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Photoinhibition in tropical forest understorey species with short- and long-lived leaves

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Summary

1. Shade-tolerant species that inhabit the understorey have a range of leaf lifetimes (from 1 to 8 years), which may indicate a variety of strategies for dealing with increases in light associated with tree-fall gaps. We hypothesized that species with long-lived leaves should be more tolerant of an increase in light levels than species with short-lived leaves.

2. In understorey plants of 12 shade-tolerant rain-forest species, photoinhibition, measured as a reduction in the chlorophyll fluorescence parameter F_v/F_m when leaf discs were exposed to 1 h at 1000 μmol $m^{-2} s^{-1}$, was greater in species with short-lived leaves than species with long-lived leaves.

3. Less photoinhibition in species with long-lived leaves was not associated with higher levels of non-photochemical dissipation (NPQ) of absorbed light, but may be the result of a higher yield of photosystem II compared with short-lived leaves.

4. Thus, species with long-lived leaves are more tolerant of abrupt increases in light that occur when tree-fall gaps are formed than species with short-lived leaves.

5. Discs from leaves of all species growing in tree-fall gaps had higher levels of NPQ, yield of photosystem II and more rapid recovery from photoinhibition than leaves developed in the understorey; however, there were no differences among species with short- and long-lived leaves.

Key-words: Acclimation in shade-tolerant species, chlorophyll fluorescence, leaf lifetimes, tolerance of high light levels

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Introduction

Across many biomes, variation among plant species in leaf longevity is related to plant growth rate as well as leaf structure and physiology (Reich, Walters & Ellsworth 1992). Species with longer leaf lifetimes tend to grow more slowly and leaves tend to be more resistant to damage and have lower rates of photosynthesis. These characteristics favour survival in environments where resources are limited (Grime 1979; Chapin 1980; Chabot & Hicks 1982; Lambers & Poorter 1992; Kursar 1997). In the understorey of tropical forests light levels are generally very low (midday photon flux densities are often less than 20 μmol $m^{-2} s^{-1}$). Because of variability in canopy height, and because tree-fall gaps are common, spatial and temporal variations in light levels are high (Chazdon & Fetcher 1984; Brokaw 1985; Smith, Hogan & Idol 1992). In general, species commonly found in the understorey have low photosynthetic rates and grow very slowly (Kitajima 1994). The environmental conditions of the forest understorey and the characteristics of the plants that grow there suggest that these species should all have similarly long-lived leaves (Reich *et al.* 1992; Reich 1993). However, leaf life spans among shade-tolerant rain-forest species are surprisingly highly variable, ranging from 1 to 8 years among several tropical forest understorey species on Barro Colorado Island in Panama (Kursar & Coley 1993; T. A. Kursar & P. D. Coley, unpublished data). The coexistence of species with a wide range of leaf life spans may occur because of the heterogeneous environment, wherein species with short-lived leaves have an advantage for carbon-gain in the relatively high-light conditions within tree-fall gaps and species with long-lived leaves have a survivorship advantage in low-light microsites.

During formation of tree-fall gaps, plants previously growing in shaded conditions may suddenly be exposed to as much as a 100-fold increase in light

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(Chazdon & Fetcher 1984; Smith *et al.* 1992). The length of the daily exposure of plants within gaps to high levels of light is dependent on the size and shape of the gap, the height of the surrounding forest, and the local topography. When shade-grown leaves are suddenly exposed to large increases in incident light levels they become photoinhibited (Langenheim *et al.* 1984; Osmond 1994; Watling *et al.* 1996). Photoinhibition is a reduction in the light-use efficiency of photosynthesis because of photo-oxidative damage to photosystem II (PSII), and/or the engagement of protective processes that dissipate much of the absorbed light energy that is in excess of what can be used in photosynthetic metabolism (Demmig-Adams & Adams 1992). Severe photoinhibition results not only in persistent loss in photosynthetic efficiency but also may promote leaf death and abscission (Lovelock, Jebb & Osmond 1994).

In understorey species with short leaf life spans photoinhibition may lead to rapid foliage turnover after gap formation, facilitating the production of a canopy acclimated to the new light regime. This, in turn, will result in faster rates of carbon gain in species with short-lived leaves compared with those with long-lived leaves. Rapid leaf turnover may also be advantageous for these species in response to decreasing light during gap closure. Meanwhile, understorey species with long-lived leaves will persist in newly formed gaps and therefore must be tolerant of high light because of their slower leaf replacement rate.

Instead of replacement of foliage after exposure to high light levels, species with long-lived leaves and slower leaf turnover may employ an alternative strategy, relying on leaf level processes to tolerate increased irradiance. Here we report the results of experiments in which leaf discs of shade-tolerant species with a range of leaf lifetimes were exposed to transient high-light treatments. The experiments are novel because the tropical forest of Panamá is one of the few natural ecosystems where leaf lifetimes of sufficient numbers of species are known such that six replicate species with either short- and long-lived leaves can be examined to establish the generality of responses across many species. We aimed to test whether there are leaf-level differences in tolerance of high-light conditions among species with contrasting leaf longevities. We hypothesized that species with long-lived leaves would be more tolerant of high-light levels than those with short-lived leaves. Chlorophyll fluorescence was used to monitor photoinhibition in leaf discs from 12 species during a 1 h high-light treatment and during the subsequent 24 h recovery period. Using leaf discs collected from the same species growing within tree-fall gaps we also determined whether species with short- and long-lived leaves differed in their capacity to acclimate to high-light conditions within a gap.

Materials and methods

To test whether species with long-lived leaves were more resistant to high levels of light than species with short-lived leaves, photoinhibition and recovery after exposure to high levels of light were measured in leaf discs of 12 species from 10 families of commonly occurring plants on Barro Colorado Island (BCI), Panamá (Table 1). Species with lifetimes of less than 2 years (short-lived) and more than 3·5 years (long-lived) were chosen for this study. Leaf lifetimes for understorey plants of seven of the 12 species had previously been assessed by marking young leaves, recensussing plants annually and determining the time to 50% mortality (T. A. Kursar & P. D. Coley, unpublished data). For *Andira inermis* (W. Wright) H.B.K. field observations indicated an annual leaf turnover. Leaf lifetime of *Psychotria horizontalis* Sw. was 1 year (Sagers 1996). Leaf lifetime was less than 2 years for *Piper aequale* Vahl (B. Engelbrecht, personal communication) and for *Acalypha diversifolia* Jaqq. (15% survival at 2 years, M. Aide, personal communication). For *Trichilia tuberculata,* leaf lifetime had been previously determined for leaves in tree-fall gaps to be 2·7 years (Coley 1988). Based on comparisons with other species for which leaf lifetimes in gaps and in the understorey were available, the leaf lifetime of understorey leaves of *T. tuberculata* was estimated to be at least 3·5 years.

One leaf per plant from five plants of each species was harvested in the early morning from the understorey and tree-fall gaps during the rainy season (April–November). Leaves collected were fully expanded. Leaf age of leaves used in the experiment were estimated to be approximately 20% of their expected leaf life span.

Leaf discs of 1·5 cm^2 were cut from the leaves and placed on moistened filter paper under low fluorescent lighting (9 $\mu mol\ m^{-2} s^{-1}$) and at 26 °C. Leaf discs were kept in the dark for at least 20 min after which an initial measurement of the chlorophyll fluorescence parameters, initial fluorescence, F_o, and maximum fluorescence after a saturating pulse of light, F_m, were made using a PAM-2000 chlorophyll fluorescence measuring device (Walz, Effeltrich, Germany), F_v/F_m, which is correlated with the efficiency of photosystem II (Krause & Weis 1991) calculated as $(F_m - F_o)/F_m$. After initial measures of F_v/F_m, leaf discs were placed within a temperature-controlled chamber set at 29 °C in normal air. Halogen light sources were suspended above the chambers providing photon flux density (PFD) at the surface of the leaf discs of 1000 $\mu mol\ m^{-2} s^{-1}$. To test for differences among species in photoinhibition owing to high PFD, leaf discs were exposed to 1000 $\mu mol\ m^{-2} s^{-1}$ for 1 h. At 10 min intervals during the hour of exposure to high light, steady-state fluorescence, F_s, and fluorescence after a saturating pulse of light, F_m', were measured. The yield of photosystem II, $(F_m' - F_s)/F_m'$,

Table 1. Identification codes and leaf lifetimes of 12 species that occur in the rain-forest understorey

Species	Family	Species code	Adult growth form	Leaf lifetime (years)
Acalypha diversifolia Jaqq.	Euphorbiaceae	ACAD	shrub	1
Alseis blackiana Hemsl.	Rubiaceae	ALSB	canopy tree	1
Psychotria horizontalis Sw.	Rubiaceae	PSYH	shrub	1
Hybanthus prunifolius (Schult.) Schultze	Violaceae	HYBP	shrub	1
Andira inermis (W. Wright) H.B.K.	Papilionoideae	ANDI	tree	1
Piper aequale Vahl	Piperaceae	PIPA	shrub	1–2
Aspidosperma cruenta Woods	Apocynaceae	ASPC	canopy tree	>8
Ouratea lucens (H.B.K.) Engler in Mart.	Ochnaceae	OURL	treelet	4·5
Calophyllum longifolium Willd.	Clusiaceae	CALL	canopy tree	3·8
Garcinia intermedia [1] (Pitt.) Hammel	Clusiaceae	GARI	tree	6·8
Trichilia tuberculata [2] H.B.K.	Meliaceae	TRIT	tree	≥3·5
Swartzia simplex Benth. in Mart.	Caesalpiniodeae	SWAS	treelet	5·0

[1] *Garcinia intermedia* (Pitt.) Hsmmel was previously referred to as *Rheedia edulis* (Seem.) Tr & Pl.
[2] *Trichilia tuberculata* H.B.K. (TRIT) was previously referred to as *Trichilia cipo* (Adr. Juss.) C.D.C.

was estimated after Genty, Briantais & Baker (1989). Non-photochemical quenching, NPQ, was calculated as $(F_m - F_m')/F_m'$ after Bilger & Björkman (1990).

After the 1 h treatment at 1000 μmol $m^{-2} s^{-1}$, leaf discs were placed in low fluorescent lighting in the laboratory to recover for 25 h. The temperature in the laboratory was 26 °C and PFD approximately 9 μmol $m^{-2} s^{-1}$. Recovery of F_v/F_m was monitored at 0·25, 0·5, 1, 2, 3, 6 and 24-h after the photoinhibitory light treatment.

Leaf absorptance was measured on 14–26 leaves of three long-lived (ALSB, OURL and SWAS) and two short-lived species (HYBP and ALSB) growing in both the understorey and tree-fall gaps. Measures were made by placing 10 cm^2 leaf discs in a 20-cm diameter Ulbricht integrating sphere coated with MgO. Light for absorption was supplied by a 12V, 75W narrow spot lamp (Sylvania, Hillsboro, NH, USA) and measured with a PFD sensor (Li-Cor, Lincoln, NE, USA).

The data were analysed by multiple analysis of variance (MANOVA). Measures at each time were considered independent response variables. Environment (either gap or understorey) and leaf lifetime (either long- or short-lived) were considered as fixed effects. Species was considered a random factor and was nested in leaf lifetime. Adequacy of the models was assessed using plots of studentized residuals against predicted values. Yield of photosystem II and non-photochemical quenching of fluorescence were logarithmically transformed before the analysis to obtain constant variance of the data.

Results

Photoinhibition, measured as a decline in F_v/F_m, was evident after 1 h in 1000 μmol $m^{-2} s^{-1}$ in leaf discs from long- and short-lived leaves grown in both gap and understorey environments (Fig. 1). In leaf discs obtained from the understorey, discs from short-lived leaves were more strongly photoinhibited, F_v/F_m was reduced from 0·79 to 0·54 at the end of the 60 min high-light treatment, compared with long-lived leaves where F_v/F_m was reduced from 0·79 to 0·62. Recovery in F_v/F_m in understorey leaves occurred rapidly within the first 2–3 h after the high-light treatment but slowed thereafter, increasing linearly for the next 22 h. After 24 h of recovery in low light, species with short-lived leaves still had lower F_v/F_m than species with long-lived leaves ($P = 0·01$).

In discs from gap-grown leaves the degree of photoinhibition after the 60-min high-light treatment was similar for species with both short- and long-lived leaves, F_v/F_m being reduced from 0·79 to approximately 0·57 (Fig. 1). In discs from leaves grown in gaps, recovery from photoinhibition in the first hour after the high-light treatment was more rapid than that of leaves grown in the understorey. F_v/F_m of gap-grown leaves had recovered to 90% of the initial value within 6 h. After 6 h, F_v/F_m of discs from gap-grown

leaves had attained greater value compared with understorey grown leaves (Fig. 1, Table 2).

Non-photochemical quenching of chlorophyll fluorescence (NPQ) is correlated with processes that dissipate absorbed light energy that exceeds what can be used in photosynthesis. NPQ was greater in discs from gap-grown leaves ($P \leq 0.001$), ranging between 2·5 and 3·0, compared with 1·6–2·3 in discs from understorey-grown leaves. Within an environment, either tree-fall gap or understorey, NPQ of leaf discs did not differ among species with either long- or short-lived leaves (Fig. 2, Table 3).

The extent of the decline in yield of photosystem II over the treatment period was similar in species with discs from both short- and long-lived leaves (Fig. 3). In leaf discs from understorey-grown leaves, yield of photosystem II was 15% higher in long-lived leaves than short-lived leaves, but owing to the high variability this trend was not statistically significant ($P > 0.10$) (Fig. 3, Table 3). In discs from gap-grown leaves, this trend was reversed, with short-lived leaves having greater yield of photosystem II than long-lived leaves.

Table 2. F_v/F_m (± standard error) of leaf discs of 12 species that occur in the rainforest understorey. The species name corresponding to the four letter species code is given in Table 1. Values are for before, after 1 h at 1000 μmol quanta $m^{-2}s^{-1}$ and after 24 h recovery at 9 μmol quanta $m^{-2}s^{-1}$. Species have leaves that are short lived (<2 years) or long lived (>3·5 years) and were developed in either the understorey or in a tree-fall gap: $n = 5$ leaf discs

		F_v/F_m		
		Initial	1 h	24 h
Understorey leaves				
Short-lived				
	ACAD	0·793 ± 0·007	0·519 ± 0·049	0·702 ± 0·039
	ALSB	0·785 ± 0·002	0·553 ± 0·024	0·677 ± 0·019
	PSYH	0·777 ± 0·005	0·588 ± 0·005	0·726 ± 0·003
	HYBP	0·790 ± 0·008	0·516 ± 0·015	0·649 ± 0·022
	ANDI	0·809 ± 0·004	0·578 ± 0·014	0·723 ± 0·010
	PIPA	0·780 ± 0·003	0·504 ± 0·037	0·671 ± 0·023
Long-lived				
	ASPC	0·803 ± 0·004	0·613 ± 0·011	0·727 ± 0·008
	OURL	0·789 ± 0·007	0·632 ± 0·013	0·730 ± 0·011
	CALL	0·796 ± 0·006	0·606 ± 0·025	0·740 ± 0·008
	GARI	0·773 ± 0·008	0·544 ± 0·034	0·670 ± 0·014
	TRIT	0·770 ± 0·007	0·591 ± 0·005	0·709 ± 0·004
	SWAS	0·795 ± 0·005	0·657 ± 0·019	0·736 ± 0·015
Gap leaves				
Short-lived				
	ACAD	0·816 ± 0·004	0·429 ± 0·026	0·772 ± 0·006
	ALSB	0·798 ± 0·005	0·516 ± 0·012	0·752 ± 0·021
	PSYH	0·784 ± 0·007	0·465 ± 0·020	0·747 ± 0·004
	HYBP	0·804 ± 0·003	0·480 ± 0·022	0·739 ± 0·018
	ANDI	0·815 ± 0·009	0·409 ± 0·015	0·747 ± 0·012
	PIPA	0·780 ± 0·006	0·472 ± 0·029	0·735 ± 0·013
Long-lived				
	ASPC	0·799 ± 0·004	0·512 ± 0·023	0·734 ± 0·017
	OURL	0·809 ± 0·008	0·490 ± 0·032	0·725 ± 0·026
	CALL	0·820 ± 0·007	0·430 ± 0·025	0·755 ± 0·010
	GARI	0·766 ± 0·006	0·405 ± 0·031	0·746 ± 0·006
	TRIT	0·771 ± 0·008	0·423 ± 0·022	0·749 ± 0·006
	SWAS	0·805 ± 0·007	0·495 ± 0·014	0·704 ± 0·035

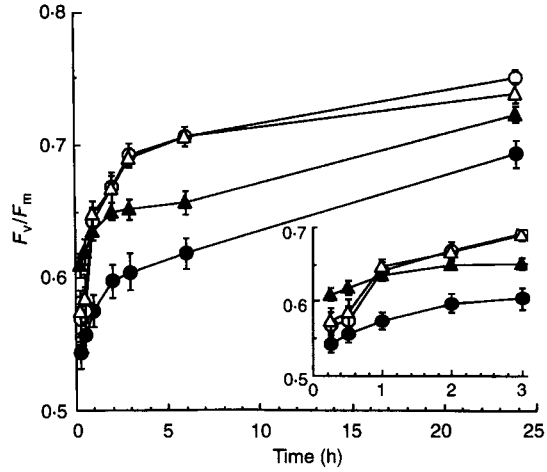

Fig. 1. Mean F_v/F_m (± standard error) of leaf discs of 12 species with either short- (circles) or long-lived (triangles) leaves during 24 h of recovery at 9 μmol $m^{-2}s^{-1}$ after exposure to 1000 μmol $m^{-2}s^{-1}$ for 1 h. Closed symbols are for leaves developed in the understorey, while open symbols are for leaves developed in tree-fall gaps. Initial mean values of F_v/F_m ± standard error were: short-lived leaves in the understorey, 0·789 ± 0·003; long-lived leaves in the understorey, 0·789 ± 0·003; short-lived leaves in tree-fall gaps, 0·791 ± 0·004; long-lived leaves in tree-fall gaps, 0·786 ± 0·003: $n = 30$ leaf discs. Inset shows details of the first 3 h of the recovery period.

This trend was also not statistically significant. There was a high variability among species in the yield of photosystem II and NPQ that was not explained by their leaf lifetime characteristics (Table 3).

To test whether greater levels of photoinhibition in short-lived compared with long-lived leaves in the understorey-grown plants could be the result of higher leaf absorptance, leaf absorptance of three species with long-lived leaves and two species with short-lived leaves was measured. Mean absorptance of short-lived leaves growing in the understorey was 0·79 ± 0·01. This was slightly lower ($P = 0.025$) than absorptances for long-lived leaves which had a mean absorptance of 0·81 ± 0·01. In tree-fall gaps mean leaf absorptance was 0·81 ± 0·01, with no significant differences between short- and long-lived leaves.

Discussion

PHOTOINHIBITION IN LEAVES DEVELOPED IN THE UNDERSTOREY

The aim of this work was to assess whether leaves of species with long-lived foliage are more resistant to photoinhibition during transiently high light conditions than leaves of species with short-lived foliage. In leaf discs from foliage developed in the understorey and exposed to transiently high irradiances, we found that species with long-lived leaves were more tolerant of high-light stress because they underwent less severe photoinhibition than species with short-lived leaves (Fig. 1, Table 2). We base this conclusion on

larger reductions in F_v/F_m observed in species with short-lived leaves compared with those with long-lived leaves, both directly after the 60 min high-light treatment, and after 24 h recovery in low light.

Leaf-level tolerance of high light can be the result of a variety of physiological processes. These include (1) a high capacity for the photoprotective dissipation of absorbed light energy (Demmig-Adams & Adams 1992), (2) a greater capacity for scavenging of reactive oxygen species which are produced under excessive light (Grace & Logan 1996), (3) higher maximum rates of photosynthetic electron transport (Öquist, Hurry & Huner 1993), (4) greater reflective leaf surfaces and (5) chloroplast movements.

Species with short- and long-lived leaves growing in the understorey had similar rates of non-photochemical fluorescence quenching (NPQ) (Fig. 2, Table 3). Non-photochemical fluorescence quenching is correlated with protective dissipation of excess light energy by the carotenoid zeaxanthin (Bilger & Björkman 1990) and can also be the result of photo-oxidative damage of photosystem II (Thiele *et al.* 1996). Differences between species with long- and short-lived leaves in susceptibility to photoinhibition were not correlated with differences in NPQ. This result is difficult to interpret and requires further study. It may indicate there are processes leading to declines in F_v/F_m that are not accounted for by measures of NPQ.

In discs from leaves that developed in the understorey, long-lived leaves had slightly higher photosystem II yields than short-lived leaves (Fig. 3, Table 3). The greater yield of photosystem II in species with

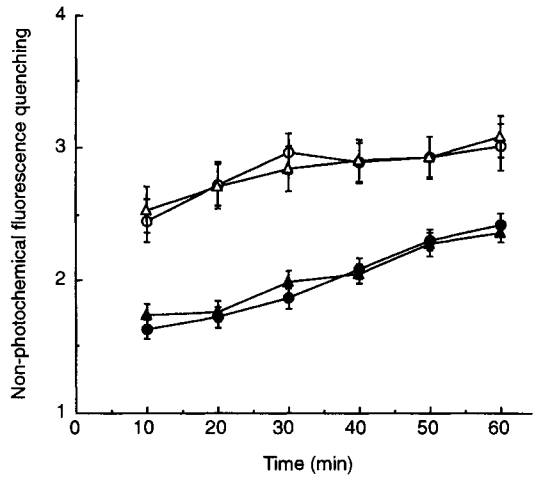

Fig. 2. Mean non-photochemical fluorescence quenching (± standard error) of leaf discs of 12 species with either short- (circles) or long-lived (triangles) leaves during exposure to 1000 μmol $m^{-2}s^{-1}$ for 60 min. Closed symbols are for leaves developed in the understorey, while open symbols are for leaves developed in tree-fall gaps: $n = 30$ leaf discs.

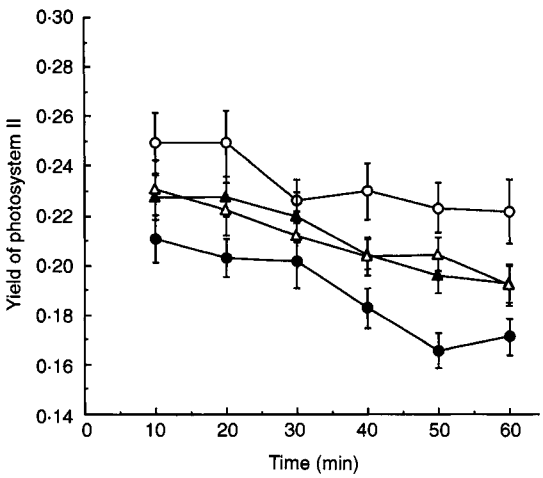

Fig. 3. Mean yield of photosystem II (± standard error) of leaf discs of 12 species with either short- (circles) or long-lived (triangles) leaves during exposure to 1000 μmol $m^{-2}s^{-1}$ for 60 min. Closed symbols are for leaves developed in the understorey, while open symbols are for leaves developed in tree-fall gaps: $n = 30$ leaf discs.

Table 3. Yield of photosystem II and non-photochemical fluorescence quenching (± standard error) of leaf discs of 12 species that occur in the rain-forest understorey. The species name corresponding to the four-letter species code is given in Table 1. Values are from the final minutes of a 1-h exposure to 1000 μmol quanta $m^{-2}s^{-1}$. Species have leaves that are short lived (<2 years) or long lived (>3·5 years) and were developed in either the understorey or in a tree-fall gap: $n = 5$ leaf discs

		Yield of photosystem II	Non-photochemical fluorescence quenching
Understorey leaves			
Short-lived			
	ACAD	0·172 ± 0·022	2·46 ± 0·21
	ALSB	0·170 ± 0·021	2·22 ± 0·13
	PSYH	0·182 ± 0·014	2·54 ± 0·08
	HYBP	0·171 ± 0·012	2·66 ± 0·15
	ANDI	0·211 ± 0·006	1·89 ± 0·12
	PIPA	0·121 ± 0·011	2·75 ± 0·28
Long-lived			
	ASPC	0·196 ± 0·013	2·21 ± 0·07
	OURL	0·170 ± 0·014	2·60 ± 0·18
	CALL	0·208 ± 0·011	2·87 ± 0·19
	GARI	0·162 ± 0·027	2·33 ± 0·21
	TRIT	0·198 ± 0·020	2·33 ± 0·13
	SWAS	0·215 ± 0·022	1·85 ± 0·11
Gap leaves			
Short-lived			
	ACAD	0·297 ± 0·009	
	ALSB	0·227 ± 0·020	3·37 ± 0·36
	PSYH	0·258 ± 0·060	
	HYBP	0·194 ± 0·022	3·03 ± 0·28
	ANDI	0·201 ± 0·026	2·71 ± 0·28
	PIPA	0·212 ± 0·029	
Long-lived			
	ASPC		
	OURL	0·191 ± 0·008	
	CALL	0·192 ± 0·018	3·76 ± 0·24
	GARI	0·161 ± 0·013	3·14 ± 0·24
	TRIT	0·202 ± 0·013	2·72 ± 0·11
	SWAS	0·214 ± 0·026	2·88 ± 0·34

long-lived leaves may have been sufficient to confer greater tolerance of light stress to species with greater leaf life spans. Enhanced photosystem II yield in species with long-lived leaves compared with those with short-lived leaves may be because of differences in various electron-transport processes (Krall & Edwards 1992). Previously, understorey species from BCI with long-lived leaves were found to have higher maximum CO_2 assimilation rates compared with those with short-lived leaves (Kursar & Coley 1993; T. A. Kursar, unpublished data). This is counter to the general pattern of declining photosynthetic capacity with increasing leaf longevity (Reich *et al.* 1992) but has also been observed in shade-acclimated temperate forest herbs of contrasting foliar life span (Skillman, Strain & Osmond 1996). Thus, higher photosystem II yields in discs from long-lived leaves from the understorey on BCI may reflect higher photosynthetic capacities in these species compared with those with short-lived leaves.

Greater tolerance of long-lived leaves to transiently high light compared with species with short-lived leaves could not be the result of lower absorptance of light because absorptance of leaves in species with long-lived leaves was actually higher than that found in species with short-lived leaves. The presence of thick epidermal layers that act as focusing lenses for light (Lee 1986) could also potentially increase the degree of photoinhibition in some species. Whether light is better focused by the epidermal layers of short-lived compared with long-lived leaves is not known and needs to be evaluated. Reduced photoinhibition in species with long-lived leaves compared with those with short-lived leaves could also have been the result of chloroplast movements that reduce light absorption (Park, Chow & Anderson 1996). It is unclear how common the phenomena of chloroplast movement is in plants (Haupt & Scheuerlein 1990; Brugnoll & Björkman 1992). We did not observe any visible bleaching of leaf discs during these experiments which might have been indicative of chloroplast movements.

COMPARISON AMONG LEAVES DEVELOPED IN TREE-FALL GAPS AND THE UNDERSTOREY

A comparison of photoinhibition of discs from leaves from gaps with those grown in the understorey (Fig. 1) showed differences that are commonly observed in sun- and shade-grown leaves (Osmond 1994). Rapid recovery of F_v/F_m in discs from gap-grown leaves compared with understorey leaves (Fig. 1), indicates enhanced protection from high light in discs from leaves developed in gaps. Reductions in F_v/F_m and rapid recovery from photoinhibition in leaf discs is consistent with the formation and subsequent removal by epoxidation of the carotenoid zeaxanthin (Demmig-Adams & Adams 1992; Thiele & Krause 1994; Thiele *et al.* 1996). All leaves, independent of lifetime, had a biphasic recovery pattern in F_v/F_m (Fig. 1). Rapid recovery occurred within the first 2–3 h after the high-light treatment, followed by a longer period of slow recovery. This has been observed in other species growing in tree-fall gaps (Krause, Virgo & Winter 1995; Krause & Winter 1996). The initial rapid recovery phase is thought to be associated with epoxidation of the carotenoid zeaxanthin (Thiele *et al.* 1996). In both understorey and gap-grown leaves, the slower recovery, beginning approximately 3 h after the high-light treatment may be associated with protein synthesis or repair (Thiele *et al.* 1996). Higher levels of NPQ and rapid recovery from photoinhibition in leaves developed in tree-fall gaps are consistent with higher concentrations of xanthophyll cycle carotenoids observed in other species growing in tree-fall gaps (Königer *et al.* 1995).

In addition to photoprotection provided by zeaxanthin, higher rates of electron transport minimize the degree of photoinhibition (Öquist *et al.* 1993). In species with short-lived foliage, gap-grown leaves had higher yields of photosystem II electron transport compared with understorey-grown leaves. (Fig. 3, Table 3). In species with long-lived foliage, leaves from the understorey and from gaps had similar yields of photosystem II electron transport. These species differences are consistent with the prediction that there will be greater photosynthetic plasticity among species with shorter leaf life spans. Species and habitat differences in photosystem II yield probably reflect differences in the capacity for photosynthetic CO_2 fixation, but may also reflect variation in other electron transport processes (Lovelock & Winter 1996).

THE RELATIONSHIP BETWEEN LEAF LONGEVITY, PHOTOSYNTHETIC PLASTICITY AND SUSCEPTIBILITY TO PHOTOINHIBITION

There is growing evidence that a predictable relationship exists between the range of maximum photosynthetic rates expressed by a species under contrasting light conditions (i.e. photosynthetic plasticity) and its relative leaf life span. Among shade-tolerant woody species on BCI with short-lived leaves (≤2 years), individuals growing in tree-fall gaps were found to have maximum photosynthesis rates of 140 to 190% greater than individuals in the understorey (Table 2 in Kursar & Coley 1993). By contrast, for co-occurring species with longer-lived leaves (≥4 years), individuals growing in tree-fall gaps were found to have maximum photosynthesis rates of 35 to 83% greater than those of understorey individuals (Table 2 in Kursar & Coley 1992). In a study of two understorey tropical herbs also on BCI, Mulkey, Smith & Wright (1991) reported that the species having a leaf lifespan of 25–30 months had a much narrower range of photosynthetic plasticity compared with the species having a leaf life span of 10–12 months. This relationship seems to apply to temperate forest species too.

Comparing two broad-leaf evergreen herbs inhabiting an Oak-Hickory forest in NC, USA, Skillman *et al.* (1996) found that the difference between maximum photosynthesis in the summer and winter was less in a species with long-lived leaves compared with one that produced short-lived leaves repeatedly over the year.

A low potential for increasing the maximum rate of photosynthetic carbon fixation at higher ambient light levels in species with long-lived leaves leads to the prediction that these species will also be more susceptible to photoinhibition (Osmond 1994). The findings of the current study contradict this prediction and suggest that species constraints in leaf longevity might lead to a compensatory enhancement of alternative modes of resistance to photoinhibition in species with long-lived leaves.

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