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Morphological and Physiological Adjustments in Juvenile Tropical Trees Under Contrasting Sunlight Irradiance

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1. Introduction

Luminosity is considered one of the most relevant environmental factors in plant growth, and it is closely associated to forest succession. It controls from morphogenetic processes of germination to morphological and physiological patterns of plant growth in different classes of forest succession.

There are several proposals to define succession classes of tree based on the placement of the species in the forest. Overall, two extreme successional groups are distinguished: a) species of the early-succession category (pioneers), which germinate, survive, and grow only in glades; and b) species of the final or late-succession category (climax), which require shady environments in the understory to grow. However, a large number of species that occupy intermediate status between these two succession classes has already been acknowledged.

In the 1980s, early species began to be categorized into sun plants; and late species into shade plants. In the beginning of this century, the concept of sun-requiring species and shade-requiring species has been adopted for plants that need high irradiance and intense shading, respectively, in order to develop. Few species suit these limitations. Studies show that most species are able to tolerate intermediate irradiance conditions. They are, therefore, categorized as facultative sun and facultative shade species.

Other terms that have often been used are shade-tolerant plants and sun-tolerant plants. Shade-tolerant plants correspond to shade-requiring plants, or simply shade plants. Sun-tolerant plants are the sun-requiring plants, also called sun plants.

Since the term *tolerance* suggests better performance under optimum environmental conditions, but able to acclimatize under conditions that are less favorable to growth, in this chapter we adopt the term *sun plants* (pioneer, sun-requiring or sun-tolerant plants), and *shade plants* (non-pioneer, shade-requiring or shade tolerant). The species in-between these two categories we call: facultative sun plants (early intermediate plants), which develop under full sunlight but tolerate moderate irradiance; and facultative shade plants (late intermediate plants), which prefer intense shading but are able to grow under moderate shading.

The initiative of categorizing the species into different status of succession is based on quantitative and qualitative criteria of the luminous spectrum occurring in natural environments, which varies significantly from the edge to the interior forest. However,

this categorization does not always correspond to the results obtained under controlled irradiance conditions. Some species considered ombrophytes of tropical forest have shown high phenotypic plasticity at the juvenile stage. They have been able to survive and grow under full sunlight. Nevertheless, the best performance occurred under moderate shading – typical characteristic of facultative shade species. Another aspect to be taken into account is phenology, because there could be different responses from juvenile to adult stage.

With so many environmental and ontogenetic variables influencing the morphological and physiological responses, it is difficult to find a scale for growth, biochemical, and physiological patterns which is able to characterize sun and shade requiring and facultative species.

Due to their high sensitivity to luminosity, the shade species have received special attention. Studies carried out with shade plants have shown that this kind of plant has lower plasticity under contrasting irradiance, which, in some cases, can compromise its growth and survival under full sunlight. When exposed to high sun irradiance, shade species suffer immediate and irreversible damages such as chlorosis, burns, and necrosis (Figure 1), followed by leaf abscission. If they are not capable of adapting to the new environment, they can collapse because of photoinhibition.

Morphological and physiological responses to variations in light intensity are well documented regarding leaves of arboreal vegetation in temperate areas. Studies on tropical tree have increasingly focused on medium term responses, leaving a gap concerning short term responses to light stress. Especially, regarding shade tolerant, semideciduous species. Based on the few tropical shade tolerant species in this study, we understand that the damages appear in the first seven days of exposure to direct solar radiation. In this period, there are photoinhibition and photo-oxidation followed by partial or complete abscission of leaves. Even so, they are able to sprout new leaves with new morphological and physiological characteristics without compromising survival.

This chapter aims at presenting up-to-date and unpublished results about the morphological, biochemical, and physiological adjustment of tropical shade arboreal vegetation after exposure to full sunlight. These data may encourage revisions to the status in forest succession of tropical species, because the descriptions of their ecological preferences concerning luminosity are quite contradictory.

2. Morphology and growth measurement

2.1 Growth

Species of the same succession group and even ecotypes of the same species have different reactions to irradiance alterations. In general, shade species of temperate climates do not survive or have low survival rates when exposed to full sunlight.

Regardless of their status in the forest succession, tropical forest plants under limiting irradiance have low root: shoot ratio (R:S); and higher leaf area ratio (LAR), leaf mass ratio (LMR), and specific leaf area (SLA). These responses provide higher photosynthetic activity in relation to breathing, allowing these species to be established inside the forest, where luminosity represents only between 2 to 8% of sunlight irradiance in the canopy.

Aiming at relating the succession status of 15 semideciduous tropical trees (Table 1) to growth measurements (Figure 2, 3 e 4), Souza & Válio (2003) verified that early-succession species (pioneer or sun plant) kept higher relative growth rate (RGR), even in the shade.

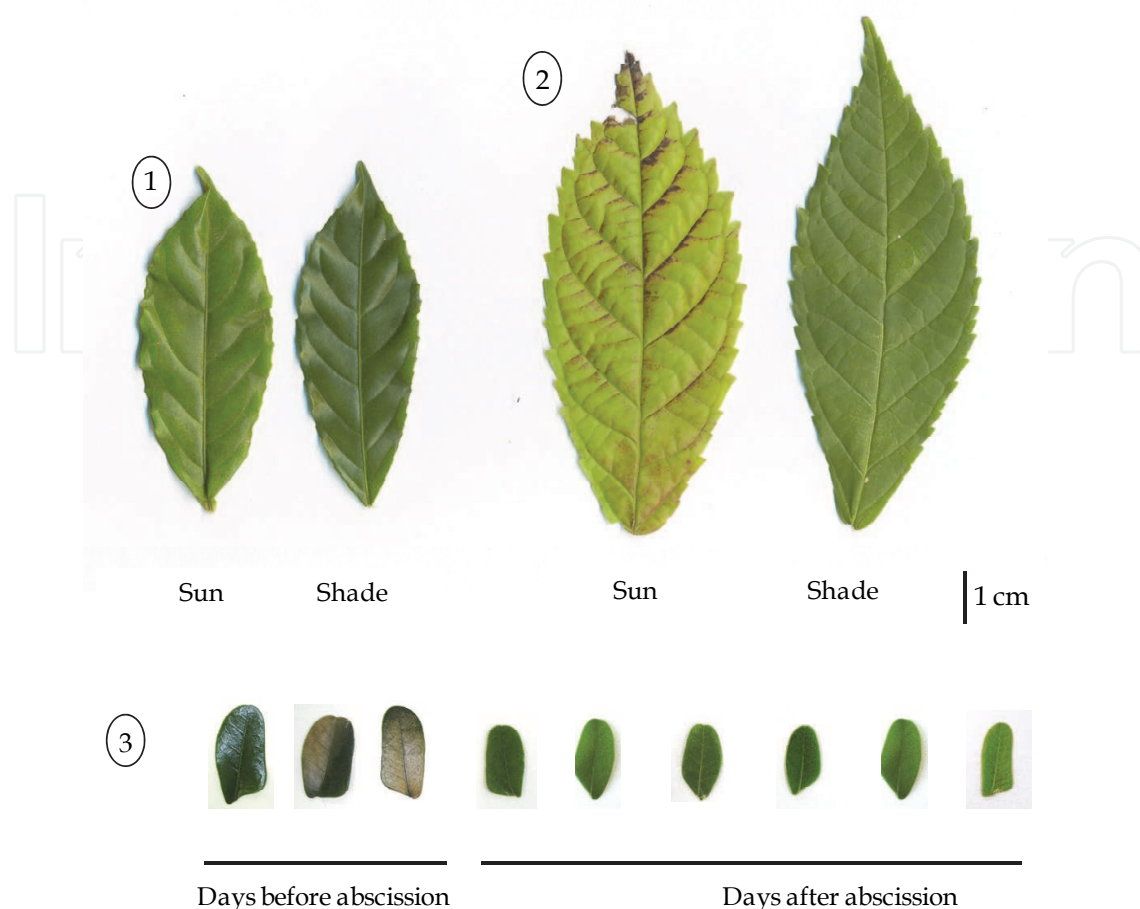


Fig. 1. Morphological features of leaves of Brazilian tropical species grown under full sunlight and shading (20% of photosynthetically active radiation). ① *Cariniana estrellensis* (Lecythidaceae), sun-tolerant; ② *Paratecoma peroba* (Bignoniaceae), shade-tolerant; ③ *Caesalpinia echinata* (Fabaceae) moderately shade-tolerant. Notice the little difference in coloration of *C. estrellensis* leaves under the two luminosity conditions. The leaves of *P. peroba* under full sunlight, however, presented chlorosis and burns at the veins. Notice the burn at the *C. echinata* pinnules before abscission. In the new pinnules sprouted after abscission, the reduced leaf area and lighter color can be noticed. Photographs provided by Paradyzo (2011) and Mengarda (2011).

For tropical forest species in the early succession stage or sun plants, RGR ranged between 40 and 60 $\text{mg.g}^{-1}.\text{day}^{-1}$ under full sunlight, whereas for late or shade plants RGR was around 20 $\text{mg.g}^{-1}.\text{day}^{-1}$ under high irradiance (Figure 2). Nevertheless, the species *Caesalpinia echinata*, considered moderately shade-tolerant (facultative shade or early intermediate plant) tropical tree, showed higher RGR under full sunlight than under shading. This shows that RGR does not always follow the value decreasing from early species (sun plants) to late plants (shade or climax plants).

As far as net assimilation rate (NAR) is concerned, the early species showed values under full sunlight in which NAR ranged from 0.3 to 0.6 $\text{mg.cm}^{-2}.\text{day}^{-1}$ (Figure 2). When under shading, the early and late species almost did not present differences regarding NAR, which was under 0.2 $\text{mg.cm}^{-2}.\text{day}^{-1}$. In some cases, NAR can reach very low values

(around 0.01 mg.cm².day⁻¹), as seen in *C. echinata*, a species moderately shade-tolerant, under high shade.

This inconsistent pattern in terms of growth and forest succession status can be attributed to ontogenesis. Therefore, one should be careful not to extrapolate results obtained in the juvenile stage to adult stage. There is also the climatic factor in which the experiments were carried out. Overall, the experiments with tropical tree plants have been carried out in areas that differ in terms of irradiance intensity, precipitation, humidity, altitude, and average temperature. Another aspect that hinders comparisons in the analysis of results regards the lack of standard growth measurements, especially for growth rates expressed using different units of measurement.

Species	Successional status
<i>Solanum granuloso-leprosum</i> (Solanaceae)	E
<i>Trema micrantha</i> (Ulmaceae)	E
<i>Cecropia pachystachya</i> (Cecropiaceae)	E
<i>Bauhinia forficata</i> (Caesalpiniaceae)	E
<i>Senna macranthera</i> (Caesalpiniaceae)	E
<i>Schizolobium parahyba</i> (Caesalpiniaceae)	E
<i>Piptadenia gonoacantha</i> (Mimosaceae)	E
<i>Chorisia speciosa</i> (Bombacaceae)	I
<i>Pseudobombax grandiflorum</i> (Bombacaceae)	I
<i>Ficus guaranitica</i> (Moraceae)	L
<i>Esenbeckia leiocarpa</i> (Rutaceae)	L
<i>Pachystroma longifolium</i> (Euphorbiaceae)	L
<i>Myroxylon peruiferum</i> (Fabaceae)	L
<i>Hymenaea courbaril</i> (Caesalpiniaceae)	L

Table 1. Species studied, classification according to the successional status (E = early-uccessional; I = intermediate, L = late-successional). Souza & Vlio (2003).

For tropical trees, low RGR values for early species under low irradiance have been associated to reduction in photosynthetic activity, as indicated by low NAR (Figure 2). However, RGR is not always related to NAR (physiological component of RGR). In some cases, RGR can be related to LAR (morphological component of RGR). These relations between RGR, NAR, and LAR depend much on the intensity of solar radiation. Not taking succession status into account, the 15 species analyzed by Souza & Vlio (2003) showed that RGR of plants under full sunlight and under natural shading is related to NAR, but not to LAR (Figure 4). This shows higher influence of the physiological component on growth rate. However, under artificial shading, the RGR was correlated to LAR, but not to NAR (Figure 4). In this case, the morphological component, particularly leaf area, had greater effect on growth rate. These differences in the correlation between RGR and NAR or LAR concerning artificial and natural shading have also been attributed to the luminous spectrum quality. Under natural shading, the red light: distant red light ratio is low, suggesting the involvement of phytochrome in the increase in SLA, component of LAR, and in LMR. These results indicate that leaf thickness and allocation of biomass to the leaves are the most pronounced morphological alterations, regardless of the species’ forest succession status.

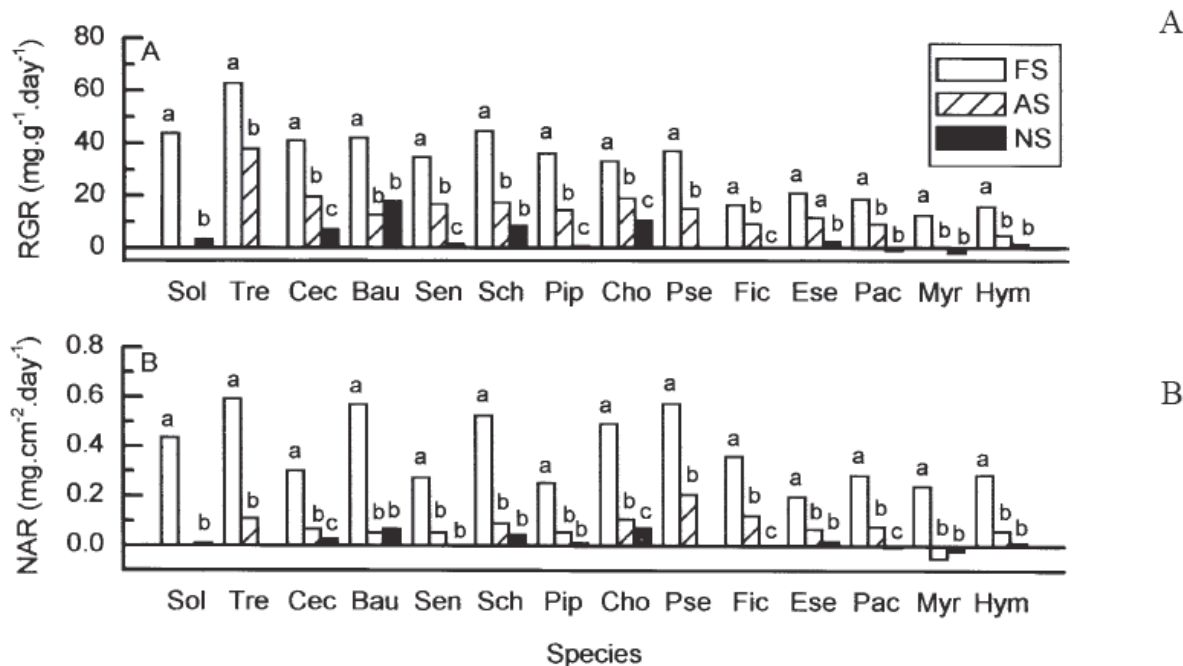


Fig. 2. A. Relative growth rate (RGR) and B. net assimilation rate (NAR) of the studied tree species under full sun (FS), artificial shade (AS) and natural shade (NS) treatments. Measurements for 0-100 days time interval. Sol = *Solanum*, Tre = *Trema*, Cec = *Cecropia*, Bau = *Bauhinia*, Sen = *Senna*, Sch = *Schizolobium*, Pip = *Piptadenia*, Cho = *Chorisia*, Pse = *Pseudobombax*, Fic = *Ficus*, Ese = *Esenbeckia*, Pac = *Pachystroma*, Myr = *Myroxylon*, Hym = *Hymenaea*. Values followed by the same letter are not significantly different. Souza & Válio (2003).

No difference in the R:S ratio has been noticed among early and late species, both under full sunlight and artificial shading (Figure 3). In general, R:S ratio ranged between 0.25 and 0.5. LMR showed higher plasticity for early species whose value ranged between 0.3 and 0.7 g.g^{-1} , especially under effect of shading (Figure 3). These results can be confirmed by the higher SLA values of early species under artificial shading (6 $\text{dm}^2.\text{g}^{-1}$). Under full sunlight, almost no difference has been found in terms of SLA of early and late plants. Early species under shading tended to present increased LAR values; around 3.4 $\text{dm}^2.\text{g}^{-1}$. Under full sunlight, the early and late species did not show significant LAR differences.

Although there are data maintaining that late species or shade plants show better performance than pioneer or sun plants under low luminous intensity, it does not always happen. Some species that are considered sun plants can show low RGR; typical of shade plants. The opposite can also happen, as seen in *C. echinata*, a moderately shade-tolerant species that showed higher RGR under full sunlight than in the shade.

Overall, the results have shown that morphological variations of tropical arboreal plants have higher influence on RGR when sun-tolerant species are under effect of shading.

Tropical tree shade species are able to develop in long periods of shading, keeping low growth rate, which favors the formation of a seedling bank. Due to their tolerance to higher irradiance, these plants show to be able to develop under increased luminosity, when glades are formed.

Therefore, the task of establishing a relation between growth measurement and successional status of tropical arboreal plants is complex. There is a paucity of more consistent data that

allow defining sun and shade plants, as well as characterizing facultative sun and shade plants (intermediate plants in forest succession).

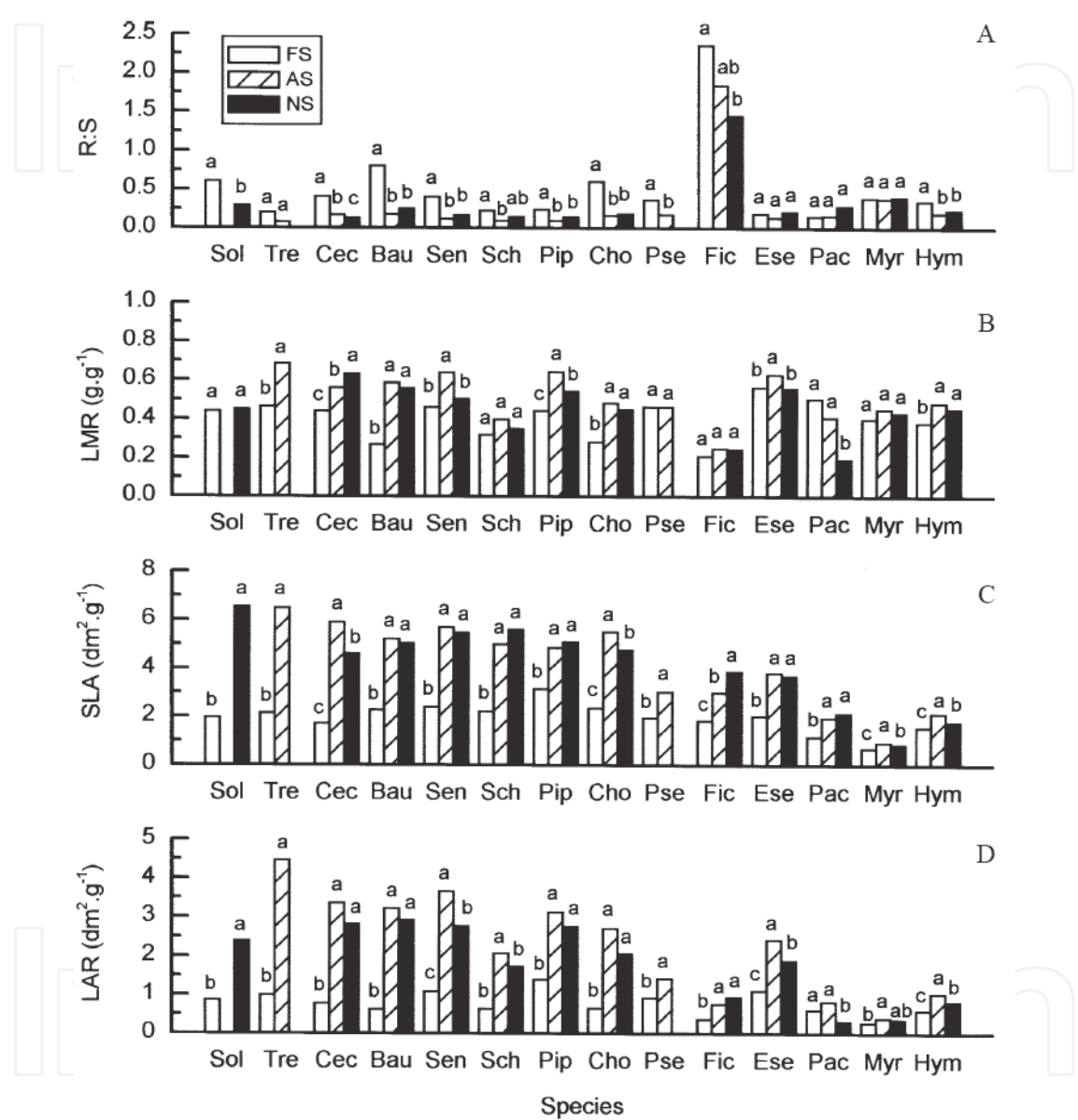


Fig. 3. A. Root:shoot ratio (R:S); B. leaf mass ratio (LMR); C. specific leaf area (SLA); and D. leaf area ratio (LAR) of the studied tree species under full sun (FS), artificial shade (AS), and natural shade (NS) treatments. Measurements after 100 days. Sol = *Solanum*, Tre = *Trema*, Cec = *Cecropia*, Bau = *Bauhinia*, Sen = *Senna*, Sch = *Schizolobium*, Pip = *Piptadenia*, Cho = *Chorisia*, Pse = *Pseudobombax*, Fic = *Ficus*, Ese = *Esenbeckia*, Pac = *Pachystroma*, Myr = *Myroxylon*, Hym = *Hymenaea*. Values followed by the same letter are not significantly different. Souza & Válio (2003).

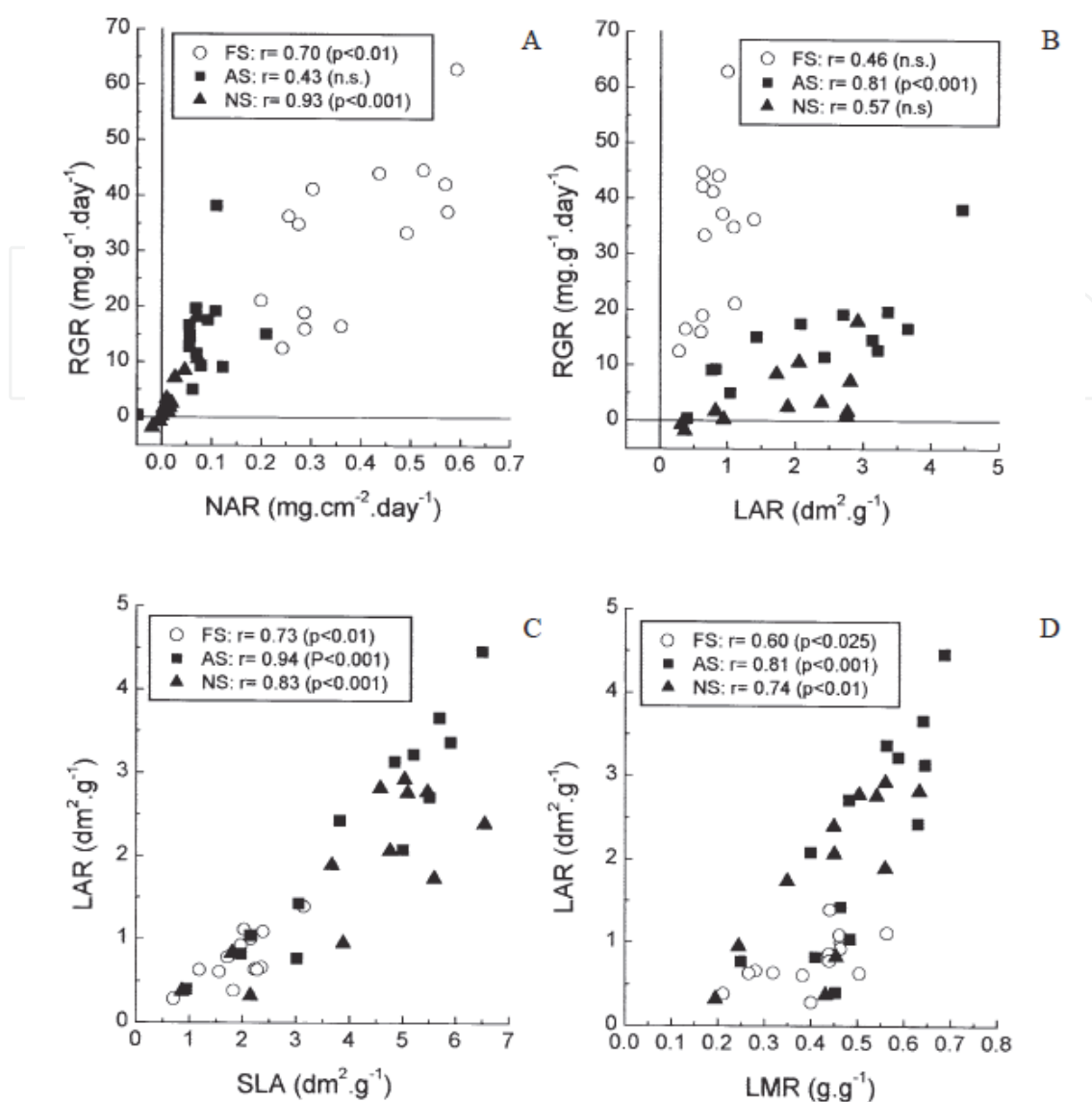


Fig. 4. Correlation between RGR and NAR (A); RGR and LAR (B); LAR and SLA (C); and LAR and LMR (D). Pooled data of all species under each one of the treatments (FS = full sun; AS = artificial shade, NS = natural shade). RGR = relative growth rate, NAR = net assimilation rate, LAR = leaf area ratio, LMR = leaf mass ratio. Souza & Válio (2003).

2.2 Leaf morphology

The ability a plant has to overcome the alarming stage is a result of physiological adjustments combined with morphological adaptations. This interaction has been considered the most relevant factor to acclimatization and survival of shade plants, when exposed to high irradiance. The morphological adjustment can start in existing plants. However, they are most pronounced in young leaves sprouted after high irradiance exposure.

In shade species, the damage caused by intense irradiance takes place already on the first days, resulting in leaf abscission. In *C. echinata*, total leaf abscission took place on the first seven days. However, in other tropical species this effect can come later, as observed in *Minquartia guianensis*, a shade species of the Amazon forest, in which 30% of its leaves collapsed before the end of the second week under full sunlight.

Differently from what had been speculated about understory species, the results have shown different degrees of sensitivity after these plants were exposed to high irradiance. Some understory species of humid tropical forest such as *Ouratea lucens* showed moderate photoinhibition, preserving most of their leaves. For *Hybanthus prunifolius*, however, there was severe photoinhibition and almost total loss of leaves.

The phenotypic plasticity of tropical arboreal plants to luminosity involves characteristics that are related to higher efficiency in capture or dissipation of light through the leaves. This essentially depends on the adjustments of morphological and anatomical components.

Among the most significant anatomical adjustments observed in shade species under high sun irradiance, we can highlight the thickening of cuticle, palisade parenchyma, and increase in stomatic density, and trichomes. For *C. echinata*, the new leaves sprouted after abscission showed thickening of palisade parenchyma (Table 2), which suggests an efficient morphological strategy to reduce photo-oxidative damage. In general, the highest stomatal density is associated to reduction in the stomatal opening area and, consequently, resistance to water loss through transpiration. Cuticle and adaxial epidermal cell thickening is also one of the adjustments often seen in tropical shade species, when exposed to full sunlight. These adaptations minimize leave surface heating by promoting of light reflection.

It is important to highlight that the intensity of these responses may vary significantly among the leaves before and after abscission. In *C. echinata*, exposure to full sunlight induced limb thinning because of thickness reduction in adaxial epidermis and palisade parenchyma during the first seven days of exposure preceding leaf abscission (Table 2). However, the new leaves sprouted after abscission showed increased thickness in palisade and spongy parenchyma, which were the main contributors to limb thickening (Table 2). In this aspect, the palisade parenchyma increased 142% under full sunlight, whereas the spongy parenchyma increased 58.3% and the adaxial epidermis 12.5% compared to plants under shading. The higher elongation of chlorophyllian tissue in the new leaves reflected the higher water content; 50% higher compared to plants under shading. These data suggest that *C. echinata* is a species that uses water effectively under full sunlight.

The reduction in SLA after solar radiation exposure is common among tropical arboreal plants. This response was observed, for example, in *M. guianensis* and *C. echinata* (Table 2). Reduction in SLA means smaller solar radiation interception area, contributing to water loss reduction and improvement of photosynthetic performance, growth, and survival of the plants under full sunlight.

Variables	7 days		60 days	
	Shade	Sun	Shade	Sun
SLA (mg.cm ²)	250±19	170±16	210±21	150±14
Limb (mm)	120±14	135±18	137±11	195±18
Palisade parenchyma (mm)	32±06	44±08	40±08	80±10
Lacunary parenchyma (mm)	60±10	60±13	67±14	88±09
H ₂ O (mg.cm ²)	18±02	19±03	18±02	27±04

Table 2. SLA values, limb thickness, palisade parenchyma, lacunary parenchyma, and water content in leaves of *Caesalpinia echinata* after 7 and 60 days of transfer of plants from shade to full sun. ± represents standard error of the mean (n=6). Data provided by Mengarda (2010).

Besides the anatomic alterations, variations in secondary metabolite content may take place in plants under intense solar radiation. Phenolic and flavonoid compounds tend to accumulate in the epidermis and mesophyll of tropical tree shade plants under higher solar intensity. Leaves of *C. echinata* under shading have shown accumulation of phenols only in the epidermis, whereas under full sunlight, they also accumulated these compounds in mesophyll cells (Figure 5). Phenol accumulation indicates that the existence of an efficient antioxidative defense system working on the sequestration of several reactive oxygen species (ROS) and O_2 singlet in chloroplasts of plants under intense solar radiation. The stress caused by excessive solar radiation also induces biosynthesis of polyphenols, among them, flavonoids. Probably, using ROS as molecular signals. Also, an increase in flavonoid concentration in leaves of arboreal plants lessens the penetration of UV wavelength.

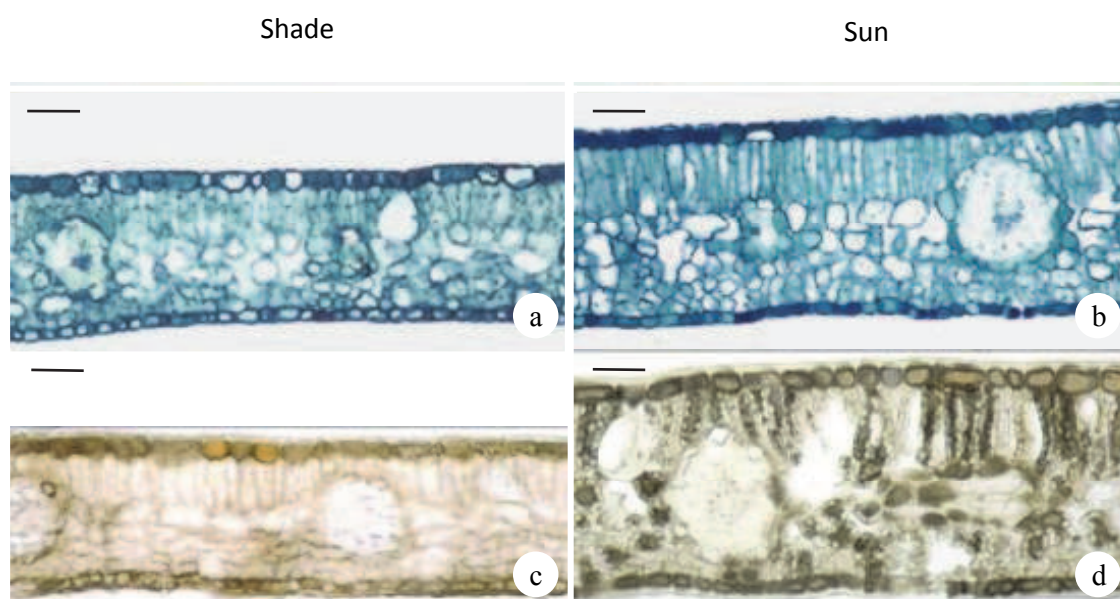


Fig. 5. Cross section of *Caesalpinia echinata* pinnules in the shade (a and c) and under full sunlight (b and d). The mesophyll of leaves under full sunlight showed chlorophyll parenchyma and adaxial epidermis thickening. Notice the higher accumulation of phenolic compounds in the limb of plants under full sunlight (d). Bar = 50 μ m. Data provided by Mengarda (2011).

3. Photosynthesis

The acclimatization strategy to high irradiance varies among species, and even among ecotypes of the same species. The physiological adjustments of shade plants exposed to high irradiance involve decrease in total chlorophyll concentration (Chl_{tot}) or increase in ratio between violaxanthin cycle pigments and Chl_{tot} . Violaxanthin and carotenoids reduce photoinhibition risks, oxidative damage, and increase dissipation of excessive energy through non-photochemical processes.

In the stage of light stress signalization of tropical shade tree species, the photoinhibition signals can be seen already in the first 24 hours of exposure to full sunlight. In *C. echinata*, a photosynthetic carbon assimilation (A), maximum quantum yield of photosystem II (F_v/F_M),

water-use efficiency (WUE), stomatic conductance (g) e transpiration (E) decreased in the first three hours (Figure 6, 7 e 8) until they reached the lowest values in 48 hours, in a 192 hour period. During this period, it was not possible to identify the restitution stage that precedes the resistance stage.

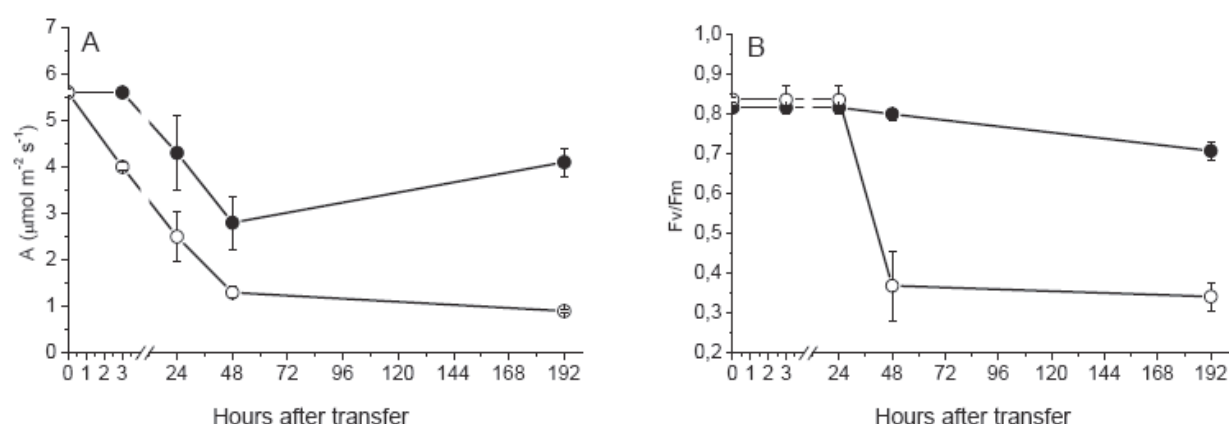


Fig. 6. Photosynthetic carbon assimilation (A) and maximum quantum yield of photosystem II (B) of *C. echinata* plants subjected to constant artificial shade of 50% (●) and transferred from shade to full sunlight (○) at 0, 3, 24, 48 and 192 h. after the start of the experiment. Vertical bars indicate standard error. Mengarda et al. (2009).

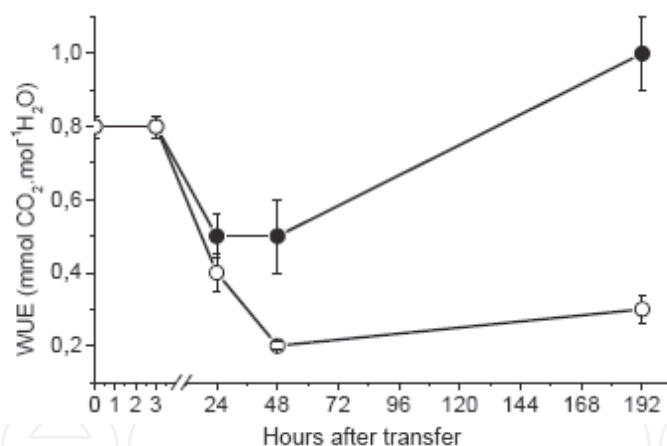


Fig. 7. Water-use efficiency of *C. echinata* plants subjected to constant artificial shade of 50% (●) and transferred from shade to full sunlight (○). Vertical bars indicate standard error. Mengarda et al. (2009).

The factors that limit photosynthesis vary according to irradiance intensity. Plants developing in shaded environments invest more in light-capturing complexes, whereas plants developing in the sun invest in Calvin cycle and electron transport proteins. Thus, irradiance variations cause alterations in A because of the differences in maximum velocity of Rubisco carboxylation (V_{c-max}) and in the maximum rate of ribulose biphosphate regeneration. The results obtained from tropical shade species show limited capacity to increase A in environments under high irradiance, due to inability to increase V_{c-max} .

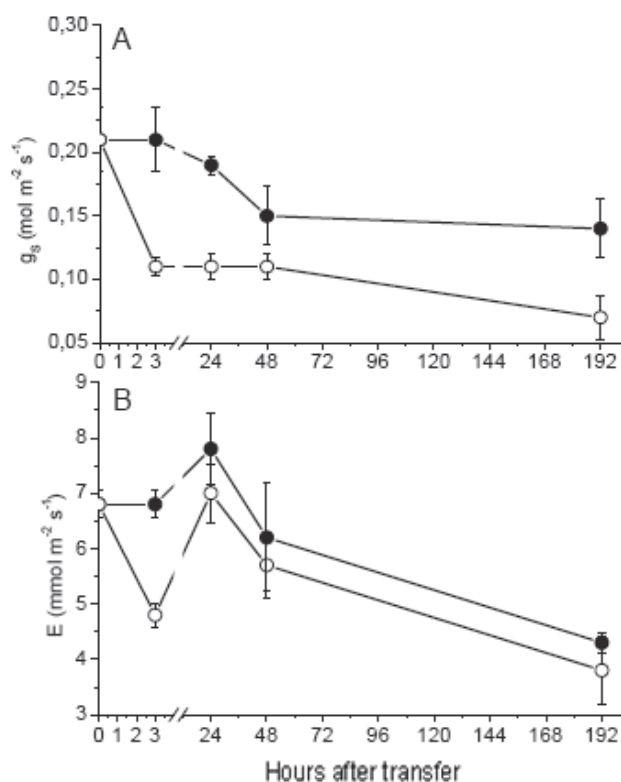


Fig. 8. Stomatal conductance (A) and transpiration (B) of *C. echinata* plants subjected to constant artificial shade of 50% (●) and transferred from shade to full sunlight (○). Vertical bars indicate standard error. Mengarda et al. (2009).

The chlorophyll fluorescence parameters have been widely used to analyze responses from shade plants exposed to intense irradiance. Especially to detect alarming and resistance stages. Overall, tropical shade tree plants show higher density of absorbed photons per reaction center of PSII (ABS/RC) when exposed to high irradiance, as seen in *C. echinata* and *Aniba roseodora*. During the first three days of exposure to full sunlight, *C. echinata* plants (Figure 9) showed an increase in energy dissipated in the form of heat or fluorescence (DI_0/RC), in absorbed energy (ABS/RC), and in energy captured and converted into redox energy for electron transport (ET_0/TR_0). These responses can indicate inactivation of the reaction center (RC). On the second day of transfer of *C. echinata* plants from the shaded environment to full sunlight, there was a significant increase in the probability that the electron captured by the reaction center of PSII remain in the transport chain beyond QA^- (ET_0/TR_0). Nevertheless, the significant reduction in the density of active reaction centers of PSII (RC/ABS) on the first seven days may have influenced the reduction in effective quantum efficiency of radiant energy conversion (F_V/F_0), and in the performance index (PI_{ABS}). The inactivation of 58 to 78% of RC in *C. echinata* (Figure 9), along with reduction in maximum quantum yield of photosystem II (F_V/F_M), indicate an increase in energy dissipation in the form of heat and fluorescence for some tropical tree plants exposed to intense irradiance. Although parameters such as RC/ABS, F_V/F_0 and PI_{ABS} have shown an increase after 20 days, the effective recovery of the photosynthetic apparatus was not observed during the 180 days of full sunlight exposure for *C. echinata* plants (Figure 9).

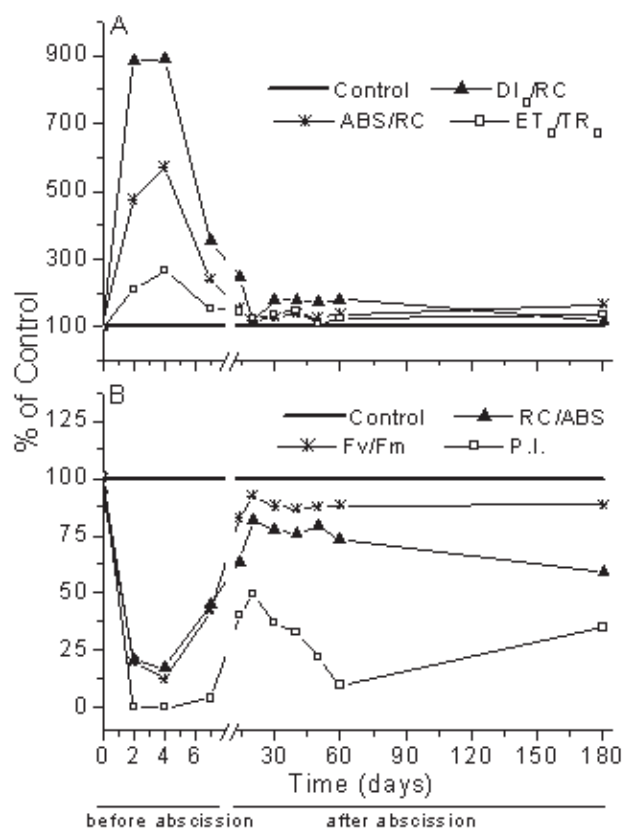


Fig. 9. Chlorophyll fluorescence emission *a* of *C. echinata* plants transferred from shade to full sunlight. Energy dissipation per reaction center (DI_0/RC), energy absorption per reaction center (ABS/RC), and probability that an exciton captured by the RC of FSII move an electron in the transport chain to beyond Q_A^- (ET_0/TR_0); (B) Ratio between number of active reaction centers of FSII and the amount of light absorbed by the antenna system (RC/ABS), maximum quantum yield of PSII (F_v/F_m), and performance index based on absorption (PI_{ABS}). Values expressed in percentage in relation to control ($n=5$). Data provided by Mengarda (2011).

The joint analysis of F_v/F_m and PI_{ABS} can be related to the ability plants have to transform luminous energy into metabolic reactions of the photosynthesis biochemical processes. Thus, taking into account the reduced F_v/F_m values and the significant drop in PI_{ABS} observed in plants under full sunlight, it can be concluded that the exposure of young *C. echinata* plants to full sunlight caused photoinhibition and reduction in primary photochemical efficiency, which can compromise photosynthesis.

In the first acclimatization weeks under high irradiance, the tropical tree plant *Mimuaritia guianensis* showed an increase in initial fluorescence (F_0), and reduction in maximum fluorescence (F_m) and F_v/F_m . Recovery only took place after four months of exposure to full sunlight, when F_v/F_m values reached 93% of the values observed for plants kept in the shade. For the tree plant *A. rosaeodora* of the Brazilian Amazon forest, reduction in F_v/F_m took place at 2 days of exposure to high irradiance, and recovery took place only at 60 days, when the values approached those observed for shaded plants.

For other tropical forest arboreal plants, the physiological adjustment process can slower. The transfer of Amazonian *M. guianensis* plants from a shaded environment to high irradiance caused a sharp decrease in F_v/F_m during the first three days, followed by gradual recovery until maximum values were reached on the 120th day, reaching the control group.

The stress condition is caused by excessive input of energy in the system, which hinders the use of this energy in the photosynthetic process. Under ideal conditions, the plants show low free energy in the system and optimum thermodynamic status, without compromising the photochemical stage in PSII. However, the photoinhibition observed in *C. echinata* plants subjected to direct solar radiation can represent a photoprotection mechanism, working on the balance between effective non-photochemical dissipation of excessive energy and the photosynthesis itself. This does not decharacterize a stress condition, but allows the adjustment and survival of the plant.

Chlorophyll fluorescence a can be considered a potential tool to differ species of particular successional status, which is useful to select species to be used for recovering degraded areas. In general, sun-requiring or facultative sun species (pioneer and early intermediate) show higher photochemical ability and increasing tendency to dissipate excessive energy as luminous intensity grows. A study carried out on three tropical tree leguminous plants (*C. echinata*, *C. ferrea* and *Machaerium obovatum*) observed higher electron transport rates and higher F_V/F_M with higher intensity of light saturation for *C. ferrea*, which suggests that this species is best adapted to environments with high irradiance, whereas *C. echinata* and *M. obovatum* do not show these responses. Therefore, *C. echinata* was characterized as late intermediate species, because it does not present photosynthetic acclimatization that is effective to high irradiance conditions. However, partial photosynthetic acclimatization and sufficient photoprotection mechanisms have been observed, allowing young plants to survive and grow under full sunlight. Thus, planting these species in reforestation has been suggested, adopting the intercropping system, in which plants receive moderate shading.

4. Soluble carbohydrates

One of the immediate metabolic signs in response to abrupt increase in irradiance is in the variation of soluble carbohydrates. These compounds are recognized as important molecular signals in the plant-environment relation and modeling agents of physiological and morphological processes.

Higher concentrations of glucose (Glu), fructose (Fru) and sucrose (Suc) were related to tolerance to water deficit during the winter for some tropical forest leguminous and tree plants. Polyols such as mannitol (Man) were also associated to water stress in *Fraxinus excelsior*. For *Olea europaea*, a Mediterranean tree, the accumulation of Man was associated to this species' tolerance to saline stress (Figure 10).

The accumulation of *monosaccharides* and Suc in leaf tissues of tree plants under water deficiency, increased salinity and intense irradiance has often been associated to osmoregulation. The relevant few studies published showed reduction in osmotic potential in leaf cells of Mediterranean tree plants such as *Ilex aquifolium* and *O. europaea* under high irradiance. For *C. echinata*, a tropical forest species, the leaves of plants under full sunlight showed higher water content (Table 2). This result was associated to higher content of total soluble carbohydrates (TCS), which possibly led to the reduction in water potential.

More recently, special attention has been paid to raffinose (Raf), which despite being found in low levels in leaves, has a significant role in the osmotic adjustment in herbaceous plants under stressing conditions, as observed in *Arabidopsis thaliana*. Raf is a trisaccharide that, along with stachyose and verbascose, is part of the oligosaccharides family of raffinose (RFO), which are synthesized from sucrose. Nevertheless, few are the publications on the

involvement of Raf in tree plants' tolerance to high irradiance. Studies on *C. echinata* showed higher concentration of Raf in leaves after 60 days of exposure to full sunlight, suggesting an antioxidant action. Besides being osmoregulators, the monosaccharides, disaccharides such as Suc and RFOs have also been related to antioxidant actions in plants that are tolerant to water deficit and high irradiance. Therefore, investigating oxidative stress and its relation to carbohydrates could provide data to better understand the mechanisms of tolerance to light stress in tropical tree plants.

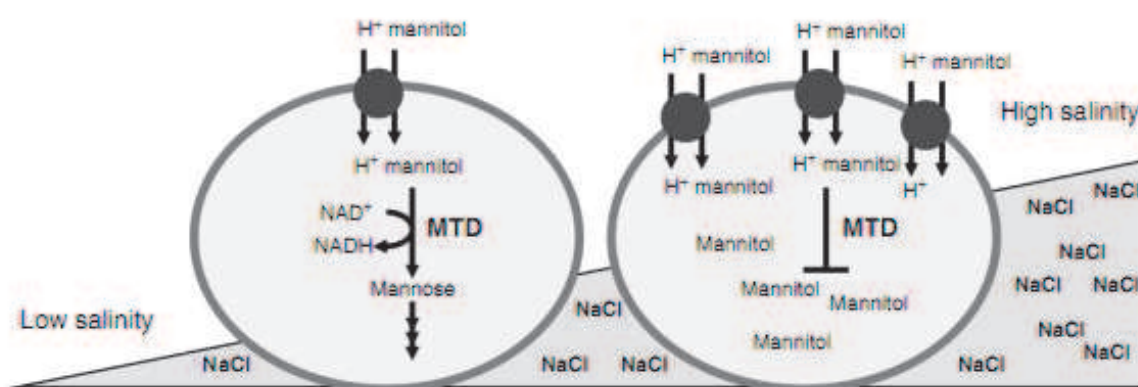


Fig. 10. Regulation of mannitol transport and metabolism as a mechanism providing salt tolerance in *O. europaea*. Conde et al. 2007.

Carbohydrates can also modify the morphological components of leaves. There are indications that the increase in palisade parenchyma thickness through elongation and periclinal cell divisions in tree plants under high irradiance is related to Suc concentration in leaves. *Chenopodium album* L. leaves, an annual herbaceous plant, showed increase in the number of layers of palisade parenchyma cells when exposed to high irradiance. This response is associated to concentration of Suc. In *C. echinata*, limb thickening because of palisade and lacunary parenchyma elongation has also been associated to higher concentration of leaf sucrose of plants under full sunlight.

There are indications that carbohydrates are also able to model plant growth, modifying biomass allocation patterns, growth rates, and R:S ratio. Under full sunlight, tree plants tend to invest more in root growth to the detriment of leaf area, resulting in RGR and NAR reduction.

In general, physiological and morphological responses associated to carbohydrates were obtained after exposing the plants to high irradiance for several days, leaving a gap concerning understanding the adjustment mechanisms at early stages of light stress. Studies on *C. echinata* have been carried out in order to categorize the alarming and resistance stages to luminous stress in a 180-day period. In this regard, carbohydrate contents and their relation to morphological and physiological adjustment have been analyzed at short periods of time (0, 2, 4, 7, 15, 30, 40, 50, 60, 120 and 180 days). The results show that the alarming stage was characterized by increased Glu and Fru contents with maximum peak at seven days. The resistance stage started with new leaves sprouting (at 15 days, Table 3), which stood out because of their higher concentrations of Suc and Raf. However, gradual reduction in Suc contents was observed by the 180th day (10 mg.g⁻¹ DW), equal to the control group (shaded plants).

Carbohydrates	7 days		60 days	
	Shade	Sun	Shade	Sun
Glu	1.2±0.68	6.0±0.27	1.0±0.65	1.0±0.25
Fru	1.1±0.41	7.0±0.15	0.7±0.09	0.5±0.05
Suc	10.3±2.53	17.0±2.16	7.0±1.25	14.0±1.36
Raf	0.26±0.07	0.26±0.08	0.04±0.00	0.7±0.06
TSC	11.2±1.58	30.0±3.86	8.0±2.95	14.0±3.25

Table 3. Leaf concentration of soluble carbohydrates in *C. echinata* plants after 7 and 60 days of transfer from shade to full sunlight. Glucose (Glu); Fructose (Fru); Sucrose (Suc); Raffinose (Raf) and total soluble carbohydrates (TSC). ± represents standard error of the mean (n=6). Data provided by Mengarda (2010).

5. Conclusion

Some tropical tree plants considered shade plants or late intermediate in forest succession are able to survive under high irradiance. Even if at the alarming stage of light stress they show partial or total abscission of leaves, survival rate is high. This is due to these plants’ ability to sprout new morphologically and physiologically adjusted leaves in environments with higher irradiance. Some tropical species considered shade plants show high plasticity to contrasting sunlight, at least in their early stages of growth. In part, physiological variables contribute more to plasticity index at the alarming stage of luminous stress. At the resistance stage, the new leaves sprouted show morphological alterations, such as SLA reduction and limb thickening. The most frequent morphological adjustment such as elongation and/or increase in the number of layers of palisade parenchyma, and reduction in SLA seem to be under the control of Suc. Photo-oxidative damage such as reduction in the *Chla:b* and *Chl_{total}:carotenoids* ratio, maximum photochemical yield of PSII, and PI_{ABS}. did not compromise the survival of shade plants when they were exposed to high solar radiation. The results point to the need of increasing the number of tropical species under controlled conditions, and assess their physiological and morphological mechanisms in field conditions at different stages of development; from seedling to adult stage. These data can support the proposal of a new forest succession classification for some tropical tree plants.

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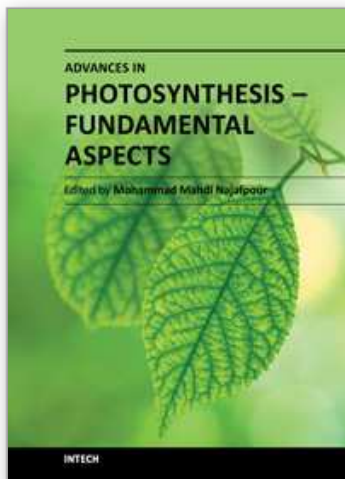
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