BIOTROPICA 32(2): 225–234 2000

Lack of Ecotypic Differentiation: Plant Response to Elevation, Population Origin, and Wind in the Luquillo Mountains, Puerto Rico[1]

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ABSTRACT

How important is ecotypic differentiation along elevational gradients in the tropics? Reciprocal transplants of two shrubs, *Clibadium erosum* (Asteraceae) and *Psychotria berteriana* (Rubiaceae), and a palm, *Prestoea acuminata* var. *montana* (Palmaceae), were used to test for the effect of environment and population origin on growth and physiology in the Luquillo Experimental Forest of Puerto Rico. Two sites were used, one at Pico del Este (1000 m in cloud forest) and one at El Verde (350 m in lower montane rain forest). At the cloud forest site, plastic barriers were erected around a subset of the plants to examine if protection from wind affected survival or biomass accumulation. Survival of *C. erosum* and *P. berteriana* was not affected by site, population origin, or the presence of barriers. For *P. acuminata* var. *montana,* survival was higher for plants with barriers, but not affected by site and population origin. Plants of *C. erosum* and *P. berteriana* at El Verde grew larger than at Pico del Este, but there was no effect of population origin or barrier treatment on biomass accumulation for these species. For *P. acuminata* var. *montana,* there was no effect of environment, population origin, or barrier treatment on biomass accumulation. Light-saturated photosynthetic rate (A_{max}) of *C. erosum, P. berteriana,* and *P. acuminata* var. *montana,* as well as leaf anatomical characteristics of *C. erosum,* were unaffected by environment, population origin, and barrier treatment. On balance, there seems to be little evidence of ecotypic differentiation in these species along the gradient.

RESUMEN

¿Cuán importante es la diferenciación ecotípica a lo largo de gradientes altitudinales en los trópicos? Nosotros hicimos transplantes recíprocos de los arbustos *Clibadium erosum* (Asteraceae) y *Psychotria berteriana* (Rubiaceae), y de la palmera *Prestoea acuminata* var. *montana* (Palmaceae), para estudiar el efecto del ambiente y de la procedencia sobre el crecimiento y la fisiología en el Bosque Experimental de Luquillo en Puerto Rico. Utilizamos dos sitios, uno en Pico del Este, a 1000 m de altitud en el bosque nuboso, y el otro en El Verde, a 350 m de altitud en el bosque lluvioso montaño bajo. En Pico del Este, construímos tapavientos de plástico alrededor de un subgrupo de plantas para examinar si el efecto de la protección al viento afectaría la sobrevivencia y la acumulación de biomasa. La sobrevivencia de *C. erosum* y de *P. berteriana* no fue afectada por el sitio, por la procedencia ni por los tapavientos. La sobrevivencia de *P. acuminata* var. *montana* fue mayor en las plantas con tapavientos, pero no hubo efecto del sitio ni de la procedencia. El crecimiento de *C. erosum* y de *P. berteriana* fue fuertemente afectado por el ambiente; las plantas que crecieron en el sito bajo fueron más grandes. No encontramos efectos de la procedencia ni de los tapavientos en la acumulación de biomasa de estas especies. En *P. acuminata* var. *montana,* no hubo efecto sobre la acumulación de biomasa debido al ambiente, la procedencia ni a los tapavientos. Ni la tasa fotosintética a saturación lumínica (A_{max}) de *C. erosum,* de *P. berteriana,* y de *P. acuminata* var. *montana,* ni las características anatómicas de *C. erosum* fueron afectadas por el ambiente, la procedencia o los tapavientos. En general, parece haber poca evidencia de diferenciación ecotípica en este gradiente altitudinal.

Key words: *biomass accumulation;* Clibadium erosum; *cloud forest; dwarf forest; ecotypes; palm; photosynthesis;* Prestoea acuminata; Prestoea montana; Psychotria berteriana; *Puerto Rico; tropical montane forest; tropical rain forest; wind.*

In the temperate zone, environmental gradients have led to the formation of ecotypes that are adapted to local environmental conditions (Clausen *et al.* 1948, Chapin & Chapin 1981, Chapin & Oechel 1983). In the tropics, there have been few studies of ecotypic differentiation along environmental gradients (Hogan 1996). Most have examined the effect of variation in moisture regime. Stemmermann (1983) identified ecotypic differentiation in the water relations of the tree *Metrosideros polymorpha,* which occupies a broad range of habitats in the Hawaiian Islands. Cordero and Molano-Flores (1996/97) found differences in the sensitivity of seed germination to water potential between populations of the tree *Tabebuia heterophylla* from the north (wetter) and south (drier) coasts of Puerto Rico. When trees of several species of *Swie-*

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tenia from provenances in Mexico and Central America were grown in a suite of common gardens in Puerto Rico, an interaction between origin of population and the moisture regime of the garden was observed (Geary *et al.* 1973).

There have been fewer studies of ecotypic differentiation along tropical elevational gradients. Smith (1975) observed that seeds from populations at higher elevations had a broader temperature range for germination than seeds from populations at lower elevations. Baruch (1979) found that ecotypes of *Espeletia schultzii* from higher elevations in the páramo of Venezuela had higher photosynthetic rates after cold acclimation and greater capacity to resist drought than ecotypes from lower elevations. Lems and Holzapfel (1971) demonstrated the existence of ecotypes of the shrub *Echium leucophaeum* along an elevational gradient in the Canary Islands. On the other hand, Williams *et al.* (1995) found little evidence for population differentiation in the introduced grass *Pennisetum setaceum* in Hawaii.

Studies from temperate, boreal, and Arctic regions have shown that ecotypes from environments with less primary productivity respond less to amelioration of their growing conditions than ecotypes from environments with more primary productivity (Clausen *et al.* 1948, Shaver *et al.* 1979, Chapin & Chapin 1981, Chapin & Oechel 1983, McGraw & Antonovics 1983, McGraw 1985, Shaver *et al.* 1986, Fetcher & Shaver 1990). In these examples, either cold temperatures or a combination of cold temperature and low nutrient availability limited productivity. Although the best-known studies from the temperate zone report ecotypic differentiation over wide geographical ranges (*e.g.,* Clausen *et al.* 1948), several studies have provided much evidence for local adaptation over distances <1 km (Musselman *et al.* 1975, McGraw & Antonovics 1983, Bennington & McGraw 1995).

On tropical mountains, climatic gradients in radiation, temperature, and precipitation can affect photosynthesis, annual carbon gain, and plant growth directly (Cordero Solorzano 1997). Climatic gradients also can affect plant growth indirectly by altering soil development, leaching, decomposition, soil aeration, and nutrient cycling (Cavelier 1996). As elevation increases, diversity of plant species, primary productivity, and stature decrease until a type of vegetation known as cloud forest or elfin forest is encountered (Howard 1968, Weaver *et al.* 1986). In the Luquillo Mountains of Puerto Rico, there is such a gradient from subtropical wet and rain forest at 300 m to elfin forest at 1000 m (Waide *et al.* 1998). Annual precipitation increases from *ca* 3460 mm at El Verde (350 m elev.) to 4200 mm at Pico del Este (1050 m), while mean maximum temperature declines 7°C and solar radiation decreases by 50 percent over the same gradient (Brown *et al.* 1983). The number of tree species declines from 153 species in tabonuco forest to 43 species in elfin forest (Little & Woodbury 1976).

In addition to slow growth rates (Walker *et al.* 1996), the trees and shrubs of the elfin forest on exposed sites at high elevations in the Luquillo Mountains are shorter and have sclerophyllous leaves characteristic of windswept areas (Howard 1969). Several factors have been proposed that may contribute to this physiognomic trend in montane forests, including mechanical (wind) stress, water stress, and nutrient limitation (Howard 1969, Ewel & Whitmore 1973, Grubb 1977, Lawton 1982, Weaver *et al.* 1986, Cavelier 1996). Mechanical stimuli, including wind, have been shown experimentally to cause increased radial growth accompanied by decreased axial growth compared to controls (Jaffe 1980), as well as increased stomatal density (Grace & Russell 1977).

We hypothesized that species with populations at both ends of the climatic gradient in the Luquillo Mountains would exhibit patterns of population differentiation similar to those observed in studies from more northern latitudes, specifically that smaller, slower-growing ecotypes would be found at the higher elevations. Furthermore, we hypothesized that plants that were protected from wind would show changes in growth, leaf anatomy, and morphology. Here we report the effects of changes in environment on growth, survival, photosynthesis, water relations, and leaf anatomy.

MATERIALS AND METHODS

Experimental design.—Reciprocal transplant gardens were established at two sites in the Luquillo Experimental Forest (LEF), one in tabonuco (*Dacroydes excelsa* Vahl) forest at El Verde (350 m elev.) and one in elfin forest at Pico del Este (1000 m). The sites were *ca* 9 km apart and located in different watersheds. The El Verde site was a 50- $\times$ 50-m clearing on a ridge in tabonuco forest in which eight rectangular plots (3×8 m) were laid out. The Pico del Este site consisted of eight similar plots placed along 1 km of road. Following the convention used by Bennington and McGraw (1995), sites will be designated by proper names

(El Verde, Pico del Este) and populations by initials (EV, PE).

Few woody species occur throughout the entire gradient that includes tabonuco and elfin forest types. Among them are the shrubs *Clibadium erosum* (Sw.) DC (Asteraceae) and *Psychotria berteriana* DC (Rubiaceae), the palm *Prestoea acuminata* (Willdenow) H. E. Moore var. *montana* (Graham) Henderson & Galeano (Palmaceae), and the trees *Micropholis garcinifolia* Pierre (Sapotaceae) and *Calycogonium squamulosum* Cogn. (Melastomaceae). *Prestoea acuminata* var. *montana* has been known as *P. montana*, but Henderson and Galeano (1996) include it with *P. acuminata* known from Central and South America. Repeated attempts to root cuttings of *M. garcinifolia* and *C. squamulosum* for transplanting were unsuccessful, so we concentrated our efforts on the two shrubs and the palm. *Prestoea acuminata* var. *montana* is found in undisturbed forest throughout the LEF (Frangi & Lugo 1985), whereas the shrubs are more likely to be found in disturbed areas and clearings.

Cuttings of *C. erosum* were taken from eight different genotypes at both El Verde and Pico del Este and propagated in a greenhouse in San Juan, Puerto Rico, for three months. In March 1990, the plants were transplanted into 25- × 25- × 25-cm holes spaced 1 m apart that were refilled with a mixture of potting mix and native soil. Seedlings of *P. acuminata* var. *montana* were collected from several locations at El Verde and Pico del Este and were maintained for two months in potting mix in the greenhouse at San Juan. They were planted at the same time as *C. erosum*. Seedlings of *P. berteriana* were collected in the field and maintained in the greenhouse for two months. An effort was made to collect seedlings from locations separated by distances of at least 10 m to ensure an adequate sample of the populations. They were planted into the transplant gardens in September 1990. At both sites, the plants were exposed to full sun for much of the day.

At El Verde, we planted 2 individuals from each population in each plot for a total of 16 individuals/population/species. At Pico del Este, we planted 4 individuals/population in each plot ($N = 32$). At Pico del Este, each of 2 individuals from each population was surrounded by a barrier of polyethylene plastic to protect it from wind. Outside the barriers, mean wind velocity ranged from 0.41 ± 0.11 (SE) to 1.1 ± 0.35 m/sec over a 24-hour period. Inside the barriers, the velocity was <0.2 m/sec. The barriers enclosed an area of *ca* 0.16 m^2 initially and later were enlarged to accommodate the growth of the plants. Barriers were elevated *ca* 5 cm above the soil surface to permit some air movement and to reduce temperature increases within the barrier.

Two months after the initial planting, dead palms (*ca* 5%) were replaced. The replacement palms were taken from the same sites as the original populations. During the course of the experiment, the plots were weeded at three- to four-month intervals, and damaged barriers were replaced.

PHYSIOLOGICAL MEASUREMENTS.—We measured gas exchange characteristics of *C. erosum* in November 1990, and those of *P. berteriana* and *P. acuminata* var. *montana* in April 1992 (19 and 25 mo after transplanting, respectively). Instantaneous gas exchange measurements were made on healthy, recently expanded, mature leaves of transplanted individuals at both sites. All measured leaves were produced after transplanting. Maximum CO_2 assimilation rate (A_{max}), stomatal conductance to water vapor (g_l), internal CO_2 partial pressure (P_i), and transpiration (E) were measured with a portable photosynthesis system (LI-6250, Li-Cor, Lincoln, Nebraska) used in its closed mode of operation during partially cloudy or sunny days. Measurements were made from late morning to midday to assure complete induction of photosynthesis. Individual measurements were made after more than five minutes of direct solar radiation onto the leaf. We used a one-liter chamber that was kept in shade when not in use. Determinations were based on 20 to 30 sec of readings of CO_2 in the chamber, depending on the rate of assimilation. Total measurement times were kept <60 sec to avoid elevated leaf temperatures. By diverting some air flow through desiccant, we adjusted relative humidity (RH) to a nearly constant value during every measurement. Measurements for which there was a 1.5°C difference between leaf and chamber temperatures were repeated. Measurements with sudden changes in radiation or RH were discarded. Means and standard errors are based on one observation per plant.

The second most recently expanded leaf on each individual of *C. erosum* was harvested for anatomical analysis in January 1991. Thicknesses of leaves, epidermis, palisade mesophyll, and spongy mesophyll were measured with an ocular micrometer from three sections/leaf that were fixed in FAA. Stomatal density was measured from three fields on each of three peels taken from the abaxial surface.

Xylem pressure potential of *C. erosum* was mea-

sured with a portable pressure chamber (Soil Moisture Corp., Santa Barbara, California) during midday on a fully and recently expanded leaf of each plant. Measurements were made on 3 June 1991, at Pico del Este and on 28 June 1991, at El Verde. These measurements were repeated at Pico del Este on 30 August 1991, and at El Verde on 3 September 1991.

All individuals of *C. erosum* were harvested between mid-September and mid-October 1991 after 18 months in the field. Individuals of *P. berteriana* were harvested in May 1992 after 19 months, and the slower-growing individuals of *P. acuminata* var. *montana* were harvested in June 1993 after 38 months. Aboveground portions of the plants were divided into leaves and stems. For most plants, we were able to excavate almost all of the roots, except for individuals of *C. erosum* that had grown too large at El Verde. Leaf areas were measured with a leaf area meter (LI-3100, Li-Cor, Lincoln, Nebraska). All plant material was dried for more than three days at 60 to 65°C and weighed.

STATISTICAL METHODS.—Discrete, or Poisson, regression was used to analyze differences in survival from the time of planting until harvest (Manly 1992). Analysis of variance (ANOVA) was used to analyze the data from the harvests and from the physiological and anatomical measurements. There were two separate experiments, one to test for the effect of site (El Verde or Pico del Este) and population (EV or PE) and the other to test for the effect of wind protection at the Pico del Este site. The first experiment, hereafter known as the reciprocal transplant experiment, was analyzed as a split plot design in which site was the whole plot factor and population of origin and plot were subplot factors. To test for ecotypic differentiation, we tested for a significant effect of the site × population interaction in addition to a population main effect. The second experiment, called the barrier experiment, was analyzed as a randomized block two-way ANOVA with population of origin and barrier as factors. Plot was used as the blocking variable. When necessary, the data were log-transformed to stabilize variances. All ANOVAs were carried out using Version 3 of the SAS JMP statistical program (SAS 1995). This program also was used in a power analysis to calculate the least significant number (LSN) to obtain a significant result (SAS 1995).

RESULTS

PLANT SURVIVAL.—The sample size for aboveground biomass given below each bar is the number of individuals surviving at harvest time from the original cohort of 16 transplants/treatment (Figs. 1–3). Neither site, population origin, nor barrier treatment significantly affected survival of *C. erosum* or *P. berteriana* ($P > 0.05$). On the other hand, survival of *P. acuminata* var. *montana* was significantly higher ($P < 0.01$) for the plants at Pico del Este that were surrounded by barriers (84%) than for those without barriers (31%). There was no effect of site or population origin on palm survival.

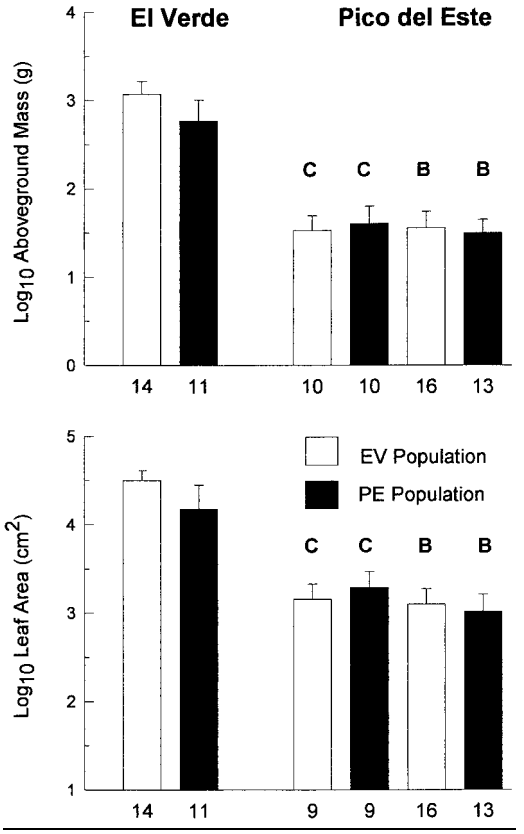

FIGURE 1. Aboveground biomass and leaf area (±SE) of *Clibadium erosum* grown at El Verde and Pico del Este in Luquillo Experimental Forest, Puerto Rico. C = exposed plants; B = plants surrounded by plastic barriers. Sample sizes are given below each bar.

EFFECTS OF PROTECTION FROM WIND ON PLANT GROWTH.—At Pico del Este, wind barriers had no significant effect on the total biomass, aboveground biomass, or total leaf area of *C. erosum*, *P. berteriana*, or *P. acuminata* var. *montana* (Figs. 1–3). They also had no effect on specific leaf mass of each species or root:shoot ratio of *P. berteriana* and *P. acuminata* var. *montana* (data not shown). Root:

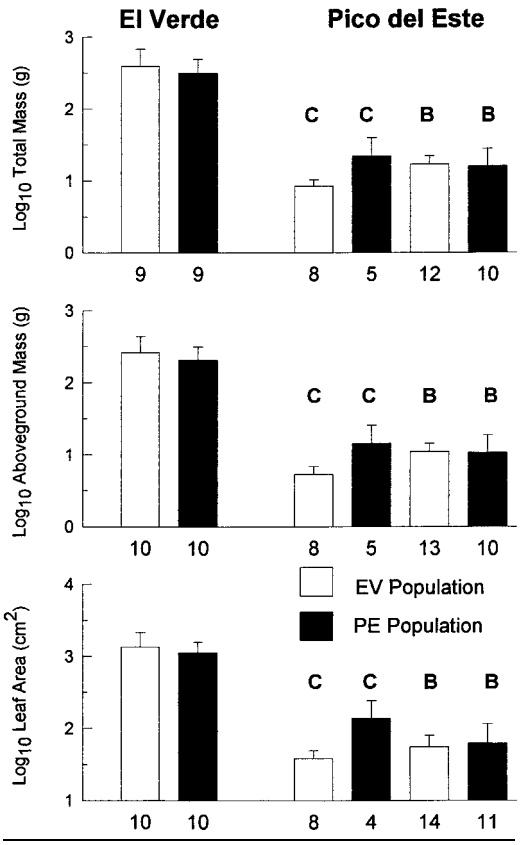

FIGURE 2. Total biomass, aboveground biomass, and leaf area (±SE) of *Psychotria berteriana* grown at El Verde and Pico del Este in Luquillo Experimental Forest, Puerto Rico. Sample sizes are given below each bar.

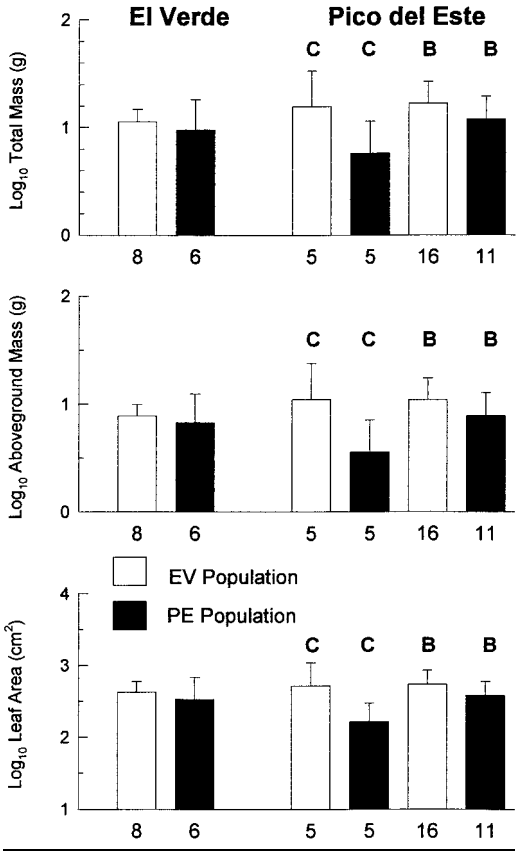

FIGURE 3. Total biomass, aboveground biomass, and leaf area (±SE) of *Prestoea acuminata* var. *montana* grown at El Verde and Pico del Este in Luquillo Experimental Forest, Puerto Rico. Sample sizes are given below each bar.

shoot ratio of *C. erosum* was not measured. Finally, there were no significant interactions between the wind barriers and population origin for any of the species.

Effect of site on plant growth.—At harvest, mean aboveground biomass of *C. erosum* at El Verde was 23 times that of the plants at Pico del Este (Fig. 1; $P < 0.001$). Leaf area also was significantly greater at El Verde than at Pico del Este (Fig. 1; $P < 0.001$). The effects of population origin and the interaction of population with site were not significant. For aboveground biomass, the LSN to detect a significant difference at the 0.05 level was 202 for population effect alone and 609 for population × site interaction. There was no effect of any of the factors on specific leaf mass (leaf mass of expanded leaves/leaf area of expanded leaves; data not shown).

Similar to *C. erosum*, total biomass, aboveground biomass, and leaf area of *P. berteriana* at Pico del Este were much smaller than those of plants at El Verde (Fig. 2; $P < 0.001$). Mean specific leaf mass at El Verde was significantly higher than at Pico del Este (65.7 vs. 51.2 g/m^2, $P < 0.01$). The effects of population origin were not significant (LSN = 68). For all three variables, the population × site interaction was marginally significant ($0.10 < P < 0.05$). The lowest probability was 0.061 for the interaction effect on aboveground biomass (LSN = 36). Because there was no barrier effect or barrier × treatment interaction (see above), plants protected by barriers at Pico del Este were included with the exposed plants for an analysis of the effect of population × site interaction. There was no significant effect (LSN = 587). Root: shoot ratio (defined as root biomass/aboveground biomass) was not affected significantly by any of the factors (data not shown).

TABLE 1. *Mean light-saturated photosynthetic rate (A_{max}), leaf conductance (g_l), transpiration, water use efficiency (WUE), and internal pressure of CO_2 (P_i) for* Clibadium erosum, Psychotria berteriana, *and* Prestoea acuminata *var.* montana *grown in gardens at El Verde and Pico del Este, Puerto Rico. Means are not given for population and barrier treatments because differences were not significant. Standard error in parentheses. * Pairs of means are significantly different* (t-*test,* $P < 0.05$).

Species	Site	*N*	A_{max} (μmol/m^2/sec)	g_l (mol/m^2/sec)	Transpiration (mmol/m^2/sec)	WUE (mol CO_2/mol H_2O)	P_i (Pa)
Clibadium erosum	El Verde	26	17.5 (0.89)	1.826 (0.145)	11.5 (0.38)*	1.53 (0.11) $\times 10^{-3}$*	28.0 (0.3)*
	Pico del Este	16	17.1 (0.76)	2.436 (0.415)	9.0 (0.58)*	1.97 (0.07) $\times 10^{-3}$*	25.9 (0.5)*
Psychotria berteriana	El Verde	8	7.96 (0.82)	0.149 (0.028)	3.67 (0.61)	2.45 (0.29) $\times 10^{-3}$	22.9 (1.6)
	Pico del Este	6	6.85 (0.62)	0.221 (0.022)	2.42 (0.31)	3.24 (0.65) $\times 10^{-3}$	26.3 (0.5)
Prestoea acuminata var. *montana*	El Verde	6	1.24 (0.28)*	0.054 (0.012)	1.67 (0.36)	0.79 (0.24) $\times 10^{-3}$*	28.9 (1.4)
	Pico del Este	8	3.00 (0.64)*	0.089 (0.023)	1.21 (0.33)	2.79 (0.45) $\times 10^{-3}$*	25.9 (1.0)

Although the transplants of *P. acuminata* var. *montana* grew during the experiment (data not shown), the mean values of total biomass, aboveground biomass, and leaf area did not respond significantly to site or population origin (Fig. 3); however, we found significant interactions between population origin and site for total biomass ($P < 0.0497$) and aboveground biomass ($P < 0.0297$). The interaction was marginally significant for leaf area ($P < 0.0666$). No difference was found between the populations at El Verde, but at Pico del Este, mean values were higher for the EV population than the PE population (Fig. 3). As with *P. berteriana*, when plants that were protected by barriers were included in the analysis, the interaction disappeared (total biomass, $P < 0.23$, LSN = 135; aboveground biomass, $P < 0.23$, LSN = 133; leaf area, $P < 0.24$, LSN = 133). This result suggests that the significant interaction was a chance occurrence and not the product of genetic differences between the populations. Specific leaf mass and root:shoot ratio were not significantly affected by site or population origin (data not shown).

PHOTOSYNTHESIS, WATER POTENTIAL, AND LEAF ANATOMY.—Mean light-saturated photosynthetic rate (A_{max}) and leaf conductance of *C. erosum* were unaffected by site, population origin, or the barrier treatment (Table 1). Transpiration rates were significantly higher at El Verde than at Pico del Este, resulting in lower water use efficiency (Table 1). This was most likely a result of the warmer leaf temperatures at El Verde (31.8°C ± 0.28 [SE]) than at Pico del Este (27.3°C ± 0.24; *t*-test, $P < 0.0001$). Mean internal CO_2 partial pressure for *C. erosum* was lower at Pico del Este than at El Verde (Table 1).

The photosynthetic characteristics of *P. berteriana* were similar to those of *C. erosum*, in that there was no significant effect of site, population origin, or barrier treatment on light-saturated photosynthesis, leaf conductance, or internal CO_2 partial pressure (Table 1). In contrast to *C. erosum*, there were no significant effects of the treatments on the transpiration rates or water use efficiency of *P. berteriana* (Table 1).

Photosynthesis of *P. acuminata* var. *montana* appeared to be adversely affected at El Verde (Table 1). Mean light-saturated photosynthesis was less than half that found at Pico del Este. Leaf conductance, transpiration, and internal CO_2 partial pressure were unaffected, but water use efficiency was significantly lower at El Verde than at Pico del Este. There were no effects of population origin or

barrier treatment on photosynthetic characteristics of *P. acuminata* var. *montana.*

Midday xylem pressure potential of *C. erosum* at Pico del Este averaged −0.76 MPa on 3 June 1991, and −0.56 MPa on 30 August 1991, when conditions were cloudier. Xylem pressure potential was not measured for the other species. There was no significant effect of population origin or barrier treatment on midday water potential for *C. erosum.* At El Verde on 28 June 1991, however, we found a significant difference (*t*-test, $P < 0.05$) between the mean water potential of the EV population (−0.61 ± 0.03 [SE] MPa, $N = 17$) and that of the PE population (−0.71 ± 0.04 MPa, $N = 22$). No significant difference was found on 3 September 1991.

Thicknesses of leaves, epidermis, palisade mesophyll, spongy mesophyll, and stomatal density of *C. erosum* did not respond to site, population origin, or barriers (Fig. 4). Thus, there was no effect of the experiment on leaf anatomy for *C. erosum.*

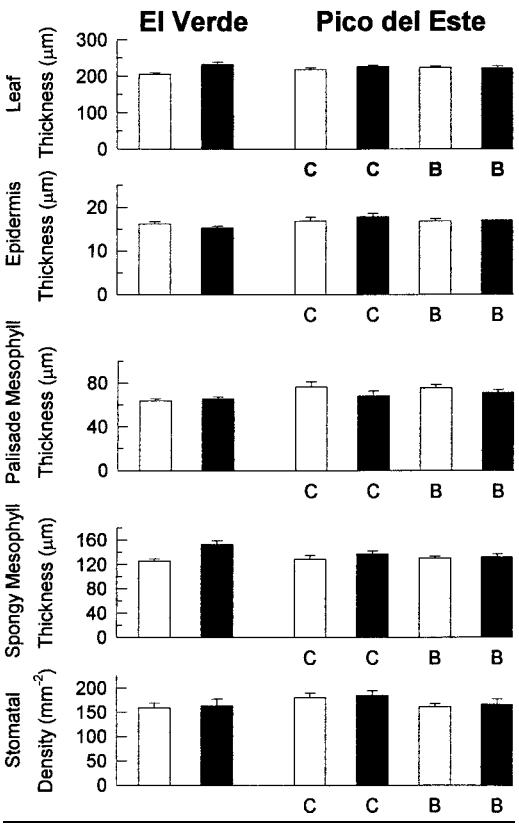

FIGURE 4. Thicknesses of the leaf, epidermis, palisade, and spongy mesophyll layers, and stomatal density of *Clibadium erosum* grown at El Verde and Pico del Este in Luquillo Experimental Forest, Puerto Rico. Figure legends as in Figure 1.

DISCUSSION

SITE DIFFERENCES.—For two of the three species, *C. erosum* and *P. berteriana,* we found a strong effect of the environment in that the plants grown at the low elevation site had more than ten times the leaf biomass as those grown at the high elevation site. For *P. acuminata* var. *montana,* we found no significant differences in plant size between sites. This latter result was quite unexpected, because the growth rate in height of *P. acuminata* var. *montana* adults at Pico del Este is less than at El Verde (A. Sabat, pers. comm.).

Differences in photosynthetic characteristics of *C. erosum* and *P. berteriana* at El Verde and Pico del Este were less pronounced than differences in growth. This may be because photosynthetic measurements were made under conditions of high photosynthetic photon flux density (PPFD) at both sites, whereas Pico del Este receives less solar radiation than sites at lower elevations (Brown *et al.* 1983). Furthermore, lower soil oxygen levels also may have restricted growth at Pico del Este (Silver *et al.* 1998). On the other hand, *P. acuminata* var. *montana* appeared to have lower photosynthetic capacity at El Verde than at Pico del Este, which may account for the lack of significant differences in growth. The individuals measured were exposed to full sun and exhibited signs of photobleaching. Seedlings normally are not found in unshaded habitats at El Verde, in part because they are overtopped by faster growing herbs and vines. Furthermore, they may be unable to acclimate to high light environments, as found by Chazdon (1986) for seedlings of understory palms from La Selva Biological Station, Costa Rica. Measurements of chlorophyll fluorescence in *P. acuminata* var. *montana* grown in a greenhouse have indicated that it is subject to photoinhibition (R. Cordero, pers. obs.).

We found little evidence for the effects of site on leaf anatomy or physiological characteristics. Although increases in stomatal density with elevation have been found for plants in New Zealand and other regions (Körner *et al.* 1986) including the Luquillo Mountains (Cintron 1970), we found no change in stomatal density or other leaf characteristics of *C. erosum.* This may be because *C. erosum* is a widespread early successional species that is similar to two introduced weedy species studied by Körner *et al.* (1986) which exhibited no variation in stomatal density with elevation.

The decline in P_i with increased elevation ap-

peared to have little effect on photosynthesis. In the case of *C. erosum*, photosynthetic rates were similar even though internal partial pressures were lower, suggesting the possibility of photosynthetic adjustment to lower P_i (Körner & Diemer 1987). An alternative explanation has been provided by Terashima *et al.* (1995), who argued on theoretical grounds that changes in P_i due to elevation should have relatively little effect on photosynthesis.

Population differences.—There seems to be little evidence for marked differentiation between high and low elevation populations in any of the species studied. We, however, cannot reject this hypothesis completely. Marginally significant or significant interactions were found between site and population origin, although these disappeared when plants from the barrier experiment were included in the analyses. Low sample size due to mortality reduced the power of many statistical tests. In the case of the palm, the experiment may not have lasted long enough for population differences to appear. Lower water potentials in *C. erosum* were found for the PE population than the EV population when measured at El Verde. Furthermore, small but significant effects of population origin were found in a greenhouse study of *C. erosum* and *P. acuminata* var. *montana* from the same populations (N. Fetcher, pers. obs.).

Our hypothesis that high elevation populations would be less responsive to a change in elevation than low elevation populations can be rejected. In contrast to studies from the temperate zone and the Arctic tundra (Clausen *et al.* 1948, Chapin & Chapin 1981, McGraw & Antonovics 1983, Fetcher & Shaver 1990), we found no indication that plants from the low elevation population (EV) responded more to the change in environment than plants from the high elevation population (PE).

There are several possible reasons for the lack of strong differences between populations. One is that the environmental gradient is not sufficiently extreme to select for locally adapted populations. The gradient, however, is sufficient to exclude many woody species found at lower elevations (Howard 1968) and to have marked effects on the growth of *C. erosum* and *P. berteriana.* Another possibility is that there has been insufficient time for population differentiation. Williams *et al.* (1995) found little differentiation along an elevational gradient in Hawaii and attributed their results to a lack of genetic variability due to a limited introduction *ca* 1917. The upper regions of the Luquillo Mountains, however, probably have had the same type of vegetation since the Oligocene (Graham & Jarzen 1969, Scatena 1989), which is longer than many montane or Arctic regions have been free of ice.

The most likely explanation for the lack of population differentiation appears to be high gene flow. Although Carromero (1996) found some evidence for population substructure, overall mean F_{ST} was 0.103. This corresponds to a mean number of migrants per generation (N_m) of 2.18, which is sufficient to overcome the effect of genetic drift (Slatkin 1985). Although they are in different watersheds, El Verde and Pico del Este are separated by only 9 km of continuous forest. Most studies of ecotypic differentiation have compared populations that were farther apart (*cf.* Musselman *et al.* 1975, Chapin & Chapin 1981, McGraw & Antonovics 1983, Bennington & McGraw 1995). Hamrick and Loveless (1989) found that gene flow was relatively high for 14 species of tropical trees with differing habits on Barro Colorado Island, Panama. Similar results have been found for the palm *Astrocaryum mexicanum* and the pioneer tree *Cecropia obtusifolia* in Mexico (Eguiarte *et al.* 1993, Alvarez-Buylla & Garay 1994).

Another factor that may contribute to the lack of differentiation is human disturbance. Both *C. erosum* and *P. berteriana* are found in recently disturbed areas. The lower regions of the LEF, including El Verde, were logged and grazed in the early 20th century (Wadsworth 1951a,b; García-Montiel & Scatena 1994) and the present populations of these species could be descended in part from migrants from higher elevation. Many patches of forest, however, were affected less severely by humans, and it seems unlikely that the low elevation representatives were eliminated completely (García-Montiel & Scatena 1994).

Effects of wind.—At the whole-plant level, the only significant result was that more *P. acuminata* var. *montana* saplings inside the barriers survived than did those without barriers, independent of population origin. These results are similar to those of Gartner (1994) who found that protection from wind enhanced survival of seedlings of *Lupinus arboreus* in stabilized dunes on the coast of California. *Prestoea acuminata* var. *montana* does not grow on exposed ridges in the Pico del Este area, in spite of the fact that we saw it growing in the understory as seedlings and saplings near edges, which suggests that establishment beyond a given size in a wind exposed area is restricted for this species.

It seems likely that wind does not affect the

overall growth of these species. Most studies of the effects of wind in relation to plant growth are based on comparisons of the growth and allometric relationships among plant parts such as stem, crown, branches, twigs, and leaves (MacMahon & Kronauer 1976, Lawton 1982, Niklas 1992). This type of analysis will be the subject of a future article.

ACKNOWLEDGMENTS

We would like to thank Steven Vogel for help in designing the wind barriers; Ligia Lebrón and Jean Lodge for greenhouse assistance; Diana García-Montiel for analyses of leaf anatomy; Humfredo Marcano, Carlos Adorno, Rafael De León, Angel Luis Méndez, Samuel Mata, and María Aponte for help in the field; Gloria Rivera, Carlos Adorno, Yolanda Castro, and Yadira Vargas for help with the harvests; Jess Zimmerman and Barbara Gartner for comments on the manuscript; and the International Institute of Tropical Forestry for use of the leaf area meter. This research was supported by NSF awards RII-8802961 and RII-8903827 to the University of Puerto Rico and the Fondo Institucional Para la Investigación of the University of Puerto Rico. We also acknowledge Dennis Willows and the staff of Friday Harbor Laboratories at the University of Washington for use of facilities while writing.

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