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Photoinhibition in seedlings of *Fraxinus* and *Fagus* under natural light conditions: implications for forest regeneration?

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Abstract Ash (*Fraxinus excelsior* L.) and beech (*Fagus sylvatica* L.) seedlings were grown in the field under three levels of natural light: (1) *open*, (2) *gap* and (3) *shade*. Light acclimation of photosynthesis was characterized by means of modulated chlorophyll *a* fluorescence of intact leaves and growth parameters were measured at the end of the growing season. Measurements of maximum photochemical efficiency (F_v/F_m) of dark-adapted leaves at intervals through the day showed that ash had a higher F_v/F_m than beech in open and gap plots but not in shade plots. This indicated a larger build-up of photoinhibition in beech under gap and open conditions. Steady-state light response curves of the operating efficiency of PSII (F'_q/F'_m), the electron transport rate (ETR) and the photochemical efficiency factor (F'_q/F'_v) showed greater variability across light treatments in ash than in beech. Both species exhibited similar responses of non-photochemical quenching (NPQ) to light. When the data were normalized to the mean maximum irradiance in the growth environment, all photochemical parameters showed a reduction in variation across treatments, indicating that light acclimation in the two species occurred primarily through adjustments in rates of photochemistry. Adjustments in thermal heat dissipation were small in both species. This pattern was stronger in ash, suggesting a greater degree of phenotypic plasticity in photosynthetic capacity in this earlier successional species. Contrary to

our expectations, the build-up of photoinhibition in beech did not appear to have a negative effect on total biomass accumulation relative to ash.

Keywords Gaps · Growth · Light acclimation · Modulated chlorophyll fluorescence · Phenotypic plasticity

Abbreviations ETR: Electron transport rate · F_m : Maximal fluorescence in the dark-adapted state · F_o : Minimal fluorescence in the dark-adapted state · F_s : Steady-state fluorescence in actinic light · $F_v = F_m - F_o$: Variable fluorescence in the dark-adapted state · F_v/F_m : Maximum photochemical efficiency of photosystem II in the dark-adapted state · F'_m : Maximal fluorescence in actinic light · F'_o : Minimal fluorescence in actinic light · $F'_v = F'_m - F'_o$: Variable fluorescence in actinic light · $F'_q = F'_m - F'_s$; F'_q/F'_m : Operating efficiency of photosystem II in actinic light · F'_q/F'_v : Efficiency factor of PSII photochemistry (also referred to as *qP*—photochemical quenching) · F'_v/F'_m : Maximum efficiency of PSII under actinic light if all reaction centres were open · NPQ: Stern-Volmer non-photochemical quenching · PPFD: Photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) refers to photosynthetically active irradiance measured with a cosine-corrected quantum sensor · PPFFR: Photosynthetic photon flux fluence rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) refers to photosynthetically active irradiance measured with a spherical quantum sensor. Fluorescence nomenclature follows Oxborough and Baker (2000).

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Introduction

The death of a tree in the forest canopy creates a gap and allows light to reach the forest floor, making way for the establishment and growth of a new generation of trees. However, this increase in light intensity can stress otherwise low-light adapted plants (Mulkey and Pearcy 1992; Lovelock et al. 1994; Krause and Winter 1996; Naidu and DeLucia 1997). The light environment in a gap

is also characterized by large amplitudes in intensity through the course of a day, another potential stress factor in shade-adapted seedlings (Percy 1994; Külheim et al. 2002). The time required and the capacity for full physiological and morphological acclimation to new light conditions differs between species (Strauss-Debenedetti and Bazzaz 1991; Lovelock et al. 1994; Percy 1994; Naidu and DeLucia 1997). Which tree species reaches the upper canopy first is ultimately determined by its ability to optimize use of the increase in light and other resources (i.e. water, nutrients) for growth in spite of the stresses an abundance of these same resources can bear.

In order to minimize the potential damage excess light can cause to the photosynthetic apparatus, plants have developed a number of non-photochemical pathways which remove this excess energy as heat. These pathways can be distinguished by the amount of time required for their subsequent relaxation upon returning to low light. Trans-thylakoid Δ pH-dependent quenching accounts for 80% of non-photochemical quenching (NPQ) (Li et al. 2000) and works by switching the antenna from a state of energy funneling into the reaction centre to one of thermal energy dissipation (Horton et al. 1996). This “fast-relaxing” component of NPQ is rapidly reversible and is associated with the build-up of zeaxanthin and antheraxanthin which increase the efficiency of the process (Björkman and Demmig-Adams 1994). The capacity for rapid energy-dissipation has been shown to decrease with increasing shade tolerance in 22 common British plant species, suggesting that a species’ capacity for NPQ is of adaptive significance (Johnson et al. 1993; see also Külheim et al. 2002). If the fast component of NPQ is insufficient, plants may experience the build-up of a slow-relaxing component. If it remains from day to day, this slow-relaxing component is referred to as *chronic photoinhibition*, and has been proposed to stem from the retention of zeaxanthin in the antenna (Demmig-Adams et al. 1998) or damage to the D1 protein of photosystem II (PSII) followed by either a period of break-down and repair (Osmond 1994) or retention of non-functional PSII to act as energy quenchers (Öquist et al. 1992a). Regardless of the mechanism, the ultimate effect of photoinhibition is a reduction in the maximum quantum yield of the leaf until recovery.

Chlorophyll fluorescence is a practical and widely used method for investigating the responses of PSII to changes in the environment. The light response of various fluorescence parameters tells us something about how plants acclimate to variation in light intensity in their growth environment. Reduction in the maximum efficiency of PSII photochemistry in the dark-adapted state (F_v/F_m) is an excellent indicator of photoinhibition in the leaf (Björkman and Demmig 1987; Öquist et al. 1992b). The operating efficiency of PSII (F'_q/F'_m) is the net photochemical yield of PSII under actinic light, when some reaction centres are reduced and NPQ is activated. F'_q/F'_m is the product of the maximum efficiency (F_v/F'_m) and the efficiency factor (F'_q/F'_v). It has been shown to be linearly correlated to the overall rate of CO_2 -assimilation by the

leaf (Genty et al. 1989). F'_v/F'_m is primarily influenced by non-photochemical processes and has indeed been used as a direct measure of thermal heat dissipation (Demmig-Adams et al. 1996). A leaf’s capacity for NPQ is, however, more often quantified by the Stern-Volmer NPQ. F'_q/F'_v , also referred to as photochemical quenching or qP , is primarily determined by the rate of photochemistry in the leaf and is non-linearly related to the proportion of open reaction centres, because this relationship is significantly influenced by connectivity between reaction centres (Govindjee 1995; Maxwell and Johnson 2000; Rosenqvist and van Kooten 2003).

Plant growth is determined by the efficiency with which light energy is converted into dry matter. Since most photosynthesis in forests occurs under light-limited conditions, ultimately controlled by the quantum yield of photosynthesis, processes which act to reduce the quantum yield should tend to reduce total biomass production (Ort and Baker 1988). Photoinhibition resulting from prolonged exposure to light much in excess of that used by the plant measurably reduces quantum yield and may therefore be expected to reduce overall plant growth (Ort and Baker 1988; Ögren and Sjöström 1990; Long et al. 1994). However, the idea that photoinhibitory damage to the system and subsequent repair reduces growth is based on the assumption that the costs of repairing damage are larger than the costs of mechanisms which help the plant avoid photoinhibition. We feel it is unclear whether this is indeed the case in all environments.

We hypothesize that light can be stressful in gaps in natural, temperate, deciduous forests and that differences among species in the degree to which light is stressful plays a role in determining the growth strategies of different co-occurring deciduous tree species. European beech (*Fagus sylvatica* L.) is the most important deciduous tree species in the cool-temperate deciduous forests of central and northern Europe. It is characterized by a remarkable dominance and competitive force due to its high shade tolerance, dark understorey, longevity and a wide range in climatic tolerances (Jahn 1991). Common ash (*Fraxinus excelsior* L.) is a common deciduous tree species found throughout the climatic range of beech and is often a major component of cool-temperate beech forests on mesic calcareous soils with ample water supply (Jahn 1991). When ash and beech are the dominant species in a stand, ash is typically more successful at invading and filling a gap than beech (Emborg et al. 1996; Diekmann et al. 1999). Not surprisingly ash is characterized as an early-to-intermediate successional species which rapidly becomes shade-intolerant with increasing size, while beech is a shade-tolerant, climax species (Emborg et al. 1996; Møller and Staun 2001). Differences between the ability of ash and beech to acclimate to periods of high light may in part explain the early success of ash over beech in a newly formed gap. In the present study, we seek to answer the following questions: (1) Do ash and beech have different capacities for photosynthetic acclimation to light and are there differences in their mode of acclimation (photochemical vs. non-photochemical)? (2) Does beech expe-

rience a greater degree of photoinhibition than ash under gap-like and open field light conditions? and (3) If so, does photoinhibition have consequences for resource allocation to growth, thereby playing a role in the early competitive balance between the species in a forest gap?

Materials and methods

Study site and plants

One-year-old dormant seedlings of *F. excelsior* (N.E. German provenance) and *F. sylvatica* (Danish provenance) were transplanted from an open field (Danish Forest Seed Centre, Humlebæk, Denmark) to 2-l pots at the Arboretum, Hørsholm, Denmark (55° 52'N, 12°30'E) in early April 2002. A soil mixture of 80% peat, 16% LECA (light expanded clay aggregate, Dansk Leca, Randers, Denmark) and 4% clay was used. Each pot received an OSMOCOTE Plus Tablet slow-release fertilizer (15-4-10 NPK, 8–9 months). Seedlings were sorted into groups of tall, intermediate and short and seedlings intermediate in height only were placed randomly in either of two replicate blocks under the three light treatments before bud-burst (6 May). Seedlings were watered manually as needed throughout the experiment.

Light treatments and measurement

The three light treatments were attained using semi-natural canopy cover at the Arboretum. High light seedlings were placed on an open field (*open*), seedlings receiving variable light were placed in a small stand of *Quercus robur* L. (English oak) trees under a small canopy gap (*gap*) and full shade seedlings were placed under a closed beech canopy, receiving relatively few sunflecks (*shade*). Seedlings in one of the two shade blocks did, however, receive increased amounts of light for a period of about 10 days after a tree fell and a gap was formed just above the block. This occurred on 4 August and the plot was moved to a position under closed canopy again on 13 August. Nevertheless, both shade plots were probably slightly influenced by the presence of this gap for the remainder of the study.

Light was monitored in the field from 7 June to 6 September using gallium arsenide phosphide photodiodes (G1126-02, Schottky, Hamamatsu Photonics, Japan) placed inside table tennis balls to produce inexpensive spherical sensors for photosynthetically active irradiance. Spherical irradiance is measured as photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$). When compared with a cosine-corrected sensor, a spherical sensor gives a better estimate of the total photosynthetically active irradiance received by 3D objects such as whole plants, shoots or bent and wrinkled leaves. Use of spherical sensors also eliminates the need for subjective pointing of cosine-corrected sensors towards the major source of light (which can change in position over a day). Sensors were calibrated against a LI-COR quantum sensor (LI-190SA, LI-COR, Lincoln, Neb., USA) placed at the back of a black box with an opening at the opposite end to allow direct sunlight but little sky light to shine on the two sensors simultaneously. Thus calibrated, spherical sensors give total amount of light intercepted per unit projected area of the sphere. The spherical sensor often gives significantly higher values of irradiance than would be measured by a cosine-corrected sensor, showing that the cosine-corrected sensor underestimates the amount of irradiance available to plants in the field. Two spherical sensors were placed in each of the two open and two shade plots and four sensors in each of the two gap plots. PPFD was logged every 5 s (every 10 s after 1 August due to technical difficulties) and the 10 min average, maximum and minimum were stored in a datalogger (DL2, Delta-T Devices, Cambridge, UK).

In contrast to the above, photosynthetically active irradiance (photosynthetic photon flux density, PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was

measured during all fluorescence measurements (see following section) using a cosine-corrected sensor adjacent to the upper leaf surface. Since a single light source was used in the laboratory (see following section) use of a spherical sensor instead of the cosine-corrected sensor built into the instrument would have given 13% more irradiance based on the cosine law and the angle of the lamp (provided corrections were made for the colour of the light).

Chlorophyll fluorescence in the field

Following the fluorescence nomenclature proposed by Oxborough and Baker (2000; see also Rosenqvist and van Kooten 2003), photosystem II (PSII) operating efficiency (F'_q/F'_m), electron transport rate (ETR) and dark-adapted maximum photochemical efficiency (F_v/F_m) were measured at 2–3 h intervals from before sunrise to after sunset on 30 July and 20 August using a pulse-amplitude modulated photosynthesis yield analyzer (Mini-PAM, Heinz-Walz, Effeltrich, Germany); 30 July was characterized by hazy but otherwise bright weather conditions and 20 August was clear and sunny (K.S. Einhorn, personal observation). The following measuring procedure was used on all leaves: F'_q/F'_m , leaf temperature and PPFD (used to calculate ETR) at the leaf surface were measured on an upper, exposed and fully developed leaf (using the 2030-B leaf clip holder, H. Walz, Effeltrich, see Bilger et al. 1995), where after the leaf was dark-adapted for 30 min (using a DLC-8 leaf clip, H. Walz, Effeltrich) and F_v/F_m was measured. This was done for each of five fully expanded, mature leaves for each species for each plot in each treatment, giving ten measurements per species per treatment. Sampling was repeated on the same leaves throughout the day. Values of F_v/F_m below approximately 0.8 indicate photoinhibition which is not reversible within 30 min of dark-adaptation.

Steady-state light response of chlorophyll fluorescence

Field measurements were supplemented with steady-state light response curves made in the laboratory from 26 June to 4 September. This allowed us to investigate the response to light with a variety of chlorophyll fluorescence parameters. Light response curves were made on seedlings taken directly into the laboratory from field conditions, alternating between which species was measured in the morning and which in the afternoon. All curves were made at room temperature using the Mini-PAM and a halogen lamp (Philips, Halogen Dichroic, 20 W 12 V) for actinic light. All leaves were flushed with humidified, CO₂-stable air during measurement. Seedlings were dark-adapted for 30 min prior to measuring the light curve to obtain minimum (F_o) and maximum (F_m) dark-adapted fluorescence. All curves were measured from the lowest light level and up, allowing the leaf to reach steady-state before changing to a new light level. Saturating flashes 0.8 s in duration were applied every minute.

The following fluorescence parameters were calculated: operating efficiency of photosystem II (F'_q/F'_m), ETR, efficiency factor (F'_q/F'_v), also termed qP , maximum quantum efficiency of PSII (F'_v/F'_m), and Stern-Volmer NPQ. Parameters were calculated as follows: the operating efficiency of PSII, $F'_q/F'_m = F'_m - F'_s / F'_m$ (Genty et al. 1989); the efficiency factor, $F'_q/F'_v = (F'_m - F'_s) / (F'_m - F'_o)$ (Dietz et al. 1985); Stern-Volmer NPQ = $(F'_m - F'_m) / F'_m$ (Bilger and Björkman 1990); and electron transport rate, $\text{ETR} = F'_q/F'_v \times \text{PPFD} \times 0.5 \times 0.84$ (Demmig and Björkman 1987; Krall and Edwards 1992). A standard leaf absorbance value of 0.84 was used, since the true leaf absorbance could not be measured. Leaf absorbance has been found to vary relatively little (0.8–0.9) across the wide range of leaf chlorophyll concentrations that are typical for both sun and shade leaves of different species (Gabrielsen 1948; Osborne and Raven 1986). Errors in calculated ETR are therefore not expected to exceed 10% as a result of variation in absorbance among species and light treatments. To determine F'_o , the formula presented by Oxborough and Baker (1997) was used.

Growth parameters

All seedlings were harvested in the 2nd week of September. Leaf area, stem diameter at base, main stem length, and leaf number were measured. Main stem length was measured as the length of the stem from the top of the soil to just below the terminal bud, and used as an indirect measure of seedling height when comparing within a species. Lengths of lateral branches were not included in this measure. Seedlings were dried at 70°C for at least 48 h and dry weight of leaves, stems (including lateral branches) and roots was determined.

Data analysis and curve fitting

All figures show means \pm 1 standard error of the mean of ten and five seedlings for diurnal and steady-state measurements, respectively. Diurnal fluorescence, leaf temperature, F_v/F_m at the beginning of each light curve and growth data were analyzed using the general linear model procedure (Proc GLM) in SAS (Version 8.2, SAS Institute, Cary, N.C., USA), with light treatment, species and their interaction as model parameters. Nine pairwise comparisons were made on species within light treatment and on light treatment within species using the sequential Bonferroni method to correct the P -values given by SAS least square means for total test number (Holm 1979; Rice 1988).

Curve fitting of steady-state, light-response data was made using Proc NLIN in SAS to find the model which gave the best, least-biased fit of the data (based on residual plots). F -tests of the model residuals were used to test for effects of treatment and species on each fluorescence parameter using the method of regression comparison described by Mead et al. (2003). Comparing response curves in this way one cannot detect effects of the interaction between treatment and species. The light response of ETR was modeled using the convexity equation of Prioul and Chartier (1977) as given in Leverenz (1987).

Results

Light treatments

The pattern of PPFFR over the course of a sunny day (29 July) in open, gap and shaded plots is shown in Fig. 1. On days with clear skies, open plants experienced stable light conditions while gap plants experienced a large amplitude in PPFFR over time and a lower daily maximum PPFFR. Shade plants experienced low light with very few sunflecks. On partly cloudy days, open plants also experienced variable light conditions and on overcast days, all treatments experienced relatively stable light conditions through the day (data not shown). The total average daily PPFFR across the season was 53.9 ± 2.1 , 10.9 ± 0.4 and 0.7 ± 0.1 mol m⁻² day⁻¹ for open, gap and shade plots, respectively. The two gap blocks proved to be slightly different in total light dose: 13.4 ± 0.6 and 8.3 ± 0.3 mol m⁻² day⁻¹. These data were pooled nonetheless. The maximum 10 min average PPFFR experienced in each treatment was $2,888 \pm 32$, $1,950 \pm 32$ and 443 ± 188 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for open, gap and shade plots, respectively. These values were used to calculate % of maximum growth irradiance (Fig. 3).

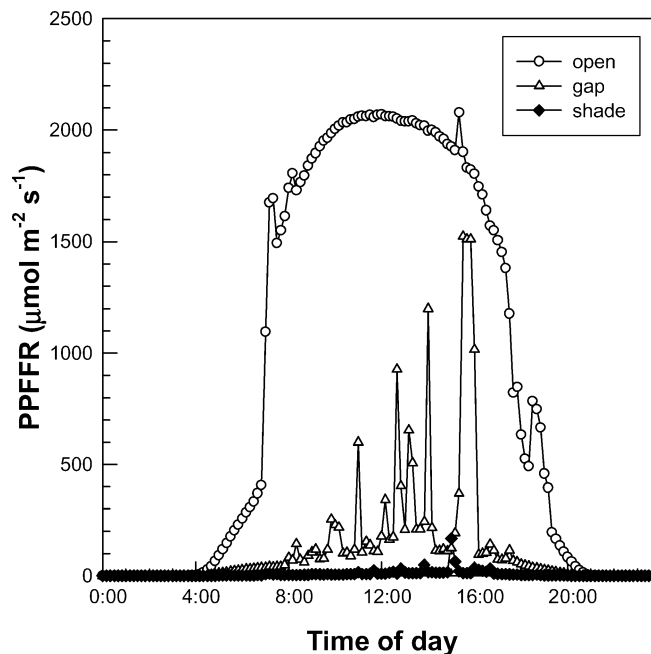


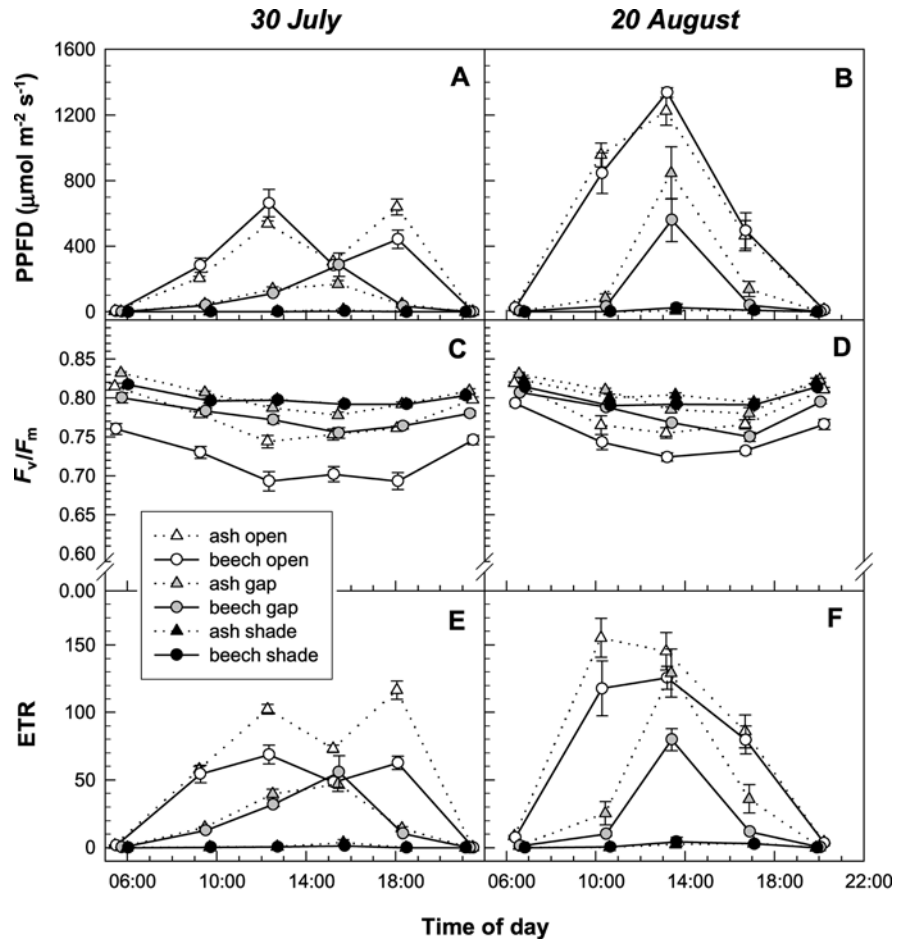
Fig. 1 Photosynthetic photon flux fluence rate (PPFFR) through the day on 29 July 2002. The data are from one sample spherical light sensor from each of the *open*, *gap* and *shade* treatments; 10 min averages of measurements made every 5 s are shown

Diurnal F_v/F_m , leaf temperature and ETR

Figure 2c, d shows the time course of F_v/F_m . For all treatment and species combinations, there was a decline in F_v/F_m towards mid-afternoon, indicating a dynamic build-up of photoinhibition in both species across all light treatments. This was followed by recovery at the end of the day as light intensity decreased (see Fig. 2a, b). The pattern of decline and recovery indicated a larger build-up of photoinhibition with increasing total light dose. The slight decline and recovery in F_v/F_m seen in the shade plants was probably caused by the few short sunflecks which, even if not very high in intensity, apparently caused a response in the very low-light adapted leaves. The response of F_v/F_m of ash and beech seedlings growing in the shade was the same throughout the day on 30 July (all P not significant in the pairwise comparisons). A difference between the species occurred in the shade treatment on 20 August, although it was only significant at 0600 and 1300 hours. This may have been associated with a tree falling over near the shaded plots in early August which increased total PPFFR in this treatment despite moving one of the plots further into the understorey.

Beech seedlings in the gap, and particularly in the open, had consistently lower maximum quantum yields than ash (all $P < 0.05$ with the exception of gap seedlings at noon on 30 July), a sign of chronic photoinhibition. F_v/F_m values higher than 0.807 were never measured for beech in the gap and open plots (pre-dawn F_v/F_m of open ash = 0.815 and 0.819, open beech = 0.760 and 0.793, gap ash = 0.832

Fig. 2 a, b Mean photosynthetic photon flux density (PPFD), c, d maximum dark-adapted quantum efficiency of photosystem II (F_v/F_m) and e, f instantaneous electron transport rate (ETR) of ash and beech seedlings grown under open, gap and shade light conditions. Measurements were taken at intervals through the day on 30 July and 20 August 2002. Points are means \pm 1 SEM of 9–10 seedlings. PPFD was measured on the leaves using the Mini-PAM leaf clip cosine-corrected quantum sensor just prior to 30 min dark adaptation



and 0.831 and gap beech = 0.800 and 0.807 on 30 July and 20 August, respectively). The 3 days preceding 30 July were particularly sunny (data for 29 July shown in Fig. 1), with almost 50% more PPFR over the day than on 30 July, and the 6 days preceding 20 August were characterized as sunny, with light levels approximately equal to those experienced on 20 August. These periods of high light may have contributed to the significant reduction in maximum quantum yield of beech seedlings.

The diurnal pattern of instantaneous ETR for all species and light treatment combinations are shown in Fig. 2e, f. There was a tendency for ETR to be lower in beech even when PPFD was higher than for ash (Fig. 2a, b). This can clearly be seen for plants growing under open conditions around midday on both sampling days.

Table 1 shows the average leaf temperatures of ash and beech seedlings just prior to dark adaptation for all light

treatments across the day. The maximum leaf temperature recorded for a single leaf is also noted. Leaf temperatures tended to be slightly higher on 20 August than 30 July ($P=0.0877$). No differences were seen in leaf temperatures among light treatments or species (all P not significant).

Steady-state light response curves

Operating efficiencies (F'_q/F'_m) were higher in ash than in beech from the gap and open light treatments, but lower in the shade (Fig. 3a). Both the effects of species and light treatment on F'_q/F'_m were significant (effect of species $F_{9, 211} = 11.82$; $P < 0.0001$; effect of treatment $F_{12, 211} = 49.69$; $P < 0.0001$). Not surprisingly, this pattern was also reflected in ETR, since this parameter is calculated directly from F'_q/F'_m (effect of species $F_{9, 211} = 8.74$; $P < 0.0001$;

Table 1 Mean \pm 1 SEM (and maximum) leaf temperature ($^{\circ}$ C) experienced throughout the day by ash (*F. excelsior*) and beech (*F. sylvatica*). Seedlings grown under open, gap and shade light

	Open		Gap		Shade	
	Ash	Beech	Ash	Beech	Ash	Beech
30 July	22.3 \pm 0.52 (28.3)	22.6 \pm 0.55 (29.6)	22.8 \pm 0.41 (26.3)	23.0 \pm 0.42 (28.4)	22.6 \pm 0.35 (26.0)	22.8 \pm 0.34 (26.4)
20 August	23.3 \pm 0.60 (28.8)	23.2 \pm 0.64 (29.7)	23.4 \pm 0.54 (30.9)	23.0 \pm 0.46 (30.6)	22.9 \pm 0.38 (26.4)	23.1 \pm 0.35 (26.5)

conditions. Leaf temperature was measured just prior to dark adaptation using the Mini-PAM leaf clip leaf temperature sensor

effect of treatment $F_{13, 211}=32.43$; $P<0.0001$; Fig. 3c). Shade plants of both species showed significantly lower F'_q/F'_m with increasing light than open and gap plants (Fig. 3a). The same pattern was seen for ETR. The maximum rate of electron transport (or minimum operating efficiency of PSII) for open and gap plants was nearly identical for both species. The variation in specific leaf area (SLA) among light treatments at the end of the

growing season (Table 2) showed that a morphological acclimation occurred in response to increased light dose from gap to open light. This occurred despite the similar response curves per unit leaf area seen in open and gap plants of both species.

Open-grown ash and beech had lower F'_q/F'_m at PPFD = 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ than all other species-treatment combinations (Fig. 3a; $P<0.0001$). This was most

Fig. 3a–j Steady-state light response curves of **a, b** the operating efficiency (F'_q/F'_m), **c, d** the electron transport rate (ETR), **e, f** the efficiency factor (F'_q/F'_v), **g, h** the maximum efficiency (F'_v/F'_m) and **i, j** non-photochemical quenching (NPQ) plotted against absolute measuring PPFD and measuring irradiance (PPFD) as a percent of maximum growth irradiance experienced in the field (PPFFR). Symbols are means \pm 1 SEM ($n=5$) of ash and beech grown under *open*, *gap* and *shade* treatments. Symbols same as in Fig. 2

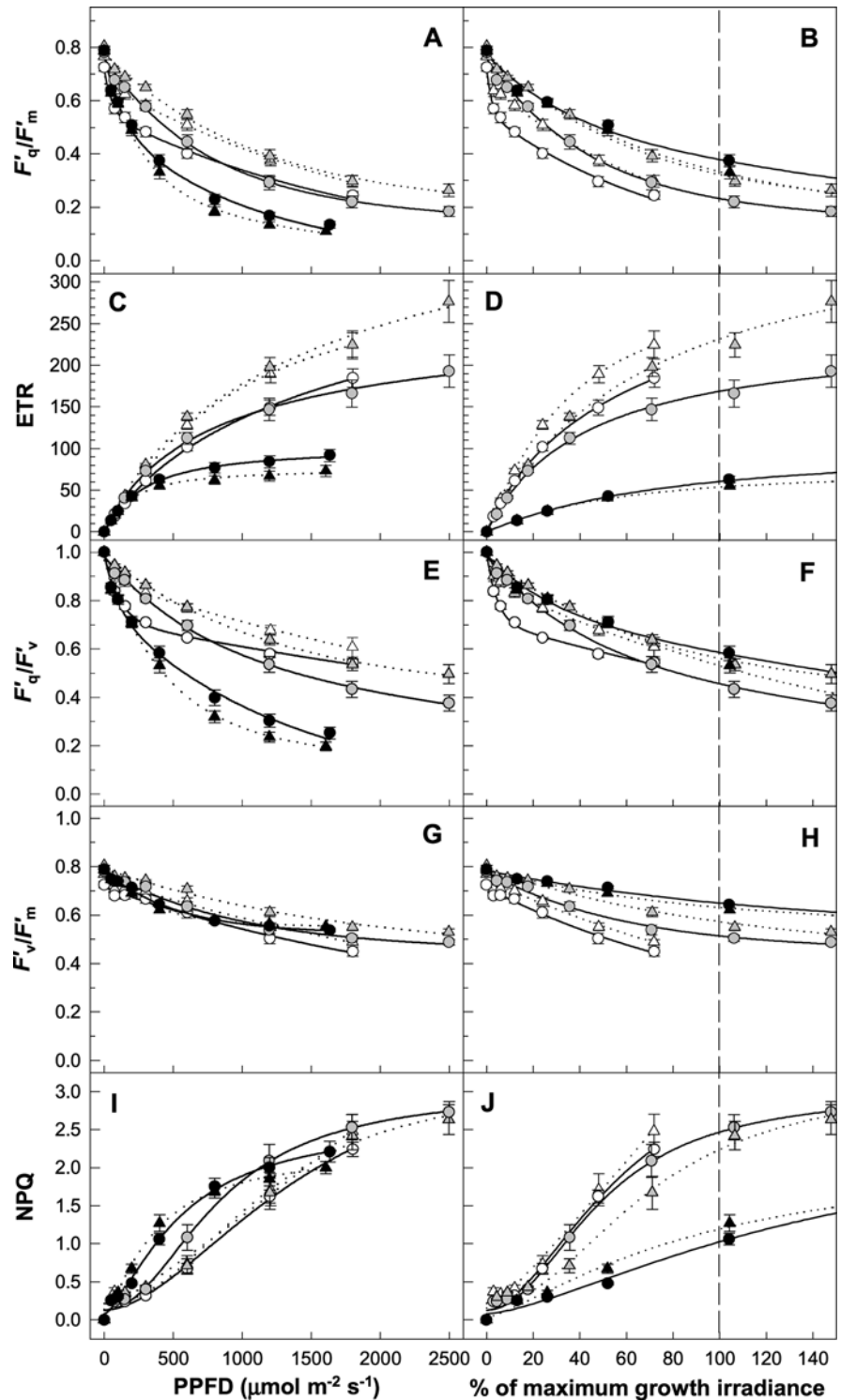


Table 2 Mean values for growth parameters at the end of the growing season of ash (*F. excelsior*) and beech (*F. sylvatica*). Seedlings grown under open, gap and shade light conditions

	Open		Gap		Shade		P-values		
	Ash	Beech	Ash	Beech	Ash	Beech	Light	Species	Interaction
Leaf area (cm ²)	1114.01	755.41	1016.96	383.06	265.87	97.24	<0.0001	<0.0001	0.0003
Leaf number	24.1	72.6	17.1	48.1	9.8	16.0	<0.0001	<0.0001	<0.0001
Specific leaf area (cm ² g ⁻¹)	217.3	131.1	494.9	192.0	781.4	377.6	<0.0001	<0.0001	0.0277
Leaf area ratio (cm ² g ⁻¹)	36.1	23.7	69.8	28.5	54.7	20.5	<0.0001	<0.0001	0.0061
Root: shoot ratio (g g ⁻¹)	1.03	0.87	0.87	0.84	1.11	0.95	0.0546	0.2924	0.6086
Main stem length (mm)	461.4	500.4	447.4	364.4	376.3	304.1	<0.0001	0.0466	0.0030
Stem diameter at base (mm)	14.7	10.7	10.9	8.2	8.2	6.3	<0.0001	<0.0001	0.3417
Leaf dry weight (g)	5.7	6.9	2.9	2.7	0.4	0.4	<0.0001	0.1245	0.0652
Stem dry weight (g)	11.4	12.9	7.2	6.3	2.3	2.3	<0.0001	0.7830	0.3739
Root dry weight (g)	17.1	16.3	8.1	6.7	2.8	2.4	<0.0001	0.2304	0.8080
Total dry weight (g)	34.3	36.1	18.2	15.6	5.5	5.2	<0.0001	0.3763	0.5215

prevalent in open-grown beech. This indicated the presence of photoinhibition in open seedlings at the start of the measurement of steady-state curves. This confirmed the measurements made on 30 July and 20 August (Fig. 2) showing chronic photoinhibition in seedlings, particularly in beech exposed to open light conditions. Open plants of both species showed a more rapid initial decline in operating efficiency where after the curves flattened out giving no considerable difference between operating efficiency of gap and open plants at higher PPFD.

The efficiency factor (F'_q/F'_v), which is one of the components of F'_q/F'_m and thus ETR, showed a similar response to growth light as F'_q/F'_m and ETR (Fig. 3e). Variation in F'_q/F'_v was significantly different among species and light treatments (effect of species $F_{12, 205} = 7.83$; $P < 0.0001$; effect of treatment $F_{16, 205} = 64.20$; $P < 0.0001$). Shade plants of both species showed the greatest reduction of the system (lowest F'_q/F'_v) with increasing light. Open- and gap-grown beech seedlings had a lower efficiency factor with increasing PPFD than open- and gap-grown ash seedlings. In general, there was more variation among treatments and species in the response curves of F'_q/F'_v than in either F'_q/F'_m or F'_v/F'_m (Fig. 3a, g respectively). This suggests that both species may have acclimated to the different growth light environments through adjustments in photochemical capacity, while the other component of F'_q/F'_m , the maximum efficiency of PSII reaction centres (F'_v/F'_m), though significantly different between species and treatments, was more stable across light environments (effect of species $F_{9, 211} = 10.29$; $P < 0.0001$; effect of treatment $F_{12, 211} = 17.83$; $P < 0.0001$). The plot of F'_q/F'_v as a function of % of maximum growth irradiance showed that both species maintained a similar range of values across growth-light environments (Fig. 3f). Ash was more successful than beech at maintaining F'_q/F'_v within the same range, regardless of environment (Fig. 3f).

Our data show no significant differences between species in the capacity for non-photochemical quenching, measured as NPQ (effect of species $F_{12, 175} = 1.63$,

$0.05 < P < 0.10$ NS; Fig. 3i). There was a significant effect of treatment which was associated with a more rapid rise in NPQ at lower PPFD in shade plants (effect of treatment $F_{16, 175} = 6.00$, $P < 0.0001$). When NPQ was plotted against % of maximum growth irradiance, the picture changed considerably (Fig. 3j). Shade plants had NPQ values much lower than the other treatments when measured within the range of light they were exposed to during growth. Under gap conditions, beech had an insignificant tendency for a higher NPQ than ash, but this was not the case in the open.

Growth

Ash had a significantly higher total leaf area than beech in all treatments and the difference was largest in the gap (Table 2). Leaf area increased significantly with increasing intensity of growth-light in beech and between shade and gap treatments in ash. Beech had a significantly greater number of leaves per seedling than ash across all treatments, but a smaller average leaf size. Ash seedlings also had a significantly higher leaf area ratio than beech in all treatments. However, the larger total leaf area in ash did not require greater total biomass, because there was no difference in total leaf dry weight between the species in any of the light treatments. Furthermore, the dry weights of stems and roots were not significantly different between the species. Both species increased total dry weight in response to increasing growth light, but there were no differences in total biomass or biomass allocation between ash and beech in any given light environment. Beech showed a significant increase in main stem length with increasing exposure to light. Only gap plants showed an effect of species ($P = 0.0371$), though caution should be used in inferring relative height of species because of differences in seedling architecture. Main stem length per stem dry weight is a measure of the length gained per unit of mass invested. Calculated as the main stem length divided by stem dry weight, we got the following values: open ash = 40.5, open beech = 38.8, gap ash = 62.1, gap

beech = 57.8, shade ash = 163.6 and shade beech = 132.2 mm g⁻¹. These values showed that increasing competition for light (increasing shade) resulted in increasing height growth per unit stem biomass within a species and that ash had a consistently higher main stem length to stem weight ratio than beech.

Discussion

Beech experiences chronic photoinhibition in the open and in forest gaps

Beech (*F. sylvatica*) and ash (*F. excelsior*) seedlings were investigated in the present study because they often co-occur in newly formed deciduous forest gaps of central and northern Europe. However, the two species exhibit very different strategies for regeneration. Ash has been called a “gap-specialist” (Emborg et al. 1996), that quickly loses its shade tolerance as it grows larger (Boysen Jensen 1929), while beech is a species known to tolerate heavy shade even as a fair-sized tree (Møller and Staun 2001). In this study, we expected ash to experience less photoinhibition in the open and in a gap than beech. We reasoned that ash might therefore allocate a greater amount of resources to total seedling biomass, while beech allocated resources to repair of damaged PSII. We therefore hypothesized that beech seedlings would have a lower total biomass accumulation relative to ash, assuming that the cost of repairing photodamage is greater than the cost of avoiding it. This might in part explain why ash is so much faster at occupying a forest gap than beech.

Beech did indeed experience chronic photoinhibition under high- and variable-light conditions in the field. This was seen as a reduction in the maximum quantum yield efficiency (F_v/F_m) at intervals through the day on two separate summer days, one sunny and one hazy (Fig. 2), as well as a low initial operating efficiency in the dark during measurements of steady-state light response curves on other days throughout the summer. F_v/F_m of beech was consistently lower than ash in the gap and open treatments. We (unpublished data) had previously seen values of F_v/F_m consistently lower in beech than in ash when growing under the same light regimes across a natural forest gap; however, it was unclear whether this pattern was attributed to a small but innate difference in F_v/F_m of the two species or to the response to the growth light environment. The current findings support the idea that differences in F_v/F_m between the species measured previously were due to different responses to the growth light environment. Furthermore, the differences in F_v/F_m between the species increased with increasing total light experienced during growth. Photoinhibition was also seen in steady-state light response curves made in the laboratory as a reduced initial operating efficiency in darkness and a larger initial drop in operating efficiency with increasing light in open-grown beech (Fig. 3a). This pattern of reduced operating efficiency of PSII at low light is consistent with previous findings that photoinhibition

affects the maximum quantum yield (Powles 1984) and the convexity of the light response curve, before affecting photosynthesis at saturating light (Leverenz et al. 1990). Shade plants are more prone to photoinhibition than sun plants (Anderson and Osmond 1987) if they are exposed to high light. This has often been attributed to a large light-harvesting antenna and lower maximum rates of photosynthesis in shade plants. Mulkey and Pearcy (1992) found that plants exposed to a combination of high light and high leaf temperatures in simulated canopy gaps experienced more severe photoinhibition than under high light alone. However, plants in their study were exposed to leaf temperatures of 40 °C, much higher than those experienced here (Table 1). It is therefore unlikely that high leaf temperatures played a measurable role in the photoinhibition seen in the present study.

A small build-up of dynamic photoinhibition was seen in both ash and beech seedlings grown under open, gap and shade light treatments as a reduction in maximum quantum yield towards midday followed by recovery as ambient light intensity declined. This could be distinguished from the chronic photoinhibition experienced particularly in open-grown beech (for a detailed discussion of chronic vs. dynamic photoinhibition, see Osmond 1994). Failure to recover by the next day could have led to an accumulation of photoinhibition over several consecutive sunny days (Krause and Winter 1996). The 3 days preceding 30 July and the week preceding 20 August were bright and sunny and could therefore have contributed to a long-term reduction in maximum quantum yield of PSII in open-grown beech. Accumulation of chronic photoinhibition can either be the result of damage to the PSII reaction centre D1 protein (Osmond et al. 1993) or of the retention of zeaxanthin and antheroxanthin which are built up in the antenna during periods of high light (Demmig-Adams et al. 1998). Slower repair of photodamage in shade-tolerant beech as compared to ash may also explain the accumulation of photoinhibition we see here (Mulkey and Pearcy 1992).

Ash shows more phenotypic plasticity of the photosynthetic apparatus

F'_q/F'_m and ETR were higher in open- and gap-grown and lower in shade-grown ash than beech (Fig. 3a, c). This indicated a higher degree of phenotypic plasticity (as defined by Valladares 2003) of the photosynthetic apparatus in ash than in beech, since operating efficiency is often linearly related to net photosynthetic rates in the leaf as long as the CO₂ supply is not affected by e.g. changes in stomatal conductance (Genty et al. 1989—though see Lovelock et al. 1994). A similar pattern was seen in the efficiency of photochemistry (F'_q/F'_v ; Fig. 3e). F'_q/F'_v was plotted against % of maximum growth irradiance to show the range of potential for photochemical quenching in the field. Both species acclimated to the ambient light conditions by maintaining the potential for photochemical quenching within a certain range of values. These findings

support those of Rosenqvist (2001) that plants normally adjust their photochemical capacity to maintain more than half of the reaction centres in an open (unreduced) state. It should be noted here that we measured growth irradiance using spherical sensors which give an upper limit for the maximum light available to the foliage. Nevertheless, our results still support the conclusions of Rosenqvist (2001) that were originally based on the use of cosine-corrected sensors for measuring maximum growth irradiance. F'_q/F'_v had a rather consistent operating range across growth light conditions. The similarity between treatments in ash was particularly striking and supports the idea that this species has a greater phenotypic plasticity of the photosynthetic apparatus. Greater phenotypic plasticity in ash is consistent with the concept that species of earlier successional and variable environments tend to show greater phenotypic plasticity of photosynthetic characters than late successional species (Bazzaz 1979; Bazzaz and Carlson 1982; Strauss-Debenedetti and Bazzaz 1991). Phenotypic plasticity in any given character acts to reduce variation in that character across environments (Saxe et al. 2001).

Photoinhibition occurs when most of the reaction centres are open

Previous studies have shown that photoinhibition occurs in plants, regardless of the light level they are acclimated to, when F'_q/F'_v falls below 0.6 (Ögren 1991; Öquist et al. 1992b; Rosenqvist 2000). Thus, photoinhibition has been reported to occur in plants even when most of the PSII reaction centres are open. Our findings support this. Beech under open and gap conditions had lower efficiency factors than ash in the field (Fig. 3f) and was clearly experiencing levels of F'_q/F'_v less than 0.6 in the field in the open and in the gap. Earlier studies have shown that beech is incapable of utilizing high light solely through increases in electron transport (Bilger et al. 1995). Thus, beech was limited by an inability to fully acclimate to the prevailing high-light conditions which ultimately led to a state of chronic photoinhibition in the field.

Resistance to photoinhibition is controlled by factors which determine the flow of photons into the reaction centre as affected by antenna size and non-radiative quenching mechanisms before energy reaches an open reaction centre, and the flow out of Q_A (Öquist et al. 1992b). Thus, a reliable way for a plant to avoid damage from excess sunlight is by acclimating the photosynthetic apparatus to process more photons through photochemistry, thereby decreasing the time spent in the reduced state (Chow 1994). Both species in this study acclimated to prevailing light conditions through adjustments in the rate of photochemistry. This is clear from the figures depicting fluorescence parameters versus % of maximum growth irradiance (Fig. 3, right-hand column). F'_q/F'_v , which is primarily determined by photochemical processes, showed little variation among growth environments under field conditions, while variation between treatments was substantial over the range of light experienced during

growth in parameters determined by non-photochemical processes, F'_q/F'_m and NPQ.

Ash and beech show the same capacity for non-photochemical energy dissipation

There may well be a trade-off between high photochemical efficiency at low light and non-photochemical protection at high light. Plants that do not experience excess light very often in the field should have a much lower NPQ in situ, since it would be wasteful to send light energy off as heat if it is a limited resource. When NPQ was plotted against % of maximum growth irradiance, we found that shade grown plants of both species operated at approximately half the NPQ of gap and open grown plants, supporting this. We found no significant effect of species on the light response of NPQ, indicating that both species have the same capacity for non-radiative heat dissipation. This is in contrast to the general trend shown by Johnson et al. (1993), however we only studied two species and the difference in shade tolerance of young ash and beech seedlings may not be that large (Emborg 1998; Møller and Staun 2001).

Non-photochemical quenching consists predominantly of rapidly reversible transthylakoid Δ pH-dependent quenching in cooperation with zeaxanthin. Our data suggest, however, that beech was in addition forced to use photoinhibition (slowly reversible quenching) to make-up for a lower maximum rate of electron transport. If this was the case, the photoinhibition seen in beech was not simply damage to the system, but rather an adaptive or regulative mechanism to deal with excess light. Photoinhibition has in fact been suggested to be a stable, long-term down-regulation of photochemistry occurring in shade species when growing under persistent high-light conditions and replaces part of the regulation usually exhibited by the transthylakoid Δ pH gradient (Öquist et al. 1992b). Öquist et al. (1992a) found that the shade plant, *Tradescantia albiflora*, growing under high light tended to retain damaged non-functional PSIIs produced by excess light instead of recycling them into new functional reaction centres. This shade plant appeared to use these non-functional PSIIs as energy quenchers, while the sun plant studied (pea) rapidly broke-down and rebuilt the PSII reaction centre into its functional form. They suggest that these results may in fact represent two strategies for dealing with excess light, a “sun-strategy” and a “shade-strategy” where the rapid recycling of PSII which requires protein synthesis is not a problem for a sun plant, where light is not limiting, while the retention of non-functional PSII in shade plants represents a cost-effectiveness more adapted to light-limited conditions (Öquist et al. 1992a). Photoinhibition has an adaptive role in protecting plants against increased light levels over prolonged time periods when down-regulation by transthylakoid Δ pH is insufficient.

Significance of photoinhibition to growth

Although photoinhibition has been shown to affect the reproductive fitness of *Arabidopsis* under dynamic light conditions (Külheim et al. 2002), photoinhibition in beech may not be detrimental, but adaptive. This is supported by the fact that our study did not show any reduction in dry matter accumulation in beech compared with ash as a consequence of higher levels of chronic photoinhibition in beech. Total carbon assimilation and dry matter accumulation may however be poor indicators of success in reaching the upper crown layer in a forest gap, due to the trade-off between height growth and crown width (Clark and Clark 2001; King 1990). It has also been suggested that measuring the significance of photoinhibition for photosynthetic production through direct measurements of growth response is unlikely to give convincing results, since the effects of photoinhibition in fully exposed leaves are probably compensated for by increased photosynthesis in other, more shaded leaves (Ögren 1994). Ash and beech seedlings exhibit very different crown morphologies; particularly in partly to deeply shaded habitats (personal observation). The effects of self-shading on photoinhibition and carbon gain in the lower parts of the crown could also have had a considerable effect on the growth of the seedlings. It is therefore difficult to make conclusions about the costs of photoinhibition repair versus avoidance and the role of photoinhibition on overall plant growth in the present study.

In the present study, the fast-growing gap specialist, ash, and the slow-growing climax species, beech, showed different capacities for photosynthetic electron transport and the ability to maintain F'_q/F'_v above 0.6, where measurable photoinhibition appears in plants. In contrast, differences in NPQ were not significant, suggesting that both species, regardless of overall growth strategy, acclimate to ambient light conditions largely through adjustments in total photochemical capacity. However, beech had a smaller range in maximum ETR which limited its ability to acclimate in this way when compared to ash. The higher degree of photochemical reduction in beech resulted in higher photoinhibition in this species. This photoinhibition did not, however, result in a measurable reduction in growth.

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References

Anderson JM, Osmond CB (1987) Shade-sun responses: compromises between acclimation and photoinhibition. In: Kyle DJ, Osmond CB, Arntzen CJ (eds) Topics in photosynthesis, photoinhibition, vol 9. Elsevier, Amsterdam, pp 1–38

- Bazzaz FA (1979) Physiological ecology of plant succession. *Annu Rev Ecol Syst* 10:351–371
- Bazzaz FA, Carlson RW (1982) Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* 54:313–316
- Bilger W, Björkman O (1990) Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*. *Photosynth Res* 25:173–185
- Bilger W, Schreiber U, Bock M (1995) Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence. *Oecologia* 102:425–432
- Björkman O, Demmig B (1987) Photon yield of O₂ evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. *Planta* 170:489–504
- Björkman O, Demmig-Adams B (1994) Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. In: Schulze ED, Caldwell MM (eds) *Ecophysiology of photosynthesis*, vol 100. Springer, Berlin Heidelberg New York, pp 17–47
- Boysen Jensen P (1929) Studier over skovtræernes forhold til lyset. *Dan Skovbrugs Tidsskr* XIV:5–31
- Chow WS (1994) Photoprotection and photoinhibitory damage. *Adv Mol Cell Biol* 10:151–196
- Clark DA, Clark DB (2001) Getting to the canopy: tree height growth in a neotropical rain forest. *Ecology* 82:1460–1472
- Demmig B, Björkman O (1987) Comparison of the effects of excessive light on chlorophyll fluorescence (77 K) and photon yield of O₂ evolution in leaves of higher plants. *Planta* 171:171–184
- Demmig-Adams B, Adams WW III, 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
- Demmig-Adams B, Moeller DL, Logan BA, Adams WW III (1998) Positive correlation between levels of retained zeaxanthin + antheraxanthin and degree of photoinhibition in shade leaves of *Schefflera arboricola* (Hayata) Merrill. *Planta* 205:367–374
- Diekmann M, Eilertsen O, Fremstad E, Lawesson JE, Aude E (1999) Beech forest communities in the Nordic countries: a multivariate analysis. *Plant Ecol* 140:203–220
- Dietz K-J, Schreiber U, Heber U (1985) The relationship between the redox state of Q_A and photosynthesis in leaves at various carbon dioxide, oxygen and light regimes. *Planta* 166:219–226
- Emborg J (1998) Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For Ecol Manage* 106:83–95
- Emborg J, Christensen M, Heilmann-Clausen J (1996) The structure of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For Land Res* 1:311–333
- Gabrielsen EK (1948) Effects of different chlorophyll concentrations on photosynthesis in foliage leaves. *Physiol Plant* 1:5–37
- Genty B, Braintais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochim Biophys Acta* 990:87–92
- Govindjee (1995) Sixty-three years since Kautsky: chlorophyll *a* fluorescence. *Aust J Plant Physiol* 22:131–160
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–79
- Horton P, Ruban AV, Walters RG (1996) Regulation of light harvesting in green plants. *Annu Rev Plant Physiol Plant Mol Biol* 47:655–684
- Jahn G (1991) Temperate deciduous forests of Europe. In: Röhrig E, Ulrich B (eds) *Temperate deciduous forests*. Elsevier, Amsterdam, pp 377–502
- Johnson GN, Scholes JD, Horton P, Young AJ (1993) Relationships between carotenoid composition and growth habit in British plant species. *Plant Cell Environ* 16:681–686

- King DA (1990) Allometry of saplings and understory trees of a Panamanian forest. *Funct Ecol* 4:27–32
- Krall JP, Edwards GE (1992) Relationship between photosystem II activity and CO₂ fixation in leaves. *Physiol Plant* 86:180–187
- Krause GH, Winter K (1996) Photoinhibition of photosynthesis in plants growing in natural tropical forest gaps. A chlorophyll fluorescence study. *Bot Acta* 109:456–462
- Külheim C, Åren J, Jansson S (2002) Rapid regulation of light harvesting and plant fitness in the field. *Science* 297:91–93
- Leverenz JW (1987) Chlorophyll content and the light response curve of shade-adapted conifer needles. *Physiol Plant* 71:20–29
- Leverenz JW, Falk S, Pilström C-M, Samuelsson G (1990) The effects of photoinhibition on the photosynthetic light-response curve of green plant cells (*Chlamydomonas reinhardtii*). *Planta* 182:161–168
- Li X-P, Björkman O, Shih C, Grossman AR, Rosenquist M, Jansson S, Niyogi KK (2000) A pigment-binding protein essential for regulation of photosynthetic light harvesting. *Nature* 403:391–395
- Long SP, Humphries S, Falkowski PG (1994) Photoinhibition of photosynthesis in nature. *Annu Rev Plant Physiol Plant Mol Biol* 45:633–662
- Lovelock CE, Jebb M, Osmond CB (1994) Photoinhibition and recovery in tropical plant species: response to disturbance. *Oecologia* 97:297–307
- Maxwell K, Johnson GN (2000) Chlorophyll fluorescence: a practical guide. *J Exp Bot* 51:659–668
- Mead R, Curnow RN, Hasted AM (2003) Statistical methods in agriculture and experimental biology. CRC, Boca Raton
- Møller PF, Staun H (2001) Danmarks Træer og Buske (in Danish). Politikens, Copenhagen
- Mulkey SS, Pearcy RW (1992) Interactions between acclimation and photoinhibition of photosynthesis of a tropical understory herb, *Alocasia macrorrhiza*, during simulated canopy gap formation. *Funct Ecol* 6:719–729
- Naidu SL, DeLucia EH (1997) Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. *Tree Physiol* 17:367–376
- Ögren E (1991) Prediction of photoinhibition of photosynthesis from measurements of fluorescence quenching components. *Planta* 184:538–544
- Ögren E (1994) The significance of photoinhibition for photosynthetic productivity. In: Baker NR, Bowyer JR (eds) Photoinhibition of photosynthesis: from molecular mechanisms to the field. BIOS Scientific, Oxford, pp 433–447
- Ögren E, Sjöström M (1990) Estimation of the effect of photoinhibition on the carbon gain in leaves of a willow canopy. *Planta* 181:560–567
- Öquist G, Anderson JM, McCaffery S, Chow WS (1992a) Mechanistic differences in photoinhibition of sun and shade plants. *Planta* 188:422–431
- Öquist G, Chow WS, Anderson JM (1992b) Photoinhibition of photosynthesis represents a mechanism for the long-term regulation of photosystem II. *Planta* 186:450–460
- Ort DR, Baker NR (1988) Consideration of the photosynthetic efficiency at low light as a major determinant of crop photosynthetic performance. *Plant Physiol Biochem* 26:555–565
- Osborne BA, Raven JA (1986) Light absorption by plants and its implications for photosynthesis. *Biol Rev* 61:1–61
- 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 Scientific, Oxford, pp 1–24
- Osmond CB, Ramus J, Levavasseur G, Franklin LA, Henley WJ (1993) Fluorescence quenching during photosynthesis and photoinhibition of *Ulva rotundata* Bild. *Planta* 106:97–106
- Oxborough K, Baker NR (1997) Resolving chlorophyll a fluorescence images of photosynthetic efficiency into photochemical and non-photochemical components: calculation of *qP* and *Fv'/Fm'* without measuring *Fo'*. *Photosynth Res* 54:135–142
- Oxborough K, Baker NR (2000) An evaluation of the potential triggers of photoinactivation of photosystem II in the context of a Stern–Volmer model of down-regulation and the radical pair equilibrium model. *Phil Trans R Soc London B* 355:1489–1499
- 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 Scientific, Oxford, pp 255–271
- Powles SB (1984) Photoinhibition of photosynthesis induced by visible light. *Annu Rev Plant Physiol* 35:15–44
- Prioul JL, Chartier P (1977) Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. *Ann Bot* 41:789–800
- Rice WR (1988) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Rosenqvist E (2000) Ecophysiological aspects of photoinhibition of photosynthesis: its relationship to light acclimation and the abiotic environment. PhD Thesis, Botanical Institute, University of Copenhagen
- Rosenqvist E (2001) Light acclimation maintains the redox state of the PS II electron acceptor QA within a narrow range over a broad range of light intensities. *Photosynth Res* 70:299–310
- Rosenqvist E, van Kooten O (2003) Chlorophyll fluorescence: a general description and nomenclature. In: De Ell JR, Toivonen PMA (eds) Practical applications of chlorophyll fluorescence in plant biology. Kluwer, Boston, pp 31–77
- Saxe H, Cannell MGR, Johnsen O, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytol* 149:369–400
- Strauss-DeBenedetti S, Bazzaz FA (1991) Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* 87:377–387
- Valladares F (2003) Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. *Prog Bot* 64:439–471