RESEARCH ARTICLE

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BRIEF COMMUNICATION

Evolutionary potential for increased invasiveness: High-Performance *Polygonum cespitosum* genotypes are competitively superior in full sun[1]

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PREMISE OF STUDY: The presence of genetic variation for traits that contribute to ecological range expansion can provide the potential for introduced taxa to evolve greater invasiveness. Genotypes that contribute to the spread of introduced range populations must have the ability to maintain fitness under changing environmental stress and competitive intensity. Previously, we identified a subset of genotypes in populations of the invasive annual *Polygonum cespitosum* that express consistently high reproductive fitness in diverse (shaded, dry, and resource-rich) conditions. Here, we investigated whether these broadly adaptive (High-Performance) genotypes also show a competitive advantage over conspecifics in full sun and/or shade.

METHODS: We grew a population-balanced sample of 13 High-Performance and 13 'Control' genotypes in intraspecific competitive arrays, comprising all four possible combinations of High-Performance vs. Control target plants and competitive backgrounds, in both full sun and shaded glasshouse environments.

KEY RESULTS: In full sun, High-Performance genotypes (1) better maintained growth and reproductive output despite competition and (2) more strongly suppressed growth and reproduction of target plants. However, genotypes did not differ significantly in shade.

CONCLUSIONS: Competitive superiority in open conditions may contribute to increasing predominance of these broadly adapted genotypes in introduced-range *Polygonum cespitosum* populations, and hence to the evolution of greater invasiveness. This study provides insight into the role of genotypic variation for ecological traits in the range expansion of a contemporary plant invader. It also highlights how such variation can be differently expressed in alternative environments (gene by environment interaction).

KEY WORDS competitive ability; competitive effect; competitive response; evolutionary potential; gene by environment interaction; general-purpose genotypes; invasive species; *Persicaria cespitosa; Polygonum cespitosum*

Evidence for rapid evolution of nonnative species in response to novel environments in their introduced ranges is abundant, but invasion biologists are still striving to describe the underlying evolutionary mechanisms (Reznick and Ghalambor, 2001; Sax et al., 2007; Buswell et al., 2011; Colautti and Lau, 2015). Understanding how genotypes respond to novel selection pressures of the introduced range may help explain changes at the population and species level (Sakai et al., 2001; Parker et al., 2003; Zenni et al., 2014). One approach to genotypic variation is an assessment of evolutionary potential, i.e., by sampling genotypes from introduced-range populations, experimenters can determine whether they display reaction norms in ecologically relevant conditions that can contribute directly to successful establishment and spread (Barrett and Schluter, 2008; Lavergne and Molofsky, 2007). If standing variation in the introduced range includes genotypes with greater fitness in novel conditions, populations can evolve to consist increasingly of these highly successful genotypes, and hence to have higher rates of reproductive output and invasive spread (Lee, 2002; Hendry, 2013). Groups of genotypes with the ability to establish and prolifically reproduce in multiple environments could contribute to rapid and widespread range expansion (Richards et al., 2006; Vellend et al., 2010; Zenni et al., 2014).

A plant species that expands its range and disrupts native communities must cope with the physiological constraints of competitive conditions (Suding et al., 2004; Maron and Marler, 2008). Plant

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ecologists have recognized that competitive ability has two distinct components: (1) *competitive response,* the ability to grow and reproduce in spite of competition from neighbors; and (2) *competitive effect,* the ability to reduce the growth and reproduction of neighboring individuals (Goldberg and Landa, 1991; Wang et al., 2010). Both components of competitive ability can contribute to the geographic spread and ecological dominance that characterize successful plant invaders (Hager, 2004; Suding et al., 2004; Hovick et al., 2011; Skálová et al., 2013). In addition, both of these dimensions of competitive ability have been shown to vary genetically (e.g., Cahill et al., 2005; Willis et al., 2010). The literature testing the Evolution of Increased Competitive Ability hypothesis (EICA; Blossey and Nötzold, 1995) has resulted in an understanding of possible ecological causes of changes in competitive ability between native- and introduced-range populations of invasive species (Felker-Quinn et al., 2013 and references therein; Joshi et al., 2014). To better understand the impact of increased competitive ability on range expansion in ongoing invasions, we must investigate the variation for competitive ability at the population and genotype levels (Moloney et al., 2009; Lachmuth et al., 2011; Svenning et al., 2014).

We examined genotypic variation for competitive ability within introduced populations of a newly invasive plant, *Polygonum* (s. l.) *cespitosum* Blume (=*Persicaria cespitosa* (Blume) Nakai (Kim and Donoghue, 2008)), a primarily self-fertilizing annual herb that was introduced to North America from Asia in the early 20th century (Paterson, 2000; Mehrhoff et al., 2003). In its native range, and for a number of decades after introduction, the species was limited to shaded, moist environments (Sultan et al., 1998). In the past two decades, northeastern North American populations have evolved altered patterns of adaptive plasticity for key functional traits associated with increased reproductive output in sunny, open conditions (Sultan et al., 2012). Field surveys show that over a similar time period these populations have expanded their ecological range to include more sites with high light (Matesanz et al., 2015). Introduced-range populations of this species contain substantial quantitative genetic variation as well as neutral (microsatellite marker) diversity (Matesanz et al., 2014a; Matesanz et al., 2014b). These populations also contain a subset of broadly adaptive, *High-Performance genotypes* that consistently reproduce at high levels relative to other genotypes, across both resource-rich and stressful greenhouse environments (Matesanz and Sultan, 2013) and thus appear to exemplify the kind of "general-purpose genotypes" (Baker, 1965) that could fuel the evolution of increased invasiveness in the species' new range. Here, we ask whether these High-Performance genotypes also differ in their ability to compete with conspecifics, a stress they are likely to confront in the dense, monotypic stands they often form in the field (Mehrhoff et al., 2003; Horgan-Kobelski, 2010; Matesanz et al., 2015).

We grew High-Performance genotypes along with a group of Control genotypes from populations across southern New England under intraspecific competition in a glasshouse. Treatments mimicked both shaded and full sun conditions to determine whether competitive interactions between the two performance groups differ between the ancestral (shaded) environment and the novel, open environments into which the species is expanding in its introduced range (Matesanz et al., 2015). We designed competitive conditions to assess both competitive response and competitive effect by establishing a target plant and a competitive background of multiple individuals within each pot. This design allowed us to address the following questions: (1) Do High-Performance genotypes of *Polygonum cespitosum* display greater competitive response and effect than a random sample of Control genotypes? (2) If High-Performance genotypes express greater competitive ability, is this pattern consistent in open and shade treatments? (3) What evolutionary potential for increased invasiveness exists within this sample of genotypes?

MATERIALS AND METHODS

Experimental sample of High-Performance and Control genotypes—In an earlier study (Matesanz and Sultan, 2013), we identified a set of consistently High-Performance genotypes to create samples for comparison based on the range of genotypic variation within northeastern North American populations of *Polygonum cespitosum*. In that study, field-collected achenes from 30 plants per population were sampled from 14 field populations of *Polygonum cespitosum* and inbred under uniform greenhouse conditions to produce 416 inbred (selfed full-sib) genetic lines (hereafter "genotypes"). Twenty achenes from each genotype were sown into pots, and those that germinated between 7-14 d after sowing were grown to maturity in high-light, full moisture conditions (details in Matesanz and Sultan, 2013). To represent the top fraction of genetic variation in introduced-range populations, those genotypes expressing the top 5% of total reproductive output (52–102% higher reproductive output than the mean of all genotypes; n = 26) were selected as putative High-Performance genotypes (Matesanz and Sultan, 2013). A subsequent greenhouse experiment comparing the performance of these genotypes to that of a Control group selected at random from the remaining 95% determined that High-Performance genotypes also had higher lifetime reproductive fitness in both dry and shaded treatments (Matesanz and Sultan, 2013). The experimental sample in the current study consisted of 13 of these previously identified High-Performance genotypes drawn from 5 northeastern North American populations (only those populations that included 2 or more such genotypes). From each of these 5 populations, an equivalent number of Control genotypes was selected, resulting in a total sample of 26 genotypes.

Treatments and growth conditions—125 inbred achenes from each genotype were stratified at 4°C for ~8 wk before germinating in flats of vermiculite. At the first true leaf stage, seedlings were transplanted (14-20 August 2013) into competitive arrays (see the following paragraphs) in 1L clay pots filled with a 1:1:1 mixture of sterilized local topsoil, Turface fritted clay (Profile, Buffalo Grove, Illinois, USA) and medium sand (Quikrete Co., Atlanta, Georgia, USA) with 2.5 grams per pot of 15:8:12 NPK fertilizer (Agway, Middlefield, Connecticut, USA). Pots were placed on greenhouse benches in full sunlight and watered regularly to field capacity moisture levels to ensure recovery from transplant shock.

To mimic the competitive conditions of the dense stands this species often encounters in the field (Mehrhoff et al., 2003; Horgan-Kobelski, 2010; Matesanz et al., 2015), each one-liter pot included a central target plant surrounded by a competitive background of six plants. One seedling (the "target plant") was transplanted into the center of each pot, then 6 seedlings at the same developmental stage as the target were transplanted around the periphery of the pot (the "competitive background"). This density of approximately 570 individuals per square meter is equivalent to the most competitive

conditions regularly observed in field populations (Horgan-Kobelski, 2010; Matesanz et al., 2015). The competitive background consisted entirely of seedlings from *either* High-Performance genotypes (High-Performance background) or Control genotypes (Control background). Each competitive background of 6 competitors consisted of 3 pairs of individuals, each pair sourced from a different genotype and population to avoid confounding the effect of performance group with the effect of a particular population or genotype.

Each pot was randomly assigned to one of two light treatments ten days after transplant. The Open treatment received full summer sunlight. Pots in the shade treatment were placed under shade tents constructed by covering metal frames with 80% neutral-density shade cloth with green plastic filters providing reduced Red: Far-Red light ratio (#138, Lee Filters, Burbank, California, USA (additional treatment details in Matesanz and Sultan, 2013). All pots were kept at field capacity soil moisture with reverse osmosis-filtered water delivered via an automatic irrigation system.

For each of the 26 target genotypes (13 High-Performance and 13 Control), we set up 8 pots with that genotype as the target plant, and randomly assigned each pot to one of two competition treatments and one of two light treatments, for a total of 4 factorial treatment combinations (Open/HP background, Open/C background, Shade/HP background, Shade/C background) with 2 replicates per genotype and treatment combination (26 target genotypes × 2 light treatments × 2 competition treatments × 2 replicates = 208 pots). Two spatial blocks were spread across 4 greenhouse benches in a randomized complete block design (Zar, 1999).

Data collection—To avoid loss of early maturing seeds, early achene collections were conducted on target plants weekly, starting 8 wk after transplant, by gently rubbing inflorescences before mature achenes were released. Plants were grown until senescence (10-11 wk after transplanting). During the final harvest (16-31 October 2013), all reproductive tissues (mature achenes, immature achenes, inflorescences, and reproductive support tissues) were removed, dried and weighed to best capture the output of this indeterminately reproducing species (see Sultan and Bazzaz, 1993; Matesanz et al., 2014a). Early achene collections and reproductive tissues collected at harvest were summed to determine lifetime *target plant reproductive output (mg)*. The remaining shoot tissue from each target plant (leaves and stems) was dried and weighed to estimate *target plant vegetative biomass (mg)*. Before weighing, all achenes were air dried at room temperature for at least 5 d, and all vegetative tissues were oven-dried at 100°C for ≥2 hours, then at 65°C for ≥48 hours.

Data analyses—ANOVA with type III sums of squares was used to test for effects on target plant reproductive output and target plant vegetative shoot biomass of: (1) *performance group* (High-Performance vs. Control); (2) *genotype* (nested within performance group); (3) *light treatment* (Open vs. Shade); (4) *competition treatment* (High-Performance background vs. Control background); (5) all two-way and three-way interactions; and (6) block. Genotype was nested within performance group and treated as a fixed effect rather than a random effect because (a) genotypes had been assigned into performance groups based on their relative fitness (Hill and Lewicki, 2006) and (b) the sample was deliberately chosen to equally represent different populations (see Matesanz and Sultan, 2013 for a similar statistical model). Data were transformed ($\sqrt{x}$ for target reproductive output and $\sqrt{(x+0.5)}$ for target vegetative biomass) to meet the ANOVA assumptions of homoscedasticity and normality (Zar, 1999). To avoid type I error, false discovery rate was controlled using the method developed by Benjamini and Hochberg (1995). Where significant treatment effects and/or interactions in the full model justified further investigation, we also carried out ANOVAs and posthoc Tukey's honest significant difference (HSD) tests within treatments.

All statistical analyses were performed in JMP version 9.0.0 (SAS Institute, Cary, North Carolina, USA). Final sample sizes were 194 pots (target plant reproductive output) and 193 pots (target plant vegetative biomass) after 14 and 15 pots, respectively, were removed from the analysis due to insect damage, mislabeling or experimental error.

RESULTS

Interaction effects between light and performance groups—Plants of all genotypes grown in the open treatment produced substantially more offspring than those grown in the shade treatment (Table 1). Compared to target plants from Control genotypes, target plants

TABLE 1. Effects of target plant performance group (Perform. Gr.), light treatment (Light), competitive background treatment (Comp. Backgr.), genotype (nested in performance group; Genotype [Perform. Gr.]), all two-way and three-way interactions, and block on target plant reproductive output and target plant vegetative biomass. Terms with bold *p*-values were significant after controlling for false discovery rate.

	Target	Plant	Reproductive	Output	Target	Plant	Vegetative	Biomass
Source	**DF**	**MS**	**F**	***p***	**DF**	**MS**	**F**	***p***
Perform. Gr.	1	0.269	10.02	**0.002**	1	0.089	4.15	0.045
Light	1	33.356	1244.63	**<0.001**	1	20.304	951.40	**<0.001**
Comp. Backgr.	1	0.138	5.16	**0.026**	1	0.141	6.59	**0.012**
Genotype [Perform. Gr.]	24	0.108	4.05	**<0.001**	24	0.073	3.41	**<0.001**
Perform. Gr. x Light	1	0.195	7.28	**0.008**	1	0.102	4.76	0.032
Perform. Gr. x Light x Comp. Backgr.	1	0.005	0.19	0.668	1	0.001	0.04	0.845
Light x Comp. Backgr.	1	0.263	9.80	**0.002**	1	0.210	9.82	**0.002**
Genotype [Perform. Gr.] x Light	24	0.065	2.42	**0.002**	24	0.050	2.33	**0.002**
Genotype [Perform. Gr.] x Comp. Backgr.	24	0.030	1.13	0.328	24	0.027	1.29	0.198
Perform. Gr. x Light x Comp. Backgr.	1	0.011	0.40	0.530	1	0.014	0.67	0.415
Genotype [Perform. Gr.] x Comp. Backgr.	24	0.022	0.83	0.694	24	0.021	0.98	0.495
Block	1	0.000	0.01	0.942	1	0.053	2.50	0.117
Error	89	0.027			88	0.021		

from High-Performance genotypes showed a greater increase in reproduction when grown in the open vs. the shade treatment (significant Light × Performance Group interaction: Fig. 1A; Table 1). Though target plants generally had higher reproductive output in the open treatment, High-Performance competitive backgrounds suppressed target reproductive output more effectively than Control competitive backgrounds in the open treatment only (significant Light × Competitive Background effect: Fig. 1B; Table 1). No difference in target plant vegetative biomass between High-Performance and Control genotypes was found in either treatment (nonsignificant Performance Group and Performance Group × Light effects), and otherwise closely matched patterns of variation observed for reproductive output (Table 1). Individual genotypes displayed significantly variable norms of reaction across the two treatments, even when the Genotype term was nested within Performance group (significant Genotype × Light effect: Table 1).

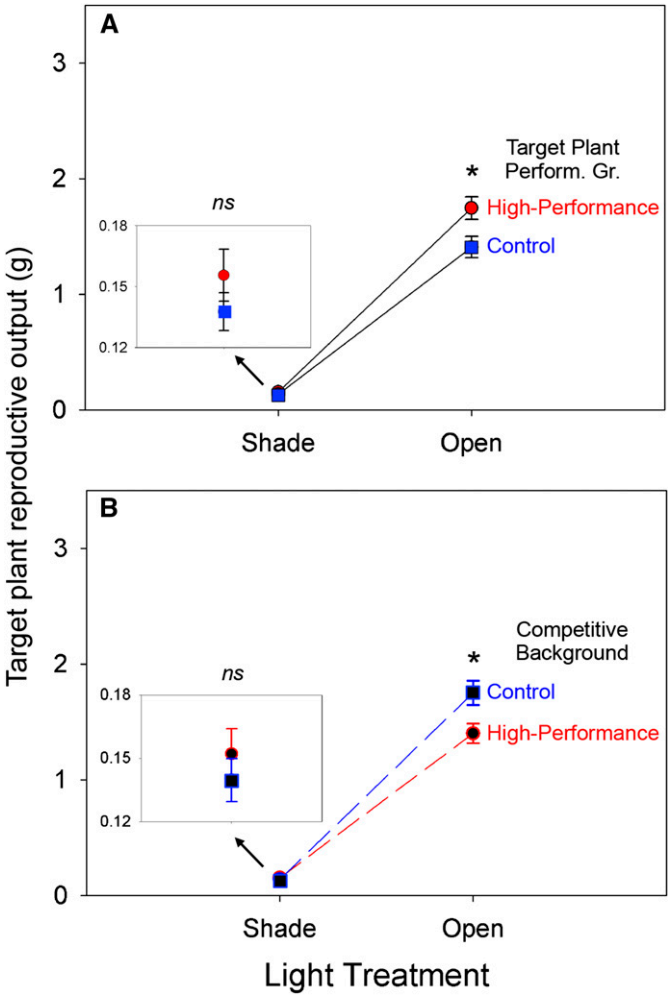

FIGURE 1 (A) Effect of target plant performance group (red circles for High-Performance, blue squares for Control) and light treatment on target plant reproductive output (mean ± SE). (B) Effect of competitive background (circles with red outlines for High-Performance, squares with blue outlines for Control) and light treatment on reproductive output of target plants from both performance groups (mean ± SE). Asterisks indicate significant differences based on *posthoc* Tukey's tests. Y-axis reflects the distribution of raw data. N = 194.

Competitive interactions in the open treatment—In the open treatment, target plants from High-Performance genotypes produced more offspring (Table 2) than those from Control genotypes. High-Performance competitive backgrounds had a significantly greater negative effect than Control competitive backgrounds on target plant reproductive output (Table 2). A *posthoc* Tukey's test of target plant performance group by competitive background showed a significant difference between the reproductive output of High-Performance target plants competing against a Control competitive background and the reproductive output of Control target plants competing against a High-Performance competitive background (Fig. 2).

DISCUSSION

The presence of genetic variation for traits that contribute to range expansion can provide the potential for introduced taxa to evolve greater invasiveness. Our study of genotypes from 5 northeastern North American populations of *Polygonum cespitosum* revealed genetic variation for the two central aspects of competitive ability, i.e., response to neighbors and suppressive effect on neighbors. High-Performance genotypes in these introduced-range populations had previously been shown to have greater fitness than Control genotypes across a range of contrasting glasshouse environments including both favorable conditions and stressful (shade and drought) treatments (Matesanz and Sultan, 2013). Here we showed that these broadly adaptive genotypes also demonstrated greater competitive ability in open habitats than a population-balanced sample of genotypes from the same populations. In light of findings from the field that this species is expanding its ecological range into open, high-light habitats (Matesanz et al., 2015), this demonstration of evolutionary potential for a highly relevant ecological trait in a novel environment provides additional insight into the invasive success of *P. cespitosum*.

Our study of evolutionary potential reveals that expression of genetic variation for competitive ability depends on environmental context in this species. Though High-Performance genotypes demonstrated a reproductive advantage over Control genotypes in both open and shaded conditions without competition (Matesanz and Sultan, 2013), when competitive conditions were incorporated, High-Performance genotypes maintained their reproductive advantage only under full sun. Individual genotypes varied in their response to the two light treatments, but the magnitude of variation was greater in the open treatment. Our results exemplify the idea that genotypes can express similar phenotypes in one environment and express meaningfully different phenotypes in another (Kruuk et al., 2008). As a result of this gene by environment ($g \times e$) interaction, we can predict that variation for competitive ability will be exposed to selection only in full sun conditions (Falconer and Mackay, 1996; Snell-Rood et al., 2010). Recent studies of biological invasions have similarly shown that exposure of introduced species to novel ecological situations can reveal genetic variation to natural selection that had not previously been expressed (Zenni et al., 2014; Dlugosch et al., 2015). In combination with the finding that introduced-range populations of *Polygonum cespitosum* have rapidly evolved adaptive responses to these novel, high-light conditions (Sultan et al., 2012), evidence presented here suggests that the competitive advantage of High-Performance genotypes in open sites could contribute to the species' increased invasiveness in the region as these genotypes come increasingly to predominate.

TABLE 2. Effects of target plant performance group (Perform. Gr.), competitive background treatment (Comp. Backgr.) and genotype (nested in performance group; Genotype [Perform. Gr.]), all two-way interactions, and block on target plant reproductive output in the open or shade treatment. Terms with bold *p*-values were significant after controlling for false discovery rate.

	Open				Shade			
Source	DF	MS	F	*p*	DF	MS	F	*p*
Perform. Gr.	1	2.713	9.79	**0.003**	1	0.003	0.94	0.338
Comp. Backgr.	1	2.438	8.80	**0.005**	1	0.006	1.96	0.168
Genotype [Perform. Gr.]	24	0.877	3.16	**0.001**	24	0.012	3.56	**<0.001**
Perform. Gr. × Comp. Backgr.	1	0.054	0.19	0.661	1	0.000	0.04	0.842
Genotype [Perform. Gr.] × Comp. Backgr.	24	0.252	0.91	0.592	24	0.005	1.57	0.094
Block	1	0.014	0.05	0.822	1	0.004	1.14	0.291
Error	43	0.283			44	0.003		

In this study we tested only the response to intraspecific competition. In some cases, competitive differences (for example, between native- and introduced-range populations) may be less apparent when plants are competing against conspecific rather than heterospecific individuals (Joshi et al., 2014). Intense intraspecific competition is a realistic scenario for *Polygonum cespitosum*, which is often found in dense, monospecific stands, particularly in high-light environments (Mehrhoff et al., 2003; Horgan-Kobelski, 2010; Matesanz et al., 2015). In general, intraspecific competition is believed to play a greater ecological role in such favorable abiotic environments (García-Cervígon et al., 2013). Because this species invades both disturbed and relatively intact habitats in its introduced range (Horgan-Kobelski, 2010; Matesanz et al., 2015), its competitive interactions with other species are also relevant. Further studies testing the responses of *P. cespitosum* genotypes to interspecific competition would further illuminate the ecological and evolutionary variation in this system.

The present dataset reflects a distinct approach that builds on previous studies of competitive ability in invasive plants. An extensive literature exists evaluating the (often greater) competitive ability of introduced taxa in comparison with native congeners (e.g., Keddy et al., 1994; Daehler, 2003; Vilà and Weiner, 2004; Skálová et al., 2013). Evolution in invasive species has been demonstrated primarily through performance comparisons of introduced vs. native range populations (Bossdorf et al., 2004; Ridenour et al., 2008; Graebner et al., 2012). Many of these studies have aimed to test the 'Evolution of Increased Competitive Ability' or *EICA* hypothesis, which posits a connection between decreased herbivory in an introduced range and a selective increase in competitive performance (Blossey and Nötzold, 1995). Although these species- and population-level studies have provided important insights, comparisons of competitive ability have heretofore been lacking at the level of genotypes within introduced populations. ("Super-genotypes," or single genotypes in apomictic species that are capable of invasion, are an exception with distinct population consequences; Le Roux et al., 2007). It is this level of variation that shapes a species' potential to evolve greater invasiveness following its introduction. Though *Polygonum cespitosum* is a primarily selfing species, these findings confirm that its North American populations contain substantial genotypic variation for competitive and fitness responses to environmental circumstances.

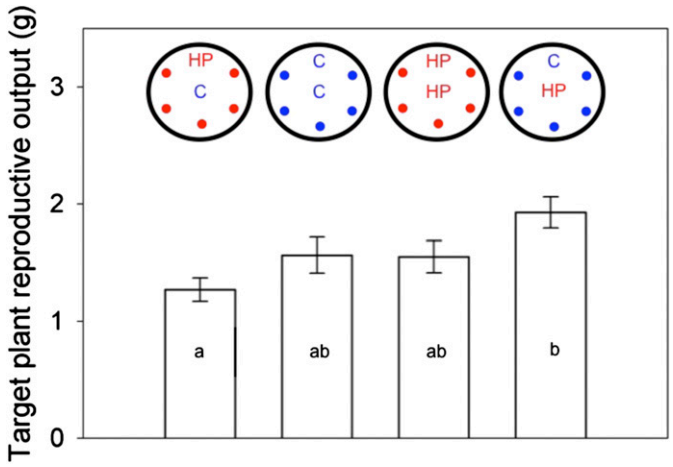

FIGURE 2 Effect in the open treatment of target plant performance group (red "HP" or blue "C" in the center of each pot) and competitive background (red "HP" and red dots or blue "C" and blue dots around the edge of each pot) on target plant reproductive output (mean ± SE). Letters indicate significant differences based on *posthoc* Tukey's tests. Y-axis reflects the distribution of raw data. N = 194.

Herbert Baker (1965) predicted that successful invasive plant species should consist of broadly adaptive, "general-purpose" genotypes that grow and reproduce successfully across a variety of conditions. Populations made up of such "general-purpose" genotypes could colonize and rapidly spread across a diverse array of sites (Parker et al., 2003; Lavergne and Molofsky, 2007). Previously, we showed that introduced-range populations of *Polygonum cespitosum* include a subset of genotypes with these characteristics (Matesanz and Sultan, 2013). The present glasshouse results suggest that in sunny, open habitats, these individuals might competitively outperform other genotypes, enhancing their reproductive advantage in these sites so as to promote their spread and eventual predominance in introduced-range populations. Because competitive dominance is a driver of colonization success in many plant invasions (Suding et al., 2004; Maron and Marler, 2008; Skálová et al., 2013), studies of quantitative genetic variation for competitive ability and response can contribute key insights to invasion dynamics. Field experiments can then play an important role in testing the realized consequences of performance differences revealed under controlled glasshouse conditions as well as this species' ability to adversely affect native plant communities.

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