typical value + effect of present environment + effect of previous environment + residual.

The effect of the present environment is generally to decrease conductance in FSH and to increase conductance in PSH. The effect of previous environment was to increase conductance in PSH. Unusually high or low residuals revealed the sources of interaction (Table 3). For *Heliocarpus* the interaction was caused by high conductance of PSH plants measured in PSH. For *Dipteryx* the interaction in the early morning was caused by high conductances of FSU plants measured in FSU; in the afternoon, it resulted from low conductances of FSU plants measured in FSU and from FSU plants measured in PSH.

Xylem pressure potential was also measured for plants grown in FSH, PSH, and FSU in each of the three environments. Xylem pressure potential of *Dipteryx* was lower than that of *Heliocarpus*. In the morning xylem pressure potentials of *Dipteryx* ranged from  $-0.52$  MPa in FSH to  $-1.52$  MPa in FSU. In the afternoon pressure potentials ranged from  $-0.24$  MPa in FSH to  $-0.93$  MPa in PSH. For *Heliocarpus* pressure potentials in the morning ranged from  $-0.26$  MPa in FSH to  $-0.84$  MPa in PSH, whereas in the afternoon they ranged from  $-0.28$  MPa in FSH to  $-0.83$  MPa in PSH.

#### Leaf angle

Both *Heliocarpus* and *Dipteryx* exhibited changes in leaf angle in response to light regime. However, the two species were quite different in the pattern of response. The analysis was the same as for leaf conductance, that is, two-way analysis of variance was used to test for the effect of previous *vs.* present environment followed by a median polish to discern what particular treatment was responsible for the results (Table 4).

Leaf angle of both species was greater in FSU than in FSH or PSH. Leaf angle of *Heliocarpus* seedlings responded to the present environment, where they had been placed at least two h before measurement. On the other hand leaf angle of *Dipteryx* was only affected by the previous environment, where the plants had been growing for four weeks. Although the response of leaf angle was the same, namely, leaves were held more vertically in FSU, the timing of the response was different. *Heliocarpus* changed leaf angle more quickly than *Dipteryx*.

#### Discussion

Growth characteristics of both *Heliocarpus* and *Dipteryx* seedlings responded to changes in light environment in a way that was unaffected by the previous environment, as shown by the lack of interaction between previous environment and present environment. In other words, they acclimated to the new environment almost completely. When significant interactions between previous and present environment did occur, the median polish procedure showed that they could be attributed to the failure of seedlings that were switched from FSH to FSU to respond appropriately. For example, total dry weight of *Dipteryx* seedlings moved from FSH to FSU was less than would be expected on the basis of the response of seedlings that were moved from PSH and FSU to FSU. The FSU environment may have been too desiccating for seedlings raised in FSH.

Because the gap environment is potentially more heterogeneous than the clearing environment we expected that the gap species, *Dipteryx panamensis*, would be more plastic than the pioneer species, *Heliocarpus appendiculatus*. This hypothesis was not supported. Adjustments in carbon allocation to photosynthetic versus non-photosynthetic tissue were equal in the two species. *Heliocarpus* was considerably more plastic than *Dipteryx* in its leaf morphology. Furthermore, *Heliocarpus* showed a greater increase in height response in FSH, which is characteristic of shade-intolerant species (Grime 1966).

Our findings are in general agreement with the conclusions of Grime (1979) and Bazzaz (1979) that early successional species acclimate better to changed environments. In a study of acclimation to irradiance by old field species in Illinois, Bazzaz and Carlson (1982) found greater plasticity in photosynthetic parameters for early successional species than for late successional species. However, ability to greatly alter a character such as leaf thickness in response to a change in light level may not always be correlated with fitness. *Heliocarpus*, although more plastic than *Dipteryx*, had lower survival in full shade. When growth in full sun was compared to growth in partial shade, *Heliocarpus* also responded less positively than did *Dipteryx*.

In addition to large changes in leaf thickness, *Heliocarpus* also experienced large changes in number and position of stomata. Leaves produced in FSH had no stomata on their adaxial surface, whereas leaves produced in FSU and PSH did. These changes are in agreement with the conclusions of a model developed by Parkhurst (1978) that predicts that stomata on both sides of the leaf are more advantageous for thicker leaves whereas stomata on only one side are more advantageous for thinner leaves. Parkhurst (1978) showed that the presence or absence of stomata on both sides of the leaf was most strongly affected by leaf thickness. As noted above, *Heliocarpus* leaves are much thinner in FSH than FSU, hence the hypostomatous condition would be more likely to be expected in FSH.

Seedling water relations were affected in the high light environment. Leaf conductance was generally lower in FSU than PSH, suggesting that stomata may have closed partially as a result of increased evaporative demand in FSU (Schulze et al. 1972). Growth of *Heliocarpus* was not enhanced in the FSU despite the availability of 5 times as much light in FSU as in PSH, which further supports the idea that partial stomatal closure may have reduced photosynthesis. Reduced growth in FSU was not observed in *Dipteryx*, despite lowered leaf conductance. Because of their generally lower conductance, the *Dipteryx* seedlings may have experienced less reduction in conductance in FSU, relative to the PSH environment. Hence photosynthesis may not have been reduced as much for *Dipteryx* seedlings as for *Heliocarpus* seedlings.

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