Invasive annuals respond more negatively to drought than native species

Justin M. Valliere[1,2], **Evelin B. Escobedo**[2], **Gary M. Bucciarelli**[2], **M. Rasoul Sharifi**[2] **and Philip W. Rundel**[2]

[1]La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, University of California, Los Angeles, CA 90095, USA; [2]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA

Author for correspondence:
Justin M. Valliere
Tel: +1 774 280 2285
Email: valliere@ucla.edu

Received: *29 November 2018*
Accepted: *12 April 2019*

New Phytologist (2019)
doi: 10.1111/nph.15865

Key words: California grasslands, Mediterranean-type ecosystems, nonnative plant invasion, phenotypic plasticity, reproductive plasticity, seed production, water stress.

Summary

- In his foundational list of 'ideal weed' characteristics, Baker (1965) proposed that weedy plants maximize reproductive output under high resource availability. Since then, the idea that invasive plant species are more responsive to fluctuating resources compared with native or noninvasive species has gained considerable traction, although few studies extend this hypothesis to include reproductive output. We revisit Baker's hypothesis in the context of invasion and drought in California grasslands, exploring whether invasives show greater growth and reproductive responses to water availability compared with the native wildflowers they displace.
- In an outdoor potted study, we grew eight native and eight invasive species of annuals commonly found in southern California grasslands to reproductive maturity under both well-watered and drought conditions.
- While drought negatively impacted plant performance overall, invasives showed more negative responses for growth and reproductive traits. Invasives also grew larger than native species, especially under well-watered conditions, and produced seed with higher rates of germination.
- Invasives may be more negatively impacted by drought compared with natives, but they are also able to capitalize on high resource conditions and greatly increase reproductive output. Such opportunistic responses exhibited by invasives might explain previously observed fluctuations in their abundance under variable precipitation.

Introduction

Baker first proposed a list of characteristics of an 'ideal weed' over 50 yr ago (Baker, 1965). This was perhaps the earliest trait-based approach to understanding plant invasions, and the resulting paradigm has left a lasting mark on invasion ecology (Pyšek & Richardson, 2007). The list included many traits typically associated with weedy species, such as rapid growth and low germination requirements. Baker also predicted that successful weeds would be able to increase seed production under favorable conditions – the first suggestion that high resource availability might be an important mechanism of invasion (Baker, 1965). Since then, the idea that invasive species are more responsive to resource availability than native or noninvasive species has gained considerable traction. Multiple studies have supported this hypothesis (Richards *et al.*, 2006; Davidson *et al.*, 2011), though not in all cases and some uncertainty remains (Hulme, 2008; Palacio-López & Gianoli, 2011).

One limitation in addressing this question is that the majority of studies examining plant responses to fluctuating resource availability do not assess effects on reproductive output. For example, in a recent meta-analysis exploring plasticity in invasive plants by Davidson *et al.* (2011), only 15% of studies examined provided data on reproduction – too few for the authors to include reproductive plasticity as a parameter in their analysis. Most work has focused on biomass or physiological traits, which may not always be related to fitness (Richards *et al.*, 2006). Globally, plant invaders have been found to express greater reproductive output compared with native species (Mason *et al.*, 2008), which probably facilitates invasion (Simberloff, 2009). But while invasive plants are often assumed to increase fecundity under high resource availability, few studies explicitly test this hypothesis. There is some evidence to suggest that reproductive traits of invasive species may be more plastic than noninvasive congeners and co-occurring native species (Goergen & Daehler, 2001; Gerlach & Rice, 2003; Richards *et al.*, 2006; Muth & Pigliucci, 2007). However, greater responsiveness to fluctuating resources in invasive species does not necessarily mean they will outperform natives under all resource conditions. For example, Goergen & Daehler (2001) found that seed production in a native Hawaiian grass was much less sensitive to drought than in an invasive competitor.

If indeed invasive plant species are more responsive to water availability than resident native species, this has particular

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relevance in the context of global change (Nicotra *et al.*, 2010), which is expected to increase the success of plant invaders (Dukes & Mooney, 1999; Bradley *et al.*, 2010). Extreme climate variability could favor more plastic species, in particular invasive species (Engel *et al.*, 2011). In California, for example, rainfall variability and the frequency and intensity of severe drought events are expected to increase in the future (Diffenbaugh *et al.*, 2015; Yoon *et al.*, 2015). It is possible that reduced precipitation and extended drought in California could exacerbate invasion and reduce plant diversity in some cases (Everard *et al.* 2010; Valliere *et al.*, 2017), but other studies have suggested that invasive annuals in California grasslands may be more negatively impacted by drought than native species (Copeland *et al.*, 2016; LaForgia *et al.*, 2018). The role of reproductive responses to drought in driving such patterns, however, is largely unexplored.

Beginning centuries ago with the arrival of Europeans, the large-scale invasion of California by Mediterranean annual grasses and forbs represents one of the most dramatic biological transformations of the modern era (Mooney *et al.*, 1986; Minnich, 2008). These invaders pose a serious threat to California's high biodiversity and unique flora (Schierenbeck, 1995). Consequently, much research has been devoted to understanding patterns and drivers of invasion in California's ecosystems. This work has taken a number of approaches, including comparative studies of native and invasive species' traits (MacKinnon *et al.*, 2014; Funk *et al.*, 2016), but few studies directly compare drought responses among species, and none, to our knowledge, has addressed effects on reproductive output.

In this study, we investigated whether nonnative invasive annuals in southern California grasslands exhibit greater (more negative) drought responses compared with co-occurring native species. We predicted that native and invasive species would exhibit diverse patterns of growth and reproduction, but that overall drought would negatively impact plant performance. We also predicted that invasives would show traits typically associated with weedy species, such as greater biomass, seed production, and rates of seed germination compared with native species, especially under well-watered conditions. Finally, we hypothesized that invasives would experience greater reductions in growth and reproductive output in response to drought compared to natives. This experiment could also be viewed as a test of Baker's original hypothesis in California annual grasslands – whether invasive plant species are able to increase seed production under favorable (well-watered) conditions (Baker, 1965).

Materials and Methods

We selected eight native and eight invasive annuals that commonly occur in annual grasslands of the Santa Monica Mountains in southern California (Table 1). This included eight native forbs (*Acmispon strigosus*, *Clarkia unguiculata*, *Collinsia heterophylla*, *Deinandra fasciculata*, *Layia platyglossa*, *Lupinus bicolor*, *Nemophila menziesii*, and *Plantago erecta*), two invasive grasses (*Avena fatua* and *Bromus diandrus*), and six invasive forbs (*Centaurea melitensis*, *Erodium cicutarium*, *Hirschfeldia incana*, *Medicago polymorpha*, *Plantago lanceolata*, and *Sonchus oleraceus*). All invasive species are native to the Mediterranean basin and are listed on the California Invasive Plant Council's Inventory of Invasive Plants (www.cal-ipc.org). Seeds of invasives and of the native species *Acmispon strigosus*, *Deinandra fasciculata*, *Lupinus bicolor*, and *Plantago erecta* were field-collected in the Santa Monica Mountains, northwest of Los Angeles. Seeds of all other native species were purchased from S&S Seeds Inc. (Carpinteria, CA, USA). We selected species based on the plant community in which they commonly co-occur (annual grasslands), and therefore our approach does not account for the lack of phylogenetic relatedness between native and invasive species (Funk *et al.*, 2015). In our system, such phylogenetic matching is not always possible. For example, some of the most problematic invasives are annual grasses – a functional group largely absent in the native flora of southern California. We instead focused on testing the response of common species that are directly competing in the same habitat and environment.

We grew plants in a rooftop garden at the University of California, Los Angeles. In January 2017, seeds were planted in 650 ml conical pots ($n = 40$ for each species) filled with potting soil. Soil consisted of a mix of sphagnum peat moss and fine and coarse perlite. Following germination, we randomly thinned plants to a density of one plant per pot. We watered pots once or

Table 1 List of species included in the study including scientific and common names, plant family, and origin (either native to California or nonnative and invasive).

Species	Common name	Family	Origin
Acmispon strigosus Brouillet	Strigose lotus	Fabaceae	Native
Clarkia unguiculata Lindl.	Elegant clarkia	Onagraceae	Native
Collinsia heterophylla Buist ex Graham	Purple Chinese houses	Plantaginaceae	Native
Deinandra fasciculata Greene	Clustered tarweed	Asteraceae	Native
Layia platyglossa A. Gray	Tidy tips	Asteraceae	Native
Lupinus bicolor Lindl.	Miniature lupine	Fabaceae	Native
Nemophila menziesii Hook. & Arn.	Baby blue eyes	Hydrophyllaceae	Native
Plantago erecta E. Morris	California plantain	Plantaginaceae	Native
Avena fatua L.	Wild oats	Poaceae	Nonnative
Bromus diandrus Roth	Ripgut brome	Poaceae	Nonnative
Centaurea melitensis L.	Maltese star thistle	Asteraceae	Nonnative
Erodium cicutarium L.	Redstem filaree	Geraniaceae	Nonnative
Hirschfeldia incana L.	Short pod mustard	Brassicaceae	Nonnative
Medicago polymorpha L.	Bur clover	Fabaceae	Nonnative
Plantago lanceolata L.	English plantain	Plantaginaceae	Nonnative
Sonchus oleraceus L.	Common sow thistle	Asteraceae	Nonnative

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twice a week. We chose to implement episodic drought treatments in which half of plants experienced severe water stress rather than continued access to low water availability. In March, 4 wk after plants established, half of each species had water withheld until they were visibly wilted (*c.*1 wk) at which point regular watering was resumed. This process was repeated after 2 wk. Following drought treatments, all plants were watered on the same schedule. Plants were fertilized with a half-strength N-P-K (24-8-16) fertilizer (Miracle-Gro; The Scotts Company LLC, Marysville, OH, USA) once after germination and again about 6 wk later when plants began to show signs of nutrient deficiency. We grew plants to reproductive maturity. Plants matured at different rates, so we harvested plants only after they senesced following seed maturation. This began in early May when temperatures rose, with the final harvest of plants occurring in June. We measured root, shoot, and total dry mass (at time of senescence), root : shoot ratio, flower number, seed number, seed mass, and percentage germination of seed produced. We counted the number of fully developed flowers at the time of harvest as well those that had gone to seed. For members of the Asteraceae and Poaceae, we counted flower heads and spikelets, respectively, not individual flowers. We used a combination of methods to collect seeds. For plants with dehiscent fruits or seed that is easily dispersed, we collected seeds daily and/or used small mesh bags secured around pedicels/inflorescences. For species with larger seeds, direct counts of seeds were possible. For those with smaller seeds, we counted a subset, determined the weight, and used the resulting equation for estimates of total seed number per plant based on total seed mass.

We conducted germination trials in January 2018 using the seed collected from plants grown in the original study. Before the experiment, seeds were stored in paper envelopes at *c.* 20°C. We randomly selected 10 seeds from 10 different maternal individuals of each species and watering treatment and sowed them in pots filled with sterile potting mix. We watered pots once or twice a week as needed to keep soil sufficiently moist. As seedlings emerged from the soil, we recorded the number of germinates in each pot, removing counted individuals to reduce overcrowding. We tracked germination for 3 months, with most germination occurring in the first 3 wk across all species, but some natives emerging after as long as 10 wk. Using these data, we calculated percentage germination and total number of germinable seeds for each species under each watering regime.

We used two distinct linear mixed effects models created in R (v.3.5.0) using the package NLME (v.3.1–137) and function ‘lme’ to evaluate the effect of species origin on plant traits and drought responses. The first model tested for effects of origin (native or invasive), watering treatment (well-watered or drought-stressed), and their interaction on absolute trait values, with a random effect for species included. Independent models were executed for total plant biomass, arcsine-transformed percentage germination, and number of germinable seeds (= seed number × mean percentage germination by treatment). To understand if native and invasive species exhibited differences in trait values under well-watered and drought conditions, we used *post hoc t*-tests to explore origin effects within treatment type. The second statistical model was used to test if relative drought responses (= (response of a drought-stressed plant − mean response of well-watered plants)/(mean response of well-watered plants)) differed by plant origin for 10 plant traits, including shoot, root, and total biomass, root : shoot ratio, seed mass, flower count, seed count, total seed mass, seed germination, and transformed, normalized values of percentage germination. As with our absolute dataset, each trait was analyzed with an independent model that included a random intercept for species. We did not include corrections for multiple comparisons. We also used Student’s *t*-tests to compare differences in trait values as a result of treatment by species.

Results

The interaction of species origin and watering treatment ($t = -7.45$, $P \leq 0.0001$) and the main effect of watering treatment ($t = 12.90$, $P \leq 0.0001$), but not origin ($t = -1.40$,

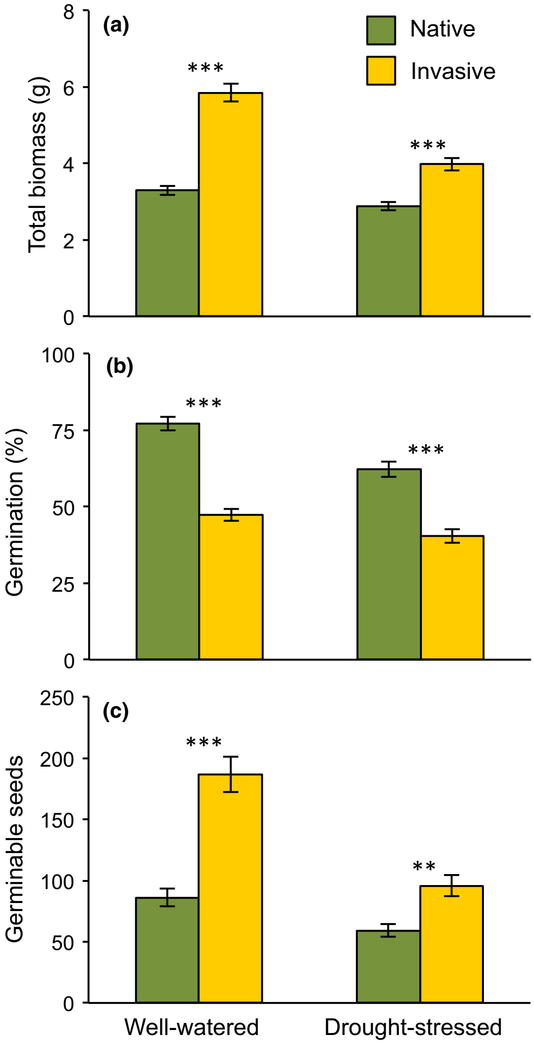

Fig. 1 Mean trait values of native and invasive species for total biomass (a), percentage germination (b), and the total number of germinable seeds (c) under well-watered and drought conditions. Bars represent means ± SE. Asterisks indicate significant differences as a result of origin within watering treatments from *t*-tests: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$.

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$P=0.1800$), had a significant effect on total plant biomass, with invasives being more impacted by drought than native species ($R^2=0.73$). Overall, invasives produced greater biomass compared with natives under both well-watered ($t=9.64$, $P\leq0.0001$) and drought ($t=5.65$, $P\leq0.0001$) conditions (Fig. 1a). The interactive effect of water and species origin showed no effect on percentage germination of produced seed ($R^2=0.55$, $t=-1.81$, $P=0.0700$). Across all species, drought reduced percentage germination ($t=4.60$, $P\leq0.0001$). Percentage germination also varied by species origin ($t=-2.36$, $P=0.0330$), and invasive plants produced seed with greater percentage germination under both well-watered ($t=7.87$, $P\leq0.0001$) and drought ($t=4.96$, $P\leq0.0001$) conditions (Fig. 1b).

The number of germinable seeds produced by plants showed a similar pattern, with the interaction of watering treatment and species origin ($t=-4.48$, $P\leq0.0001$) and the main effect of watering treatment ($t=9.15$, $P\leq0.0001$), but not origin ($t=-0.82$, $P=0.4200$), having a significant effect on the number of germinable seeds produced by plants ($R^2=0.63$). Invasives produced a greater number of germinable seeds under both well-watered ($t=6.23$, $P\leq0.0001$) and drought ($t=3.65$, $P\leq0.0001$) conditions (Fig. 1c).

We observed significant differences in relative drought responses for measures of plant growth between native and invasive species (Figs 2a–d, 3a–d; Table 2). Drought generally reduced plant growth, but invasives exhibited greater reductions in biomass in response to drought compared with natives for shoot mass ($R^2=0.17$, $t=3.91$, $P=0.0016$; Figs 2a, 3a), root mass ($R^2=0.16$, $t=3.98$, $P=0.0014$; Figs 2b, 3b), and total plant biomass ($R^2=0.21$, $t=4.68$, $P\leq0.0001$; Figs 2c, 3c). Most species increased the proportion of root biomass under drought (Fig. 3d), but this effect did not vary by origin ($R^2=0.05$, $t=0.52$, $P=0.606$; Fig. 2d).

Reproductive responses also revealed some dissimilar patterns between native and invasive species (Figs 2e–j, 3e, 4a–e; Table 3). Multiple species exhibited reductions in flower number as a result of drought (Fig. 3e), but, overall, invasive species experienced more severe reductions compared with native species ($R^2=0.24$, $t=2.57$, $P=0.0220$; Fig. 2e). Species exhibited a diversity of seed sizes, morphology, and dispersal mechanisms (Supporting information Fig. S1). Drought reduced seed mass in only a single species, *Avena fatua* (Fig. 4a), and species origin had no effect on relative drought responses for seed mass ($R^2=0.21$, $t=0.38$, $P=0.7060$; Fig. 2f). Overall, invasives showed more negative drought responses for both seed number ($R^2=0.22$, $t=2.38$, $P=0.0310$; Figs 2g, 4b) and total seed mass ($R^2=0.27$, $t=0.3.63$, $P=0.0190$; Figs 2h, 4c). Drought responses for percentage germination of seed produced ($R^2=0.09$, $t=0.26$, $P=0.7900$; Figs 2i, 4d) and the total number of germinable seeds ($R^2=0.37$, $t=1.61$, $P=0.1300$; Figs 2j, 4e) did not differ significantly by species origin.

Discussion

Resource availability is thought to play a key role in the invasion process (Davis *et al.*, 2000), with invasive species often exhibiting

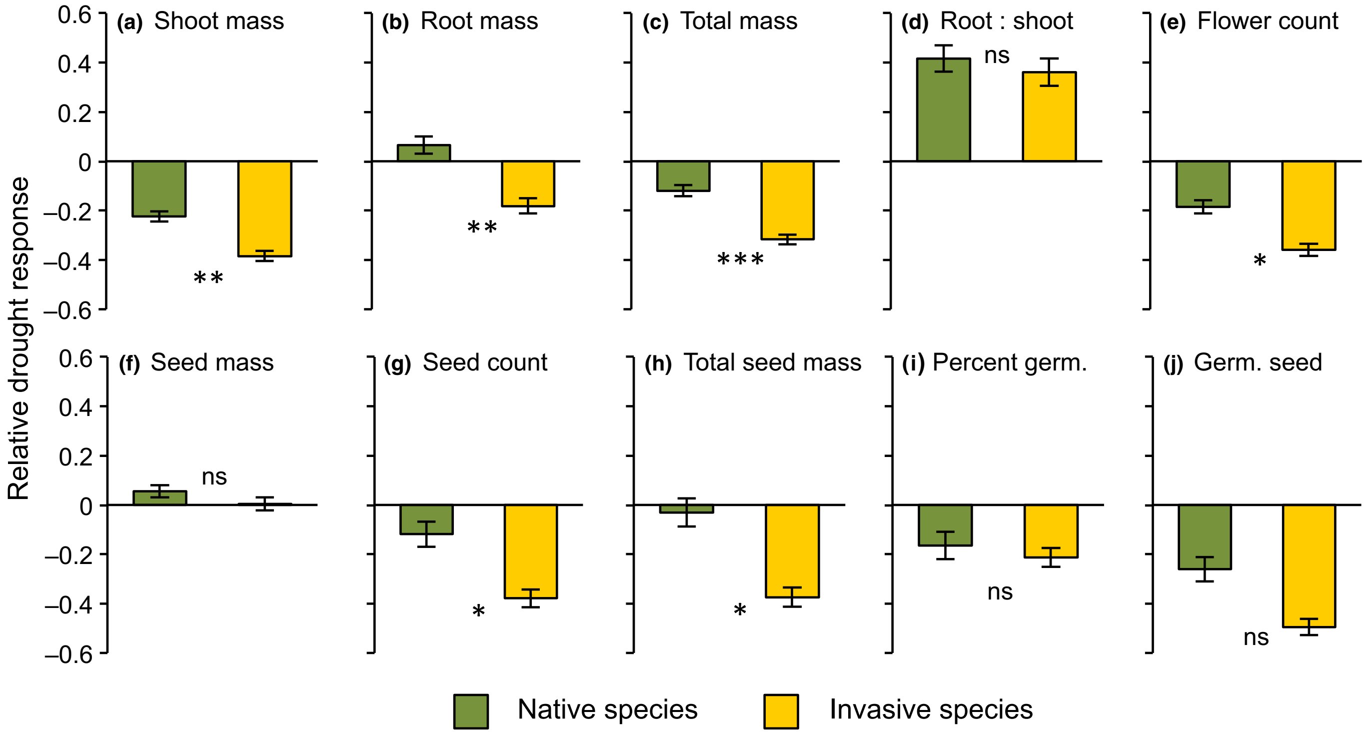

Fig. 2 Relative drought responses of native and invasive species (by origin) for shoot mass (a), root mass (b), total plant mass (c), root : shoot ratios (d), flower number (e), seed mass (f), seed number (g), total seed mass (h), percentage germination (i), and number of germinable seeds (j). Bars represent means ± SE. Asterisks indicate significant differences in drought responses between natives and invasives from linear mixed models: *, $P<0.05$; **, $P<0.01$; ***, $P<0.0001$; ns, not significant.

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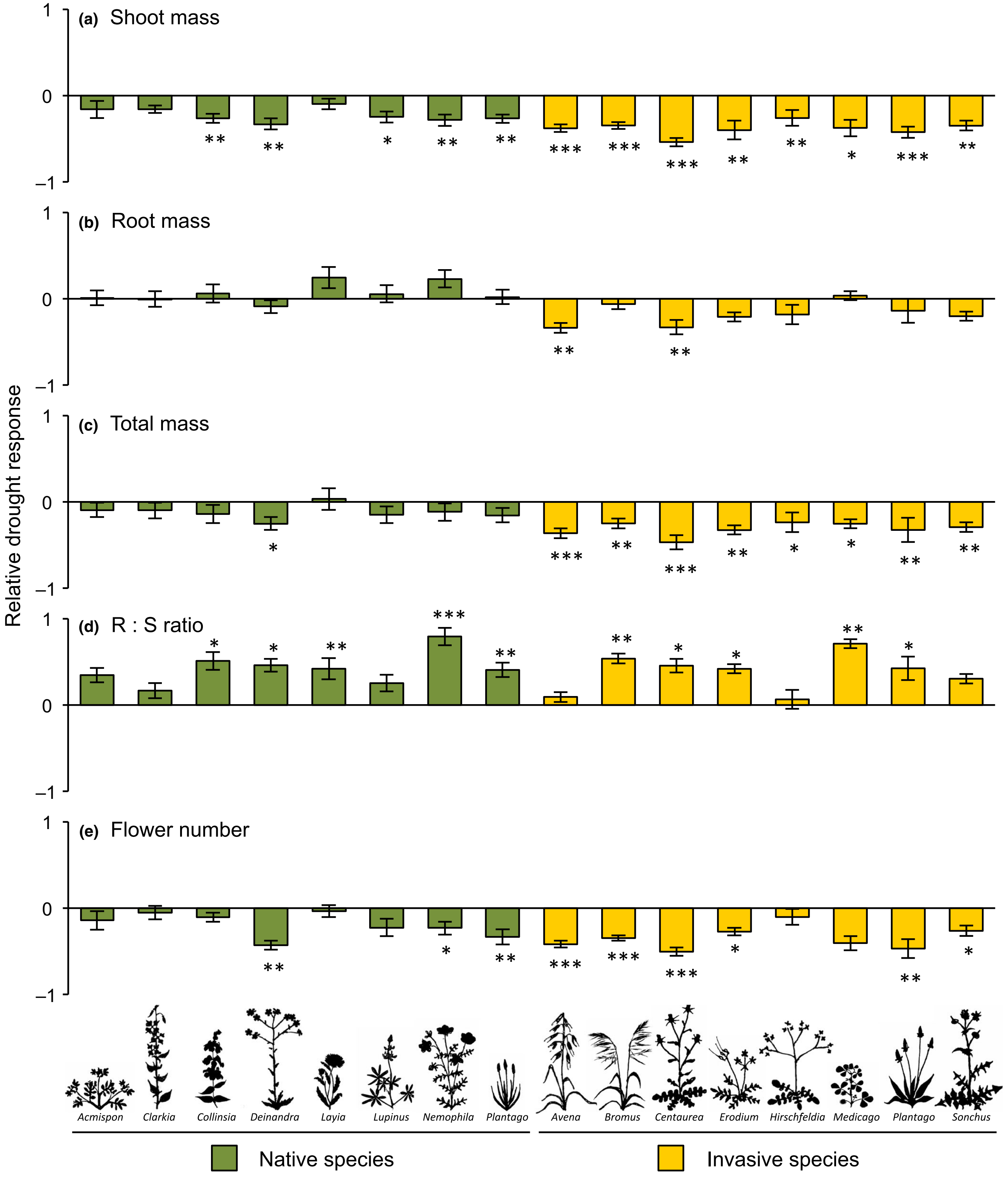

Fig. 3 Relative drought responses for shoot mass (a), root mass (b), total plant mass (c), root : shoot (R : S) ratios (d), and flower number (e) for each native and invasive species. Bars represent means ± SE. Asterisks above bars for each species indicate a significant drought response from *t*-tests comparing trait values of drought-stressed plants with those of well-watered controls: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$. Full *t*-test results are shown in Table 2.

traits associated with rapid growth and resource acquisition compared with native species (Leishman *et al.*, 2007; Van Kleunen *et al.*, 2010; MacKinnon *et al.*, 2014). The ability to increase reproductive output under favorable resource conditions probably facilitates invasion success (Baker, 1965; Mason *et al.*, 2008), yet relatively few studies examining the response of invasive species to resource availability include measures of reproductive output (Davidson *et al.*, 2011). Here, we show that invasive annuals of California grasslands may experience greater reductions in growth and reproduction as a result of drought compared with the native forb species they displace. However, invasive plant species also achieved greater biomass overall and produced a greater number of seeds with higher rates of germination compared with native species, especially under well-watered conditions. These invasives therefore appear to express a life-history strategy that allows them to rapidly capitalize on high resource conditions. Thus, our results support Baker's (1965) original hypothesis regarding the ability of weedy species to dramatically increase reproductive output under high resource availability.

The greater overall size of invasive species we observed is perhaps unsurprising, as a number of studies comparing native and invasive plants have reported similar results, including in California (MacKinnon *et al.*, 2014; Funk *et al.*, 2016). This is probably the net effect of a number of superior functional traits, including early germination, high relative growth rates, and rapid carbon assimilation (Wainwright & Cleland, 2013; Funk *et al.*, 2016). Plants often adjust biomass allocation in response to resource availability (McConnaughay & Coleman, 1999; Weiner, 2004), and, predictably, our study species responded to drought by increasing root : shoot ratios. This effect was similar across native and invasive species. Previous work has shown that invasives may display greater shoot allocation compared with noninvasive species (Van Kleunen *et al.*, 2010), but our results revealed no such pattern. Interestingly, while native and invasive species showed similar adjustments in root : shoot ratios in response to drought, the total biomass of natives was less responsive to drought than that of invasives. It is possible that native annuals in this system rely more on shifting allocation rather than altering plant mass in response to fluctuating water availability, and this growth strategy could buffer against more severe effects of drought, as experienced by invasives. While we harvested all plants at the same developmental stage (reproductive maturity), it should be noted that the observed root : shoot ratios were probably influenced by changes to growth rate as a result of drought in addition to optimal partitioning (McConnaughay & Coleman, 1999).

Seed size may be an important component of invasion (Rejmánek & Richardson, 1996; Willis *et al.*, 2000), but we observed no differences in seed mass between the native and invasive annuals examined. It is possible that a wider taxonomic sampling might reveal different patterns. Seed mass is thought to be one of the least plastic of plant traits (Fenner, 1985), and this is consistent with our findings, as we observed little effect of drought. However, the environment can exert a strong influence on seed size and viability, and one invasive species did exhibit significant reductions in seed mass as a result of drought: *Avena fatua*. This was also one of the few species to show reduced rates of germination as a result of drought.

We observed significantly higher rates of germination in invasives compared with natives, and previous work in California has documented similar results (Wainwright & Cleland, 2013). In some cases, more prolific germination may even be an adaptive response in introduced species (Hierro *et al.*, 2009). It is possible that the germination rates we report do not reflect actual seed viability, but instead different degrees of dormancy among species. We also cannot rule out the influence of maternal effects, as the environment can exert strong transgenerational effects (i.e. maternal effects) on seed germination (Fenner, 1991). Many native species from ecosystems with variable rainfall possess high degrees of seed dormancy (Ellner, 1987). This bet-hedging ability allows some seed to germinate and grow each year, while protecting most propagules until a reliably wet season arrives (Levine *et al.*, 2008). These invasives exhibit a different strategy, producing as much readily germinable seed as possible, with little dependence

Table 2 Results of Student's *t*-tests comparing trait values of drought-stressed plants with those of well-watered controls for each native and invasive species, including for mean shoot mass, root mass, total plant mass, root : shoot (R : S) ratio, and number of flowers.

		Shoot mass		Root mass		Total mass		R : S		No. of flowers	
Species	Origin	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Acmispon strigosus	Native	−1.03	0.3164	0.25	0.8039	−0.57	0.5730	1.47	0.1567	−1.57	0.1317
Clarkia unguiculata	Native	−1.96	0.0601	0.18	0.8594	−1.12	0.2699	1.39	0.1737	−0.43	0.6690
Collinsia heterophylla	Native	**−3.09**	**0.0045**	0.46	0.6513	−1.55	0.1333	**2.50**	**0.0187**	−0.80	0.4317
Deinandra fasciculata	Native	**−3.89**	**0.0006**	−1.02	0.3168	**−3.39**	**0.0021**	**2.59**	**0.0152**	**−3.13**	**0.0041**
Layia platyglossa	Native	−1.09	0.2826	1.62	0.1141	0.21	0.8381	**2.91**	**0.0065**	0.16	0.8722
Lupinus bicolor	Native	−2.22	0.0391	0.32	0.7543	−1.98	0.0629	**2.00**	**0.0602**	−1.67	0.1118
Nemophila menziesii	Native	**−3.16**	**0.0045**	1.88	0.0731	−1.47	0.1570	**4.77**	**< 0.0001**	**−2.24**	**0.0357**
Plantago erecta	Native	**−2.75**	**0.0100**	0.35	0.7267	−1.34	0.1909	**2.86**	**0.0077**	**−2.97**	**0.0059**
Avena fatua	Invasive	**−5.55**	**< 0.0001**	**−3.10**	**< 0.0001**	−4.96	< 0.0001	0.69	0.4941	**−6.43**	**< 0.0001**
Bromus diandrus	Invasive	**−4.79**	**< 0.0001**	−0.26	0.7962	−3.62	**0.0012**	**3.00**	**0.0057**	**−5.65**	**< 0.0001**
Centaurea melitensis	Invasive	**−6.95**	**< 0.0001**	**−2.85**	**0.0088**	−6.57	< 0.0001	**2.18**	**0.0494**	**−5.56**	**< 0.0001**
Erodium cicutarium	Invasive	**−4.18**	**0.0005**	−0.41	0.6834	−3.78	**0.0015**	**2.22**	**0.0388**	**−2.22**	**0.0390**
Hirschfeldia incana	Invasive	**−3.34**	**0.0039**	−1.65	0.1178	−2.39	**0.0274**	0.59	0.5644	−1.34	0.1991
Medicago polymorpha	Invasive	**−2.84**	**0.0118**	0.49	0.6316	−2.42	**0.0279**	**3.22**	**0.0054**	−1.93	0.0718
Plantago lanceolata	Invasive	**−4.82**	**< 0.0001**	−1.49	0.1509	−3.59	**0.0016**	**2.20**	**0.0378**	**−3.12**	**0.0048**
Sonchus oleraceus	Invasive	**−3.30**	**0.0032**	−1.59	0.1268	−2.97	**0.0071**	1.84	0.0791	**−2.77**	**0.0113**

Significant differences ($P < 0.05$) as a result of watering treatment are shown in bold.

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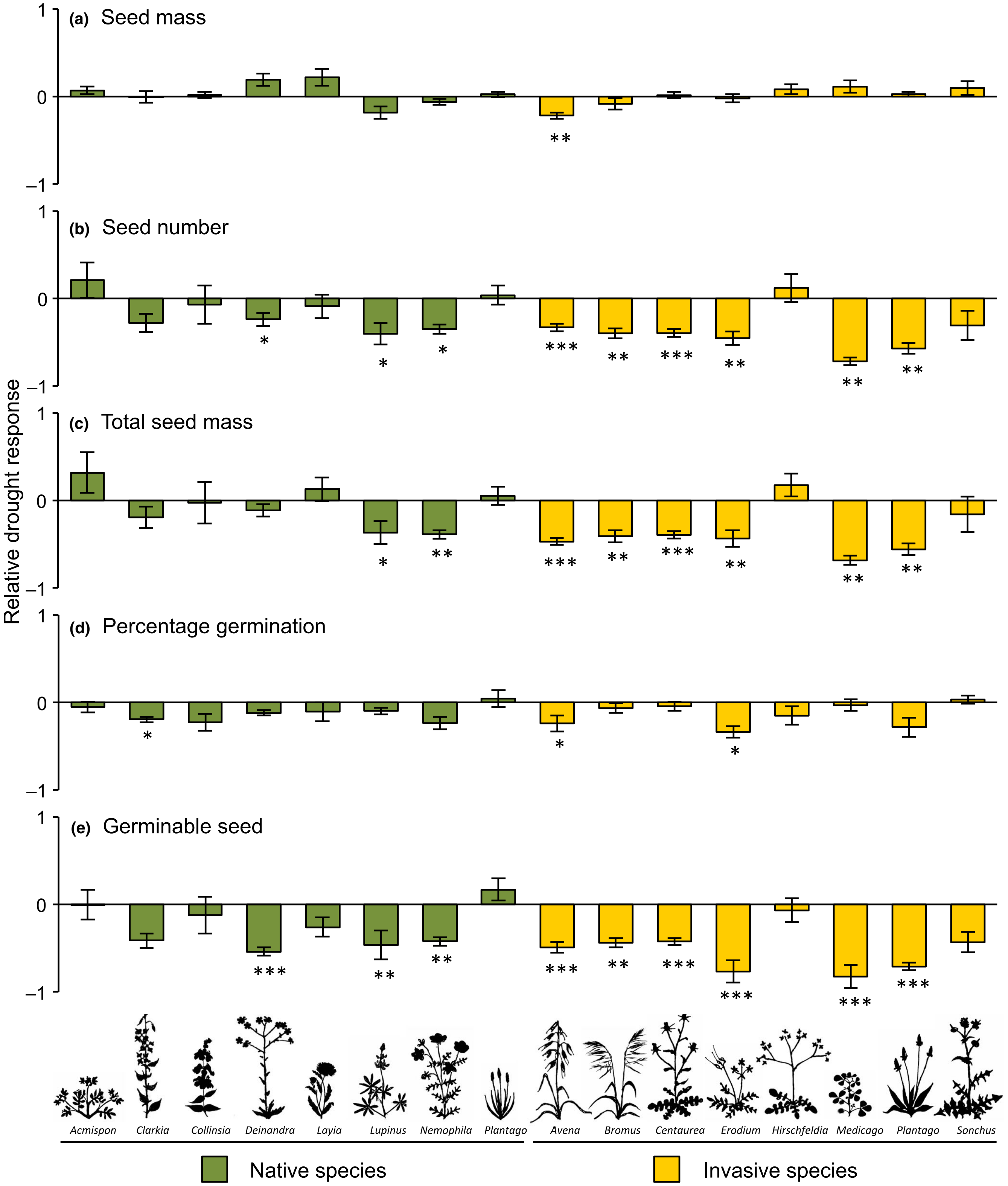

Fig. 4 Relative drought responses for seed mass (a), seed number (b), total seed mass (c), percentage germination (d), and number of germinable seeds (e) for each native and invasive species. Bars represent means ± SE. Asterisks above bars for each species indicate a significant drought response from *t*-tests comparing trait values of drought-stressed plants with those of well-watered controls: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$. Full *t*-test results are shown in Table 3.

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on soil seed-banking (Wainwright & Cleland, 2013; LaForgia *et al.*, 2018).

Although our results showing negative effects of drought on seed production in invasive species might suggest the existence of potential benefits of drought for native ecosystems, it is important to note that the dominance of invasives is probably facilitated by a number of other factors, such as earlier germination phenology, rapid growth, and increased competition for resources (Wainwright & Cleland, 2013; Funk *et al.*, 2016). Furthermore, even though invasive species exhibited more negative drought responses for several reproductive traits, overall they produced more germinable seed than native species under both well-watered and drought conditions. This suggests that their superior fitness may be maintained regardless of watering conditions as long as plants are able to reach reproductive maturity. Prolific seed production during wet years may also overwhelm any negative impacts of periodic drought on seed banks of these species, as evidenced by their persistence and even spread under prolonged drought (Minnich, 2008; Valliere *et al.*, 2017). It may therefore be more instructive to consider the inverse relationship – that invasive species are able to capitalize on favorable resource conditions and dramatically increase seed production – rather than the negative drought response ratios reported. This pattern best fits the 'master of some' strategy proposed by Richards *et al.* (2006).

Our results may help to explain vegetation dynamics in the field. For example, as a result of their less sensitive germination cues and reduced fecundity under drought, invasive species may be exhausted from the seed bank during extended dry periods while native forb species persist (LaForgia *et al.*, 2018). Previous field studies in California grasslands have found that nonnative invasive plant species may be more negatively impacted by drought than native species both above and below ground (Copeland *et al.*, 2016; LaForgia *et al.*, 2018). It is for this reason that some of the most spectacular wildflower blooms in California often occur during wet years following periods of drought – years when natives are not outcompeted by invasives (Minnich, 2008). This could have important implications for native plant restoration, as practitioners might be able to take advantage of low invasive propagule pressure to meet management goals (Bradley *et al.*, 2009). We should, however, caution against assuming all invasive annuals in this system will respond similarly to drought, and indeed the species composition of annual plant communities in California shows considerable interannual variability; in some years annual grasses predominate whereas other years may yield prolific stands of mustards or, most famously, carpets of wildflowers (Minnich, 2008). It is also unclear if such patterns will continue to manifest under future climate variability, as one recent study by Harrison *et al.* (2018) showed that native forb species did not recover in a wet year following a multiyear drought.

Because we selected species based on community type (annual grasslands) and not phylogenetic relatedness, it is important to note the potential bias that this may have introduced to the study (reviewed in Funk *et al.*, 2015). For example, two of the invasive study species were annual grasses, a functional group that is largely absent in the native flora of southern California, and annual grasses may exhibit different suites of traits compared with annual forbs (Kindscher & Wells, 1995; Larson & Funk, 2016). The source of plant material used may also influence results of experiments such as these, as some species may exhibit population-level differences in their response to varying soil moisture (e.g. Dyer *et al.*, 2016). Future experiments utilizing pairs of closely related natives and invasives (e.g. Muth & Pigliucci, 2007), a wider taxonomic sampling, and/or plant material from multiple populations of species across climate gradients will be useful for further evaluating the importance of these drought responses in the invasion process. Maternal environmental effects may also play an important role in shaping plant responses to

Table 3 Results of Student's t-tests comparing trait values of drought-stressed plants with those of well-watered controls for each native and invasive species, including for mean seed mass, number of seeds, total seed mass, percentage germination, and number of germinable seeds.

		Seed mass		No. of seeds		Total seed mass		Germination (%)		No. of germinable seeds	
Species	Origin	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Acmispon strigosus	Native	1.46	0.1598	0.47	0.6404	0.72	0.4826	−0.58	0.5703	−0.28	0.7826
Clarkia unguiculata	Native	0.17	0.8661	−0.95	0.3508	−0.93	0.3586	**−2.82**	**0.0114**	−1.65	0.1105
Collinsia heterophylla	Native	0.40	0.6952	−0.96	0.3439	−0.93	0.3591	−0.37	0.7160	−1.19	0.2466
Deinandra fasciculata	Native	1.99	0.0621	**−2.11**	**0.0488**	−0.77	0.4529	−1.80	0.0890	**−5.87**	**< 0.0001**
Layia platyglossa	Native	1.82	0.0777	−0.54	0.5958	0.47	0.6381	−0.90	0.3823	−1.34	0.1900
Lupinus bicolor	Native	−0.39	0.7038	**−2.16**	**0.0459**	**−2.19**	**0.0434**	−1.52	0.1468	**−3.68**	**0.0020**
Nemophila menziesii	Native	−1.56	0.1356	**−2.55**	**0.0202**	**−3.33**	**0.0037**	−0.75	0.4632	**−3.31**	**0.0039**
Plantago erecta	Native	0.57	0.5716	0.31	0.7605	0.52	0.6076	0.32	0.7532	1.04	0.3071
Avena fatua	Invasive	**−3.90**	**0.0005**	**−4.61**	**< 0.0001**	**−6.49**	**< 0.0001**	**−2.28**	**0.0348**	**−7.60**	**< 0.0001**
Bromus diandrus	Invasive	−1.77	0.0899	**−2.70**	**0.0119**	**−3.47**	**0.0018**	−0.90	0.3823	**−3.12**	**0.0042**
Centaurea melitensis	Invasive	0.31	0.7574	**−5.59**	**< 0.0001**	**−5.44**	**< 0.0001**	−0.73	0.4746	**−6.08**	**< 0.0001**
Erodium cicutarium	Invasive	−0.30	0.7696	**−3.76**	**0.0011**	**−3.04**	**0.0063**	**−3.40**	**0.0032**	**−6.03**	**< 0.0001**
Hirschfeldia incana	Invasive	1.20	0.2460	0.50	0.6260	1.00	0.3312	−1.32	0.2037	−0.60	0.5560
Medicago polymorpha	Invasive	1.15	0.2695	**−4.21**	**0.0008**	**−3.89**	**0.0014**	−1.24	0.1381	**−5.45**	**< 0.0001**
Plantago lanceolata	Invasive	0.70	0.4915	**−4.07**	**0.0007**	**−3.51**	**0.0025**	−2.10	0.0501	**−5.80**	**< 0.0001**
Sonchus oleraceus	Invasive	1.66	0.0616	−1.47	0.1575	−0.85	0.4065	0.34	0.7349	−1.34	0.1972

Significant differences ($P < 0.05$) as a result of watering treatment are shown in bold.

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drought, and understanding how these transgenerational effects may differ among native and invasive plant species in this system warrants further investigation (Bossdorf *et al.*, 2008; Fenesi *et al.*, 2014).

Another important consideration is that in this study we chose to implement an episodic drought treatment in which we withheld water from plants to induce severe drought stress as opposed to an approach where plants are continually supplied with lower amounts of water than are controls. The response of plants to water manipulations is influenced by multiple factors, including the timing, duration, and severity of drought treatments applied. Therefore it is possible that an alternative experimental design might yield different results from those observed here.

A key question that arises from this work is what is the role of phenotypic plasticity in driving the observed plant responses to drought? High phenotypic plasticity has been reported in a number of invasive plant species and may be an important mechanism of invasion success (Richards *et al.*, 2006; Davidson *et al.*, 2011), although it should be noted this has not been observed in all cases (Hulme, 2008; Palacio-López & Gianoli, 2011). Phenotypic plasticity undoubtedly influenced plant responses to drought, but our experimental approach is better suited to assessing drought resistance in these species and not phenotypic plasticity *sensu stricto* (Valladares *et al.*, 2006). For example, reduced plant performance under drought conditions may reflect a lack of adaptations for stress tolerance rather than genetically based plasticity. Although the invasive species studied here may indeed be more responsive to resource availability compared with natives, future work that includes more than two levels of water availability (and/or other resources) and multiple measurements of growth/traits over time will be useful to evaluate potential differences in plasticity among these species.

This study provides a critical piece of empirical evidence in support of Baker's original hypothesis (Baker, 1965). Given the importance of propagule pressure in the invasion process (Simberloff, 2009), studies such as this, which include measures of reproductive output, are crucial for assessing the role of resource availability in determining invasion success (Davidson *et al.*, 2011). Opportunistic responses to water availability along with other superior functional traits may facilitate the dominance and spread of these species under more extreme environmental variability, exacerbating ecosystem impacts under global change (Dukes & Mooney, 1999). However, these observed responses may also help to explain why drought has a more negative impact on nonnative invasives compared with native species in California grasslands (Copeland *et al.*, 2016; LaForgia *et al.*, 2018). Future studies that include a broader taxonomic sampling, more levels of resource availability, and demographic data will be useful in further evaluating the importance of these responses *in situ*.

Acknowledgements

This work was supported by a UCLA La Kretz Center for California Conservation Science Postdoctoral Fellowship and USDA NIFA postdoctoral fellowship (grant 12108962) awarded to JMV and a Stunt Ranch Research Grant awarded to EBE.

Author contributions

JMV and EBE designed and performed the experiment. JMV and GMB analyzed the data and interpreted results. MRS and PWR advised on experimental design, analysis, and presentation of results. All authors contributed to preparation of the manuscript.

ORCID

Gary M. Bucciarelli https://orcid.org/0000-0003-3345-1361
Justin M. Valliere https://orcid.org/0000-0003-3599-2911

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Images of seeds for each of the native and invasive plant species included in the study.

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