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Chlorophyll fluorescence and photosynthetic gas exchange responses to irradiance of Tree of Heaven (*Ailanthus altissima*) in contrasting urban environments

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Abstract

Sun-and shade-adapted plants of *Ailanthus altissima* utilized thermal-dissipative photoprotection (NPQ) across a range of photosynthetic photon flux densities (PPFD), with higher NPQ and lower maximum quantum yield of photosystem 2 photochemistry (F_v/F_m) in sun-adapted individuals, suggesting increased engagement of antennae-based quenching. Photosynthetic quantum requirements (Q_{req}; number of photons per CO_2) were similar in sun and shade plants, but were low and comparable to forest understory species. Diurnal measurements showed that PPFDs in both habitats were consistently above photosynthetic compensation irradiance, and frequently exceeded saturating values. In addition, sun- and shade-adapted individuals possessed stomata that tracked short-term fluctuations in PPFD. Thus *A. altissima* may be unique in that it couples high, shade-plant like photosynthetic efficiency with high photosynthetic capacity in high-irradiance, while stomatal attributes that optimize water use efficiency are maintained in the shade. These features may contribute to success of *A. altissima* in establishing in disturbance-prone urban systems, and facilitate its spread into more PPFD-limited and competitive natural ecosystems.

Additional key words: areal leaf mass; diurnal courses of photosynthetic characteristics; fluorescence induction; irradiance; leaf dimensions; photoprotection; photosystem 2; quantum yield; stomatal conductance.

Introduction

Studies of urban plant systems have generalized most members of the world's urban flora as disturbance-tolerant, radiant energy-demanding, ruderal species, characteristics attributed to plants adapted to early successional or other disturbance-prone systems (Gilbert 1989). However, urban habitats are highly heterogeneous resource mosaics (Pouyat *et al.* 1995), especially in the case of irradiation (Gilbert 1989). The patterns of radiant energy availability imposed by human built structures result in the novel feature of highly contrasting irradiances in a highly disturbance-prone system (Gilbert 1989, Pearcy 1998). Thus, effective exploitation of a wide range of PPFD may be an important feature in plants that are successful urban colonizers. Understanding such phenomenon may provide mechanistic insight on the invasive potential of such plants, since many non-native invasive plant species have first established in open urban settings prior to spreading into more irradiance limited, competitive native systems (Gilbert 1989, Facelli 1994).

Ailanthus altissima (Tree of Heaven) is a highly successful, invasive tree common to urban areas around the Northern Hemisphere (Garber 1987, Gilbert 1989, Kowarik 1995), and is an excellent case study for ecophysiological responses to urban irradiances. *A. altissima* is a rapidly growing clonal woody species capable of establishing from seed or vegetatively in contrasting irradiances (Facelli 1994, Kowarik 1995). Kowarik (1995) attributed the persistence of *A. altissima* clones in deeply shaded environments to resource relocation from more exposed portions of the genet, and postulated that shaded ramets were maintained in a quasi-dormant state to maximize colonization potential following canopy disturbance. However, the actual photosynthetic responses of *A. altissima* to PPFD variability—processes important to the maintenance of positive carbon balance and persistence in highly heterogeneous irradiances (Sims and Pearcy 1994, Sims *et al.* 1994, Pearcy 1998)—has yet to be established.

Plant responses to PPFD occur at a variety of organ-

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izational levels (Lichtenthaler 1981, 1984, Lichtenthaler and Burkart 1999, Sims and Pearcy 1994, Sims *et al.* 1994, Kozlowski *et al.* 1997, Pearcy 1998). At the membrane level, sun-adapted leaves or plants possess a greater capacity to thermally dissipate excess radiant energy across a wide range of PPFD in the antennae complexes of photosystem 2, PS2 (Demmig-Adams and Adams 1992, Björkman and Demmig-Adams 1994, Osmond 1994). In contrast, shade-adapted leaves or species have a greater reliance on slower reversing, reaction center-based mechanisms for photoprotection (Osmond 1994, Osmond and Grace 1995). As a result, shade-leaves or plants can achieve greater photochemical efficiency compared to sun-adapted counterparts, especially at lower PPFD (Pearcy 1998). However, increased photosynthetic efficiency is usually not the case, especially in woody species, which tend to have similar photosynthetic quantum requirement between sun and shade leaves (Hamerlynck and Knapp 1994a, Kozlowski *et al.* 1997). In addition, leaves from locations experiencing high integrated daily PPFD have higher specific leaf masses, nitrogen contents, and have greater respiration and photosynthetic capacities compared to shade-adapted plants (Pearcy 1998). *A. altissima* has a high investment to thermal dissipation capacity, a feature that may contribute to its high tolerance to ozone and other common urban pollutants (Rank 1997). However, how sun and shade-adapted individuals of this species establish photoprotective mechanisms is unknown.

In addition to acclimatory responses, many plant species possess stomata capable of tracking short-term (5–8 min) fluctuations in PPFD (Knapp and Smith 1989, Fay and Knapp 1995). This trait is an important adaptation in woody species native to highly variable PPFD and moisture environments (Knapp 1992, Hamerlynck and Knapp 1994b, Whitehead and Teskey 1995), a condition common in built-up urban areas (Gilbert 1989). Stomatal tracking is conserved in leaves differing in photosynthetic capacity, but this has only been established for fully exposed leaves (Hamerlynck and Knapp 1994a,b). To date, it is not known if this behavior is maintained in between sun and shade adapted leaves within a species. Given the highly variable PPFD environments that *A. altissima* occupies, we hypothesized that *A. altissima* possesses stomatal tracking ability, and that this trait would be conserved in shade leaves.

This paper presents the results of a study that examined the leaf-level anatomical and photosynthetic responses of naturally occurring clonal ramets of *A. altissima* to PPFD variability under field conditions in an urban landscape. It was hypothesized that *A. altissima* would show leaf-level PPFD responses that could optimize radiant energy harvesting, maintain significant positive leaf-level carbon gain, and maximize integrated water-use efficiency. This hypothesis would be supported by evidence of: (*1*) Greater engagement of thermal dissipation of excess PPFD (*i.e.*, greater NPQ, Osmond 1994) in response to increasing PPFD. (*2*) Photosynthetic PPFD saturation kinetics that would maintain net assimilation rates above photosynthetic compensation over the diurnal period (Sims and Pearcy 1994, Pearcy 1998). Of specific interest were alterations to photosynthetic quantum requirement [mol photon needed to fix 1 mol CO_2], an indicator of the efficiency of photosynthetic PPFD conversion), compensation irradiance, and saturation irradiance between sun and shade leaves. (*3*) Possession of stomata capable to track short-term (5-8 min) fluctuations in PPFD. Together, these features could provide mechanistic insights on the success of this species in occupying and persisting in highly disturbed urban systems.

Materials and methods

Study area and environmental measurements: Research was done from July 10 to August 25, 1999 on naturally occurring clonal ramets of *Ailanthus altissima* in three typical urban habitats: a parking lot at the intersection of Raymond Blvd. and University Ave. and the northern and western sides of New Jersey Institute of Technology in Newark, New Jersey (40.7 N, 74.2 W), and a city park in Bayonne, New Jersey (40.6 N, 74.1 W). Shade ramets were sampled from locations that were shaded by buildings and other man-made structures. After photosynthetic gas exchange measurement, ages of aboveground stems were determined from ring counts. Stem ages ranged from 2-4 years old, and originated from well-established rootstocks of undetermined age.

Diurnal courses of PPFD were measured under typical clear to mixed cloud conditions at the Raymond Boulevard site over two days using a *Li-1400* (*LiCOR Instruments*, Lincoln, NE, USA) data logger. Values were recorded from two silicon-photodiodes, one located in the fully exposed and other in the fully shaded areas occupied by *A. altissima.* PPFD was gathered from 04:00 to 21:00 EST, logged every minute, averaged over five minutes, then recorded.

Anatomical and morphological measurements: Eighteen leaves from individual sun and shade stems (total n = 36) of *A. altisima* were measured for petiole length, number of leaflets per leaf, and distance between each leaflet pair. Individual leaflet area [cm^2] was measured using a *LI-Cor 3000* Area Meter (*LiCOR Instruments*, Lincoln, NE, USA), with whole leaf area estimated by summing the leaflet areas. Leaflets were dried at 70 °C for a minimum of 48 h, then weighed to estimate area leaf mass (ALM) of the entire compound leaf [g m^{-2}]. Ten stems from sun and ten shade *A. altissima* clones were measured to quantify inter-node length, beginning from the top most bud to the last.

Photosynthetic measurements: Chlorophyll (Chl) fluorescence and photosynthetic gas-exchange responses to PPFD were generated for the fifth leaf from the shoot terminus on five different ramets growing in sun and shade. Pulse-amplitude-modulated (PAM) Chl fluorescence using a *FMS 2 PAM* fluorimeter (*Hansatech Instruments*, Kings Lynn, UK) was used to estimate dark-adapted and light-adapted responses of *A. altissima.* Leaves were dark-adapted for 30 min prior to sampling, with PPFD at sampling measured at the leaf-level by holding a *LiCOR 190A* silicon-photodiode parallel to the leaf surface and averaging for 15 s prior to dark-adaptation. Baseline fluorescence (F_0) was established by exposing the dark-adapted tissue for 10 s to a weak modulated beam and averaging fluorescence yield. Maximum fluorescence yield (F_m) was obtained by a saturating flash of 0.8 s duration and 8 500 µmol m^{-2} s^{-1} irradiance. Optimal PS2 efficiency (F_v/F_m) was calculated as $(F_m - F_o)/F_m$. Immediately following determination of F_m, an actinic radiation source was turned on to 4.5 µmol m^{-2} s^{-1}, and increased to 2 000 µmol m^{-2} s^{-1} in 3-min steps. At the end of each actinic exposure, PPFD-adapted maximum fluorescence yield (F_m') was induced by a 0.8 s exposure to the saturating source. Steady-state fluorescence (F_s) was averaged over a 5-s period 10 s after F_m determination. The sample was then exposed to low far-red radiation for estimation of PPFD-induced adjustments to F_0 (F_0'). These parameters (F_0, F_m, F_m', F_s, and F_0') were used to estimate rate of electron flow forom PS2 $(1 - q_P)$, where $q_P = (F_m' - F_s)/(F_m' - F_o')$, thermal dissipation of excess PPFD energy, NPQ, where NPQ = $(F_m - F_m')/F_m'$), maximal yield of PS2 photochemistry, $F_v'/F_m' = (F_m' - F_o')/F_m'$, and effective quantum yield of PS2, $\Phi_{PS2} = (F_m' - F_s)/F_m'$ as per Schreiber *et al.* (1998).

Photosynthetic gas exchange response to PPFD was generated in the field by changing a high density red-blue irradiance of LED display of a *LI-6400* portable photosynthesis system (*LiCOR Instruments,* Lincoln, NE, USA) from saturating values (2 000 µmol m^{-2} s^{-1}) to darkness. Leaf temperature (T_{leaf}) was maintained at 25 to 30 °C, with a leaf air vapor pressure deficit (VPDL) of 1.6 to 2.1 kPa. Leaves were allowed to equilibrate for at least 5 min before each measurement. Photosynthetic PPFD response parameters of dark respiration (R_D), maximum photosynthetic capacity (P_{max}), quantum requirement [mol(PPFD) mol^{-1}(CO_2)], and photosynthetic compensation irradiance were calculated using *Photosynthesis Assistant* software version *2.0* (*Dundee Scientific*, Dundee, UK). Six leaves from individual ramets in sun and shade habitats were sampled.

Responses of net photosynthetic rate, P_N [µmol m^{-2} s^{-1}], stomatal conductance to water vapor, g_s [mol m^{-2} s^{-1}], and internal CO_2 concentration, C_i [mmol mol^{-1}] to short-term fluctuation in PPFD were made using an open-flow portable photosynthesis system (*LI-6400, LiCOR Instruments*, Lincoln, NE, USA) with a high intensity LED source. The variable PPFD regime was determined after examination of the saturation PPFD responses obtained above. Initial cuvette conditions were set to 2 000 µmol m^{-2} s^{-1} PPFD, T_{leaf} of 25 °C, and vapor pressure deficit (VPDL) of 0.8 to 1.2 kPa. The leaf was allowed to equilibrate for a minimum of 5 min prior to initiating a sun/shade cycle. Measurements were made every 60 s over 7 min at 2 000 µmol m^{-2} s^{-1}, then PPFD was reduced to 300 µmol m^{-2} s^{-1} 30 s after the last full PPFD point was logged. Leaf-to-air VPDL and leaf temperature (T_{leaf}) were allowed to reduce with irradiance (300 µmol mol^{-1} was selected because it was below saturation PPFD for sun leaves, above shade-leaf photosynthetic LSP). The first shade value was logged 30 s into the shade period, with measurements made every 60 s for an additional 6 min. Irradiation was returned to 2 000 µmol m^{-2} s^{-1} 30 s after the last shade measurement, with 7 subsequent measurements. Single leaves from four individual aboveground stems from each PPFD environment were sampled.

Statistical analysis: One-way ANOVA (*Statistix* version *4.0, Analytical Software*, St. Paul, MN, USA) was used to test for significance differences between anatomical, F_v/F_m, and all parameters derived from photosynthetic PPFD saturation curves of sun and shade *A. altissima.* Repeated measures two-way ANOVA was used to test for differences between sun and shade leaf Chl fluorescence PPFD response and gas exchange responses to short-term PPFD fluctuation. PPFD was the whole-plot factor, using the PPFD environment-by-replicate stem interaction as the whole-plot error term. The sub-plot factors were PPFD and PPFD-by-leaf type interaction (in the case of Chl fluorescence measurements) and time period, and the leaf type-by-time interaction (in the case of stomatal tracking measurements), using the appropriate three way interaction (type-by-light-by-replicate or type-by-time-by-replicate) as the sub-plot error term. Of specific interest were the two-way interactions, since these would indicate habitat-specific responses to PPFD and short-term fluctuations in PPFD. *Post-hoc* linear contrasts using Scheffe's F-test were used to test the significance of specific contrasts contributing to any observed significant interactions. All fluorescence data was arcsine transformed to meet ANOVA assumptions (Zar 1974).

Results

Environmental measurements: Comparison of typical *A. altissima* PPFD environments showed marked abbreviation in total daily integrated and maximum incident PPFD was common between fully exposed and shaded habitats (Fig. 1). On a clear day in sun habitats, PPFD exceeded 1 000 µmol m^{-2} s^{-1} for over ten hours, while PPFD was usually between 10 and 15 µmol m^{-2} s^{-1} in shaded locations (Fig. 1). The PPFD spikes apparent in shaded habitats in late afternoons resulted from low sun angles that allowed deeper light penetration (Fig. 1).

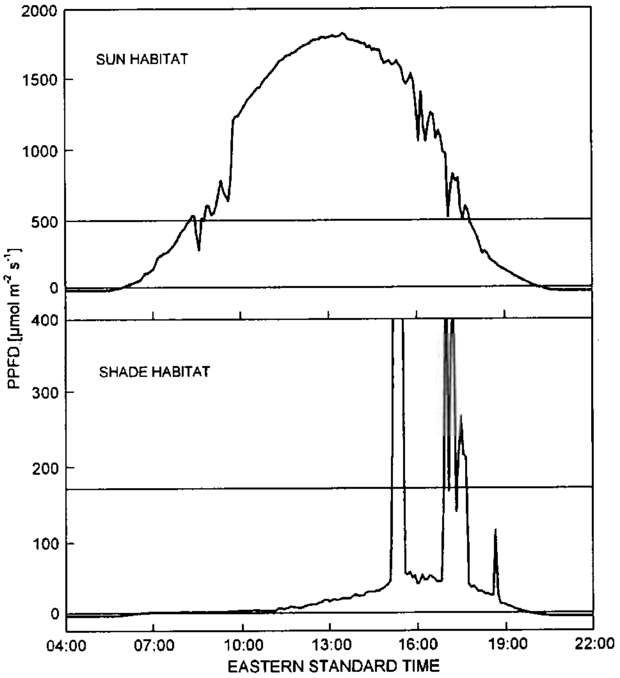

Fig. 1. Typical diurnal course of photosynthetic photon flux density (PPFD) in fully exposed (*top*), and shaded (*bottom*) habitats of *Ailanthus altissima*. Lines indicate PPFD saturation and compensation irradiance of sun- and shade-adapted *A. altissima*, respectively.

Anatomical and morphological responses: Stem lengths of sun and shade leaves were not significantly different, but sun leaves had individual leaflet areas that were 55 % smaller and inter-leaflet distances reduced by 19 % compared to shade leaf counterparts (Table 1). Sun plant leaves also had 18 % more leaflets per leaf than shade adapted plants. As a result, leaves in *A. altissima* sun plants were 48 % smaller than in shade plants, while ALM was 13 % greater in leaves from fully exposed *A. altissima* (Table 1). On a whole stem basis, stem internode length reduced by 42 % in sun plants compared to shade plant *A. altissima* (Table 1).

Table 1. Differences in anatomical and morphological attributes of *Ailanthus altissima* growing in contrasting urban light environments with associated ANOVA results (1, 34 degrees freedom). NS – not significant.

Parameter	Sun	Shade	F	$p \leq 0.05$
Petiole length [cm])	56.00	52.30	1.28	NS
Number of leaflets per leaf	20.50	17.40	9.23	*
Leaflet area [cm^2]	19.10	42.50	195.00	*
Inter-leaflet space [cm]	3.00	3.70	36.34	*
Total leaf area [cm^2]	373.70	718.10	15.55	*
Areal leaf mass [g m^{-2}]	4.36	3.84	5.26	*
Internode length [cm]	2.96	5.11	13.61	*

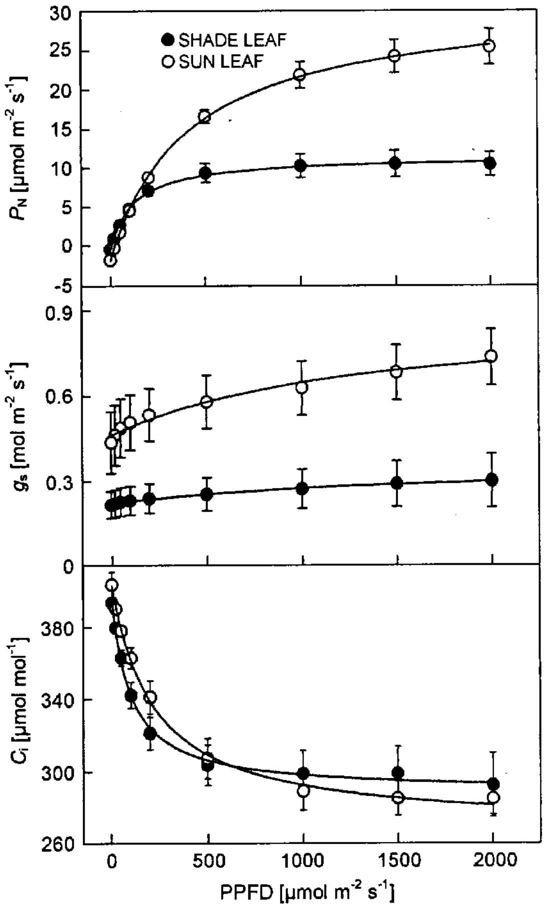

Fig. 2. PPFD saturation response curves of net photosynthetic rate (P_N), stomatal conductance to water vapor (g_s), and internal CO_2 concentration (C_i) of *Ailanthus altissima* growing in contrasting irradiances. Means of six independent measurements, bars indicate ± one SE.

Physiological responses: Leaves from *A. altissima* growing in full sun had significantly lower baseline fluorescence (–15.6 %), F_m (–42.2 %), and F_v/F_m (–7.1 %) compared to shade-adapted counterparts (Table 2). Analysis of PPFD saturation responses showed significantly higher compensation irradiance (+408 %), saturation irradiance (+158 %), and maximum PPFD-saturated P_N (+160 %) in sun leaves compared to shade leaves (Table 2). However, apparent quantum requirement (Q_{req}) did not differ between leaf types (Table 2 and Fig. 2). Sun plant R_D was also significantly higher by 433 % in sun leaves (Table 2).

Table 2. Differences in dark-adapted chlorophyll (Chl) fluorescence yields and photosynthetic irradiance response parameters of *Ailanthus altissima* growing in sun and shade contrasting urban PPFD. Means of five (Chl fluorescence) or six (gas exchange) independent measurements, standard error of the mean in parentheses. Letters differ significantly at $^*p \leq 0.05$, $^{**}p \leq 0.0001$ (one-way ANOVA).

Parameter	Sun	Shade
F_0 [relative]	216.60 (7.07)^{a*}	256.60 (10.72)^{b*}
F_m [relative]	1018.40 (33.19)^{a**}	1761.00 (59.19)^{b}
F_v/F_m [relative]	0.79 (0.009)^{a**}	0.85 (0.003)^{b}
LCP [μmol m^{-2} s^{-1}]	23.40 (1.05)^{a**}	4.60 (+1.05)^{b}
LSP [μmol m^{-2} s^{-1}]	452.20 (47.56)^{a*}	177.50 (+18.40)^{b}
Q_{req} [mol mol^{-1}]	14.10 (+0.56)	15.30 (+0.63)
P_{max} [μmol m^{-2} s^{-1}]	30.10 (2.72)^{a**}	11.60 (1.52)^{b}
R_D [μmol m^{-2} s^{-1}]	1.60 (0.14)^{a**}	0.30 (+0.08)^{b}

Table 3. Repeated-measures ANOVA results comparing the PPFD-response curves of chlorophyll fluorescence-based parameters of sun and shade-adapted *Ailanthus altissima.* F-test results differ significantly at $^*p \leq 0.05$ and $^{**}p \leq 0.0001$.

	Dependent variable				
	$1 - q_p$	NPQ	F_v'/f_m'	Φ_{PS2}	df
Type	278.31**	6.31*	5.34*	39.69*	1,8
PPFD	2303.95**	316.69**	269.58**	1451.65**	6,48
Type × PPFD	134.94**	7.62**	1.42^{ns}	30.02**	6,48

Significant habitat-specific PPFD-response of $1 - q_P$, non-photochemical thermal dissipation (NPQ), and effective PS2 yield (Φ_{PS2}) were apparent between sun and shade adapted *A. altissima* (Table 3 and Fig. 3). Only F_v'/F_m' did not show the expected two-way interaction between PPFD and irradiance (Table 3). Pooled across all PPFD, $1 - q_P$ decreased 43.6 % in sun adapted plants, while NPQ increased by 29.2 % compared to shade-adapted *A. altissima* (Fig. 3). F_v'/F_m' decreased by 9.1 %, while Φ_{PS2} was 35.9 % greater in sun plants compared to shade plants (Fig. 3). At some lower irradiances, $1 - q_P$ (at 4.5 μmol m^{-2} s^{-1} PPFD), NPQ (at 4.5, 20, and 85 μmol m^{-2} s^{-1} PPFD), and Φ_{PS2} (at 4.5 and 20 μmol m^{-2} s^{-1} PPFD), no significant differences between sun and shade-adapted *A. altissima* were found (Fig. 3). This likely resulted in the significant type-by-PPFD interactions in these parameters (Table 3).

Photosynthetic gas exchange in leaves from both PPFD tracked changes in short-term fluctuations in PPFD (Fig. 4). Upon shading, P_N in sun and shade plant leaves showed a post-lower irradiation burst of photorepiratory CO_2 (Vines *et al.* 1983), the recovery from which was longer in sun compared to shade plants, which rapidly reached new equilibrium P_N under lower PPFD (Fig. 4). Pooled across the shade period, mean P_N was not significantly different between sun and shade plant leaves, even though P_N in fully exposed *A. altissima* was

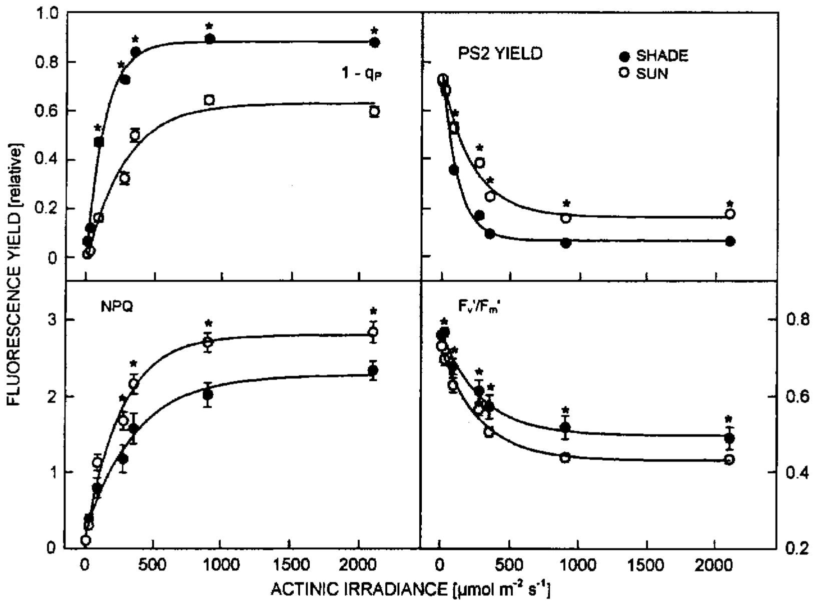

Fig. 3. PPFD response curves of chlorophyll fluorescence parameters of $1 - q_P$, non-photochemical thermal dissipation (NPQ), maximal yield of PS2 photochemistry (F_v'/F_m'), and effective yield of PS2 (Φ_{PS2}) in sun- and shade-adapted *Ailanthus altissima.* Means of five independent measurements, bars indicate ± one SE, * indicate significant differences within PPFD (linear contrasts, Scheffe's F, $p \leq 0.05$)

86 % higher prior to shading (Fig. 4). These PPFD-specific differences resulted in a significant two-way type-by-time interaction (Table 4). Upon re-irradiation, P_N in sun *A. altissima* was slightly depressed below pre-shading levels, but not significantly so (Fig. 4). Stomatal conductance (g_s) in both sun and shade *A. altissima* reduced significantly in response to shading (Table 4, Fig. 4). Proportional changes in g_s with shading were greater in sun plant leaves (*ca.* –32 %), which had much higher g_s prior to shading (0.92 ± 0.006 mol m^{-2} s^{-1}) compared to shade plants, which reduced 25 % from pre-shade levels (0.44 ± 0.002 mol m^{-2} s^{-1}). Sun plant leaf g_s did not fully recover from shading, even seven minutes following re-irradiation, remaining 18 % lower compared to pre-shade levels. Stomatal conductance in dynamics gave rise to a leaf type-by-time interaction (Table 4). Changes in C_i in response to changes in PPFD shade plant leaves, however, fully recovered to pre-shade levels upon re-irradiation (Fig. 4). These differences in g_s were also irradiance-specific (Table 4). Proportional changes in C_i under shade were much greater in sun plant leaves (+17 %) compared to shade plant leaves (+5 %). Before shading, sun plant leaf C_i (258.8 ± 0.20 µmol mol^{-1}) was markedly lower than in shade plants (273.4 ± 0.25 µmol mol^{-1}), then exceeded shade plant C_i throughout the shade period (Fig. 4). Upon re-irradiation, C_i in shade plant leaves immediately achieved pre-shading levels, while sun plant C_i showed a continuous decline (Fig. 4), a dynamic that likely resulted in the significant type-by-time interaction (Table 4).

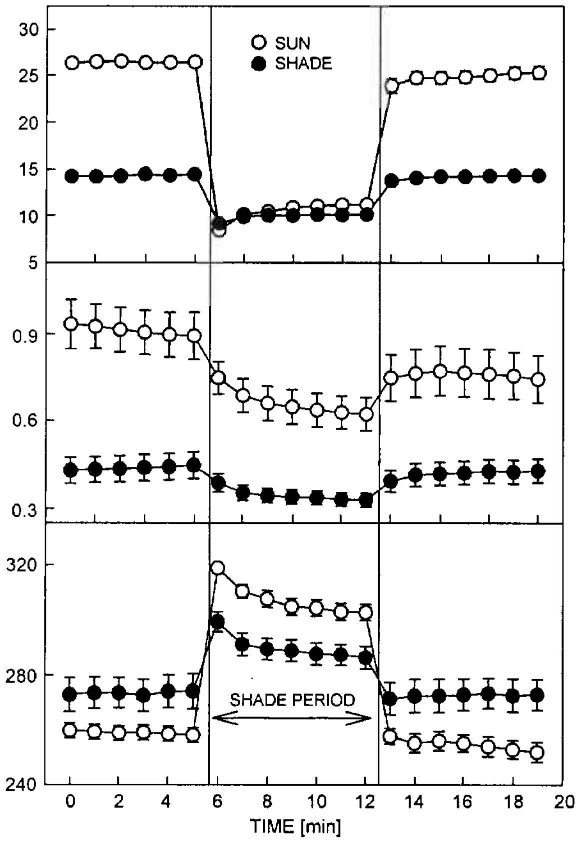

Fig. 4. Responses of net photosynthetic rate (P_N), stomatal conductance to water vapor (g_s), and internal CO_2 concentration (C_i) to short-term variation in photosynthetic photon flux density (PPFD) in *Ailanthus altissima* growing in contrasting urban PPFDs. Pre- and post-shade PPFD were 2 000 or 300 µmol m^{-2} s^{-1} for shade period PPFD. Means of four measurements, error bars indicate ± one SE.

Table 4. Repeated-measures ANOVA results that compare photosynthetic gas exchange responses to short-term variation in PPFD level of *A. altissima* growing in full sun or shaded microenvironments. F-test results differ significantly at $^{*}p \leq 0.05$ and $^{**}p \leq 0.0001$.

	Dependent variable			
	P_N	g_s	C_i	df
Type	328.54^{**}	16.52^{*}	0.46^{ns}	1,6
Time	531.57^{**}	33.35^{**}	370.25^{**}	9,114
Type × time	164.51^{**}	9.42^{**}	91.21^{**}	19,114

Discussion

As hypothesized, leaves from sun-adapted *A. altissima* showed higher thermal dissipation of excess radiant energy (Fig. 3). However, unlike most sun and shade-adapted plants, photochemical quenching in shade-adapted *A. altissima* was markedly lower compared to levels in sun-adapted plants (Björkman and Demmig-Adams 1994, Osmond 1994, Osmond and Grace 1995, Anderson *et al.* 1997), as indicated by higher $1 - q_P$ (Fig. 2). Lower q_P is indicative of fewer open PS2 reaction centers (Osmond 1994), and hence lower effective PS2 yields (Fig. 3). It might be possible that the similar NPQ (Fig. 2) and slightly higher F_0 (Table 2) in shade adapted plants indicate reliance on more slowly relaxing forms of photoprotection. In slow-relaxing photoprotective down-regulation, limitations to D1-protein turnover results in an accumulation of non-functional reactions PS2 centers that enhance NPQ by diverting energy from operational PS2 reaction centers (Anderson *et al.* 1997). Thus, the reductions in q_P in shade-adapted *A. altissima* (Fig. 2) might reflect the accumulated effects of periodic exposure to saturating PPFD (Fig. 1), and why F_v'/F_m' is higher compared to that in sun plants (Fig. 3). However, without supporting molecular values, this remains conjectural. Rather, the decreased levels of F_0, F_m, and F_v/F_m in sun plants (Table 2) and the slight differences in sun and shade plant NPQ (Fig. 3) are more strongly indicative of different capacities and degree of engagement of antennae-based, energy-dependent photoprotection (Osmond 1994, Osmond and Grace 1995, Gilmore 1997). Thus, it is more reasonable to assert that *A. altissima* primarily utilizes protective thermal-dissipative mechanisms common in plants adapted to systems characterized by high PPFD (Björkman and Demmig-Adams 1994, Osmond 1994, Huxman *et al.* 1998).

The differences in the dynamics in photoprotective down-regulation of PS2 efficiency may contribute to the similar quantum requirement (Q_{req}) in sun and shade *A. altissima* (Table 2 and Fig. 2). Differences in photosynthetic PPFD responses (Table 2 and Fig. 2) can be attributed to changes in respiration accompanying alterations in leaf mass (Table 1). The parallel photosynthetic and anatomical adjustments *in A. altissima* and invariant Q_{req} also occur in other high-PPFD preferring woody species (Hamerlynck and Knapp 1994a, Kozlowski *et al.* 1997). However, there are some aspects of the photosynthetic PPFD responses of *A. altissima,* both in terms of acclimation to irradiance (Fig. 2), and in response to short-term variation in PPFD (Fig. 4) that make *A. altissima* unique from other "high light" plants.

First, in its acclimation response, R_D in leaves from both sun and shade adapted *A. altissima* are considerably lower than reported in other woody species, even when correcting for leaf mass (Hamerlynck and Knapp 1994a, Kozlowski *et al.* 1997, Reich *et al.* 1998). This suggests that nighttime respiratory losses in shade-adapted *A. altissima* could be low. Secondly, photosynthetic quantum requirement of *A. altissima* is very low (*ca.* 15 photons per carbon fixed), indicative of highly efficient conversion of radiant energy. Q_{req} in *A. altissima* is much lower than in other heliophilic tree species that possess similar maximum photosynthetic capacity (Hamerlynck and Knapp 1994a, Kozlowski *et al.* 1997). It is also more comparable to values in understory tree species with much lower photosynthetic capacities (Mulkey *et al.* 1993, Kozlowski *et al.* 1997, DeLucia and Thomas 2 000, Singsaas *et al.* 2 000). Thus, *A. altissima* could be characterized as a "high capacity shade plant" in terms of its photosynthetic capacity and PPFD conversion efficiency.

Lastly, leaves from fully shaded *A. altissima* ramets showed dynamic stomatal responses to irradiance (Fig. 4), suggesting that leaves in such plants are fully active under PPFD that would be highly limiting to most high-irradiance adapted species (Kozlowski *et al.* 1997, Hamerlynck and Knapp 1994a). The advantage of stomatal tracking is that costs to carbon gain imposed by stomatal limitations upon re-irradiation are offset by the benefit of minimizing water loss during low P_N under low PPFD (Knapp and Smith 1989, Knapp 1992, Fay and Knapp 1995, Whitehead and Teskey 1995). Stomatal tracking in shaded portions of the plant may be advantageous in that photorespiration is reduced in shaded conditions, as evidenced by the smaller post-lower irradiation burst of photorespiratory CO_2 (Fig. 4; see Vines *et al.* 1983). By altering stomatal aperture in shade-adapted foliage, the plant could realize considerable water savings in tissue that proportionally fixes more CO_2 than exposed leaves, which realize considerable photorespiratory losses (Osmond and Grace 1995). This could likely optimize whole-plant water-use, and could contribute to the ability of clones of *A. altissima* to co-ordinate and integrate plant water eco-nomy across locations with contrasting water and light resources.

Given these findings, it seems likely that heavily shaded ramets of *A. altissima* are not in a quasi-dormant state, as previously hypothesized (Kowarik 1995). Rather, our results suggest that shaded portions of this clonal plant are important and active positive contributors to overall plant carbon balance (Sims and Pearcy 1994, Sims *et al.* 1994). The leaf-level attributes quantified in this study (Fig. 2) suggest that *A. altissima* remains above compensation irradiance during most of the daylight hours in deeply shaded locations, and that it is very efficient at utilizing both low and saturating PPFD in fully exposed and shaded locations (Figs. 1 and 2). Also, *A. altissima* is capable of optimizing water use efficiency both in fully exposed and deeply shaded microenvironments (Fig. 4). Taken together, these features could allow *A. altissima* to maximize integrated daily carbon acquisition across highly heterogeneous resource mosaics. These features likely fit into a suite of co-ordinated characteristics that make *A. altissima* well suited for success in human-impacted ecosystems. In addition to having highly stress-tolerant photochemical attributes (Rank 1997), roots in seedlings of *A. altissima* can better withstand soil compaction compared to other tree species (Pan and Bassuk 1985). *A. altissima* produces allelopathically active compounds (Heisey 1990). Such compounds have an ecologically relevant impact on surrounding seeds and seedlings (Lawrence *et al.* 1990). These features, and the leaf-level responses noted in this study, could contribute to the great success of *A. altissima* in invading and persisting in highly disturbed systems, but also facilitate its subsequent success in more light-limited and competitive natural ecosystems (Facelli 1994, Kowarik 1995, Smith and Knapp 1999).

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