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Photosynthetic acclimation to light in juveniles of two cloud forest tree species

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Abstract The photosynthetic response of juveniles of *Decussocarpus rospigliosii*, an emergent primary forest species and shade tolerant in its juvenile stages and *Alchornea triplinervia*, a gap-colonizing species of tropical cloud forest in Venezuela was studied. Daily courses of microenvironmental variables and gas exchange under contrasting light conditions (gap and understory) were carried out in their natural environment and transplanted to different light regimes (shade and sun) in the field. The photosynthetic response and some anatomical characteristics of plants from different treatments were analyzed in the laboratory. Photosynthetic rates were low for both species, and were negative during some diurnal periods, related to the low photosynthetically active radiation levels obtained at both gap (6% of total radiation) and understory (2%). *A. triplinervia* shows higher rates (1.5–3.0 $\mu molm^{-2}s^{-1}$) than *D. rospigliosii* (0.7–1.1 $\mu molm^{-2}s^{-1}$). Both species showed increased photosynthetic rates when grown in gaps. *A. triplinervia* did not adjust its maximum photosynthetic rates to the prevailing light conditions. In contrast, *D. rospigliosii* responded to increased light levels. Both species showed low light compensation points when grown under total shade. There was a partial stomatal closure generally during midday in *D. rospigliosii*. *A. triplinervia* presented lower leaf conductances, transpiration rates and lesser stomatal control. Some leaf anatomical characteristics, in both species, were affected by variations in the light regime (i.e. increased leaf thickness, leaf specific weight and stomatal density). These results suggest that both species have the ability to respond to variations in their natural light environments, therefore maintaining a favorable carbon balance during the day.

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Key words *Alchornea triplinervia* · *Decussocarpus rospigliosii* · Photosynthetic acclimation · Sun/shade adaptation · Tropical cloud forest

Introduction

Tropical rain forests are complex ecosystems, both in their biological diversity, as well as in their spatial arrangement, characterized by a structure of multiple strata which also determine a complex light environment. Gap formation accentuates spatial heterogenity in terms of environmental conditions, and at the same time dominates the dynamics of these forests and plays an important role in the evolution of life history characteristics of plant populations and in the distribution of individuals within the forest (Bazzaz 1984).

Under non-disturbed conditions, the forest's complex structure determines the existence of a vertical profile in light intensity, as well as air humidity, CO_2 concentration, temperature and wind velocity. Light intensity is the factor that most influences the vegetation density of the understory, photosynthesis, leaf area index and leaf structure (Mooney et al. 1984; Medina 1986). Most of the emergent tree species in tropical humid forests require an opening in the canopy in order to grow and develop and, furthermore, species may be distinguished by the size of the gap and the microsite within the gap where they may regenerate (Hartshorn 1978, 1980; Whitmore 1978, 1989; Denslow 1980, 1987; Bazzaz 1984; Clark and Clark 1987; Swaine and Whitmore 1988). As a consequence of this hypothesis, it has been suggested that important characteristics of tropical forests such as richness of tree species and diversity of growth forms may be explained, at least partially, in terms of the frequency with which trees fall and by the heterogenity of the created conditions within those gaps (Orians 1982).

The environmental characteristics of gaps, especially with respect to light and its distribution, are determined by size, form, orientation and the manner in which it was created, and, additionally, by the severity of the disturbance (Bazzaz 1984). The succession that follows gap formation

is likely to depend upon key characteristics of the species as seedlings and seeds, and specially their response to the new light climate and their capacity to compete with each other (Kwesiga et al. 1986). Some specific physiological adaptations of species which colonize gaps are similar to those found in pioneer species, generally presenting higher light-saturated photosynthetic rates, transpiration and respiration rates, stomatal conductivities and nitrogen content than those of shade-tolerant species (Boardman 1977; Bazzaz and Pickett 1980; Lebron 1980; Oberbauer and Strain 1984; Fetcher et al. 1987).

Rapid changes which occur in the light environment of a particular area due to the creation of a gap greatly influence the photosynthetic rates and water balance of the upcoming regeneration and forest understory species. Plant responses can be through acclimation or by forming new leaves which are adapted to the new light conditions (Bazzaz and Carlson 1982). Differences between sun and shade adapted plants in tropical forests are not clear, since a plant may germinate in a particular environment and develop in another or in a series of contrasting, alternating environments before reaching the canopy. Therefore, there may be changes in morphological, physiological and biochemical properties during the trees' development which would determine its capacity to acclimate to different light regimes, in order to increase its growth rate to a maximum (Bazzaz 1984; Fetcher et al. 1987; Clark and Clark 1987).

In this work we examine the photosynthetic and stomatal response and some anatomical characteristics to contrasting light conditions (understory and gap) in juveniles of two cloud forest tree species, and evaluate the hypothesis that tree species with different regeneration patterns should have different physiological responses in relation to CO_2 assimilation and acclimation capacity to a range of light environments. The species, with different successional characteristics, are *Decussocarpus rospigliosii*, an emergent species of the primary forest which in its juvenile stages is shade-tolerant, and *Alchornea triplinervia*, a species which colonizes gaps; both are dominant species of Andean cloud forests (Sarmiento et al. 1971).

Materials and methods

Site characteristics and plant material

The study site was located in La Carbonera, Cordillera de los Andes (8°39'N; 71°24'W), between 2200 and 2500 m asl. Mean annual temperature is 14.9 °C with a maximum below 20 °C and minimum above 8.5 °C. Mean annual precipitation is between 1500 and 1800 mm, with a wet season (March–November) and a mild dry season (December–March). Cloud cover and fog occur almost daily due to the condensation of saturated air from the Lago de Maracaibo Basin.

Sarmiento et al. (1971) classifies the vegetation as a high montane cloud forest, dominated by evergreen species with a mixed and irregular canopy. As a consequence of the high humidity, cellular and vascular epiphytes and epiphyles (Araceae, Orchidaceae, Bromeliaceae, mosses and lichens) are frequent. The understory is dense, composed mainly of shrubs and young trees of the species from the higher strata (Lamprecht and Veillon 1957). *Decussocarpus rospigliosii* (Pilger) de Laubenfels (Podocarpaceae) is an emergent tropical conifer which may reach 45 m. Leaves are oval-lanceolate, opposite, amphistomatic, coriaceous, between 7 and 22 mm long and 3 to 6 mm in width. *Alchornea triplinervia* (Spren.) M. Arg. (Euphorbiaceae) is a species from the early successional stages. It may reach up to 30 m at the study site and it is found as seedlings or young plants in gaps produced by fallen trees. Leaves are single alternate, coriaceous from 20 to 70 mm long and 20 to 50 mm in width (Huber 1986; Steyermark and Huber 1978).

Field studies

A 100 m^2 gap produced by several fallen trees was chosen as the study site for seedlings and juveniles (20–40 cm) of *A. triplinervia*. Juveniles of *D. rospigliosii* (20–40 cm) were located in a non-disturbed forest area adjacent to the gap.

Fourteen daily courses of carbon balance and microclimatic variables were carried out at each site monthly from September 1989 to January 1991. A fully portable system, consisting of a leaf chamber, an air supply unit, and an infrared gas analyser unit, operating in the open mode was used to measure gas exchange in the field (LCA-2, The Analytical Development Co. Ltd. Hoddesdon, Herts, England). The leaf chamber contained a solid state humidity sensor, a thermistor for chamber temperature measurements, and a quantum sensor for photosynthetically active radiation (PAR) measurements. Gas exchange rates were calculated from flow rates, projected leaf surface area sealed within the chamber, and CO_2 and water vapor concentration differences between reference and analysis air (von Caemmerer and Farquhar 1981). The gas exchange measurements [conductance (Gs), CO_2 assimilation (A) and transpiration (E) rates] were conducted on five newly and completely expanded leaves of five individuals of each species, at 1–2 h intervals.

In order to study plant responses to changes in the forest's light microenvironment, individuals of each species were transplanted to polyethylene bags (0.0182 m^3) with a 50:50 sand, forest soil mixture. These plants were placed in a partially shaded site for 4 months as a recuperating period. Afterwards, ten plants of each species were placed in their natural habitat (*A. triplinervia* in gaps; *D. rospigliosii* in the understory) for 3 months. Individuals of each species were randomly divided into two groups, one remained under natural conditions while the other was transferred to the contrasting environment for 9 months. After this period, plants were brought to the laboratory for measurements under controlled conditions. Leaf conductance and CO_2 assimilation rates were measured before and after transferring plants to the different light treatments. Air and leaf temperatures were measured with copper-constantan thermocouples connected to a digital microvoltmeter (Data Precision, Model 258). Relative humidity was measured with Assmann ventilated psychrometers placed at 1.5 m at each site (gap and understory). Vapor pressure difference between leaf and air (VPD) were calculated from these temperatures and relative humidities (Pearcy et al. 1987). Total radiation was measured with a pyranometer.

Laboratory studies

Transplanted juveniles of both species were used to obtain CO_2 assimilation-leaf temperature and CO_2 assimilation-PAR curves. A detailed description of the system used in these laboratory experiments is given in Rada et al. (1992). For the former curves, leaf temperature was decreased from 32 °C down to 3 °C at approximately 4 °C intervals. PAR was maintained constant at saturating levels (650 $\mu molm^{-2}s^{-1}$). For the latter ones, leaf temperature was maintained constant at its optimum for photosynthesis (18 ± 1 °C). For both curves, 20 min elapsed before taking measurements at each interval in order to stabilize the plant's response.

Leaf material from the different treatments was used for total nitrogen determinations (microkjeldahl method; Müller 1961) and chlorophyll content (Arnon 1949). Some leaf morphological and anatomical characteristics were studied on material sampled in the field and placed in formalin (5 cc)-acetic acid (5 cc)-70% ethyl alcohol (90 cc; Johansen 1940). Epidermal sections were observed under a light microscope (Leitz, Dialux 20 EB) with a 1.25 XX light camera. Specific leaf weight was obtained after drying leaves of known area at 80 °C until reaching a constant weight.

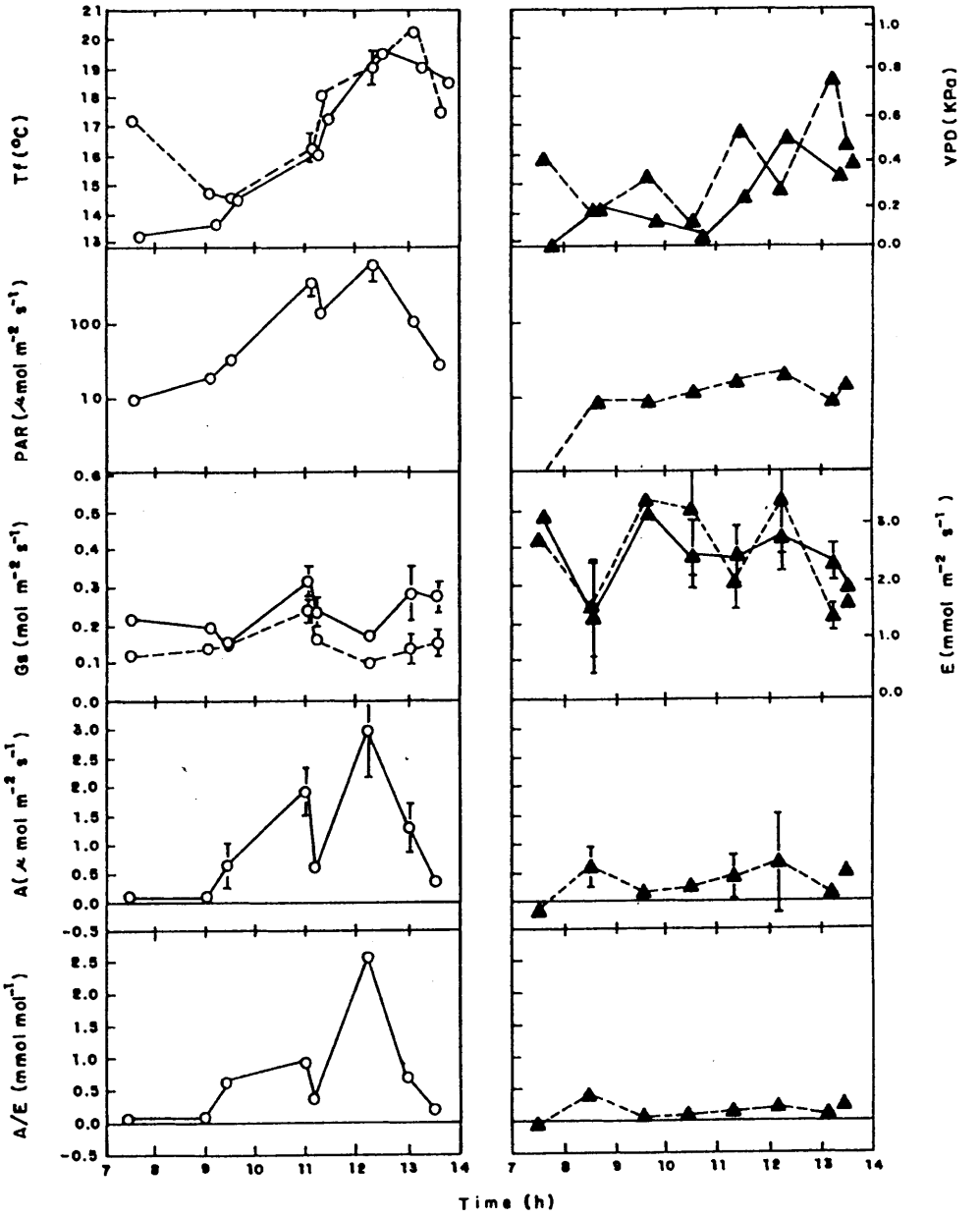


Fig. 1 Daily course of leaf temperature (Tf---), leaf-air VPD (——), photosynthetically active radiation (PAR), leaf conductance, (Gs– – –), transpiration rate (E——), photosynthetic rate (A) and water use efficiency (A/E) for *A. triplinervia* in a gap (○) and *D. rospigliosii* in the understory (▲) during the wet season (29 September 1989). *Vertical bars* are standard errors ($n = 4$)

Kruskall-Wallis (non parametric 1-way Analysis by ranks) and Friedman (2-way analysis by ranks; $P < 0.05$) was used for the statistical analysis. A rectangular hyperbola was used to describe the relationship between photosynthetic rate (A) and photosynthetically active radiation (PAR; Landsberg 1977).

Results

Daily courses of plant responses to their natural light environment

Figures 1 and 2 show representative mean daily variations in the microclimatic parameters and responses of *A. triplinervia* and *D. rospigliosii* juveniles, in their respective habitats, during wet (29 September 1989) and dry (17 January 1991) seasons. Maximum leaf temperatures and VPD were reached during midday (1130–1330 hours) for both species, when maximum radiation and air temperature were, generally, obtained (Fig. 1, 2). The difference in mean VPD between both species is approximately 0.1 KPa with a maximum of 0.85 KPa in *A. triplinervia* during the wet season (Fig. 1). Leaf conductance and transpiration rates for both species tend to follow each other throughout the day. For *A. triplinervia*, these variables were low and were not significantly different between wet and dry seasons (mean Gs 0.108–0.190 molm^{-2}s^{-1}, mean E 0.9–1.7 mmolm^{-2}s^{-1} t-test, $P < 0.05$). Even though *D. rospigliosii* showed higher values and greater fluctuations during both seasons, differences were not significant (mean Gs 0.176–0.388 molm^{-2}s^{-1}, mean E 1.22–2.86 mmolm^{-2}s^{-1}, t-test, $P < 0.05$).

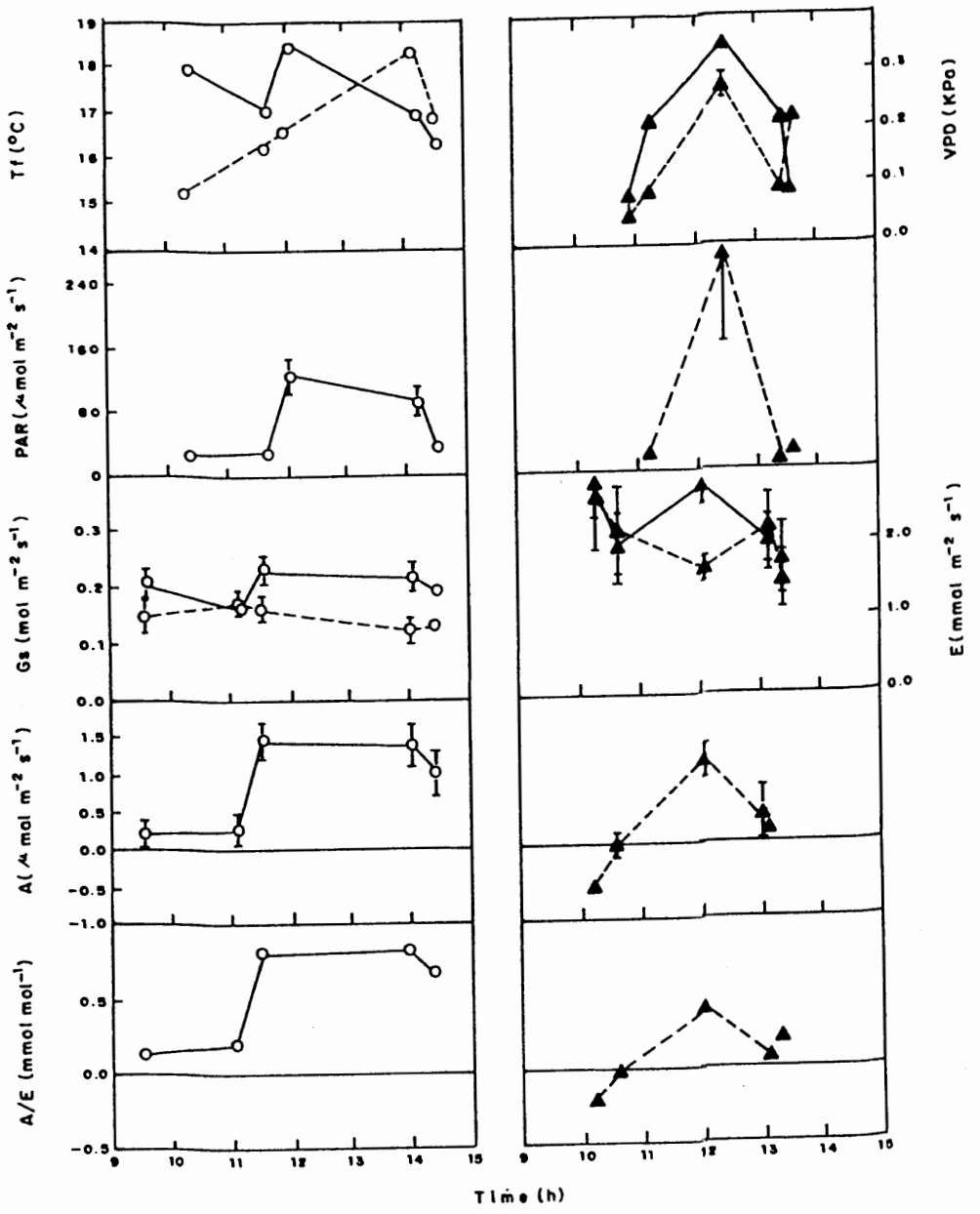


Fig. 2 Daily course of leaf temperature (T_f---), leaf-air VPD (——), photosynthetically active radiation (*PAR*), leaf conductance, (*Gs*---), transpiration rate (*E*——), photosynthetic rate (*A*) and water use efficiency (*A/E*) for *A. triplinervia* in a gap environment (○) and *D. rospigliosii* in the understory (▲) during the dry season (17 January 1991). *Vertical bars* are standard errors ($n = 4$)

Leaf conductance decreases during midday hours in *D. rospigliosii* when an increase in VPD was observed (Fig. 2). There is a negative exponential correlation between *Gs* and VPD ($r = 0.62$), which is not as evident for *A. triplinervia* (Fig. 3). However, for the daily course in Fig. 1, which corresponds to an exceptionally clear day during the wet season, the VPD for this latter species in the gap reached maximum values of 0.9 KPa. As a consequence, a partial stomatal closure together with a decrease in the transpiration rate were produced at midday (Fig. 1). Photosynthesis did not seem to be related to leaf conductance in either of the species during both wet and dry seasons (Fig. 1, 2). Maximum CO_2 assimilation rates were reached when PAR and VPD were greater (generally at midday).

Differences between the two light environments are observed in the mean PAR frequency distributions shown in Fig. 4, which correspond to 175 measurements for both seasons. The highest percentage for the gap was found in the 25–50 $\mu molm^{-2}s^{-1}$ interval (32%) with just 18.8% exceeding 100 $\mu molm^{-2}s^{-1}$. In the case of the understory, 53% of the measurements were found in the 0–10 $\mu molm^{-2}s^{-1}$ interval and approximately 81% between 0–25 $\mu molm^{-2}s^{-1}$. If we assume that values above 50 $\mu molm^{-2}s^{-1}$ are due to sun flecks (Chazdon 1988), only 12.5% of the measurements fell above this value; however, it contributed on average to 58% of the total PAR measured for the different dates. Hardly 6% of the measurements were above saturating light intensities for photosynthesis (100 $\mu molm^{-2}s^{-1}$).

Net photosynthesis-PAR relationships (Fig. 5) show that *A. triplinervia* in gaps reached maximum photosynthetic rates of 2–3 $\mu molm^{-2}s^{-1}$, at saturating PAR levels of 200 $\mu molm^{-2}s^{-1}$. *D. rospigliosii*, in the understory, showed maximum photosynthetic rates of 1 $\mu molm^{-2}s^{-1}$, saturating at PAR of 100 $\mu molm^{-2}s^{-1}$.

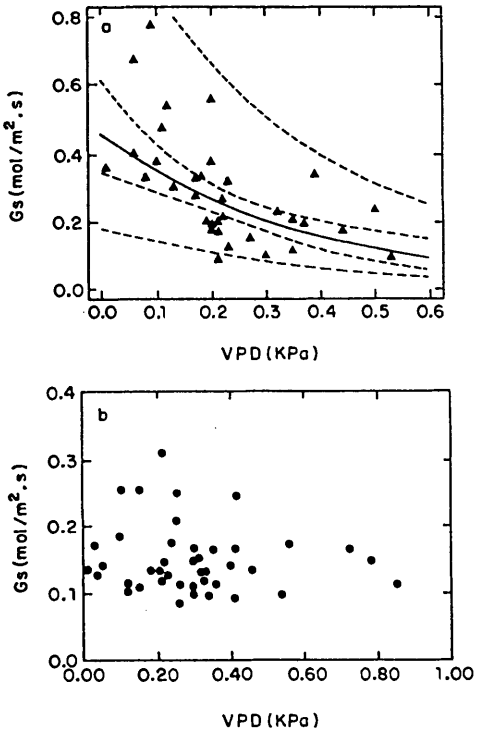


Fig. 3 Relationship between leaf conductance, (*Gs*), and leaf-air vapor pressure difference (*VPD*), for (**a**) *D. rospigliosii,* in the understory (▲), $Gs = e^{(-0.773-2.698\ VPD)}$, $r = 0.62$, SE = 0.43, and (**b**) *A. triplinervia* in a gap environment (●). All data for 10 days of field observations are included in the figure

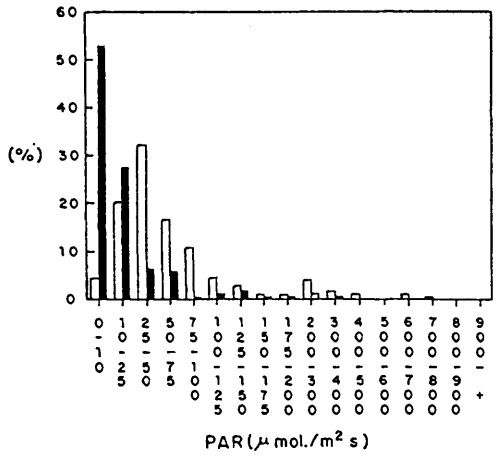
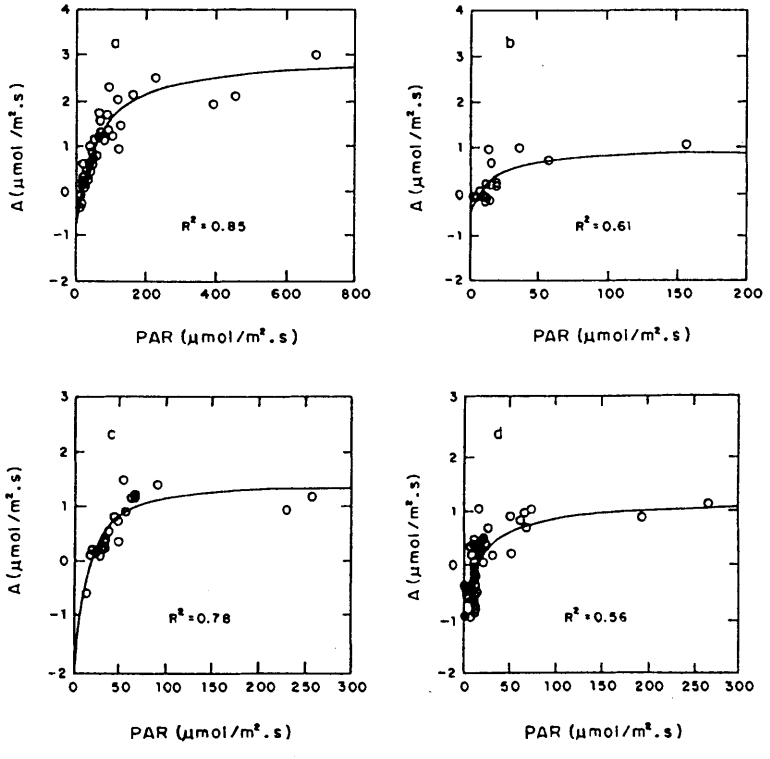


Fig. 4 Frequency distributions of photosynthetically active radiation (*PAR*) in a gap (□) and the understory (■). Values are representative of dry and wet seasons

Daily courses of plant responses in different treatments

Daily variations of microclimatic parameters and responses of transplanted *A. triplinervia* and *D. rospigliosii* in their natural light environment (gap and understory, respectively) and in contrasting light conditions (*A. triplinervia* in shade and *D. rospigliosii* in gaps), for the wet season are shown in Fig. 6. *A. triplinervia* in the gap shows a VPD in average 0.1 KPa higher than in the understory, with maximum values of 0.4 KPa in both treatments. Leaf conductance and transpiration in the gap were higher than in the

Fig. 5 Relationship between the photosynthetic rate (*A*) and photosynthetically active radiation (*PAR*) for *A. triplinervia* in a gap (**a**) and in the understory (**b**) and *D. rospigliosii* in a gap (**c**) and in the understory (**d**). Values are representative of dry and wet seasons



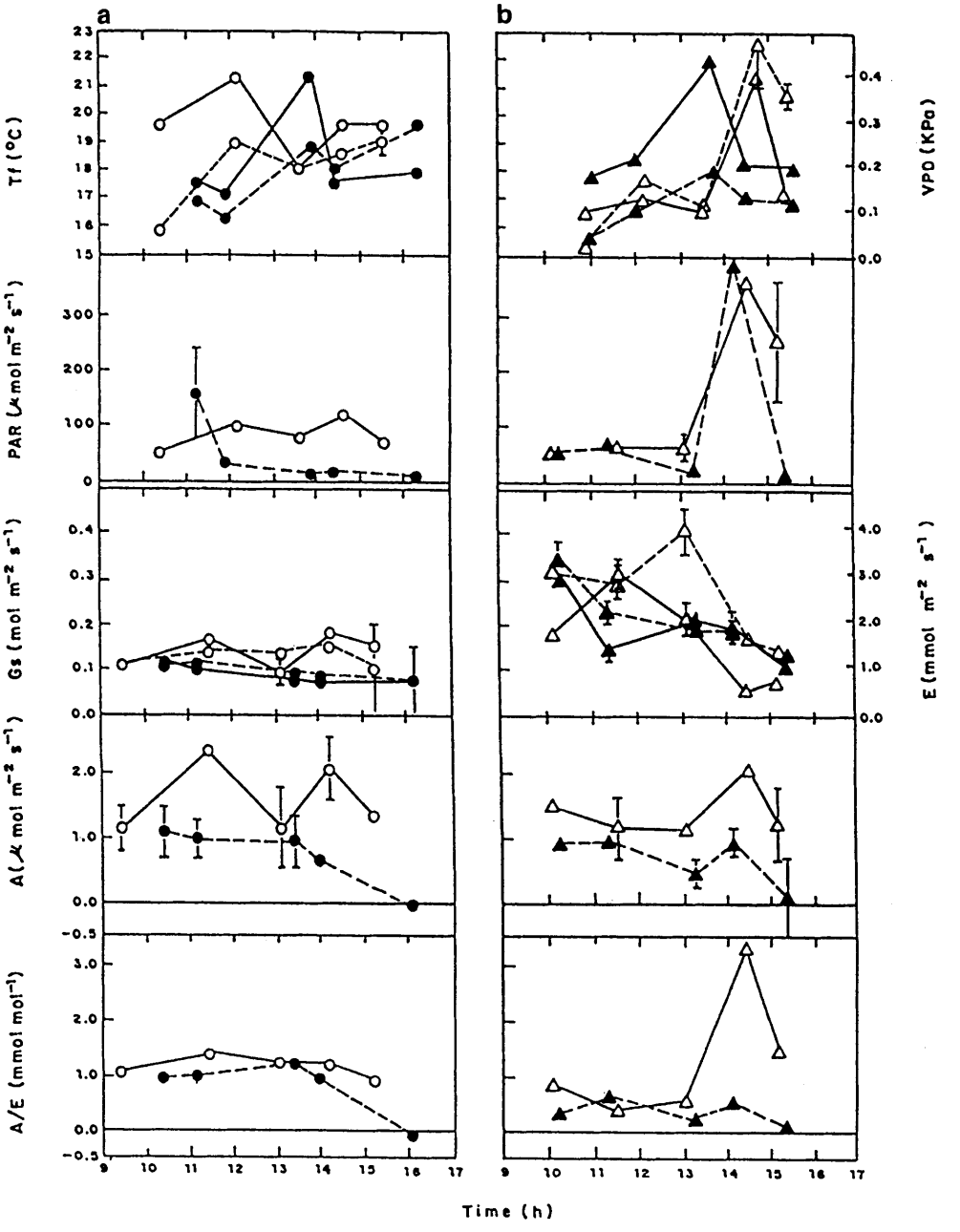


Fig. 6 Daily course of leaf temperature (T_f---), leaf-air VPD (——), photosynthetically active radiation (*PAR*), leaf conductance, (*Gs*---), transpiration rate (E ——), photosynthetic rate (*A*) and water use efficiency (*A/E*) during the wet season (13 September 1990) for (a) *A. triplinervia* in the understory (●) and in a gap (○) and (b) *D. rospigliosii* in the understory (▲) and gap (△). *Vertical bars* are standard errors ($n = 4$)

understory, a trend which is maintained throughout all the daily courses (García-Núñez 1992).

Mean VPD of 0.2 KPa for both light environments was observed for *D. rospigliosii*, with maximum values of 0.4 KPa at midday. Even though there is a significant increase in stomatal frequency for *D. rospigliosii* plants developed in the gap (Table 1), leaf conductance and transpiration rates are higher for the understory. Since VPD in the gap, for this species, is slightly higher than in the understory, the lower leaf conductances in exposed environments may be related to the type of stomatal control presented by *D. rospigliosii* (Fig. 3).

Net photosynthetic rates for both species were 1.7 times higher in gaps compared to the understory values; with maximum values of 1.26–2.32 μmolm^{-2}s^{-1} for *A. triplinervia* and 0.85–2.08 μmolm^{-2}s^{-1} for *D. rospigliosii*, following closely the PAR response for both light environments (Fig. 6).

Both species maintained a positive carbon balance in the understory, with low CO_2 assimilation rates, and which were slightly higher in *A. triplinervia* and reaching light saturation at approximately 100 μmolm^{-2}s^{-1} (Fig. 6). Despite higher photosynthetic rates and lower leaf conductances in *A. triplinervia*, water use efficiency (WUE) for both light environments (0.8 and 0.5 mmol CO_2/mol H_2O in gap and understory, respectively), were not significantly different when compared to *D. rospigliosii* (0.5 and 0.2 mmol CO_2/mol H_2O in gap and understory, respectively, *t*-test, $P < 0.05$).

Table 1 Photosynthetic and anatomical characteristics of fully expanded leaves from *A. triplinervia* and *D. rospigliosii*; $n = 4$, * $P < 0.05$ between treatment, ** $P < 0.05$ between species

Treatments	*A. triplinervia*	*D. rospigliosii*	
Dark respiration rate ($\mu molm^{-2}s^{-1}$)			
Gap	−0.34 ± 0.07	−0.66 ± 0.09*	
Understory	−0.18 ± 0.00	−0.04 ± 0.03	
Light compensation point ($\mu mols\ m^{-2}s^{-1}$)			
Gap	6.50 ± 1.09	7.50 ± 2.12*	
Understory	3.50 ± 2.12	1.67 ± 0.82	
Quantum efficiency (mol CO_2 $molph^{-1}$)			
Gap	0.06 ± 0.02	0.06 ± 0.02	
Understory	0.08 ± 0.06	0.04 ± 0.01	
Maximum photosynthetic rate ($\mu mol\ m^{-2}s^{-1}$)			
Gap	4.40 ± 0.64	4.01 ± 0.26*	
Understory	2.87 ± 0.63	1.57 ± 0.04	
Maximum photosynthetic rate ($\mu mol\ moIN^{-1}s^{-1}$)			
Gap	59.30 ± 7.16	56.74 ± 8.84*	
Understory	52.84 ± 13.68	27.13 ± 0.76	
Nitrogen content ($mg\ g^{-1}$)			
Gap	23.57 ± 0.80* **	12.96 ± 0.39**	
Understory	21.25 ± 0.63	11.13 ± 0.41	
Chlorophyll content ($mg\ g^{-1}$)			
Gap	9.20 ± 0.25	6.98 ± 0.40*	
Understory	8.31 ± 1.30	9.56 ± 0.33	
Chlorophyll a/b ratio			
Gap	3.10 ± 0.33	1.82 ± 0.16	
Understory	2.59 ± 0.36	2.14 ± 0.17	
Chlorophyll/Nitrogen relationship			
Gap	0.39 ± 0.02**	0.54 ± 0.03* **	
Understory	0.39 ± 0.07	0.85 ± 0.05	
Specific leaf weight ($g\ m^{-2}$)			
Gap	44.11 ± 1.03* **	76.48 ± 2.74* **	
Understory	35.82 ± 1.55	68.15 ± 1.97	
Stomata number (mm^{-2})		Abaxial	Adaxial
Gap	132 ± 0.23	134 ± 0.26*	131 ± 0.26
Understory	127 ± 0.49	117 ± 0.20	115 ± 0.14

Photosynthetic responses under controlled conditions

Photosynthetic responses to light per unit leaf area in *A. triplinervia* and *D. rospigliosii* grown in gaps (6% of total insolation) and understory (2% of total insolation) are shown in Fig. 7. Maximum photosynthetic rates for both species were found in individuals developed in the gap (approximately 4 $\mu molm^{-2}s^{-1}$). Light saturation for the gap-adapted trees was reached between 200 and 300 $\mu molm^{-2}s^{-1}$ and for the understory between 100 and 200 $\mu molm^{-2}s^{-1}$ for both species (Fig. 7).

The light compensation point (Table 1) was low for both species grown in the understory (3–4 $\mu molm^{-2}s^{-1}$ for *A. triplinervia* and 1–2 $\mu molm^{-2}s^{-1}$ for *D. rospigliosii*). In the gap, *D. rospigliosii* showed a slightly higher point (7–8 $\mu molm^{-2}s^{-1}$) compared to *A. triplinervia* (6–7 $\mu molm^{-2}s^{-1}$). These low compensation points for both species are similar to the light levels registered in the forest's understory. The apparent quantum yield (based on incident radiation) is higher in *A. triplinervia* (Table 1). There were no significant differences ($P < 0.05$) in this parameter between the different light treatments for both species (Table 1), which indicates that there is no photoinhibition.

Plants developed in the understory showed lower dark respiration rates (Table 1). On the other hand, dark respiration rates on a leaf area basis, showed a linearly increasing tendency with respect to leaf weight/leaf area and the amount of total nitrogen per unit dry weight in the range of light available to which they were exposed (García-Núñez 1992).

Optimum temperature for photosynthesis was approximately 18 °C for both species (Fig. 8), a value which is, generally, close to the mean air temperature experienced in their respective environments. It is important to note that *D. rospigliosii* has a broader range than *A. triplinervia*, which partially indicates a greater acclimation response.

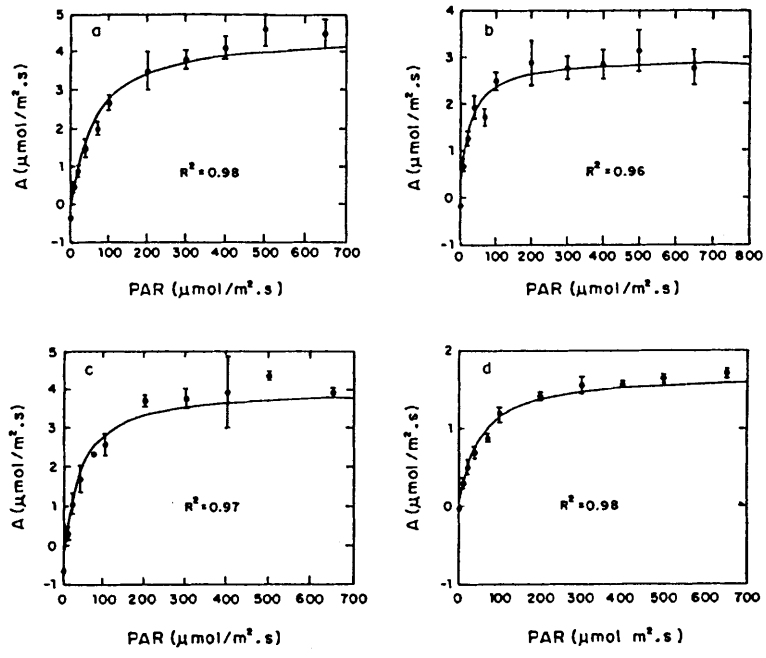


Fig. 7 Relationship between photosynthetic rate (*A*) and photosynthetically active radiation (*PAR*) under controlled conditions for *A. triplinervia* in a gap (**a**) and in the understory (**b**) and *D. rospigliosii* in a gap (**c**) and understory (**d**). Values are representative of dry and wet seasons. *Vertical bars* are standard errors ($n = 4$)

Nitrogen content, leaf chlorophyll and anatomical characteristics

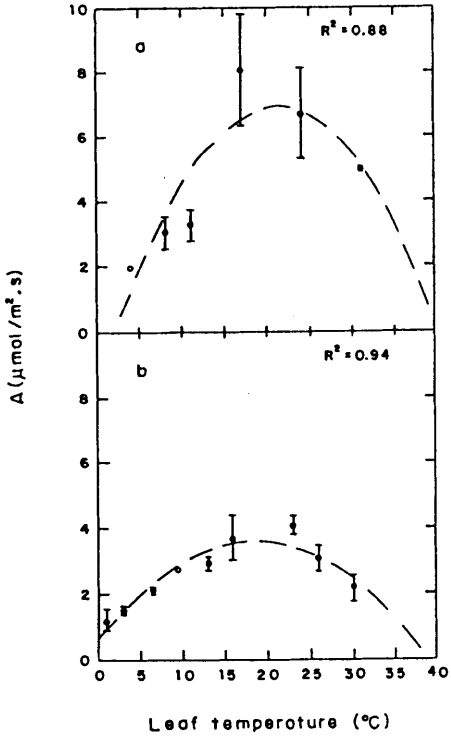
In both species total nitrogen content per unit leaf weight was higher in plants developed in the gap, being significantly higher in *A. triplinervia* for both light environments (Table 1). There were no significant differences in the amount of chlorophyll per unit weight between both species, even though the values of *A. triplinervia* in the gap were slightly higher than in the understory, while for *D. rospigliosii*, chlorophyll concentration in the understory was significantly higher than for the gap (Table 1).

Significant differences were also found in the chlorophyll/nitrogen relationship between both species. *A. triplinervia* showed similar values in gap and understory, while in *D. rospigliosii* the values were lower in the gap (Table 1). The chlorophyll a/b ratio was higher in *A. triplinervia* for the two light environments, although there were no significant differences between treatments (Table 1). Values for *A. triplinervia* in the understory were lower than the gap. On the other hand, the understory results were higher than the gap values for *D. rospigliosii*. *A. triplinervia* presented a higher instantaneous nitrogen use efficiency (INUE) in both light environments, even though the differences were not significant.

A. triplinervia leaves developed in both gap and understory have medium-sized leaves (20–100 cm²). Both leaf thickness and specific leaf weight (SLW) were significantly higher in the gap (160.25 µm; 44.11 g/m², respectively) than in the understory (145.25 µm; 35.82 g/m²). This leaf thickness decrease in the understory was due, principally, to a decrease in the thickness of the epidermis of the upper surface and in the spongy parenchyma. The palisade/spongy parenchyma relation was similar in both environments and the stomatal density was slightly higher in leaves grown in the gap and significantly larger than in the understory.

D. rospigliosii leaves grown in the gap presented higher values of leaf thickness and SLW (263.10 µm; 76.48 g/m², respectively) compared to those grown in the understory

Fig. 8 Relationship between photosynthetic rate (*A*) and leaf temperature under controlled conditions. (**a**) *A. triplinervia* in a gap, $y = -2.1069 + 0.8771x - 0.0215x^2$, (**b**) *D. rospigliosii* in the understory, $y = 0.6192 + 0.3193x - 0.0086x^2$. *Vertical bars* are standard errors ($n = 4$)



(240.61 μm; 68.15 g/m², respectively). This greater leaf thickness was due to a larger spongy parenchyma, while the palisade parenchyma and the epidermis remained the same. Stomatal density was significantly higher in both surfaces for leaves grown in the gap. Stomatal cell size was similar for both light environments.

Discussion

Mechanisms of stomatal regulation

Our results show two distinct patterns in relation to transpiration rates and stomatal regulation in the studied species. *A. triplinervia*, the gap-colonizing species, maintains low and relatively constant leaf conductances and transpiration rates throughout the day. In contrast, *D. rospigliosii* presented higher leaf conductances and transpiration rates, together with a partial stomatal closure due to changes in the environment's evaporative demand. This type of stomatal control has been reported for many different life forms and, particularly, in conifers (Kaufmann 1976; Grieu et al. 1988; Meinzer et al. 1984). In adult individuals of *D. rospigliosii* which constitute the emergent stratum where water deficits may generate due to high VPD and to the high hydraulic resistance presented by conifers (Edward and Jarvis 1982), this mechanism would be effective in controlling water losses. Meinzer et al. (1984) found that in *D. rospigliosii* stomatal closure occurs with increments in the evaporative demand, being independent of the general water status of the leaf. This high sensitivity of stomata to VPD has been reported in several species from tropical rain forests (Huc and Guehl 1989; Granier et al. 1992).

Lower conductance and transpiration rates and a lesser stomatal control in *A. triplinervia*, contradicts what has generally been found, i.e. species in early succesional stages present much higher transpiration rates compared to shade-tolerant species (Bazzaz and Pickett 1980). However, this species maintains its stomatal conductance constant and lower during the daily cycles compared to *D. rospigliosii*, but with higher assimilation rates than this latter species. These characteristics permit *A. triplinervia* to maintain a higher intrinsic water use efficiency (A/Gs), which would have a greater adaptive value in exposed habitats (large gaps) and in those individuals which reach the higher stratum in the forest's canopy. The greater stomatal conductance found in *D. rospigliosii* may give it an advantage to profit from light flecks and increase the assimilation rate by increasing the internal CO_2 concentration as has been proposed for other species (Mooney et al. 1983; Pearcy et al. 1987; Chazdon and Fetcher 1984; Pearcy and Calkin 1983).

Photosynthetic responses

The light environment where the measurements were carried out was not homogeneous due to the variability of microsites, furthermore in our acclimation experiment shaded housing was not used to control and homogenize light levels. The results are, therefore, heterogeneous, and will be discussed in terms of the trends which in many cases are consistent and clear, showing significant differences between treatments and species.

Some of our results, such as photosynthetic rates and the photosynthetic acclimation capacity to changes in the light environment, do not coincide with the species' successional stage and its degree of shade tolerance as described by Bazzaz and Pickett (1980) and Bazzaz and Carlson (1982). Similar results have been reported in tree species from tropical rain forests (Denslow 1980; Langenheim et al. 1984; Walters and Field 1987; Fetcher et al. 1987). The fact that there were no significant differences in the maximum photosynthetic rate, measured under optimum laboratory conditions, when both species were grown in the gap, may be due to the light environment where the experiment was carried out (100 m² gap, receiving 6% of total insolation), an amount which was, probably, not optimum to obtain the maximum photosynthetic capacity in *A. triplinervia*. *D. rospigliosii*, which has a shade tolerant seedling bank, is able to adjust its photosynthetic capacity, responding to increases in radiation levels without showing signs of photoinhibition. These results suggest that *D. rospigliosii* would benefit from the opening of small gaps, increasing its growth rate, in the same manner as has been described for other tropical rain forest seedlings (Fetcher et al. 1983; Popma and Bongers 1988; Sanchez-Coronado et al. 1990). Studies of the influence of light on the development of *D. rospigliosii* show that, although it may resist complete shade in the understory, it can grow better under medium to high light conditions (Lamprecht and Liscano 1957).

Both *A. triplinervia* and *D. rospigliosii* showed low and very similar light compensation points when grown in complete shade. Therefore, it is difficult to classify them as shade-tolerant, since the light compensation points seem to be more affected by the treatments than by the species. The small difference found with respect to quantum yield between treatments for both species, may be possibly due to the small difference between the amount of radiation received by the gap compared to the understory, and, therefore, no damage was produced in the photosynthetic apparatus when moved from shade to light. *D. rospigliosii* showed low dark respiration when grown in the understory, which permits it to maintain a positive carbon balance throughout the day, compared to *A. triplinervia* grown in the understory. These differences in respiration rates may be the factor which determines the success or failure of seedlings growing in the understory, where the plants may spend many hours below the light compensation point (Loach 1967).

Total nitrogen content in leaves differ between species and may show their successional status. The higher nitrogen content per unit dry weight in the gap species (*A. triplinervia*), indicates a better nutritional status found in rapid growing species of the early succession. In contrast, the lower nitrogen content found in *D. rospigliosii*, together

with a higher specific leaf weight, are characteristics of late succession species and/or slow growing primary species (shade-tolerant; Mooney et al. 1984; Medina 1986; Evans 1989). *A. triplinervia* is equally photosynthetically efficient in its nitrogen use in both gap and understory which means that there is no acclimation response. In contrast, *D. rospigliosii* increases its INUE when placed in the gap, which supports the idea that this species depends on gaps to reach the higher forest strata and to reproduce. However, the phylogenetic difference between an angiosperm and a gymnosperm must be taken into account when comparing physiological and morphological attributes and their relation to the successional status.

Maximum photosynthetic rates and leaf nitrogen found for both species growing in the gap are low when compared to Amazonian species (Reich et al. 1991), but are similar to values reported for tree species from other cloud forests (Añez 1987) and to understory species from tropical rain forests (Koyama 1981; cited in Mooney et al. 1984). These results support Grubb's (1977) prediction with respect to low photosynthetic rates in mountain cloud forests.

The light regime also affected leaf structure in both species. *A. triplinervia* shows a decrease in leaf thickness, SLW and stomatal frequency when grown in the understory, while *D. rospigliosii* presents an increase in these parameters when grown in the gap. As a consequence, the photosynthetic rate shows a linear relationship with respect to SLW in the range of light availability to which these plants were exposed (data not shown). Similar results have been reported in leaves of species developed under different light regimes (Chabot et al. 1979; Jurik et al. 1979; Fetcher et al. 1987; Sims and Pearcy 1989).

In general, our results suggest that both species have the capacity to respond to changes in the natural light environment, maintaining a favorable carbon balance, even though the CO_2 assimilation rates are low. Although *A. triplinervia* is generally found in exposed habitats, its high maximum photosynthetic rates, INUE and quantum yield suggest that this species may also occupy shaded habitats. *D. rospigliosii's* characteristics such as lower dark respiration rate, light compensation points, chlorophyll a/b ratio and a higher chlorophyll/nitrogen relationship and leaf conductance, may give this species a competitive edge which may assure its survival as a seedling bank in the understory. The photosynthetic acclimation in this shade-tolerant species permits it to be more competitive when a gap occurs.

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