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Tradeoffs between growth rate and water-use efficiency in seedlings of native perennials but not invasive annuals

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Abstract Tradeoffs among species' traits play an important role in shaping communities. These relationships may also mediate community response to environmental change. In plants of water-limited ecosystems, tradeoffs between growth and water use may impose an important physiological constraint within and across species. I investigated how functional traits associated with this tradeoff differ between seedlings of native perennials in California and the invasive annuals displacing them. I created plant community mesocosms of native and invasive species grown under altered N and water availability, measuring multiple plant functional traits. Natives responded positively to N and water when grown separately, but grew best under low resources when in competition with invasives. Invasives grew much larger than natives and exhibited traits associated with rapid growth. Native species also suffered a tradeoff between relative growth rate (RGR) and water-use efficiency (WUE), while nonnatives exhibited both high RGR and high WUE, especially under high resource availability. The ability to grow rapidly and use limiting resources efficiently undoubtedly contributes to the dominance of these invasive species over native seedlings. Such superior trait combinations and differences in physiological tradeoffs could explain reduced native seedling establishment and restoration success in the presence of these invasives.

Keywords Nitrogen deposition · Drought · Relative growth rate · Water-use efficiency · Ecological tradeoffs · Coastal sage scrub

Introduction

In plants, carbon gain through photosynthesis comes at the cost of water lost via transpiration. This imposes a major physiological constraint, particularly in water-limited ecosystems, which may result in tradeoffs among underlying plant traits. For example, in a desert annual community, a key tradeoff has been identified between relative growth rate (RGR) and water-use efficiency (WUE), where fast-growing species have low WUE and vice versa (Angert et al. 2007; Huxman et al. 2008). Species with high RGR respond rapidly to resource pulses, but have low drought tolerance.

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Conversely, species with greater WUE may be better suited to withstand drought, but could be outcompeted by faster-growing species. This tradeoff has been useful in explaining long-term variation in plant population sizes and the assembly of plant communities (Angert et al. 2007; Huxman et al. 2008).

Natural communities are increasingly subjected to multiple components of global change, including climate change and anthropogenic N deposition (Tylianakis et al. 2008), which may fundamentally alter the ecological context in which species' traits evolved. Nonnative plant invasion may also be exacerbated by environmental change (Dukes and Mooney 1999; Davis et al. 2000; Blumenthal 2005; Vilà et al. 2007). A better understanding of functional trait differences between native and invasive species and the role of resource availability in driving these differences may increase our ability to predict future invasions under global change (Lavorel and Garnier 2002). For example, in California, multiple drivers of global change may interact to negatively impact the severely threatened and biodiverse coastal sage scrub (CSS) plant community (Kimball et al. 2014; Allen et al. 2016; Valliere et al. 2017), and examinations of relevant plant traits may help elucidate the mechanisms of community-level changes (Kimball et al. 2016).

In southern California, elevated N deposition is a major driver of vegetation-type conversion of native CSS to invasive annual grasslands (Talluto and Suding 2008; Cox et al. 2014). Reduced precipitation also promotes shrub loss and invasion, especially in conjunction with elevated N (Valliere et al. 2017; Vourlitis 2017). During a recent multi-year drought, a previous study documented dramatic loss of native CSS and concomitant nonnative plant invasion, especially under high N (Valliere et al. 2017). N addition also reduced plant WUE of the dominant shrub species, likely contributing to drought-induced mortality (Valliere et al. 2017). A similar effect was observed in CSS seedlings, where growth in high N soils increased the negative effects of drought (Valliere and Allen 2016). Together, these results suggest that CSS species might suffer a tradeoff between growth and water use that is exacerbated under N deposition.

I sought to understand if the RGR-WUE tradeoff might be useful in explaining the dominance of nonnative invasive annuals over native CSS seedlings (in terms of plant biomass) and whether or not invasives experience the same tradeoffs as natives. Previous work, for example, has shown that the invasive *Erodium cicutarium* (also a dominant invader in CSS) exhibits the "forbidden trait combination" of high RGR and high WUE, making it more competitive than natives (Gremer et al. 2013; Kimball et al. 2013, 2014b). Given the strong influence of resource availability on plant traits, I was also interested in understanding how N and drought might differentially impact this relationship in native and invasive species. If natives are disproportionately impacted by physiological tradeoffs, or if invasive species possess the superior trait combination of high RGR and high WUE, this could help explain the reduced seedling recruitment and limited restoration success often observed in invaded areas (Eliason and Allen 1997; Allen et al. 2000; Kimball et al. 2014a).

Methods

I chose five native CSS species, including four shrub species (*Acmispon glaber, Artemisia californica, Encelia californica,* and *Salvia mellifera*) and a perennial grass (*Stipa pulchra*), and five nonnative annual species that are invasive throughout California, including annual grasses (*Avena fatua* and *Bromus diandrus*) and forbs (*Centaurea melitensis, Erodium cicutarium,* and *Hirschfeldia incana*). Plants were propagated from untreated seeds, which were germinated directly in the experimental mesocosms described below and thinned to the desired plant density. Native seed was procured from S & S Seeds Inc., Carpinteria, California. Nonnative seed was field-collected in the Santa Monica Mountains, California.

I created plant community mesocosms with natives and invasives planted either separately or together. Plant communities were grown under differential N and water availability in a full factorial design: community type (native, invasive, or native + invasive) × N treatment (low N or high N) × water treatment (well watered or drought), with four replicates of each combination ($3 \times 2 \times 2 \times 4 = 48$ mesocosms). The experiment was conducted from January to April 2016 in a glasshouse at the University of California, Riverside. Mesocosms consisted of plastic bins with drainage holes, each measuring $35 \times 30 \times 15$ cm and filled with a 1:1 mixture of live

field soil and sand. Field soil was collected from a disturbed stand of CSS at Rancho Sierra Vista, a park unit within the Santa Monica Mountains National Recreation Area of southern California. Soil texture was approximately 64% sand, 23% silt, and 13% clay. Soil was sieved through 1 cm^2 hardware cloth before use, and sand was added to improve water drainage. Extractable N of the field soil used was approximately 14 μg N g^{-1} soil prior to mixing with sand.

In a substitutive design (20 plants per mesocosm), mesocosms were planted with one of the three community types from seed: all natives, all invasives, or natives + invasives. Plants were randomly placed in a grid (five rows with four plants each) with equal distances between plants. Placement of species was decided at random, with replicates of every species included in each mesocosm.

After plants were established, high N mesocosms received N in solution from ammonium nitrate (NH_4NO_3) in a single treatment of $\sim$50 μg N g^{-1} soil. Low N mesocosms received an equal amount of unfertilized water. Mesocosms were watered 2–3 times per week, with well-watered and drought mesocosms maintained at 50 ($\sim$ 0.12 ml g_{soil}^{-1}) and 20 ($\sim$ 0.05 ml g_{soil}^{-1}) percent water-holding capacity by weight, respectively. Concurrently, I grew bins of each species under the same conditions and harvested individuals over time, using data to generate simple linear regressions of leaf number with shoot mass to estimate biomass within mesocosms (R^2 = 0.66 to 0.84 for all regressions; Fig. S1). Mesocosms were randomly distributed on greenhouse benches and rearranged each week. I measured leaf number at week 6 and harvested plants after 12 weeks. I measured plant dry mass, root:shoot (RS), total leaf area, and specific leaf area (SLA). RGR was calculated as [RGR = (ln W_2– ln W_1) /(t_2– t_1)], where W_1 and W_2 are plant dry weights at times t_1 (week 6) and t_2 (week 12), respectively. This calculation of RGR assumes exponential plant growth. RGR was determined only for shoot biomass. I also calculated total shoot biomass in each mesocosm by origin (either native or invasive).

Leaf tissue was analyzed for CN and C isotope ratio ($\delta^{13}C$) to infer plant WUE at the University of California Riverside Facility for Isotope Ratio Mass Spectrometry. These C isotope ratios provide information on the longer-term intrinsic WUE efficiency of plants as opposed to measurements of instantaneous WUE obtained by analyzing leaf gas exchange. Observed differences in plant WUE could indicate differences in stomatal control and/or differences in photosynthetic capabilities.

I used mixed effects linear modeling to analyze data for plant biomass and functional traits, with separate models fit for each response variable. All analyzes were performed using JMP (version 14.0.0, SAS Institute Inc.). Across species and treatments, biomass data were not normally distributed and resistant to transformation. Therefore, I analyzed biomass data using generalized linear models. First, to understand if native and invasive species responded differently to the community type in which they were grown, I analyzed biomass data with species' origin, community type (either monotypic or mixed), and the interaction as fixed effects and mesocosm and species (nested in origin) included as random effects. Next, I analyzed biomass within the different community mesocosm types with species' origin (native or invasive), N treatment, watering regime, and their interactions included as fixed effects and mesocosm and species (nested in origin) included as random effects. I also compared proportions of native to invasive biomass in mixed mesocosms using paired *t* tests.

I then analyzed each plant functional trait separately (RGR, WUE, root:shoot, SLA, and leaf CN ratio) using a standard least squares model, with species' origin, N treatment, watering regime, and their interactions included as fixed effects. Mesocosm and species identity (nested in origin) were included as random effects in all models. Prior to analysis, I confirmed all functional trait data were normally distributed. Data for root:shoot ratios and leaf CN ratios were log-transformed to meet this assumption of normality. For each model, I also assured that residuals were normally distributed. For these analyses, I focused on mesocosms in which native and invasive species were grown together.

Finally, I used simple linear regression to evaluate the relationships between RGR and WUE, including data from all community types and resource treatments in order to capture the full range of trait expression for each species.

Results

Invasive species accrued much greater biomass than natives, both when grown separately and in mixed-community mesocosms (Fig. 1; Table S1). Natives and invasives responded differently to the community type in which they were grown, with origin ($F_{1,8} = 12.7$, $p = 0.0073$) and the interaction of origin and community type ($F_{1,8} = 60.4$, $p < 0.0001$) having significant effects on plant biomass. Invasives responded similarly to N and water when grown in both community types. Native species responded positively to higher N and/or water availability only when grown with other natives; in invaded communities, all natives achieved the greatest biomass in the lowest resource treatment: low N and drought (Fig. 1).

Invasive species exhibited the highest RGR values, especially under high resource availability (Fig. 2a).

Fig. 2 Mean trait values (±SE) of native and invasive species from mixed-community mesocosms (n = 4) in each resource treatment including RGR (**a**), WUE (**b**), root:shoot ratio (**c**), SLA (**d**), and foliar CN ratio (**e**). Significant direct and interactive effects of species' origin (*O*), nitrogen (N), and water (*W*) are shown (*$p < 0.05$, **$p < 0.01$, ***$p < 0.0001$)

The effect of resources on traits also differed between natives and invasives (Fig. 2; Table S2). For example, invasives responded to increased N and water with more rapid growth, while natives showed the highest RGR under low N and drought (Fig. 2a). Species' origin had either a direct or interactive effect on all traits (Fig. 2a–e). In addition to exhibiting higher RGR and WUE values, overall invasives displayed lower root:shoot ratios (Fig. 2c), higher SLA (Fig. 2d), and lower CN of leaf tissue (Fig. 2e).

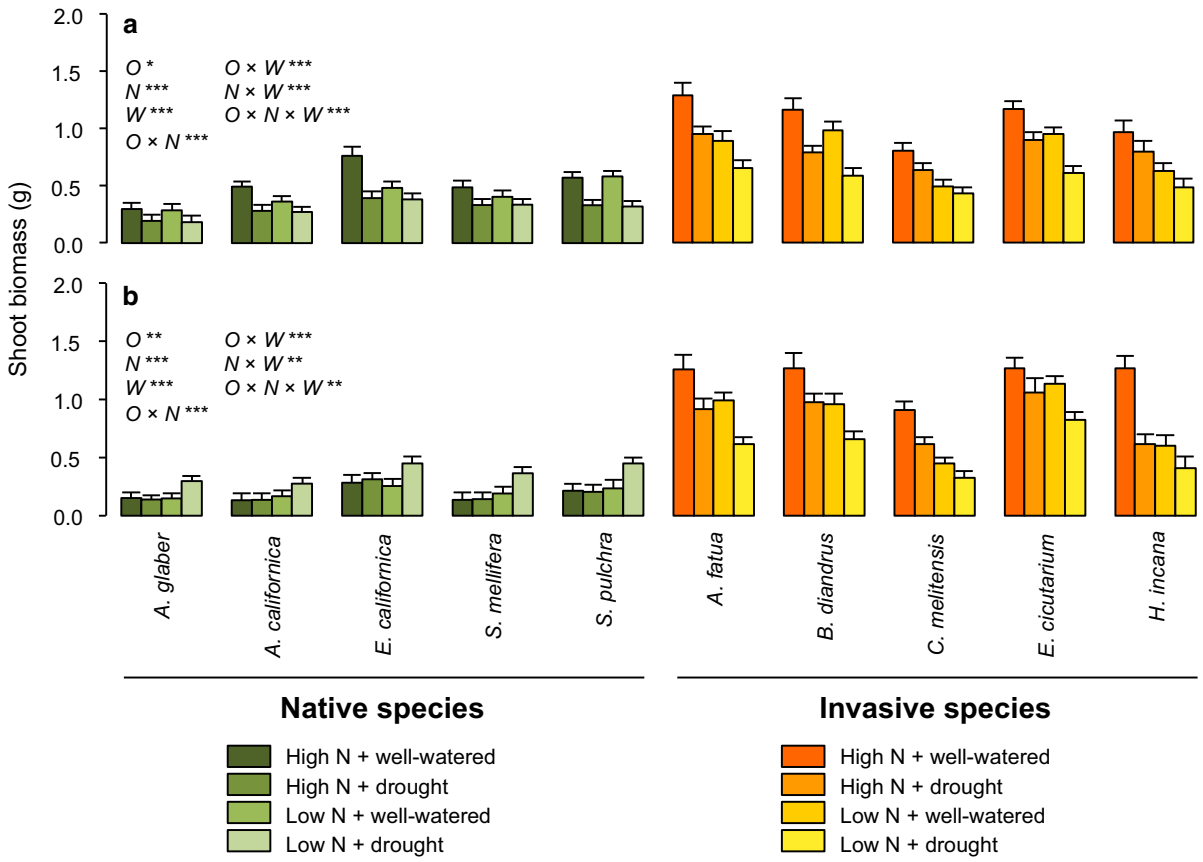
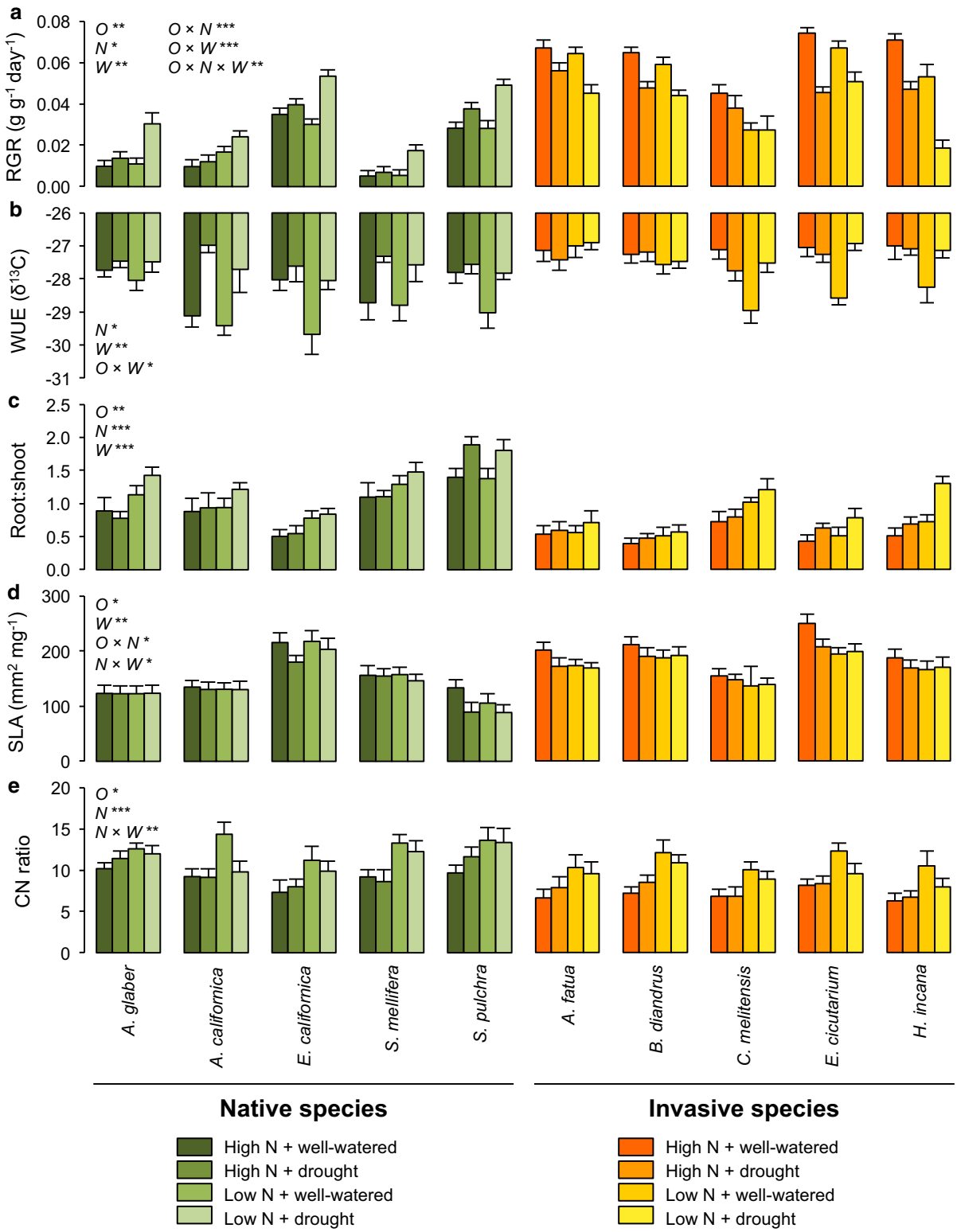


Fig. 1 Mean biomass of native and invasive species grown in monotypic (**a**) or mixed-community (**b**) mesocosms under altered N and water availability ($n = 4$ for each treatment combination). Significant direct and interactive effects of species' origin (*O*), nitrogen (*N*), and water (*W*) are shown (*$p < 0.05$, **$p < 0.01$, ***$p < 0.0001$)


a
RGR (g g-1 day-1)
0.08
0.06
0.04
0.02
0.00
O **
N *
W **
O × N ***
O × W ***
O × N × W **
b
WUE (δ13C)
-26
-27
-28
-29
-30
-31
N *
W **
O × W *
c
Root:shoot
2.5
2.0
1.5
1.0
0.5
0.0
O **
N ***
W ***
d
SLA (mm2 mg-1)
300
200
100
0
O *
W **
O × N *
N × W *
e
CN ratio
20
15
10
5
0
O *
N ***
N × W **
A. glaber
A. californica
E. californica
S. mellifera
S. pulchra
A. fatua
B. diandrus
C. melitensis
E. cicutarium
H. incana
Native species
High N + well-watered
High N + drought
Low N + well-watered
Low N + drought
Invasive species
High N + well-watered
High N + drought
Low N + well-watered
Low N + drought

Natives and invasives also showed different patterns of intraspecific variation in RGR and WUE (Fig. 3). All but one native species, *E. californica*, showed a negative relationship between RGR and WUE (Fig. 3a–e). No invasive species exhibited this tradeoff, though *A. fatua* showed a positive correlation (Fig. 3f–j). While RGR and WUE were not significantly correlated across species, invasives exhibited higher values for both RGR and WUE, especially under high N and water availability (Fig. 4a–d). The treatment in which natives and invasives showed the most similarity in trait expression was under low N and water conditions, which was also the treatment where natives performed best when grown with invasives (Figs. 1a–e , 4a–d).

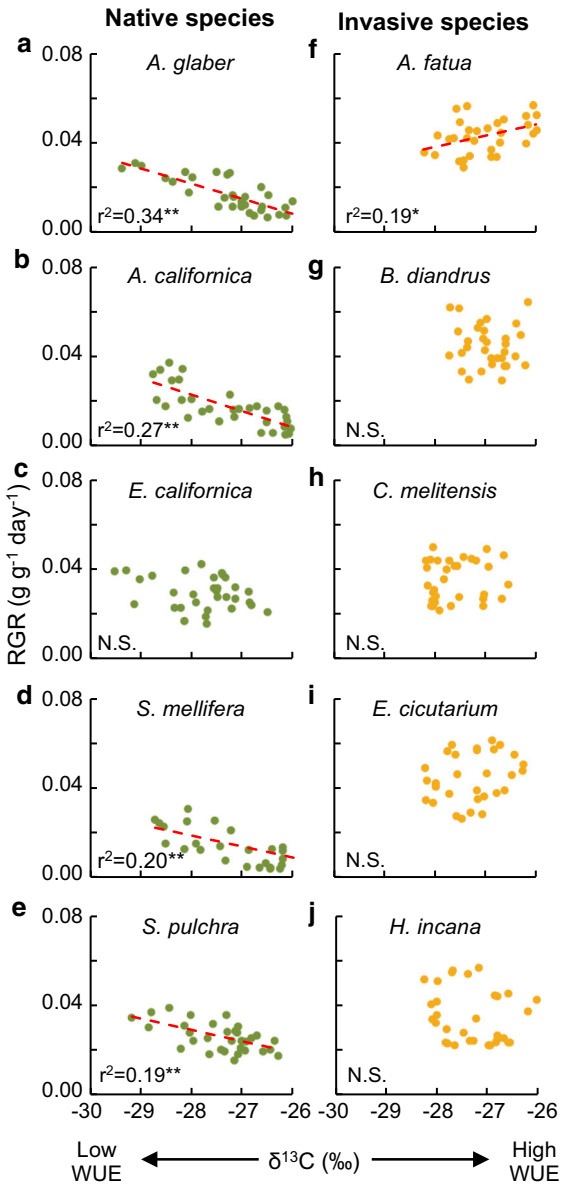


Fig. 3 Regressions of relative growth rate (RGR) and water-use efficiency (WUE) for native (**a**–**e**) and invasive (**f**–**j**) species across all treatments ($n = 32$). Significant trendlines and coefficients of determination are shown ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.0001$)

Discussion

These results illustrate key differences in traits and tradeoffs between seedlings of native CSS perennials and the invasive annuals displacing them throughout California and may provide insight into the invasion of this ecosystem observed under elevated N deposition and drought (Kimball et al. 2014a; Valliere et al. 2017). As predicted, invasives accrued greater biomass than natives, especially under high resource availability. Native species responded positively to added N and water but only in the absence of invasives; in invaded communities, native species accrued the greatest biomass under low resource availability. This strongly suggests that the negative impacts of N deposition on native CSS seedlings are largely due to the presence of invasives and not direct effects of N fertilization. This supports the hypothesis that increased resource availability promotes invasion success (Dukes and Mooney 1999; Davis et al. 2000; Blumenthal 2005), which has been observed in multiple field studies exploring N addition in CSS (Kimball et al. 2014a; Valliere et al. 2017; Vourlitis 2017). Despite the improved growth of natives under low resources, they were still outperformed by invasives, highlighting the ability of these invaders to succeed in both low- and high-resource environments and under high and low water availability.

Natives and invasives also exhibited contrasting suites of plant functional traits. Overall, natives exhibited traits typically associated with a conservative growth strategy: low RGR, high R:S, and more carbon-rich leaves (Pierce et al. 2013; Díaz et al. 2016). In contrast, invasives showed traits characteristic of more acquisitive species, including rapid growth, increased shoot allocation, higher foliar N, and thinner leaves (Pierce et al. 2013; Díaz et al. 2016). This is consistent with previous research comparing native and invasive plant traits (Funk and

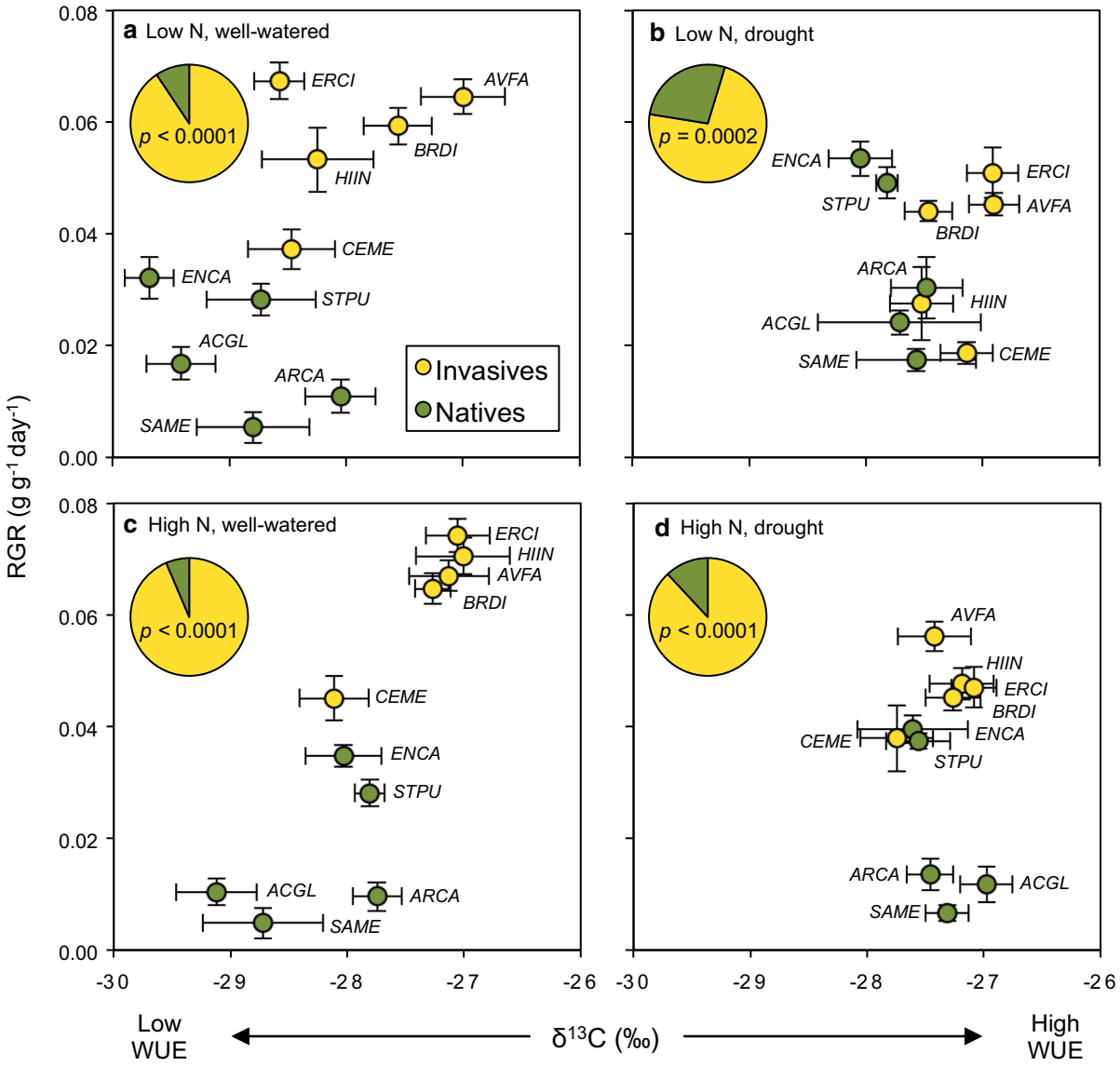


Fig. 4 Relative growth rate (RGR) and water-use efficiency (WUE) for all species in mixed-community mesocosms under each resource treatment ($n = 4$), including low N + well watered (**a**), low N + drought (**b**), high N + well watered (**c**), and high N + drought (**d**). Pie charts illustrate relative biomass of native versus invasive species in each treatment (t tests; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.0001$)

Vitousek 2007; Leishman et al. 2007). These differences may reflect the contrasting life history strategies of these species, and it is not surprising that annuals would express more "weedy" characteristics than native perennial seedlings (Funk et al. 2016). The ability of invasives to rapidly accumulate biomass even under low resource availability undoubtedly contributes to their success in this ecosystem.

While I predicted invasives would display traits associated with rapid growth, I also found that these species are capable of achieving high WUE, often even greater than natives. The ability of invasives to express high WUE along with high RGR runs somewhat counter to traditional theories regarding invasive plant traits, as it is often assumed that invasive species possess traits associated with rapid resource acquisition and growth at the expense of

resource conservation (Rejmánek and Richardson 1996; Craine 2009; Funk 2013). However, previous work has demonstrated invasives in low-resource environments may also be highly resource-use efficient (Funk and Vitousek 2007; Matzek 2011; Funk 2013). Interestingly, the invasive species studies here showed high WUE in all resource treatments, particularly under high N and water availability. This suggests the expression of resource-conserving traits in invasive species is not limited to low resource environments and may also occur in conjunction with rapid growth. Such novel trait combinations may enhance the capacity of these species to outcompete resident natives at the seedling recruitment stage (Molina-Montenegro et al. 2012; Kimball et al. 2013).

The ability of native seedlings to persist in the presence of invasives may be further hampered by the intraspecific tradeoffs they experience between RGR and WUE. This may be due, in part, to the pulse-driven nature of Mediterranean-type habitats such as CSS. Many native perennials in this ecosystem senesce and remain inactive during the summer dry season but are adapted to respond quickly to winter rains and may exhibit high rates of gas exchange (Harrison et al. 1971). Poor regulation of water-loss at the leaf level could be responsible for the relatively low WUE values observed in these native species. In contrast, invasives maintained high WUE even during rapid growth, possibly due to greater photosynthetic capabilities (McDowell 2002).

These invasive annuals may also have the advantage of being more competitive for water (Eliason and Allen 1997), perhaps due to greater biomass and superior ability to take up water compared to native perennials (Everard et al. 2010), as well as higher rates of root growth and elongation (Larson and Funk 2016). Together, these trait differences could explain the ability of these invasive annuals to outperform native seedlings even (or especially) when water is limiting.

While mesocosm experiments such as this may yield useful information, they also have some inherent limitations. For example, this experimental design may preclude the potential for resource partitioning due to rooting depth and neglect the spatial patchiness and stoichiometry of belowground resources that would be found in the field (Seabloom et al. 2003; Cleland and Harpole 2010). It is also important to note that the native species studied here are long-lived perennials. Therefore, the trait expression of seedlings may not reflect plant functioning of mature individuals later in life. Nevertheless, these results are useful in explaining the lack of native seedling recruitment and reduced restoration success in the presence of invasive annuals (Eliason and Allen 1997; Allen et al. 2000; Kimball et al. 2014a).

A greater understanding of the traits and environmental perturbations that underlie invasion may aid in predicting and managing future invasions under global change (Lavorel and Garnier 2002). Here I show that plant functional trait differences, as well as tradeoffs between traits, may contribute to the success of invasive annuals over native CSS seedlings. Anthropogenic disturbances such as N deposition, severe drought, and frequent fire, all contribute to the loss of CSS and spread of invasive species in this system (Talluto and Suding 2008; Cox et al. 2014; Valliere et al. 2017). The superior trait combinations observed in these invasive plant species along with other characteristics, such as earlier phenology, greater rates of seed germination, and competitive advantages, may facilitate this process (Eliason and Allen 1997; Everard et al. 2010; Wainwright and Cleland 2013).

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