UC Irvine

UC Irvine Previously Published Works

Title

Photosynthetic acclimation within individual *Typha latifolia* leaf segments

Permalink

<https://escholarship.org/uc/item/3mg8d62j>

Journal

Aquatic Botany, 111

ISSN

0304-3770

Authors

Tinoco Ojanguren, C
Goulden, ML

Publication Date

2013-11-01

DOI

10.1016/j.aquabot.2013.08.007

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

Photosynthetic acclimation within individual *Typha latifolia* leaf segments

Clara Tinoco Ojanguren^{a,*}, Michael L. Goulden^b

^a Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 1354, Hermosillo, Sonora, C.P. 83000, Mexico

^b Department of Earth System Science, University of California, 3319 Croul Hall, Irvine, CA 92697, USA

ARTICLE INFO

Article history:

Received 10 January 2012

Received in revised form 26 August 2013

Accepted 29 August 2013

Available online 16 September 2013

Keywords:

Freshwater marsh

Light profile

CO₂ assimilation capacity

Dark respiration

Nitrogen content

ABSTRACT

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

© 2013 Elsevier B.V. All rights reserved.

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; Percy, 1987; Percy 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 Percy, 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 Percy, 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 (Sebaa 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 multiflorum* (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

* Corresponding author at: Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 1354, Hermosillo, Sonora, C.P. 83000, Mexico. Tel.: +52 662 213 93 03; fax: +52 662 213 93 03.

E-mail addresses: claral@unam.mx (C. Tinoco Ojanguren), mgoulden@uci.edu (M.L. Goulden).

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 $2.7 \text{ mol m}^{-2} \text{ d}^{-1}$ and a maximum of $159 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, which was created with 80% neutral shade cloth, or high light with a mean PPFD of $19.4 \text{ mol m}^{-2} \text{ d}^{-1}$ and a maximum of $990 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$. Each pot had one plant, and the pots were widely spaced. The lower segments of leaves were unshaded by either neighboring plants or 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 ($A_{\text{full sun}}$), stomatal conductance (g_s) and dark respiration rate (R_d) 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 6400). $A_{\text{full sun}}$ was measured at a PPFD of $2000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ and R_d was measured in darkness after allowing 3–5 min for equilibration. Leaf temperature was controlled at 25 °C and reference CO_2 concentration at $370 \text{ } \mu\text{mol mol}^{-1}$. 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 Biscoe, 1980; Thornley and Johnson, 1990; <http://landflux.org/Tools.php>). $A_{\text{full sun}}$ was calculated as the photosynthetic rate at $2000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$; A_{max} was calculated by extrapolating the regression to infinite light; R_d was calculated as the y-intercept; the apparent quantum yield (Φ_y) was calculated as the slope extrapolated to darkness.

The light response curves were started at high light ($2000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$), 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 dim to bright 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 $2000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ for ~15 min exhibited a steady CO_2 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 recorded with a datalogger (CR10X, Campbell Scientific Inc., Logan, UT, USA) at 0.0, 0.6, 1.2, and 3.0 m above the sediment surface. The 3.0 m measurement was above the canopy. LAI was measured at the base of the canopy with a LI-COR LAI-2000, assuming non-clumped leaves and without distinguishing between live leaves and litter. Photosynthetic light response curves were measured on three segments (30, 50 and 100 cm from the tip) of fully expanded leaves from 5 different plants. The cross section of leaves changed from flat at the tip to triangular at the base, and it was not possible to

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_{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_{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 (Φ_y) showed no significant differences. When compared within plants that started in sun, $A_{\text{full sun}}$ and A_{max} of SU-SU segments (10–15 and 30–35 cm) differed significantly from SU-SH segments. The same pattern was found for R_d and g_s , but not Φ_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 and 30–35 cm) and SH-SH segments were significantly different for most parameters ($A_{\text{full sun}}$, A_{max} , R_d , g_s) except Φ_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 SU-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

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 $\pm$ SD. The continuous line is the best-fit non-rectangular hyperbola.

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

Table 1

Average and standard deviation of parameters derived from light response curves ($n = 6$). Photosynthesis under bright light ($A_{\text{full sun}}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum photosynthetic capacity (A_{max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), apparent quantum yield (Φ_y , $\text{mol CO}_2 \text{ mol photons}^{-1}$), and dark respiration rate (R_d , $\mu\text{mol m}^{-2} \text{s}^{-1}$) were calculated from a non-rectangular hyperbola fit. $A_{\text{full sun}}$ was calculated for the regression at $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$, and A_{max} was calculated by extrapolating the regression to infinite light. Stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) and intercellular CO_2 concentration (C_i , $\mu\text{mol mol}^{-1}$) were calculated from the observations at $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$.

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

Lower case letters indicate significant differences among treatments at $P \leq 0.05$

Table 2

(A) Student's t -test results comparing sun and shade segments, and Univariate ANOVAs and Tukey test results evaluating differences in parameters derived from light response curves among light treatments after acclimation. Photosynthesis under bright light ($A_{\text{full sun}}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum photosynthetic capacity (A_{max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), apparent quantum yield (Φ_y), dark respiration rate (R_d), and stomatal conductance (g_s). (B) Results of multivariate analysis of variance (MANOVA) comparing gas exchange characteristics ($A_{\text{full sun}}$, A_{max} , g_s and R_d) of *Typha latifolia* leaf segments in response to light transfers and time since transfer.

(A) Treatments comparison	$A_{\text{full sun}}$	A_{max}	Φ_y	R_d	g_s	C_i
Sun segments vs. shade segments.	$t = 11.587$ $P < 0.0001$	$t = 10.211$ $P < 0.0001$	$t = 14.864$ $P = 0.196$	$t = -5.573$ $P < 0.0001$	$t = 5.708$ $P < 0.0001$	$t = 1.353$ $P = 0.185$
SU-SU 10–15 cmSU-SU 30–35 cmSU-SH 30–35 cm	$F_{2,15} = 61.775$ $P < 0.0001$	$F_{2,15} = 29.95$ $P < 0.0001$	$F_{2,15} = 1.057$ $P = 0.371$	$F_{2,15} = 17.57$ $P < 0.0001$	$F_{2,15} = 5.491$ $P < 0.05$	$F_{2,15} = 0.881$ $P = 0.434$
SH-SU 10–15 cmSH-SU 30–35 cmSH-SH 30–35 cm	$F_{2,15} = 24.079$ $P < 0.0001$	$F_{2,15} = 27.326$ $P < 0.0001$	$F_{2,15} = 1.088$ $P = 0.362$	$F_{2,15} = 7.849$ $P < 0.0047$	$F_{2,15} = 8.685$ $P < 0.01$	$F_{2,15} = 0.703$ $P = 0.510$
(B) Effects comparison	F	$P > F$	Degrees of freedom			
Light treatment	31.868	0.0001	15, 20			
Time	4.630	0.0001	18, 620			
Time $\times$ treatment	3.496	0.0001				

content per weight ($F_{5,28} = 1.8777$, $P > 0.05$) or nitrogen content per area ($F_{5,28} = 0.275$, $P > 0.05$; Table 3).

3.4. Light environment and photosynthetic characteristics at the SJFM

The fully developed *Typha* canopy at the SJFM had a Leaf Area Index of $4.75\text{--}6.39 \text{ m}^2 \text{m}^{-2}$. The midday PPFD in August 2004 decreased from $1930 \mu\text{mol m}^{-2} \text{s}^{-1}$ above the canopy to $85 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the sediment surface (Fig. 5a). $A_{\text{full sun}}$ was similar for leaf segments that were 30 and 50 cm from the tip, and 30–40% reduced for segments 100 cm from the tip (Fig. 5b). Paired t -test comparisons of the light response parameters between 30 and 100 cm showed significant differences for $A_{\text{full sun}}$ ($t = -6.142$, $P < 0.01$) but not R_d ($t = -0.749$, $P = 0.495$) or Φ_y ($t = 0.423$, $P = 0.693$).

Table 3

Leaf mass per area (LMA), nitrogen content per weight (N_w), and nitrogen content per area (N_a), for *Typha latifolia* leaf segments after acclimation to light transfer (average $\pm$ S.D.; $n = 4\text{--}6$).

Treatment	LMA (g m^{-2})	N_w (mg g^{-1})	N_a (g m^{-2})
SH-SU 10–15 cm	85.3 ± 12.6	19.6 ± 6.7	1.7 ± 0.5
SH-SH 30–35 cm	87.4 ± 7.1	17.0 ± 1.9	1.5 ± 0.2
SH-SU 30–35 cm	88.2 ± 20.7	21.1 ± 4.1	1.7 ± 0.5
SU-SU 10–15 cm	89.9 ± 6.4	19.4 ± 2.1	1.7 ± 0.1
SU-SH 30–35 cm	90.9 ± 16.4	14.6 ± 3.7	1.4 ± 0.3
SU-SU 30–35 cm	100.7 ± 9.5	17.6 ± 4.4	1.7 ± 0.4

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 $A_{\text{full sun}}$ of $\sim 15 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 $A_{\text{full sun}}$ of $\sim 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 photoinhibition following the shift from low to high light; $A_{\text{full sun}}$ increased by $\sim 30\%$ within three days of transfer to sunny conditions. Sun-acclimated leaf segments were capable of impressive rates of CO_2 uptake ($\sim 30 \mu\text{mol m}^{-2} \text{s}^{-1}$), which are comparable to those observed for other rapidly growing herbaceous plants.

Dark respiration (R_d) changed in concert with $A_{\text{full sun}}$. The R_d of segments grown in shade and transferred to sun (SH-SU) increased from -1 to $-2 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $\sim -3 \mu\text{mol m}^{-2} \text{s}^{-1}$; the R_d of segments grown in sun and transferred to shade (SU-SH) decreased from -2.5 to $-3 \mu\text{mol m}^{-2} \text{s}^{-1}$ to -1 to $-1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (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 $A_{\text{full sun}}$ 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;

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., 1980b; 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; Percy 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

Fig. 3. Temporal patterns of stomatal conductance 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 $p \leq 0.05$.

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 3). Acclimation appears to be unrelated to changes in either C_i (Fig. 4) or gross leaf morphology (leaf mass per area). 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 CO_2 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 $p \leq 0.05$.

higher rates of CO_2 uptake (Fig. 5b). Previous field studies on *T. latifolia* have also reported large CO_2 assimilation and g_s gradients along leaves (Knapp and Yavitt, 1995).

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

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.

that experienced later in life. The strategy of investing in leaves that have a morphological capability for high rates of CO_2 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 Burkey, 1990a, b; 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 Burkey, 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.

Acknowledgments

This study was supported by a University of California–Consejo Nacional de Ciencia y Tecnología (UCMEXUS-CONACYT) sabbatical scholarship to CTO, and also by the University of California Water Resources Center. This work was performed at the San Joaquin Freshwater Marsh Reserve (SJFM), which is a component of the University of California Natural Reserve System. We thank Bill Bretz and Peter Bowler for managing and supporting the SJFM, Dr. Steve Weller for greenhouse facilities at University of California at Irvine, Dr. Juan Fornoni and Dr. Carlos Anaya for statistical advice, Enrique Solis for N analysis and Anabel Díaz Martínez for lab assistance.

References

- Anderson, J.M., Osmond, C.B., 1987. Shade-sun responses: compromises between acclimation and photoinhibition. In: Kyle, D.J., Osmond, C.B., Arntzen, C.J. (Eds.), *Photoinhibition*. Elsevier Science Publishers, Amsterdam, pp. 2–34.
- Anderson, J.M., Chow, W.S., Park, Y.I., 1995. The grand design of photosynthesis: acclimation of the photosynthetic apparatus to environmental cues. *Photosynth. Res.* 46, 129–139.
- Anderson, T.W., 2003. *An Introduction to Multivariate Statistical Analysis*, 3rd edition. Wiley Series in Probability and Statistics, USA, pp. 721.
- Avalos, G., Mulkey, S., 1999. Photosynthetic acclimation of the liana *Stigmaphyllon lindenianum* to light changes in a tropical dry forest canopy. *Oecologia* 120, 475–484.
- Boardman, N.K., 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28, 355–377.
- Chow, W.S., Anderson, J.M., 1987. Photosynthetic responses of *Pisum sativum* to an increase in irradiance during growth. I. Photosynthetic activities. *Aust. J. Plant Physiol.* 14, 1–8.
- De la Torre, W.R., Burkey, K.O., 1990a. Acclimation of barley to changes in light intensity: chlorophyll organization. *Photosynth. Res.* 24, 117–125.
- De la Torre, W.R., Burkey, K.O., 1990b. Acclimation of barley to changes in light intensity: photosynthetic electron transport activity and components. *Photosynth. Res.* 24, 127–136.
- Dreccer, M.F., Oijen, M., van Schapendonk, A.H.C.M., Pot, C.S., Rabbinge, R., 2000. Dynamics of vertical leaf nitrogen distribution in a vegetative wheat canopy, impact on canopy photosynthesis. *Ann. Bot.* 86, 821–831. <http://dx.doi.org/10.1006/anbo.2000.1244>.
- Evans, J.R., Porter, H., 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.* 24, 755–767.
- Frank, E., Le Roux, J., Millard, P., Dreyer, E., Jaouen, G., Saint-Joanis, B., Wendler, R., 2001. Changes in total nitrogen and partitioning of leaf nitrogen drive photosynthetic acclimation to light in fully developed walnut leaves. *Plant Cell Environ.* 24, 1279–1288.
- Goulden, M.L., Litvak, M., Miller, S.D., 2007. Factors that control *Typha* marsh evapotranspiration. *Aquat. Bot.* 86, 97–106.
- Grace, J.B., Harrison, J.S., 1986. The biology of Canadian weeds. 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha x glauca* Godr. *Can. J. Plant Sci.* 66, 361–379.
- Hikosaka, K., 1996. Effects of leaf age, nitrogen nutrition and photon flux density on the organization of the photosynthetic apparatus in leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. *Planta* 198, 144–150.
- Kamaluddin, M., Grace, J., 1992. Photoinhibition and light acclimation in seedlings of *Bischofia javanica*, a tropical forest tree from Asia. *Ann. Bot.* 69, 47–52.
- Knapp, A.K., Yavitt, J.B., 1995. Gas exchange characteristics of *Typha latifolia* L. from nine sites across North America. *Aquat. Bot.* 49, 203–215.
- Marshall, B., Biscoe, P.V., 1980. A model for C3 leaves describing the dependence of net photosynthesis on irradiance. I. Derivation. *J. Exp. Bot.* 31, 29–39.
- Miao, S., 2004. Rhizome growth and nutrients resorption: mechanisms underlying the replacement of two clonal species in Florida everglades. *Aquat. Bot.* 78, 55–66. <http://dx.doi.org/10.1016/j.aquabot.2003.09.001>.
- Murchie, E.H., Horton, P., 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity and habitat preference. *Plant Cell Environ.* 20, 438–448.
- Murchie, E.H., Hubbert, S., Chen, Y., Peng, S., Horton, P., 2002. Acclimation of rice photosynthesis to irradiance under field conditions. *Plant Physiol.* 130, 1999–2010.
- Naidu, S.L., De Lucia, E.H., 1998. Physiological and morphological acclimation of shade grown tree seedlings to late season canopy gap formation. *Plant Ecol.* 138, 27–40.
- Nilsen, E.T., Stetler, D.A., Gassman, C.A., 1988. Influence of age and microclimate on the photochemistry of *Rhododendron maximum* leaves. II. Chloroplast structure and photosynthetic light response. *Am. J. Bot.* 75, 1526–1534.
- Niinemets, U., Valladares, F., 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. *Plant Biol.* 6, 254–268. <http://dx.doi.org/10.1055/s-2004-817881>.
- Niinemets, U., Kull, O., Tenhunen, J.D., 2004. Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. *Plant Cell Environ.* 27, 293–313.
- Niinemets, U., 2007. Photosynthesis and resource distribution through plant canopies. *Plant Cell Environ.* 30, 1052–1071.
- Noguchi, K., Nakajima, N., Terashima, I., 2001. Acclimation of leaf respiratory properties in *Alocasia odora* following reciprocal transfers of plants between high and low light environments. *Plant Cell Environ.* 24, 831–839.
- Oguchi, R., Hikosaka, K., Hirose, T., 2003. Does the photosynthetic light acclimation need change in leaf anatomy? *Plant Cell Environ.* 26, 505–512.
- Oguchi, R., Hikosaka, K., Hirose, T., 2005. Leaf anatomy as a constraint for photosynthetic acclimation: differential responses in leaf anatomy to increasing growth irradiance among three deciduous trees. *Plant Cell Environ.* 28, 916–927.
- Pearcy, R.W., 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. *Funct. Ecol.* 1, 169–178.
- Pearcy, R.W., Sims, D.A., 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. In: Caldwell, M.M., Pearcy, R.W. (Eds.), *Exploitation of Environmental Heterogeneity by Plants – Ecophysiological Processes Above and Belowground*. Academic Press, San Diego, pp. 145–174.
- Pons, T.L., Pearcy, R.W., 1994. Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiol. Plant.* 92, 636–644.
- Prioul, J.L., Brangeon, J., Reyss, A., 1980a. Interaction between external and internal conditions in the development of photosynthetic features in a grass leaf. I. Regional responses along a leaf during and after low-light or high-light acclimation. *Plant Physiol.* 66, 762–769.
- Prioul, J.L., Brangeon, J., Reyss, A., 1980b. Interaction between external and internal conditions in the development of photosynthetic features in a grass leaf. II. Reversibility of light induced responses as a function of developmental stages. *Plant Physiol.* 66, 770–774.
- Rejmánková, E., 2005. Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytol.* 167, 471–482. <http://dx.doi.org/10.1111/j.1469-8137.2005.01449.x>.
- Rocha, A.V., Goulden, M.L., 2009. Why is marsh productivity so high? New insights from eddy covariance and biomass measurements in a *Typha* marsh. *Agric. For. Meteorol.* 149, 159–168.
- Rocha, A.V., Potts, D.L., Goulden, M.L., 2008. Standing litter as a driver of interannual CO₂ exchange variability in a freshwater marsh. *JGR Biogeosciences* 113, G04020. <http://dx.doi.org/10.1029/2008JG000713>.
- Sailaja, M.V., Rama Das, V.S., 1995. Photosystem II acclimation to limiting growth light in fully developed leaves of *Amaranthus hypocondriacus* L., NAD-ME C₄ plant. *Photosynth. Res.* 46, 227–233.
- Sebaa, E., Prioul, J.L., Brangeon, J., 1987. Acclimation of adult *Lolium multiflorum* leaves to changes in irradiance: effect on leaf photosynthesis and chloroplast structure. *J. Plant Physiol.* 127, 431–441.
- Shawna, L.N., De Lucia, E.H., 1998. Physiological and morphological acclimation of shade grown tree seedlings to late season canopy gap formation. *Plant Ecol.* 138, 27–40.
- Sims, D.A., Pearcy, R.W., 1991. Photosynthesis and respiration in *Alocasia macrorrhiza* following transfers to high and low light. *Oecologia* 86, 447–453.
- Sims, D.A., Pearcy, R.W., 1992. Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Araceae) to a transfer from low to high light. *Am. J. Bot.* 79, 449–455.
- Sims, D.A., Pearcy, R.W., 1994. Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole plant performance. I. Carbon balance and allocation at different daily photon flux densities. *Plant Cell Environ.* 17, 881–887.

- Sims, D.A., Gebauer, R.L.E., Percy, R.W., 1994. Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole-plant performance. II. Simulation of carbon balance and growth at different photon flux densities. *Plant Cell Environ.* 17, 889–900.
- Thornley, J.H.M., Johnson, I.R., 1990. *Plant and crop modelling. A mathematical approach to plant and crop physiology.* Oxford Science Publications, Oxford.
- Von Ende, C.N., 1993. Repeated measures analysis: growth and other time-dependent measures. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments.* Chapman & Hall, New York, pp. 113–137.
- Walters, R.G., 2005. Towards an understanding of photosynthetic acclimation. *J. Exp. Bot.* 56, 435–447.