Michael E. Loik · Karen D. Holl

Photosynthetic responses of tree seedlings in grass and under shrubs in early-successional tropical old fields, Costa Rica

Abstract Only recently have studies addressed the effect of early-colonizing vegetation on tree seedling survival and growth during secondary succession in tropical old fields, and few studies have elucidated the physiological responses of tree seedlings to different vegetational communities. We compared growth and various photosynthetic parameters for seedlings of four rain-forest tree species, *Cedrela tonduzii*, *Inga punctata*, *Ocotea whitei*, and *Tapirira mexicana*, growing in areas of pasture grass and shrubs in early-successional abandoned pasture in Costa Rica; in addition, we made measurements for two species in forest gaps. We tested the general hypothesis that early-colonizing shrubs facilitate growth of forest tree seedlings. Specifically, we measured microclimate, growth, CO_2 assimilation, stomatal conductance, photosystem II quantum yield (ΦPSII), and xanthophyll pigment pools for all seedlings. Photosynthetic flux density (PFD) was higher under grass than shrubs or forest gaps, but was highly variable in each growth environment. For three of the four species, height growth was greatest in the grass compared to the shrubs and forest gaps; growth was similar below grass and shrubs for *O. whitei*. Photosynthetic capacity, apparent quantum yield, and stomatal conductance did not vary across habitats, but light compensation point and PFD at light saturation tended to be higher in the grass compared to forest and shrub growth environments. Water use efficiency differed across growth environments for three of the species. For plants in ambient PFD and dark-adapted plants, the efficiency of excitation energy transfer through PSII was lowest for plants in the grass compared to shrubs and forest gaps and also differed across species. Measurement of steady-state responses of ΦPSII to increasing PFD indicated a significant effect of growth environment at low PFD for all species and sig-nificant effects at high PFD only for *I. punctata*. All species exhibited a high degree of midday xanthophyll de-epoxidation in the different growth environments. Xanthophyll pigment pool size on an area basis was highest in the grass compared to shrubs and forest gaps for all four species. The results suggest that shrubs do not provide a facilitative effect for growth or photosynthesis for ~1.5-year-old seedlings of these four species. We conclude that site differences in success of tree seedlings during succession are a result of complex interactions of facilitation and competition and are not simply based on physiological responses to PFD.

Keywords Competition · Facilitation · Photoprotection · Photon flux density · Xanthophylls

Introduction

The effects of existing vegetation on the establishment of forest trees in abandoned old fields has been studied extensively in the temperate zone (e.g., McDonnell and Stiles 1983; Pickett et al. 1987; de Steven 1991a, 1991b; Myster 1993; Berkowitz et al. 1995). Only recently, however, have studies focused on the role of shrubs in tropical old-field succession (e.g., Vieira et al. 1994; Aide et al. 1995; Holl et al. 2000). Research in the temperate zone suggests that early successional shrubs may have variable effects on different stages of seedling re-generation (Pickett et al. 1987; Walker and Chapin 1987; Myster 1993; Callaway and Walker 1997). For example, shrubs often enhance seed dispersal by animals and woody seedling establishment (Werner and Harbeck 1982; McDonnell and Stiles 1983; Li and Wilson 1998), but shrubs may also compete with larger seedlings for nutrients, light, and water (Walker and Chapin 1986; Putz and Canham 1992; Berkowitz et al. 1995). Similarly, the few studies of succession in abandoned agricultural land in the tropics suggest that early successional shrubs enhance seed dispersal compared to areas of grass (Saab and Petit 1992; Vieira et al. 1994; Cardoso da

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Silva et al. 1996; Duncan and Chapman 1999) and provide a more favorable light environment for growth of recently germinated seedlings (Vieira et al. 1994; K.D. Holl, unpublished work). As seedlings grow larger, however, they may increasingly compete with shrubs for light (Holl 1998).

The few studies of the effect of early-colonizing shrubs on tree seedling establishment in abandoned tropical pastures have documented vegetation patterns without investigating the underlying physiological mechanisms. Understanding the physiological responses of seedlings planted in different habitats allows for a greater comprehension of the relative importance of facilitation in comparison to competition (Bertness and Callaway 1994) and for predicting patterns of succession. For example, seedlings growing in the shade of shrubs may be less susceptible to coincident light, temperature, and water stress effects on photosynthesis (Valladares and Pearcy 1997; Niinements et al. 1999) that might occur in open pasture. On the other hand, seedlings in shade may not receive enough light to drive the photosynthetic carbon uptake necessary for growth (Murphy and Briske 1994; Humphrey and Swaine 1997; Anten and Hirose 1998).

It has been argued that light is one of the primary factors limiting growth of tropical forest seedlings (Denslow and Hartshorn 1994; Chazdon et al. 1996). Therefore, much previous research has focused on the response of tropical forest tree seedlings to the light environment of sunflecks or treefall gaps (Chazdon and Pearcy 1991; Königer et al. 1995; Barker et al. 1997; Valladares et al. 1997; Davies 1998; Adams et al. 1999; Allen and Pearcy 2000). This work suggests that many species can survive in low-light conditions and can rapidly acclimate to a higher light environment, although there are differences in the range of preferred photon flux density (PFD) levels across species. The ability to persist in low-light environments is often associated with a reduced ability to acclimate to varying light regimes (Fetcher et al. 1983; Kobe 1999). In this regard, we would predict that *Ocotea whitei*, a species for which numerous seedlings are present in the forest understory at our study site (K. Holl, personal observations), would have a lower ability to acclimate to the high-light environment in the pasture compared to species such as *Inga punctata* which generally establish in more open areas.

Much less research has focused on the responses of rain-forest seedlings to light levels in large disturbed areas such as abandoned agricultural fields. Light levels in large, open areas are typically two orders of magnitude higher than in intact forest (Chazdon and Fetcher 1984; Oberbauer et al. 1988; Holl 1999). Existing old-field vegetation, however, may intercept light, providing a light environment intermediate between forest and pasture for seedlings in the vegetation understory (Vieira et al. 1994; Loik and Holl 1999). In our previous work (Loik and Holl 1999) at the present study site, seedlings planted in the shade of remnant pasture trees generally exhibited greater growth than seedlings planted in the

exposed, open pasture or in the deep shade of adjacent primary forest understory. The ability to adapt to the different environments varied across species. This research, as well as other work demonstrating much higher growth of recently germinated seedlings below shrubs compared to pasture grass (K.D. Holl, unpublished work), led us to predict that the microenvironment under shrubs would facilitate seedling growth compared to the microenvironment among pasture grass.

Shrubs may affect seedling growth by reducing light intensity and coincident water and temperature stresses. Numerous studies of seedlings in sunflecks and treefall gaps suggest that native tropical forest seedlings may experience a decrease of photosystem II (PSII) efficiency when exposed to PFDs (400–700 nm) in excess of photosynthetic capacity (Lovelock et al. 1994; Osmond 1994; Pearcy 1994; Castro et al. 1995). PSII efficiency can be further reduced under multiple simultaneous stresses (Björkman 1987; Gamon and Pearcy 1990; Havaux 1992). The energy from PFD is used to drive photochemistry, and the excess is non-photochemically dissipated as heat to avoid potential damage to PSII (Demmig-Adams and Adams 1996). The impact of PFD and thermal dissipation of excess energy can be detected by changes in the quantum yield of PSII chlorophyll fluorescence, and by changes in the relative amounts of the xanthophyll pigments violaxanthin, antheraxanthin, and zeaxanthin (Demmig-Adams et al. 1996; Gilmore 1997; Niyogi et al. 1997). The degree to which xanthophyll cycle-dependent energy dissipation is engaged depends upon the reversible conversion of violaxanthin to antheraxanthin and zeaxanthin, as well as thylakoid acidification (Walters et al. 1996; Adams et al. 1999) and changes in pigment-binding protein complexes (Gilmore 1997; Ruban et al. 1997). In our previous work (Loik and Holl 1999) seedlings exhibited minimal differences in photosynthetic capacity in open pasture, remnant tree shade and primary forest, yet there were differences in PSII downregulation across growth environments and species. In other words, growth differences in the three light environments may have been due, in part, to the downregulation of photo0synthetic electron transport and reduced carbon gain for seedlings in the high compared to low PFD environments.

The primary objective of this study was to compare the effects of pasture grasses and early-successional shrubs on the growth, photosynthesis, water relations, PSII efficiency, and xanthophyll pigment content for four species of tropical tree seedlings. For comparative purposes we also measured these factors for two of the species in forest treefall gaps. If early-colonizing shrubs facilitate growth via impacts on photosynthesis and photoprotection for certain tree species, then shrubs may play an important role in determining patterns of tropical forest succession in abandoned pastures.

Materials and methods

Site description

This study was conducted in abandoned pasture adjacent to primary, seasonal montane wet forest (Holdridge et al. 1971) in southern Costa Rica (8°57′N, 82°50′W, 1500 m elevation). Average annual rainfall is approximately 3000 mm, >95% of which normally falls between April and December, and average annual maximum and minimum temperatures are 24.6 and 13.2°C (Holl 1999). The 5-ha pasture where the study was conducted was used for 15 years for the cultivation of coffee and for the subsequent 10 years for cattle grazing. Cattle were removed from the pasture in February 1995. At that time, the pasture vegetation consisted predominantly of African grasses such as *Axonopus scoparius* (Flügge) Kuhlm., *Digitaria decumbens* Stent, and *Melinis minutiflora* Beauv which grow up to 1.5 m tall. While the pasture was used the land owner periodically cleared all shrubs with machetes, so some shrubs re-grew from sprouts when the pasture was abandoned. Isolated trees, primarily *Inga edulis* Mart. and *I. punctata* Willd., are scattered throughout the pasture, but all seedlings, both under grass and shrubs, were planted at least 5 m beyond the crowns of remnant trees.

Shrubs covered 2.4% and 6.1% of the pasture in February 1996 and February 1998, 1 and 3 years after abandonment (Holl et al. 2000). Almost all the patches included multiple species of shrubs and vines, the most common of which were *Heterocondylus vitalbae* (D.C.) King and H. Robins, *Piper arboreum* Aublet, *Pithecoctenium echinatum* (Jacq.) Baill., *Rubus urticaefolius* Poir., *Solanum rudepannum* Dunal, *S. umbellatum* Willd., and *Vernonia patens* H. B. K. Small trees of *I. edulis, I. punctata*, and *Saurauia montana* Seem. were occasionally present in shrub patches. Shrub patches generally ranged in height from 1 to 5 m.

Experimental design

In July 1997, 15 seedlings of each of four native tree species (*Cedrela tonduzii* L. (Meliaceae), *Inga punctata* Willd. (Fabaceae), *Ocotea whitei* Woodson (Lauraceae), and *Tapirira mexicana* Marchand (Anacardiaceae)) were planted in areas of dense pasture grass and under large shrub patches in the pasture. The four species were chosen as they are all found in the surrounding forest, but naturally colonize both under shrubs and in open areas of abandoned pasture (Holl 1999; Holl et al. 2000). *C. tonduzii* and *O. whitei* are common components of mature forest; *I. punctata* and *T. mexicana* tend to be more common in forest gaps or second growth areas, although their specific habitat requirements are unknown. *C. tonduzii, O. whitei*, and *T. mexicana* are used for reforestation efforts in the region (Nichols and González 1991). *I. punctata* is often interplanted in agroforestry systems as a nitrogen-fixing species (Kettler 1997).

Seedlings of all species were obtained from a nursery located ~1 km from the experimental site. Seeds were collected from at least five individuals of each species, within 5 km of the experimental sites and were immediately germinated in field-collected soil. When seedlings were approximately 5 cm tall, they were transplanted into black plastic nursery bags (11.5 cm diameter×30 cm deep) where they were grown in full sunlight until outplanting. They were watered as needed during periods of low rainfall, but were not fertilized. Seedlings were 5–11 months old at the time of planting. Mean heights at the time of outplanting were: *C. tonduzii* 34.1±1.6 cm, *I. punctata* 13.2±0.6 cm, *O. whitei* 17.4±1.0 cm, and *T. mexicana* 23.0±1.2 cm.

Five seedlings of each species were planted in each of three blocks in grass and in shrub patches. In the pasture, the seedlings were randomly located in grids with 3×3 m spacing. In the shrub patches, seedlings were planted less systematically, due to existing vegetation, but all planted seedlings were separated by a minimum of 3 m. Fifteen seedlings of *Cedrela tonduzii* and *T. mexicana* (the two species for which there were sufficient healthy seedlings) were also planted in recent (<6 months old) treefall gaps in the adjacent forest for comparison purposes. We planted seedlings in treefall gaps rather than dense forest canopy given that our previous research showed that light levels in the intact forest understory were below light compensation, and most tropical forest seedlings grow faster in treefall gaps (Denslow and Hartshorn 1994; Chazdon et al. 1996; Press et al. 1996). Seedlings were given 1 l of water at the time of outplanting but were neither watered nor fertilized thereafter. All plants were fenced with 20 cm diameter×45 cm high chicken wire to prevent rabbit herbivory which was shown to be an important cause of mortality in a previous study (Holl and Quiros-Nietzen 1999).

Microclimate

Daily maximal and minimal air temperatures and precipitation for the study period were obtained from a weather station of the Instituto Costarricense de Electricidad located 1 km from the study site. PFD (400–700 nm) was recorded using the external quantum sensor of a portable photosynthesis system (Model LI-6400, Li-Cor, Inc. Lincoln, Neb., USA) during light curve measurements. Measurements were made in the plane of the leaf used for photosynthesis measurements at approximately 50 cm above the soil surface. Air temperatures were measured with a shaded thermistor. Air vapor pressure deficit was calculated by the LI-6400 based on measurements of water vapor content and air temperature.

Plant morphology and leaf water potential

Seedling survival and height of the tallest meristem were measured for all 15 seedlings at the initial planting time (July 1997) and in February 1998. Leaf number and surface area for five plants per species per growth environment were measured in February 1998. Leaf surface area was non-destructively determined by tracing the leaf on paper, weighing the image, and comparing the weight to that of a known area of paper.

Physiological measurements were made between 5 and 20 February 1998 (dry season), approximately 7 months after planting. Physiological measurements were made on five randomly selected seedlings of each species in the pasture grass, under shrubs, and for *C. tonduzii* and *T. mexicana*, within the primary forest gaps; in two cases one sample was lost so *n*=4 (*C. tonduzii*, under grass, photosynthetic curves; *C. tonduzii*, under shrub, xanthophyll pigments). The three growth environments are subsequently referred to as grass, shrub, and forest gaps, respectively. The order of measurements across growth environment was randomly assigned.

To determine leaf water potential (Ψ), leaf discs were removed with a cork borer (1.0 cm diameter) between 1200 and 1300 hours and placed in the sample chamber of a Decagon SC-10 thermocouple psychrometer (Pullman, Wash., USA). The leaf discs were allowed to equilibrate for 3 h indoors at an average air temperature of 26°C. Ψ was determined by measuring the voltage across the thermocouple with a Decagon NT-3 nanovoltmeter compared to voltages obtained with NaCl standards. Ψ was calculated based on the van't Hoff relation at 25°C (Loik and Harte 1997). Leaf temperature was measured using a nickel-chromel-constantan thermocouple (1.3 mm diameter) appressed to the abaxial surface of the same leaves that were used for gas exchange, chlorophyll fluorescence and pigment determinations.

Photosynthetic responses to light

The responses of photosynthetic CO_2 uptake to PFD were measured on the fifth fully-expanded leaf from the apical meristem; when such leaves were absent, wilted, necrotic, or infested with insects (<5% of leaves), the next lower leaf was used. Measurements were made between 0600 and 1100 hours when ambient PFD in open areas was at least 750 µmol m^{-2} s^{-1} in the horizontal plane (1100 hours generally marks the onset of dense cloudiness).

Net assimilation, stomatal conductance to water vapor, transpiration, and ambient PFD were measured using the LI-6400 open-mode portable photosynthesis system. CO_2 in the reference chamber was maintained at 365 μmol mol^{-1} added from an external canister. Leaf temperature was maintained with a Peltier thermoelectric block. Water vapor concentration was measured by water infrared gas analyzers (IRGAs). Vapor pressure deficit within the chamber was maintained at pre-measurement ambient levels by passing a portion of the incoming airstream through 10–20 mesh $CaSO_4$.

Light response curves were determined using a light-emitting diode (LED) light source. Upon enclosure within the chamber, each leaf was allowed to dark adapt for 10–15 min. PFD started at 0 μmol m^{-2} s^{-1} and increased stepwise to 2000 μmol m^{-2} s^{-1} measured with a gallium-arsenide-phosphide sensor. Measurements were recorded at 4-s intervals, and PFD levels were changed to the next level when CO_2 uptake stabilized. The apparent quantum yield, light compensation point, PFD at incipient saturation of CO_2 assimilation, and photosynthetic capacity were estimated from each light response curve using a non-rectangular hyperbola model (Sims and Pearcy 1991) and Photosynthesis Assistant version 1.1 (Dundee Scientific, Dundee, Scotland, UK). Water use efficiency was calculated using instantaneous values of assimilation and transpiration for PFD=100 μmol m^{-2} s^{-1}.

Chlorophyll fluorescence

Measurements of chlorophyll fluorescence were obtained with a pulse-modulated fluorimeter (Model FMS1, Hansatech, Kings Lynn, UK), which has routines for recording various fluorescence parameters (F_0, F_M, F_M', F, F_V', and F_0'; nomenclature of van Kooten and Snel 1990). For leaves exposed to ambient PFD, the intrinsic efficiency of excitation transfer from light harvesting complexes to reaction centers (Schreiber et al. 1995; Barker and Adams 1997) was calculated by the fluorimeter software as $F_V'/F_M'=(F_M'-F_0')/F_M'$. F_0' was determined by the fluorimeter following transient shading of the leaf using FMS1 leaf clips, and application of a pulse of far-red light to excite photosystem I (PSI) to open PSII reaction centers. To assess the recovery of excitation energy transfer, leaves were dark-adapted for 15 min using the clips. The saturating light pulse lasted 0.7 s at an intensity of 5000 μmol m^{-2} s^{-1}. Efficiency of excitation transfer for dark-adapted leaves was calculated as $F_V/F_M=(F_M-F_0)/F_M$.

In order to examine the potential for downregulation of PSII over a range of PFD typical of the different growth environments, we measured the quantum efficiency of PSII (ΦPSII) for the four species. Controlled steady-state light response curves were generated using a quartz halogen actinic light source within the fluorimeter and delivered to the leaf by an optical fiber. Leaves were exposed to actinic light at 10, 500, 1000, 1500 or 2000 μmol m^{-2} s^{-1} in a step-wise fashion. Following a 15-min dark-adaptation period, the leaf was exposed to a particular actinic PFD within the leaf clips for 10 min. This particular set of PFD values and timing was chosen to span the range of ambient PFD levels, balanced by the battery limitations at our remote field site (batteries were recharged at night by a diesel generator). Preliminary experiments indicated that all species reached a steady-state of photosynthetic gas exchange and ΦPSII within 10 min of exposure to altered PFD. After exposure to each PFD for 10 min, ΦPSII was calculated as $(F_M'-F)/F_M'$.

Xanthophyll pigments

Pigment pool size was compared for leaf samples removed with a 1-cm-diameter cork borer. Samples were removed from the same leaves that were used for previous physiological measurements. Samples were removed between 0900 and 1100 hours under full sun conditions, on the last day of the field work. Because liquid nitrogen was not available and electricity was only sporadically available, leaf samples were immediately placed into 1 ml of dimethylformamide (DMF) in glass vials (Bergweiler and Lütz 1986) and transported to the laboratory on ice within a picnic cooler. The transit time was 2 days and ice was periodically replaced. Upon return to the laboratory, the samples were stored at –20°C until further processing.

Pigments were separated and quantified using high-performance liquid chromatography, using modified methods of Bergweiler and Lütz (1986) and Thayer and Björkman (1990). Pigment extracts in DMF were mixed with 2 volumes of 50% methanol before injection of 100 μl into a Perkin-Elmer Series 4 liquid chromatograph. Separation was conducted on a 250×4.6 mm C_{18} 5-μm reversed phase column (Vydac, Hesperia, Calif., USA). The mobile phase consisted of 80% (v:v) methanol to 100% MeOH over a 20-min linear gradient. Detection and quantification were conducted with a Beckman 160 absorbance detector at 440 nm and a Perkin-Elmer LC 100 laboratory computing integrator. Peaks were identified by comparisons to pigments isolated and quantified according to Yamamoto et al. (1974).

Statistical analyses

One-way analysis of variance (ANOVA) was used to analyze the effect of growth environment on each of the continuous dependent variables when there were three growth environments. T-tests were used to compare variables when only two growth environments were compared. Analyses were done for each species separately. Most data were log$_e$-transformed when necessary to meet assumptions of normality and homoschedasticity. Ratio data (e.g., some fluorescence and pigment values) were arcsine-square-root transformed (Sokal and Rohlf 1981) when necessary to meet these assumptions. Tukey's LSD multiple comparison procedure was used to test differences among growth environment when it was found to be a significant factor in the ANOVA.

For comparisons of steady-state ΦPSII responses to increasing PFD across growth environments, univariate repeated measures analyses were used since measurements on individual plants at different PFD levels were not independent of one another. Because of the correlation of the variance-covariance matrix the Huynh-Feldt adjustment was used (Huynh and Feldt 1976). All analyses were done using SAS Version 6.12 (SAS Institute, Cary, N.C., USA). Throughout means and SEs are reported, and $P<0.05$ is considered significant.

Results

Microclimate

Daily maximum and minimum temperatures averaged 27.3°C and 13.3°C, respectively over the 16-day measurement period. A total of 150 mm of rain fell during this time. Photosynthetic photon flux density (PFD) was highly variable in all growth environments (Table 1). The median PFD in the grass was approximately 10 times higher than in the shrub or forest gaps, although there were a couple of high instantaneous values of PFD (509 and 1849 μmol m^{-2} s^{-1}) in the forest gaps. On average, both air and leaf temperature were approximately 7°C higher in the grass than in either the shrub or pasture. Likewise, the vapor pressure deficit of the air was similar under shrubs and in forest gaps, but was higher in the grass.

Plant survival and morphology

Seedling survival ranged from 80 to 100% for the four species across the growth environments (Table 2).

Table 1 Photosynthetic photon flux density (PFD; 400–700 nm), air temperature (T^{air}), and vapor pressure deficit of the air (VPD) measured at the site and time of photosynthetic measurements (approximately 50 cm above the ground) in pasture grass, under shrubs, and in forest gaps. PFD data are medians with range in parentheses because of high variation. T^{air}, T^{leaf}, and VPD data are means±SE; $n=20$ measurements under grass and shrubs and $n=10$ in the forest gaps. Measurements were recorded between 0600 and 1100 hours

Growth environment	PFD (μmol m^{-2} s^{-1})	T^{air} (°C)	T^{leaf} (°C)	VPD (kPa)
Grass	311 (35–2000)	33.3±0.9	32.3±0.9	2.97±0.25
Shrub	27 (1–130)	26.3±0.3	25.6±0.3	1.67±0.05
Forest gap	44 (3–1849)	25.6±0.9	25.1±1.0	1.42±0.11

Table 2 Growth rates, leaf number, and leaf area for seedlings in pasture grass, under shrubs, and in forest gaps. Data are means±SE; $n=5$ plants per growth environment for leaf number and leaf area and $n=$number surviving for change in height. Means with the same letter are not significantly different ($P<0.05$) across growth environment type, based on Tukey's LSD or t-tests

Species	Growth environment	Number surviving[a]	Increment in height (m)	Leaf number	Leaf area (cm^2)
Cedrela tonduzii	Grass	14	0.129±0.050[a]	3.2±1.0[a]	70±30[a]
	Shrub	12	0.005±0.040[b]	2.8±0.5[a]	80±40[a]
	Forest gap	12	0.049±0.022[ab]	7.6±3.6[a]	140±30[a]
Tapirira mexicana	Grass	15	0.293±0.042[a]	6.0±0.3[a]	60±10[a]
	Shrub	14	0.031±0.015[b]	8.4±1.6[ab]	60±20[a]
	Forest gap	14	0.089±0.027[b]	12.0±2.0[b]	160±40[b]
Inga punctata	Grass	15	0.169±0.041[a]	6.8±1.6[a]	30±10[a]
	Shrub	13	0.011±0.007[b]	6.6±0.9[a]	20±10[a]
Ocotea whitei	Grass	13	0.041±0.022[a]	18.6±6.5[a]	30±20[a]
	Shrub	15	0.017±0.006[a]	29.8±3.8[a]	10±10[a]

[a] 15 seedlings of each species were planted

Table 3 Light compensation point (LCP), light saturation point (PFD$_{sat}$), apparent quantum yield, light-saturated photosynthetic capacity (A_{max}), g_s stomatal conductance to water vapor, and water use efficiency (WUE) derived from light response curves for seedlings in pasture grass, under shrubs, and in forest gaps. Data are means±SE for $n=5$ plants per growth environment except for $n=4$ for *Cedrela* under grass. Means with the same letter are not significantly different ($P<0.05$) across growth environment type based on Tukey's LSD or t-tests

Species	Growth environment	LCP (μmol m^{-2} s^{-1})	PFD$_{sat}$ (μmol m^{-2} s^{-1})	Apparent quantum yield	A_{max} (μmol m^{-2} s^{-1})	g_s (mol m^{-2} s^{-1})	WUE
C. tonduzii	Grass	37.0±6.45[a]	108.3±15.4[a]	0.035±0.017[a]	3.4±1.7[a]	0.051±0.030[a]	1.89±0.58[a]
	Shrub	7.23±1.65[b]	41.6±11.5[a]	0.023±0.009[a]	1.2±0.1[a]	0.017±0.003[a]	3.91±1.37[ab]
	Forest gap	8.48±3.36[b]	171.4±57.7[a]	0.037±0.016[a]	3.0±0.7[a]	0.033±0.009[a]	7.44±0.84[b]
T. mexicana	Grass	13.9±1.93[a]	132.9±22.9[a]	0.046±0.003[a]	5.5±1.1[a]	0.159±0.042[a]	3.40±0.58[a]
	Shrub	2.94±1.87[b]	61.8±10.2[a]	0.065±0.011[a]	4.6±1.1[a]	0.112±0.045[a]	4.92±0.50[ab]
	Forest gap	6.02±1.55[b]	65.6±16.7[a]	0.066±0.013[a]	3.6±0.6[a]	0.107±0.017[a]	5.62±0.37[b]
I. punctata	Grass	18.1±5.93[a]	100.6±7.9[a]	0.062±0.015[a]	5.3±1.5[a]	0.097±0.051[a]	3.75±1.03[a]
	Shrub	6.75±0.57[b]	63.6±9.0[b]	0.081±0.018[a]	4.6±1.1[a]	0.066±0.019[a]	8.95±0.94[b]
O. whitei	Grass	10.9±3.73[a]	83.8±19.1[a]	0.044±0.013[a]	2.7±0.8[a]	0.068±0.030[a]	2.85±0.64[a]
	Shrub	4.19±2.33[a]	60.3±10.5[a]	0.076±0.021[a]	4.2±0.7[a]	0.115±0.023[a]	4.44±0.43[a]

Height increments were higher in the grass compared to shrubs for three of the four species; height growth was slightly although not significantly higher in forest gaps compared to shrubs for *C. tonduzii* and *T. mexicana*. *O. whitei* exhibited similarly low growth rates below both grass and shrubs. The effect of growth environment on number of leaves per plant and leaf area was significant only for *T. mexicana,* for which leaf number and area were higher in the forest gaps compared to the grass (Table 2).

Photosynthetic responses to PFD

The light compensation point (LCP) was significantly lower for seedlings of *T. mexicana* and *C. tonduzii* in the shrubs and forest gap sites compared to the grass, and lower in the shrubs compared to the grass for *I. punctata* (Table 3). For all species LCP was below the median PFD in all three growth environments. The PFD leading to saturation of CO_2 assimilation (PFD$_{sat}$) was significantly higher in the grass compared to shrubs for *I. punctata*. PFD$_{sat}$ was marginally higher in the grass for *T.*

Fig. 1A–D Quantum yield of PSII photochemistry (*ΦPSII*) as a function of Photon flux density (*PFD*) for seedlings in pasture grass (●), under shrubs (■), and forest gaps (▲). Data are means±SE for *n*=5 plants per growth environment. For statistical analyses see Table 5
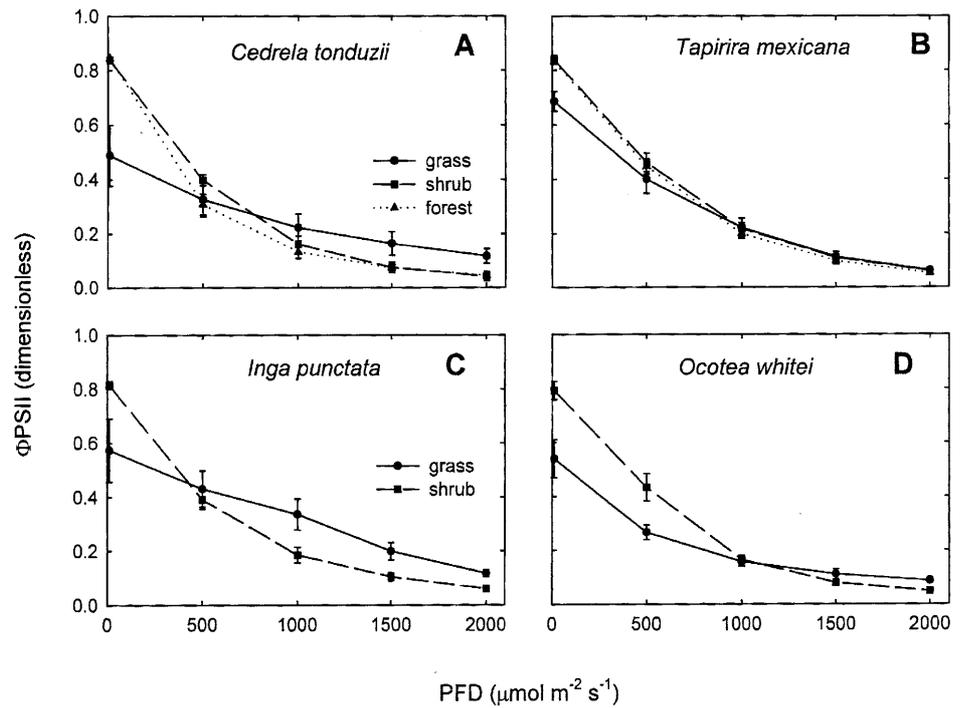
mexicana (*P*=0.05), and for *C. tonduzii* PFD_{sat} was highest in the forest, intermediate in the grass, and lowest in the shrubs (*P*=0.07). Mean PFD_{sat} for each species was above the median PFD under shrubs and in forest gaps and below the median PFD under grass. Photosynthetic capacity and apparent quantum yield for CO_2 uptake did not differ for seedlings under shrubs compared to grass for any of the four species, and the variance within growth environments was high (Table 3).

Stomatal conductance to water vapor (g_s) did not differ for any of the species across the different growth environments (Table 3). In general, g_s was lowest for *C. tonduzii* compared to the other three species. Instantaneous water use efficiency (WUE) differed significantly across growth environments for all species except *O. whitei* (Table 3). WUE was higher in the forest gaps compared to the grass for *C. tonduzii* and *T. mexicana*, and higher in shrubs compared to grass for *I. punctata*.

For three of the species, *C. tonduzii, I. punctata,* and *O. whitei*, midday water potential averaged –1.30 to –2.09 MPa and did not significantly differ across growth environments (data not shown). For *T. mexicana*, midday water potential was significantly more negative (*df*=2, *F*=4.634, *P*=0.032) in the forest gaps (–2.00±0.14 MPa) compared to the grass (–1.45±0.10) or shrubs (–1.47± 0.18).

Chlorophyll fluorescence

The efficiency of excitation energy transfer through PSII was compared for leaves in ambient PFD (F_V'/F_M') and after dark adaptation (F_V/F_M; Table 4). For *C. tonduzii* F_V'/F_M' was highest in forest gaps, followed by seed-

Table 4 Efficiency of excitation energy transfer through PSII for leaves under ambient light (F_V'/F_M') and following dark adaptation for 15 min (F_V/F_M) for seedlings in pasture grass, under shrubs, and in forest gaps. Data are means±SE for *n*=5 plants per growth environment. Means with the same letter are not significantly different (*P*<0.05) across growth environment type based on Tukey's LSD or *t*-tests

Species	Treatment	Grass	Shrub	Forest gap
C. tonduzii	Ambient	0.188±0.016[a]	0.747±0.029[b]	0.849±0.006[c]
	Dark	0.609±0.106[a]	0.764±0.038[a]	0.757±0.047[a]
T. mexicana	Ambient	0.261±0.075[a]	0.796±0.018[b]	0.782±0.022[b]
	Dark	0.190±0.108[a]	0.710±0.078[b]	0.761±0.045[b]
I. punctata	Ambient	0.265±0.095[a]	0.737±0.057[b]	–
	Dark	0.457±0.147[a]	0.683±0.091[a]	–
O. whitei	Ambient	0.391±0.114[a]	0.739±0.030[b]	–
	Dark	0.506±0.058[a]	0.743±0.039[b]	–

lings in shrubs and then those under grass, whereas there was no difference for dark-adapted plants. Likewise, F_V'/F_M' was higher for *I. punctata* in the shrubs compared to the grass for light-adapted plants with no difference for dark-adapted plants. For *O. whitei* and *T. mexicana,* however, there were differences for both light- and dark-adapted plants, with values for plants in forest gaps and under shrubs always higher than in grass.

For all species ΦPSII decreased with increasing PFD and there was a significant growth environment×PFD interaction (Fig. 1; Table 5); in other words, the effect of growth environment on ΦPSII varied depending on PFD. For all species ΦPSII was lower for plants in the grass compared to the other growth environments at low PFDs

Table 5 Univariate repeated measures analyses of ΦPSII by growth environment and PFD (*df*s for *Inga* and *Ocotea* are in parentheses when they differ from the other two species)

Source of variation	df	Cedrela	Tapirira	Inga	Ocotea
Growth environment	2 (1)	0.9	1.1	0.1	3.3
PFD	4	66.7***	1062.8***	111.1***	212.6***
Growth environment×PFD	8 (4)	4.1*	6.4***	11.0**	7.6***

*$P<0.05$, **$P<0.01$, ***$P<0.001$, *F*-values using the Huynh-Feldt adjustment.

Table 6 Pigment composition on an area basis for seedlings in pasture grass, under shrubs, and in forest gaps. Data are means±SE for *n*=5 plants per growth environment except for *n*=4 for *Cedrela* under shrubs. Means with the same letter are not significantly different (*P*<0.05) across growth environment type based on Tukey's LSD or *t*-tests. *V, A*, and *Z* refer to violaxanthin, antheraxanthin, and zeaxanthin, respectively

Species	Growth environment	V+A+Z (μmol m^{-2})	(A+Z)/ (V+A+Z)	Chl $a+b$ (μmol m^{-2})	Chl a/b	Neoxanthin (μmol m^{-2})
C. tonduzii	Grass	89±12[a]	0.82±0.08[a]	302±49[a]	2.86±1.20[a]	49±15[a]
	Shrub	58±5[b]	0.77±0.09[a]	343±147[a]	3.00±1.52[a]	24±6[a]
	Forest gap	26±4[c]	0.38±0.15[a]	766±281[a]	3.89±0.75[a]	68±16[a]
T. mexicana	Grass	121±13[a]	0.85±0.08[a]	346±17[a]	2.51±0.73[a]	70±22[b]
	Shrub	30±5[b]	0.82±0.12[a]	411±167[a]	2.74±0.58[a]	18±12[a]
	Forest gap	51±3[b]	0.75±0.04[a]	534±98[a]	3.09±0.55[a]	10±3.0[a]
I. punctata	Grass	227±8[a]	0.88±0.06[a]	1003±157[a]	3.88±1.94[a]	142±29[a]
	Shrub	131±17[b]	0.90±0.05[a]	846±180[a]	3.00±0.76[a]	69±18[a]
O. whitei	Grass	159±12[a]	0.72±0.03[a]	473±104[a]	3.75±0.62[a]	57±8[a]
	Shrub	88±3[b]	0.78±0.05[a]	371±50[a]	3.53±1.62[a]	85±15[a]

(10 μmol m^{-2} s^{-1}). For three of the species, *C. tonduzii, O. whitei,* and *T. mexicana,* there were no growth environment differences in ΦPSII for PFD greater than 1000 μmol m^{-2} s^{-1}. For *I. punctata* ΦPSII was lower under shrubs compared to plants in grass for PFD >500 μmol m^{-2} s^{-1}.

Xanthophyll pigments

For all four species, xanthophyll pigment pool size (V+A+Z; violaxanthin+antheraxanthin+zeaxanthin) on an area basis was significantly higher for plants in grass compared to other growth environments (Table 6). For *C. tonduzii*, V+A+Z was about twice as high in grass compared to the forest gaps, but there was no significant difference between shrub and forest gap plants for *T. mexicana*. There were no significant growth environment differences in the ratio of A+Z to V+A+Z for any species, which suggests that a large portion of the pigments were in the de-epoxidated state despite the PFD differences across growth environments. Chlorophyll *a*+*b* and chlorophyll *a/b* content did not differ significantly for any species across growth environments. Neoxanthin content on an area basis was significantly higher for *T. mexicana* under grass compared to the other growth environments, but did not differ across growth environments for the other three species.

Discussion

Effects of pasture vegetation on forest seedling growth

Our past research shows that seedlings (>1 m tall) of the tree species studied are found both below shrubs and in open areas of abandoned pasture at the current study site, but that the proportion of seedlings under shrubs is much higher than in open areas (Holl et al. 2000; K.D. Holl, unpublished work), suggesting that shrubs facilitate tree seedling establishment at certain life-history stages. We and others have previously demonstrated that early-colonizing shrubs facilitate the earliest stages of tree seedling establishment, primarily by enhancing seed dispersal and by increasing seedling survival of recently germinated seedlings (Vieira et al. 1994; Cardoso da Silva et al. 1996; K.D. Holl, unpublished work). The results from this study and one previous study (Holl 1998) suggest that as tree seedlings increase in size shrubs no longer have a facilitative effect on seedling growth relative to grass. In other words, the pattern of higher numbers of seedlings below shrubs appears to be primarily due to shrub facilitation of the earliest life-history stages of tree seedlings.

This change in the relative effects of facilitation and competition by shrubs on tree seedlings may be due to changes in the light environment as the seedlings grow. Daily PFD at the height of recently germinated seedlings is an order of magnitude higher below shrubs than grass (K.D. Holl, unpublished work). The reverse is true in this study, as the seedlings overtopped the grass canopy but were still well within the shrub canopy. Large seedlings may also increasingly compete with shrubs for nutrients as they grow in size, but we cannot make any conclusions regarding above- vs. below-ground competition based on the current study. Previous studies in abandoned moist tropical pasture (Holl 1998), abandoned dry tropical pasture (Gerhardt and Fredrikkson 1995), and moist tropical forest treefall gaps (Denslow et al. 1998), however, all suggest that growth of tree seedlings is reduced more by above-ground competition for light than below-ground competition for nutrients. It is important

to note that we did not study the relative effects of mammalian herbivory in different growth environments since we caged seedlings; differential herbivory may also lead to differences in survival and growth in the different growth environments and warrants further study.

We know of no studies testing competition between different types of early-successional vegetation and tree seedlings at different seedling stages in abandoned agricultural land in the tropics. Our results concur with previous work in the temperate zone indicating that shrubs facilitate the early stages of seedling establishment but that the interaction shifts towards increasing competition as plants become older (Archer et al. 1988; Callaway and Walker 1997; Barnes and Archer 1999). These results highlight the importance of long-term studies to assess interactions between vegetation types in order to assess the relative importance of competition and facilitation. From a management perspective, the results suggest that reduction of competition from either pasture grasses or early-colonizing shrubs may help to enhance growth of seedlings planted for reforestation or restoration.

Physiological responses

It was somewhat surprising that there were no differences in photosynthetic capacity and apparent quantum yield for the four species across growth environments. Light-saturated photosynthetic capacity (A_{max}) and PFD_{sat} values for these species were low, but in the general range measured for other tropical rain-forest tree seedlings and understory plants (Chazdon et al. 1996). Photosynthetic capacity, dark respiration, and LCP are generally higher for plants grown in high compared to low PFD (Barker et al. 1997; Davies 1998; Huante and Rincón 1998). In the present study, the growth patterns across environments for *C. tonduzii*, *I. punctata,* and *T. mexicana* are likely due to the higher overall PFD in the grass compared to the shrubs. Assimilation for most individuals in the grass should be at A_{max} because median PFD was above PFD_{sat}, whereas under shrubs and in forest gaps the median PFD was below the PFD_{sat}, leading to assimilation rates below A_{max}. Growth and photosynthesis were also highly variable in the forest gaps, likely due to the variability in PFD. It is important to note that our PFD data represent point measurements and do not take into account the full range of temporal and spatial variability in each of the growth environments (Denslow and Hartshorn 1994; Chazdon et al. 1996). They should be treated as approximate rather than precise descriptions of the PFD environments.

It is notable that *O. whitei* exhibited the lowest growth in height compared to the other species. Compared to the other species PFD_{sat} in the grass was lowest for *O. whitei*, and did not differ for seedlings under grass and shrubs. Observations indicate that seedlings of *O. whitei* are common within the understory of the primary forest (K.D. Holl, unpublished work). It appears that *O. whitei* has limited photosynthetic acclimation ability in response to differing PFD levels, as none of the photosynthetic parameters deduced from light curves were different across growth environments. Other studies have shown that species that are more tolerant of low light levels tend to be less able to acclimate to a varying light environment (Fetcher et al. 1983; Björkman 1987; Kobe 1999). These results imply that patterns of biochemical and stomatal adjustments during light acclimation may limit growth for some species in early successional abandoned fields.

The ability to direct excitation energy to photochemistry or non-photochemical energy dissipation can be important for carbon balance in variable PFD environments (Königer et al. 1995; Adams et al. 1999). The four species studied exhibited significant differences across growth environments in terms of excitation energy transfer through PSII for leaves in ambient light and after dark adaptation. Such differences are likely due to the degree of de-epoxidation of the xanthophyll pigments (Demmig-Adams and Adams 1996) in the different growth environments, allowing for appreciable thermal energy dissipation for leaves under excess PFD (Gilmore 1997). Following a dark adaptation period, the maximum potential efficiency of PSII electron transport increased for seedlings in the grass for *Cedrela*, *Inga*, and *Ocotea*, but there was no dark recovery of F_V/F_M for *Tapirira*. For all four species there was no significant relationship between apparent quantum yield and F_V/F_M. These observations may be related to species-specific differences in epoxidation resulting in interconversion of antheraxanthin and zeaxanthin back to violaxanthin (Adams et al. 1999). Other factors may have also accounted for the differences in PSII efficiency, including differences in the spatial patterns of chlorophyll a binding proteins and light harvesting proteins (Tanaka and Melis 1997). The ability to undergo non-photochemical quenching to avoid permanent photo-oxidative damage at PFD greater than median ambient levels would confer an advantage to species in the highly variable PFD of forest gaps. Moreover, this would pre-adapt some species to establishment in shrub and grass environments.

Changes in PSII efficiency are strongly correlated with PFD, xanthophyll pool size and xanthophyll de-epoxidation (Demmig-Adams and Adams 1996; Gilmore 1997). In the present study, the degree of xanthophyll pigment de-epoxidation during midday was generally high for all species in all growth environments. Adams et al. (1999) showed that the ratio A+Z/(V+A+Z) varied across growth environments for *Stephania japonica* and *Smilax australis* growing in deep shade, forest understory, and full sun. Thermal energy dissipation rapidly engaged during sunflecks, suggesting a role of thylakoid energization in xanthophyll cycle-dependent energy dissipation (Adams et al. 1999). Although we did not measure rapid kinetics of xanthophyll pigment interconversions, this response would be advantageous for the seedlings in our study, as PFD varied greatly over short temporal scales in all three growth environments due to the angle of the sun, clouds, and wind-blown canopy movement.

Factors other than PFD may have contributed to the observed differences in photosynthesis and growth. Developmental plasticity in response to light quality can influence plant morphology and photosynthetic acclimation (Kwesiga et al. 1986; Chazdon and Kaufmann 1993). The higher growth rates in the grass occurred despite higher air and leaf temperatures and air vapour pressure difference (VPD) in comparison to shrub and forest gap sites. Temperature and VPD could also have lead to a higher driving force for water loss in the grass compared to the forest gaps for *C. tonduzii*, *T. mexicana* and compared to the shrubs for *I. punctata*, and may account for the significantly lower WUE for these species in grass compared to shrubs or forest gaps. The reduced WUE may have contributed to the downregulation of the photosynthetic apparatus (Mulkey and Pearcy 1992; Chazdon et al. 1996). Midday water potential did not differ for the four species across growth environments (except for *T. mexicana* in forest gaps), similar to results from a previous study (Holl 1999). Water potential has not been previously measured for our four study species, but Ψ ranges from –0.90 to –2.50 MPa across a wide range of tropical species (Cavelier 1996).

Differences in soil nutrient content in the growth environments also might help explain differences in plant growth but were not measured in the current study. Previous studies, however, suggest that phosphorus, the primary limiting nutrient, is higher in the forest than the pasture (Holl 1999) and there are no differences between grass and shrubs (K.D. Holl, unpublished work); therefore, these results do not help to explain higher growth rates in grass. However, higher P levels (Holl 1999) may help to explain the greater leaf number and area in the forest gaps compared to the shrubs for *T. mexicana*. In other words, in habitats where PFD levels are similar, nutrients may affect photosynthesis and growth. Previous soil measurements were taken at single sampling points, so further measurements assessing interactions between light and nutrient limitations are warranted.

Species adaptations to different growth environments

It has been suggested that spatial distribution of tropical trees may be based on niche partitioning of photosynthetic patterns (Kitajima 1994; Barker et al. 1997; Davies 1998). Our results, as well as numerous previous studies (Augspurger 1984a; Langenheim et al. 1984; Clark et al. 1993; Lieberman 1996) suggest that seedlings of many tropical forest species are able to acclimate in varying ways to different temporal and spatial patterns of light. This ability is not surprising given that seedlings of numerous tropical forest tree species grow slowly in the understory by making use of sunflecks (Chazdon and Fetcher 1984; Chazdon and Pearcy 1991; Allen and Pearcy 2000), and generally increase growth rapidly in response to treefall gap formation (Uhl et al. 1988; Denslow and Hartshorn 1994;

Press et al. 1996). A growing body of evidence suggests that biotic interactions, such as limited seed dispersal, seed and seedling herbivory, and pathogens, may be important driving factors that determine spatial patterns of establishment, survival, and growth in intact tropical forests as well as abandoned agricultural lands (Augspurger 1984b; Nepstad et al. 1991; Aide and Cavelier 1994; Barker et al. 1997; Chapman and Chapman 1999; Holl and Kappelle 1999; Hubbell et al. 1999; Harms et al. 2000). In addition, soil type and topography may play an important role in tree distribution (Clark et al. 1999). Determining the degree to which light is an important factor limiting species distributions requires data on light requirements of species over a range of life-history stages (Clark and Clark 1992; Clark et al. 1993).

References

Adams WW, Demmig-Adams B, Logan BA, Barker DH, Osmond CB (1999) Rapid changes in xanthophyll cycle-dependent energy dissipation and photosystem II efficiency in two vines, *Stephania japonica* and *Smilax australis*, growing in the understory of an open eucalyptus forest. Plant Cell Environ 22:125–136

Aide TM, Cavelier J (1994) Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restor Ecol 2:219–229

Aide TM, Zimmerman JK, Herrera L, Rosario M, Serrano M (1995) Forest recovery in abandoned tropical pasture in Puerto Rico. For Ecol Manage 77:77–86

Allen MT, Pearcy RW (2000) Stomatal behavior and photosynthetic performance under dynamic light regimes in a seasonally dry tropical rain forest. Oecologia 122:470–478

Anten NPR, Hirose T (1998) Biomass allocation and light partitioning among dominant and subordinate individuals in *Xanthium canadense* stands. Ann Bot 82:665–673

Archer S, Scifres C, Bassham CR, Maggio R (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol Monogr 58:111–128

Augspurger CK (1984a) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. J Ecol 72:777–795

Augspurger CK (1984b) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712

Barker DH, Adams WW (1997) The xanthophyll cycle and energy dissipation in differently oriented faces of the cactus *Opuntia macrorhiza*. Oecologia 109:353–361

Barker MG, Press MC, Brown ND (1997) Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning? Oecologia 112:453–463

Barnes PW, Archer S (1999) Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation? J Veg Sci 10:525–536

Bergweiler P, Lütz C (1986) Determination of leaf pigments by high-performance liquid chromatography after extraction with N,N-dimethylformamide: ecophysiological applications. Environ Exp Bot 26:207–210

Berkowitz AR, Canham CD, Kelly VR (1995) Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology 76:1156–1168

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Björkman O (1987) High-irradiance stress in higher plants and interaction with other stress factors. In: Biggens J (ed) Progress in photosynthesis. Martinus Nijhoff, Dordrecht, pp 11–18

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965

Cardoso da Silva JM, Uhl C, Murray G (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conserv Biol 10:491–503

Castro Y, Fetcher N, Fernandez DS (1995) Chronic photoinhibition in seedlings of tropical trees. Physiol Plant 94:560–565

Cavelier J (1996) Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 399–439

Chapman CA, Chapman LJ (1999) Forest restoration in abandoned agricultural land: a case study from East Africa. Conserv Biol 13:1301–1311

Chazdon RL, Fetcher N (1984) Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. J Ecol 72:553–564

Chazdon RL, Kaufmann S (1993) Plasticity of leaf anatomy of two rain forest shrubs in relation to photosynthetic light acclimation. Funct Ecol 7:385–394

Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants: photosynthetic machinery appears adapted to brief unpredictable periods of radiation. Bioscience 41:760–766

Chazdon RL, Pearcy RW, Lee DW, Fetcher N (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 5–55

Clark DA, Clark DB (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecol Monogr 62:315–344

Clark DB, Clark DA, Rich PM (1993) Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. Biotropica 25:397–407

Clark DB, Palmer MW, Clark DA (1999) Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80:2662–2675

Davies SJ (1998) Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. Ecology 79:2292–2308

Demmig-Adams B, Adams WW (1996) Chlorophyll and carotenoid composition in leaves of *Euonymus kiautschovicus* acclimated to different degrees of light stress in the field. Aust J Plant Physiol 23:649–659

Demmig-Adams B, Adams WW, Barker DH, Logan BA, Bowling DR, Verhoeven AS (1996) Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. Physiol Plant 98:253–264

Denslow JS, Hartshorn GS (1994) Tree-fall gap environments and forest dynamic processes. In: McDade LA (ed) La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, pp 120–127

Denslow JS, Ellison AM, Sanford RE (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. J Ecol 86:597–609

Duncan RS, Chapman CA (1999) Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecol Appl 9:998–1008

Fetcher N, Strain BR, Oberbauer SF (1983) Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. Oecologia 58:314–319

Gamon JA, Pearcy RW (1990) Photoinhibition in *Vitis californica* – interactive effects of sunlight, temperature and water status. Plant Cell Environ 13:267–275

Gerhardt K, Fredrikkson D (1995) Biomass allocation by broadleaf mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. Biotropica 27:174–182

Gilmore AM (1997) Mechanistic aspects of xanthophyll cycle-dependent photoprotection in higher plant chloroplasts and leaves. Physiol Plant 99:197–209

Harms KE, Wright SJ, Calderón O, Hernández A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495

Havaux M (1992) Stress tolerance of photosystem II in-vivo antagonistic effects of water, heat and photoinhibition stresses. Plant Physiol 100:424–432

Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JA Jr (1971) Forest environments in tropical life zones: a pilot study. Pergamon Press, Oxford

Holl KD (1998) Effects of above- and below-ground competition of shrubs and grass on *Calophyllum brasiliense* (Camb.) seedling growth in abandoned tropical pasture. For Ecol Manage 10:187–195

Holl KD (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31:229–241

Holl KD, Kappelle M (1999) Tropical forest recovery and restoration. Trends Ecol Evol 14:378–379

Holl KD, Quiros-Nietzen E (1999) The effect of rabbit herbivory on reforestation of abandoned pasture in southern Costa Rica. Biol Conserv 87:391–395

Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical forest restoration in abandoned pastures in Costa Rica: obstacles and opportunities. Restor Ecol 8:339–349

Huante P, Rincón E (1998) Responses to light changes in tropical deciduous woody seedlings with contrasting growth rates. Oecologia 113:53–66

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, De Lao SL (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557

Humphrey JW, Swaine MD (1997) Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. I. Competition from *Pteridium aquilinum*. J Appl Ecol 34:577–584.

Huynh H, Feldt LS (1976) Estimation of the box correction for degrees of freedom from sample data in the randomized block and split plot designs. J Educ Stat 1:69–82

Kettler JS (1997) Fallow enrichment of a traditional slash/mulch system in southern Costa Rica, comparisons of biomass production and crop yield. Agrofor Syst 35:165–176

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428

Kobe RK (1999) Light gradient partitioning among tropical tree species through differential seedling mortality and growth. Ecology 80:187–201

Königer M, Harris GC, Virgo A, Winter K (1995) Xanthophyll-cycle pigments and photosynthetic capacity in tropical forest species: a comparative field study on canopy, gap and understory plants. Oecologia 104:280–290

Kooten O van, Snel JFH (1990) The us of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth Res 25:147–150

Kwesiga FR, Grace J, Sandford AP (1986) Some photosynthetic characteristics of tropical timber trees as affected by the light regime during growth. Ann Bot 58:23–32

Langenheim JH, Osmond CB, Brooks A, Ferrar PJ (1984) Photosynthetic responses to light in seedlings of selected Amazonian and Australian rainforest tree species. Oecologia 63:215–224

Li X, Wilson SD (1998) Facilitation among woody plants establishing in an old field. Ecology 79:2694–2705

Lieberman D (1996) Demography of tropical tree seedlings: a review. In: Swaine MD (ed) The ecology of tropical forest tree seedlings. Parthenon, New York, pp 131–138

Loik ME, Harte J (1997) Changes in water relations for leaves exposed to a climate-warming manipulation in the Rocky Mountains of Colorado. Environ Exp Bot 37:115–123

Loik ME, Holl KD (1999) Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. Restor Ecol 7:382–391

Lovelock CE, Jebb M, Osmond CB (1994) Photoinhibition and recovery in tropical plant species: response to disturbance. Oecologia 97:297–307

McDonnell MJ, Stiles EW (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia 56:109–116

Mulkey SS, Pearcy RW (1992) Interactions between acclimation and photoinhibition of photosynthesis of a tropical forest understory herb, *Alocasia macrorrhiza,* during simulated canopy gap formation. Funct Ecol 6:719–729.

Murphy JS, Briske DD (1994) Density-dependent regulation of ramet recruitment by the red:far-red ratio of solar radiation: a field evaluation with the bunchgrass *Schizachyrium scoparium*. Oecologia 97:462–469

Myster RW (1993) Tree invasion and establishment in old fields at Hutcheson memorial forest. Bot Rev 59:251–272

Nepstad DC, Uhl C, Serrao EAS (1991) Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio 20:248–255

Nichols D, Gonzalez E (1991) Especies nativas y exóticas para la reforestación en la zona sur de Costa Rica. Organización para Estudios Tropicales, San José, Costa Rica

Niinemets U, Bilger W, Kull O, Tenhunen JD (1999) Responses of foliar photosynthetic electron transport, pigment stoichiometry, and stomatal conductance to interacting environmental factors in a mixed species forest canopy. Tree Physiol 19: 839–852

Niyogi KK, Björkman O, Grossman AR (1997) The roles of specific xanthophylls in photoprotection. Proc Natl Acad Sciences USA 94:14162–14167

Oberbauer, SF, Clark DB, Clark DA, Quesada M (1988) Crown light environments of saplings of two species of rain forest emergent trees. Oecologia 75:207–212

Osmond CB (1994) What is photoinhibition? Some insights from comparisons of shade and sun plants. In: Baker NR, Bowyer JR (eds) Photoinhibition of photosynthesis: from molecular mechanisms to the field. BIOS, Oxford, pp 1–24

Pearcy RW (1994) Photosynthetic response to sunflecks and light gaps: mechanisms and constraints. In: Baker NR, Bowyer JR (eds) Photoinhibition of photosynthesis: from molecular mechanisms to the field. BIOS, Oxford, pp 255–271

Pickett STA, Collins SL, Armesto JJ (1987) Models, mechanisms, and pathways of succession. Bot Rev 53:335–371

Press MC, Brown ND, Barker MG, Zipperlen SW (1996) Photosynthetic responses to light in tropical rain forest seedlings. In: Swaine MD (ed) The ecology of tropical forest tree seedlings. Parthenon, New York, pp 41–48

Putz FE, Canham CD (1992) Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. For Ecol Manage 49:267–275

Ruban AV, Phillip D, Young AJ, Horton P (1997) Carotenoid-dependent oligomerization of the major chlorophyll a/b light harvesting complex of photosystem II of plants. Biochemistry 36:7855–7859

Saab VA, Petit DR (1992) Impact of pasture development on winter bird communities in Belize, Central America. Condor 94:66–71

Schreiber U, Bilger W, Neubauer C (1995) Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis. In: Schulze ED, Caldwell MM (eds) Ecophysiology of photosynthesis. Springer, Berlin Heidelberg New York, pp 49–70

Sims DA, Pearcy RW (1991) Photosynthesis and respiration in *Alocasia macrorrhiza* following transfers to high and low light. Oecologia 86:447–453

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, New York

Steven D de (1991a) Experiments on mechanisms of tree establishment in old-field succession; seedling emergence. Ecology 72:1066–1075

Steven D de (1991b) Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076–1088

Tanaka A, Melis A (1997) Irradiance-dependent changes in the size and composition of the chlorophyll a-b light-harvesting complex in the green alga *Dunaliella salina*. Plant Cell Physiol 38:17–24

Thayer SS, Björkman O (1990) Leaf xanthophyll content and composition in sun and shade determined by HPLC. Photosynth Res 23:331–344

Uhl C, Clark K, Dezze N, Maquirino P (1988) Vegetation dynamics in Amazonian treefall gaps. Ecology 69:751–763

Valladares F, Pearcy RW (1997) Interactions between water stress, sun-shade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. Plant Cell Environ 20:25–36

Valladares F, Allen MT, Pearcy RW (1997) Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. Oecologia 111:505–514

Vieira ICG, Uhl C, Nepstad D (1994) The role of the shrub *Cordia multispicata* Cham. as a "succession facilitator" in an abandoned pasture, Paragominas, Amazonia. Vegetatio 115:91–99

Walker LR, Chapin FS III (1986) Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67:1508–1523

Walker LR, Chapin, FS III (1987) Interactions among processes controlling successional change. Oikos 50:131–135

Walters RG, Ruban AV, Horton P (1996) Identification of proton-active residues in a higher plant light-harvesting complex. Proc Natl Acad Sci USA 93:14204–14209

Werner, PA, Harbeck, AL (1982) The pattern of tree seedling establishment relative to staghorn sumac cover in Michigan old fields. Am Midl Nat 108:124–132

Yamamoto H, Chenchin EE, Yamada DK (1974) Proceedings of the third international congress on photosynthesis. Elsevier, Amsterdam