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ORIGINAL ARTICLE

# Diurnal physiological behavior of seedlings in the Amazon rainforest: generalist versus specialist species of shade and sun

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## Abstract

The regenerative success of generalist and specialist species may be due to differences in their physiology. Measurements of stomatal conductance (gS) provide an efficient way to infer immediate physiological responses of plants to diurnal environment variation. Radiation, air temperature, and relative humidity were measured in the Colombian Amazon rainforest, to identify the extreme environmental conditions that limit the gS of seedlings in three site types: small gap, open forest, and closed forest. We hypothesized that the diurnal physiological performance of generalist species must be plastic in these three environments. Morphological traits, gS, and leaf temperature were evaluated in seedlings of four species: one generalist, common to all sites, and one specialist from each site. The gap site was warmer and more irradiated than the other two sites, which caused several midday physiological depressions, limited seedling survival, and facilitated the specialized strategy. Leaf and air temperatures were strong determinants of overall gS. The generalist species was physiologically plastic and, at some hours of the day, more efficient than the specialists from open forest and closed forests. This factor interplay could allow the coexistence of both types of plants.

**Keywords:** Heliophyte; gap dynamics; leaf temperature; seedling; shade-tolerance; stomatal conductance.

## Introduction

The Amazon rainforest is the most extensive tropical forest in the world, covering 6.8 million km$^2$, and accumulating 10 % of global primary productivity (Chazdon & Montgomery, 2002; Rivera, 2008). Light energy in a tropical forest is distributed in multiple foliage layers from the canopy to the ground. In the understory; diffuse radiation reaches values around 2 %, while in gaps and in the upper canopy direct radiation levels exceed 40 % (Smith *et al*., 1992; Clark *et al*., 1993; Romo 2005). Treefall gaps are random events that change about 2 % of the canopy each year (Lobo & Dalling 2013), and many authors agree that gap dynamics contribute to high productivity and diversity in tropical forests (Martínez-Ramos 1985, Whitmore 1998, Hubbell *et al*., 1999; Schnitzer *et al*. 2008).

Gaps contribute considerably to heterogeneity in radiation, temperature, humidity, soil nutrient availability and biotic components (Denslow 1980, Brokaw 1985, Denslow 1987), affecting plant physiology and recruitment (Brokaw 1985, Gravel *et al*., 2010; Ashton *et al*. 2011). Without gaps, the dense cover of vegetation and high tropical temperatures would make the Amazonian forest a place with limiting conditions of low light and high humidity.

The successional process for gap recovery begins with the colonization of fast growing, heliophyte and short-lived pioneer species. They are replaced by shade-intolerant shrubs and trees that require the opening of gaps to increase their lifespan and at the end the site is colonized by slow growing, long-lived and shade-tolerant species (Whitmore 1989, Collantes *et al*., 2000; Krause *et al*., 2001; Wright *et al*. 2003).

Plants can be classified as generalist or specialist according to their regenerative habitat preferences (Fetcher *et al*., 1987; Van Der Meer *et al*., 1998). Generalist species possess a set of morpho-physiological attributes that allows their fast spread and recruitment in a wide range of light conditions (Brunet *et al*. 2011). These plants are considered facultative shade-tolerants (Collins *et al*., 1985; Santos-Filho *et al*. 2008) and are favored by the microclimate created by previously established pioneer species in a forest gap (Luken *et al*. 2008). By contrast, specialist species, either heliophytes or shade-tolerants, only persist in homogeneous environments of gaps or understory respectively, which implies a lower competitive capacity under the effects of disturbance (Denslow 1980).

Gap dynamics determine responses in the content of photosynthetic pigments and quantum yield (Valladares *et al*., 1997; Krause *et al*. 2001), rate of carbon assimilation (Valladares *et al*., 1997; Bonal & Guehl 2001, Leakey *et al*., 2003; Hölsher *et al*., 2004), biomass distribution (Fetcher *et al*. 1987, Claussen 1996, Saldaña *et al*., 2009; Craven *et al*. 2010), and the structural and morphological features of plants (Ehleringer & Werk 1986, Rundel *et al*. 1998, Hölsher *et al*. 2004). However, little is known about the physiological responses of generalist and specialist plant species to environmental conditions in tropical forests.

Stomatal conductance is a physiological trait that determines photosynthesis and plant growth, since stomatal opening regulates the $CO_2$ entry into the leaf. There is substantial evidence that, in environments with elevated relative humidity, diffusive limitations of photosynthesis, measured through the stomatal conductance, are more variable and better correlated with carbon assimilation than biochemical limitations (Carswell *et al*., 2000; Santiago & Wright 2007; Damour *et al*., 2010; Kamakura *et al*. 2011). The maximum stomatal conductance in tropical rainforests can vary between 100 mmol $m^{-2}$ $s^{-1}$ in shade-tolerant species and around 1 000 mmol $m^{-2}$ $s^{-1}$ in heliophyte species (Roberts *et al*., 1990; Domingues *et al*., 2007; Kosugi *et al*. 2012). Stomatal conductance variation may reflect a prompt response to water, heat or light stress (Valladares *et al*., 1997; Leakey *et al*., 2003; Slot & Poorter 2007). Therefore, the study of stomatal conductance could explain differences in competitiveness and survival of generalist and specialist species in relation with gap opening.

In a conserved rainforest of the Colombian Amazon, we measured environmental variables and estimated the seedlings diversity in three different sites: small gap, open forest and closed forest, to identify the most extreme environmental conditions that could limit the growth and survival of seedlings. We hypothesized that the diurnal physiological performance of one generalist species must be plastic in these three environments, probably emulating the performance of species specialized to light or shade. Some differences in morphological traits could be associable with responses of generalist and specialist species to extreme conditions. Findings from this study will assist us to explore some eco-physiological mechanisms behind the regenerative dynamics of tropical rainforests.

## Materials and Methods

### Study Area

A total of 7 % of the Amazon rainforest is located in Colombia, hosting about 10 % of the global biodiversity, which represents more than 6 000 species (Rivera 2008, WWF 2010). Our study was conducted in the Amacayacu National Natural Park (PNNA) located in the southern part of Colombia (3°49’3.11" S; 70°15’48.4" W) in the municipality of Leticia, in the Colombian department of Amazonas. The park comprises a protected area of 2 930 $km^2$ of vegetation classified as tropical rainforest (Holdridge 2000), with altitude around 100 m.a.s.l. The average temperature is close to 27 °C, the annual rainfall ranges between 3 000 and 4 500 mm and the relative humidity normally exceeds 90 % (Martino 2007, Peña *et al*. 2010). The soils are ferralsols and oxisols with low cation exchange capacity, high acidity and high iron and aluminum content (Malagón 1997). It is a sedimentary region of flood plain rivers coming from the eastern slopes of the Andes Range (Räsänen *et al*., 1987; Uhl *et al*. 1988). The most frequent event of natural disturbance in the Amacayacu forest is the opening of small gaps or spaces of direct sunlight created by the fall of a unique tree.

### Pre-sampling of generalist and specialist species.

Three sampling sites in the PNNA: small gap, open forest, and closed forest were selected for our study. Within each site one plot of 5 x 2 m (10 $m^2$) was established to survey all seedlings less than or equal to 30 cm in height. A total of 166 seedlings, represented by 62 species were sampled. Three species were common to all sites but only *Qualea psidiifolia* (Spruce ex Warm) was considered as the principal generalist because it was the most frequent from the seedlings bank (8.5 %). Likewise, the specialist species, occurring exclusively in one site, were: *Bahuinia guianensis* (Aubl.) in the small gap (16.3 %), *Calathea* sp. in the open forest (16.9 %), and *Capirona decorticans* (Spruce) in the closed forest (11.5 %). These four species (one generalist and three specialists) were destined for the physiological measurements. The physiological and environmental monitoring took place during seven consecutive days in the middle of the dry season in September of 2012.

### Environmental measurements

One plot of 10 m x 10 m (100 $m^2$) surrounding the seedlings plot was delimited in each site (Small gap, open forest and closed forest) for the placement of thermo-hygrometers. Ten readings of photosynthetically active radiation (PAR) were taken using MQ-100 quantum integral reader device (Apogee Instruments, Inc. USA), and four readings of air temperature (AT) and relative humidity (% RH), using digital thermohygrometers (Control Company. USA), were taken in each plot at one-hour daylight intervals. One additional variable, the vapor pressure deficit (VPD) was estimated from data of air temperature, leaf temperature, and relative humidity (Sullivan *et al*. 1996). Also, the distance among trees was measured using a portable digital laser distance meter (PrexisoX2. Switzerland).

During the monitoring period there were three extreme rainfall events, typical to the study area. During each of this rainfall episodes measurements were not taken. Normalized data of tree spacing, maximum PAR, air temperature, and relative humidity were analyzed by two-way ANOVA (Statistica 13.3, TIBCO Software Inc.) to evaluate the effect of site and time of day. The post-hoc Fisher's LSD was applied to find differences among pair-wise comparisons.

### Diversity per site

The abundance (N) and number of species (S) were used to calculate the diversity indices of Shannon and Margalef, as well as the Simpson's dominance index in gap, in open forest and closed forest. In addition, Morisita-Horn and Bray-Curtis similarly indices were computed to establish the compositional divergence among sites. The analysis of diversity was performed by PAST software (Paleontological Statistic, v.3.25 © Hammer, 1999-2020).

### Physiological variables

For each site, four individuals of the generalist species and five individuals of the specialist species were selected for the monitoring of physiological variables at one-hour daylight intervals. Leaf area (LA) was measured with an AM350 portable leaf area meter (Opti-Sciences Inc. USA). Stomatal conductance (gS) and leaf temperature (LT) were measured using a SC-1 leaf digital porometer (Decagon Devices Inc. USA).

ANOVA and the Fisher's LSD post-hoc tests were used to detect overall differences in physiological parameters among the sites. Stomatal conductance data were $\text{Log}_{10}$ transformed, and an analysis of covariance was applied for variables LT and gS, with time of day as a covariate. We compared the stomatal conductance and leaf temperature between generalist and specialist seedlings using the non-parametric Mann-Whitney test. The linear relationship between environmental variables and stomatal conductance were analyzed by Pearson correlation coefficients (using the normalized variable $\text{Log}_{10}$ gS) and their coefficient of determination was calculated to extract the multivariate linear regression model. Statistica 13.3 software was used to statistical analysis (TIBCO Software Inc.).

## Results and Discussion

The three sites revealed stark environmental contrasts (**Fig. 1**). In the small gap site, the spacing among trees was around 3 m, enough to have a photosynthetic radiation 15 and three-fold higher than that of closed forest and open forest respectively. The maximum air temperature in the gap site was 7 °C higher than that of closed forest and its relative humidity was lower than that in open forest and closed forest. The presence of unique species exceeding 59 % in all sites confirms that the environmental heterogeneity differentially influences germination and seedling survival (**Table 1**). The combination of high radiation and high temperature causes photoinhibition in most plants (Claussen 1996, Leakey *et al.* 2003, Houter & Pons 2005), and it is associated with a high mortality of seedlings in gaps

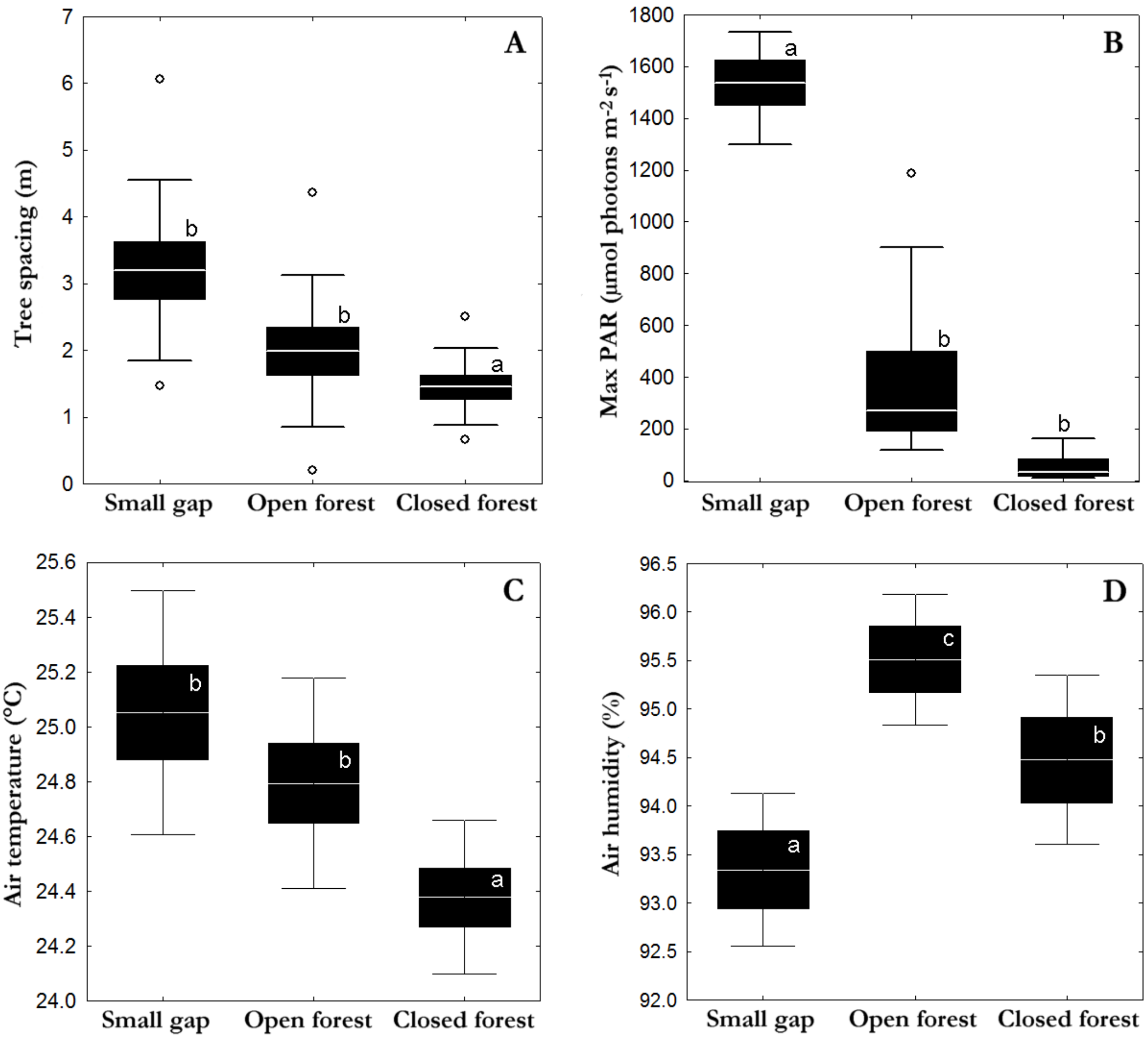

**Figure 1.** Environmental features at three successional sites in the PNNA Amazon rainforest. Photosynthetically active radiation (PAR) was highly variable and a non-normalized parameter, but its maximum values (12 measurements per site) were parametrically analyzed. Line: mean; box: standard error; wisker: 95 % confidence interval; points: outlayers. Letters denote ANOVA significant differences at $p < 0.01$.

(Dupuy & Chazdom 2008). The maximum radiation recorded around noon in the small gap far exceeded the light saturation point of young tropical plants and, even, heliophytes (Larcher 2003, Lambers *et al.* 2008); whereas, the understory of the closed forest received photosynthetic radiation below 200 $\mu$mol m$^{-2}$ s$^{-1}$ (**Table 2**).

**Table 1.** Alpha and beta diversity of the seedling community in the PNNA Amazon rainforest. Three sites at different successional stages were sampled: Small gap, open forest and closed forest. N: Abundance; S: Richness.

**α - Diversity**

| | Gap | Open forest | Closed forest | Total |
|---|---|---|---|---|
| N | 50 | 64 | 52 | 166 |
| S | 22 | 26 | 30 | 62 |
| Margalef | 5.40 | 6.01 | 7.34 | 12.32 |
| Shannon | 2.75 | 3.07 | 3.17 | 3.81 |
| Simpson | 0.91 | 0.95 | 0.95 | 0.97 |
| % Unique species | 59.1 | 69.2 | 60 | --- |

**β - Diversity**

| SITE 1 | SITE 2 | Shared Species | Morisita-Horn | Bray-Curtis |
|---|---|---|---|---|
| Gap | Open forest | 4 | 0.09 | 0.11 |
| Gap | Closed forest | 8 | 0.18 | 0.20 |
| Open Forest | Closed forest | 7 | 0.32 | 0.24 |

The Shannon, Margalef, and Simpson indices showed that biodiversity was higher in the closed forest than in the open forest, and, in turn, the open forest was more biodiverse than the gap site. Although the open forest had the highest abundance (64 individuals) and proportion of unique species (69 %), the closed forest had the highest richness (30 species). Total diversity was very high, since the Simpson index showed a 97 % chance of choosing randomly two seedlings of different species in the study area. Gap and open forest were the most dissimilar sites in composition (Table 1).

Opposite to what we observed, due to its low photosynthetic radiation, the closed forest was not expected to exhibit the highest diversity. This agrees with the idea that light is not necessarily the most important factor for germination and seedling recruitment. (Augspurger 1984, Whitmore 1989, Hubbell *et al*. 1999, Schnitzer *et al*. 2008). Although little light availability limits the biochemical process of photosynthesis, tropical forests seem to have a wide diversity of species able to survive and grow with low rates of physiological performance (Denslow 1987, Oberbauer *et al*. 1993, Dalling *et al*. 1999, Leakey *et al*. 2003, Ashton *et al*. 2011). More than quantity, quality of light and phytochrome specific responses have a crucial role in growth

**Table 2**. Physiological variables of seedlings in the gap, open forest and closed forest sites (Mean ± SD). SH: Stem height; LN: Leaf number; LA: Leaf area; gS: Stomatal conductance; LT: Leaf temperature. *Q. psidiifolia* is a generalist species, while *B. guianensis*, *Calathea sp.* and *C. decorticans* are specialist in each successional site. Letters denote significant differences at $p < 0.05$.

| | **Gap** | | **Open forest** | | **Closed forest** | |
|---|---|---|---|---|---|---|
| | *Q. psidiifolia* | *B. guianensis* | *Q. psidiifolia* | *Calathea sp.* | *Q. psidiifolia* | *C. decorticans* |
| SH (cm) | 22.8 8.4 | 23.9 1.4 | 15.6 3.0 d | 4.7 ± 0.2 e | 15.6 1.9 | 17.7 4.6 |
| LN | 2.5 0.6 | 5 0.7 | 2.3 ± 1.2 b | 2.8 ± 2.4 b | 2.3 ± 1.3 b | 3.2 ± 1.8 ab |
| LA (cm$^2$) | 23.8 3.9 | 43.5 11.9 | 15.5 6.4 | 13.4 ± 6.5 b | 20 ± 6.7 b | 22.9 ± 10.6 b |
| LA/SH | 1.2 0.7 | 1.8 0.5 | 1 ± 0.3 b | 2.9 ± 1.5 a | 1.3 ± 0.5 b | 1.4 ± 0.9 b |
| gs mmolm$^{-2}$s$^{-1}$) | 172 37 | 175 19.4 | 285 16.6 | 264 23.4 | 220± 26.9 | 174 20.2 |
| LT (°C) | 28.4 1.8 | 28.3 2 | 28.1 1.9 | 28 1.3 | 28.3 1.5 | 27.9 1.9 |

and coexistence of seedlings in the understory (Vázquez-Yanes & Smith, 1982; Leite & Takaki, 2001; Wagner *et al.* 2011). Moreover, non-structural carbohydrates in root and stem are apparently involved in the first-year survival of shade-tolerant species (Myers & Kitajima, 2007).

The most extreme diurnal conditions occurred in the small gap site between 11 and 14 h, when seedlings were exposed to high radiation and temperatures above 28 °C (**Fig. 2**). Peaks of air temperature in the closed forest, two degrees cooler than air temperatures in the small gap, were more favorable for gas exchange and persistence of diversity. In the small gap site, the larger leaf area of seedlings optimizes the ability to dissipate excess energy as heat, mitigating the effect of photoinhibition (Table 2) (Phillips *et al.* 1998, Dalling *et al.* 1999). Nevertheless, the joint effect of high leaf temperature and photoinhibition at noon has negative effects in stomatal conductance (Table 2, **Fig. 3**) and photosynthesis (Yu *et al.* 2001). In the open forest, high relative humidity and intermediate radiation favor stomatal conductance, photosynthesis, and survival (Pearcy 1987, Ni & Pallardy 1992, Myers & Kitajima, 2007); however, the resulting high

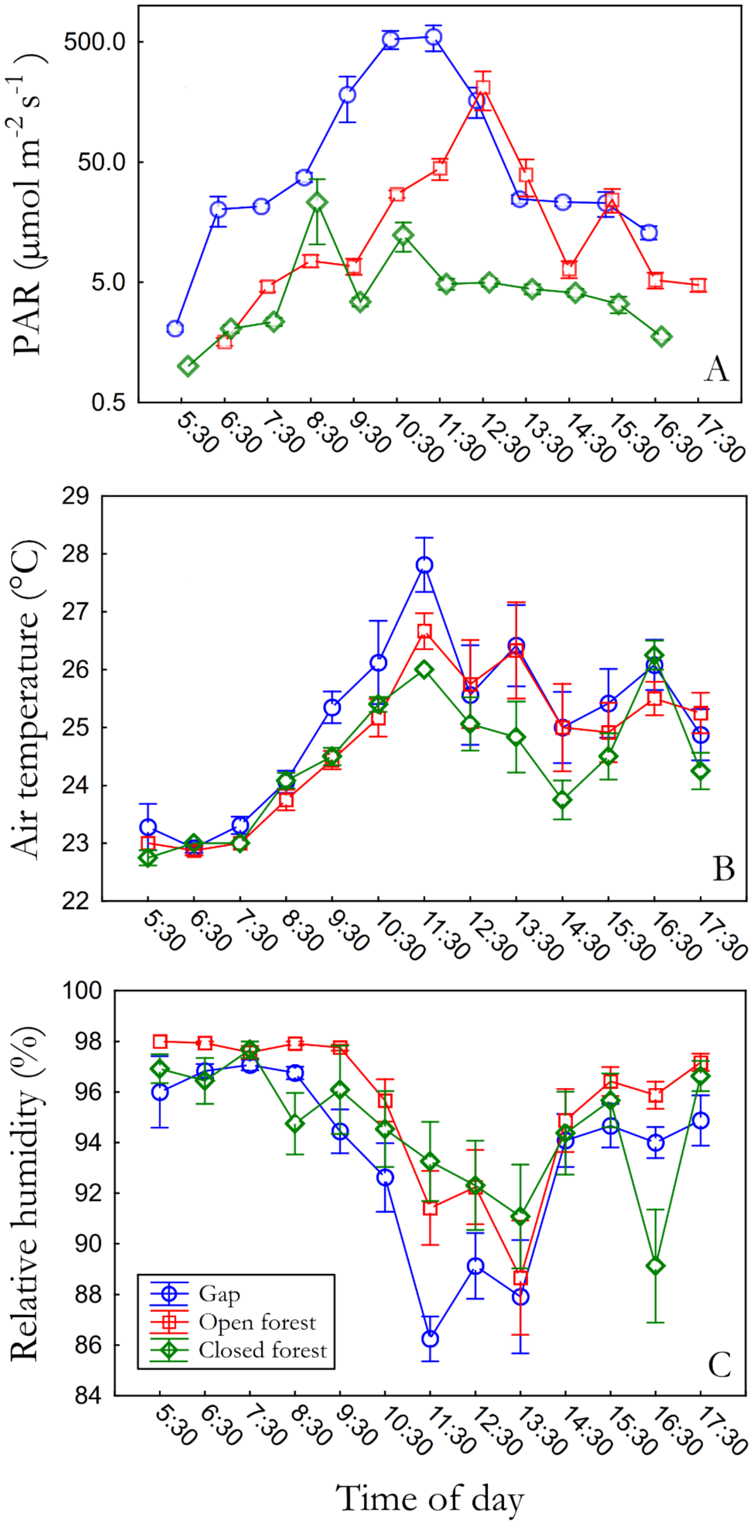

**Figure 2.** Diurnal variation (mean ± standard error) of three environmental features at three successional sites in the PNNA Amazon rainforest. Photosynthetically active radiation (PAR), air temperature, and relative humidity were recorded during seven days at three successional sites: small gap, open forest, and closed forest.

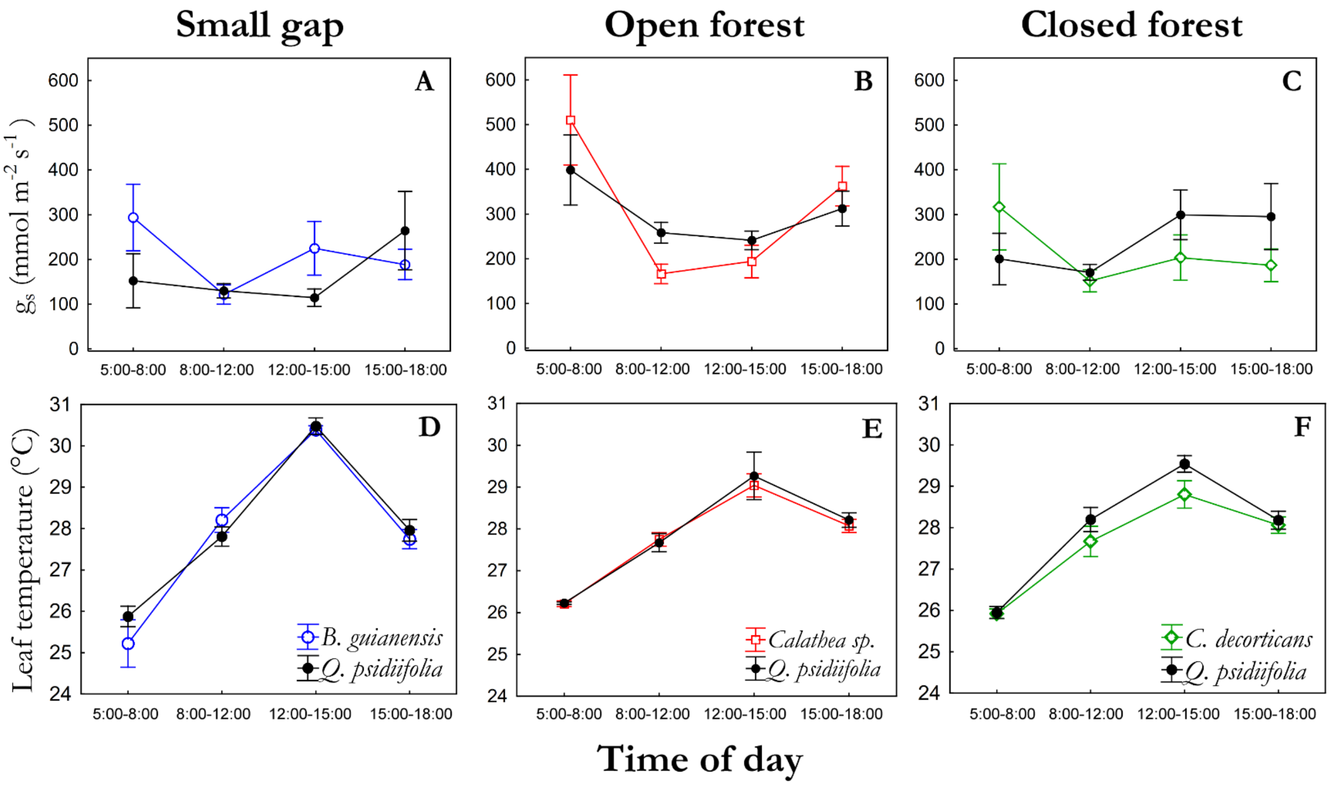

**Figure 3.** Diurnal change (mean ± standard error) of two physiological variables measured at three sites in the PNNA Amazon rainforest. A, B, C): stomatal conductance (gS) and D, E, F): leaf temperature of generalist (filled square) Q. *psidiifolia* and specialist (open square) *B. guianensis* seedlings from small gap, open forest (*Calathea sp.*), and closed forest sites (*C. decorticans*), respectively.

abundance of seedlings could promote competition for space, nutrients, and light (Denslow *et al.*, 1991; Harms *et al.*, 2000; Dalling *et al.*, 2004). This can lower richness in the open forest site, compared to the closed forest site.

We found significant differences in seedling morpho-physiological traits between generalist and specialist plants (Table 2). The specialist plant of the gap site, *B. guianensis*, showed the tallest seedlings, with more leaves and the highest leaf area; whereas the specialist of the open forest *Calathea sp.* showed the highest proportion of leaves per height. Seedlings of the generalist Q. *psidiifolia* were taller in the gap site than in the forest site, despite having similar number of leaves in all sites. A similar plasticity in specific leaf mass was found by Valladares *et al.* (2000) through experiments of gap site species that underwent shaded environments. Stomatal conductances in the open forest site were higher than those recorded in the gap and closed forest sites ($F_{(2578)} = 4.49$, $p = 0.011$). For the particular case of the generalist species Q. *psidiifolia*, the stomatal conductance showed the pattern: open forest

> closed forest > gap site (H = 49.77, N = 270, $p < 0.01$). Average leaf temperature was similar in all sites ($F_{(2512)} = 1.46$, $p = 0.231$).

Generalists are plants with acclimation capacity, which means a wide range of adjustment of the light saturation point; however that capacity depends of the environment where the seedlings grew (Rundel *et al.* 1998, Lambers *et al.* 2008, Ishii & Ohsugi 2011). This acclimation capacity was demonstrated by *Q. psidiifolia*, the most abundant species in the seedling bank, that showed a stomatal conductance and a leaf area/stem height ratio similar to those of the specialist *B. guianensis* in the gap site.

In general, stomatal conductance varied widely during the day, from values below 10 mmol m-2 s-1 to values around 1 000 mmol $m^{-2}$ $s^{-1}$ (Fig. 3). Comparisons among hour ranges showed that seedlings of the open forest had the highest stomatal conductance peaks from 5 to 8 h and from 15 to 18 h ($F_{(3,187)} = 22.59$, $p < 0.01$). Furthermore, seedlings of the gap site endured their highest leaf temperature from 12 to 15 h ($F_{(3,180)} = 68.77$, $p < 0.01$). The effect of time of day over leaf temperature was persistent; we found a general increase of around 4° C from 12 to 15 h (Fig. 3). The combined effect of air temperature and radiation caused that stomatal conductance of the gap site to be around 30 % lower than in the open forest site (MS = 59 071, N=578, $p = 0.02$) and 20 % lower than in the closed forest site (MS = 59 071, N=578, $p = 0.09$).

A physiological midday decrease of stomatal conductance and an increase of leaf temperature was common to all three sites. This results from a high vapor pressure difference between air and leaf (Pons & Welschen 2003, Kamakura *et al.* 2011). Differences of stomatal conductance were evident with a recovery after 15 h in seedlings of the open and closed forest sites that did not happened in seedlings of the gap site (Fig. 3). Such recovery could be possible through a fast energy dissipation and activation of alternative pathways of electron transport during a stress period (Krause *et al.* 2001, Leakey *et al.* 2003, Houter & Pons 2005). In general, stomatal conductance along the day was higher in the generalist *Q. psidiifolia* than in the specialists *C. decorticans* and *Calathea sp.*, in the closed forest (U = 4 097, $p < 0.01$) and open forest (U = 3 716, $p < 0.01$). These differences were noticeable from 9 to 15 h. In the gap site, early in the morning, stomatal conductance values of the specialist *B. guianensis* were 10-fold higher than the values observed in the generalist *Q. psidiifolia*.

The most significant correlations confirmed linear and negative relationships between stomatal conductance and photosynthetically active radiation, vapor pressure deficit, leaf temperature, and air temperature (**Fig. 4**). Despite

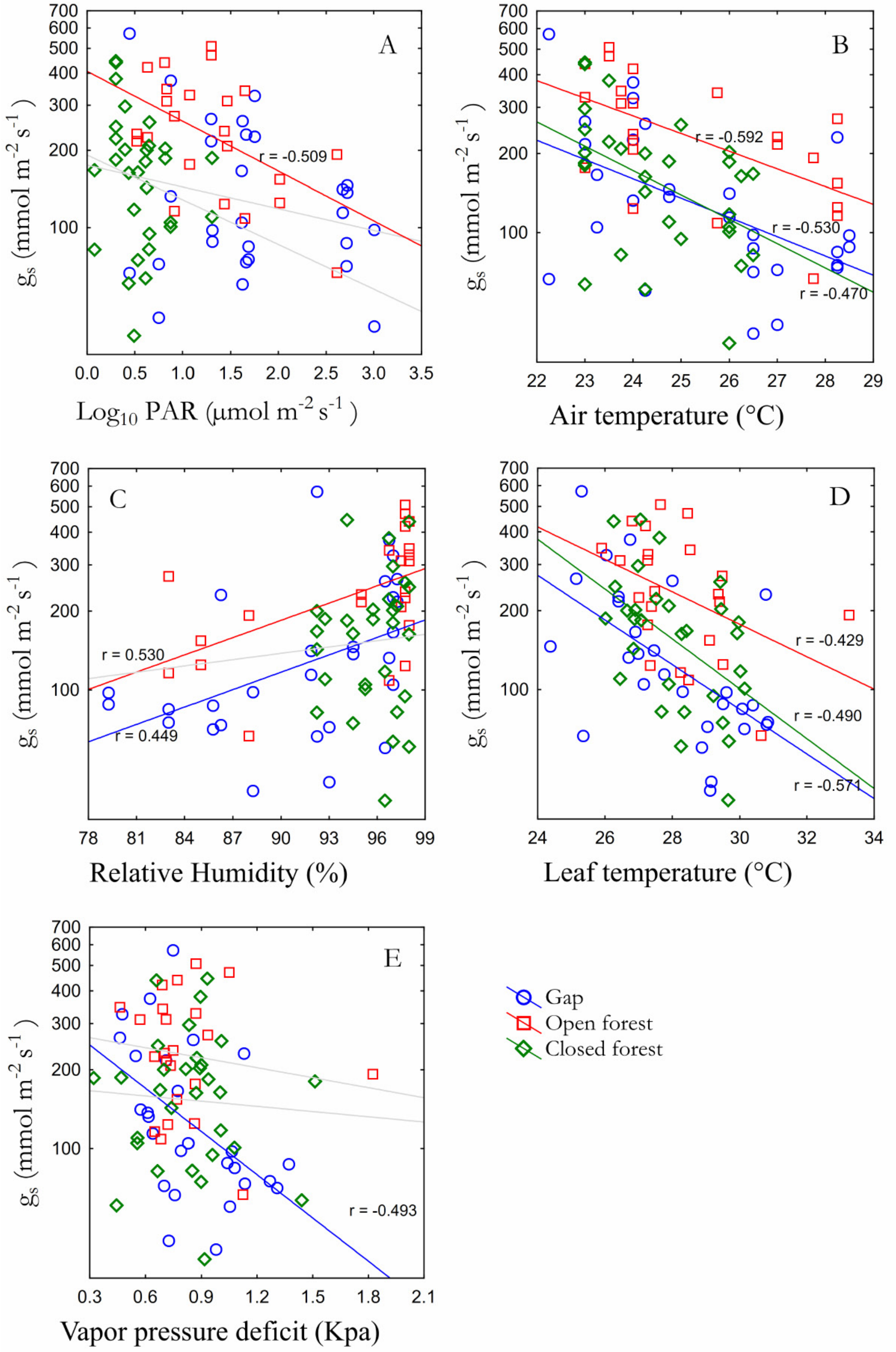

**Figure 4**. Pearson's correlations between stomatal conductance (gS) and five environmental variables at three sites in the PNNA Amazon rainforest. **A)** Photosynthetically active radiation (PAR), **B)** air temperature, **C)** relative humidity, **D)** leaf temperature, **E)** vapor pressure deficit. ($N = 82$, $p < 0.01$). Fitting lines correspond to significant correlation coefficients ($p < 0.05$).

these relationships, the general model of the multivariate linear regression ($\text{Log}_{10}$ gS = 0.47 – 2.1 LT+ 1.48 AT + 1.36 VPD + 0.96 RH – 0.15 PAR; $R^2 = 0.322$, $p < 0.001$) could explain only 32.2 % of the stomatal conductance. Separating the responses into gap ($R^2 = 0.388$, $p = 0.042$), open forest ($R^2 = 0.514$, $p = 0.021$), and closed forest sites ($R^2 = 0.442$, $p = 0.011$) resulted in more predictive models, explaining more than 38 % of variance of stomatal conductance in each case. The main weights of partial effects were of PAR in the open and LT and VPD in the closed forests. All variables seem to contribute equally to responses of stomatal conductance. The fact that air and leaf temperature sustain a marked overall linear relationship with stomatal functioning, supports the argument that temperature is also a limiting factor for plant growth in rainforest ecosystems (Roberts *et al.* 1990, Pearson *et al.* 2002, Leakey *et al.* 2003).

The interplay of the different variables measured and its effect on stomatal conductance is complex, and it depends on the environmental heterogeneity of the Amazon rainforest. The leaf temperature of seedlings in the closed forest did not exceed 30° C throughout the day, and this variable was the main limiting factor to gas exchange. There is evidence that seedlings of late-successional species experience a marked reduction of their relative growth at high temperatures (Cheesman & Winter 2013) and the most suitable explanation is the influence of dark respiration on the light compensation point (Baltzer & Thomas 2007). In the open forest, radiation was the most limiting factor for stomatal conductance. Plants in the understory of tropical forests are normally exposed to densities below 400 $\mu$mol photons $m^{-2}$ $s^{-1}$ (Carswell *et al.* 2000), the majority of these species could reach its maximum rate of carbon assimilation at flux densities around 350 $\mu$mol $m^{-2}$ $s^{-1}$ (Ashton *et al.* 2011) and these rates are usually lower to 5 $\mu$mol C $m^{-2}$ $s^{-1}$ (Valladares *et al.*, 1997; Carswell *et al.*, 2000; Nascimento & Marenco 2013). Therefore, seedlings in open forest, showing slow growth and being adapted to shade, are likely to be more susceptible to photoinhibition.

A considerable fraction of the variation in stomatal conductance was not explained by the models, which led us to wonder if intrinsic characteristics of seedling, such as leaf area, height, and leaf number could modulate the physiological response to environmental heterogeneity. **Table 3** shows linear relationships based on the full set of seedlings, suggesting that tall individuals with large leaf area delay temperature rise during the early hours of the day, while individuals with large leaf area and high leaf number dissipate heat quickly in the afternoon, after the peaks of radiation and temperature.

**Table 3**. Spearman correlations between morpho-physiological traits and leaf temperature of seedlings at different hours of day. Asterisk denotes significant values at $p < 0.01$.

| Variable correlated with leaf temperature | Time of day | | | |
|---|---|---|---|---|
| | **5-8h** | **8-12h** | **12-15h** | **15-18h** |
| LA | -0.613* | 0.413* | 0.445* | -0.668* |
| SH | -0.604* | 0.161 | 0.437* | -0.333 |
| LN | -0.308 | 0.187 | 0.107 | -0.541* |

However, individuals with large leaf area (not necessarily large leaf number) also undergo overheating in the hours of highest radiation. Apparently there is a pattern of intrinsic modulation of thermal acclimation that increases with ontogeny (Claussen 1996). This subject has been incipiently investigated (Cheesman & Winter 2013), and will be important for a full understanding of plant growth and regenerative dynamics in tropical forests.

## Conclusions

The environmental contrast among small forest gaps, open forest, and closed forest promotes the establishment of a large number of specialist plant species in the PNNA Amazon rainforest. Low radiation in the understory does not limit the physiology of seedlings, and other sources of stress, like herbivory or desodependant factors should be studied to explain the recruitment of seedlings in these environments.

The effect of environmental factors on seedling stomatal conductance varies according to site. However, leaf temperature and air temperature constitute two of its determinants. In turn, our findings suggest that leaf temperature could be partially regulated by individual morphological characteristics.

The generalist plant *Q. psidiifolia*, present in all three sites, showed a physiological plasticity that set its competitive advantage against specialist plants, thus persisting for longer time.

The small gap is the most unfavorable site for seedling survival and only a few heliophyte species persist. This indicates that gaps opening do not contribute substantially in the high alpha diversity of the Amazon rainforest.

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## Conflict of Interests

The authors declare no conflict of interest.

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# Comportamiento fisiológico diurno de plántulas en la pluviselva amazónica: especies generalistas versus especialistas de sombra y de sol

**Resumen:** El éxito regenerativo de especies generalistas y especialistas puede deberse a diferencias en su fisiología. Las medidas de conductancia estomática (gS) proporcionan una forma eficiente de inferir respuestas fisiológicas inmediatas de las plantas a la variación ambiental. Se midió radiación, temperatura del aire y humedad relativa en la pluviselva amazónica colombiana, para identificar condiciones ambientales extremas que limitan la gS de las plántulas en tres tipos de sitios: un claro pequeño, bosque abierto y bosque cerrado. Se planteó la hipótesis de que la actividad fisiológica diurna de especies generalistas debe ser plástica en estos tres ambientes. Se evaluaron las características morfológicas, la gS, y la temperatura de la hoja en plántulas de cuatro tipos de especies: una generalista, común a todos los sitios, y una especialista de cada sitio. El sitio del claro fue más cálido y más irradiado que los otros dos sitios, lo que causó algunas depresiones fisiológicas del mediodía y supervivencia de plántulas limitada, y facilitó la estrategia especialista. Las temperaturas de las hojas y del aire fueron fuertes determinantes de la gS global. Las especies generalistas fueron fisiológicamente plásticas y, a ciertas horas del día, más eficientes que las especialistas de los bosques abiertos y cerrados. Esta interacción de los factores podría permitir la coexistencia de ambos tipos de plantas.

**Palabras clave:** Heliófitas; dinámica de claros; temperatura de las hojas: plántulas; tolerancia a la sombra; conductancia estomática.

## Comportamento fisiológico diurno de mudas na Floresta Amazônica: espécies generalistas versus espécies especialitas de sombra e sol

**Resumo:** O sucesso regenerativo de espécies generalistas e especialistas pode ser devido a diferenças em sua fisiologia. As medidas de condutância estomática (gS) proporcionam uma forma eficiente de inferir respostas fisiológicas imediatas das plantas a variação ambiental. Foram medidas radiação, temperatura do ar e humidade relativa na Floresta Amazônica Colombiana, para identificar condições ambientais extremas que limitam a gS das mudas em três tipos de locais: uma pequena abertura, bosque aberto e bosque fechado. Planteou-se a hipóteses de que a atividade fisiológica diurna de espécies generalistas deve ser plástica em estes três ambientes. Avaliaram-se as características morfológicas, a gS e a temperatura da folha em cada muda de quatro tipos de espécie: uma generalista comum em todos os locais, e uma especialista de cada local. O local aberto foi mais caloroso e mais irradiado que os outros dois locais, o que causou algumas depressões fisiológicas do meio-dia e sobrevivência limitada das mudas, e facilitou a estratégia especialista. As temperaturas das folhas e do ar foram determinantes fortes da gS global. As espécies generalistas foram fisiologicamente plásticas e, a certas horas do dia, mais eficientes que as especialistas de bosques abertos e fechados. Estas interações dos fatores poderiam permitir a coexistência de ambos os tipos de plantas.

**Palavras-chave:** Heliofitas; dinâmica de abertos; temperatura das folhas; mudas; tolerância à sombra; condutância estomática.

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