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## PLASTIC PHENOTYPIC RESPONSE TO LIGHT OF 16 CONGENERIC SHRUBS FROM A PANAMANIAN RAINFOREST

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**Abstract.** The comparative phenotypic plasticity of 16 species of tropical rainforest shrubs (genus *Psychotria*, Rubiaceae) was investigated by growing plants in three light environments on Barro Colorado Island (BCI, Panama). The three light environments gave daily photon flux densities (PPFD) similar to the natural light gradient from shaded forest understory to small and large canopy gaps. Six of the species are principally found in gaps or forest edge environments, whereas the other ten species are principally found in shaded understories. Interactions between light treatment and species resulted in unpredictable mean phenotypic expression across light treatments. Shoot relative growth rates (RGR) were similar for understory and gap species in the low light treatment. Gap species had significantly greater shoot RGR in the intermediate light treatment than in the high light treatment. Mean plasticity was significantly lower for morphological variables when compared to physiological variables, while variation in plasticity was significantly greater for structural variables. Significant differences between gap and understory species were found in the plasticity of six out of the seven variables. The mean phenotypic plasticity of the seven variables was significantly greater for gap than for understory species. The high plasticity of gap species was consistent with the hypothesis that specialization in a more favorable environment increases plasticity. The species exhibited a wide range of leaf longevities, from four to 29 months, with gap species having, on average, shorter leaf span than understory species. Mean phenotypic plasticity decreased with increasing leaf longevity. Selection for greater plasticity may be stronger in the gap species because gaps exhibit a relatively predictable decrease in PPFD for which plasticity could be adaptive. While we have found a significant correlation between phenotypic plasticity and habitat affiliation, phylogeny (subgenus ascription) was not correlated with plasticity or with plant performance in any given PPFD treatment, reinforcing the hypothesis that phenotypic plasticity has evolved through natural selection in this diverse genus.

**Key words:** Barro Colorado Island, Panama; leaf longevity; light acclimation; phenotypic plasticity; predictability of environmental change; *Psychotria*; stress syndrome; tropical forest.

### INTRODUCTION

Evolution has been hypothesized to lead to greater specialization, resulting in ever increasing biological diversity. The specialization hypothesis proposes that genotypes are subject to strong habitat-based selection, resulting in specialized ecotypes (Lortie and Aarssen 1996). The supposed superiority of specialized ecotypes or taxa over generalists has led biologists to focus on evolutionary specialization, and to neglect plastic responses of the phenotype to the environment (Schlichting 1986, Sultan 1992). Phenotypic plasticity may be essential for survival in heterogeneous and var-

iable environments, especially for sessile photosynthetic organisms (Bradshaw 1965, Sultan 1992, Pintado et al. 1997). Though the implications of plasticity for fitness-related variables have been recognized (e.g., Hirose 1987), plasticity has been traditionally viewed as an alternative to specialization. A new approach has postulated that plasticity in some plant traits may represent specialization (Lortie and Aarssen 1996). These predictions for plasticity of specialized genotypes depend on whether specialization is associated with favorable ends of an environmental gradient (Lortie and Aarssen 1996). Specialization in favorable environments increases plasticity, whereas specialization in less favorable environments decreases plasticity.

Tropical rainforests, with their mosaic of different light environments ranging from shaded understories to treefall gaps of varying size, provide a setting to test the specialization–plasticity hypothesis, and to explore the evolutionary role of phenotypic plasticity in plants.

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Differing dependence of species on gaps for regeneration has been associated with a range of shade tolerant physiologies (Denslow 1987). The high species richness of tropical forests provides congeneric species that specialize along this light gradient. Species typical of gaps (favorable end of the light gradient) usually exhibit high growth rates and rapid leaf turnover, while species typical of shaded understories (adverse end) exhibit low growth rates and slow leaf turnover (Coley 1988, Mulkey et al. 1991a, Chapin et al. 1993, Mulkey et al. 1993, Kitajima 1994, Strauss-Debenedetti and Bazzaz 1996). Previous studies have found greater photosynthetic plasticity in gap-dependent as compared to shade-tolerant species (Bazzaz and Carlson 1982, Strauss-Debenedetti and Bazzaz 1991, 1996). We extend these results to explore plasticity for morphological and growth variables as well as photosynthetic variables.

To examine the relationships between phenotypic plasticity and adaptation to the light gradient, we studied 16 species of the genus *Psychotria* occurring on Barro Colorado Island (BCI), Panama. This pantropical genus of mostly shrubs is remarkably diverse (Gentry and Dodson 1987, Hamilton 1989a) and 21 species occur within the 16 km<sup>2</sup> of BCI (Croat 1978; S. J. Wright, *personal observation*). The genus is common in the understory on BCI with a mean density of 0.7 stems/m<sup>2</sup> (S. J. Wright, *unpublished data*). The different species range from 25 cm tall subshrubs to 2–4 m tall shrubs or small trees that exhibit a range of habitat preferences with respect to light. In this study, we examined the plastic response of physiological and morphological variables of seedlings from 16 species of *Psychotria* to three light treatments in a screened growth house. We addressed the following questions. (1) How different is the plastic response to light among species occurring on different parts of the light gradient in the field with regard to seven variables? These variables are: leaf mass per unit area, leaf area ratio, supporting biomass, root:shoot ratio, photosynthetic capacity, dark respiration, and relative growth rate. (2) Are species that are adapted to more favorable light environments (gaps) more plastic than species that are adapted to less favorable environments (shaded understories), as predicted by Lortie and Aarssen (1996)? Based on the classic view of specialization, our working hypothesis was that in low light, shade-tolerant species should perform better than gap-dependent species, and in high light, the opposite should be true.

Leaf longevity is likely to affect phenotypic plasticity, not only due to its reported influence on acclimation to different environments (Chabot and Hicks 1982, Kitajima et al. 1997), but also due to its potential influence on the speed at which a given genotype can track environmental changes by replacing the existing leaves with phenotypically different ones. For this reason, we also address the following question: is a short leaf lifespan associated with higher plasticity at the leaf and

TABLE 1. Species studied (genus *Psychotria*; Rubiaceae) arranged according to their occurrence in different light environments in the field.

Gap species		Understory species	
<i>P. brachiata</i> (BRA)	H	<i>P. acuminata</i> (ACU)	H
<i>P. grandis</i> (GRD)	H	<i>P. chagrensis</i> (CHA)	P
<i>P. micrantha</i> (MIC)	P	<i>P. emetica</i> (EME)	H
<i>P. psychotriifolia</i> (PSY)	P	<i>P. graciliflora</i> (GRC)	P
<i>P. pubescens</i> (PUB)	P	<i>P. horizontalis</i> (HOR)	P
<i>P. racemosa</i> (RAC)	H	<i>P. ipecacuanha</i> (IPE)	H
		<i>P. limonensis</i> (LIM)	P
		<i>P. marginata</i> (MAR)	P
		<i>P. pittieri</i> (PIT)	H
		<i>P. tenuifolia</i> (TEN)	P

Note: Abbreviations used in the figures are shown in parenthesis, and the subgenus is indicated by P (*Psychotria*) or H (*Heteropsychotria*).

at the whole plant level? Besides the large number of species compared, which allows for more solid generalizations than in most previous studies (typically, only two to six species are compared; see references in Bazzaz 1996, Strauss-Debenedetti and Bazzaz 1996), the strength of this study relies on addressing plasticity not only at the leaf level (as in previous studies of tropical plants, e.g., Walters and Field 1987, Mulkey et al. 1993, Kitajima et al. 1997) but also at the whole plant level. Leaf-level studies are likely to miss many important aspects of the plastic response of plants to the environment (Percy and Sims 1994, Valladares 1999), such as those involving resource allocation, which are crucial for growth and survival (Newell et al. 1993, Coleman et al. 1994, Kitajima 1994, Zipperlen and Press 1996).

## MATERIALS AND METHODS

### *Plant material and experimental design*

Seeds of 16 tropical rainforest shrub species belonging to the genus *Psychotria* (Rubiaceae) were planted in 50-L pots containing a 50:50 mixture of forest topsoil and river sand. Pots were placed in a screened growing house at the Smithsonian Tropical Research Institute Station on Barro Colorado Island (BCI, Panama). Plants were maintained under natural air temperature and relative humidity, and were watered daily with an automatic irrigation system. The 16 species were separated into two main groups, gap species and understory species (Table 1). The grouping of species was based on previous studies (Mulkey et al. 1991b, 1993, Wright 1991, Wright et al. 1992, Mulkey and Wright 1996; S. J. Wright, *personal observation*). Three light environments were created with neutral density shade cloth, providing a range of total daily photosynthetic photon flux densities (PPFD) similar to those experienced by natural populations (Table 2). For more information regarding the natural light environment of the species see Valladares et al. (1997). The daily course of incident PPFD (3–12 May and 2–19 October 1995, dry and wet seasons, respectively) was

TABLE 2. Daily and maximum PPFD in light microhabitats in the field and in the three experimental light treatments.

Habitat or treatment	Total daily PPFD (% of a totally open site)	Total daily PPFD (mol·m <sup>-2</sup> ·day <sup>-1</sup> )	Average PPFD at midday (μmol·m <sup>-2</sup> ·s <sup>-1</sup> )
Light microhabitat			
Forest gap	35.3 ± 6.7	12.1 ± 5.2	550 ± 132
Forest understory	1.5 ± 0.4 to 9.5 ± 2.2	0.3 ± 0.2 to 4.3 ± 2.3	10 ± 2 to 175 ± 42
Light treatment			
High light	31.3 ± 3.7	8.8 ± 3.1	320 ± 65
Intermediate light	8.8 ± 1.1	2.5 ± 0.3	115 ± 32
Low light	1.4 ± 0.2	0.4 ± 0.1	12 ± 3

Note: Data are the average of 2–6 sensors for eight days in the dry season, and 17 days in the wet season (May and October 1995, respectively) ± SD.

measured with Model G1118 GaAsP photocells (Hamamatsu, Bridgewater, New Jersey, USA) connected to a Model 21X datalogger (Campbell Scientific, Logan, Utah, USA). For each species, several pots with three to five seedlings were placed in each light treatment. After some weeks of growth, all seedlings except one were removed from each pot. The three largest plants per species per treatment were used in the analyses. Plants were allowed to grow for one to two years before the final harvest. Typically this was one year for fast-growing plants, mostly in the medium and high light treatment; and two years for slow-growing plants, mostly in the low light treatment.

#### *Structural, physiological, and growth variables*

Three individuals of each species were harvested from each light treatment. Leaves, petioles, stems, branches, and roots of each plant were dried to a constant mass at 70°C. Leaf area was measured with a portable LI-COR Model 3000 area meter (LI-COR, Lincoln, Nebraska, USA) before drying. Seven variables were considered: leaf mass per unit area, leaf area ratio (total leaf surface area per whole plant mass, m<sup>2</sup>/kg), supporting biomass (percentage of aboveground plant mass represented by petioles, branches, and stems), root:shoot ratio (root mass per shoot mass, g/g), photosynthetic capacity ( $A_{\max}$ , μmol CO<sub>2</sub>·m<sup>-2</sup>·s<sup>-1</sup>), dark respiration (μmol O<sub>2</sub>·m<sup>-2</sup>·s<sup>-1</sup>), and aboveground relative growth rate (RGR, mg·g<sup>-1</sup>·wk<sup>-1</sup>). Length and diameter of all stems, branches, and petioles, and the surface area of all leaves were measured as soon as the plants had two to three fully developed leaves. The aboveground biomass of each plant was then calculated from allometric relationships obtained in parallel, destructive measurements carried out in replicate seedlings. The process was repeated on the very same plants each month for fast-growing plants and every two months for slow-growing plants in order to calculate the aboveground biomass increase as a function of time. We minimized the possibility of an ontogenetic component in the differences among species and among light treatments by harvesting plants at a similar size rather than at the same age, as much as possible. Since

relative growth rates (shoot RGR, mg·g<sup>-1</sup>·wk<sup>-1</sup>) tend to decline with plant size and age, maximum shoot RGR was determined as the initial slope of the natural logarithm of mass plotted against time. Consequently, the shoot RGR values reported here represent the maximum value for a given species under a given light treatment. This minimizes ontogenetic effects on this variable and allows for a better interpretation of phenotypic plasticity (Coleman et al. 1994).

Two to three fully expanded leaves were chosen at random from each plant for gas exchange measurements. Photosynthetic capacity was calculated from assimilation light curves carried out with a portable IRGA, Model Ciras-I (PP-Systems, Hitchin Herts, UK). A 12-V quartz-iodide lamp connected to an external battery provided irradiance. Neutral density filters were used to obtain different PPFDs at the leaf surface. Due to the very low respiration rates of certain leaves, especially those acclimated to low light, we used an oxygen electrode (Hansatech, Norfolk, UK) to measure dark respiration rates in the laboratory. The possible induction of photoinhibition in the high light treatment was checked by measuring the photochemical efficiency of photosystem II in the dark with a PAM 103 fluorometer (Walz, Effeltrich, Germany).

Leaf longevity was estimated for three to 12 individuals for each of the 16 *Psychotria* species. Study individuals were reproductively mature and growing naturally in sites with light environments characteristic of each species. A total of 8172 leaves were registered in monthly censuses from October 1991 to October 1996. Leaves that were lost due to fallen objects, death of the whole branch or plant, or herbivory were discarded. Only leaves that were initiated and died during the censuses were used in the calculations. Just 0.3% of the leaves survived beyond October 1996.

#### *Index of phenotypic plasticity and statistical analyses*

An index of phenotypic plasticity ranging from zero to one was calculated for each variable and species as the difference between the minimum and the maximum mean values among the three light treatments divided by the maximum mean value. Means were calculated

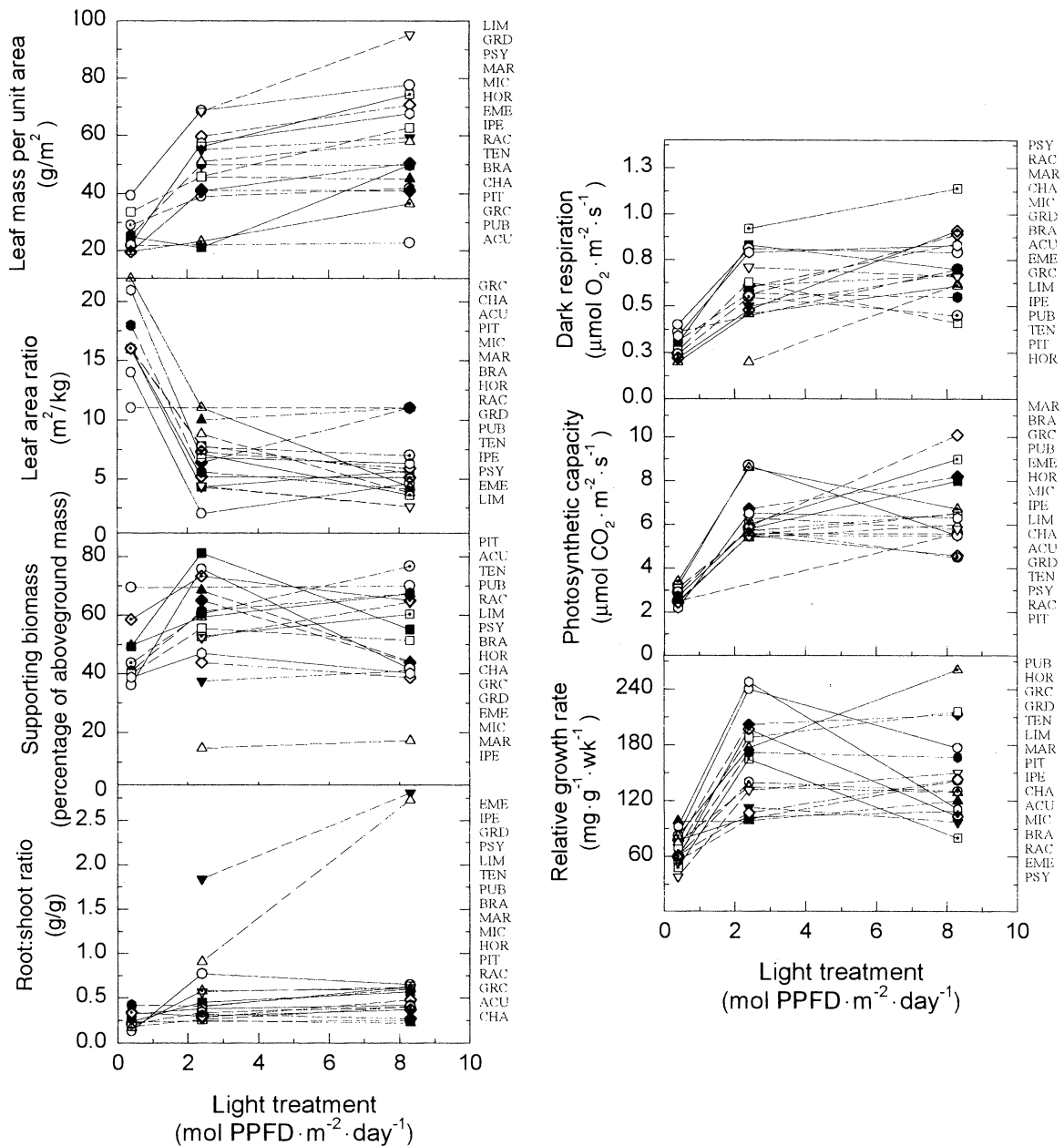


FIG. 1. Light response of understory (dashed lines) and gap (continuous lines) species of *Psychotria*. All species may not be discernible due to overlapping symbols and lines. The species abbreviations (see Table 1) have been ordered according to the mean value for the high light treatment and are shown at the right-hand side of each graph. Each data point is the mean of all plants for each light treatment and species.

for three individuals for each species and light treatment, omitting individuals that developed abnormally (due to herbivory, physical damage, or other factors). Mean phenotypic plasticity was calculated for each species by averaging the indices of plasticity obtained for each of the seven variables. The plastic response of growth was also explored as the slope in the plots of shoot RGR vs. light treatments (Fig. 1). In such analyses not only the intensity of the change but also

the sign of the change in growth due to the different PPFD treatments could be compared. Slopes were calculated separately for low to intermediate PPFD and for intermediate to high PPFD. Even though plants were harvested at a similar final size, plant biomass at the time of harvest was used as a covariate to neutralize possible ontogenetic effects in the comparisons among species and treatments.

Two-way analysis of variance (ANOVA) was used

TABLE 3. Two-way ANOVA of the seven selected variables with species nested within habitat.

Variable	Source of variation				
	Treatment (TMT) (df = 2)	Habitat (HAB) (df = 1)	Species (SP[HAB]) (df = 14)	Interactions (TMT × HAB) (df = 2)	Interactions (TMT × SP[HAB]) (df = 28)
Leaf mass per unit area	372.3**	1.6	50.6**	10.5**	37.9**
Leaf area ratio	994.9**	2.5	34.0**	16.8**	27.1**
Supporting biomass	53.1**	3.5*	56.1**	1.6	10.6**
Root:shoot ratio	329.1**	4.4*	353.2**	0.7	50.9**
Photosynthetic capacity	208.5**	7.0**	16.0**	8.5**	15.9**
Dark respiration	738.1**	25.6**	30.6**	5.3**	15.2**
Shoot relative growth rate	599.4**	4.9*	39.4**	6.8**	21.4**

Notes: Sixteen species, three PPFD treatments, and gap vs. understory species are compared. Table entries are *F* ratios; df for the error = 96.

\* *P* < 0.05, \*\* *P* < 0.01.

to test for differences among habitats, light treatments, and their interactions. Species were nested within habitats according to the preferred light environment in the field (i.e., gap and understory species). In all cases, the data met the assumptions of normality and homocedasticity. Since many structural variables (e.g., LAR, root:shoot ratio) vary with plant size, plant biomass was used as a covariate.

In order to check the significance of separating the species in two main groups according to their habitat affiliation, and to explore the existence of internal trends within gap and understory species, we conducted

a principal components analysis of average response to PPFD and of phenotypic plasticity of all species. Principal component analysis was performed using a correlation matrix since the variables used were measured on very different units. A varimax rotation produced the simplest possible structure among the component loadings. All analyses were performed with SYSTAT 6.0 (Wilkinson 1990).

RESULTS

The light treatments had large effects on phenotypic expression for most variables in most species (Fig. 1). There were significant differences among species for a given variable in a given treatment. Species differed in their phenotypic plasticity. The interaction between light treatment and species nested within the appropriate habitat affiliation was significant for all seven variables (Table 3; graphically, this can be seen in Fig. 1 where the responses of gap or understory species frequently cross). Thus, mean phenotypic expression was unpredictable across light treatments. Understory species did not have greater shoot relative growth rate (RGR) than gap species in the low light treatment (Fig. 2). Gap species had significantly greater shoot RGR in the intermediate light treatment but not in the high light treatment (Fig. 2). Apparent photosynthetic quantum yield, obtained from assimilation-irradiance curves, was lower in the high PPFD treatment than in the other two treatments for both understory and gap species. This was linked to a slight but chronic photoinhibition measured by “in vivo” chlorophyll fluorescence and revealed by a 5–10% reduction in the photochemical efficiency of photosystem II ( $F_v/F_m$  in dark adapted leaves), from which the plants only partially recovered overnight.

Plasticity indices were significantly lower for structural than for physiological variables (median for structural parameters = 0.35; median for physiological parameters = 0.61; Mann-Whitney *U* rank sum test, *P* = 0.03). However, interspecific variations in plasticity indices were greater for structural variables. The largest

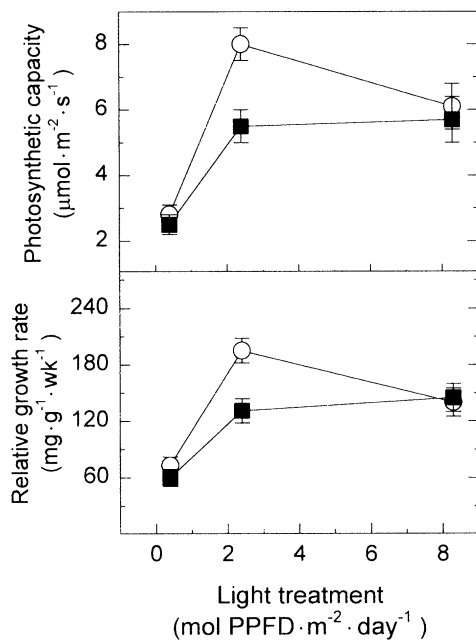


FIG. 2. Photosynthetic capacity and relative growth rate for the three PPFD treatments for gap (open symbols) and understory (closed symbols) *Psychotria* species. Values are the mean of all the species belonging to each habitat (see Table 1) ± 1 SD. Differences among gap and understory species were significant only for the intermediate light treatment (ANOVA, *P* < 0.01).

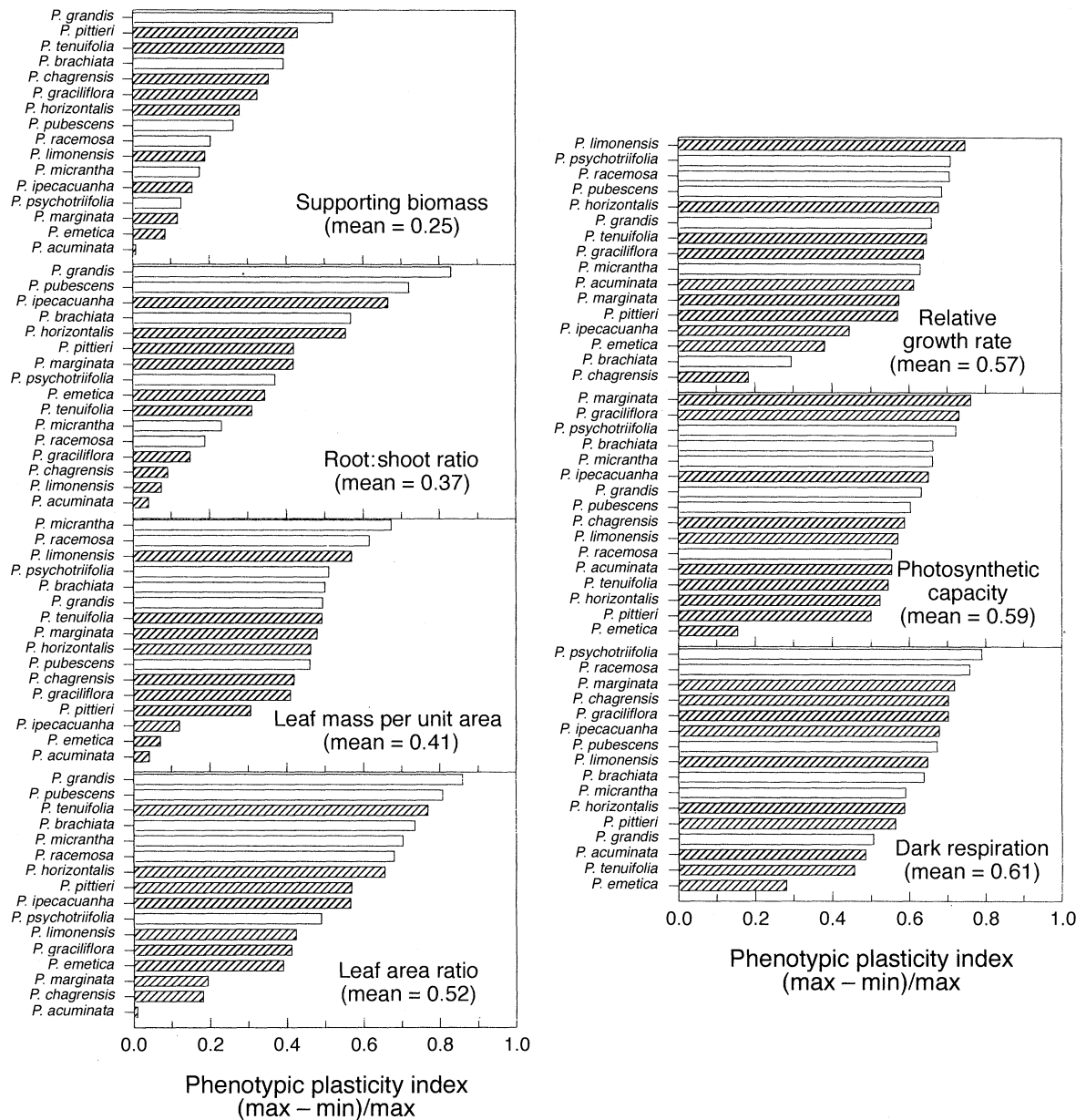


FIG. 3. Phenotypic plasticity index, (maximum – minimum)/maximum, for gap (open bars) and understory (hatched bars) species of *Psychotria* for each of the seven structural and physiological variables. Graphs within the figure and species within each graph are ordered by mean phenotypic plasticity.

differences among species were found for structural variables such as root:shoot ratio or leaf area ratio (Fig. 3, Table 4). Significant differences between gap and understory species were found in the plasticity of six out of the seven variables (Table 4). The mean phenotypic plasticity of the seven variables was significantly greater for the six gap species than for the ten understory species (Table 4). When the mean phenotypic plasticity for the seven variables was calculated for each species independently, gap species exhibited the highest values. Only the mean plasticity of the gap

species *P. micrantha* was not statistically higher than that of understory species (Tukey's test,  $P < 0.05$ , Fig. 4).

Large differences between species were also found when the plasticity of shoot RGR in response to PPFD was studied as the slope of the growth response. Different responses were found not only between but also within the gap and the understory species. Some gap species such as *P. grandis*, *P. micrantha*, and *P. racemosa* exhibited a large increase in shoot RGR in response to low to medium PPFD, and a large decrease

TABLE 4. ANOVA of the phenotypic plasticity index for the seven selected variables for the 16 *Psychotria* species grouped according to their habitat affiliation (gap and understory; see Table 1).

Variable	Gap species	Under-story species	F
Leaf mass per unit area	0.57	0.39	14.0 **
Leaf area ratio	0.71	0.41	7.9**
Supporting biomass	0.27	0.29	0.5
Root:shoot ratio	0.50	0.28	4.8*
Photosynthetic capacity	0.64	0.55	5.3*
Dark respiration	0.66	0.58	6.3*
Shoot relative growth rate	0.63	0.52	4.7*
Mean	0.62	0.46	5.2*

\*  $P < 0.05$ , \*\*  $P < 0.01$ .

in response to medium to high PPF (Fig. 5). Two subgroups of understory species could be observed. One subgroup exhibited relatively small increases in response to both low to medium and medium to high PPF changes (e.g., *P. chagrensis*, *P. acuminata*, and *P. marginata*). The other, more heterogeneous subgroup exhibited a large increase in response to low to medium PPF and a small decrease in response to medium to high PPF (e.g., *P. horizontalis*, *P. tenuifolia*, and *P. pittieri*).

The 16 species of *Psychotria* exhibited very different mean leaf longevities, ranging from <4 to >29 mo (Table 5). Gap species had, on average, shorter leaf life-span than understory species (460 vs. 540 d, respectively; significant for  $P < 0.05$ , ANOVA). The mean phenotypic plasticity for the seven variables decreased significantly with increasing leaf longevity (Fig. 6). Remarkably, leaf longevity was not related to mean values of structural or physiological variables at the leaf level, such as leaf mass per unit area or photosynthetic capacity at a given treatment.

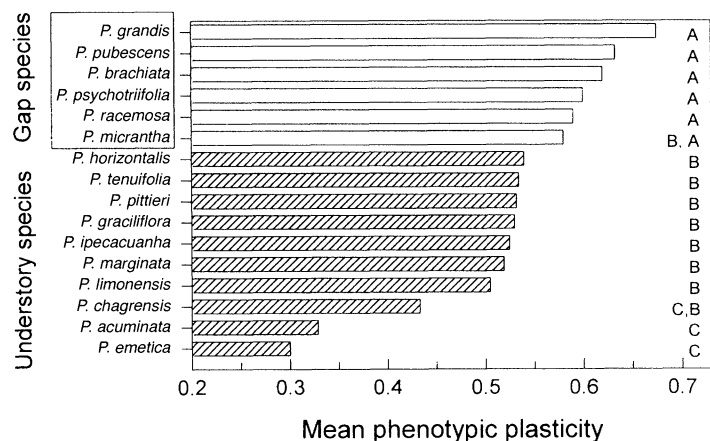
Multivariate comparisons of species were carried out with both mean values under the intermediate PPF treatment (the one rendering the highest number of significant differences among species) and phenotypic

plasticity indices. Understory and gap species were rather scattered and intermingled in the principal component plot of mean values (Fig. 7). Eight understory species clustered together, but two understory species, *P. emetica* and *P. ipecacuanha*, both with unusually high root:shoot ratios, were positioned far from the centroid for understory species. Five gap species clustered together, but one gap species, *P. pubescens*, with an unusually large shoot RGR, was positioned far from the centroid for gap species. Factor loadings revealed a tendency towards low values of supporting biomass and high values of leaf area ratio in understory species. Gap and understory species were better segregated in principal components space when the plasticity indices were used in the analyses instead of the mean values (Fig. 7). Gap species shared high plasticity in shoot RGR in response to PPF and had greater plasticity in the structural variables than understory species.

DISCUSSION

Plant evolution in a heterogeneous environment leads to one of two alternatives: specialization to a fraction of the environmental heterogeneity; or generalized adaptation to a broad range of environments (Bazzaz 1996). In opposition to expectations from the classical approach to adaptation and specialization, our study shows that understory species of *Psychotria* did not perform better in terms of relative growth rate than their gap counterparts in the low light treatment (Figs. 1 and 2). Gap species performed better than understory species in the intermediate PPF treatment, and exhibited greater plasticity (Figs. 2–4). Even though phenotypic plasticity is often cited as a characteristic of generalists (Spitze and Sadler 1996), it can be the result of specialization to a fraction of the environmental heterogeneity (Lortie and Aarssen 1996). The specialization hypothesis (habitat selection processes resulting in specialized taxa or ecotypes) can be accepted in our comparison of gap and understory species, but following the approach of Lortie and Aarssen (1996) that reconciles specialization and phenotypic plasticity by

FIG. 4. Sixteen *Psychotria* species ordered by mean phenotypic plasticity for seven variables (supporting biomass, root:shoot ratio, leaf mass per unit area, leaf area ratio, relative growth rate, photosynthetic capacity, and dark respiration). Species from gaps (open bars) exhibited larger values than species from the forest understory (hatched bars). The letter code indicates significant differences among species (ANOVA, Tukey's test  $P < 0.05$ ).





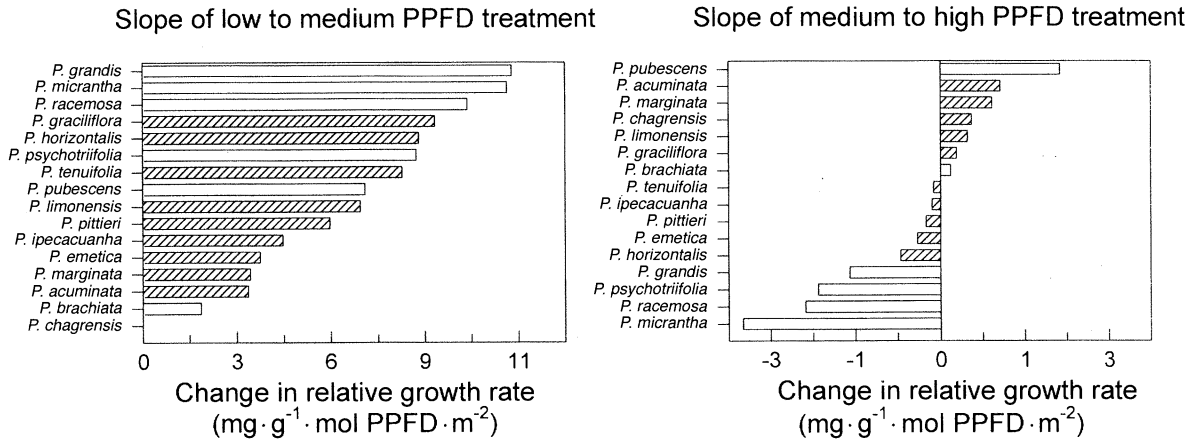


FIG. 5. Plastic growth response to an increase in the light treatment from low to medium PPFD (left graph), and from medium to high PPFD (right graph) for gap (open bars) and understory (hatched bars) species of *Psychotria*. Each value represents the slope of the corresponding part of the relative growth rate vs. PPFD graph.

considering the position along environmental gradients to which plants are specialized. In this approach, phenotypic stability is considered to be more adaptive than plasticity in adverse environments (for instance the dark understory of the rainforest), while plants from more favorable environments (e.g., forest gaps) are more plastic as a consequence of selection for specialization to this environment (Lortie and Aarssen 1996).

While it is easy to recognize the ecological advantages of phenotypic plasticity, it is less straightforward to find scenarios where a plastic response to the environment could be maladaptive. Examples of the latter have been pointed out for plants growing under extreme conditions, and usually in the absence of strong competition (Chapin 1991, Chapin et al. 1993). Such plants tend to show a conservative pattern involving slow, steady growth and nutrient storage even when condi-

tions are temporarily favorable (Chapin 1980, Chapin et al. 1986, Mulkey et al. 1991a, Waller 1991) in order to avoid the production of a plant too large or structures too expensive to be sustained once conditions deteriorate. Specialization to a low-resource environment seems to start with modification in a key growth-related variable. This results in a cascade of effects that triggers the entire “stress resistance syndrome” reported by Chapin et al. (1993); i.e., low rates of growth, photosynthesis, and nutrient absorption, high root:shoot ratios, low rates of tissue turnover, and high concentrations of secondary metabolites. The understory species of *Psychotria* had lower shoot growth rates in the intermediate PPFD treatment, lower photosynthetic rates in each PPFD treatment (Figs. 1 and 2), and lower rates of leaf turnover (Table 5). These results are consistent with a stress resistance syndrome in understory species of *Psychotria*. However, there is limited eco-physiological information to explain the trade-offs between the different traits involved in successful per-

TABLE 5. Leaf longevity (days) of the 16 species of *Psychotria* studied.

Species	Mean	1 SD	n
<i>P. limonensis</i>	870.2 a	292.9	52
<i>P. ipecacuanha</i>	696.3 b	363.2	44
<i>P. marginata</i>	690.1 b	307.1	161
<i>P. horizontalis</i>	685.7 b	337.6	190
<i>P. acuminata</i>	648.3 b	152.3	154
<i>P. chagensis</i>	644.6 b	288.2	248
<i>P. grandis</i>	629.1 b	326.9	51
<i>P. micrantha</i>	535.6 c	192.4	226
<i>P. racemosa</i>	513.2 c	181.4	170
<i>P. psychotriifolia</i>	498.8 c	320.1	99
<i>P. pittieri</i>	415.1 d	197.3	336
<i>P. brachiata</i>	382.2 d	147.8	570
<i>P. graciliflora</i>	339.1 e	145.0	287
<i>P. tenuifolia</i>	303.4 e	204.0	145
<i>P. pubescens</i>	212.4 f	100.6	196
<i>P. emetica</i>	118.8 g	141.7	91

Note: A letter code following the mean is used to indicate significant differences (ANOVA,  $P < 0.01$ ).

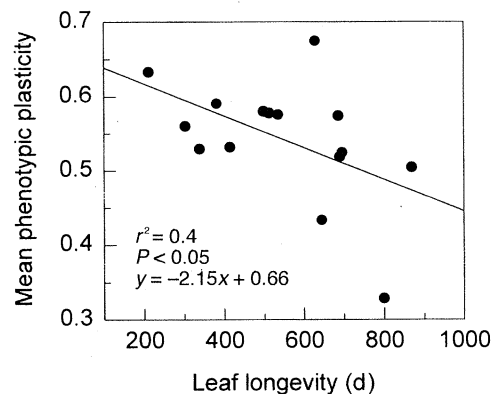


FIG. 6. Mean phenotypic plasticity vs. mean leaf longevity for 15 *Psychotria* species. *P. emetica* was removed from the regression after testing for outliers.

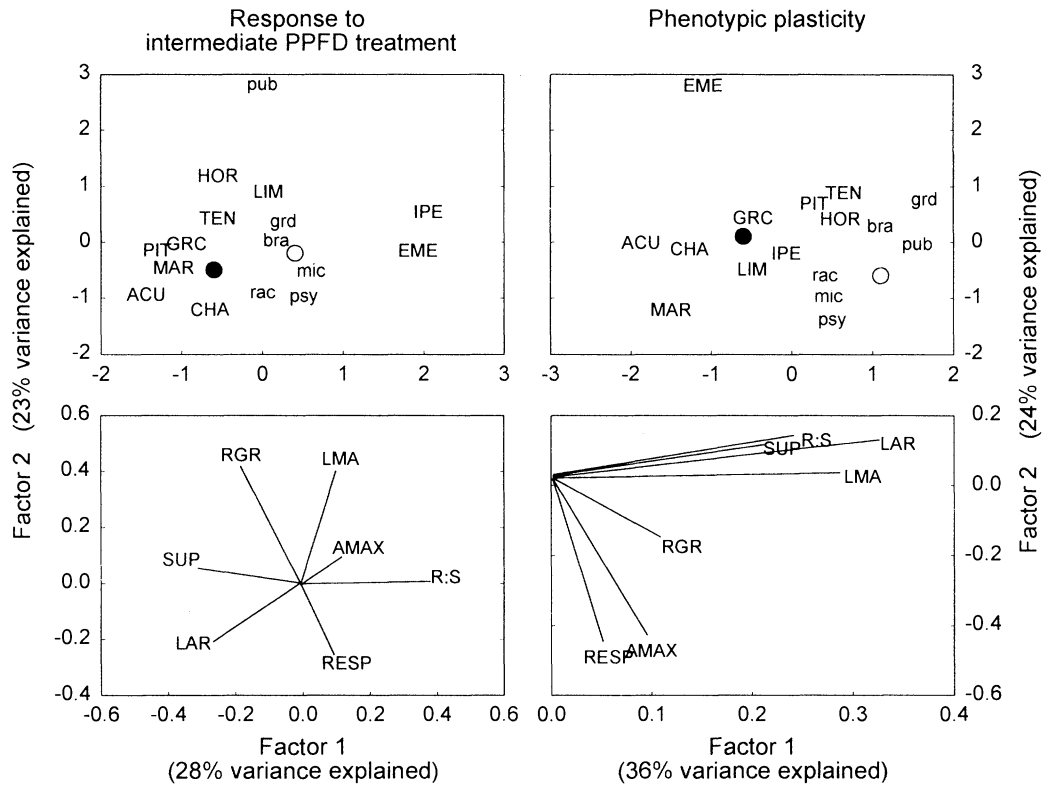


FIG. 7. Principal components ordination of 16 species of *Psychotria* (upper graphs) according to their mean response to the intermediate PPFd treatment (left) and to their phenotypic plasticity (right) for seven variables (LMA = leaf mass per unit area, R:S = root:shoot ratio, SUP = percentage of supporting biomass, LAR = leaf area ratio, RESP = dark respiration, AMAX = photosynthetic capacity, and RGR = shoot relative growth rate). Lower graphs show factor loadings. Abbreviations in the upper graphs indicate species (see Table 1); uppercase abbreviations indicate understory species, and lowercase abbreviations indicate gap species. Solid and open circles indicate the centroids of understory and gap species, respectively.

formance under adverse conditions (Lambers and Poorter 1992, Atkin et al. 1996).

The greater plasticity in response to PPFd of gap *Psychotria* species could also be related to the predictable environmental change (gap closure) experienced by gap species. Predictability of environmental heterogeneity determines the direction of evolutionary changes in phenotypic plasticity (Scheiner 1993, Huber 1996). Since the formation of canopy openings that influence any individual in the understory is unpredictable (Lorimer and Frelich 1988), plasticity in long-lived understory plant species might not be directly enhanced by selection. In contrast, species that are dependent on gaps experience a predictable progression of light environments once a gap is created (vegetation regeneration leads to a gradual decrease in the available light; Denslow 1987, Uhl et al. 1988). This predictable change may select for phenotypic plasticity in gap-dependent species.

Phylogenetic analysis of species used in comparative plant ecophysiological studies has been infrequent, despite its potential to elucidate important evolutionary questions (Monson 1996), and may enhance the understanding of the forces responsible for evolutionary

changes in plasticity. As argued by Schlichting (1986), if changes in phenotypic plasticity have arisen solely via drift (random changes not driven by selection), then the degree of similarity in plasticity between taxa should directly reflect their relatedness. Within the genus *Psychotria* two subgenera, *Psychotria* and *Heteropsychotria*, have been described (Hamilton 1989a, 1989b). Subgenus *Psychotria* is monophyletic and the species of subgenus *Heteropsychotria* used in this study appear to form a monophyletic group as well (M. Nepokroeff, *personal communication*). While we have found a significant correlation between phenotypic plasticity and habitat affiliation, phylogeny (subgenus ascription) was not correlated with plasticity or with plant performance in any given PPFd treatment, suggesting that phenotypic plasticity has evolved repeatedly through natural selection in this genus.

Several studies have found that light-demanding trees requiring gaps for successful regeneration had higher and more flexible metabolic rates than did shade-tolerant trees (Bazzaz 1979, Bazzaz and Pickett 1980, Bazzaz and Carlson 1982, Chazdon 1992, Strauss-Debenedetti and Bazzaz 1996). Gap species typically have greater ability to acclimate photosyn-

thesis to low light than do understory species to high light (Mulkey et al. 1991a, Fredeen and Field 1996, Strauss-Debenedetti and Bazzaz 1996). But there is not a general consensus, and there seems to be a number of exceptions to the prediction that high light species have greater photosynthetic acclimation potential than low light species. For example, Fetcher et al. (1987) could not correlate successional status with photosynthetic acclimation potential in six rainforest tree species. Gas exchange characteristics in response to light availability did not differ between gap and understory species in a comparison of seedlings of 13 tropical tree species, although greater plasticity in total biomass and RGR was observed for more light demanding species (Kitajima 1994). Temperate forest, mid-successional tree species were found to have greater phenotypic plasticity than either early or late successional species (Neuner and Bannister 1995), which was suggested to be an adaptation to a broader range of ecosystem conditions in midsuccession. Similar photosynthetic acclimation to light was observed in a gap specialist and a generalist *Piper* species (Walters and Field 1987, Field 1988).

Even though the *Psychotria* species studied were, in general, more plastic for gas exchange variables than for structural variables, the largest differences in plasticity among species were found for structural variables such as root:shoot ratio or leaf area ratio (Fig. 3). Gap species (e.g., *P. grandis*, *P. pubescens*, and *P. brachiata*) were more plastic in their allocation to roots or leaves than were understory species (e.g., *P. chagrensis*, *P. limonensis*, and *P. acuminata*). While much of the research on plant response to variation in forest light environment has focused on the photosynthetic responses of leaves, net whole plant carbon gain and photosynthate allocation are crucial to define seedling ecology and to understand plant persistence beneath a closed canopy (Canham 1988, Zipperlen and Press 1996). Inherently slow growth rates are often not due to low photosynthetic rates but to morphological features such as low leaf area per leaf dry mass (Lambers and Poorter 1992, Kitajima 1994, Atkin et al. 1996). Our results point to the existence of higher genetic restrictions in morphological plasticity in understory species than in gap species of *Psychotria*. The functional implications of this reduced morphological plasticity on light harvesting via leaf display and crown architecture can be very relevant in the ecological segregation of similar species co-occurring in a given forest (Canham 1988).

Higher leaf longevity diminishes nutrient losses and is a factor contributing to success in resource-limited environments (Lambers and Poorter 1992). Moreover, the light environment influences leaf longevity, with shade leaves typically having longer life-spans than sun leaves (Chabot and Hicks 1982, Sims and Pearcy 1992). Sun plants, however, typically have higher rates of leaf production, compensating for the more rapid leaf se-

nescence (Pearcy and Sims 1994). In agreement with this pattern, gap species of *Psychotria* exhibited shorter leaf life-spans than understory species. Since a component of plasticity involves structural changes in leaves on a developmental time scale (i.e., sun vs. shade leaves), leaf longevity interacts with phenotypic plasticity due to its influence on the speed at which a given genotype can track environmental changes. In the *Psychotria* species we studied, mean phenotypic plasticity increased with decreasing leaf longevity (Fig. 6), in agreement with the expected relationship between plasticity and leaf turnover rates. Leaf life-span is closely interrelated with several other plant traits (e.g., growth rate, leaf mass per unit area, photosynthetic capacity), and general trends in these relationships, such as fast growth and high leaf turnover in high resource environments, have been found across diverse ecosystems (Reich et al. 1991, 1992, Ryser 1996, Prado and De Moraes 1997), although some of these traits are not always correlated within a given habitat (see Reich 1993). Since plasticity of the *Psychotria* species has been explored in a controlled environment, while leaf longevity was estimated in field populations, the correlation found here between plasticity and leaf turnover requires confirmation by additional studies. Besides, leaf longevity itself can exhibit phenotypic plasticity (Ackerly and Bazzaz 1995, Kitajima et al. 1997), which also requires further research.

In most ecophysiological studies of light responses of plants, only a small group of species is compared. With a few exceptions (e.g., Popma and Bongers 1988, Osunkoya et al. 1994, and Veenendaal et al. 1996), these studies only include two or three species, one from each different light environment. Patterns of plastic responses to the light environment based on a few species, each representing a contrasting ecological strategy, should be interpreted with caution. As we have shown here, a given shade tolerance can be associated with a different plasticity in response to light even within a taxonomically close group of species (i.e., subgenus). We have found different levels of plasticity and leaf turnover within both gap and understory species, and within each of the two phylogenetic groups of species of *Psychotria*. However, mean phenotypic plasticity for a set of structural and physiological variables was positively related to light availability of natural populations and to leaf longevity. Even though understory species did not perform better than gap species in the low PPFD treatment, the larger plasticity of gap species was consistent with a reappraisal of the specialization hypothesis (Lortie and Aarssen 1996). Gap and understory species of *Psychotria* differed more in their plastic response to the light environment than in the mean phenotypic response to each light environment. Ecological studies comparing sympatric plant species sharing resources in very diverse environments would probably benefit more from the combined exploration of plasticity and specialization than

from only the search for species differences regarding specialization following the classical NeoDarwinian view of adaptation.

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## LITERATURE CITED

- Ackerly, D. D., and F. A. Bazzaz. 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* **101**:289–198.
- Atkin, O. K., B. Botman, and H. Lambers. 1996. The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland *Poa* species. *Functional Ecology* **10**:698–707.
- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**:351–371.
- Bazzaz, F. A. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge, UK.
- Bazzaz, F. A., and R. W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* **54**:313–316.
- Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* **11**:287–310.
- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**:115–155.
- Canham, C. D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* **69**:786–795.
- Chabot, B. F., and D. J. Hicks. 1982. The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**:229–259.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**:233–260.
- Chapin, F. S. 1991. Integrated responses of plants to stress. *BioScience* **41**:29–36.
- Chapin, F. S., K. Autumn, and F. Pugnaire. 1993. Evolution of suites of traits in response to environmental stress. *American Naturalist* **142**:S78–S92.
- Chapin, F. S., A. J. Bloom, C. B. Field, and R. H. Waring. 1986. Plant responses to multiple environmental factors. *BioScience* **37**:49–57.
- Chazdon, R. L. 1992. Photosynthetic plasticity of two rain forest shrubs across natural gap transects. *Oecologia* **92**:586–595.
- Coleman, J. S., K. D. M. McConaughay, and D. D. Ackerley. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* **9**:187–191.
- Coley, P. D. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**:531–536.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California, USA.
- Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**:431–451.
- Fetcher, N., S. F. Oberbauer, G. Rojas, and B. R. Strain. 1987. Effects of light regime on photosynthesis and growth in seedlings of tropical rainforest trees. *Revista de Biología Tropical (Supplement)* **35**:97–110.
- Field, C. B. 1988. On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. *Australian Journal of Plant Physiology* **15**:343–358.
- Fredeen, A., and C. Field. 1996. Ecophysiological constraints on the distribution of *Piper* species. Pages 597–618 in S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York, USA.
- Gentry, A. H., and C. Dodson. 1987. Contribution of non trees to species richness of a tropical rain forest. *Biotropica* **19**:149–156.
- Hamilton, C. W. 1989a. A revision of mesoamerican *Psychotria* subgenus *Psychotria* (Rubiaceae). Part I: introduction and species 1–16. *Annals of the Missouri Botanical Garden* **76**:67–111.
- Hamilton, C. W. 1989b. A revision of mesoamerican *Psychotria* subgenus *Psychotria* (Rubiaceae). Part II: introduction and species 17–47. *Annals of the Missouri Botanical Garden* **76**:386–429.
- Hirose, T. 1987. A vegetative plant growth model: adaptive significance of phenotypic plasticity in dry matter partitioning. *Functional Ecology* **1**:195–202.
- Huber, H. 1996. Plasticity of internodes and petioles in prostrate and erect *Potentilla* species. *Functional Ecology* **10**:401–409.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**:419–428.
- Kitajima, K., S. S. Mulkey, and S. J. Wright. 1997. Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. *Oecologia* **109**:490–498.
- Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**:188–261.
- Lorimer, C. G., and L. E. Frelich. 1988. Estimating gap origin probabilities for canopy trees. *Ecology* **69**:778–785.
- Lortie, C. J., and L. W. Aarssen. 1996. The specialization hypothesis for phenotypic plasticity in plants. *International Journal of Plant Sciences* **157**:484–487.
- Monson, R. K. 1996. The use of phylogenetic perspective in comparative plant physiology and developmental biology. *Annals of the Missouri Botanical Garden* **83**:3–16.
- Mulkey, S. S., A. P. Smith, and S. J. Wright. 1991a. Comparative life history and physiology of two understory Neotropical herbs. *Oecologia* **88**:263–273.
- Mulkey, S., and S. J. Wright. 1996. Influence of seasonal drought on the carbon balance of tropical forest plants. Pages 187–216 in S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York, USA.
- Mulkey, S. S., S. J. Wright, and A. P. Smith. 1991b. Drought acclimation of an understory shrub (*Psychotria limonensis*; Rubiaceae) in a seasonally dry tropical forest in Panama. *American Journal of Botany* **78**:579–587.
- Mulkey, S. S., S. J. Wright, and A. P. Smith. 1993. Comparative physiology and demography of three Neotropical forest shrubs: alternative shade-adaptive character syndromes. *Oecologia* **96**:526–536.
- Neuner, G., and P. Bannister. 1995. Frost resistance and susceptibility to ice formation during natural hardening in re-

- lation to leaf anatomy in three evergreen tree species from New Zealand. *Tree Physiology* **15**:371–377.
- Newell, E. A., E. P. McDonald, B. R. Strain, and J. S. Den-slow. 1993. Photosynthetic responses of *Miconia* species to canopy openings in a lowland tropical rain forest. *Oecologia* **94**:49–56.
- Osunkoya, O. O., J. E. Ash, M. S. Hopkins, and A. W. Graham. 1994. Influence of seed size and seedling ecological attributes on shade tolerance of rain forest tree species in Northern Queensland. *Journal of Ecology* **82**:149–163.
- Pearcy, R. W., and D. A. Sims. 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. Pages 145–174 in M. M. Caldwell and R. W. Pearcy, editors. *Exploitation of environmental heterogeneity by plants: ecophysiological processes above and below ground*. Academic Press, San Diego, California, USA.
- Pintado, A., F. Valladares, and L. G. Sancho. 1997. Exploring phenotypic plasticity in the lichen *Ramalina capitata*: morphology, water relations and chlorophyll content in North- and South-facing populations. *Annals of Botany* **80**:345–353.
- Popma, J., and F. Bongers. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* **75**:625–632.
- Prado, C. H. B. A., and J. A. V. P. De Moraes. 1997. Photosynthetic capacity and specific leaf mass in twenty woody species of Cerrado vegetation under field conditions. *Photosynthetica* **33**:103–112.
- Reich, P. B. 1993. Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates—the blind men and the elephant retold. *Functional Ecology* **7**:721–725.
- Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf life span as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* **86**:16–24.
- Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**:365–392.
- Ryser, P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology* **10**:717–723.
- Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* **24**:35–68.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* **17**:667–693.
- Sims, D. A., and R. W. Pearcy. 1992. Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Araceae) to a transfer from low to high light. *American Journal of Botany* **79**:449–455.
- Spitze, K., and T. D. Sadler. 1996. Evolution of a generalist genotype: multivariate analysis of the adaptiveness of phenotypic plasticity. *American Naturalist* **148**:S108–S123.
- Strauss-Debenedetti, S., and F. A. Bazzaz. 1991. Plasticity and acclimation to light in tropical moraceae of different successional positions. *Oecologia* **87**:377–387.
- Strauss-Debenedetti, S., and F. A. Bazzaz. 1996. Photosynthetic characteristics of tropical trees along successional gradients. Pages 162–186 in S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York.
- Sultan, S. E. 1992. What has survived of Darwin's theory? Phenotypic plasticity and the Neo-Darwinian legacy. *Evolutionary Trends in Plants* **6**:61–71.
- Uhl, C., K. Clark, N. Dezzee, and P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**:751–763.
- Valladares, F. 1999. Architecture, ecology and evolution of plant crowns. Pages 121–194 in F. I. Pugnaire and F. Valladares, editors. *Handbook of functional plant ecology*. Marcel Dekker, New York, New York, USA.
- Valladares, F., M. T. Allen, and R. W. Pearcy. 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. *Oecologia* **111**:505–514.
- Veenendaal, E. M., M. D. Swaine, R. T. Lecha, M. F. Falsch, I. K. Abebrese, and K. Owusu-Afriyie. 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* **10**:501–511.
- Waller, D. M. 1991. The dynamics of growth and form. Pages 291–320 in M. J. Crawley, editor. *Plant ecology*. Blackwell Scientific Publications, Wiltshire, UK.
- Walters, M. B., and C. B. Field. 1987. Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. *Oecologia* **72**:449–456.
- Wilkinson, L. 1990. SYSTAT: The system for statistics. Version 6.0. SYSTAT, Evanston, Illinois, USA.
- Wright, S. J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology* **72**:1643–1657.
- Wright, S. J., J. L. Machado, S. S. Mulkey, and A. P. Smith. 1992. Drought acclimation among tropical forest shrubs (*Psychotria*, Rubiaceae). *Oecologia* **89**:457–463.
- Zipperlen, S. W., and M. C. Press. 1996. Photosynthesis in relation to growth and seedling ecology of two dipterocarp rain forest tree species. *Journal of Ecology* **84**:863–876.