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SEEDLING ESTABLISHMENT AND ENDURANCE IN TROPICAL FORESTS: ECOPHYSIOLOGY OF STRESS DURING EARLY STAGES OF GROWTH

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Resumo:

"Estabelecimento e persistência de plântulas em florestas tropicais: ecofisiologia de estresse durante os estágios iniciais de crescimento"

A regeneração natural de vegetações requer produção sazonal de unidades de dispersão capazes de germinar e se estabelecer sob condições estressantes. Estabelecimento depende de processos (germinação, crescimento radicular e produção de folhas) que são limitados por fatores físico-químicos como umidade, luz e textura e química do solo. Adicionalmente, competição intra- ou interespecífica de indivíduos estabelecidos reduz o espaço para o desenvolvimento de raiz e copa de plantas em crescimento. Nas florestas tropicais, os principais estresses regulando crescimento, relações hídricas e fotossíntese são as reduzidas intensidades luminosas e disponibilidade de nutrientes. A exigência por elevadas intensidades luminosas decresce das plantas pioneiras e espécies arbóreas de estágios iniciais de sucessão, para as espécies de estágios tardios que toleram sombra. Competição radicular e simbiose mutualista (micorrizas) regulam ganho de carbono a longo prazo no sub-bosque florestal. As altas concentrações de CO_2 próximo ao solo florestal, possivelmente facilitam a sobrevivência de plântulas por melhorar seu balanço de carbono. Em florestas secas e savanas, a sobrevivência de plântulas é associada à duração da estação seca e à intensidade de competição radicular. Espécies não-arbóreas, como gramíneas e pteridófitas, são capazes de extrair a maior parte da água e nutrientes disponíveis nas camadas superiores do solo. Em pântanos, inundação periódica ou permanente interage com intensidade luminosa para determinar crescimento e sobrevivência de plântulas e jovens.

Abstract:

Regeneration of natural vegetation requires seasonal production of dispersal units (seeds, propagules) able to germinate and become established under stressful conditions. Establishment depends on several processes (seed germination, root growth and leaf production) constrained by physico-chemical factors such as humidity, light intensity, and soil texture and chemistry. Furthermore, intra- or interspecific competition of established individuals reduces the space for root and canopy development of growing seedlings. In tropical forests low light intensity and nutrient availability are often the main stresses regulating growth, water relations and photosynthesis. Light intensity requirement decreases from the light-demanding pioneer and early successional tree species to the late successional, shade-tolerant tree species. Root competition and mutualistic symbiosis (mycorrhizae) regulate long-term carbon gain in the forest understory. Higher CO_2 concentrations near the forest floor possibly increase seedling survival by improving their carbon balance. In dry forests and savannas, seedling survival is associated with the length of the dry season and the intensity of root competition. Non-tree species (grasses and forbs) are able to take up most of the water and nutrients available in the upper soil layers. In swamp forests recurrent or permanent flooding interacts with light intensity in determining growth and survival of seedlings and saplings.

Introduction

Forest regeneration requires the establishment of seedlings and saplings within the same (or similar) environment where the parent trees grow. However, in rain forests environmental conditions determining performance of adult trees contrast with those under which their seeds germinate and develop. Adult trees occupy a volume of the forest canopy, with levels of light availability at least one order of magnitude higher than those prevalent in the forest understory (Chazdon & Fetcher, 1984). Photosynthetically active radiation is the driving force in the production of organic matter, therefore it has been assumed that openings in the canopy (gaps) allowing enough light to reach the understory are required for the regeneration of forest trees (for a review see Strauss-Debenedetti & Bazzaz, 1996). However, it seems clear that the establishment of seedlings within natural forests depends on the interaction of multiple external factors, both biotic and abiotic, with the physiological and morphological properties of the seedlings (Fig. 1).

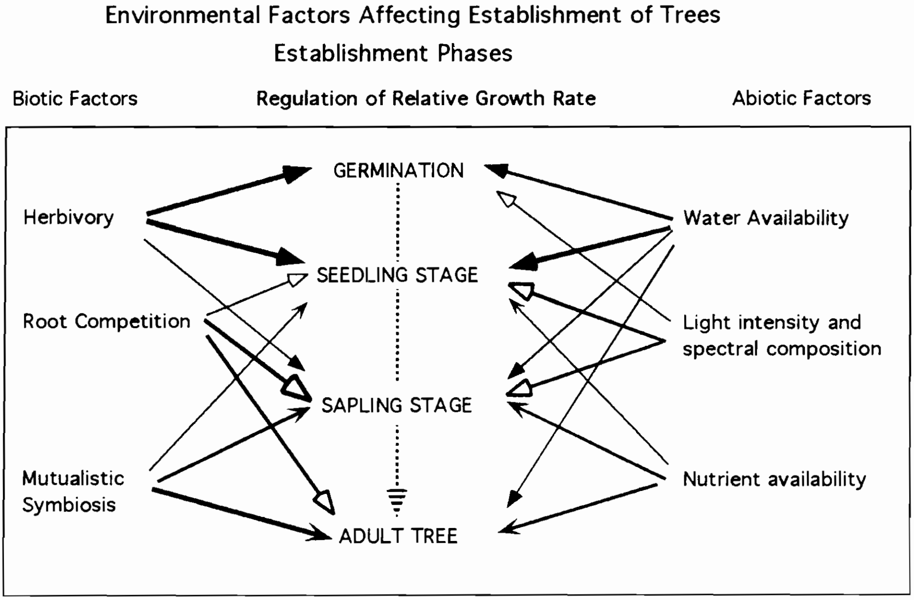

Figure 1. Multilevel interactions of abiotic and biotic factors affecting seedling and sapling survival in tropical forests. Arrow thickness indicates the magnitude of the interaction. The arrow heads differentiate the environmental factors.

Among the abiotic factors, light intensity has been identified as the main limitation for seedling establishment in tropical rain forests. In addition, nutrient availability may also be critical because it is a strong regulator of seedling growth rate.

Among the biotic factors root competition and mutualistic symbiosis seem to affect seedling establishment, at least in forests growing on acid, highly leached soils. Their influence is mainly related to the regulation of nutrient availability. Intrinsic genetic factors that regulate growth rate determine the demand for environmental resources, and therefore may influence the carbon balance in the shady understory of tropical forests. Herbivory is certainly a most important process affecting seedling survival and composition of plant populations (Coley, 1983), but I will not discuss it here because it would require special consideration of secondary plant metabolism.

Based on observations of population dynamics under natural conditions it has been recognized that tropical rain forest trees present a large range of variation in shade tolerance. The extremes of this continuum have been conceptualized as early successional or pioneer trees that grow rapidly in gaps under high light intensity, and those that are found in the forest understory and persist for prolonged periods with slow or nil growth rates while light availability remains low, denominated late successional (mature forest trees)(Swaine & Whitmore, 1988).

Recent reviews on the ecophysiological traits of tropical tree seedlings and saplings have been published by Kitajima (1996) and Strauss-Debenedetti & Bazzaz (1996) and in a recent UNESCO book (Swaine & Alexander, 1995). These reviews provide an in-depth discussion of the processes of growth and survival, in association with photosynthetic and anti-herbivore traits, that explain the light requirements for establishment of tropical trees under natural conditions. It appears that less attention has been given to the impact of nutrient availability and the differences in air CO_2 concentration as possible co-determining factors of shade tolerance or capacity for exploitation of high light intensity environments.

In this paper I summarize selected aspects of plasticity and acclimation of both photosynthetic traits and growth responses, related to adaptation to the low light environment of tropical forests understory. Both light intensity as well as spectral composition will be taken into account. In addition I will emphasize two points: a) the possible role of nutrient availability, associated with substrate fertility or the occurrence of mutualistic symbiosis, and b) the potential significance of higher CO_2 concentration in the air of the forest understory as a partial compensation for lower light intensity. Finally I will highlight some aspects of seedling establishment in seasonal tropical forests that require more research in the future.

Environmental Factors Affecting Establishment of Tree Seedlings

There are a number of generalizations regarding the properties of forest seedlings according to their occurrence or preferences under natural conditions. This characterization takes the form of a dichotomy where extreme behaviors are depicted according to the experience of the researcher (for summaries of these dichotomies see

Givnish, 1988; Huston, 1994; Kitajima, 1996; Strauss-Debenedetti & Bazzaz, 1996). The usual designations found in the literature are associated with the successional status of the species considered: early, intermediate and late successional species. It is hypothesized that light requirements and drought tolerance decrease with successional position. A convenient way of expressing the range of variation found in plants that grow under different light regimes or levels of water availability has been devised by Huston (1994). The essential formulation is: plants that photosynthesize at high rates and grow and or reproduce rapidly under conditions of high light (or high soil water availability) are unable to survive at low light levels (or under dry conditions) (Huston, 1994). The corollary to this proposition is that shade tolerant plants are drought intolerant and *vice versa*. Fig. 2 is a graphic representation of Huston's statement with the addition that atmospheric CO_2 concentrations above present atmospheric concentration may displace the curves towards higher levels of potential carbon gain for a given level of light or water availability. This graphic representation is useful to understand the contrasting properties of shade tolerant (or drought intolerant) and light demanding (or relatively drought tolerant) plants in tropical rain forests. The concept expressed in Fig. 2 will be used in the rest of the paper to interpret the results obtained with different rain forest species.

Seedling Establishment in Tropical Rain Forests

Plasticity and acclimation of photosynthetic traits in tropical rain forest species

The bulk of the literature dealing with the effect of light intensity on the growth of rainforest tree seedlings has been thoroughly revised elsewhere (Kitajima, 1996; Strauss-Debenedetti & Bazzaz, 1996). A summary from those reviews indicates:

a) independently of successional status, survival and growth rates of all species are lower under light regimes similar to those prevalent in the understory of tropical rain forests,

b) photosynthetic traits of species classified as late successional are generally less plastic than those of species classified as early successional or pioneers,

c) there appears to be a continuum in shade tolerance among tropical forest trees.

Growth under low light regimes in the forest understory represents significant stress, jeopardizing seedling establishment and regeneration of the tree species that dominate these forests. The conclusion is that some kind of forest disturbance, that results in gap formation of various sizes, might be indispensable for forest regeneration.

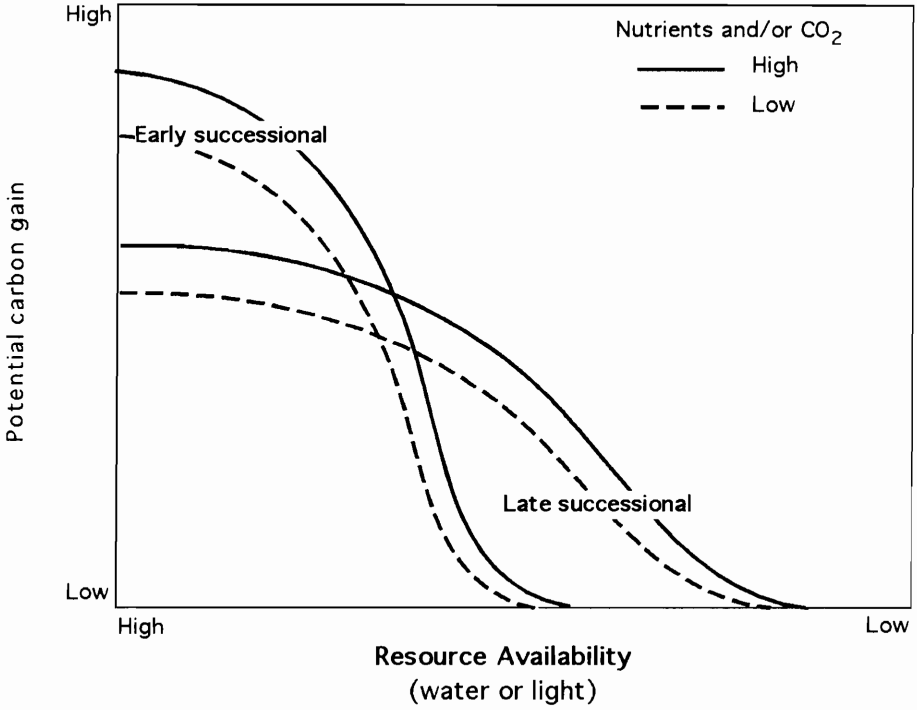

Fig. 2. Hypothetic responses of potential carbon gain by seedlings and saplings belonging to contrasting successional groups along gradients of resource availability. Analogous to Huston (1994).

Among the multiple responses of the photosynthetic machinery of different species to contrasting light regimes, the interactions between regulation of maximum photosynthetic rate (Amax) and the allocation of biomass to photosynthetic structures or roots still have to be analyzed and explained in detail. Is the enhanced growth under relatively high light regimes due to increased photosynthesis or to increased allocation to photosynthetic structures (leaf area)? In an experiment with early and late successional species of Mexican rain forests seedlings cultivated under high (HL) and low light (LL), the ratio Amax (HL/LL) was 3 to 4 in early successional species, but only 1.5 in a late sucessional species (Tinoco-Oranjuren & Pearcy, 1995) (Table 1).

Table 1. Differences in Amax, leaf area development and leaf mass per area in pioneer and mature phase tropical forest trees grown in high light (36.3 mol day^{-1} and Red:FarRed ratio= 1.25) and low light (0.98 mol day^{-1} and Red:FarRed=0.26). * Indicate that differences among treatments are statistically significant (Tinoco-Ojanguren & Pearcy, 1995).

		Amax(μmol m^{-2} s^{-1})	Leaf Area (cm^2)	Leaf mass/area (g m^{-2})
Heliocarpus appendiculatus	L	3.7	185	14.0
	H	11.6*	1856*	32.7*
Cecropia obtusifolia	L	5.2	712	39.0
	H	22.4*	2647*	116.1*
Rheedia edulis	L	3.8	113	75.7
	H	5.6*	194*	113.6*

Similarly, the ratio of leaf mass per area (HL/LL) was 2-3 in the early successional compared to 1.5 in the late successional species. However, the leaf area ratio (HL/LL) varied from 4 to 10 in the early successional but it was only 1.7 in the late successional. In the case of *Heliocarpus appendiculatus*, enhanced growth was more the result of increased allocation to leaf area development, while in *Cecropia obtusifolia* Amax seemed to be slightly more important in enhancing growth than leaf area. In the late successional species, enhanced growth in high light was due equally to increased Amax and leaf area. Ramos & Grace (1990) reached the conclusion that it is the amount of photosynthates allocated to the construction of leaves, and not the photosynthetic rates, that determines overall growth under contrasting light regimes.

The dynamics of acclimation to changes in the predominant light environment are also of great physiological and ecological relevance. The differentiation of sun and shade types may be understood on the basis of the original analysis by Björkman (1981). Sun plants can modify their allocation of nitrogen to photosynthetic proteins according to the light energy available during growth, therefore they are more plastic in the sense of Bazzaz & Pickett (1980). Shade types cannot take advantage of the higher light availability, although their growth may be enhanced, because their photosynthetic protein content does not increase as much as in the sun types (Gauhl, 1976; Björkman, 1981). Plants grown under a certain light regime adapt their morphology and biochemical characteristics so that carbon gain is maximized. The degree of change in these properties for a species cultivated under contrasting light regimes represents its photosynthetic plasticity (Fetcher *et al.*, 1983; Oberbauer & Strain, 1985; Ramos & Grace, 1990; Riddoch *et al.*, 1991a,b; Strauss-Debenedetti & Bazzaz, 1991; Turnbull, 1991; Ashton & Berlyn, 1992; Kamaluddin & Grace, 1992a,b; Tinoco-Ojanguren & Pearcy, 1995). Changes in light conditions during growth, from low to high or in the reverse direction, generate strong physiological changes that can be measured as responses in growth and leaf photosynthetic rates. The speed and efficiency with which these changes take place constitute the acclimation capacity of the species (Bazzaz & Carlson, 1982). The acclimation of photosynthesis can take place within the same leaves developed in a different light regime, or in new modules that develop after a shift in light conditions (Kamaluddin and Grace, 1992a,b; Strauss-Debenedetti & Bazzaz, 1996). The dynamics of these processes of plasticity and acclimation have been abundantly documented in the literature and in general agree with known biochemical processes regulating synthesis of proteins of the photosynthetic machinery. Turnbull *et al.* (1993) conducted an experiment that summarizes most of the results in the literature (Table 2).

Three species of different successional positions from Australian rainforests were cultivated under contrasting light regimes, and after several months, plants were transferred to the opposite light regime and the changes in photosynthetic behavior were followed. Low light plants, independently of their successional status, showed lower Amax than the same species cultivated under high light. When transferred to the opposite light regime Amax and Rdark decreased when plants were transferred from high to low, while the opposite occurred when plants were transferred from low to high light regime (Table 2). However, acclimation of leaves formed previously to the new light regime was not as complete as that observed in the newly formed leaves. It should be noted that changes in photosynthetic rates were always more pronounced in early or mid successional species when compared to late successional. This result supports the view of Bazzaz and co-workers that light demanding species are more plastic and acclimate faster to contrasting light regimes than late successional species. Further, the reduction of respiration in plants transferred from high to low light intensity was of similar magnitude regardless of successional status. On the contrary, increases in Rdark in transfers from low to high light were significantly larger than reductions, and were less pronounced in late successional species than in the other two types. This point seems to be of potential significance for the maintenance of a positive carbon balance in the shady forest understory. It seems that regulation of respiration of leaves, and possibly of all tissues of seedlings developed under low light, may play a more important role in shade tolerance than has been appreciated so far.

Kitajima (1996) raised the point that the higher photosynthetic plasticity of early successional plants does not help them to survive in the long run under shady conditions. The answer appears to be related to the intrinsic high relative growth rates characteristic of the early successional types and their capability to withstand herbivory. In a detailed study on the growth rates of saplings in a Panamanian lowland humid forest, King (1994) found that light-demanding species grew as rapidly as shade-tolerant species in the shade. However, their shorter leaf lifespan required higher production rates and this lowered probability of survival in the understory.

Most studies on the photosynthetic plasticity and acclimation capacity of tree seedlings have been conducted at the leaf level only. Conclusions regarding light requirements for survival based on this type of analysis may be erroneous because leaf area development has a number of costs associated with its own construction and maintenance, and costs associated with support and transport of water and nutrients (Givnish, 1984). Ecologically significant light compensation points have to be calculated on a daily basis, taking into account the photosynthetic surplus of the leaves and the consumption of assimilates by leaf night respiration, and amortization of construction costs. Givnish (1988) calculated that the light compensation points of *Liriodendron tulipifera*, a shade intolerant temperate forest tree, increased from 13 µmol $m^{-2} s^{-1}$ for instantaneous photosynthesis, to 93 µmol $m^{-2} s^{-1}$ if night respiration and leaf construction costs are included. When whole plant gas exchange is considered the light requirements for a positive carbon gain increase rapidly. This type of analysis is required for a more fundamental understanding of seedling survival in the understory of tropical forests.

Table 2. Percentage change in photosynthesis (Amax) and respiration (Rdark) of mature leaves of *Omalanthus populifolius*, *Duboisia myoporoides* and *Acmena ingens* 28 days after transfer to a new light environment. Treatments: High (H), Low (L) and Very Low (VL) Light. * and ** significance at p<5% and 1% respectively (Turnbull *et al.*; 1993).

	Transfer	*Omalanthus populifolius*	*Duboisia myoporoides*	*Acmena ingens*
Amax	H-L	-58.4*	-64.0*	-43.8 ns
	L-H	+2.5 ns	+53.8*	+45.8**
	VL-H	+52.2*		
Rdark	H-L	-63.6**	-62.6*	-62.7**
	L-H	+165**	+196**	

Morphogenetic responses associated with changes in the R:FR ratios

Tinoco-Ojanguren & Pearcy (1995) found that changes in the ratio of red to far-red light (R:FR ratio) of the incoming radiation influenced morphogenetic aspects of early successional species but did not modify steady-state photosynthetic characteristics. The leaf area ratio and the leaf weight ratio of pioneer species (*Heliocarpus appendiculatus* and *Cecropia obtusifolia*) are significantly reduced under low R:FR ratios, while no response was detected in the late successional species studied (*Rheedia edulis*). On the other hand, carboxylation capacity and Rdark under low light was not affected by the R:FR ratio. Amax was influenced weakly only in the case of *H. appendiculatus*, being higher under high R:FR ratios.

Lee *et al.* (1996) found that species of rain forest trees differing in their successional status responded differently to cultivation under contrasting light intensities and R:FR ratios. Early successional species (*Endospermum malaccense* and *Parkia javanica*) drastically change their growth rates and architectural characteristics in relation to light intensity. Some properties, particularly the ratio leaf area/stem length, tend to decrease more in light demanding compared to shade tolerant species under conditions of lower R:FR ratios. That means that early successional species allocate more carbon to stems than to leaves when grown under low R:FR ratios.

Kitajima (1994) did not find any influence of the R:FR ratio on gas exchange, allocation patterns, or growth rates in 13 species with different successional status in Panamá. Seedlings were grown under the different light treatments during only two months, therefore they may still have been dependent on seed reserves.

Growth and mortality of tree seedlings: regulation of growth rates

Shade tolerance of tropical rain forest trees has been measured as the survival after one year of growth under low light comparable to understory light intensity, and medium light intensity comparable to the light conditions characteristic of small gaps or the border of large gaps (Augspurger, 1984). Successional status was evaluated using wood density. In general, pioneer, fast growing species have lower wood densities. Augspurger (1984) found that shade tolerance (slope of the log number of surviving shaded seedlings plus one) was highly correlated with wood density of the adult tree, meaning that late successional trees are more shade-tolerant than early successional. Seedlings in medium light intensity grew faster than those in low light. Correspondingly, longevity of photosynthetic cotyledons was longer under shady conditions. In addition, shade tolerant seedlings also proved to be less damaged by pathogens (particularly fungi). The results point out to a continuum in shade tolerance rather than to a clearcut differentiation among extreme types.

Sunfleck frequency and efficiency of utilization

Most of the studies relating survival or photosynthetic plasticity to light intensity during early stages of growth have used uniform light regimes. However, for many tropical rainforests the light environment in the understory is very dynamic because of the occurrence of sunflecks. Pearcy and co-workers have shown that seedlings and saplings growing in the understory of natural forests respond significantly to the frequency and intensity of sunflecks. These short-term pulses of light contribute to improving the carbon balance of plants in the shade (Chazdon & Pearcy, 1986; Pearcy, 1988). Photosynthetic capacity of shade plants is induced by sunflecks of several minutes of duration (light activation of RubP-carboxylase). Afterwards, photosynthetic responses to subsequent sunflecks are quite rapid. Fully induced leaves show higher carbon gain than expected under steady state assimilation rates because of the post-illumination CO_2 fixation (Pearcy, 1988). Even in non-induced leaves carbon gain can be equal to or higher than that expected under steady state, light-saturated photosynthesis. The induced state of the photosynthetic machinery is reduced during succeeding periods of low light intensity. Therefore, frequency of light flecks is critical to attain higher carbon balances than those expected under steady state of photosynthesis.

Nutrient availability

Soon after exhaustion of seed reserves seedling growth is strongly dependent on the availability of nutrients from the forest soils (Kitajima, 1996). The enhancement of seedling growth and survival under conditions of medium light intensity and sufficient water supply brought about by increased supply of nutrients has been demonstrated under experimental and natural conditions by many authors (Denslow *et al.*, 1987; Thompson *et al.*, 1988; Riddoch *et al.*, 1991b ; Burslem *et al.*, 1994; Huante *et al.*, 1995). Tropical forest soils are commonly deficient in phosphorus (Grubb, 1977; Vitousek, 1984;

Medina & Cuevas, 1994), but other nutrients become strongly limiting once phosphorus limitation has been removed. Seedlings of *Melastoma malabathricum* grown on native forest soil were shown to be extremely dependent on the supply of P. Mixtures of P plus Ca, micronutrients, Mg, K and N produced additional stimulation of growth during a 3-month period (Burslem *et al.*, 1994; Fig. 3).

Light intensity and nutrient availability during early stages of growth interact quite strongly. Under low light intensity nutrient requirements for the development of the photosynthetic machinery are smaller. In herbaceous, light demanding species, photosynthetic capacity of plants cultivated under high light intensity with low nutrients is similar to that of plants cultivated under low light intensity (Medina, 1971). It is noteworthy that low nutrient, high light plants appear to be less healthy than low light, low nutrient plants and accumulate considerable amounts of chloroplast starch. Comparison of photosynthetic properties of early successional and late successional species under contrasting light intensities and nutrient supply produced more complex results. High availability of nutrients resulted in higher maximum photosynthetic rates both in low and high light for both successional types (Riddoch *et al.*, 1991b; Table 3).

The ratio leaf area/weight decreases under high light intensity for both nutritional treatments. In a study of *Flindersia brayleyana*, a tree species with a wide range of shade tolerance, seedling growth and leaf area development were greater at intermediate light intensities, both at high and low nutrient availability levels (Thompson *et al.*, 1988; Table 4). Maximum photosynthetic rate, photosynthetic electron transport and carboxylation efficiencies were also higher at intermediate light intensities. Conversely, Rdark increased with light intensity during growth. Nutrient availability did not affect respiration rates, however, assimilation rates were reduced markedly in the treatment high light/low nutrient, falling below the treatment low light/low nutrient. Rate of electron transport and carboxylation efficiency behaved in a similar fashion (Table 4).

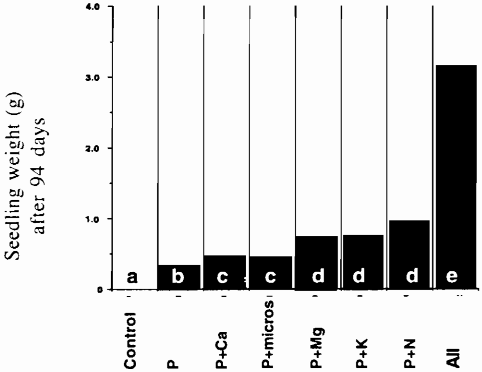

Fig. 3. Growth response of seedlings of *M. malabathricum* growing on natural forest soil (control) and amended with different combinations of fertilizers (data from Burslem *et al.*, 1994).

Table 3. Photosynthesis (Amax), nitrogen content (N) and specific leaf area (SLA) of a pioneer (*N. diderrichii*) and a late successional (*E. angolense*) species from a semi-evergreen African rainforest (Riddoch *et al.*, 1991b).

Species	Light/Nutrient	Amax (µmol m^{-2} s^{-1})	N(mmol kg^{-1})	SLA (m^2 kg^{-1})
Nauclea diderrichii	Low/low	4.73	1307	36
	Low/high	7.31	1986	43
	High/low	14.2	514	12
	High/high	20.8	1493	16
Entandrophragma angolense	Low/low	4.82	800	22
	Low/high	5.59	1186	24
	High/low	11.4	843	11
	High/high	16.9	1400	14

Table 4. Growth and photosynthetic characteristics of *Flindersia brayleyana* seedlings after 180 days of growth under low (1.3), medium (5.6) and high irradiance (23.1 mol quanta m^{-2} day^{-1}) at low (N: 1 mg l^{-1} and P: 0.2 mg l^{-1}) and high nutrient supply (N: 71 mg l^{-1} and P: 11 mg l^{-1}) (Thompson *et al.*, 1988). The numbers in bold indicate the maximum significant value of the corresponding parameter.

	High nutrients			Low nutrients		
	Low	Medium	High	Low	Medium	High
Whole plant weight (g)	0.8	6.6	**7.3**	1.0	**3.0**	1.6
Leaf area (cm^2)	130	**600**	530	110	**200**	50
Chlor (a+b) (mmol m^{-2})	0.76	**1.11**	0.72	**0.66**	0.57	0.32
Total N (mmol m^{-2})	94	144	**156**	61	**81**	77
Total P (mmol m^{-2})	5.8	5.2	4.8	0.9	1.0	1.2
A(µmol CO_2 m^{-2} s^{-1})	6.5	**8.0**	7.2	5.1	**5.4**	3.4
R dark (µmol CO_2 m^{-2} s^{-1})	0.7	1.1	**1.3**	0.7	0.9	**1.1**
Photosynthetic electron transport (µmol e^- m^{-2} s^{-1})	64	**86**	65	39	**49**	34
Carboxylation efficiency (µmol CO_2 m^{-2} s^{-1})	23	**32**	**31**	**19**	**22**	13

Mutualistic symbiosis

Growth responses of tropical tree seedlings are strongly dependent on the occurrence of mutualistic symbiosis of the mycorrhizal association type. In a classic paper, Janos (1980) showed that a large proportion of tree seedlings in a tropical rain forest were dependent on the establishment of mycorrhizal symbiosis for survival and growth under natural conditions. He was able to differentiate among obligate mycotrophic and facultative mycotrophic species (Fig. 4).

Mycorrhizal symbiosis, frequently of the vesicular-arbuscular type, plays an important role in the supply of nutrients to seedlings, saplings and adult trees in forests growing on highly leached soils such as those found in large tracts of the Amazon basin. Burslem *et al.* (1995) showed recently that VA-mycorrhizal seedlings growing in native forest soils deficient in P do not respond to the addition of P.

Root competition

Under natural conditions nutrient availability in a given soil may be markedly affected by root competition. Particularly in forests growing on nutrient poor soils, fine roots tend to accumulate near and above the soil surface developing a root mat that can exert a strong competitive pressure for water and nutrients (Stark & Jordan, 1977; Jordan *et al.*, 1979; Cuevas & Medina, 1988). One excellent demonstration of the effect of root competition on the nutrient supply of tree seedlings was carried out by Karpov in temperate forests (1969, after Walter & Breckle, 1984). This author analysed the growth of *Picea* seedlings on the floor of dense *Betula* dominated forests in eastern Europe. The experiment consisted of trenching the roots around the tree seedlings and fertilizing with phosphorus marked with ^{32}P. The experiments showed that trenching the roots of the *Betula* trees allowed the absorption of significantly higher amount of ^{32}P by the *Picea* seedlings, giving a direct demonstration of the effect of root competition. This effect was more pronounced in poorer soils.

Similar results have been reported recently by Coomes (1995) in a tropical rainforest of the upper Orinoco basin. Trenching roots around saplings of 13 tree species growing in understory of natural forests resulted in increased concentration of N and P in the trenched saplings, and also in a marked increase in leaf area development and branching. These experiments may be considered as support for the hypothesis that root competition reduces sapling growth and perhaps survival in the understory due to the competition for nutrients exerted by root biomass of established trees.

Photosynthetic independence and the concentration of CO_2 in the understory

In the understory of rain forests CO_2 concentrations are frequently above the average concentrations in the atmospheric air above the forest (Wofsy *et al.*, 1988). The higher CO_2 concentration in the forest understory is a result of CO_2 production by soil respiration (root respiration + respiration of decomposing organisms in the soil). Higher CO_2 concentration surrounding leaves limited by low light intensity may improve the carbon gain of these leaves by maintaining a gradient of CO_2 concentration between the air and the carboxylating sites in the chloroplasts. Plants in the understory of tropical forests have a lower abundance of carbon 13 in their tissues (van der Merwe & Medina, 1989; Medina *et al.*, 1991), as measured by the $\delta^{13}C$ value. $\delta^{13}C$ values of plants are determined by the carbon 13 content of the CO_2 being actually assimilated by the leaf, and the ratio of internal to external CO_2 concentrations (C_i/C_a) in the leaves (Farquhar *et al.*, 1989). In the forest understory $\delta^{13}C$ of the air decreases because of the influence of soil respiration (oxidation of soil organic matter produces CO_2 depleted in ^{13}C), and the C_i/C_a ratio of seedling and saplings leaves increases due to the reduction in photosynthetic activity of the chloroplasts as a result of low light intensity (Farquhar *et al.*, 1989; van der Merwe & Medina, 1989). Both factors contribute to produce plant tissues depleted in carbon 13 (Table 5). The $\delta^{13}C$ values can be used as an indication of the photosynthetic activity of the plants in the understory, and perhaps also to measure the photosynthetic independence of the seedlings from reserves provided by the mother tree (Medina *et al.*, 1991). As far as I know, there is no experimental evidence indicating that the increased availability of CO_2 in the understory can compensate for the constraints to photostynthesis imposed by low light intensity. The obvious procedure should be to measure the light responses and A/C_i response of the understory leaves to demonstrate whether or not the proposed compensation truly exists.

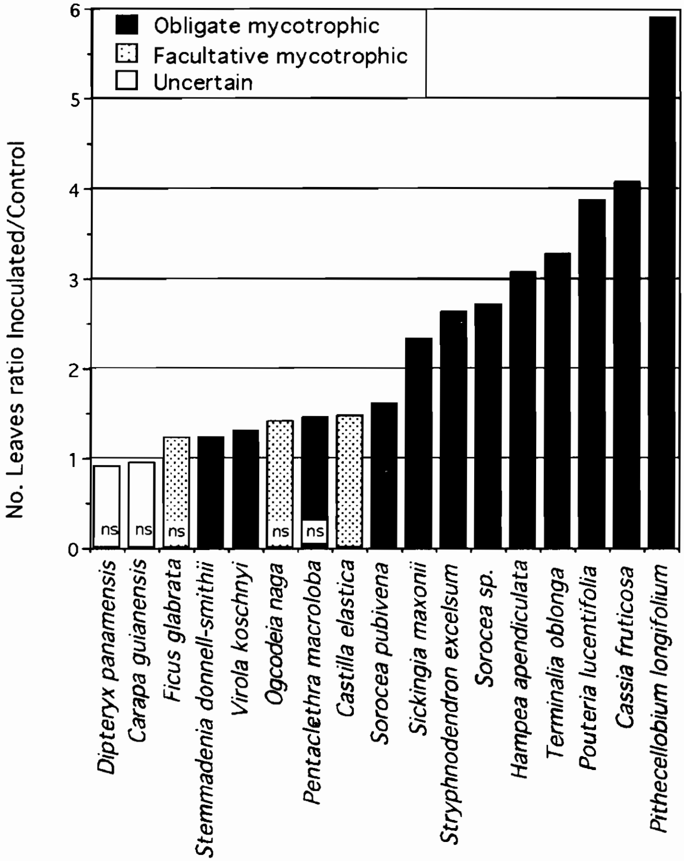

Fig. 4. Relative increase in leaf production in seedlings of tropical rain forest trees inoculated with native mycorrhizal spores (data from Janos, 1980).

Table 5. $\delta^{13}C$ values of seedlings, saplings and canopy leaves of selected species in El Verde forest and in a hybrid mahogany plantation (*S. macrophylla* x *S. mahogany*) in the Luquillo mountains, Puerto Rico (Medina *et al.*, 1991).

Leaf material	***Swietenia hybrid***	***Buchenavia capitata***	***Dacryodes excelsa***	***Manilkara bidentata***	***Ormosia krugii***
Seedling	-32.3	-33.3	-31.7	-31.3	-32.0
Sapling	-32.5	-34.3	-33.3	-33.7	-33.3
Canopy	-29.7	-30.1	-28.6	-28.7	-28.5

Average difference seedling-sapling= 1.3, P (two-tailed)= 0.02; sapling=canopy= 3.0, P (two-tailed)= 0.02

Seedling Establishment in Highly Seasonal Tropical Vegetation

Dry forests

In highly seasonal tropical dry forests the problem of seedling establishment is not light availability but drought stress. There is an abundant literature showing the role of perennial vegetation in arid areas in fostering regeneration by protecting seedlings and young plants from desiccation (Yeaton, 1978; Franco & Nobel, 1989). A clearcut example from the seasonally dry tropics is provided by the analysis of water stress in seedlings, saplings, and adult trees from *Swietenia mahogany* plantations in southern Puerto Rico. Seedlings and saplings have lower water potentials than adult trees, because the latter have access to underground water during the dry season. This behavior contrasts with the water relations of seedlings in wet forests (Fig. 5).

Survival of seedlings is associated with the length of the rainy season. Prolonged water availability may allow the roots to grow deep enough to reach soil layers that provide the small amounts of water required by the seedling to get through the dry season. During years with average or shorter than average rainy seasons, mortality of the current seedling crop is complete.

Savannas

Savannas are characterized by the coexistence of trees within a continuous matrix of C_4 grasses. Establishment of trees within the grass matrix follows the same pattern as the establishment of seedlings in dry forests. In this case, however, root competition for water and nutrients by grasses is usually more intense. Therefore, successful establishment of tree seedlings requires a sequence of humid years that allow the accumulation of water reserves in the upper soil layers to cover the demand of grasses and leave enough water for the tree seedlings (Baruch *et al.*, 1996). Fire must be added to this picture. Grass dominated vegetation in the tropics is very susceptible to fire. Many savanna trees are fire resistant only after they have grown above the level of the grass fire, and to reach this height certainly takes several years (Medina & Silva, 1990).

Fresh water swamps

Very little is known about the regeneration of trees in forested wetlands. Several of these forests are dominated by palms in the South American tropics (*Mauritia flexuosa, Euterpe oleracea*) with a tendency to reach high densities and present a strong stratification in juvenile and adult plants (Kahn & de Granville, 1992). In most cases swamp forests can be highly diverse and productive. Morphological and physiological characteristics allowing the regeneration and permanence of these forests are reviewed in the second section of this volume. This is certainly an important research venue in tropical forest ecology.

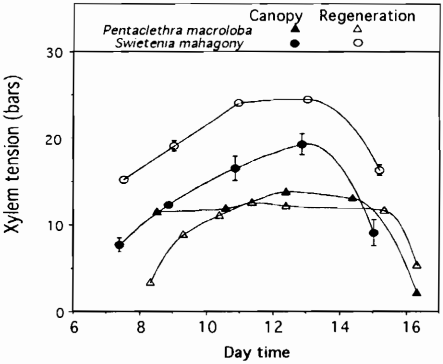

Fig. 5. Daily course of xylem tension in adult trees and saplings of *Swietenia mahogany* in Guánica Puerto Rico (E. Medina, unpubl.), and *Pentaclethra macroloba* in La Selva, Costa Rica (Oberbauer & Strain, 1985).

Concluding Remarks

During the last 15 years substantial advances have been made in the characterization of the establishment processes of tree seedlings in tropical rainforests. The picture that has emerged is complex. It shows that although light intensity in the forest understory is the main driving force selecting shade tolerant species, the interactions between light intensity, occurrence of light flecks, light spectral composition, nutrient availability, and CO_2 concentrations produce a multidimensional space. The set of species that constitute a dynamic forest are distributed within that space in a continuum fashion rather than distinct groups.

It appears that acclimation of dark respiration of leaves to contrasting light environments is faster than that of the photosynthetic machinery. It is fair to assume that this acclimation capacity would also be observable in non-photosynthetic tissues such as stems and roots. It seems to me that the level of understanding of biochemical regulation of respiration is not as advanced as in the case of photosynthesis and would require intensified research.

Plasticity and acclimation of tree seedlings can be explained on the basis of biochemical adjustment of the photosynthetic machinery maximizing utilization of environmental resources, light, nitrogen, and CO_2. However, survival of seedlings in the forest understory cannot be inferred from the gas exchange properties of the leaves alone, but from the carbon balance of the whole individual. These types of measurements are scarce in the literature and positive carbon balances can be assumed only from those studies where growth and survival under natural conditions have been measured.

The measurement of gas exchange in seedlings under natural conditions should lead to experiments aiming to detect the effect of nutrient availability, as determined by soil fertility, mutualistic symbiosis, or root competition, on photosynthetic performance and carbon balance of whole seedlings and saplings. These experiments should also lead to the examination of the effect of elevated CO_2 concentrations in the air near the forest floor on the efficiency of light utilization by seedlings grown under shady conditions.

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