High-Light Stress does not Impair Biomass Accumulation of Sun-Acclimated Tropical Tree Seedlings (*Calophyllum longifolium* Willd. and *Tectona grandis* L. f.)

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Abstract: Studies with seedlings of tropical rainforest trees (*Calophyllum longifolium* Willd.; *Tectona grandis* L. f.) were designed to test whether high-light stress affects photosynthetic performance and growth. Seedlings were cultivated in pots at a field site in Central Panama (9°N) and separated into two groups: (1) plants exposed to full solar radiation; (2) plants subjected to automatic neutral shading (48%) whenever visible irradiance surpassed 1000, 1200, or 1600 μmol photons m^{-2} s^{-1}. After 2–4 months, chlorophyll fluorescence (F_v/F_m ratio), photosynthetic net CO_2 uptake, pigment composition, α-tocopherol content of leaves, and plant biomass accumulation were measured. Fully sun-exposed, compared to periodically shaded plants, experienced substantial high-light stress around midday, indicated by photoinhibition of photosystem II and depressed net CO_2 uptake. Higher contents of xanthophyll cycle pigments, lutein, and α-tocopherol showed an enhancement of photoprotection in fully sun-exposed plants. However, in all experiments, the maximum capacity of net CO_2 uptake and plant dry mass did not differ significantly between the two treatments. Thus, in these experiments, high-light stress did not impair productivity of the seedlings studied. Obviously, the continuously sun-exposed plants were capable of fully compensating for any potential costs associated with photoinhibition and repair of photosystem II, reduced CO_2 assimilation, and processes of high-light acclimation.

Key words: Biomass accumulation, CO_2 assimilation, midday depression, photoinhibition of photosystem II, α-tocopherol, xanthophyll cycle, *Calophyllum longifolium* Willd., *Tectona grandis* L. f.

Abbreviations:

Ax:	antheraxanthin
β-Car:	β-carotene
Chl:	chlorophyll
F_v/F_m:	ratio of maximum variable to maximum total chlorophyll *a* fluorescence yield
Lut:	lutein
Neo:	neoxanthin
PFD:	photon flux density (spectral range 400–700 nm)
PSII:	photosystem II
Vx:	violaxanthin
Zx:	zeaxanthin

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Introduction

Full, direct sunlight during midday hours is highly in excess of that required for driving photosynthesis in sun-acclimated leaves of most plant species. Many studies have shown that, in nature, absorption of excess photons causes photoinhibition of photosystem II (PSII) (e.g., Ögren and Rosenquist, 1992; Long et al., 1994), leading primarily to a reduction in photon yield and, to a lesser extent, of the capacity for photosynthetic CO_2 assimilation. Photoinhibition of PSII is often associated with "midday depression" of net CO_2 uptake, which is observed when photon flux density (PFD) and leaf temperatures reach their daily maxima (Raschke and Resemann, 1986; Demmig-Adams et al., 1989; Muraoka et al., 2000; Franco and Lüttge, 2002). In leaves acclimated to excess light, photoinhibition appears to be based partly on persistent effects of the xanthophyll zeaxanthin (Zx) and partly on inactivation of the D1 protein in the PSII reaction centre (Thiele et al., 1996, 1997, 1998). In both cases, a decrease in the ratio of the "dark-adapted" variable to maximum chlorophyll (Chl) *a* fluorescence emission, F_v/F_m, indicates that, in photoinhibited PSII, enhanced thermal dissipation of absorbed light energy occurs (see Krause and Jahns, 2003, 2004). Under most circumstances, photoinhibition is reversible in low light, when Zx is reconverted to violaxanthin (Vx) via the xanthophyll cycle, and the inactivated D1 protein is degraded and replaced by new synthesis. Upon strong and extended impact of excess light, complete PSII recovery may require more than one day (Björkman et al., 1988; Krause et al., 1999; Werner et al., 2002), indicating "chronic" photoinhibition.

Reductions in PSII photochemistry due to high-light stress, i.e., photoinhibition, can be the cause and the result of reductions in photosynthetic CO_2 fixation. Keeping this in mind, the present study addresses whether potential losses in carbon gain caused by high-light stress, including effects of high leaf temperatures, results in a reduction in biomass accumulation of plants in their natural environment. Several investigations have demonstrated that carbon gain becomes considerably reduced by high-light stress in sun-exposed canopy leaves, although effects on biomass production were not assessed. For

example, Ögren and Sjöström (1990) estimated the reduction in net carbon assimilation by peripheral leaves of willow (*Salix* sp.) in northern Sweden at about 10% on clear days. Jifon and Syvertsen (2003) showed that moderate (50%) shade compared to full sun increased net CO_2 uptake by outer canopy leaves of citrus trees *(Citrus paradisi* and *C. sinensis)* in Florida. The effect was attributed to reduced photoinhibition of PSII and midday depression of CO_2 uptake. Net photosynthesis of leaves of apricot trees *(Prunus armeniaca)* was substantially lower under full sunlight than in moderate (about 35%) shade (Nicolás et al., 2005). Furthermore, based on model calculations, Zhu et al. (2004) suggested that, on transition from high to low light, i.e., under fluctuating light in the field, the relatively slow reversibility of protective thermal energy dissipation in PSII causes losses in net carbon uptake by canopies.

Contrasting data on long-term effects of high-light stress on biomass production at the level of the whole plant have been reported. Reduced plant growth and productivity observed at suboptimal temperatures has been suggested to be caused, in part, by excessive light (Farage and Long, 1991; Königer and Winter, 1991; Winter and Königer, 1991; Laing et al., 1995; Egerton et al., 2000). It is well known that low temperatures aggravate photoinhibition at a given photon flux (for reviews see Baker et al., 1988; Krause, 1994). However, direct proof as to what extent photoinhibition *per se* caused a reduction in growth rate is difficult to obtain in those cases.

In the absence of low temperature stress, seedlings of *Picea engelmannii* did not exhibit significant differences in dry mass accumulation when cultivated at limiting or high levels of nitrogen supply, either in full or 33% sunlight (McKinnon and Mitchell, 2003). Under both forest gap and full sunlight conditions, field-grown seedlings of beech *(Fagus sylvatica)* exhibited higher photoinhibition in comparison with ash *(Fraxinus excelsior),* but not less biomass accumulation (Einhorn et al., 2004).

Building on previous studies of tropical plants (Krause et al., 1995; Krause and Winter, 1996; Barth et al., 2001; Krause et al., 2003, 2004), we used an automatic shading device to find out whether conditions of full solar radiation in a tropical environment can have negative effects on plant productivity. Seedlings of tropical forest trees were cultivated at an open site, either in full sunlight (with PFD up to about 2400 µmol photons m^{-2} s^{-1}) or under the shading device, which provided 48% neutral shade whenever PFD exceeded light saturation of photosynthesis or reached levels that promote strong photoinhibition of PSII. Following long-term acclimation to those contrasting light conditions, photoinhibition and net CO_2 assimilation during the day-course, as well as photosynthetic light-use efficiency and capacity, the contents of photosynthetic pigments and of the antioxidant α-tocopherol of leaves were analysed. At the end of the cultivation periods, biomass accumulation and various growth parameters of whole plants were determined.

Materials and Methods

Experiments were performed at a field site in Parque Natural Metropolitano, Panama City (9°N) (Holtum and Winter, 2005). Pigment and α-tocopherol analyses were carried out at the Institute of Plant Biochemistry, Düsseldorf, Germany.

Plant material and experimental procedure

Seedlings of two species were studied: (i) *Calophyllum longifolium* Willd. (Moraceae), a late-successional tree of neotropical lowland forests, and (ii) *Tectona grandis* L. f. (Verbenaceae), teak, a fast-growing pioneer tree originating in South-East Asia.

Three long-term experiments with *C. longifolium* were performed in 2001/2002, 2002/2003, and 2003/2004, in which growing conditions and experimental procedure were varied.

1. Seeds were germinated and seedlings cultivated in soil (Pro-Mix Bx, Les Tourbieres Premier LTEE, Quebec, Canada; pots of 7.5 L, height 40 cm) for 1.5 months under deep shade (midday PFD 10 – 30 µmol photons m^{-2} s^{-1}; mean temperature about 30 °C) in a greenhouse. The plants were transferred to larger pots (15 L, 50 cm high), filled with a mixture of forest soil and 50% leaf litter, and acclimated in four steps to 65% of ambient PFD within 3.5 months. The pots were shielded with aluminium foil to avoid heating from sunlight. Subsequently, 5 – 6 plants of average size were harvested for determination of dry mass and other growth parameters. The remaining seedlings were separated into two groups and placed at an open site receiving potentially 9.5 h direct sunlight per day. One group was exposed to full sunlight, whereas the other group was automatically shaded (about 48% neutral shade) whenever ambient PFD exceeded 1000 µmol photons m^{-2} s^{-1}. The plants were watered when rain was insufficient to keep the soil permanently moist. The seedlings were kept under these contrasting light conditions for 3.5 months, starting in the late rainy season (6 Dec. 2001) and continuing during the dry season (late Dec. 2001 to March 2002), when leaf samples were taken and physiological measurements performed. On 22 March 2002, the plants were harvested to determine dry mass and further growth parameters.
2. Seeds were germinated, starting on 15 July 2002, in 15-L pots under a plexiglass roof covered with shade cloth transmitting 25% of ambient PFD. On 25 Oct. 2002, the light level was increased to 70% of ambient PFD for 12 days. The plants were then divided into two groups that were exposed to full sunlight and partial shade, respectively. The threshold for automatic shading (see above) was set at an ambient PFD of 1200 µmol photons m^{-2} s^{-1}. Leaf samples and measurements were taken from Dec. 2002 to March 2003. Plants were harvested on 7 March 2003.
3. Seeds were germinated, starting on 24 Oct. 2003, in 15-L pots under either fully sun-exposed or partly shaded conditions, with automatic shading set at a threshold of 1600 µmol photons m^{-2} s^{-1}, ambient PFD. By the end of November 2003, the first leaf pairs had developed. Leaf samples and measurements were taken in February and March 2004, and the plants were harvested on 11 March 2004.

In addition, an experiment was done with *T. grandis* in 2001/2002. Seeds were germinated at a site exposed for about 4 h d^{-1} to full sunlight, and seedlings were transferred to 15-L pots. On 3 Dec. 2001, after reaching an average height of 6 cm (age of plants about 6 weeks), one group of plants each was exposed to full sunlight or partial shade. The threshold for shading was set to 1000 µmol photons m^{-2} s^{-1}. Plants were harvested on 2 Feb. 2002.

Automatic shading device

Partial shading above a specified threshold of ambient PFD (spectral range 400 – 700 nm) was done with a folding screen made of black shade cloth, absorbing about 48% of PFD and UV light. A metal frame, 2 m high and covering an area of 4 × 6 m, supported the shade cloth. When unfolded, it shaded the plants from the top, as well as from SE and SW sides; when folded, the plants were exposed to full sunlight. Folding and unfolding, by means of a power-driven motor, required 45 s and was initiated by a quantum sensor (LI-190SA, LI-COR, Lincoln, NE) connected to a data logger (CR10X Measurement and Control System, Campbell Scientific Inc., Logan, Utah). The quantum sensor was placed in a horizontal position on top of the frame. That measuring system also served to record ambient PFD during the course of the day. At the partially shaded site, PFD was recorded using a second LI-190SA sensor. Additionally, PFD was monitored with a third LI-190SA sensor connected to a LI-189B data logger. UV-B and UV-A were measured with a radiometer (IL 1400 A, International Light, Newburyport, MA) that was calibrated against an OL 754-O-PMT spectroradiometer (Optronics, Orlando, FL).

Chlorophyll a *fluorescence*

As a measure of potential PSII efficiency, the ratio of maximum variable to maximum total Chl *a* fluorescence emission, F_v/F_m, was determined from attached leaves with a portable PAM 2000 or MINI-PAM fluorometer (Walz, Effeltrich, Germany) after 10 min dark adaptation. DLC-8 leaf clips (Walz) were used for darkening. The mode of PAM 2000 measurements has been described by Barth and Krause (1999). The measuring light frequency of the MINI-PAM fluorometer was set low (0.6 kHz); for exact recording of initial fluorescence, F_o, the "measuring light burst" mode was used. The duration of the saturating light pulses to record F_m was 0.8 or 1.0 s.

Measurements of non-photochemical Chl fluorescence quenching in dark-adapted leaf disks (1 cm diameter) with a PAM 101 fluorometer (Walz) have been described previously (Thiele et al., 1997; Krause and Jahns, 2003; Krause et al., 2004). Actinic white light was 1850 µmol photons m^{-2} s^{-1} and the saturating pulse intensity was 5300 µmol photons m^{-2} s^{-1}.

CO_2 gas exchange

During the course of the experiments, measurements of CO_2 gas exchange were performed with an LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE) on the youngest fully developed leaves oriented towards the SE, i.e., strongly sun-exposed from morning to early afternoon. Ambient air containing 360 – 380 µL L^{-1} CO_2 was used. Net CO_2 assimilation under solar radiation at ambient temperatures was followed during the day. In addition, light response curves under controlled conditions (up to 1000 µmol photons m^{-2} s^{-1}; air temperature 30 °C) were obtained with a 6400-02B LED red and blue light source (LI-COR). Measurements were conducted between morning and midday after the plants had been adapted to a solar PFD of 200 – 500 µmol photons m^{-2} s^{-1} for at least 30 min. To avoid high-light stress before measurements, plants were temporarily taken to a partially shaded area. Light saturation of net CO_2 assimilation was reached at 500 to 1000 µmol photons m^{-2} s^{-1}. Photon use efficiency was calculated from the initial linear slopes of the light response curves; linear regression coefficients were $r^2 = 0.98$ or higher.

Photosynthetic pigments and α-tocopherol

Leaf disks (1 cm diameter) were frozen in liquid nitrogen and stored at – 70 to – 80 °C or on dry ice until analysis. For quantification of chlorophylls and carotenoids, a modified procedure of Färber et al. (1997) was used as described by Krause et al. (2003).

In experiment 2 with *C. longifolium* (2002/2003), pigments and the antioxidant α-tocopherol were determined in the same leaf extract according to García-Plazaola and Becerril (1999). One leaf disk was ground in a mortar with liquid nitrogen in the presence of sodium carbonate and extracted twice with 0.5 mL acetone (100%). The extracts were centrifuged (20 400 g) for 10 min, adjusted to a total volume of 1.0 mL and filtered. α-Tocopherol was analyzed by HPLC with System LaChrom (Merck/Hitachi, Darmstadt, Germany) using an RP-18 endcapped column (LiChroCART 125-4) and Fluorescence Detector L7485 (Merck/Hitachi; excitation wavelength at 295 nm; emission at 325 nm). A linear solvent gradient was applied to elute α-tocopherol. Solvent A consisted of methanol (30% v/v)/0.1 M ammonium acetate, pH 5.2 (10% v/v)/water (60% v/v). Solvent B was 100% methanol. The gradient started with 6% Solvent A, 94% Solvent B, ending after 10 min with 1% A, 99% B, followed by 13 min of further elution with the latter mixture. The injection volume was 10 µL and the flow rate was 1 mL min^{-1}. The retention time of α-tocopherol was about 10.5 min. Calibration was done with DL-α-tocopherol (Tocopherol Set, Calbiochem/Merck Biosciences, Darmstadt, Germany).

Growth parameters

Leaf blades, stems (including leaf petioles), and roots were separated. Leaf area was measured with an LI-3100 area meter (LI-COR, Lincoln, NE). Dry mass was determined after drying the plant material at 70 °C for 72 to 96 h. Based on these data, specific leaf area (SLA = leaf area per leaf dry mass) and shoot to root dry mass ratio were calculated.

Statistics

Means and standard deviations (SD) of data are presented. The significance of differences between data from fully sun-exposed and partially shaded plants were assessed by unpaired *t*-tests. The probability of error (P) is noted in figure legends and tables where appropriate.

Results

Light and temperature conditions

The daily integrated PFD received by the plants cultured under partially shaded, as compared to open, fully sun-exposed conditions, is presented in Fig. **1** for an experiment with *C. longifolium* in which about 48% neutral shade was provided whenever PFD exceeded a threshold of 1200 µmol photons m^{-2} s^{-1} (see "Materials and Methods", experiment 2). The relative reduction in daily integrated PFD in the shade treatments increased during the transition from the rainy to the dry season

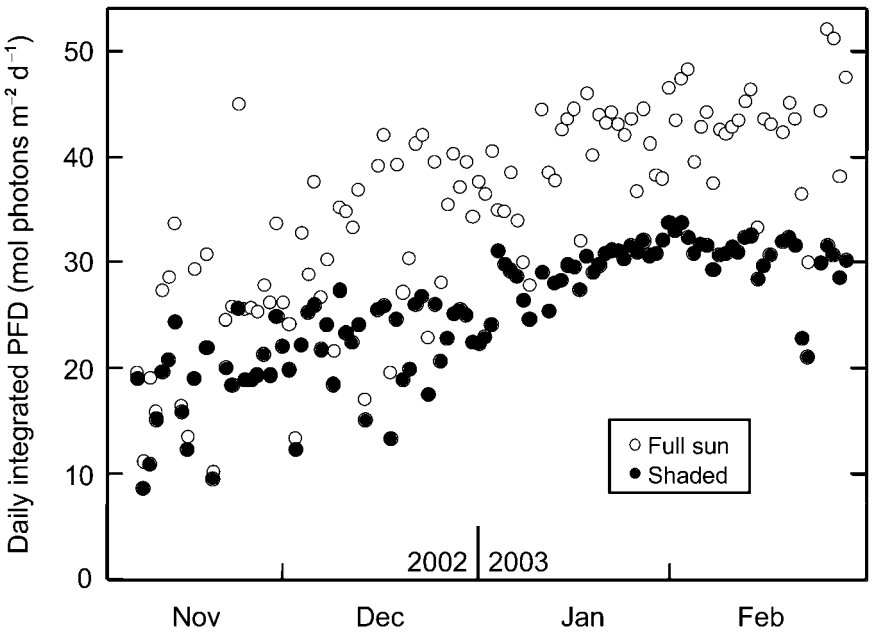

Fig. 1 Daily integrated PFD (spectral range 400 – 700 nm) from November 2002 to February 2003 under fully sun-exposed and partially shaded growth conditions. Automatic 48% shading occurred whenever ambient PFD exceeded 1200 µmol photons m^{-2} s^{-1}. PFD was recorded with horizontally placed quantum sensors. Open symbols, full sunlight; closed symbols, partial shade.

Table 1 Daily integrated PFD in the spectral range 400 – 700 nm (means ± SD) recorded with horizontally placed quantum sensors under fully sun-exposed and partially shaded conditions, obtained with different PFD thresholds for shading (n, number of days with records[a])

PFD threshold (µmol photons m^{-2} s^{-1})	Month/ year	Integrated PFD (mol photons m^{-2} d^{-1})			n
		Full sun	Shaded	(%)[b]	
1000	Feb. 2002	40.0 ± 6.6	21.9 ± 2.4	55	21
1200	Nov. 2002	24.9 ± 8.1	18.4 ± 4.7	74	24
	Dec. 2002	33.8 ± 6.9	23.0 ± 3.4	68	30
	Jan. 2003	40.6 ± 5.2	30.2 ± 2.2	74	30
	Feb. 2003	42.7 ± 5.1	30.2 ± 2.8	71	23
1600	Dec. 2003	28.2 ± 7.6	26.9 ± 6.2	95	29
	Feb. 2004	40.2 ± 5.4	27.5 ± 6.2	68	27

[a] PFD recording was not done on all days due to technical problems.
[b] Mean integrated PFD under partially shaded conditions as percentage of integrated PFD under fully exposed conditions.

(December/January). Means of daily integrated PFD in the months of the study are presented in Table **1** for PFD thresholds at 1000 (recorded in February only), 1200, and 1600 µmol photons m^{-2} s^{-1}. The daily integrated PFD was not substantially reduced under partial shading above 1600 µmol photons m^{-2} s^{-1} in December 2003, due to a largely cloudy sky and the high PFD threshold applied; but daily integrated PFD was strongly decreased in February 2004.

UV-B and UV-A radiation were attenuated by the shading cloth to approximately the same extent as PFD in the spectral range of 400 – 700 nm. At a typical ambient midday PFD (2173 ± 20 µmol photons m^{-2} s^{-1}) under a clear sky, 2.55 ± 0.02 W m^{-2} UV-B and 46.7 ± 1.1 W m^{-2} UV-A were measured, as compared to 1.32 ± 0.02 and 24.2 ± 0.4 W m^{-2}, respectively, under shading conditions (means ± SD of 3 measurements).

Although air temperatures were not significantly different between the two light treatments, *C. longifolium* leaf temperatures (adaxial surface; 8 – 17 leaves) were slightly elevated under full solar exposure compared to partial shade in the absence of wind. Under 1900 – 2300 µmol photons m^{-2} s^{-1} PFD (full sun), leaf temperatures were typically between 38 and 43 °C (air temperature 32 – 37 °C), whereas under shade conditions leaf temperatures were 35 – 37 °C (air temperature 33 – 37 °C). Moderate wind abolished these differences.

Potential PSII efficiency and CO_2 assimilation

Fully sun-exposed leaves of the tree seedlings studied experienced substantial photoinhibition of PSII during the course of the day, indicated by a decline in the fluorescence ratio F_v/F_m (Figs. **2a – d**, lower panels). This response was largely reversible when the PFD level declined in the afternoon. PFD values recorded during the days of measurements under full sun and partial shade are shown in the upper panels of Figs. **2a – d**. The degree of photoinhibition was reduced when the leaves were shaded above a PFD threshold of 1000 (Figs. **2a,b**) or 1200 µmol photons m^{-2} s^{-1} (Fig. **2c**). In the case of Fig. **2b**, the leaves did not fully recover over night, indicating slight chronic photoinhibition. The fast-growing pioneer species *T. grandis* (teak) showed considerably less photoinhibition under full sunlight than the late-successional species *C. longifolium* (Figs. **2a,b**). When the PFD threshold for partial shading was at 1600 µmol photons m^{-2} s^{-1} (Fig. **2d**), strong photoinhibition occurred in the morning in plants of both treatments before shading set in. After shading had started, leaves of the shaded plants recovered, whereas under full sunlight a high degree of photoinhibition prevailed around midday (Fig. **2d**).

Data on photosynthetic CO_2 assimilation during the course of two consecutive days under fully sun-exposed and partially shaded conditions (PFD threshold for shading, 1000 µmol photons m^{-2} s^{-1}) are presented in Figs. **3b,d** for leaves of *C. longifolium.* Figs. **3a,c** show PFD values simultaneously measured

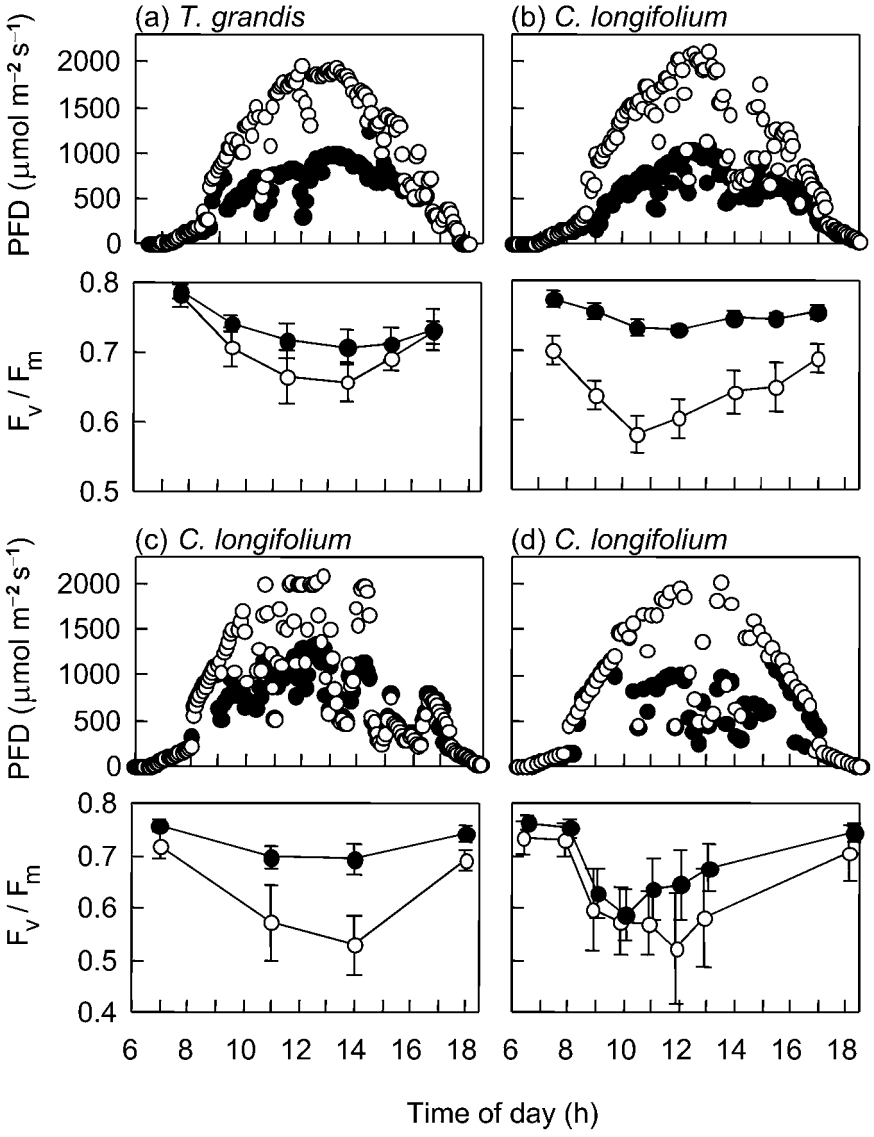

Fig. 2 Photoinhibition of PSII, measured as a decrease in F_v/F_m, during the course of the day in leaves of *T. grandis* and *C. longifolium* seedlings that were either exposed to full sunlight or partially shaded when ambient PFD exceeded 1000 (**a, b**), 1200 (**c**), or 1600 µmol photons m^{-2} s^{-1} (**d**). Upper panels show PFD (µmol photons m^{-2} s^{-1}). Decline in F_v/F_m (lower panels) indicates a reduction in potential PSII efficiency. Measurements were done after the plants had grown under the two light regimes for 57 d (**a**), 103 d (**b**), 106 d (**c**), and 92 d (**d**). Means ± SD are given for F_v/F_m; n = 5 (**a, b**); n = 8 – 10 (**c, d**); leaves of different plants. In **a**, differences in F_v/F_m between "full sun" and "shade" were significant at 9.30 h, 11.30 h, and 13.40 h, local time; in **d**, differences were significant at 12.00 and 13.00 h ($p < 0.05$). Open symbols, full sunlight; closed symbols, partial shade.

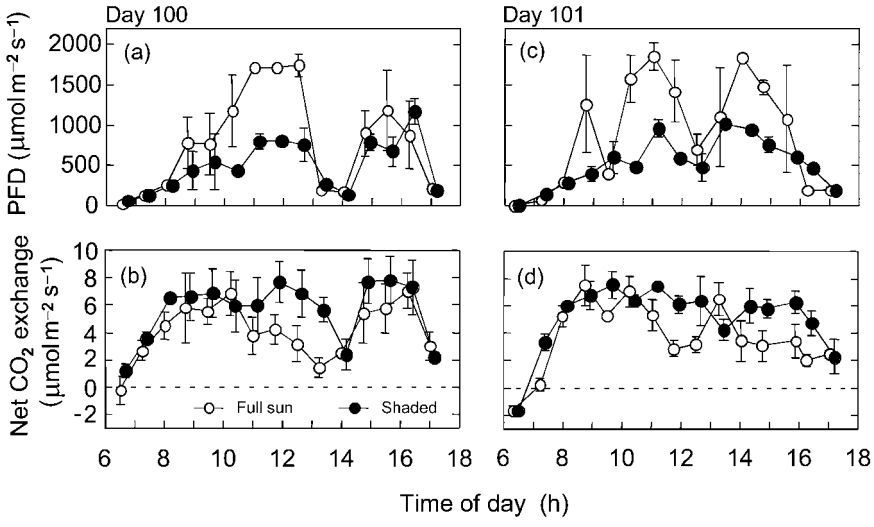

Fig. 3 Day course of net CO_2 exchange by leaves of *C. longifolium* after 100 d (**a, b**) and 101 d (**c, d**) of acclimation to full sunlight or automatic shading whenever PFD exceeded 1000 µmol photons m^{-2} s^{-1}. Upper panels (**a, c**), PFD (µmol photons m^{-2} s^{-1}) recorded at leaf level; lower panels (**b, d**), rates of net CO_2 exchange. Means ± SD are given (n = 4 – 5; leaves from different plants; SD not shown when smaller than symbols). Open symbols, full sunlight; closed symbols, partial shade.

Table 2 Capacity (A_{max}) and photon use efficiency of net CO_2 assimilation, obtained from light response curves using an artificial light source. Means ± SD of n leaves from different plants are given. Seedlings of *C. longifolium* were acclimated to full sunlight or were automatically shaded whenever ambient PFD exceeded 1200 µmol photons m^{-2} s^{-1}. Plants were randomly chosen for measurements; on 5 Feb. 2003, all leaves used had newly developed after the start of treatments. Photoinhibitory light levels were avoided on days of measurements until recordings were completed (see "Materials and Methods")

Date	A_{max} (µmol CO_2 m^{-2} s^{-1})			Photon use efficiency (mol CO_2 mol^{-1} incident photons)		
	Start	Full sun	Shaded	Start	Full sun	Shaded
4 Nov. 2002 (start)	10.2 ± 0.3 (n = 5)			0.064 ± 0.003 (n = 4)		
15 Nov. 2002 (day 10)		8.8 ± 1.6[a] (n = 7)	7.2 ± 1.3[a] (n = 7)		0.051 ± 0.004[a] (n = 4)	0.050 ± 0.005[a] (n = 4)
25 Nov. 2002 (day 20)		8.2 ± 0.6[a] (n = 4)	6.9 ± 1.0[a] (n = 4)		0.049 ± 0.004[a] (n = 4)	0.056 ± 0.009 (n = 4)
5 Feb. 2003 (day 93)		8.0 ± 0.8[a] (n = 6)	9.9 ± 1.3[b] (n = 6)		0.057 ± 0.006 (n = 6)	0.062 ± 0.005 (n = 6)

[a] Significantly different from start of experiment ($p < 0.01$).
[b] Significantly different from "full sun" ($p < 0.05$).

at the leaf level. Typical midday depression of net CO_2 uptake was observed in fully exposed leaves, when the sun was not obscured by clouds. In contrast, high rates of CO_2 assimilation were maintained under partial shade. Similar results were obtained with the threshold for shading set to 1200 µmol photons m^{-2} s^{-1}. When the shading threshold was at 1600 µmol photons m^{-2} s^{-1}, no significant differences in CO_2 uptake between the two treatments were found (data not shown). The day course of CO_2 assimilation by the pioneer species *T. grandis* was not investigated.

The light-saturated capacity of CO_2 assimilation of *C. longifolium* (PFD of shading threshold, 1200 µmol photons m^{-2} s^{-1}) declined significantly in both treatments during the first 20 days of the experiment and then recovered within 3 months at the shaded site only (Table **2**). After 10 days, photon use efficiency had also declined, but recovered later in both treatments (Table **2**). Capacity and photon use efficiency of CO_2 assimilation did not show significant differences between the two treatments in the other experiments (see "Materials and Methods").

Acclimative responses to high-light stress

As shown for *T. grandis* (PFD of shading threshold, 1000 µmol photons m^{-2} s^{-1}; Fig. **4**) and *C. longifolium* (shading theshold 1200 µmol photons m^{-2} s^{-1}; Fig. **5**), leaves of fully sun-exposed seedlings built up a larger pool of xanthophyll cycle pigments, viola-, anthera-, and zeaxanthin (Vx, Ax, Zx), as compared to partially shaded seedlings. Fig. **4** demonstrates, moreover, the conversion of a higher fraction of Vx to Zx via the xanthophyll cycle in fully sun-exposed leaves at midday. A very high Zx level under full sun at midday was also observed with *C. longifolium* (Fig. **5**). In addition, Fig. **5** shows that the level of lutein (Lut) increased, whereas levels of β-carotene (β-Car) and neoxanthin (Neo) remained unaltered. Very similar data as in Fig. **5** were obtained already 29 days after the start of the experiment. No significant differences in total Chl contents and Chl *a*/Chl *b* ratios between fully sun-exposed and partially shaded leaves were found (data not shown). When the shading threshold was set to 1600 µmol photons m^{-2} s^{-1} PFD, high pools of xanthophyll cycle pigments were observed that did not differ significantly between the two treatments (data not shown).

The capacity for non-photochemical Chl fluorescence quenching, an indicator of potential harmless dissipation of excess photon energy, was determined on detached leaf disks of *C. longifolium* after 109 days of acclimation to full sunlight or partial shading (PFD threshold, 1200 µmol photons m^{-2} s^{-1}). Despite the larger pool size of xanthophyll cycle pigments in fully sun-exposed leaves, both total non-photochemical quenching, qN, and "energy-dependent" quenching, qE, which is known to depend on the presence of Zx and a high trans-thylakoid proton gradient (Demmig et al., 1987; Thiele and Krause, 1994; Horton et al., 1996), were not different between the two treatments. Stern-Volmer type quenching parameters (see Thiele et al., 1997; Krause and Jahns, 2003, 2004) of leaves grown under "sun" or "shaded" light conditions were, respectively, qN(sun) = 3.02 ± 0.58; qN(shaded) = 3.27 ± 0.53; qE(sun) = 2.14 ± 0.35; qE(shaded) = 2.28 ± 0.36 (n = 4; leaves from different plants).

The level of α-tocopherol, an antioxidant in the thylakoid membranes (Havaux et al., 2003), was significantly increased in fully sun-exposed compared to partially shaded leaves (PFD of shading threshold, 1200 µmol photons m^{-2} s^{-1}) of *C. longifolium* (Table **3**).

The contents of UV-B absorbing compounds in *C. longifolium* leaves, assessed from the relative absorbance at 305 nm (A_{305}), were close to the level of sun leaves from other species (cf. Krause et al., 2003) at the start of the experiment (A_{305} = 13.9 ± 1.8). Levels did not change over 29 days either under full sunlight (A_{305} = 13.9 ± 1.2) or in the plants that were shaded when ambient PFD exceeded 1200 µmol photons m^{-2} s^{-1} (A_{305} = 14.3 ± 0.9; n = 4).

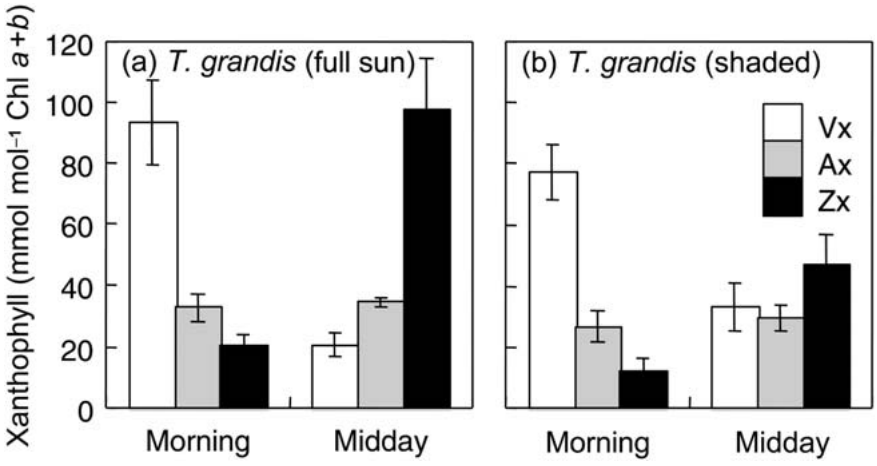

Fig. 4 Contents of xanthophyll cycle pigments in the morning and at midday in leaves of *T. grandis* after 57 d of acclimation to full sunlight (**a**) or automatic shading when PFD exceeded 1000 µmol photons m^{-2} s^{-1} (**b**). Samples were taken in the morning, before PFD rose above 50 µmol photons m^{-2} s^{-1}, and at midday when the sky was clear. Means ± SD of violaxanthin (Vx), antheraxanthin (Ax), and zeaxanthin (Zx) contents based on Chl are given (n = 3; leaves from different plants). At midday, Zx content was significantly higher in fully sun-exposed compared to partially shaded plants ($p < 0.05$). The sum of xanthophyll cycle pigments (VxAxZx) was larger in leaves of fully sun-exposed (150 ± 16 mmol mol^{-1} Chl $a+b$) than shaded plants (113 ± 14 mmol mol^{-1} Chl $a+b$) ($p < 0.01$; n = 6, morning and midday values pooled).

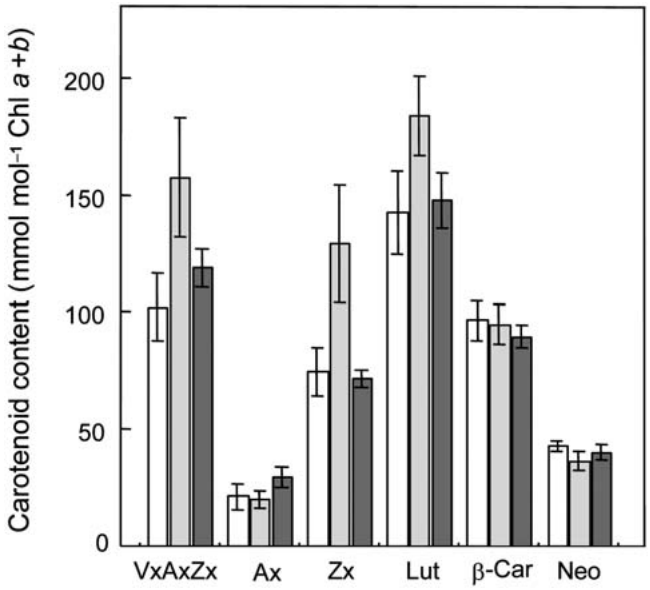

Fig. 5 Contents of carotenoids at midday under clear sky in leaves of *C. longifolium* after 120 d of acclimation to full sunlight or automatic shading (PFD threshold at 1200 µmol photons m^{-2} s^{-1}). Means ± SD of the sum of viola-, anthera-, and zeaxanthin (VxAxZx), of antheraxanthin (Ax), zeaxanthin (Zx), lutein (Lut), β-carotene (β-Car), and neoxanthin (Neo) are presented (n = 5 – 6; leaves from different plants). Columns: open, start of experiment; light grey, full sunlight; dark grey, partial shade. Differences between fully sun-exposed and partially shaded plants are significant for VxAxZx ($p < 0.05$), Zx ($p < 0.01$), and Lut ($p < 0.01$).

Table 3 Content of α-tocopherol in leaves of *C. longifolium*. Seedlings were acclimated for 123 days to full sunlight or were automatically shaded whenever PFD exceeded 1200 µmol photons m^{-2} s^{-1}. Means ± SD are given (n = 5; leaves from different plants)

Light condition	α-tocopherol (µmol m^{-2})
Full sun	79.9 ± 14.8
Shaded	60.6 ± 10.8 [a]

[a] Significant difference $p < 0.05$

Biomass accumulation and allocation

Fig. **6** shows the dry mass of *T. grandis* and *C. longifolium* seedlings acclimated to full sunlight or to 48% neutral shade above threshold PFD values of 1000 (Figs. **6a, b**), 1200 (Fig. **6c**), or 1600 µmol photons m^{-2} s^{-1} (Fig. **6d**). Total dry mass of *T. grandis* seedlings (Fig. **6a**) increased about 17-fold during the experimental period of 59 days. Total dry mass of *C. longifolium* (Figs. **6b, c**) increased about five-fold within 116 and 123 days (see Legend to Fig. **6**). Significant differences in total dry mass or in dry mass of leaves, stems, and roots between the two light conditions were not found in any of these experiments. As demonstrated for *C. longifolium* in Table **4** (threshold for shading, 1200 µmol photons m^{-2} s^{-1} PFD), leaf number, total leaf area, specific leaf area (SLA), stem height, and shoot to root biomass ratio also did not vary between plants grown under full sunlight or partial shade. No significant differences in total leaf area between the two light conditions were observed in the other experiments (data not shown).

Discussion

Under full solar radiation, mature sun leaves of the late-successional species *C. longifolium* exhibited clear effects of high-light stress, such as photoinhibition of PSII (Figs. **2b – d**) and midday depression of CO_2 assimilation (Fig. **3**). In general agreement with an earlier study of outer canopy leaves of tropical trees (Krause et al., 1995), the decline in F_v/F_m, indicating a reduction in potential PSII efficiency (see Krause and Weis, 1991), was largely or fully reversible when PFD declined in the afternoon. Chronic photoinhibition of PSII was either absent or observed at a low degree only, in agreement with a previous study of tropical tree seedlings (Castro et al., 1995). The fast-growing early-successional species *T. grandis* showed less PSII photoinhibition than *C. longifolium* when exposed to full sunlight (Fig. **2a**). In a previous study of tropical tree seedlings cultivated in simulated tree-fall gaps (Krause et al., 2001), potential PSII efficiency was less affected by direct sunlight in pioneer than in late-successional species.

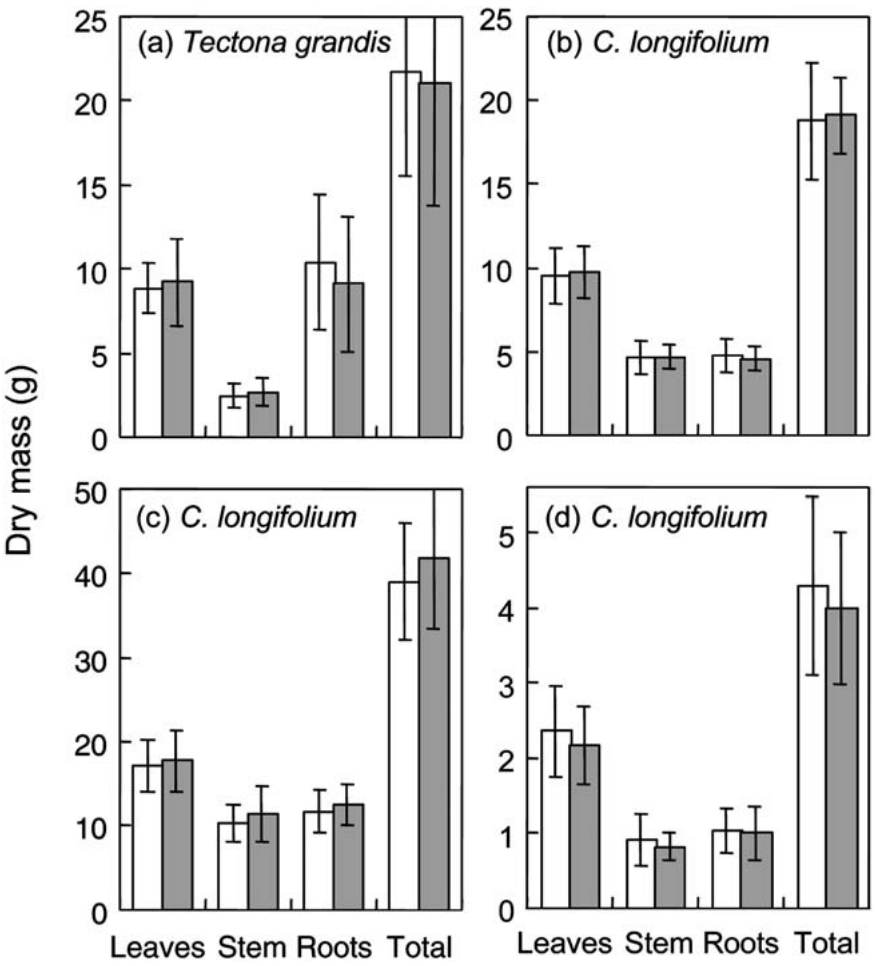

Fig. 6 Dry mass of *T. grandis* and *C. longifolium* seedlings that were either exposed continuously to full sunlight or partially shaded when ambient PFD exceeded 1000 (**a, b**), 1200 (**c**), or 1600 µmol photons m^{-2} s^{-1} (**d**). Periods of acclimation to the respective light conditions were 59 d (**a**), 116 d (**b**), 123 d (**c**), and 100 d (**d**). Means ± SD of dry mass of leaves, stems (including leaf petioles), roots, and total dry mass are given for n = 10 plants (**a, b**) and n = 12 plants (**c, d**). Total dry mass at the start of experiments (means ± SD; n = 5–6 plants) was 1.24 ± 0.20 (**a**), 3.55 ± 0.35 (**b**), and 7.44 ± 1.06 g (**c**). In the experiment shown in **d**, seedlings were subjected to the respective light conditions starting from germination. Open columns, full sunlight; grey columns, partial shade. No significant differences between fully sun-exposed and partially shaded plants were seen.

Table 4 Growth parameters of seedlings of *C. longifolium*. Seedlings were acclimated for 123 days to full sunlight or were automatically shaded whenever PFD exceeded 1200 µmol photons m^{-2} s^{-1}. Means ± SD of total leaf area, specific leaf area (SLA, total leaf area per total leaf dry mass), stem height, and shoot/root dry mass ratio are presented (n = 12 plants)

	Full sun	Shaded
Leaf number	20.8 ± 2.8	20.2 ± 2.5
Total leaf area (cm^2)	1366 ± 214	1367 ± 255
SLA (cm^2 g^{-1})	80.3 ± 4.7	77.4 ± 3.9
Stem height (cm)	53.5 ± 5.5	52.8 ± 6.6
Shoot/root ratio (g g^{-1})	2.40 ± 0.51	2.34 ± 0.42

A decline in potential PSII efficiency is known to affect the light-saturated capacity of CO_2 assimilation (A_{max}) less readily than photon yield (Long et al., 1994). Our data do not allow a determination as to whether the reduction in PSII photochemistry was partly responsible for the midday depression of net CO_2 uptake occurring in highly excessive light. There was no close correlation between the decline in F_v/F_m and the depression of CO_2 uptake around midday in leaves of *C. longifolium*. During the midday depression (Fig. **3**), reduced conductance and lowered calculated intercellular CO_2 concentration (c_i) were observed as a tendency only. Owing to the considerable fluctuations of PFD caused by clouds from day to day and during all days of measurements, we did not attempt to study in detail the contributions of stomatal and non-stomatal components to the midday depression (cf. Demmig-Adams et al., 1989; Muraoka et al., 2000; Franco and Lüttge, 2002; Haldimann and Feller, 2004; Nicolás et al., 2005).

Partial (48%) shading of the plants above certain thresholds of ambient PFD to selectively reduce the amount of excess light received by the leaves (Fig. **1**, Table **1**) strongly diminished both photoinhibition of PSII (Fig. **2**) and midday depression of CO_2 uptake (Fig. **3**). However, shading had little or no effect on A_{max} and photon use efficiency of CO_2 assimilation measured under controlled conditions in the absence of high-light stress. In only one experiment (Table **2**) was an impact on photon yield and photosynthetic capacity observed: full sun exposure of *C. longifolium* in comparison with partial shading reduced A_{max} by about 20% and transiently affected photon use efficiency.

Long-term exposure to full solar irradiance resulted in strengthened photoprotection. This is obvious from greater pool sizes of xanthophyll cycle pigments, higher Zx levels at midday (in leaves of *C. longifolium* and *T. grandis*; Figs. **4, 5**), and increased levels of α-tocopherol (in *C. longifolium,* Table **3**),

as compared to partially shaded plants. Only when the shading threshold for *C. longifolium* was set high (PFD 1600 µmol m^{-2} s^{-1}) was an equally large pool of xanthophyll cycle pigments found in fully exposed and partially shaded plants (data not shown). This was probably an acclimative response to strong light stress also experienced by the shaded plants in the morning and afternoon, when PFD was below but close to 1600 µmol photons m^{-2} s^{-1}.

The high pool size of xanthophyll cycle pigments in the fully sun-exposed compared to partially shaded leaves did not result in a higher capacity of total non-photochemical fluorescence quenching, qN, or "energy-dependent" quenching, qE, recorded under laboratory conditions. Obviously, the amount of Zx formed under high-light was sufficient or, in the case of full sun exposure, in excess of saturation of those quenching parameters, indicating thermal dissipation of absorbed photon energy. Presumably, part of the Zx present around midday in fully sun-exposed leaves is not bound to the light-harvesting complexes of the photosystems, but resides freely in the lipid phase of the thylakoid membrane where it exerts a general photoprotective antioxidative function (cf. Havaux, 1998). Such a function can also be assumed for the increased level of Lut found in fully sun-exposed leaves of *C. longifolium*.

There is ample evidence that α-tocopherol, which counteracts lipid peroxidation, is an effective antioxidant in the thylakoid membranes (Havaux et al., 2003; García-Plazaola et al., 2004). However, it has been reported that α-tocopherol accumulates in many species as leaves age (García-Plazaola et al., 2003; Hansen et al., 2003). In these leaves, α-tocopherol may be largely located outside the thylakoids, in plastoglobuli (Tevini and Steinmüller, 1985), and may not be involved directly in photoprotection. In the present study, relatively young, recently fully expanded leaves of similar age were analysed, and the increased level of α-tocopherol found in fully sun-exposed leaves (Table **3**) presumably represents an acclimation to high-light stress.

The complete absence of significant differences in biomass accumulation and growth between plants cultivated under full sun and partially shaded conditions (Fig. **6**, Table **4**) was unexpected. Enhanced biomass production and growth would have been expected from the relief of high-light stress, particularly for seedlings of *C. longifolium* shaded above PFD thresholds of 1000 or 1200 µmol photons m^{-2} s^{-1} (Figs. **2 b, c, 3**). However, the data show that the seedlings growing under full and frequently excessive solar radiation were capable of compensating for any losses of carbon gain and costs of strengthened photoprotection at the level of the whole plant. Growth limitation by lack of nutrients and restricted root expansion was avoided by using fertile soil and large pot sizes for seedling culture. We cannot rule out that beneficial effects of the automatic shading treatment on carbon gain in the upper, most exposed leaves have been partly offset by reduced photosynthesis in older leaves shaded by younger ones or by shading due to unfavourable leaf angles. However, seedlings did not develop dense crowns during the course of these experiments, and their leaves tended to be oriented horizontally. Further experiments are in progress to determine whether biomass accumulation is affected by excess light in species with a lower capacity for high-light acclimation.

Consistent with our results, in a study of *Picea engelmannii* seedlings grown under 100% compared to 33% of full sunlight, McKinnon and Mitchell (2003) observed a reduction in potential PSII efficiency (F_v/F_m) and higher levels of xanthophyll cycle pigments, Lut, and β-Car, indicating adjustment of photoprotection, whereas no effects on biomass accumulation were seen. Similarly, for leaves of *Quercus crispula* seedlings, Matsuki et al. (2003) reported lower A_{max} and F_v/F_m values and a higher de-epoxidation state of xanthophyll cycle pigments at midday under full sun than under shaded (10% of sunlight) conditions; but the authors did not find a difference in dry mass accumulation over 5 months of growth. Thus, present evidence does not support the assumption that full solar radiation, except when combined with low-temperature stress (see "Introduction"), negatively affects biomass productivity in sun-acclimated plants. Our data are in general agreement with findings of Adams et al. (2005), who reported that, in photoinhibited leaves of *Vinca minor* and *Monstera deliciosa*, contents of carbohydrates such as sugars and starch were increased. This supports the view discussed by Adams et al. (2005) and suggested by earlier studies (e.g., Demmig-Adams et al., 1995; Demmig-Adams and Adams, 1996; Krause et al., 1995; Thiele et al., 1996; Adams et al., 2002) that photoinhibition largely represents a regulatory phenomenon preventing severe leaf damage, rather than a destructive process.

In conclusion, the present study of tree seedlings, cultivated either under full sun or partial shade, showed that shading ameliorated adverse effects of high-light stress and diminished the need for the build-up of photoprotective capacity, but did not enhance dry mass production. Obviously, complex regulatory and compensatory processes in the whole plant were capable of achieving a homeostatic growth rate under these contrasting environmental conditions.

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