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Physiological performance and growth under low and high light treatments in three neotropical species of *Cecropia*

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Resumen. *Tres especies de* Cecropia *mostraron aclimatación lumínica en parámetros asociados a fotosíntesis medidos en condiciones de vivero. Dos de estas especies son especialistas respecto del recurso luz (*C. tessmannii*, de sombra, y* C. membranacea*, de sol), mientras que la tercera,* C. pachystachya*, es generalista. La especie de sombra fue la que mostró menor flexibilidad en los parámetros medidos. La tasa fotosintética varió positivamente con la intensidad lumínica, transpiración .y conductancia. El orden relativo de las tasas fotosintéticas y de crecimiento file el mismo para coda una de las tres especies siendo la especie generalista la que presentó los mayores valores.*

Abstract. *Light acclimation in gas exchange properties was found in three different Neotropical species of* Cecropia *under greenhouse conditions. Two species are habitat specialists (*C. tessmannii*, a shade species and* C. membranacea*, a sun species), and the third ís a generalist (*C. pachystachya*). The shade species showed the least flexibility. Rates of photosynthesis were positively correlated with light intensify, transpiration and conductance. Photosynthetic rates for each species ranked in the same order as growth rates. The generalist species,* C. pachystachya *performed, oil average, better than any of the specialists in their own light environment.*

Introduction

It has been observed that plants adapted to growing in low light habitats are not able to attain high photosynthetic rates when exposed to high light, but can perform efficiently under low light conditions. Conversely, plants adapted to growing in high light conditions have relatively high photosynthetic rates at a saturating light intensity but are less efficient photosynthetically in shade habitats (Boardman 1977). Due to the fact that photosynthesis is a light dependent process, the ability of a plant to adjust both structurally and biochemically to the light environment is very important for the survival of species growing in variable light environments. In fact, a broad suite of plant species show these characteristics (Boardman 1977, Bazzaz and Carlson 1982, Chazdon and Pearcy 1986, Walters and Field 1987, Sims and Pearcy 1989, Seeman 1989, but see Clough et al. 1979). Acclimation capability is very important for plants that may germinate in habitats with different irradiances or in gaps that are transformed later in the understory of mature forests. For example, the daily photon flux density can be ten-fold greater in large gaps than in understory habitats (Walters and Field 1987).

Cecropia (Moraceae) is a common genus of myrmecophytic plants which are found in the early successional habitats in neotropical forests where disturbance and sunlight are high (Davidson et al. 1990). While some species of *Cecropia* can be found growing across a wide range of light conditions (Folgarait, pers.obs., Berg, pers.com), very few species can be considered shade tolerant (Smith 1982) and are found only in the understory of tropical forests (Davidson et al. en prensa). In this study, three different species of *Cecropia* were compared in terms of instantaneous photosynthetic rate, stomatal conductance, transpiration, and water-use efficiency. *C. tessmannii,* a shade species, and *C. membranacea,* a sun species, are both native to Peru, while *C. pachystachya* is found growing in several habitats in Argentina ranging from high to low light availability. Early successional species are known to have high photosynthetic flexibility (Bazzaz and Carlson 1982). If a large degree of plasticity is needed to be a habitat generalist, and this comes at a significant cost, then generalists should perform worse under any light condition than specialists for a particular habitat (Walters and Field 1987). Therefore, I expected to find: 1) a lower photosynthetic and growth performance for the generalist species in comparison with the specialist species, 2) a higher photosynthetic and growth performance for each specialist species in its own light regime, 3) a higher photosynthetic acclimation capacity for the generalist species, and 4) a lower capacity for photosynthetic acclimation for the specialist species.

Methods

The three *Cecropia* species were grown from seed in the Department of Biology's tropical greenhouse at the University of Utah. Plants were randomly assigned to one of two treatments after germination: sun (which received 30% of full sunlight, to protect sensitive tropical leaves from light damage) or shade (adding a layer of shade cloth so 10% of full sunlight was received). All plants received the same water and nutrient regimes standard for the tropical greenhouses (3 heavy watering/day; 20% N, 20%v P, 20% K fertilizer twice weekly). Plants were transferred to bigger pots when they needed more space for the roots. Plants were rotated weekly to minimize block effects.

C. tessmannii and *C. membranacea* germinated at the end of July 1989 so they were 10 months old at the time of the measurements. *C. pachystachya* had germinated at the end of October 1989; and was 7 months old at the time of the measurements. Photosynthetic measurements were made during May of 1990 from 11 am to 3 pm, the period of highest light intensity and photosynthetic rates. Due to the fact that I worked with natural irradiances that could not be controlled precisely (although, they were registered), an ANCOVA (Analysis of covariance) was performed to account for variation in light intensity differences among species or treatments during the analysis of the data.

Gas exchange parameters were obtained using a LiCor 6200 portable photosynthetic system (Lincoln, NE.). Two mature leaves (of similar age among individuals and species) per plant, six plants per species, in both a shade and a sun treatment were used. The data were *In* transformed to 6t the assumptions necessary to run the Analysis of Covariance. JMP (SAS) package was used in statistical analyses. ANCOVA were performed to establish gas exchange differences between light treatments and among species using light intensity as a covariate. ANCOVA for different slopes were used when the interaction term between the independent variable and the covariate was significant. Otherwise, an ANCOVA for equal slopes was performed.

Table 1. Mean and standard deviation in the number of leaves produced and final height (cm) after the first 7 months of growth for the shade specialist (N=16). sun specialist (N=16) and the generalist species (Nsu=10, Nsh=15) under a low and high light treatmen

	C. tessmannii		*C. membranacea*		*C. pachystachya*	
	Low	High	Low	High	Low	High
# leaves	8.1±0.3	8.8±0.5	13.1±1.2	12.3±3.7	22.5±1.8	25.5±1.7
Height	16.6±2.2	20.8±2.1	72.6±19.5	65.6±13	67.7±19	89.4±6.9

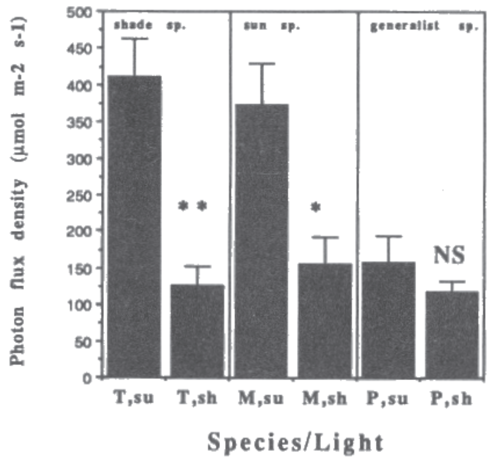

Fig. 1. Mean and standard error of photon flux density for *C. tessmannii* (T)*, C. membranaceae* (M) and *C. pachystachya* (P) under high (su) and low (sh) light treatments. Probability values are the result of t-test comparisons between treatments for each species. NS: P>0.05, *: 0.01<P<0.05, **: P<0.01.

Results

Light intensities differed significantly between light treatments for two of the three species at the time of the measurements (Fig. 1). In general, mean instantaneous photosynthetic rate averages were higher at higher photon flux densities (Fig. 1 and 2A). Therefore, in general, photosynthetic rates were significantly higher for each species in the high light treatment (Fig. 2A). Results of ANCOVA showed significant differences in photosynthetic rates among species when light intensity differences were taken into account (ANCOVA P<0.0001; species: P<0.0013, light intensity: P<0.0001). Significant differences in photosynthesis were also found among species within each treatment (ANCO VA sun: P<0.0001, species: P<0.0002, light intensity: P<0.0001, species*light intensity: P < 0.0001; ANCOVA shade: P < 0.0002, species: P < 0.0473, light intensity: P < 0.0001). The photosynthetic rank for each species under the high light treatment changed when the adjusted means were considered (Fig. 2A).

Conductance values differed significantly between light treatments for *C. membranacea* and *C pachystachya,* being higher under the high light treatment. This was not seen, however, in the shade specialist, *C. tessmannii* (Fig. 2B). Significant differences among species for conductance values were also found (ANCOVA P<0.0001, species: P<0.005, light intensity: P<0.0096, species*light intensity: P<0.0015). As with the measurements of stomatal conductance, the highest transpiration rates were found for each species under the high light treatment (Fig. 2C). Transpiration rates also differed significantly among species (ANCOVA P<0.0001; species: P < 0.0034, light: P < 0.0001, species*light: P < 0.0004). Significant differences in photosynthetic rates and transpiration among species lead to marked significant differences in water-use efficiency (ANCOVA P<0.0015; species: P>0.0082, light intensity: P<0.0013, species*light intensity: P<0.0024). However, the specialist species, *C. tessmannii* and C *membranacea,* showed a consistent, significantly higher water use efficiency under the low light treatment (Fig. 2D).

The shade species showed the least flexibility in the gas exchange characteristics measured, although all the species, in general, had shown the ability to change their performance according to the environment (Fig. 2).

The generalist species showed higher leaf production rates and final height at the end of the first 7 months of life in comparison with the specialist species. When comparing the specialist species, the sun species grew faster than the shade species (Table 1).

Discussion

Early successional species (Bazzaz and Carlson 1982), generalist species (Walters and Field 1987), and understory species (Chazdon and Pearcy 1986, Sims and Pearcy 1989) have all been reported to be able to light acclimate. The data presented here demonstrate that, for the three species of *Cecropia,* there was a high degree of photosynthetic flexibility, as predicted for generally early successional species. However, the shade species showed the least flexibility, having the lowest overall instantaneous photosynthetic rate under the high light treatment, even though it was the species under highest irradianees during the time of the measurements (Fig. 1 and 2A).

In agreement with Walter and Field (1987), f did not find strong evidence that, at least for the gas exchange characteristics, these specialists were better suited or performed better in their own light regime than the generalist (Fig. 2). Since the light saturation levels were not known for these species, caution should be taken especially in the comparison between species that performed under very different irradianees, such as in the high light treatment. However, when light irradiance differences were considered (see adjusted means) the generalist species had a higher average photosynthetic rate than the other two species under high light treatment. If the average irradiance for the generalist species had been similar to that used for the sun species under high light conditions, *C. pachystachya* would have had photosynthetic rates as high or higher than *C. membranacea* (Figs. 1 and 2A). Under similar irradianees, such as in the low light treatment, *C. pachystachya* attained higher photosynthetic rates than the other two species. If the photosynthetic performance of each species is combined across light treatments (for means or adjusted means) and then ranked, *C. pachystachya* show a better performance than the specialist species. This ranking was concordant with the number of leaves produced and the height attained during their first 7 months of life (Table 1). Although the generalist species was the only species growing during par(of its seven months under an increasing photoperiod (spring), my personal experience of working with these plant can predict that the differences found in Table 1 would also be found if the plants were grown simultaneously. These data support the idea that growth rates are dependent on both photosynthetic properties of the plants as well as key environmental resources, such as light availability.

Higher conductance and transpiration values were found more often in high light than in low light treatments. This may be due to the higher heat loads, leaf temperatures and different energy budgets. Under higher heat loads, stomatal apertures were larger or more common leading to larger values of conductance and transpiration, as well as photosynthesis. These results also reflected the acclimation response of the plants under different conditions of light availability (Fig. 2A, B and C). Water use efficiency differed between light treatments, being higher in the shade treatment for the specialist species (Fig. 2D). This pattern may had resulted from 1) a higher ratio of transpiration to photosynthesis in the high light treatment and/or 2) lower ratios of transpiration to photosynthesis under low light due to lower photosynthesis (below the light saturating levels of photosynthesis). The generalist species, *C. pachystachya,* seemed to had a more conservative strategy in terms of transpiration rates, combined with a very high photosynthetic capacity, resulting in a higher water use efficiency (see adjusted means in Fig. 213) under high light conditions.

The results shown here suggested that generalist species did not perform worse than any specialist at least under the low light level. Moreover, the generalist species performed better than the specialists without detrimental effects on the growth parameters measured. This does not mean that there is no cost associated with physiological fexibility but, at least, it was not evident when compared in this study to other species in the same genus. When the two specialist species were compared, *C. tessmannii* had the highest photosynthetic performance under the low light treatment, while *C. membranacea* did better in the high light treatment (Fig. 2A). As expected, each specialist performed better in a light regime similar to its native light environment. However, both species had the flexibility to acclimate to a different light regime. Therefore, it can be suggested that the

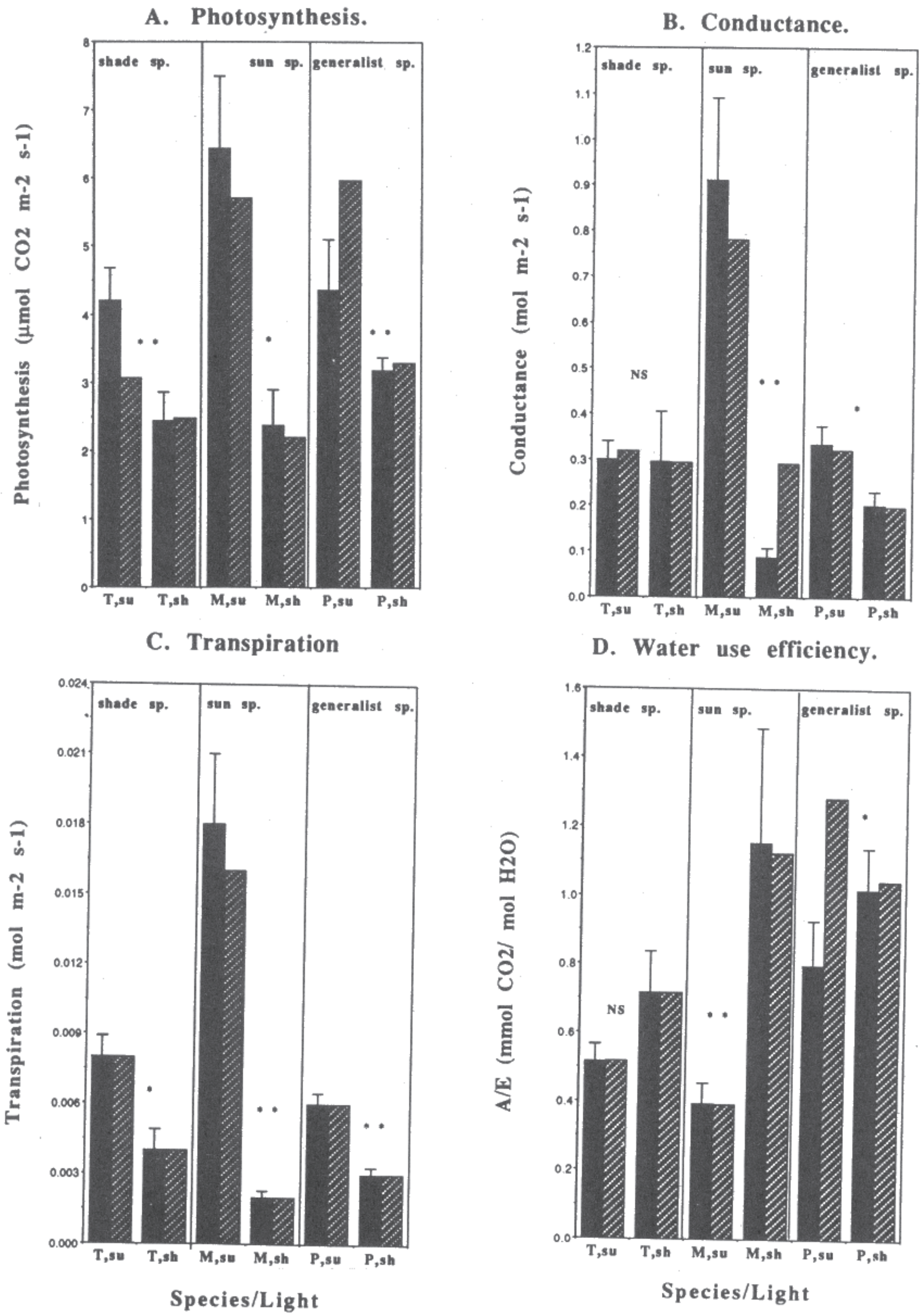

Fig 2. Mean (black columns). adjusted means (hatched columns) and standard errors for photosynthetic rates (A), conductance (B), transpiration rates (C) and water use efficiency (D) for *C. tessmannii* (T), *C. membranacea* (M), and *C. pachystachya* (P) under high (su) and low (sh) light treatments. Probability values were the result of ANCOVA comparisons for each gas exchange property between treatments calculated separately for each species. Significance symbols as in fig. 1.

absence of each specialist in habitats with opposite light availability may be related with other selective pressures (e.g. dispersal, competition, herbivory) rather than with physiological-photosynthetic constraints such as light acclimation capabilities. There was a general tendency for the fast growing species (i.e. *C. pachystachya* and *C. membranacea*) to show, on average, higher photosynthetic rates than the slow growing species (*C. tessmannii*) (Fig. 2A and Table 1).

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