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ORIGINAL PAPER

Physiological responses to short-term water and light stress in native and invasive plant species in southern California

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Abstract As climate variability increases in low-resource environments, the ability of native and invasive species to tolerate stress and respond to large, ephemeral resource pulses will strongly influence plant fitness and, consequently, competitive outcomes. We examined how native and invasive species occurring in arid coastal sage scrub communities in southern California responded to water and high-light stress. We also examined how plants responded to irrigation following short-term water stress. While species responded differently to water and light treatments, no general pattern emerged between native and invasive species. Photosynthetic function of *Ricinus communis* (invasive) and *Salvia mellifera* (native) was most robust to water stress and most responsive to irrigation following water stress. Leaf transpiration data suggested that *Ricinus* and *Salvia* maintained photosynthetic function by high water use efficiency rather than higher water status via large root biomass. *Brassica nigra* (invasive) and *Encelia californica* (native) were more resistant to photoinhibition in response to high-light stress than *Ricinus*, *Salvia*, *Artemesia californica* (native) or *Nicotiana glauca* (invasive). Our data suggest that native and invasive species in these arid systems display a range of physiological responses to stress and that strategies for invasive species control or native ecosystem restoration based on plant responses to stress may require species-specific approaches.

Keywords Resource availability · Water stress · Photoinhibition · Resource use efficiency · Precipitation pulses · Plasticity

Introduction

One of the most widely accepted hypotheses explaining the success of invasive plant species is the fluctuating resource hypothesis, which posits that invasion is facilitated by high resource availability resulting from disturbance or low resource uptake by the native plant community (Davis et al. 2000). Invasive species generally possess physiological, morphological or life history traits that allow them to quickly colonize disturbed areas (e.g., copious small seeds) or grow rapidly in response to high resource availability (e.g., high growth rate, leaf area ratio, photosynthetic rate; Grotkopp et al. 2002; Hamilton et al. 2005; Rejmanek et al. 2005), thereby outperforming native species. However, numerous invasive species inhabit low-resource systems, which are characterized by extreme limitation of light, water or nutrient availability, and few studies have examined the mechanisms by which invasive species

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succeed in these systems (Baruch and Goldstein 1999; Funk 2008; Funk and Vitousek 2007; Krueger-Mangold et al. 2006; Leishman and Thomson 2005; Muth and Pigliucci 2007; Reed et al. 2005).

Low-resource systems are often temporally or spatially variable with plants receiving resource pulses, defined as episodes of increased resource availability that combine low frequency, large magnitude and short duration (Yang et al. 2008). Plant fitness can depend on utilization of resources during these pulses. For example, it is thought that a large percentage of annual carbon assimilation in desert plants occurs during the few days following each large precipitation event (Loik 2007). A rapid response to water availability is advantageous given the threat of immediate evaporation (particularly from shallow soil layers) and competition for water from other plant species (Chesson et al. 2004; Loik 2007; Noy-Meir 1973). Thus, the ability of species occurring in low-resource environments to respond to resource pulses at physiological (e.g., photosynthesis) and morphological (e.g., increased root growth) levels and on short time scales will strongly influence plant fitness and, ultimately, community composition (Chesson et al. 2004).

Several studies have shown that invasive species are more phenotypically plastic than natives in response to changes in environmental factors on time scales of weeks to months (Burns and Winn 2006; Funk 2008; Gleason and Ares 2004; Muth and Pigliucci 2007; Niinemets et al. 2003; Padgett and Allen 1999; Williams and Black 1994). Fewer studies have examined how native and invasive species respond to shorter-term changes (days) in environmental factors (Durand and Goldstein 2001; Yamashita et al. 2000) and many of these studies have focused on grasses (Huxman et al. 2004; Ignace et al. 2007; Resco et al. 2008). In this study, we conducted two experiments to investigate stress and stress-recovery of native and invasive species over a seven day period. In the first experiment, we examined how species responded to the resumption of irrigation following moderate drought. In the second experiment, we examined how shade-acclimated plants coped with high-light stress. We examined physiological responses indicative of carbon assimilation and stress in plant species that are native to or invasive in southern California coastal sage scrub communities. Sage scrub communities occur throughout California in semi-arid habitats receiving no more than 300 mm of annual precipitation (Rundel and Gustafson 2005). These communities are dominated by short-statured, shallow-rooted shrubs that drop their leaves during the summer drought season, which typically lasts for six months or more.

Our objective was to determine if native species in this arid system would be more stress tolerant than invasive species by maintaining higher rates of carbon assimilation in response to both water stress and high-light stress. Species growing in arid systems commonly experience simultaneous water and high-light stress. As stomata close to reduce transpiration loss, lower intercellular CO_2 concentration decreases the activity of the Calvin cycle and, consequently, demand for products of the light-harvesting photosystems and electron transport chain. These compounds have very negative redox potentials and their accumulation in chloroplasts causes photoinhibition as they react with cellular components (proteins, lipids) associated with photosynthesis (Lawlor and Tezara 2009). Additionally, a large proportion of annual rainfall is delivered during multi-day winter and spring storms (http://cdec.water.ca.gov) where light availability can fall below 25% of full sunlight (JL Funk, unpublished data). Thus, the ability to minimize photoinhibition during conditions of high soil water availability following storms is likely to improve plant fitness. Our previous work in arid regions of Hawaii demonstrated that invasive species maintained high carbon assimilation despite low water availability, which may allow them to persist in these low-resource systems; however, tolerance of high-light stress was not examined (Funk and Vitousek 2007). Based on our previous work in Hawaii, we predicted that invasive and native species in this arid system would be similarly tolerant to both water and light stress.

Materials and methods

In February 2008, seedlings of three species native to southern California coastal sage scrub communities (*Encelia californica, Artemesia californica, Salvia mellifera*) were obtained from a local nursery and seeds for three common invasive species in these vegetation communities (*Brassica nigra, Nicotiana glauca, Ricinus communis*) were germinated. It is widely thought that rooting depth explains interspecific patterns of water use across functional groups (Noy-Meir 1973; Weltzin and McPherson 1997, Gebauer and Ehleringer 2000; Schwinning and Ehleringer 2001, Jenerette et al. 2008); thus, we selected co-occurring native and invasive species with similar rooting depths. All native species are perennial subshrubs with fibrous root systems that penetrate less than 2 m into the soil (Hellmers et al. 1955). *Nicotiana* and *Ricinus* are perennial shrubs. In its native range, *Ricinus* has course major roots growing downwards but not exceeding 1.5 m in depth (Comar et al. 2004). *Brassica* is an annual herb with a fibrous root system not exceeding 1 m in depth. All species employ the C3 photosynthetic pathway and all species co-occur throughout disturbed coastal sage scrub habitat in southern California.

Plants were grown in a 4:1 mixture of potting soil (cactus mix, E.B. Stone Organics) and perlite. For the first two months, all plants were grown in the Chapman University greenhouse where light levels averaged 300 μmol photon m^{-2} and average daily maximum temperature ranged from 21–38°C. Plants received monthly doses of 7 g of 8-7-6 (N–P–K plus micronutrients, percent by volume) fertilizer (Miracle Gro, The Scotts Company, Marysville, OH). A foliar systemic insecticide was applied monthly (Orthenex, The Ortho Group, Marysville, OH). In April 2008, all plants were moved outside of the greenhouse and exposed to full sunlight (2,000 μmol photon m^{-2} s^{-1}) and ambient temperature conditions. Plants were allowed to acclimate to these environmental conditions for one month prior to water and light manipulation studies.

Water manipulation

In May, five individuals each of *Encelia, Salvia, Nicotiana* and *Ricinus* were randomly placed into one of three treatments: control (watered every day, soil volumetric water content (*VWC*) 25–30%), stress (*VWC* < 10%), and stress-recovery (*VWC* < 10% before watering resumed). Each treatment included five plants per species. Because of the large number of measurements required with three treatments, we only used four of the six species for this experiment. *Encelia* and *Salvia* were selected as the two native species because their planar leaves permit easy gas exchange measures. *Nicotiana* and *Ricinus* were chosen as the two invasive species because they are most similar to *Encelia* and *Salvia* in life form (perennial shrub) and rooting depth. *VWC* was measured daily with a soil moisture meter (Delta-T HH2 with ML2x probe). For the stress and stress-recovery treatments, water was withheld from plants until *VWC* was less than 10% (approximately one week). When *VWC* fell below 10%, initial physiological measures (Day 0) were conducted (see below). Following physiology measurements, irrigation was resumed in the stress-recovery treatment and *VWC* was maintained at 25–30% for the remainder of the experiment. No natural precipitation occurred during the study period.

One recently mature leaf on each plant was selected for physiology measurements, tagged and repeatedly measured over the course of the experiment. Physiological traits were measured on Day 0 (before and after resuming irrigation for the stress-recovery treatment), and on Days 1, 2 and 7. Photosynthetic capacity (A_{max}, μmol m^{-2} s^{-1}), transpiration rates (*E*, mol m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}) and chlorophyll fluorescence were measured with a LI-6400 portable photosynthesis system with a fluorescence chamber (LI-COR, Lincoln, NE). All measures were conducted at saturating light levels (1,900 μmol photon m^{-2} s^{-1}), at 400 μL L^{-1} CO_2, at 40–60% relative humidity, and under ambient temperature (26–30°C). The effective quantum yield of PSII ($\Phi PSII$) was calculated as $(F_m'-F_s)/F_m'$, where F_s is the fluorescence yield of a light-adapted leaf and F_m' is the maximal fluorescence during a saturating light flash. Leaf chlorophyll content (*Chl*, μmol m^{-2}) was determined with a SPAD-502 meter (Spectrum Technologies, IL, USA).

After physiological measures on Day 7, leaves were collected, scanned to determine leaf area, dried at 65°C for 3 days, and weighed to determine leaf mass per area (*LMA*, g m^{-2}). All plants were then harvested and separated into above- and below-ground biomass. To minimize fine root loss, roots were carefully separated from soil and washed. All material was dried and weighed to determine root to shoot ratio (*R:S*) and total biomass.

Light manipulation

In May, after plant species had acclimated to 2,000 μmol photon m^{-2} s^{-1} conditions for one month, five individuals each of *Encelia, Artemesia,* *Salvia, Brassica, Nicotiana,* and *Ricinus* were moved to the greenhouse (300 μmol photon m^{-2} s^{-1}) for one week. At the end of the week (Day 0), measures of A_{max}, *E*, *ΦPSII*, and *Chl* were conducted as described above. In addition, pre-dawn fluorescence measurements were taken to assess the fraction of absorbed photons that are used for photochemistry (F_v/F_m) which was calculated as (F_m-F_o/F_m), where F_o is the fluorescence in total darkness and F_m is fluorescence of a dark-adapted leaf during a saturating light flash. F_v/F_m is around 0.8 for healthy plants, with smaller values indicating photoinhibition (Cavender-Bares and Bazzaz 2004). Photoinhibition is caused when more energy is generated by light harvesting than can be used by the Calvin cycle. Severe photoinhibition over a long time period can lead to the production of highly reactive free oxygen radicals, which degrade photosynthetic components.

Because of the various patterns of branching and leaf initiation employed by the six species, stem diameter at the base of the plant was used as a measure of plant productivity. While we did not conduct allometric measures for these species, stem diameter is highly correlated with total plant biomass in many species (Coyle and Coleman 2005; Monclus et al. 2006; Yamashita et al. 2000). After Day 0 measures, plants were returned to a high-light environment (2,000 μmol photon m^{-2} s^{-1}) and the physiological and growth traits were measured again on Day 1, 2 and 7.

Statistical analysis

The influence of light stress, water stress, and irrigation following water stress on physiological and morphological variables was determined by planned (*a priori*) orthogonal contrasts among treatments within species at Day 0 and Day 7 and among species within a treatment. Data that violated the ANOVA assumptions of normality were Box Cox transformed. Following Quinn and Keough (2002); Moran (2003); Gotelli and Ellison (2004), sequential Bonferroni corrections for multiple statistical tests were not conducted. Because we lacked enough degrees of freedom to contrast native and invasive species, we discuss how individual species responded to light and water treatments. All analyses were performed in JMP 8.0 (SAS Institute Inc., Cary, NC).

Results

Water manipulation

Volumetric water content for plants in the control treatment was maintained between 25–30% for all species (Fig. 1). *VWC* for plants in the stress and stress-recovery treatments fell below 10% at the beginning of the experiment (Day 0) and *VWC* quickly returned to control levels after irrigation was resumed in the stress-recovery treatment. *VWC* for plants in the stress treatment was maintained at 10% for the duration of the experiment.

Physiological and morphological traits differed among the four species examined and across the three treatments (Figs. 1, 2) with the exception of *Chl* content, which did not vary across treatments (data not shown). *Encelia* displayed the highest A_{max} and *ΦPSII*, followed by *Salvia* and *Ricinus*. *Nicotiana* had the lowest A_{max} and *ΦPSII* (Fig. 1). However, while *Encelia* displayed the highest A_{max} under control conditions, A_{max} fell to less than 18% of control values when water stressed (Fig. 1).

All traits except *Chl* content were lower in stressed plants relative to control plants at Day 0 (Fig. 1). However, traits in some species recovered to control values by Day 7 despite the maintenance of $VWC < 10\%$. In *Encelia, Salvia* and *Ricinus*, *ΦPSII* recovered over the 7-day experiment. Similarly, A_{max} recovered to control values in *Salvia* and *Ricinus*, although g_s and *E* remained low in *Ricinus* (high water use efficiency). Only *Ricinus* showed changes in morphological traits following prolonged water stress. Stressed *Ricinus* plants had lower biomass and higher *LMA* relative to control plants following the 7-day measurement period (Fig. 2).

Photosynthetic function (A_{max}, *ΦPSII*) recovered in three of the four species when irrigation was resumed (Fig. 1). *Ricinus* and *Salvia* recovered to levels of the control treatment by Day 1 while *Encelia* recovered by Day 7 (Fig. 1). Photosynthetic function in *Nicotiana* never recovered in the stress-recovery treatment. After resuming irrigation at Day 0, g_s and *E* recovered to control-level values in all species by Day 7 (Fig. 1). Species in the stress-recovery treatment showed no morphological changes relative to control plants (Fig. 2).

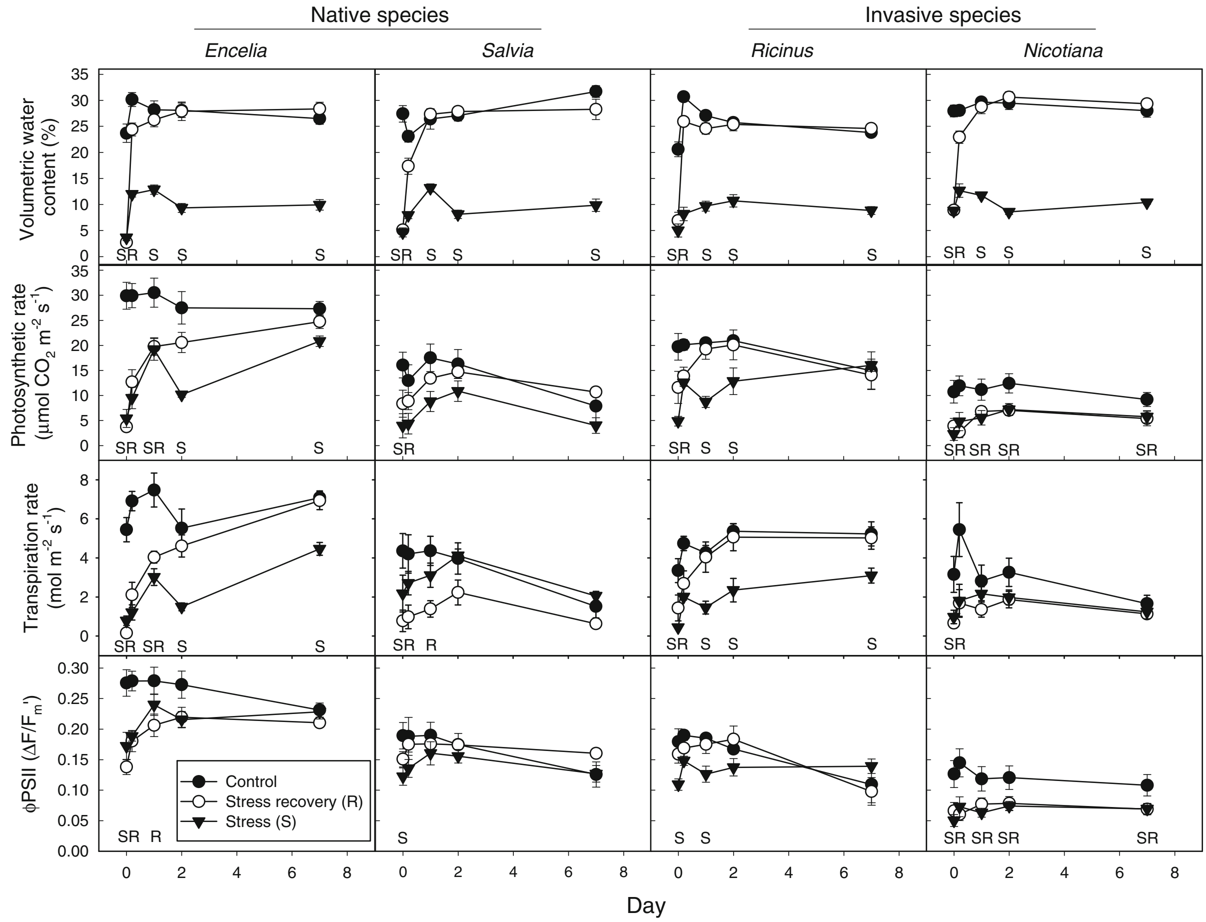

Fig. 1 Soil volumetric water content (*VWC*), leaf photosynthetic rate, leaf transpiration rate, and the effective quantum yield of PSII in control (closed circles), stress-recovery (open circles), and stress (closed triangles) treatments for two native (*Encelia californica, Salvia mellifera*) and two invasive species (*Nicotiana glauca, Ricinus communis*) over seven days ($n = 5$ individuals per species). For the stress-recovery treatment, plants were initially water stressed ($VWC < 10\%$) and irrigation was resumed on Day 0. *VWC* was maintained at 10% in the stress treatment for the duration of the experiment. Data are means and standard errors. Significant differences ($P < 0.05$) between the control and stress treatment (*S*) and the control and stress-recovery treatment (*R*) are shown for each species

Light manipulation

Many species decreased $A_{\max}$ and *ΦPSII* (except *Artemisia*) and experienced photoinhibition (low F_v/F_m, except *Encelia* and *Brassica*) when transitioning from shade to sun (Fig. 3). Leaf *Chl* content decreased in the three invasive species (*Ricinus, Nicotiana, Brassica*) and remained unaltered in two of the native species (*Encelia, Salvia*; Fig. 3). *Artemesia* leaves were too small to be measured for *Chl* content. Stomatal response to high-light availability was extremely variable across species (Fig. 3). Stomatal conductance decreased in two natives and one invasive (*Encelia, Salvia, Ricinus*), increased in one native (*Artemesia*) and remained unaltered in two invasive species (*Nicotiana, Brassica*). Species increased growth over the 7-day period to varying degrees (Fig. 4). Two of the three species that displayed the highest growth (34% increase in stem diameter) were invasive (*Ricinus*, *Nicotiana*). Growth (change in stem diameter) was negatively correlated with three measures of leaf function ($A_{\max}$, *ΦPSII*, g_s), but these relationships were not statistically significant ($P > 0.10$).

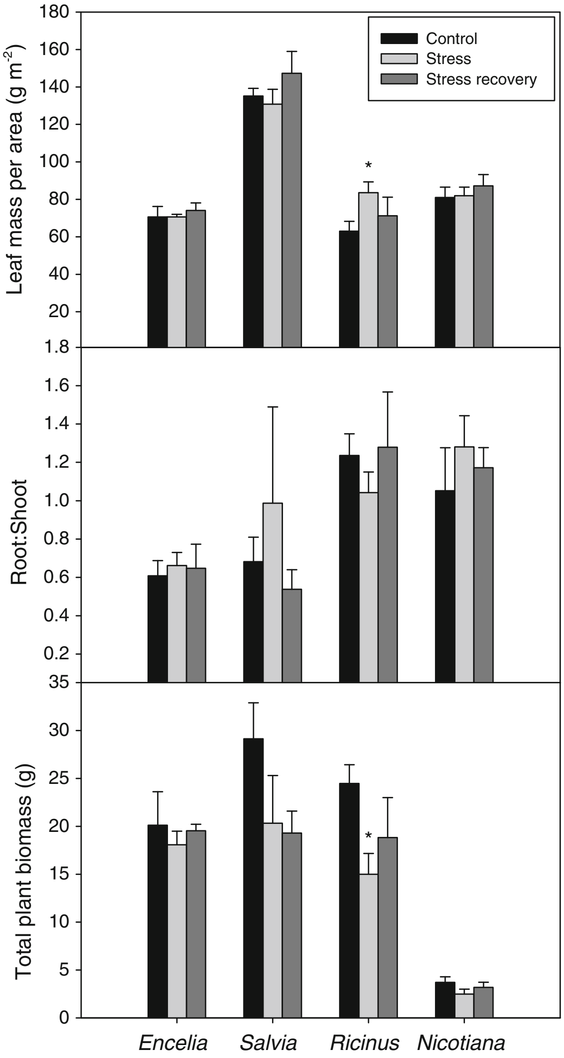

Fig. 2 Leaf morphological and plant-level growth data for two native and two invasive species in control, water stress (stress), and stress-recovery treatments after 7 days. See text for description of treatments. Data are means and standard errors. Asterisks denote statistically significant differences between stress treatments and the control treatment ($P < 0.05$)

Discussion

The ability of invasive species to tolerate stress (Funk and Vitousek 2007) and respond to resource pulses when available (Davis et al. 2000) will strongly influence invasion dynamics in low-resource systems. Here, stress tolerance was examined by subjecting plants to water and high-light stress, which are commonly experienced by species growing in arid habitats. In response to water and high-light stress, we found that species differentially responded to stress; however, there were no consistent differences between invasive and native species. Thus, our data neither support nor refute our hypothesis. Instead, our data suggest that species in arid systems display a range of physiological responses to stress.

Stress response

In the water manipulation experiment, one native (*Salvia*) and one invasive (*Ricinus*) species showed partial photosynthetic recovery during severe water stress ($VWC < 10\%$) while one native (*Encelia*) and one invasive (*Nicotiana*) species did not. Unexpectedly, these species patterns were reversed for high-light stress. Upon transfer from low light (300 μmol $m^{-2}\ s^{-1}$) to high-light (2,000 μmol $m^{-2}\ s^{-1}$), *Encelia* and *Nicotiana* showed smaller reductions in photosynthetic function ($A_{\max}$, $\Phi PSII$) than *Salvia* and *Ricinus*. In response to high-light stress, photoinhibition (as measured by F_v/F_m) was lower in native species relative to invasive species, although one invader (*Brassica*) showed no photoinhibition and low reductions in $A_{\max}$. Collectively, the data from our stress treatments demonstrate that some invasive species have the ability to retain physiological function while living in water stressed conditions (*Ricinus*) or when exposed to high-light stress following shade acclimation (*Brassica*).

Does the ability to maintain photosynthetic function during water stress preclude a plant from protecting itself from photoinhibition? Leaf adaptations for water stress should be similar to those for high-light stress. For example, species in arid systems typically have trichomes or increased pigment content (i.e., xanthophyll pigments) to deflect or dissipate excess radiation (Demmig-Adams and Adams 1992; Ehleringer and Mooney 1978), which lowers the amount of radiation absorbed (i.e., decreases photoinhibition) and lowers leaf temperature (i.e., lowers evaporative loss and maintains an optimal temperature range for photosynthesis). While morphological traits such as trichome density and carotenoid content were not measured, the gas exchange results are inconsistent with the idea that species should have integrated stress responses (Chapin 1991) and respond similarly to water and high-light stress. As stated above, $A_{\max}$ recovered in *Ricinus* and *Salvia* following water stress while *Brassica* and *Encelia* were most robust to photoinhibition.

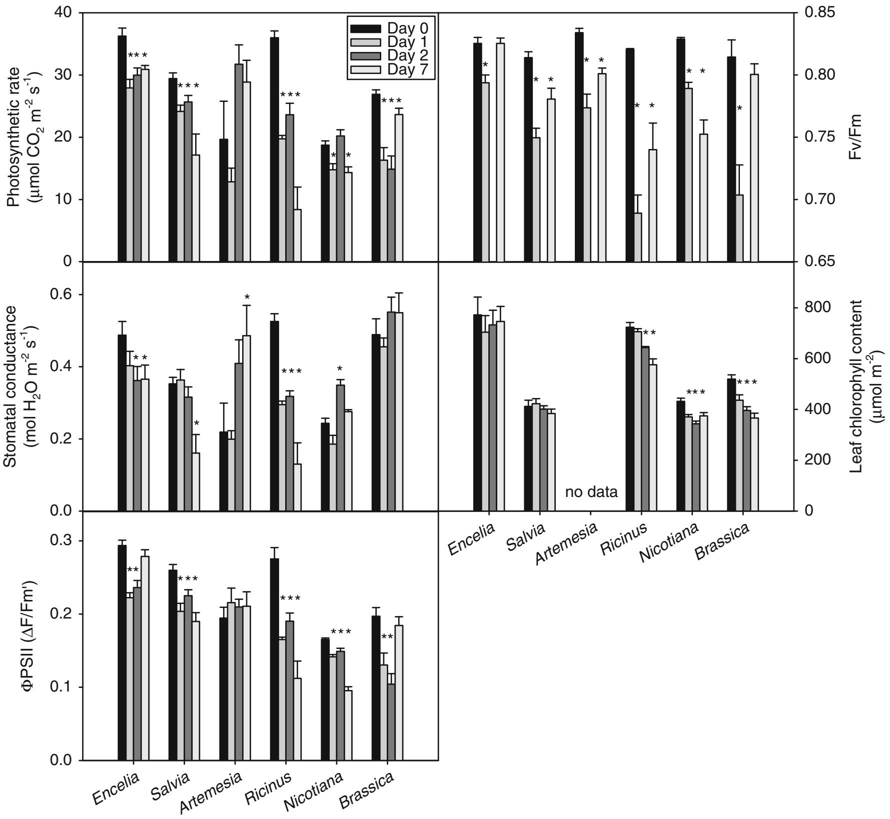

Fig. 3 Leaf-level physiological data for three native and three invasive species before (Day 0, 300 μmol m^{-2} s^{-1}) and after (Day 1, 2, and 7, 2,000 μmol m^{-2} s^{-1}) transferring plants to a high-light environment ($n = 5$ individuals per species). Data are means and standard errors. Asterisks denote statistically significant differences between high-light (Day 1, 2, 7) and low-light (Day 0) conditions ($P < 0.05$)

Recovery from stress

Few studies have examined plant responses on short time scales to determine how plants respond to rapidly changing environmental conditions or to precipitation pulses (Barker et al. 2006; BassiriRad et al. 1999; Gebauer and Ehleringer 2000; Ignace et al. 2007; James and Richards 2005; Loik 2007; Nobel and Sanderson 1984; Peek and Forseth 2009; Resco et al. 2008). We found that photosynthetic function in three of four species (all but *Nicotiana*) fully recovered from water stress after irrigation was resumed. Recovery was fastest in *Salvia* and *Ricinus*, occurring after just one day, while *Encelia* recovered after seven days. Although there have been many studies examining photosynthetic recovery following drought stress (e.g., BassiriRad et al. 1999; Gebauer and Ehleringer 2000), few generalizations can be made regarding the mechanistic basis of recovery. Ennahli and Earl (2005) found that partial recovery of photosynthesis following severe water stress resulted from chloroplast limitations of photosynthesis (e.g., reduced Rubisco activity, increased photoinhibition) rather than stomatal limitations (e.g., low intercellular CO_2 concentration). It seems unlikely that photoinhibition inhibited photosynthetic recovery during

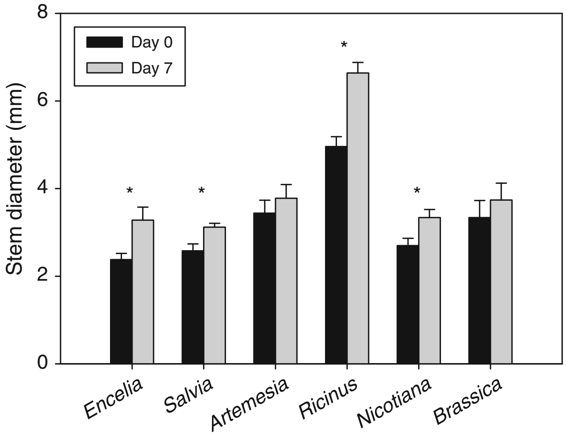

Fig. 4 Above-ground growth data for three native and three invasive species before (Day 0, 300 μmol m^{-2} s^{-1}) and after (Day 7, 2,000 μmol m^{-2} s^{-1}) transferring plants to a high-light environment ($n = 5$ individuals per species). Data are means and standard errors. Asterisks denote statistically significant differences between high-light (Day 7) and low-light (Day 0) conditions ($P < 0.05$)

water stress in *Encelia* and *Nicotiana* given their resilience to photoinhibition in the high-light study. Thus, it is plausible that stomatal limitations to photosynthesis resulted in slow or incomplete recovery after seven days in these two species.

Root to shoot ratios strongly influence stomatal limitation of photosynthesis by controlling plant water status. For example, high *R:S* of a non-native C4 bunchgrass (*Eragrostis lehmanniana*) in southeastern Arizona is believed to contribute to the ability of this species to increase g_s and, consequently, to rapidly increase $A_{\max}$ following a precipitation pulse (Ignace et al. 2007). Plants may also increase *R:S* immediately following a precipitation event. Nobel and Sanderson (1984) found that root growth in cactus (*Agave deserti*) can be induced within six hours of soil wetting, highlighting the potential importance of new root growth in response to precipitation pulses. Root to shoot ratios remained unchanged in our stress-recovery treatment for all four species relative to control plants, suggesting that root growth was not rapidly initiated and that new root growth is unlikely to explain the rapid photosynthetic recovery that we observed in *Ricinus* and *Salvia*. Across treatments, *R:S* was higher in *Ricinus* (1.24 ± 0.11) and *Nicotiana* (1.05 ± 0.22) than in either native species (*Encelia*, 0.61 ± 0.08; *Salvia*, 0.68 ± 0.13), which may partially explain faster photosynthetic recovery in *Ricinus*, but not *Salvia*. However, low *E* observed for *Ricinus* and *Encelia* suggests that rapid photosynthetic recovery of these species resulted from increased water use efficiency (WUE) rather than increased g_s mediated by root dynamics.

While *Chl* content was unaffected by water stress in all species, all three invasive species displayed lower *Chl* content in response to high-light stress, suggesting that invaders were adjusting to the new light environment by reallocating N away from light-harvesting pigments to carboxylation components of photosynthesis (Yamashita et al. 2000) or possibly initiating senescence of existing leaves. A recent study found that an invasive species (*Ageratina adenophora*) allocates more nitrogen to photosynthetic protein at the expense of structural protein [(e.g., cell walls; Feng et al. (2009)], but the timescale on which plants can reallocate nitrogen to various protein fractions, and the potential for nitrogen biochemistry to explain how species will respond to rapid changes in environmental factors, is unknown. Because there was no significant difference between leaf function ($A_{\max}$, *ΦPSII*, g_s) and stem diameter, we cannot conclude that invasive species decreased the function of existing leaves while diverting resources to new structures (e.g., Ackerly and Bazzaz 1995). However, future resource-pulse studies should monitor the potential trade-off between the function of existing leaves and new leaf growth over longer time periods.

In conclusion, we found no universal differences between native and invasive species in response to high-light stress, water stress and irrigation following water stress. Instead, responses were species specific. Climate change projections for the southwestern United States call for intensified intra-annual precipitation resulting in larger precipitation events with longer intervening dry periods (Diffenbaugh et al. 2005; Knapp et al. 2008). Thus, species will need to both tolerate stress and respond to large precipitation pulses. Understanding how species use water and light during pulse events may suggest strategies for the restoration of invaded systems by identifying native species with similar resource use patterns (thereby increasing community resilience to invasion) or through manipulation of pulsed resources (Funk et al. 2008).

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