Photosynthetic acclimation within individual *Typha latifolia* leaf segments

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**A B S T R A C T**

Growing *Typha latifolia* leaf segments traverse a wide range of light environments as they are pushed upward from basal meristems through sediment, water, and dense litter and leaf layers. We used light transfer experiments in a greenhouse to investigate the photosynthetic acclimation of individual *Typha* leaf segments. Fully expanded leaf segments exhibited strong and symmetrical acclimation to increases or decreases in light. The photosynthetic light response curves of shade grown segments that were transferred to high light acclimated within 10–15 days to match those of segments that grew and remained in high light. Acclimation was highly localized; the light response curves of shade grown segments that remained shaded did not change, even as adjacent segments acclimated to high light. Leaf segments exposed to various treatments did not differ significantly in leaf mass per area; *Typha* leaves are apparently morphologically preformed to function in high light and allow high photosynthetic capacity, regardless of the growth environment. Likewise, nitrogen content did not differ significantly between treatments, and photosynthetic acclimation may involve a reallocation or activation of nitrogen within a leaf segment, rather than a net nitrogen translocation into or out of a segment. We interpret these patterns as an adaptive strategy that maximizes carbon gain by monocot leaves growing in a vertically heterogeneous light environment.

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1. Introduction

The light-saturated rates of leaf photosynthesis vary between sunny and shady environments (Boardman, 1977). Leaves growing in sunny locations have comparatively high photosynthetic capacities, Rubisco activity, rates of electron transport, and rates of dark respiration (Anderson et al., 1995). Some species are restricted to sunny or shady locations, and the leaves of these plants are often genetically adapted to their characteristic light environment. The leaves of other species, including those that are naturally exposed to particularly variable light environments, acclimate to local conditions (Murchie and Horton, 1997; Shawna and De Lucia, 1998; Niinemets, 2007). Acclimation to extended (days or longer) changes in light enhances net assimilation and nitrogen use efficiency while decreasing vulnerability to high light stress (Anderson and Osmond, 1987; Pearcy, 1987; Pearcy and Sims, 1994; Dreccer et al., 2000; Niinemets and Valladares, 2004; Niinemets et al., 2004).

Either anatomical or biochemical mechanisms may be involved in acclimation (Sims and Pearcy, 1994; Murchie and Horton, 1997; Evans and Porter, 2001). The local light environment influences the morphological development of leaves in many species, resulting in comparatively thick leaves in bright locations (Sims et al., 1994; Hikosaka, 1996; Niinemets, 2007). Fully expanded leaves have a limited capacity for morphological change (Sims and Pearcy, 1992; Evans and Porter, 2001; Niinemets et al., 2004), and acclimation by these leaves requires biochemical changes in carboxylation, electron transport, and light harvesting, as well as modifications to chloroplast structure and orientation (Sébba et al., 1987; De la Torre and Burkey, 1990a, b; Avalos and Mulkey, 1999; Frank et al., 2001; Murchie et al., 2002; Oguchi et al., 2003, 2005; Walters, 2005).

Monocotyledons with basal meristems, long leaves, and dense canopies may represent a case where photosynthetic acclimation by biochemical change is particularly advantageous. The grass *Lolium multilorum* (Italian ryegrass) exhibits a strong capacity for local photosynthetic acclimation along the length of a leaf (Prioul et al., 1980a, b). The leaves of plants like *Lolium* are produced in dark or dim conditions at the base of plants, and, over time, are pushed to the upper part of the canopy. *Typha latifolia* (Broadleaf Cattail), a
tall monocot that forms dense and highly productive monospecific stands in wetlands (Grace and Harrison, 1986; Rocha and Goulden, 2009), may provide an even more extreme example. T. latifolia ramets originate from rhizomes that are buried in sediment, submerged under water, and often shaded by a dense layer of litter and existing plants. Initial leaf growth is supported by carbohydrates that are either mobilized from rhizomes or translocated from older leaves. Depending on sediment thickness and water depth, and the density of the litter layer and existing canopy, the lower (younger) 50–100 cm of a Typha leaf may experience almost total darkness (Rocha et al., 2008).

These characteristics make Typha a useful experimental system for investigating the acclimation capacity of morphologically mature leaves. Basal growth in Typha allows the separation of leaf age from light environment; the oldest segments of Typha leaves are exposed to the brightest light, as opposed to plants with apical meristems, where the youngest leaves are in bright conditions. We investigated the photosynthetic capacity of T. latifolia leaves over time following step changes in shading at different locations (ages) along leaves. We hypothesized that morphologically mature Typha leaves have a strong ability for local acclimation, and that individual leaf segments acclimate to the local light level autonomously from the rest of the leaf.

2. Materials and methods

2.1. Plant material

*T. latifolia* (L.) rhizomes and crowns were collected in April 2004 at the San Joaquin Freshwater Marsh (SJFM; Goulden et al., 2007), located in Orange County, California (33°39′30″ N 117°51′30″ W). Rhizomes with an average weight of 49.7 ± 2.5 g (±1 standard deviation) were planted in 20-l pots filled with sand. Plants were grown in a greenhouse under either low light with a mean PPFD of 2.7 mol m⁻² d⁻¹ and a maximum of 159 μmol m⁻² s⁻¹, which was created with 80% neutral shade cloth, or high light with a mean PPFD of 19.4 mol m⁻² d⁻¹ and a maximum of 990 μmol m⁻² s⁻¹. Each pot had one plant, and the pots were widely spaced. The lower segments of leaves were unshaded by either neighboring plants, upper leaf segments, and the light levels were approximately constant along the length of leaves. The water level in the pots was maintained 5 cm above the sand surface with daily additions of deionized water. The pots were fertilized every 2 weeks with Flora Grow (mainly nitrogen and potassium) and Flora Micro (micronutrients, nitrogen and calcium) following the manufacturer’s instructions (General Hydroponics-USA, Sebastopol, California). The pots were drained before fertilization to avoid salt buildup.

2.2. Sun and shade transplant experiments

Two-month-old sun and shade grown plants (6 replicates) with several fully expanded leaves were placed on a bench under high light, and a pair of fully expanded leaves from each plant were selected for experimentation. Individual leaf segments between 20 and 45 cm from the tip were exposed to either sun or shade during the 15-day transfer experiment using cylinders of 80% neutral shade cloth, creating the full combination of segments exposed to (1) constant low light (SH-SH; segments that grew in shade and remained in shade throughout the transfer experiment), (2) constant high light (SU-SU; segments that grew in sun and remained in sun), (3) low to high light (SH-SU; segments that grew in shade and were transferred to sun), or (4) high to low light (SU-SH; segments that grew in sun and were transferred to shade). Additionally, a set of segments on the same leaves (uppermost 20 cm) were exposed to either constant high light (SU-SU) or low to high light (SH-SU). All treatment combinations and locations were replicated six times.

The photosynthesis rate under bright light (*A* full sun), stomatal conductance (*g*ₛ) and dark respiration rate (*R*₅) were measured every two or three days for two weeks in the middle of the sun and shade segments (10–15 and 30–35 cm from the tip), on six replicate plants using a portable gas exchange system (LI-COR Inc., Lincoln, NE, model LI6400). *A* full sun was measured at a PPFD of 2000 μmol m⁻² s⁻¹ and *R*₅ was measured in darkness after allowing 3–5 min for equilibration. Leaf temperature was controlled at 25 °C and reference CO₂ concentration at 370 μmol mol⁻¹. The leaf to air vapor pressure deficit ranged from 0.6 to 1.5 kPa.

Photosynthetic light response curves were measured after leaves had fully acclimated to a change in light (15 days). The light response curves were fit using a non-rectangular hyperbola (Marshall and Bisio, 1980; Thornley and Johnson, 1990; http://landflux.org/Tools.php). *A* full sun was calculated as the photosynthetic rate at 2000 μmol m⁻² s⁻¹; *A*₅₇ was calculated by extrapolating the regression to infinite light; *R*₅ was calculated as the y-intercept; the apparent quantum yield (*Φ*ₚ) was calculated as the slope extrapolated to darkness.

The light response curves were started at high light (2000 μmol m⁻² s⁻¹), and assimilation was measured in response to stepwise PPFD decreases until full darkness. Stomatal conductance decreased gradually in response to light decreases, and increased gradually in response to light increases. This sluggish stomatal response either led to lower rates of photosynthesis for light curves run from bright to dim conditions relative to curves run from bright to dim conditions, or forced unreasonably long equilibration times. Moreover, midday field and greenhouse observations showed that leaves exposed to a continuous PPFD of 2000 μmol m⁻² s⁻¹ for ~15 min exhibited a steady CO₂ assimilation. We therefore opted to carry out light curves from bright to dark conditions, but acknowledge that lags in stomatal adjustment may have resulted in somewhat higher *C*ᵢ for the light curves than would have been observed for fully equilibrated leaves. Nonetheless, we emphasize that our study is comparative, and the key is consistency across treatments; we executed the light curves the same way for all treatments and leaf segments.

Nitrogen concentration (per weight mg g⁻¹, and per area g m⁻²), and leaf mass per area (g m⁻²), were measured on the leaf segments used for gas exchange. Nitrogen was determined using the micro Kjeldahl technique; samples were oven dried, ground in a Wiley mill, weighed, digested, and nitrogen concentration was determined with an auto analyzer (Alpkem model RFA 300).

2.3. Light and photosynthesis measurements in the field

We characterized the vertical gradients of light and photosynthetic characteristics during midday sunny conditions in August 2004. The PPFD profile was measured through the canopy at 48 different locations in the SJFM using a horizontal quantum sensor (LI-190SB, LiCor Inc., Lincoln, NB, USA) mounted on a 2 m hand-held pole. Each profile consisted of ten individual measurements used for gas exchange. Nitrogen was determined using the micro Kjeldahl technique; samples were oven dried, ground in a Wiley mill, weighed, digested, and nitrogen concentration was determined with an auto analyzer (Alpkem model RFA 300).
seal the chamber on leaf segments further than 100 cm from the tip.

2.4. Statistical analysis

The parameters derived from the light response curves, the nitrogen content, and the leaf mass per area, were compared between treatments using Univariate ANOVA or t tests. The effect of light treatment was analyzed by Student’s t-test. Univariate ANOVAs and Tukey tests were used to compare \( A_{\text{full, sun}} \), \( A_{\text{max}} \), \( g_s \), and \( R_d \) between the light treatments within each sampling period. The effects and interactions of treatment and time following transfer were analyzed with multivariate analysis of variance (MANOVA); this analysis corrected \( F \) values due to temporal autocorrelation. MANOVA does not require the response variables to be equally correlated, assuming an unstructured variance–covariance matrix (Von Ende, 1993; Anderson, 2003). The effect of leaf position on the photosynthetic parameters of leaves growing in natural conditions was analyzed with three paired t-tests, because of the high variation among leaves. Statistical analyses were performed with JMP software version 7.0 (SAS Institute, Cary, NC, USA) and Minitab statistical software version 15.

3. Results

3.1. Photosynthetic acclimation

Fully expanded \( T. \) latifolia leaf segments exhibited strong acclimation to a change in light. The light response curves of individual segments of shade grown leaves that were transferred to high light (SH-SU) were similar to those of segments that remained in high light throughout the experiment (SU-SU; Fig. 1a and b). This acclimation was highly localized: the response curves of SH-SH segments did not change, even as adjacent SH-SU segments acclimated to high light. Likewise, the response curves of SU-SU segments did not change, even as adjacent SU-SH segments acclimated to shade (Fig. 1b).

Photosynthesis in bright light \( (A_{\text{full, sun}}) \), maximum photosynthetic capacity \( (A_{\text{max}}) \), dark respiration \( (R_d) \), and stomatal conductance \( (g_s) \) differed significantly between sun and shade segments following acclimation, regardless of initial growth conditions (Table 1 and Table 2). In contrast, intercellular CO\(_2\) concentration \( (C_i) \) and apparent quantum yield \( (\Phi_Y) \) showed no significant differences. When compared within plants that started in sun, \( A_{\text{full, sun}} \), \( A_{\text{max}} \), \( R_d \), and \( g_s \) differed significantly between sun and shade segments following acclimation, regardless of initial growth conditions (Table 1 and Table 2). In contrast, intercellular CO\(_2\) concentration \( (C_i) \) and apparent quantum yield \( (\Phi_Y) \) showed no significant differences. When compared within plants that started in sun, \( A_{\text{full, sun}} \), \( A_{\text{max}} \), \( R_d \), and \( g_s \) differed significantly from SU-SU segments. The same pattern was found for \( R_d \) and \( g_s \), but not \( \Phi_Y \) and \( C_i \), where no significant differences among treatments were found. When light treatments were compared within plants that started in the shade, SH-SU segments (10–15 or 30–35 cm) and SH-SH segments were significantly different for most parameters \( (A_{\text{full, sun}}, A_{\text{max}}, R_d, g_s) \) except \( \Phi_Y \) and \( C_i \) (Table 1 and Table 2A).

3.2. Rate of acclimation

Acclimation to a change in light occurred over a 10 to 15 day period. The MANOVA showed significant effects of light treatment and time, as well as an interaction, on leaf gas exchange (Table 2B). The rate of \( A_{\text{full, sun}} \) by SH-SU segments increased over time, and was significantly greater than that of adjacent SH-SH segments beginning on day 8 (Fig. 2a). The \( A_{\text{full, sun}} \) observed for the SH-SU segments after ~10 days was comparable to that of SU-SU segments (Fig. 2a and b). Broadly similar, or somewhat faster, responses were observed for the SH-SH treatments; \( A_{\text{full, sun}} \) decreased, reaching a rate that was comparable to that of SH-SH segments (Fig. 2b). Sun grown segments exposed continuously to high light (SU-SU) also showed a decrease in \( A_{\text{full, sun}} \) over time (Fig. 2b), though this trend was smaller than that observed for the SU-SH segments, and \( A_{\text{full, sun}} \) by the SU-SH segments was significantly less than that by the SU-SU segments beginning on day 8.

Stomatal conductance \( (g_s) \) paralleled the changes in \( A_{\text{full, sun}} \); the \( g_s \) of SH-SU segments increased over time, becoming significantly different from that of SH-SH segments on day 4, and reaching a maximum after ~10 days that was comparable to that of SU-SU segments (Fig. 3). Likewise, the \( g_s \) of SU-SH segments decreased significantly, reaching a rate that was comparable to that of SH-SH segments (Fig. 3b).

The respiration rate of shade grown segments that were shifted to high light became significantly more negative (a higher respiration rate) four days after transplant (Fig. 4a). The shade grown segments exposed continuously to low light (SH-SH) showed small changes in \( A_{\text{full, sun}} \) and \( R_d \) relative to the SH-SU segments. \( R_d \) acclimation in SU-SH segments took about 13 days, with an initial rapid change followed by a more gradual change (Fig. 4b).

3.3. Leaf nitrogen

Leaf segments exposed to the various treatments did not differ significantly in leaf mass per area \( (F_{5,28} = 1.611, P > 0.05) \), nitrogen

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**Fig. 1.** Photosynthetic light response curves on fully expanded \( Typha \) latifolia leaf segments (10–15 or 30–35 cm from the leaf tip) after acclimation to contrasting light conditions. (a) Shade grown segments shifted to high light (SH-SU) or maintained in shade (SH-SH); (b) sun grown segments shifted to low light (SU-SH) or maintained in sun (SU-SU). Each curve is the average for six different plants ± SD. The continuous line is the best-fit non-rectangular hyperbola.
Table 1
Average and standard deviation of parameters derived from light response curves (n = 6). Photosynthesis under bright light (A_{full\,sun}, μmol m^{-2} s^{-1}), maximum photosynthetic capacity (A_{max}, μmol m^{-2} s^{-1}), apparent quantum yield (Φ_{a}, μmol mol CO₂ mol photons^{-1}), and dark respiration rate (R_{d}, μmol m^{-2} s^{-1}) were calculated from a non-rectangular hyperbola fit. A_{full\,sun} was calculated for the regression at 2000 μmol m^{-2} s^{-1}, and A_{max} was calculated by extrapolating the regression to infinite light. Stomatal conductance (g_{s}, mmol m^{-2} s^{-1}) and intercellular CO₂ concentration (C_{i}, μmol mol^{-1}) were calculated from the observations at 2000 μmol m^{-2} s^{-1}.

| Treatments | A_{full\,sun} | A_{max} | Φ_{a} | R_{d} | g_{s} | C_{i} |
|-------------|---------------|---------|-------|-------|-------|-------|
| Sun segments | 31.7 ± 4.2a | 48.1 ± 10.3a | 0.055 ± 0.009a | −1.231 ± 0.5b | 831 ± 226a | 287 ± 21a |
| Shade segments | 17.9 ± 2.8b | 22.6 ± 4.6b | 0.048 ± 0.016b | −0.39 ± 0.3b | 521 ± 325b | 273 ± 21b |
| SH-SU 10–15 cm | 33.0 ± 2.4a | 53.6 ± 11.3a | 0.046 ± 0.008a | −0.9 ± 0.7b | 796 ± 161a | 286 ± 15a |
| SH-SU 30–35 cm | 35.5 ± 3.6a | 56.6 ± 3.6a | 0.052 ± 0.007a | −1.0 ± 0.4b | 871 ± 356a | 278 ± 35a |
| SH-SH 30–35 cm | 18.7 ± 2.4b | 24.1 ± 4.9b | 0.042 ± 0.016b | −0.3 ± 0.1b | 350 ± 105b | 267 ± 29b |
| SU-SU 10–15 cm | 28.2 ± 3.0a | 39.6 ± 5.5a | 0.059 ± 0.004a | −1.5 ± 0.2b | 710 ± 142b | 289 ± 11b |
| SU-SU 30–35 cm | 30.2 ± 4.1a | 42.5 ± 6.1a | 0.062 ± 0.008a | −1.5 ± 0.3b | 891 ± 232b | 295 ± 17b |
| SU-SH 30–35 cm | 17.1 ± 3.3b | 21.2 ± 4.3b | 0.054 ± 0.013a | −0.7 ± 0.2b | 345 ± 078b | 279 ± 7b |

Lower case letters indicate significant differences among treatments at P ≤ 0.05.

4. Discussion

4.1. Typha's capacity for photosynthetic acclimation

Individual Typha leaf segments have a strong ability for acclimation. Leaf segments that grew in sun and were transferred to shade (SU-SH) developed an A_{full\,sun} of ~15 μmol m^{-2} s^{-1} within ~15 days, which was similar to that observed for segments that grew and remained in shade. Likewise, leaf segments grown in shade and transferred to sun (SH-SU) developed an A_{full\,sun} of ~30 μmol m^{-2} s^{-1} within ~10 days, which was similar to that observed for segments that grew and remained in sun (Figs. 1 and 2). We found no evidence of photo-inhibition following the shift from low to high light; A_{full\,sun} increased by ~30% within three days of transfer to sunny conditions. Sun-acclimated leaf segments were capable of impressive rates of CO₂ uptake (~30 μmol m^{-2} s^{-1}), which are comparable to those observed for other rapidly growing herbaceous plants.

Dark respiration (R_{d}) changed in concert with A_{full\,sun}. The R_{d} of segments grown in shade and transferred to sun (SH-SU) increased from ~1 to ~2 μmol m^{-2} s^{-1} to ~3 μmol m^{-2} s^{-1}; the R_{d} of segments grown in sun and transferred to shade (SU-SH) decreased from ~2.5 to ~3 μmol m^{-2} s^{-1} to ~1.5 μmol m^{-2} s^{-1} (Figs. 1 and 2). Acclimation was largely independent of leaf age; comparatively old (10–15 cm from the leaf tip) and young (30–35 cm) segments responded in similar ways to changing light (Figs. 1 and 2).

The changes in A_{full\,sun} and R_{d} occurred over 10 to 15 days following the light shift. This rate of acclimation is consistent with previous reports of 7–15 days (Prioul et al., 1980b; Sebaa et al., 1987; De la Torre and Burkey, 1990a; b; Sims and Pearcy, 1991;
C. Tinoco Ojanguren, M.L. Goulden / Aquatic Botany 111 (2013) 54–61

Fig. 2. Temporal patterns of photosynthesis under bright light ($A_{\text{full sun}}$) following light changes by *Typha latifolia* leaf segments (10–15 or 30–35 cm from the leaf tip). (a) Shade grown segments shifted to high light (SH-SU) or maintained in shade (SH-SH); (b) sun grown segments shifted to low light (SU-SH) or maintained in sun (SU-SU). Each point is the average for six different plants. Lower case letters indicate significant differences between treatments for a sampling period; a lack of letters indicates insignificant differences at $p \leq 0.05$.

Naidu and De Lucia, 1998; Oguchi et al., 2005). *Typha* leaf segments that were continuously exposed to high light showed a slow $A_{\text{full sun}}$ decline. This decline may have resulted from leaf aging, which has been reported to accelerate in high light (Sebaa et al., 1987; Nilsen et al., 1988).

The intercellular CO$_2$ concentration remained constant among the treatments (Table 1), and the changes in $A_{\text{full sun}}$ were attributable to shifts in photosynthetic capacity rather than CO$_2$ supply. Stomatal conductance paralleled the changes in $A_{\text{full sun}}$ (Figs. 2 and 3). We did not find evidence of changing patterns of stomatal control, and the simplest explanation is that conductance simply responded to $A_{\text{full sun}}$ acclimation.

Leaf acclimation was highly localized; individual leaf segments acclimated to local light autonomously from the rest of the leaf. Previous studies of leaf acclimation have focused on entire leaves, and acclimation by segments of mature leaves has received less attention (Prioul et al., 1980a; Sebaa et al., 1987). The ability for mature leaf acclimation varies among species, and has been reported in several herbaceous and a few woody species (Kamaluddin and Grace, 1992; Pearcy and Sims, 1994). Our findings of segmented acclimation are most closely related to those of Prioul et al. (1980a), who found that $A_{\text{full sun}}$ chlorophyll content, and Rubisco activity changed markedly from the base to tip of *Lolium multiflorum* leaves. Likewise, reciprocal transplants to contrasting light conditions in *L. multiflorum* showed the capability for rapid photosynthetic reacclimation to high and low light along the leaf, even in fully expanded leaves (Prioul et al., 1980b; Sebaa et al., 1987).

Detailed investigations of leaf anatomy and biochemistry are beyond the scope of this study, but our observations provide evidence of the mechanisms responsible for acclimation. Photosynthetic acclimation in *Typha* appears to result from biochemical or cellular changes, and a general up or down regulation of metabolic activity within individual leaf segments (Figs. 2 and 5). Acclimation did not involve a significant change in nitrogen content on either a mass or area basis. We did not find evidence that a morphological change in leaf thickness, or a net movement of nitrogen into or out of a leaf segment, were required for photosynthetic acclimation.

4.2. Adaptive significance of acclimation in *Typha*

Our results confirm previous reports that species from highly variable light environments have a strong capacity for photosynthetic acclimation. In the case of *T. latifolia*, light heterogeneity is created by the combination of a basal meristem and a dense canopy of live leaves and litter (Rocha et al., 2008). *Typha* leaves are exposed to markedly different light environments as they grow and individual segments are pushed upward (Fig. 5a). The upper segments of leaves in the field, which occurred in a brighter environment, had
Fig. 4. Temporal patterns of dark respiration rate in response to light changes by *Typha latifolia* leaf segments (10–15 or 30–35 cm from the leaf tip). (a) Shade grown segments shifted to high light (SH-SU) or maintained in shade (SH-SH); (b) sun grown segments shifted to low light (SU-SH) or maintained in sun (SU-SU). Each point is the average for six different plants. More negative rates of CO2 flux signify a greater loss of carbon and a higher rate of respiration. Lower case letters indicate significant differences between treatments for a sampling period; a lack of letters indicates insignificant differences at $p \leq 0.05$.

Fig. 5. (a) Midday photosynthetic photon flux density at 0, 0.6, 1.2, and 3.0 m above the soil surface (PPFD; means ± 1 standard deviation; $n=48$) at the San Joaquin Freshwater Marsh (SJFM). The lower three locations were within the canopy; the 3.0-m observation was above the canopy. (b) *Typha latifolia* light response curves measured at the SJFM as a function of distance from the leaf tip (30, 50, 100 cm). Each curve is the mean ± 1 standard deviation of 5 curves on different plants. The continuous line is the best-fit non-rectangular hyperbola.

We hypothesize that the patterns of leaf photosynthesis and conductance in *Typha* reflect four properties. (1) Mature *Typha* leaf segments are morphologically preformed to function in high light and allow high rates of $A_{\text{full sun}}$, regardless of the current or growth environment. (2) Mature *Typha* leaf segments contain sufficient amounts of nitrogen to support high rates of $A_{\text{full sun}}$, regardless of the current or growth environment. (3) Mature *Typha* leaf segments rapidly reallocate nitrogen between active and inactive pools in response to local light availability; acclimation occurs at a local level and does not require nitrogen translocation into or out of a leaf segment. (4) The controls on stomatal conductance remain constant over time; the patterns of conductance (Fig. 3) can be explained based on simple, short-term adjustments that act to maintain a nearly constant $C_i$ concentration despite the changes in $A_{\text{full sun}}$ and the physical environment.

We interpret these patterns as a highly plastic strategy that maximizes carbon gain by a monocot growing in a vertically heterogeneous light environment. The construction of leaves that are morphologically capable of high rates of $A_{\text{full sun}}$ is a simple consequence of the spatial decoupling of the growth environment from that experienced later in life. The strategy of investing in leaves that have a morphological capability for high rates of CO2 uptake appears advantageous given a situation where it is difficult to predict which leaves will ultimately experience high light conditions, and where fully expanded leaves are unable to morphologically adjust to a change in light.

High rates of $A_{\text{full sun}}$ come at the cost of high $R_d$. A leaf with a low $A_{\text{full sun}}$ in a shady site has a more favorable carbon balance than a leaf with a high $A_{\text{full sun}}$ in the same environment; the carbon savings associated with reduced $R_d$ more than offset the loss of potential photosynthesis during occasional sunflecks. The rapid down regulation of $A_{\text{full sun}}$ following transfer to shade would be expected to improve the C balance of leaf segments by decreasing $R_d$. The initial changes in $R_d$ following light change were probably tied to the changes in leaf photosynthetic activity, and the energy requirements to process and export carbohydrates, as well as changes in protein turnover (Sims and Pearcy, 1991; Pons and Pearcy, 1994; Noguchi et al., 2001). Subsequent changes in $R_d$ may have been associated with changes in the biosynthesis and/or
degradation of cellular components, such as Rubisco, cytochrome f, and chloroplast ATPase (Chow and Anderson, 1987; De la Torre and Burke, 1990a; Sims and Pearcy, 1991).

The amount of nitrogen in leaf segments remained nearly constant over time, leading us to hypothesize a fraction of the nitrogen in shaded segments is stored in inactive pools and is rapidly activated following transfer to high light. These changes may include adjustments in partitioning among carboxylation, electron transport and light harvesting, chloroplast ultrastructure, volume, and orientation (Sebaa et al., 1987; De la Torre and Burke, 1990a; Sailaja and Rama Das, 1995; Frank et al., 2001; Oguchi et al., 2003, 2005). The high N content of shaded segments should not be viewed as wasteful. These nutrients can be reabsorbed and reallocated to the rhizome during senescence; a high reabsorption efficiency of P and N (45–75%) has been reported for Typha domingensis (Miao, 2004; Rejmánková, 2005). Moreover, this strategy allows a leaf segment to rapidly and autonomously respond to a change in light availability, without importing or exporting nitrogen to or from other leaf segments or organs.

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