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Using native and invasive populations as surrogate ‘species’ to predict the potential for native and invasive populations to shift their range

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ABSTRACT

Background: The wetland grass, *Phalaris arundinacea*, is invasive in North America but native to Europe.

Aim: Compare experimentally how a native species and an invasive species may respond to changing environmental conditions.

Methods: Sample both native and invasive populations from near the centre and the margin of their ranges. Native, centre: Czech Republic; native, range margin: Mediterranean France; invasive, centre: Vermont; invasive, range margin: North Carolina. Use 18 invasive and 18 native genotypes of *P. arundinacea*. Plant them into four common gardens along a latitudinal gradient in the eastern USA (Vermont, North Carolina, Georgia, Florida). Measure mean phenotypic traits, phenotypic plasticity, and genetic variances in each garden.

Results: The plants grew best in the North Carolina garden, where the invasive genotypes are larger, taller, and produce more tillers than their native counterparts. But these differences did not appear in the other gardens. In addition, although we predicted higher phenotypic plasticity for the invasive genotypes, we found only modest differences in phenotypic plasticity between native and invasive genotypes. Populations growing close to their presumed ideal growing conditions (as measured by plant biomass) have similar and relatively high genetic variances. Thus, populations growing under favourable conditions have the greatest potential to evolve in response to changing environmental conditions. However, where conditions became stressful (as defined by high mortality), only the southern marginal invasive individuals (North Carolina) showed higher genetic variances than the native marginal populations (Mediterranean France).

Conclusions: When confronted with a new environment, invasive populations at the range margin had a higher evolutionary potential than native populations.

Keywords: genetic variance, invasive plants, *Phalaris arundinacea*, range margin.

INTRODUCTION

Being able to predict which plant species can persist under environmental change has important implications for the maintenance of our current plant communities (Jump and

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Penuelas, 2005). Because plant species are primarily sessile and move only through dispersal, they are especially vulnerable to change in the environment (Higgins and Richardson, 1999; Ronce, 2001). Some plant species may persist because they can adapt to changing climate, whereas others may persist through phenotypic plasticity (Miner *et al.*, 2005; Lavergne *et al.*, 2010). Phenotypic plasticity – an alteration in a phenotypic trait in response to the environment – is likely to be particularly important in long-lived perennial plants in which recruitment through seeds occurs infrequently (Schlichting, 2002). While phenotypic plasticity can function as a short-term mechanism to allow individuals to grow under new conditions, populations that harbour genetic variation among individuals may be able to evolve in response to changes in the environment (Lavergne *et al.*, 2010). Both mechanisms may function to allow a species to survive in different local populations within its current range and different mechanisms may be at play in different parts of that range (Bridle and Vines, 2007). For example, populations in the middle of a species range may be larger and thus harbour greater genetic variation than populations at the leading edge of the range (Kirkpatrick and Barton, 1997; Bridle and Vines, 2007; Hill *et al.*, 2011). If this is the case, the larger central populations may possess sufficient genetic diversity to adapt to changing environmental conditions (Kirkpatrick and Barton, 1997). In addition to possessing greater genetic diversity, these populations may also contain individuals that exhibit a greater range of phenotypic variation and thus individuals that are phenotypically plastic and can adjust to a new environment. In contrast, environmental conditions at the edge of a species distribution may be more extreme than environmental conditions at the centre of the range, and in general population sizes are smaller (García-Ramos and Kirkpatrick, 1997; Kawecki and Ebert, 2004). This suggests that these small marginal populations will have lower genetic and genotypic diversity and may have already undergone strong directional selection to the environment (García-Ramos and Kirkpatrick, 1997; Kawecki and Ebert, 2004; Johannesson and André, 2006). Alternatively, an influx of individuals from the centre of the range margin may prevent population differentiation and subsequent adaptation to the environmental conditions (Bridle and Vines, 2007). If this second scenario is the case, one would predict that successful individuals at the edge of the range are those that are phenotypically plastic in traits that are important for fitness.

However, these general observations about how plant populations may differ from the centre of the range to the range margin in their response to the environment may not hold for invasive species because recently invasive populations of a species may differ in some fundamental ways from native populations. First, invasive species can be more phenotypically plastic than their native counterparts (Bossdorf *et al.*, 2005; Richards *et al.*, 2006; Van Kleunen *et al.*, 2011). This is largely thought to be a pre-adaptation to invasiveness – that is, those introduced species that successfully establish are those that exhibit phenotypic plasticity, which allows them to grow in a foreign environment (Bossdorf *et al.*, 2005; Richards *et al.*, 2006; Van Kleunen *et al.*, 2011). Once in residence in a new location, the ability to grow under a wide range of conditions may allow them to persist and survive in the new environment (Nicotra *et al.*, 2010). Second, although some invasive species arise from a few dispersal events resulting in them being genetically depauperate, many invasive species have been introduced multiple times into the new environment, becoming admixed in the new range resulting in invasive species that have the same or greater genetic diversity than native populations (Lavergne and Molofsky, 2007; Kolbe *et al.*, 2008; Keller and Taylor, 2010). This disparity in genetic diversity between native species and invasive species will be exacerbated at the current geographic limit of a species range because native species are expected to have reduced genetic diversity at the range margin (Blows and Hoffmann, 1993; Arnaud-Haond *et al.*, 2006; Johannesson and André, 2006; Bridle and Vines, 2007;

Kunin *et al.*, 2009; Vergeer and Kunin, 2013), while invasive species at the range margin, depending on their introduction history, can have similar levels of genetic diversity within their populations compared with central native populations (Lavergne and Molofsky, 2007). More relevant for this study is the fact that individuals found at the margin of the invasive range may be introduced from multiple different locations, and because they are recently introduced will not have been subject to consistent directional selection. Thus, we would predict that invasive populations at the margin would contain greater phenotypic and genetic variance than populations at the margin from native populations. A natural consequence of these purported differences at the range margin is that invasive species may have greater potential to evolve than the native species, which suggests that invasive species may be able to evolve in response to climate change whereas native species may not.

To test this idea experimentally requires that we have representative populations of both native species and invasive species and that the populations are grown at their current ecological range limit and beyond. However, a comparison of native and invasive species can be confounded by phylogenetic differences, making direct comparisons difficult. A comparative study of individuals of the same species taken from their native range with individuals of the same species from the introduced range provides a mechanism to explore these issues (Lavergne and Molofsky, 2004). In this way, we can evaluate the phenotypic plasticity and genetic variance of individuals taken from the native range with individuals of the same species that have been introduced (Lavergne and Molofsky, 2007). Moreover, by using plants that reproduce readily by clonal spread, we can create identical copies of individuals [phytometers (Dietrich *et al.*, 2013)] that can be reared in a common environment and then planted out in gardens along a climatic gradient, allowing for a direct comparison of the response of individuals across different environments and among individuals of native and invasive populations within a single environment.

Such conditions would allow us to test the following specific hypotheses: (1) invasive individuals will have higher survival and be larger than native individuals, and the differences in survival and growth will be greatest beyond the range margin; (2) invasive individuals will have greater phenotypic plasticity than native individuals, and these differences will be greater for the populations at the edge of the range; and (3) invasive individuals at the range margin will have higher genetic variances than native individuals at the range margin. We test these hypotheses using individuals collected from populations of the wetland plant *Phalaris arundinacea* collected from the centre and the range margin in the native range in Europe (Czech Republic and Mediterranean France) and the invasive range in North America (Vermont and North Carolina), and planted in common gardens in eastern North America at and beyond their current range margin.

METHODS

Study species

The experimental species, reed canarygrass (*Phalaris arundinacea*), is a C-3 wetland grass that has a cosmopolitan distribution (Lavergne and Molofsky, 2004). Native to Eurasia, *P. arundinacea* is highly invasive in North American wetlands (Galatowitsch *et al.*, 1999). Originally introduced repeatedly to the United States as a wet forage grass and as part of a conservation mixture for ditch stabilization, it has since become an aggressive invader in wetlands in the northern and midwestern United States (Lavergne and Molofsky, 2004, 2006).

Selection of populations

We collected *P. arundinacea* from both the centre and southernmost range margin in its native range in Europe (Czech Republic and Mediterranean France, respectively) and from the centre and southernmost range margin in its invasive range in North America (Vermont and North Carolina, respectively). Selecting populations from the centre and range margin also allowed us to sample populations from different climatic regions. At each location, we selected at least three populations from each of four locations in both northern and southern regions of *P. arundinacea*'s range: two in the native European range [Czech Republic (CZ) and Mediterranean France (FR)] and two in the invasive United States range [Vermont (VT) and North Carolina (NC)]. Genotypes were identified through allozyme analysis (Lavergne and Molofsky, 2007) and a subset were chosen for common garden experiments. All sampled individuals from one French population were hexaploid while all other populations were tetraploid. We thus excluded the hexaploid population and chose an additional three genotypes from a fourth Czech Republic population. We thus selected 18 invasive genotypes (9 VT and 9 NC) and 18 native genotypes (12 CZ and 6 FR). Chosen genotypes were transplanted into pots in the University of Vermont greenhouse, where they were maintained, and then sequentially propagated before experimentation to minimize any maternal environmental effects.

Nine replicate blocks of the 18 native (12 CZ and 6 FR) and 18 (9 VT and 9 NC) invasive genotypes were planted into four common gardens along a north–south climatic gradient in North America (Vermont, 44°46′N, 73°15′W; North Carolina, 35°48′N, 82°55′W; Georgia, 31°46′N, 83°51′W; and Florida, 27°48′N, 81°91′W). The locations of the four gardens were chosen to be open grassland areas in which *Phalaris* either was present or, in the case of beyond the range, could potentially grow. Two of the gardens were located within the species' current introduced range (Vermont and foothills of North Carolina) and two gardens were located outside their current introduced range (piedmont area of Georgia and central grassland area of Florida). Mean temperature, maximum and minimum temperature, and mean annual precipitation are shown in Table 1. The main axis of differentiation was the temperature, although there were also differences in precipitation and soil substrate among other factors. The mean temperature in the Vermont garden was much lower than that in the North Carolina garden and because the low temperatures were above freezing in the North Carolina garden, plants never died back and continued to grow all year resulting in overall larger, more robust plants (Table 1). The main difference we observed between the North Carolina garden and the Georgia garden was that the maximum temperature was higher in the Georgia garden and this was coupled with overall lower precipitation (Table 1).

In each garden, the nine replicate 5 × 5 m blocks were specifically chosen to encompass the natural variation present in our field sites. Each experimental garden was run for at least 12 months except in Florida, where all plants died after 6 months (Vermont, June 2005 to September 2006; North Carolina, May 2006 to September 2007; Georgia, April 2007 to June 2008; Florida, October 2005 to March 2006). Each of the experimental plants was measured monthly for survivorship, stem height, number of leaves, and number of tillers. Plants were not allowed to flower and set seed in the common gardens. Thus, fitness was assessed by survivorship and two surrogate measures of fitness (tiller number and total biomass). Tiller number, which is a measure of the plant's ability to spread and take over an

Table 1. The coordinates of the study regions (latitude/longitude) together with descriptive climatic variables for the study populations and the four garden locations

Population sample/ garden location	Coordinates	Temperature (°C) Mean	Maximum	Minimum	Mean rainfall (mm)
Czech Republic	49°00′N, 14°77′W	8.0	23.6	−5.2	717
Mediterranean France	43°61′N, 3°87′W	13.8	28.5	1.4	743
Vermont	44°46′N, 73°15′W	7.7	27.2	−12.1	1141
North Carolina	35°48′N, 82°55′W	18.5	27.7	−5.6	1584
Georgia	31°46′N, 83°51′W	18.6	33.0	2.6	1201
Florida	27°48′N, 81°91′W	23.5	34.8	10.6	1248

Note: The Vermont and North Carolina gardens are from the sites where the plants were sampled.

area within the plant community following colonization, is a reasonable proxy for vegetative plant fitness. Total biomass provides a crude measure of plant fitness in perennial grass species that can persist for many years and spread through rhizomes. However, we were unable to document reproductive fitness in any of our plants. All plants were harvested for above- and below-ground biomass at the end of the second growing season. Plant biomass was dried (60°C for 48 hours) and dry mass was determined for both above- and below-ground biomass.

Statistical analyses

We examined differences in survivorship among field sites, genotype range (invasive or native), and genotype region nested within range (native range: Czech Republic and Mediterranean France; invasive range: Vermont and North Carolina). We used a logistic regression model in SAS, PROC LOGISTIC (Stokes *et al.*, 2010), to test for differences in survivorship among sites, blocks within site, genotype range, and genotype region nested within range.

Our plants were not allowed to flower in any of the common gardens; therefore, we analysed vegetative traits only. Two vegetative traits (biomass and tiller number) are related to plant size, which can be correlated with fitness because larger plants have greater survival; we also analysed one morphological trait (stem height). Biomass is an integrated measure of plant fitness, with bigger plants having overall greater survival and flowering. Tiller number represents one measure of local spread.

For each trait, we analysed the data using a mixed-effect model of the form:

$$\text{Trait} = \text{block} + \text{range} + \text{region(range)} + \text{genotype(region range)}$$

Range and region were treated as fixed effects, and block and genotype were treated as random effects using PROC MIXED (SAS). Significant differences were determined between regions using least square means (LSMEANS) (Stokes *et al.*, 2010).

We also tested whether native and invasive genotypes differed in their phenotypic plasticity. Each genotype's phenotypic plasticity was determined by calculating the norm of the reaction [slope of the line (Pigliucci *et al.*, 1995; Pigliucci and Schlichting, 1998)], calculated as the mean performance of each genotype in the northern garden (Vermont) versus the mean performance of the same genotype in the southern garden (North Carolina). Plants were always heavier in the North Carolina garden but not always taller, so to remove negative values for stem height we calculated the absolute difference in stem height.

For each garden along our climatic transect (Vermont, North Carolina, and Georgia), we estimated regional differences in genetic variance for three traits (ln biomass, ln stem height, and ln tiller number). We estimated the variance components with REML using the PROC MIXED procedure in SAS (SAS v. 9.1.3). Our model consisted of the random effects of genotype and block and we calculated confidence intervals for all variance estimates by bootstrapping the data 1000 times.

RESULTS AND DISCUSSION

Hypothesis 1: Invasive individuals will have higher survival and greater growth than native individuals, and the differences in survival will be greatest beyond the range margin

The proportion of experimental plants surviving in each garden declined along the latitudinal gradient. Survival was high in the Vermont garden (approximately 90%), lower in the North Carolina garden (70%), and extremely low in the Georgia garden (approximately 40%) (Fig. 1).

In the Vermont garden, we found no significant differences in survival among ranges or regions. In the North Carolina garden, we found no significant differences in survival between ranges or between regions, but for both ranges southern genotypes had a slightly but significantly higher survival than the northern genotypes. In the Georgia garden, this pattern was repeated with slightly higher survival for the southern genotypes than for the

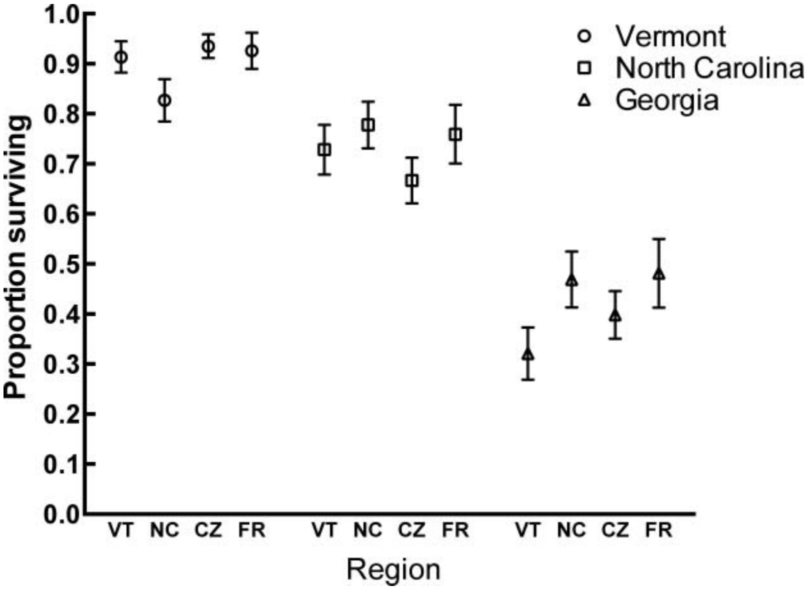

Fig. 1. Regional differences in proportion plants surviving in the three gardens. The Florida garden is not shown since no plants survived past 6 months. VT = Vermont genotypes, NC = North Carolina genotypes, CR = Czech Republic genotypes, FR = Mediterranean France genotypes.

northern genotypes (Fig. 1). However, we did not find support for our hypothesis that NC genotypes have higher survival than the native FR genotypes, as there were no differences between native and invasive southern genotypes.

We also predicted that invasive genotypes would be larger than the native genotypes and the differences would be more pronounced when plants were grown beyond the range margin in the Georgia garden. For the three growth measurements (stem height, tiller number, and biomass), we found modest to no differences in the Vermont garden; however, in the North Carolina garden where the plants grew best, the invasive genotypes and the FR genotypes produced significantly more tillers and greater biomass (Fig. 2) than the CZ genotypes. For our third metric, height, the NC genotypes were significantly taller than plants from the other three regions. In the Georgia garden where the plants were the smallest, FR genotypes produced slightly more tillers and biomass than plants from the other three regions. Thus, support for invasive genotypes growing better than native ones was generally not upheld. In the harsher environments, differences among native and invasive genotypes were modest or non-existent. We found no evidence that invasive genotypes performed better than native genotypes in the harsher climate conditions.

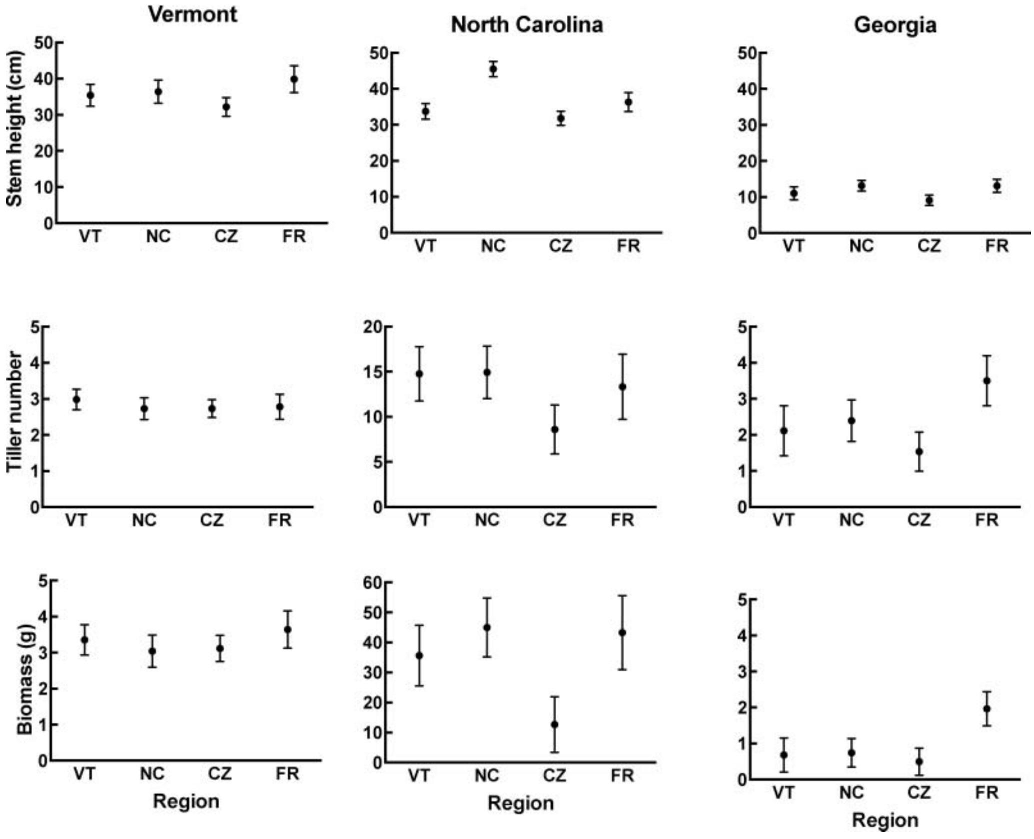

Fig. 2. Regional differences in stem height, tiller number, and total biomass for each region (VT = Vermont, NC = North Carolina, CZ = Czech Republic, FR = Mediterranean France) in each of the three gardens (Vermont, North Carolina, and Georgia).

Hypothesis 2: Invasive genotypes will have greater phenotypic plasticity than native genotypes, and the differences will be greater for the invasive genotypes at the edge of the range

Phenotypic plasticity of traits related to fitness is often cited as a mechanism whereby invasive plants that have undergone a genetic bottleneck can survive and grow in a new environment (Miner *et al.*, 2005). If an introduced species' presence in a new environment is the result of multiple introductions, rather then a genetic bottleneck, the role of phenotypic plasticity in facilitating the invasion is less clear. By comparing native and invasive genotypes of *Phalaris arundinacea*, we can determine whether or not plasticity occurred in fitness traits and whether it is a preadaptation present in the native populations or may have evolved *in situ* in the new range (Van Kleunen *et al.*, 2011). Because of genotypic sorting post-introduction, we expected invasive *Phalaris* genotypes to have higher phenotypic plasticity than native genotypes.

Our results on phenotypic plasticity are clear. With respect to individual genotypes altering their phenotypes between the northern and southern gardens, there were no differences in the slopes of the reaction norms between native and invasive genotypes for the two traits we examined: stem height (SS = 0.367, d.f. = 1, $F = 0.842$, $P =$ N.S.) and biomass (SS = 2.07, d.f. = 1, $F = 1.794$, $P = 0.19$). Thus, we found that any plasticity for these two traits was likely a preadaptation. When we examined regional differences within range, there were no significant differences in plasticity with respect to stem height (SS = 0.1617, d.f. = 2, $F = 0.1856$, $P =$ N.S.) but a significant difference in plasticity with respect to biomass (SS = 11.169, d.f. = 2, $F = 4.839$, $P = 0.0148$). The significant regional difference is due to the CZ plants, which had a flatter reaction norm than plants from the other regions. Because we only measured two traits in the field and had limited numbers of native and invasive populations, it is possible that a wider sampling would have indicated that, on average, native plants had a more canalized phenotype that is less likely to be modified with the environment. In a related study performed in the Vermont garden that examined differences in phenotypic trait plasticity along a moisture gradient in which several morphological traits (leaf number, leaf width, stem height) were combined using principal components analysis, we did find that invasive genotypes had significantly greater phenotypic plasticity, when measured as plastic variance (see Scheiner and Goodnight, 1984), than native genotypes (Lavergne and Molofsky, 2007). However, for our reaction norm approach using only two traits measured in the Vermont and North Carolina gardens, there was limited support for the hypothesis that invasive genotypes had greater phenotypic plasticity than native genotypes.

Hypothesis 3: Invasive individuals will have higher overall genetic variances than native individuals; and, moreover, the differences between native and invasive individuals will be greatest at the range margin where the native individuals are predicted to have the lowest genetic variances; a corollary of this is that in a new environment, invasive individuals will have greater genetic variances than native individuals

We predicted that if invasive populations are the result of multiple introductions, as was the case here, genetic variances should be higher in the invasive populations than in the native populations, especially under favourable environmental conditions where the greatest genetic variance can be expressed. In the present study, the most favourable environment was the North Carolina field site where the plants were tallest, produced the most tillers, and produced the greatest biomass. However, in North Carolina support for this hypothesis was mixed. For biomass and tiller number, contrary to that which we hypothesized, the invasive populations did not have the highest genetic variances. Rather, the FR populations had the highest genetic variance, followed by the NC, VT and, finally, CZ populations (Fig. 3). In fact, it appeared that the populations collected from the warmer part of the species ranges expressed higher genetic variances in North Carolina. This may be because for these southern populations, the North Carolina environment represented the least stressful and most benign environment. The results for stem height, however, did not follow the same pattern. For stem height, we found that NC plants had higher genetic variance than CZ and FR plants and these had higher genetic variance than the VT plants (Fig. 3).

In the Vermont garden, survival was uniformly high but plants were smaller than in the North Carolina garden; this most likely represents a more stressful environment than the North Carolina garden. We hypothesized that populations from the invasive range would have higher genetic variances than populations from the native range, which we did not observe for biomass or tiller number but was upheld for stem height (Fig. 3). Additionally, we broke our comparison into central and marginal populations. In this case, we predicted VT populations would have greater genetic variances than CZ populations, and that NC populations would have greater genetic variances than FR populations. However, we only observed this pattern for variance in tiller number in the marginal populations (Fig. 3). For our third trait, stem height, our results matched our expectation. The VT populations had higher genetic variances than the CZ populations, and the NC populations had higher genetic variances than the FR populations.

The Georgia garden represents a potentially new environment for all of the genotypes at least with respect to temperature, since the maximum temperature in this location exceeds the maximum temperature that any of our populations would have experienced in their home environment (Table 1). Moreover, mortality was high in this environment (approximately 60% of the plants died), indicating it was a harsh environment for *Phalaris*. Additionally, there were no differences in survival between native and invasive populations or between regions. Thus, our estimates of genetic variance for traits should not be biased by differential death rates by range or region within range. However, the general poor growth in the Georgia garden resulted in overall low levels of genetic variances, suggesting that the surviving plants are under strong environmental constraints that limit their trait expression. We predicted that in a new stressful environment, invasive populations would have higher genetic variances than native populations; moreover, we predicted that marginal invasive populations would be highest because these individuals come from an environment that is most similar to the novel environment. Indeed, we found that in the Georgia garden, the marginal NC populations had the highest genetic variances for all three traits. This was not the case for our central populations; instead, we found that VT populations had higher genetic variances than CZ populations for stem height but not for biomass or tiller number. Although our results support the hypothesis that invasive marginal populations have higher genetic variances than native marginal populations and invasive central populations, we need to examine this hypothesis with a greater number of traits and populations and for a greater number of central versus marginal comparisons of native and invasive species. Nevertheless, our results suggest that invasive populations at the range margin may contain greater evolutionary potential than native range marginal populations, and thus may be better able to evolve in response to environmental changes.

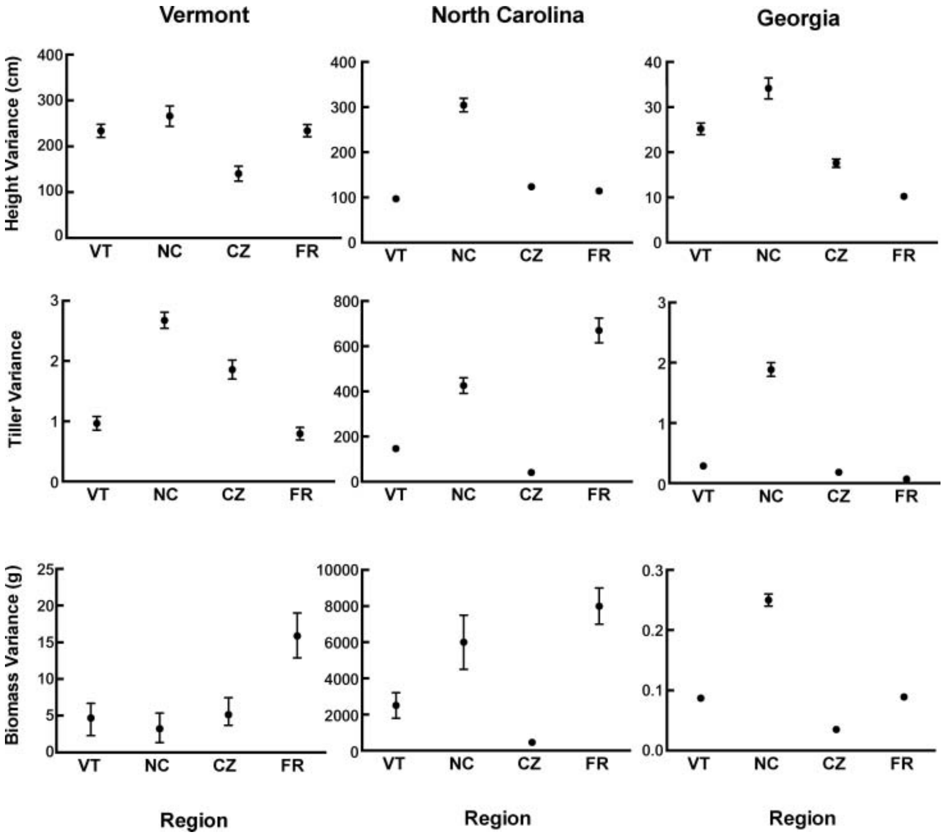

Fig. 3. Genetic variance for the three traits (stem height, tiller number, and biomass) for each region (VT = Vermont, NC = North Carolina, CZ = Czech Republic, FR = Mediterranean France) in each of the three gardens (Vermont, North Carolina, and Georgia).

CONCLUSIONS

Environmental changes, especially predicted temperature increases over the coming years, will not affect all species equally and differences in evolutionary response to climate change will contribute to which species ultimately survive (Salamin *et al.*, 2010). Understanding how species will respond to environmental change depends on knowing how populations at the range margin will respond, because these populations are most likely to harbour individuals that have traits that will allow them to grow under changed conditions (Hill *et al.*, 2011). For native species, populations at the range margin generally have lower genetic diversity and genotypic diversity because populations there tend to have fewer individuals, and have been subject to strong directional selection (Mandák *et al.*, 2005; Arnaud-Haond *et al.*, 2006). However, these limiting conditions are not met for invasive populations at the margin because these populations may have resulted from multiple introductions, not been subject to selection over the same time period, and come from an environment different to that in which they are currently growing (Kilkenny and Galloway, 2013). In this study, we provide one test for this idea by studying central and marginal populations of the same species as surrogates for how native versus invasive species may evolve in response to changing environmental conditions, especially temperature. Our experimental planting of central and marginal native and invasive genotypes close to the climatic centre, their current range margin, and beyond the current range limit allowed us to assess directly how central versus marginal populations of each group should perform; specifically, marginal invasive populations may not be subject to the same constraints as native marginal populations due to their different evolutionary histories. Their stored genetic potential suggests that these southern marginal invasive populations may possess the evolutionary potential to evolve further in response to changing climate. The present study highlights the difficulty in predicting species' response to climate change and underlines the need to understand the population history before robust predictions can be made.

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