

High-performance genotypes in an introduced plant: insights to future invasiveness

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Abstract. Maintaining high reproductive output in diverse conditions has consistently been found to promote invasiveness in introduced taxa. Following on this key observation, studies have compared the performance across environments of invasive vs. native congeners, and of introduced vs. native populations within invasive species. Performance differences among genotypes within introduced species have received far less attention, although such genetic variation could be critical to invasive potential. If an introduced species contains genotypes that can maintain high fitness across contrasting environments, such broadly adaptive, high-performance genotypes could promote and shape the species' immediate spread across multiple habitats. Furthermore, their presence could lead to the evolution of greater aggressiveness in the species, as these high performers increase in frequency. We investigated the existence and distribution of high-performance genotypes in *Polygonum cespitosum*, a newly invasive Asian annual. We raised 416 genotypes, collected from 14 North American populations, under resource-rich conditions to identify potential high-performance genotypes (the top 5% in total reproductive output). We then compared their fitness, life history, and functional traits to a random group of the remaining genotypes in three contrasting environments to ask the following: (1) Do consistently high-performance genotypes (i.e., genotypes with high relative fitness in diverse conditions) exist within introduced-range populations? (2) If so, do these high-performance genotypes possess distinctive life history and/or functional traits? (3) Do these genotypes occur in all populations or in only a subset of populations?

Genotypes initially identified as high-performance in favorable conditions also had higher reproductive output in resource-limited environments. Their fitness advantage compared with control genotypes varied in magnitude from one environment to another but was significant within all three test environments. High-performance genotypes shared a developmental syndrome characterized by rapid and high germination, fast seedling growth, early reproductive onset, and high reproductive allocation, but they did not differ in other functional traits.

P. cespitosum includes a subset of genotypes with accelerated development and significantly greater fitness in both favorable and stressful conditions. The nonrandom distribution of these high-performance genotypes among populations in the species' introduced range highlights the importance of genotypic and population-level variation for invasion dynamics.

Key words: ecological generalist; genetic variation; invasive species; life history; norms of reaction; northeastern North America; *Persicaria cespitosa*; phenotypic plasticity; *Polygonum cespitosum*.

INTRODUCTION

A central goal of contemporary ecology has been to identify key traits that promote aggressive spread in a novel range, in order to predict the invasive potential of introduced taxa. Baker (1965, 1974) determined the characteristics of an “ideal weed” by comparing aggressively colonizing vs. non-weedy plant congeners. These foundational papers predict that aggressive species will be characterized by rapid seedling growth, early reproductive onset, high phenotypic plasticity, and

most importantly, the ability to establish and reproduce successfully across a wide range of environments. Recent meta-studies have confirmed that life history traits such as high germination rate, early and longer flowering, and high fecundity may indeed contribute to the spread of introduced species (Hayes and Barry 2007, Pyšek and Richardson 2007, van Kleunen et al. 2010). In particular, the ability to maintain high reproductive output in diverse conditions has consistently been found to promote invasiveness in both plants and animals (Lockwood et al. 2005, Simberloff 2009).

Most studies of traits important to invasiveness have compared fitness, life history, and/or functional plasticity of invasive species to that of native (or noninvasive) congeners, or have compared traits of introduced vs.

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native populations of an invasive taxon (e.g., Bossdorf et al. [2005] and references therein, van Kleunen et al. [2011]). Performance differences among genotypes within introduced species have received far less attention, although such genetic variation could be critical to invasive potential (Vellend et al. 2009, 2010); (also see Schlaepfer et al. [2008], Treier et al. [2009], Hahn et al. [2012], te Beest et al. [2012] for work on differential performance among ploidy levels of invasive species). If an introduced species contains certain genotypes that can maintain high fitness in multiple environments, such high-performance genotypes (broadly similar to the “Jack-of-all-trades” concept discussed by Richards et al. [2006]) could influence invasion dynamics in two key ways. First, these genotypes could directly promote the species’ immediate geographic spread across diverse habitats and sites in its introduced range, as individuals with higher reproductive output will likely have greater colonization success due to increased propagule pressure (i.e., the number of individuals arriving at a site; Lockwood et al. 2005). Second, high-performance genotypes could fuel the evolution of increased aggressiveness in an introduced species, since its populations will increasingly come to consist of such genotypes over time due to natural selection following the initial introduction. Accordingly, populations that contain high-performance genotypes are likely to be the major contributors to a species invasion, so the precise distribution of high-performance genotypes (i.e., their occurrence and prevalence in various populations) may provide important insight to invasion trajectories.

Here we present a two-stage study testing for the existence, nature, and distribution of high-performance genotypes in a newly invasive plant. *Polygonum* (s.l.) *cespitosum* Blume (*Persicaria cespitosa*; Kim and Donoghue 2008) is an annual, primarily self-fertilizing herb introduced to North America from eastern Asia in the early 20th century (Paterson 2000). In its native and initial introduced range, *P. cespitosum* populations were largely restricted to shaded, moist, disturbed habitats such as forest understories. However, in the last two decades, the species has expanded its ecological range in northeastern North America to include open, moist habitats characterized by high light availability. Rapid, recent evolution of phenotypic plasticity patterns to express enhanced ecophysiological function and increased reproductive output in high light conditions has accompanied this change in ecological distribution (Sultan et al. 2012). Due in part to its rapid spread to new habitats, *P. cespitosum* has recently been classified as invasive in North America (Mehrhoff et al. 2003). As an invasion in progress, this scenario provides an excellent model system in which to investigate high-performance genotypes.

We screened a large sample of *P. cespitosum* genotypes from introduced-range populations in a high light, moist greenhouse environment to identify as potential high-performance genotypes those with high

reproductive output in this favorable treatment. We designed this test environment to mimic an open, moist habitat because (a) *P. cespitosum* is successfully invading this type of site in North America, and (b) reproductive output can be extremely high in such conditions. For both reasons, performance differences among genotypes in this resource-rich environment are of particular relevance to the species’ invasive potential in its introduced range (see Lockwood et al. [2005], Simberloff [2009] on propagule pressure and invasion success).

To determine whether these potential high-performance genotypes maintained their relative fitness advantage across diverse conditions, we then compared their expression patterns for a variety of life history and functional traits to a randomly selected control group of genotypes, in three greenhouse environments simulating current habitats of the species in its introduced range. Such naturalistic, controlled treatments make it possible to precisely characterize the performance of individual genotypes in response to key environmental variables and are a standard approach in plasticity and ecological development studies (Sultan 2000, 2007). Because *P. cespitosum* is highly cleistogamous (existing in nature as multiple homozygous lines [S. Matesanz, K. Theis, K. Holsinger, and S. Sultan, *unpublished data*]), comparisons among inbred genotypes are an appropriate way to assess variation among genetic individuals.

We addressed the following specific questions: (1) Do consistently high-performance genotypes (i.e., genotypes that express high relative fitness in diverse conditions) exist within introduced-range populations of *P. cespitosum*? (2) If so, do these high-performance genotypes possess distinctive life history and/or functional traits? (3) Do all populations of the species include such genotypes, or do they occur in only a subset of populations?

MATERIALS AND METHODS

Stage 1: Inbreeding generation and identification of potential high-performance genotypes

Achenes were collected in October 2008 from 14 well-established *Polygonum cespitosum* populations representing the species’ current habitat range in northeastern North America (Appendix A). In March 2009, achenes collected from 30–35 field individuals per population were raised to maturity in uniform greenhouse conditions to produce inbred (selfed full-sib) genetic lines (hereafter “genotypes”) lacking any maternal–environment differences. (See Appendix B for growth conditions). Mature achenes were collected from each of 469 inbred genotypes.

In April 2010, 20 achenes from each genotype were sown into 1-L clay pots. Seedlings that emerged between day 7 and day 14 (representing 416 genotypes) were grown to maturity under open/moist greenhouse conditions (see Appendix B) to identify those showing the highest total reproductive output in a favorable, introduced-range environment at a common age (eight

weeks after germination). All plants were monitored daily and their reproductive onset (date of first flowering) recorded. Starting at week 5, mature achenes were collected from each plant weekly. At week 8, all remaining (mature and immature) achenes were harvested together with flowers and reproductive support tissue, and the percentage of senescent leaves was estimated for each plant. Achenes were air dried for at least five days and weighed. Data were excluded from 23 individuals that suffered an aphid infestation.

Total reproductive output for each genotype was calculated as the sum of the early-maturing achenes plus all reproductive material collected at harvest. To account for compartment effects (i.e., slight differences in environmental conditions between greenhouse compartments) on reproductive output, relative fitness for each genotype was calculated as its total reproductive output divided by the compartment's mean reproductive output. Genotypes were ranked based on relative fitness in this treatment, with those in the top $\approx 5\%$ ($N = 22$) categorized as potential high-performance genotypes. The 5% threshold was used because relative fitness of the top 5% genotypes differed markedly from other genotypes (52–102% higher reproductive output than the mean of all genotypes; relative fitness 1.52–2.02); also, a 5% threshold is conventionally used to denote significant differences between groups (Zar 1999). Because the species reproduces indeterminately, four genotypes with relative fitness very close to the threshold (1.48–1.51) and fewer than 5% senescent leaves were included, since in natural conditions these nonsenescent plants would likely produce additional achenes, for a total of 26 high-performance (HP) genotypes (see *Results* section for population distribution). For comparison, a control group of genotypes was chosen from the remaining 95%. To create a robust control sample that accounted for among-population differences (Matesanz et al. 2012), we included two randomly selected genotypes from each of the 14 populations ($N = 28$ genotypes; relative fitness 0.51–1.46).

Stage 2: Comparison of potential high-performance vs. control genotypes in three habitat treatments

Experimental sample.—In June 2010, 70–100 achenes (from the inbreeding generation) per genotype were sown into flats of moist vermiculite. At the first true-leaf stage, three replicate seedlings per genotype were randomly assigned to each of three greenhouse treatments. The final experimental sample was 443 plants: 26 high-performance genotypes and 24 control genotypes (28 minus 4 removed due to low germination and/or abnormal growth) \times 3 treatments \times 3 replicates per treatment.

Experimental habitat treatments.—Plants were grown for nine weeks in three greenhouse treatments designed to mimic environmental conditions in contrasting introduced-range habitats (T. Horgan-Kobelski, S. Matesanz, and S. Sultan, *unpublished manuscript*): a

high-resource, open/moist treatment, a moisture-limited open/dry treatment, and a light-limited understory/moist treatment, with corresponding subtle differences in daytime temperature (details in Appendix B). The open/dry and understory/moist treatments represent substantial environmental stresses compared to the favorable open/moist treatment (see Plate 1). Seedlings were individually transplanted into 1-L clay pots and given ample water and 75% sun for 48 h, after which one replicate seedling per genotype was assigned to a random position in each of three plots for each treatment. In order to create habitat treatments that differed consistently in light availability, moisture, and temperature, we assigned the three plots of each treatment to the same greenhouse compartment. This design was appropriate because the goal of the experiment was to assess performance differences among genotypes within each of these naturalistic, combinatorial habitat treatments rather than to document responses to replicated versions of these complex treatments (see Brock and Weinig [2007] and Chivers et al. [2009] for similar experimental designs).

Plants in the open/moist and open/dry treatments received full sun (mean midday photosynthetically active radiation [PAR] $\sim 1300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Understory/moist plants were grown under metal frames covered with woven, neutral-density shade cloth that blocked 80% of the incident light (PAK Unlimited, Cornelia, Georgia, USA; mean midday PAR was $\sim 260 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). To mimic understory conditions, we created sunflecks to simulate the moments of direct solar radiation that occur in shaded *P. cespitosum* populations (sunflecks lasting ≤ 15 minutes represent $\sim 90\%$ of all sunflecks occurring in these sites). The center of each pot received a ~ 15 minute-sunfleck at noon (details in Appendix B). Green plastic filter strips (#138, Lee Filters, Burbank, California, USA) were overlaid between the sunfleck rows to simulate light spectral quality beneath the forest canopy.

Soil moisture was maintained by automatic systems that delivered reverse-osmosis filtered water to one watering tube per pot (Chapin Watermatics, New York, USA). Plants in the open/dry treatment were maintained at 50% field capacity. Open/moist and understory/moist plants were maintained at 100% and 95% field capacity, respectively (details in Appendix B).

Data collection.—Germination was censused daily. On day 10 in treatment, we measured seedling height (elongation above the cotyledons to the base of the most recent fully expanded leaf) and number of nodes; average internode length was calculated as seedling height/number of nodes.

Physiological measurements were taken during six comparable sunny days (17–30 August). Data were collected between 09:00 and 14:00 hours on half of a randomly selected plot of each treatment each day; all plants were watered 30 min before measuring. In situ instantaneous photosynthetic rate and stomatal conduc-



PLATE 1. Inbred replicates of a single *Polygonum cespitosum* high-performance genotype grown in understory/moist (left), open/dry (center), and open/moist (right) greenhouse treatments. Phenotypic differences among these genetically uniform individuals include changes to the root system and to leaf structure, phenology, and biomass. Photo credit: S. Matesanz.

tance were measured on one new, fully-expanded leaf of a primary branch per plant using a LI-COR 6400 infrared gas analyzer (LI-COR, Lincoln, Nebraska, USA). Leaf temperature and relative humidity were kept constant and close to ambient conditions; measurements were logged only when the stability criteria suggested by the manufacturer were met. Whole-plant photosynthetic rate was calculated as photosynthetic rate \times total estimated leaf area.

After nine weeks in treatment, aboveground tissues of each plant were harvested and separated, oven-dried (at 100°C for 1 h and then at 65°C for ≥ 48 h), and weighed to determine leaf and stem biomass. Three nonsenescent leaves from one primary branch per plant were scanned on an LI-3100 leaf area meter (LI-COR, Lincoln, Nebraska, USA), oven-dried, and weighed to determine specific leaf area (SLA, leaf area/leaf biomass). Whole-plant total estimated leaf area (TELA) was calculated as SLA \times leaf biomass. Root systems were stored at 4°C before being washed, oven-dried, and weighed to determine root biomass. Plant biomass was calculated as the sum of leaf, stem, and root biomass. Whole-plant ratio of root biomass to leaf area (root biomass/TELA) and leaf area ratio (TELA/plant biomass) were calculated.

Reproductive onset (date of first flowering) was determined for each plant through a daily census.

Mature achenes were collected weekly. At final harvest, all remaining mature and immature achenes, flowers, and reproductive support tissue were harvested. Achenes were air-dried for ≥ 5 d and weighed; total reproductive output was determined as in stage 1. Mean individual achene mass was determined based on a random sample of 20 mature achenes per experimental plant. Achene number was estimated as total reproductive output/mean individual achene mass, and reproductive allocation was calculated as (total reproductive output/[plant biomass + total reproductive output]) $\times 100\%$.

Data analyses

The Kaplan-Meier method was used to calculate cumulative germination curves of genotypes from each performance group (Kaplan and Meier 1958). Differences among germination curves were tested using Gehan's Wilcoxon test, and differences between high-performance and control groups in final germination proportion were tested using the χ^2 test (Zar 1999).

For other traits, mixed ANOVA models were used to test for the fixed effects of performance group (high performance vs. control), treatment, and genotype (nested within performance group) and their interactions, and the random effect of plot (nested within treatment). Genotype was treated as a fixed factor since a specific criterion (relative fitness) was used to assign

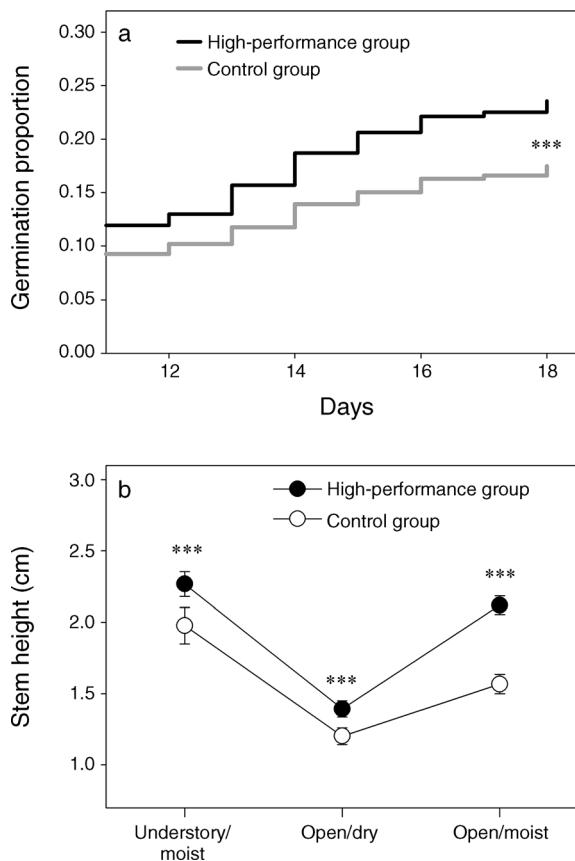


FIG. 1. Germination and seedling performance of high-performance and control genotypes of *Polygonum cespitosum* from the introduced range in northeastern North America. (a) Kaplan-Meier germination curves for high-performance and control genotypes. Cumulative germination proportion is shown at each time point. Curves were calculated based on 2800 and 2940 high-performance and control genotype seeds, respectively. (b) Stem height (mean \pm SE) in high-performance and control genotypes in the three habitat treatments. Significance is indicated by asterisks (see Appendix B). *** $P < 0.001$.

the genotypes to each group; therefore, genotypes could be assigned to only one of the two groups and only those genotypes were of interest (Hill and Lewicki 2005). Results were robust: analyses treating genotype as a random factor showed nearly identical significance results for main effects and their interactions. When the performance group and/or performance group \times treatment terms were significant, individual analyses were performed within each treatment to test for fixed effects within that treatment of performance group and genotype (nested in performance group) and random plot effects.

Variables were log-transformed (reproductive output, achene number, leaf area ratio, photosynthetic rate, and root biomass/TELA) or squared-root transformed (stem height, plant biomass, reproductive onset, SLA, and stomatal conductance) to meet the assumptions of the models (Zar 1999). Seventeen plants were excluded from

the data set due to treatment or measurement error. All analyses were performed using Statistica 6.0 (Statsoft, Tulsa, Oklahoma USA).

RESULTS

Distribution of high-performance genotypes among populations

The high-performance (HP) genotypes initially identified in open/moist conditions occurred only in certain populations, in frequencies varying from 3–21% of genotypes in those populations (Appendix C). Genotypes classified as HP were found in eight of the 14 populations sampled.

Germination and seedling traits

On average, achenes of HP genotypes germinated faster (Gehan's Wilcoxon $Z = -5.694$, $P < 0.001$; Fig. 1a) and in higher proportion ($\chi^2 = 30.25$, $P < 0.001$) than those of control genotypes.

All genotypes significantly increased seedling height in the understory/moist and open/moist treatments compared to the open/dry treatment (42–63% mean increase; Fig. 1b) and produced longer internodes on average in the understory/moist treatment (Table 1a). By day 10, seedlings of HP genotypes were 15–35% taller and had 17–27% longer internodes than control seedlings across treatments (performance group effect; Table 1a; Appendix D), with the most pronounced height difference in the open/moist treatment (significant performance group \times treatment interaction; Table 1a). There was significant genetic variation within each performance group for seedling traits and their plasticity (significant genotype and genotype \times treatment effects; Table 1a; Appendix D).

Reproductive fitness traits

Fitness components differed significantly among performance groups as well as treatments (Table 1b). All genotypes sharply increased total reproductive output and achene number in the favorable open/moist treatment compared to the open/dry treatment and, especially, the understory/moist treatment (Figs. 2 and 3a). HP genotypes had significantly higher total reproductive output and produced significantly more achenes than control genotypes in all three habitat treatments (Figs. 2 and 3a, Table 1b; Appendix D), with large differences in the understory/moist treatment (39% higher reproductive output and 45% higher achene number) and open/moist treatment (38% and 39% higher) and a less pronounced difference in the open/dry treatment (6–8%).

All genotypes delayed reproductive onset in the understory/moist treatment by an average of 16 days (Fig. 3b) and sharply reduced reproductive allocation (Fig. 3c) and achene size (Fig. 3d; 43% reduction) compared to the two open (high light) treatments. HP genotypes flowered earlier than control genotypes in all three treatments (Table 1b, Fig. 4b; Appendix D);

TABLE 1. Effects of performance group (high-performance vs. control), habitat treatment, and genotype on seedling traits, fitness traits, and functional traits of introduced populations of *Polygonum cespitosum* in northeastern North America.

Trait	R^2	Performance group, PG (df = 1)	Treatment (df = 2)	PG × treatment (df = 2)	Genotype (PG) (df = 48)	Genotype (PG) × treatment (df = 96)	Plot (treatment) (df = 6)
a) Seedling traits							
Seedling height	0.57	66.75***	114.12***	3.47*	5.36***	1.83***	0.75 ^{ns}
Average internode length	0.75	68.60***	71.90***	2.14 ^{ns}	7.66***	2.62***	5.25***
b) Fitness traits							
Total reproductive output	0.97	125.25***	15 847.03***	31.17***	6.61***	3.59***	0.99 ^{ns}
Achene number	0.97	65.91***	3236.74***	12.75***	4.05***	2.12***	1.82 [†]
Reproductive onset	0.80	45.24***	337.79***	1.63 ^{ns}	4.15***	1.90***	1.99 ^{ns}
Reproductive allocation	0.96	269.43***	827.08***	37.26***	9.71***	4.46***	5.12***
Individual achene mass	0.78	0.61 ^{ns}	83.54***	1.34 ^{ns}	17.65***	0.88 ^{ns}	4.03***
c) Functional traits							
Plant biomass	0.97	1.09 ^{ns}	978.63***	11.46***	2.32***	2.26***	6.80***
Photosynthetic rate	0.92	1.35 ^{ns}	670.87***	4.96**	2.09***	1.91***	3.39***
Stomatal conductance	0.54	5.88*	23.89**	1.80 ^{ns}	1.83**	1.61**	6.42***
Whole-plant photosynthetic rate	0.87	0.46 ^{ns}	1132.41***	0.424 ^{ns}	1.90***	1.76***	1.66 ^{ns}
SLA	0.83	0.33 ^{ns}	157.60***	0.06 ^{ns}	1.26 ^{ns}	1.15 ^{ns}	5.78***
TELA	0.90	0.48 ^{ns}	382.89***	9.66***	1.93***	1.78***	4.33***
Root biomass:TELA	0.93	0.01 ^{ns}	749.40***	2.70 [†]	2.06***	1.09 ^{ns}	3.21**
Leaf area ratio	0.96	1.68 ^{ns}	460.17***	1.15 ^{ns}	2.67***	1.52**	10.64***

Notes: Adjusted R^2 and F ratios are shown. For all traits the error df = 255. Abbreviations are: specific leaf area, SLA; total estimated leaf area, TELA.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † $P < 0.1$; ns, not significant.

differences were 4.3 d (understory/moist treatment), 1.5 d (open/dry treatment), and 2.6 d (open/moist treatment) (mean ± SE). HP genotypes also consistently allocated more biomass to reproduction than control genotypes (12%, 24%, and 28% higher in the open/dry, understory/moist, and open/moist treatments, respectively; Table 1b, Fig. 4c; Appendix D). Variation among treatments in the magnitude of differences between HP and control genotypes resulted in significant performance group × treatment interaction effects on reproductive output, achene number, and reproductive allocation (Table 1b). HP and control genotypes produced achenes of similar size in all treatments (nonsignificant performance group and performance group × treatment interaction effects; Fig. 3d, Table 1b). There was significant genetic variation within performance groups for fitness traits and their plasticity (genotype and genotype × treatment effects; Table 1b; Appendix D).

Morphological, allocational, and physiological traits

All genotypes produced more plant biomass in the open/moist treatment than the open/dry and understory/moist treatments (+215% and +1000%, respectively; Fig. 4a, Table 1c). Biomass differences between the performance groups varied from one treatment to another (Appendix D); although HP genotypes had significantly higher biomass than control genotypes in the understory/moist treatment, they had lower biomass in the open/dry treatment and equivalent biomass in the open/moist treatment (Fig. 4a; nonsignificant main effect of performance group, significant performance group × treatment interaction, Table 1c; Appendix D);

the same pattern of differences between performance groups was found for total estimated leaf area (TELA; Table 1c; Appendix D).

All genotypes sharply increased specific leaf area (SLA) and leaf area ratio in the understory/moist treatment compared to the open/dry and open/moist treatments (105–215% and 279–390% increases, respectively; Fig. 4b, Table 1c). These plastic responses were similar in HP and control genotypes (nonsignificant effects of performance group and performance group × treatment; Table 1c). Root allocational responses were also similar in HP and control genotypes: all genotypes increased the ratio of root biomass:TELA in the open/dry treatment compared to the open/moist and understory/moist treatments (by 117% and 996%, respectively; Fig. 4c; nonsignificant effects of performance group and performance group × treatment; Table 1c).

All genotypes increased instantaneous photosynthetic rate >100% in the high light, open treatments compared to the understory/moist treatment (Fig. 4d), and increased stomatal conductance in the open/moist treatment compared to both resource-limited treatments (Fig. 4d). Although there was a marginally significant main effect of performance group on stomatal conductance (Table 1c), physiological differences between the groups were not consistent across treatments. HP genotypes had higher photosynthetic and conductance rates than control genotypes in the open/dry treatment, but lower photosynthetic rates and similar conductance in the understory/moist treatment (Appendix D). Whole-plant photosynthetic rate did not differ significantly between performance groups in any treatment (nonsignificant effects of performance group and per-

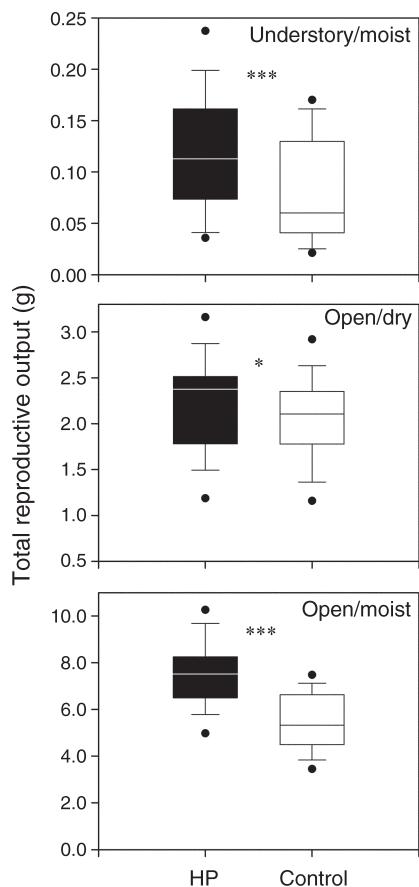


FIG. 2. Total reproductive output in high-performance (HP; solid boxes) and control genotypes (open boxes) under three habitat treatments; note the different habitat-specific y-axis values. The boxes depict the median, 10th, and 25th percentiles of distribution; lower and upper whiskers show the 75th and 90th percentiles, respectively. The 5th and 95th percentiles are also shown (as dots). Significant differences between performance groups within treatments are indicated by asterisks (see Appendix B).

* $P < 0.05$; *** $P < 0.001$.

formance group \times treatment; Table 1c) because differences in photosynthetic rates and total leaf area (and plant biomass) were inversely related in the two treatments in which the groups differed (compare Fig. 4a to 4d). With the exception of SLA, functional trait means and plasticities varied among genotypes within the performance groups (significant effects of genotype and genotype \times treatment, Table 1c; Appendix D).

DISCUSSION

*Existence of high-performance genotypes in introduced-range populations of *Polygonum cespitosum**

The *Polygonum cespitosum* genotypes with extremely high reproductive fitness in full-sun, moist conditions (open/moist treatment) also had significantly higher reproductive output, in terms of both total mass and

achene number, in moisture- and light-limited environments. Dramatic treatment differences in plant biomass and fitness confirm that both of these treatments represented substantial environmental stresses compared to the favorable open/moist treatment. The fitness advantage of high-performance over control genotypes varied in magnitude from one environment to another but was significant within every one of the test environments. As is predicted for broadly adaptive genotypes (Baker 1965, 1974, Sultan 2001, Richards et al. 2006), these genotypes were thus able to more successfully exploit a favorable, resource-rich environment as well as to reproduce at higher levels in contrasting, resource-limited conditions.

Interestingly, there was no evidence of the trade-off between offspring size and number that characterizes a wide range of species (Leishman 2001 and references therein): despite their significantly higher offspring number, the high-performance genotypes produced equally large offspring (individual achene mass) as control genotypes in all three habitats. Together, these results confirm the existence in *P. cespitosum* of genotypes capable of achieving high reproductive output across a broad environmental range, the kind of general-purpose genotypes hypothesized by Herbert Baker to characterize the ideal weed.

Life history and functional traits of high-performance genotypes

Across the range of experimental habitats, high-performance genotypes consistently expressed a suite of accelerated life history traits: faster and higher germination rates, faster seedling growth, earlier transition to flowering, and higher allocation to reproductive tissues. The accelerated life history syndrome shared by high-performance genotypes is consistent with predicted features of highly invasive taxa (Baker 1965, 1974, Hayes and Barry 2007, Pyšek and Richardson 2007, van Kleunen et al. 2010) and corresponds to traits that characterize several aggressive plant invaders at the species level (e.g., Leger and Rice 2003, Blair and Wolfe 2004, Garcia-Serrano et al. 2005, Schlaepfer et al. 2010). Clearly these are aspects of plant life history that will contribute to increased propagule pressure (Lockwood et al. 2005, Simberloff 2009) and competitive ability, and that are likely to promote the establishment of populations under natural conditions (Sakai et al. 2001, Maron et al. 2004, Fenesi and Botta-Dukat 2010). Accordingly, this subset of genotypes may increase the potential invasiveness of *P. cespitosum*, and can be expected to contribute disproportionately to the species' spread in its introduced range.

Surprisingly, the high-performance genotypes did not differ consistently from control genotypes with respect to other growth traits. Instead, genotypes from both groups expressed similar patterns of adaptive plasticity for functionally important traits in response to resource limitations. These plastic responses included dramati-

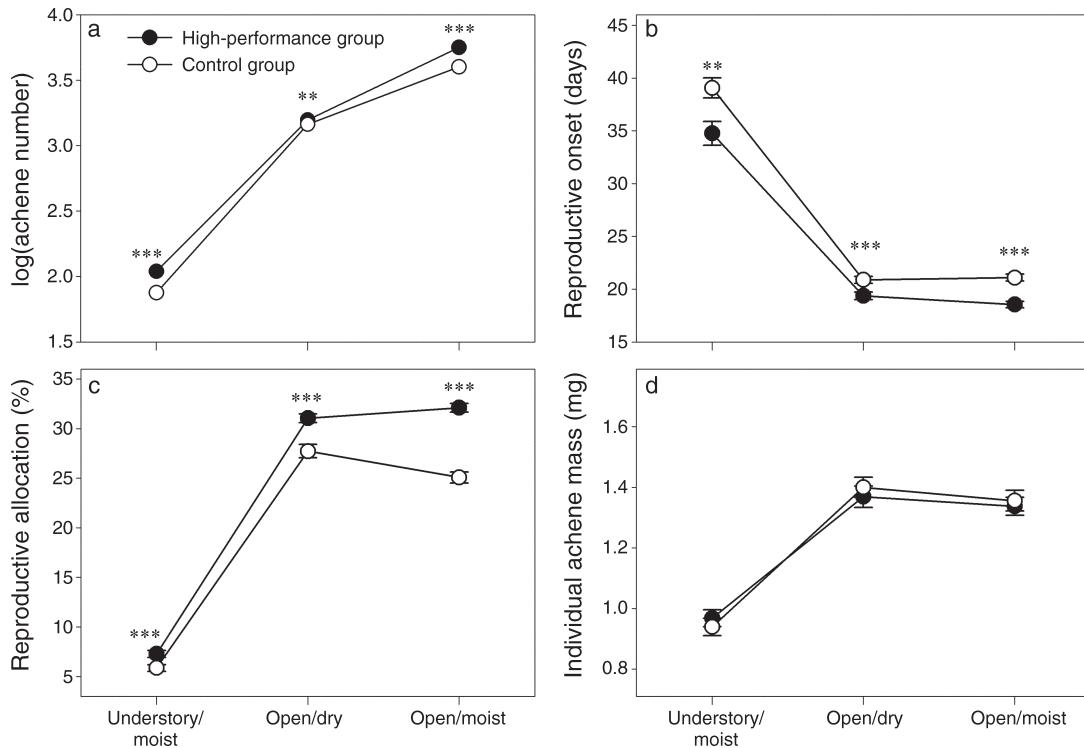


FIG. 3. Fitness traits (mean \pm SE) in high-performance and control genotypes are shown as (a) log-transformed number of achenes, (b) reproductive onset, (c) reproductive allocation, and (d) individual achene mass. Significant differences between performance groups within treatments are indicated by asterisks (see Appendix B).

** $P < 0.01$; *** $P < 0.001$.

cally increased root allocation in dry conditions, and morphological and allocational changes to maximize photosynthetic area (specific leaf area and leaf area ratio) in simulated understory shade. Patterns of biomass reduction in the resource-limited treatments were also similar for the high-performance and control genotypes. Broadly similar results were reported by Blair and Wolfe (2004) for introduced plants of *Silene latifolia*, which germinated earlier, grew faster, and produced more flowers than their native conspecifics, while morphological traits remained relatively unchanged.

Population origin of the high-performance genotypes

High-performance genotypes occurred in eight of the 14 *P. cespitosum* populations studied from the introduced range in northeastern North America, in proportions varying from a few percent to one-fifth of genotypes sampled within those populations. Populations that include these distinctive genotypes, and in particular those populations in which they comprise a substantial proportion, seem likely to be the source of much of the species' future spread in this region (see Lee and Gelembiuk [2008] and references therein).

A possible explanation for the presence of high-performance genotypes in North American populations

is postintroduction evolution in this region. The role of rapid evolution in plant invasions is increasingly a focus of study (Dlugosch and Parker 2008, Buswell et al. 2011, Dormontt et al. 2011). Previous studies have revealed significant adaptive evolution within introduced-range populations of *P. cespitosum* in as few as 11 generations, indicating that these populations have considerable potential for rapid selective evolution (Sultan et al. 2012). High-performance genotypes might have resulted from novel genetic combinations following multiple introductions to this region. The admixture of previously isolated genotypes in a new range, through repeated introductions from different native-range sources, can play a critical role in the origin of novel invasive genotypes (Ellstrand and Schierenbeck 2000, Wolfe et al. 2006, Lavergne and Molofsky 2007). Adaptive evolution in the introduced range may also explain the lag time that often occurs between the initial introduction of nonnative plants and their transition to invasiveness (Ellstrand and Schierenbeck 2000, Richards et al. 2006), also observed in *P. cespitosum*, and the species' recent expansion in northeastern North America to include novel habitats (secondary phase invasions sensu Dietz and Edwards [2006]).

The possibility of postintroduction evolution is supported by the fact that a sample of four Asian *P.*

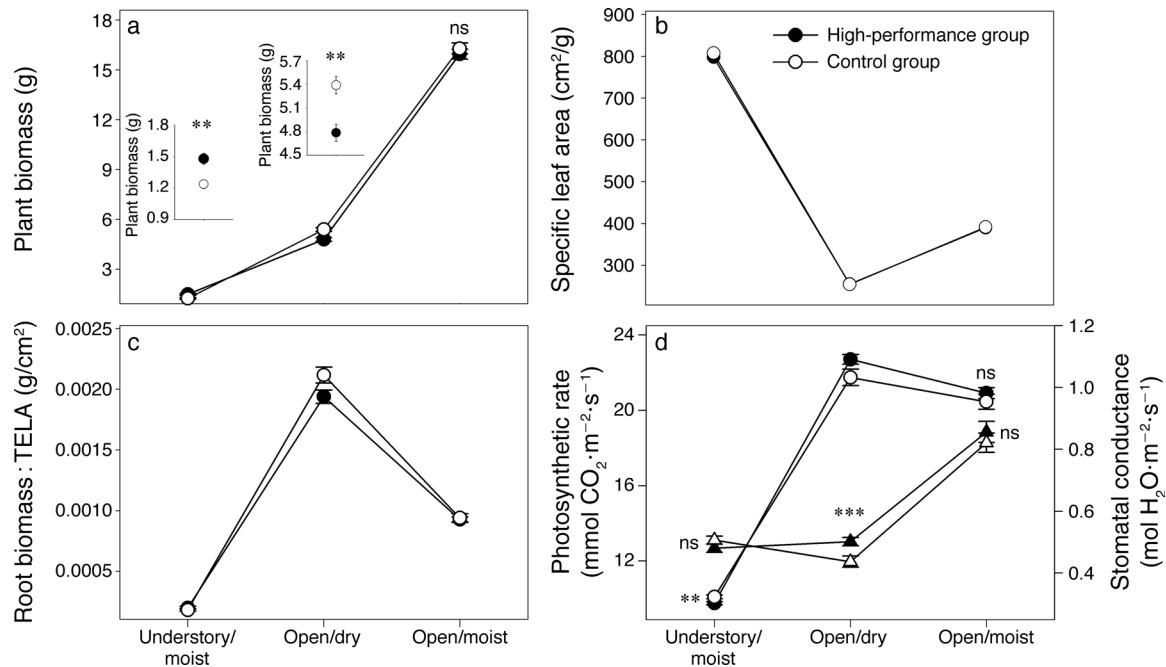


FIG. 4. Growth and functional traits (mean \pm SE) in high-performance and control genotypes with different habitat treatments. (a) Plant biomass (note that the same pattern of significance was found for total estimated leaf area [TELA; see Table 1]), (b) specific leaf area (the same pattern of significance was found for leaf area ratio), (c) root biomass:TELA, and (d) photosynthetic rate and stomatal conductance. Insets in panel (a) show details of results in the understory/moist and open/dry treatments, respectively. Significant differences between performance groups within treatments are indicated by asterisks (see Appendix B).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

cespitosum populations lacked the broadly high-performance genotypes found in the introduced-range populations (see Appendix E for details). However, although the absence of high-performance genotypes from the native-range populations suggests that such genotypes may have arisen in North American populations, this absence may simply reflect the limited number of native-range populations and/or the smaller genotypic samples from those populations (Appendix E). If high-performance genotypes do occur in the species' native range, their existence in North American populations could result from the introduction (and possibly enhanced spread) of these genotypes rather than from their evolution in the introduced range (see Bossdorf et al. 2008, Caldera et al. 2008, Schlaepfer et al. 2010).

Interestingly, high-performance genotypes of *P. cespitosum* were found in ecologically diverse, geographically distant populations in the species' introduced North American range, from moist forest understory to open and relatively dry roadside (Appendix A). Furthermore, high-performance genotypes were evidently as genetically diverse as the control genotypes that were randomly sampled from *P. cespitosum* populations; both performance groups showed considerable quantitative genetic variation as well as similar amounts of variation for neutral microsatellite markers (expected heterozygosity 0.639 ± 0.054 for control genotypes and

0.607 ± 0.028 for high-performance genotypes [mean \pm SE]; S. Matesanz, K. Theiss, K. Holsinger, and S. Sultan, *unpublished data*). These findings are not consistent with a scenario in which one or a few distinctive high-performance genotypes (whether evolved in situ or introduced) have spread across the introduced range, as has been found for some species (e.g., single "super-genotype" of the invasive grass *Pennisetum setaceum*; Le Roux et al. 2007, Saltonstall 2002, 2003). Instead, they suggest that genotypes with accelerated life histories and consistently high reproductive output may have evolved independently a number of times in *P. cespitosum* from genetically diverse origins. These events would be expected to vary among populations depending on founder genotypes, genetic variation and outcrossing levels, population size and age, gene flow, and so forth (Baker 1965, Ellstrand and Schierenbeck 2000, Etterson 2004, Novak and Mack 2005, Wares et al. 2005, Simberloff 2009, Dormontt et al. 2011).

Implications for future invasiveness of *Polygonum cespitosum*

This study identified a subset of highly successful, broadly adaptive genotypes in northeastern North American populations of the newly invasive plant *P. cespitosum*. The occurrence of these genotypes may be

an important factor shaping the invasion trajectory of *P. cespitosum* in North America. Because these genotypes have higher reproductive output in both resource-rich and stressful conditions, they are likely to fuel the species' immediate spread across contrasting habitats in the introduced range. Furthermore, as a result of their superior reproductive fitness, the high-performance genotypes will be selectively favored in introduced-range populations. As the frequency of these genotypes increases due to natural selection, the species can be predicted to evolve in its introduced range to be increasingly aggressive. The existence of these high-performance genotypes and their nonrandom distribution highlights the importance of combining genotype-level and population studies to investigate the dynamics of species invasions. Our results suggest that genotypes of introduced taxa may contribute differently to the invasive potential of such organisms. Further investigations of high-performance genotypes may contribute to the understanding, and possibly the management, of other aggressive invaders.

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SUPPLEMENTAL MATERIAL

Appendix A

Location and habitat description of the study populations ([Ecological Archives E094-226-A1](#)).

Appendix B

Detailed description of the methods ([Ecological Archives E094-226-A2](#)).

Appendix C

Proportion of high-performance genotypes in each population ([Ecological Archives E094-226-A3](#)).

Appendix D

ANOVA results testing for the effects of performance group and genotype within each treatment on seedling traits, fitness traits, and functional traits ([Ecological Archives E094-226-A4](#)).

Appendix E

Performance of Asian genotypes in a high-light, moist environment ([Ecological Archives E094-226-A5](#)).