

Expansion of a globally pervasive grass occurs without substantial trait differences between home and away populations

A. Leifso · A. S. MacDougall · B. Husband ·
J. L. Hierro · M. Köchy · M. Pärtel ·
D. A. Peltzer

Received: 24 August 2011 / Accepted: 11 May 2012 / Published online: 6 June 2012
© Springer-Verlag 2012

Abstract The global expansion of species beyond their ancestral ranges can derive from mechanisms that are trait-based (e.g., post-establishment evolved differences compared to home populations) or circumstantial (e.g., propagule pressure, with no trait-based differences). These mechanisms can be difficult to distinguish following establishment, but each makes unique predictions regarding trait similarity between ancestral ('home') and introduced ('away') populations. Here, we tested for trait-based population differences across four continents for the globally distributed grass *Dactylis glomerata*, to assess the possible role of trait evolution in its worldwide expansion. We used a

common-environment glasshouse experiment to quantify trait differences among home and away populations, and the potential relevance of these differences for competitive interactions. Few significant trait differences were found among continents, suggesting minimal change during global expansion. All populations were polyploids, with similar foliar carbon:nitrogen ratios (a proxy for defense), chlorophyll content, and biomass. Emergence time and growth rate favored home populations, resulting in their competitive superiority over away populations. Small but significant trait differences among away populations suggest different introductory histories or local adaptive responses following establishment. In summary, the worldwide distribution of this species appears to have arisen from its pre-adapted traits promoting growth, and its repeated introduction with cultivation and intense propagule pressure. Global expansion can thus occur without substantial shifts in growth, reproduction, or defense. Rather than focusing strictly on the invader, invasion success may also derive from the traits found (or lacking) in the recipient community and from environmental context including human disturbance.

Communicated by Melinda Smith.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2370-4) contains supplementary material, which is available to authorized users.

A. Leifso · A. S. MacDougall (✉) · B. Husband
Department of Integrative Biology, University of Guelph,
Guelph, ON N1G 2W1, Canada
e-mail: amacdo02@uoguelph.ca

J. L. Hierro
Facultad de Ciencias Exactas y Naturales, (INCITAP)
CONICET-UNLPam, Universidad Nacional de La Pampa,
Santa Rosa, La Pampa, Argentina

M. Köchy
Department of Biochemistry and Biology,
Universität Potsdam, 14469 Potsdam, Germany

M. Pärtel
Institute of Ecology and Earth Sciences,
University of Tartu, Lai 40, 51005 Tartu, Estonia

D. A. Peltzer
Ecosystems Processes Landcare Institute,
Lincoln 7640, New Zealand

Keywords Invasion ecology · Common-environment trial · Competition · Plant functional traits · Orchard grass

Introduction

The increasing global homogenization of the world's biota, typically in association with anthropogenic influences, has long been recognized as a substantial threat to the diversity and function of many biological communities. However, what remains unclear for many globally pervasive species are the mechanistic causes of their widespread expansion. The naturalization or invasion of these species across

continents is paradoxical, because they lack evolutionary experience with local conditions yet often become widespread, locally abundant, or both (Sax and Brown 2000; Bossdorf et al. 2005; Rout and Callaway 2009; Firn et al. 2011). Explanatory models fall into two main categories that are not necessarily mutually exclusive. Models focusing on trait evolution predict that these species undergo some form of trait-based alteration upon leaving their ancestral territory, through processes such as hybridization, polyploidy, and other mechanisms of adaptation including responses to enemy escape (Gaskin and Schaal 2002; Rout and Callaway 2009). Models focusing on circumstance predict that no trait-based changes occur, with invasion success deriving from trait novelty (e.g., novel traits that happen to be absent in the recipient community), or anthropogenic influences relating to propagule pressure, disturbance, or both (Petitpierre et al. 2012).

Empirically differentiating between these two models can be difficult, especially after dominance has been attained for decades or longer (Bossdorf et al. 2005; Hierro et al. 2005; Colautti et al. 2009). Each has the capacity to explain expansion success. Each can also explain factors such as high annual net primary productivity, regulation of resource pools, and recruitment that characterize many successful species, albeit by different mechanisms (MacDougall and Turkington 2005; Didham et al. 2005; Firn et al. 2010; HilleRisLambers et al. 2010). For example, globally prevalent species that thrive by trait-based changes associated with enemy escape typically grow larger than native flora and compared to their home populations, thereby capturing a greater proportion of available resources in the away range and restricting recruitment by other species (e.g., Callaway et al. 2004). However, agronomic plant species established over wide areas by cultivation and the persistent addition of seed may similarly capture most incoming resources and regulate recruitment of native species, simply because they are abundant (MacDougall and Turkington 2005). If their establishment is coupled with land use practices that also enhance productivity (e.g., fertilization), then away populations may be composed of larger and taller individuals compared to home ones, but by plasticity rather than evolved trait advantages.

Here, we use home-and-away experiments in a common glasshouse environment to test these predictions for the perennial grass *Dactylis glomerata* L., a globally distributed species that is frequently invasive in its introduced ranges (Firn et al. 2011). Home-and-away experiments (i.e., comparisons between ancestral population vs. those introduced outside the ancestral range) have emerged as the primary means by which to quantify trait-based performance differences between ancestral populations versus those that have established elsewhere (Hierro et al. 2005; Lambdon 2008; Mason et al. 2008; Ricklefs et al. 2008;

Colautti et al. 2009). Widespread graminoids such as *Dactylis* are among the world's most successful plant species, whose expansion is often associated with loss of native grassland species and the transformation of community structure and function (D'Antonio and Vitousek 1992; Norton 2009). The mechanisms explaining this success have been variously attributed to the two models described above, ranging from hybridization (e.g., *Spartina*; Ainouche et al. 2009) and intentional selection by humans for pre-adapted traits including rapid emergence and growth (Lolicato and Rumball 1994), to high propagule pressure following cultivation (MacDougall et al. 2004). Many such grasses continue to be introduced given their economic value for factors including erosion stabilization, rangeland forage, and biofuels. Many also have the potential to expand into non-targeted grassland communities, but the mechanisms that are likely to determine this expansion remain unclear.

To test for home and away differences, we combined a common environment trial with competition experiments using 14 *Dactylis* populations from along a 9° latitudinal gradient in the home range of western Europe, and away populations in Canada, Argentina, and New Zealand. The common environment trial quantified differences in growth and related traits associated with invasiveness among the populations, including seed emergence, biomass, ploidy level, carbon:nitrogen ratios in the foliage, and the ability to draw-down a limiting resource (soil moisture). We then used competition experiments to investigate the potential ecological significance of trait differences, examining the outcome of intraspecific interactions between home and away populations to test whether the latter are better competitors (i.e., as would occur if evolved advantages developed upon leaving the home range) (Lortie et al. 2009).

Materials and methods

Study species

Dactylis is a cool-season C₃ perennial that grows to heights from 0.45 to 1.5 m, with flowering from May to September in the northern hemisphere, and November–March in the south. Its ancestral range extends from Europe and western Asia to the Mediterranean including northern Africa. Most of its populations have been classified as diploid ($2n = 2x = 14$), but it also exhibits tetraploidy in some regions, with triploid and hexaploid forms occasionally reported (Zohary 1959; Lolicato and Rumball 1994). The phenotypes of diploid and tetraploid forms are morphologically similar and can co-occur geographically, but do not generally interbreed (Lolicato and Rumball 1994).

Dactylis introductions globally began as early as the 1700s, for a range of purposes including forage and soil stabilization. *Dactylis* seed was also used extensively in Europe and North America as packing material for explosive armaments in the early to mid-1900s, resulting in the widespread global movement of seed, including from North America back to Europe. This species now occurs across temperate and subtropical regions of North America, South America, and Australasia, and has been classified as invasive in parts of its introduced range, although not always (Firn et al. 2011).

The ploidy dynamics, growth characteristics, and introductory history of *Dactylis* have been extensively investigated (Lumaret 1988; Lolicato and Rumball 1994; Gauthier et al. 1998; Lindner et al. 1999; Sugiyama 2003). As is typical for many agronomic grasses, however, the mechanisms underlying its global expansion are unknown and can be variously attributed to trait differences or circumstance. Success could derive from polyploid vigor, traits relating rapid emergence and growth, enemy escape including soil pathogens, or selective breeding that occasionally occurred at agricultural research stations in the away ranges prior to widespread introduction (Casler et al. 2000; MacDougall et al. 2011). *Dactylis* has many different cultivars, of which there are two broad categories: ‘early-emergence’ and ‘late emergence’. It is typically assumed that these differences are derived from the specific selection of cultivars by agronomists in the home range (Casler et al. 2000), although this has not been explicitly tested. Alternatively, *Dactylis* was typically introduced in association with intensive cultivation and repeated seeding at high densities (MacDougall et al. 2004), such that ‘circumstance’ could largely explain its establishment and persistence in many areas. It continues to be widely and intentionally planted, despite its association with species loss in some native grassland communities.

Seed collection

Seeds were collected from ancestral populations in Europe spanning a latitudinal gradient from 51° to 59°N in Germany and Estonia (five sites), and from introduced populations in Canada, Argentina, and New Zealand (nine sites). Seeds were obtained in late summer (August–October 2008 in the northern hemisphere; December 2008–February 2009 in the southern hemisphere) and were air-dried at room temperature until shipping to Canada.

Common-environment trial

Two complementary ‘home and away’ glasshouse projects were conducted in the summer of 2009: a common-environment trial to quantify differences among home and

away populations, and pair-wise competition trials to test the significance of these trait differences on interactions among individuals from these populations.

The common-environment trial was run for 3 months at the University of Guelph Phytotron. Plants were grown in 5-l pots with greenhouse soil (peat moss–perlite–gypsum), with ten replicates per population. In each pot, 20 seeds were added initially before being thinned to one plant (the first to emerge), with the seeds spread 1 cm under the soil surface in each pot. Since the seeds came from many plants at each site, the selection of seeds for planting was done randomly, such that each seed had the possibility of being from 20 different individuals. The length of the trials (3 months) is similar to the duration of establishment to maturation for *Dactylis* in the field (MacDougall and Turkington 2004). Glasshouse temperatures were 22–24 °C during the day and 17–19 °C at night. Plants were fertilized once, at 60 days, when signs of slight nutrient deficiency became evident.

We examined population differences among a range of traits associated with plant performance, competitive ability, and widespread population expansion (Table 1) (van Kleunen et al. 2010). Seed mass was determined by averaging the total weight of 25 groups of ten seeds, after they had been air-dried following collection in the field. Emergence time was defined as the time of the first emerging seedling per plot (days since planting); a twist-tie was placed loosely around the first plant to emerge and all others were weeded. Percent emergence was the number of seeds to emerge from the 20 planted seeds per pot. Four measurements—plant height (cm), soil moisture draw-down, number of leaves per plant, and chlorophyll content—were taken at 30, 60, and 90 days, to test if growth and performance varied with time. Plant height and number of leaves were measured as the rate of increase [e.g., height (cm)/time (days)]. These measures allowed us to test whether size differences at the end of the experiment were positively correlated with emergence time and growth at the earlier intervals (e.g., are plants bigger only because they emerged earlier?). The draw-down of soil moisture (an estimate of R^* ; Tilman 1988) in each pot was determined by watering the pots to saturation, and then measuring soil moisture levels 24 h later (volumetric water content; Hydrosense TDR meter; Campbell Scientific, Edmonton, Alberta). Chlorophyll content was measured with a chlorophyll meter (Hansatech Instruments, Norfolk, England), with three wide, healthy leaves measured and averaged per plant. Chlorophyll content is an indication of photosynthetic activity, which is closely related to the amount of leaf nitrogen (e.g., Schepers et al. 1992). After 90 days, aboveground biomass (g) was determined by harvesting each plant at the soil surface, and drying at 68 °C for 48 h before weighing. We attempted to measure root biomass

Table 1 Mean functional trait values (± 1 SE) for home and away populations of *Dactylis glomerata*

Trait	<i>F</i> value	Home populations (Estonia, Germany)	Away populations (Canada, Argentina, New Zealand)
Seed mass (g)	1.91	0.08 (0.002)	0.07 (0.001)
Days to emerge	12.68 ^a	7.7 (0.3)	9.1 (0.3)
% Emerged	0.13	45.6 (4.1)	46.7 (2.9)
Height (cm)	3.17	76.4 (2.1)	71.7 (1.9)
Volumetric soil moisture	3.55	7.7 (0.6)	6.6 (0.4)
Number of leaves per plant	2.12	17.9 (0.6)	16.9 (0.5)
Chlorophyll content index	0.77	15.3 (0.9)	16.1 (0.7)
Growth rate (30 days)	27.75 ^a	1.00 (0.04)	0.80 (0.03)
Growth rate (60 days)	3.69	1.2 (0.06)	1.3 (0.05)
Growth rate (90 days)	1.27	0.4 (0.06)	0.5 (0.06)
Total % carbon	6.41	44.5 (0.08)	44.1 (0.05)
Total % nitrogen	2.76	1.8 (5.5)	2.0 (5.9)
C/N ratio	3.57	25.5 (0.8)	23.7 (0.6)
Biomass (g)	0.4	13.7 (0.48)	14.1 (0.35)

F values are derived from ANOVA for each trait by origin

^a Significant trait differences ($P \leq 0.05$), derived from post hoc Tukey's tests after Bonferroni corrections. Soil moisture is percent water content following a 24-h imposed drought. Chlorophyll content index is the ratio of light absorbance between the red and near-infrared wavelengths. Growth rate is measured as plant height (cm day⁻¹) after 30, 60, or 90 days

and the draw-down of soil nitrogen, but all pots were root-bound, such that we could not accurately separate roots and soil. Total foliar carbon and nitrogen were measured using a C/N analyzer (Leco, MI, USA), with samples consolidated from all leaves of each plant in case there was wide variability among leaves (Soil and Nutrient Lab, University of Guelph, Canada).

Ploidy number was determined using flow cytometry. Leaf tissue samples (~6 cm length) were cut from young, fully expanded leaves and dried in an envelope with silica gel. Although desiccated tissue is not currently recommended for estimating genome size, it has been used for determining ploidy (Suda and Trávnicek 2006) and worked successfully here. Barley (*Hordeum vulgare*) was used as an internal standard. Sample tissue was finely chopped with an approximately equal amount of *Hordeum* in a Petri dish with 0.75 ml of LB01 buffer (Dolezel et al. 1989) containing 50 $\mu\text{g ml}^{-1}$ propidium iodide and 50 $\mu\text{g ml}^{-1}$ RNase. Samples were stained for approximately 1 h (20 min to 2 h). After filtering through a 30 μm 'CellTrics' filter (Partec), samples were run on a FACSCalibur Flow Cytometer (BD Biosciences, San Jose, USA). Each sample was run on low until we had screened approximately 1,000 events (nuclei) per peak. The FL2 detector (585/42 nm) was used to measure fluorescence, and the parameter FL2-Area (integrated fluorescence) was used to quantify DNA content. Mean fluorescence, coefficients of variation (CV) and nuclei number per peak were measured using Modfit LT software (Verity Software House, 2000). The 2C DNA content values for each sample were calculated as the *Dactylis* mean fluorescence/*Hordeum* mean fluorescence \times *Hordeum* 2C

DNA content (11.12 pg; Bennett and Smith 1976). Ploidy was assigned by comparing the sample 2C DNA content values to those reported in the literature (Creber et al. 1994; Vilhar et al. 2002; Tuna et al. 2004).

Competition experiment

We conducted pair-wise competition trials among individuals from the ancestral and introduced ranges, using two randomly selected away populations (Argentina, Canada) and four randomly selected home populations (two from Germany and Estonia) due to bench space restrictions. These trials consisted of all possible combinations of the six populations, including competition trials between individuals from the same site. There were ten replicates per combination, with a single individual of each population in a separate pot. Measurements for height, number of leaves, soil moisture, and chlorophyll content were taken on days 30, 60, and 90, with final biomass determined as above after 90 days.

Statistical analysis

For the garden trials, trait differences among populations were compared with univariate multi-factor nested ANOVAs, and multiple linear regression models using principal component scores as the dependent variables (Ramette 2007). The first analysis allowed us to separate the effects of origin (home, away), country (Estonia, Germany, Argentina, New Zealand, Canada), and population (14 populations) on the variation of each measured trait. The

second analysis allowed us to quantify correlations among the measured traits and to test whether these correlations differ by origin (e.g., are traits associated with disturbance more prevalent in away populations?) (Küster et al. 2008).

For the univariate analyses, we emphasized ‘country’ given the possibility that the management history of *Dactylis*, including the timing and method of introduction, may vary by jurisdiction (Casler et al. 2000). All values were log-transformed to increase normality, except for the probability values for ‘percent emergence’ (arcsine-transformed), and for ‘seed mass’ (normally distributed). For traits measured at multiple intervals, we used repeated-measures univariate ANOVAs. Post hoc comparisons for all analyses were conducted using Tukey’s HSD tests. Because multiple univariate tests can inflate the α value and increase the probability of a Type 1 error, all comparisons were conducted using sequential Bonferroni-corrected alpha levels. That being said, the Bonferroni corrections did not change the outcome of any analysis.

For the multiple linear regressions, ordination scores were derived using principal components analysis (PCA), given that data were unimodal, continuous, and had relatively narrow ranges for each of our measured traits (Ramette 2007). The scores were taken from the first four ordination axes, which explained 71.6 % of the total variation. This allowed us to explicitly test the relationship between biogeographical origin (home vs. away) and the distribution of the component loadings on the four axes.

For the competition trials, we focused on the relative differences in tolerating the competitive effects of other individuals (Goldberg and Landa 1991). This was done at three levels: within the same population, from other populations within the same origin (e.g., away vs. away trials), and from different origins (home vs. away trials). These differences were quantified by contrasting the performance of individuals from each population when grown in isolation (‘monoculture’) versus when grown with other individuals (‘mixture’), using the following formula: [(monoculture biomass – mixture biomass)/monoculture biomass]. We then used ANOVA and post hoc Tukey’s HSD tests to contrast these competition values by origin, country, and site. This allowed us to construct a competitive hierarchy among the populations tested within the competition trials.

All statistical analyses were conducted with JMP 8 (SAS, Cary, NC, USA) or SPSS 13, which was used for the PCA (SPSS, Chicago, IL, USA).

Results

There were few trait differences between home and away *Dactylis* populations, suggesting an absence of substantial

life history changes underlying its global expansion (Table 1). This includes an absence in trait differences in total foliar N content, total foliar C content, plant height, leaf chlorophyll content, the ability to draw-down soil moisture, and final biomass. All plants but one were tetraploids, based on the known tetraploid 2c value of *Dactylis* (8.6 pg DNA; Vilhar et al. 2002) versus our measured value (9.37 pg DNA). The one exception was one individual from Argentina that appeared to be a hexaploid, based on the reference DNA content (15.36 pg DNA).

There were two significant trait differences that we detected by origin (i.e., home vs. away populations), which also influenced the outcome of the competition trials (Table 1; Fig. 1). Plants from the home populations, on average, germinated more quickly and grew faster within the first 2 months of the common-environment trial. As a result, individuals from the home populations were more likely to suppress the height and final biomass of their neighbors while tolerating their effects (Fig. 2). Neither of these results would have changed if we ran the garden or competition trials longer than 3 months, given how biomass accumulation dropped substantially after 60 days likely due to the pots becoming root-bound (Fig. 3). Growth rates for all individuals, regardless of population, sharply declined after 60 days as plants became root-bound and started flowering (Fig. 3).

Some of our measured traits were correlated (e.g., emergence time vs. final biomass, final height vs. final biomass), as would be expected given the large number of characteristics that we quantified (Table 1). These correlations, however, did not differ between home and away populations (whole model using PCA scores: $F_{43,87} = 1.39$, $P = 0.14$), as might have been expected if different sets of traits resulted in fitness advantages in the home versus away environments.

Of the total variation that occurred among the measured traits, most was explained by differences at the country level that were unrelated to origin. Foremost, this result was influenced by the two New Zealand *Dactylis* populations, which emerged and grew the slowest, produced the least amount of final biomass, but were also most effective at drawing-down soil moisture (Fig. 1). There were also several less extreme but significant differences among other countries, for measures including height, emergence time, and final biomass (Appendices 1, 2). Among the home countries, for example, German populations had significantly higher percentage of seeds to emerge than Estonian ones, which was positively correlated with seed mass (Appendix 1). Estonian sites, however, were quicker to emerge.

There was also significant trait variation among some sites, possibly reflecting selection for local climate regimes or different introduction histories (Appendix 2). Among the

Fig. 1 Trait measurements for *Dactylis glomerata* populations in away (Canada, Argentina, New Zealand) and home (Estonia and Germany) ranges. Data are mean (± 1 SE) for **a** final height (3 months), **b** emergence success (percent total germination), **c** an estimate of R^* for soil moisture draw-down at peak biomass (percent water content), **d** final dry-weight biomass of individual plants per pot, **e** time to first germination (days), and **f** seed mass. Data are mean and ± 1 SE. Bars with different letters indicate significant differences among sites using Tukey's HSD test ($P \leq 0.05$). All analyses were conducted on log transformed data, except for seed emergence (arcsine) and seed mass (not transformed)

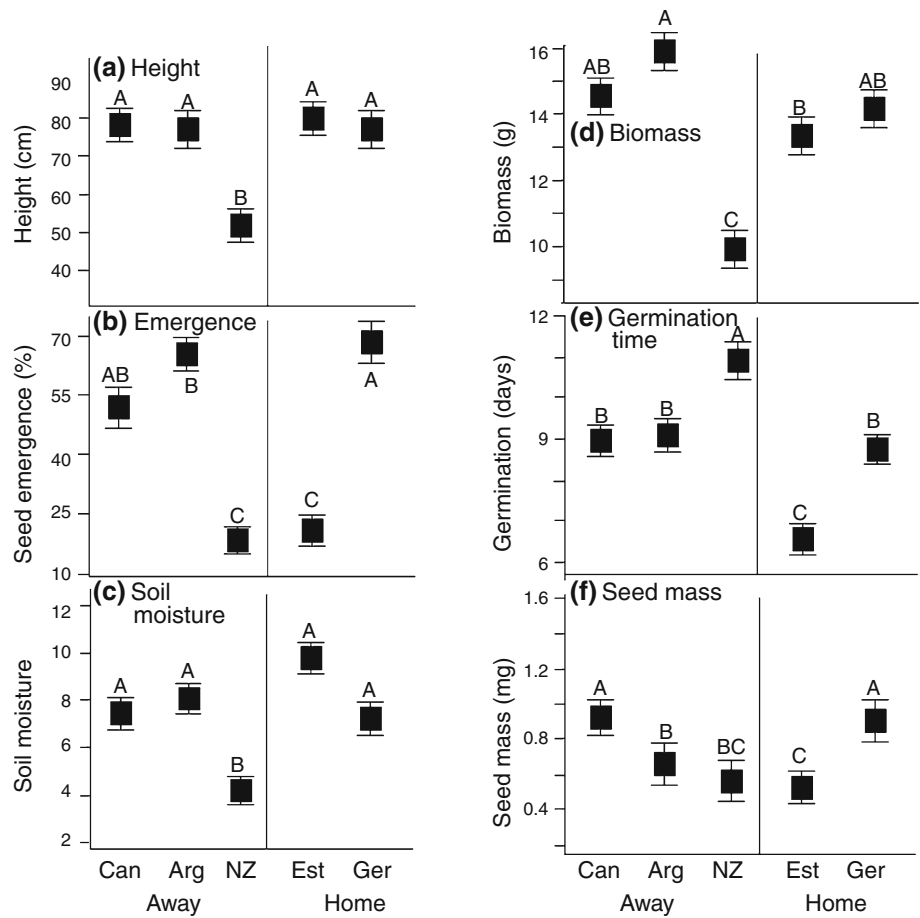
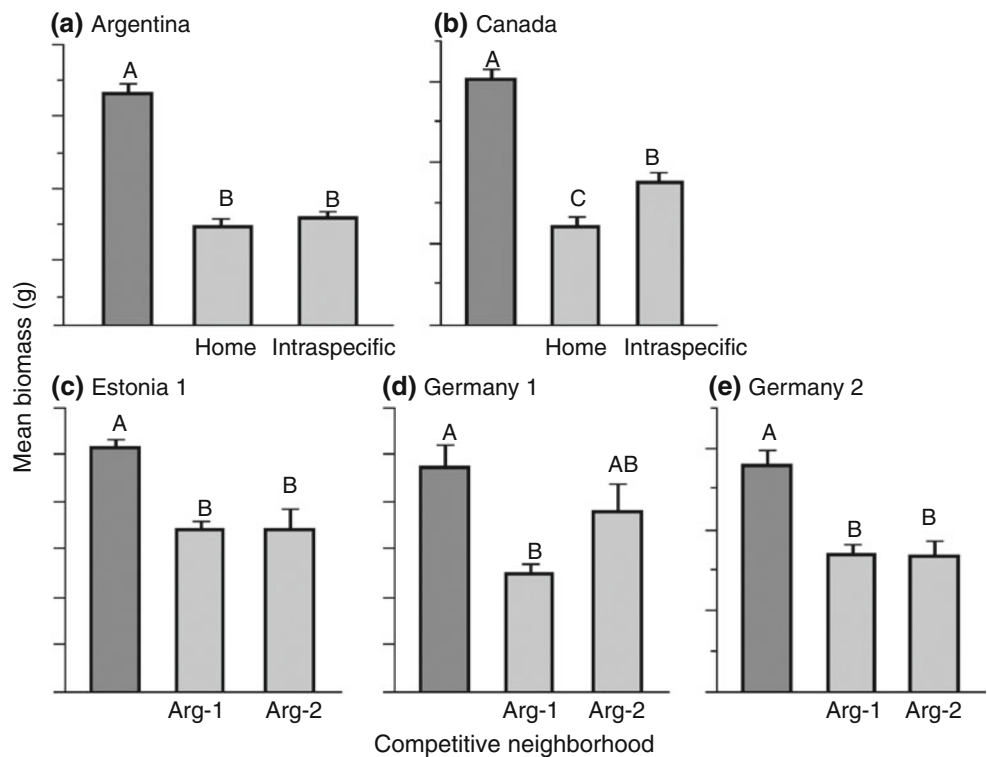


Fig. 2 Mean biomass (± 1 SE) in competition trials, contrasting monoculture performance (i.e., single plant without neighbors), and biomass when grown in mixtures with another plant. Home interactions with *Dactylis glomerata* home populations, intraspecific interactions between individuals from the same site, *Arg-1* interactions with the A1 Argentinian population of *D. glomerata*, *Arg-2* interactions with the A2 Argentinian population. Canada, Estonia 1, and Germany 1 and 2 refer to *D. glomerata* populations from those sites. Bars with letters indicate significant differences amongst sites (Tukey's HSD test, $P \leq 0.05$)



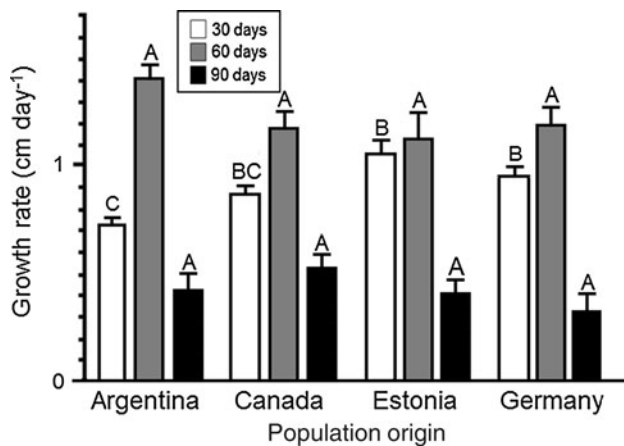


Fig. 3 Growth rates (mean \pm 1SE) for four populations of *Dactylis glomerata* over three intervals. Bars with different letters at each time interval indicate significant differences (Tukey's HSD test, $P \leq 0.05$)

Argentinean populations, for example, leaf production per plant ranged from 207.4 leaves (SE = 14.3) to 148.1 leaves (SE = 16.8). In contrast, the New Zealand populations did not significantly differ in any trait (Appendix 2). For the home sites, two of the German populations differed significantly in seed mass and final biomass.

Discussion

The global expansion of plants is often assumed to relate to superior trait-based performance by away populations (Sax and Brown 2000). Results from our common environment and competition trials among home and away populations of the globally distributed *D. glomerata* did not support this hypothesis. Many of the mechanisms that could explain superior performance in away plants, including higher ploidy level, changes in the allocation of total carbon and total nitrogen in the leaf tissues, higher chlorophyll content reflecting increased photosynthetic activity, and plant biomass, were similar to European home populations. The few divergences we detected either favored the home populations (e.g., growth rate, competitive ability in the glasshouse environment), or varied more at the level of country or site, regardless of biogeographical origin.

Rather than succeeding due to changes that develop during the expansion process, the mechanisms explaining *Dactylis* success appears to derive from other sources. This likely includes the importance of the pre-adapted traits that we observed in the home populations, including rapid emergence and large aboveground biomass production, which may contribute to establishment and persistence in away settings. An implication of this finding is that invader success may sometimes derive more from differences between invaders and species in the recipient community

(e.g., trait novelty), rather than differences between home and away populations. We attempted to test this, collecting functionally similar native grass species in all away areas but encountered low germination for most species. This could reflect methodological problems relating to collection or storage, although all native seed was collected and stored identically to *Dactylis*, which suffered no difficulties. An alternative explanation is the occurrence of specialized stratification requirements, common in native grasses and tied to seed age or environmental cues, with dormancy protecting against germination in unsuitable conditions (Simpson 2007). This may be ecologically important for native grasses under non-anthropogenic conditions, but could be a huge disadvantage in systems transformed by disturbance (Harnden et al. 2011), to which *Dactylis* appears better adapted.

Another explanation for success could be circumstance, again meaning that trait differences among home and away populations could be relatively unimportant. Historical records often describe frequent (multi-year) and high-density introductions of *Dactylis*, typically preceded by the reduction or elimination of the native community by heavy grazing or some form of cultivation (Lumaret 1988; Lolcato and Rumball 1994; Casler et al. 2000; MacDougall et al. 2004).

One of the challenges in determining the influence of trait-based factors on global expansion is the tight covariance of trait differences with disturbance and other environmental-based changes (e.g., fertilization, irrigation, climate change), which can also produce growth increases in the away range. Populations in the away ranges may thus contain, for example, large plants with N-rich foliage that are explained by plasticity, rather than trait-based changes in resource allocation. Our common-environment trial allows us to distinguish between these possibilities, and few trait-based differences were apparent. Also, shifts in the allocation of carbon and nitrogen are predicted to derive from changes in the selective environment in the away territory, where the absence of enemies allows individuals to allocate resources towards growth or reproduction instead of defense (Blossey and Nötzold 1995). We examined this issue by measuring total C, total N, and chlorophyll content, hypothesizing that, if away *Dactylis* populations were investing less in defense, then chlorophyll content might be elevated while total C levels would be reduced relative to both N levels in away plants and C levels in home plants. This hypothesis was also not supported, which may reflect an absence of any form of enemy escape or similar levels of herbivory in home and away ranges, given that *Dactylis* is often introduced as a forage species. An alternative explanation, which we did not test, is that shifts in the type of C allocation (i.e., simple sugars vs. complex carbohydrates) have occurred in response to

lower enemy attack. These shifts could have resulted in reductions in the production of metabolically expensive complex carbohydrates such as lignin that are associated with plant defense (Chapin et al. 2002).

Polyploidy is associated with establishment and population spread in away ranges through its potential for positive impacts on plant performance including growth and biomass (Stebbins 1985; Henery et al. 2010; Thebault et al. 2011). *Dactylis* has been reported to commonly occur in both diploid and polyploid forms at home, such that its global success could derive from the introduction of polyploids or even the creation of polyploids from human-constructed hybrid swarms in the away ranges (e.g., Gaskin and Schaal 2002). These hypotheses, however, were also rejected as all the *Dactylis* populations we examined, including the European ones, were polyploids. It is difficult to determine the role of polyploidy in establishment, or the possible significance of the European populations all being polyploids. We did not examine differences in competitive ability compared to native species in the away communities, although other studies have shown *Dactylis* to be superior to its native competitors (MacDougall and Turkington 2004). There is some evidence that *Dactylis* polyploids generally outperform and outcompete *Dactylis* diploid individuals, with these advantages deriving from trait differences including greater tiller weight, heavier seed mass, faster leaf production, and more rapid onset of flowering (Maceira et al. 1993; Bretagnolle and Thompson 2001). If these same differences exist between expanding pre-adapted polyploid *Dactylis* genotypes and the herbaceous native species that they interact with, then this may help explain establishment success and eventual dominance by the invader.

Although origin differences were not substantial, there were significant contrasts in performance among countries, and even among sites within countries. This applied to both the home and away populations. The Estonian populations, for example, produced less biomass on average than the German ones. In the away ranges, this result may derive from the possible interaction of two factors: the variety of *Dactylis* that happened to be introduced to a given area, combined with the habitat suitability of that area including factors such as climate, soil substrate, and even the timing and intensity of human land use practices associated with *Dactylis* establishment. The mechanism by which *Dactylis* established could vary widely by population depending on how these two factors combine (Mack and Pyke 1983; Hierro et al. 2009).

We do not have explicit data on the patterns of distribution, abundance, and invasiveness (i.e., the ability to invade nearby native plant communities) for the populations that we used, and we did not sample the full extent of *Dactylis* populations in the home and away ranges. The

general trends, however, support the notion that *Dactylis* functions differently in different regions. On Vancouver Island, for example, the species is highly aggressive, associated with the displacement of co-occurring rare flora, and is subject to extensive eradication management programs. In Argentina, in contrast, the species is widespread along a large latitudinal gradient within the country, but it is relatively uncommon in non-cultivated areas. Similar variations in distribution and abundance characterize European populations, suggesting that performance in home and away habitats is similar and its global expansion is not based on evolutionary change in traits (Firn et al. 2011).

It is impossible to determine the exact significance of the one substantial difference that we did observe between home and away populations—that the latter tended to be slower to emerge and slower growing. This pattern reached its extreme in New Zealand, with individuals germinating slowly and in low numbers, having low rates of increase, and producing relatively small amounts of biomass. One explanation for this result could derive from the initial introductions, where the founder populations happened to derive from a home population possessing these various traits. An alternative explanation derives from some of the other trait differences observed in the New Zealand populations, especially the R^* estimates based on water draw-down. R^* measures have been shown to predict the outcome of competition including for abundant non-native plants (Seabloom et al. 2003, Harpole and Tilman 2005). This suggests that, at least for these populations, some trait-based changes have occurred since *Dactylis* left home, albeit not the typical traits associated with rapid population expansion including rapid growth and large size. Our experimental work simulated conditions expected of a disturbed environment—seeds were planted on bare soil with unlimited resources (initially) and in the absence of a plant canopy. This would favor ‘weedy’ traits such as rapid emergence and growth, which the home populations possess. The sorts of traits seen in the New Zealand populations are more consistent with species of less disturbed habitats, such as old-fields with limited grazing and cultivation.

In summary, large increases in plant size and abundance compared to ancestral ‘home’ ranges are often assumed for globally pervasive species, but the generality of these assumptions has not been widely tested (Thebaud and Simberloff 2001; Firn et al. 2011). Here, we found little supporting evidence, observing few differences in size or other performance-based traits between home and away populations of one of the world’s most widespread species. Global expansion, therefore, appears possible without profound ecological or evolutionary based changes relating to growth and reproduction. These findings are likely

influenced by the agronomic history of *Dactylis* introductions, as the traits that favor this species in disturbed pastures of Eurasia may also favor establishment and expansion elsewhere, given that seed additions are often accompanied by European-style land management (Firn et al. 2011). As such, it may be no surprise that the traits that favor persistence in the home range are similarly effective at driving high abundances in the away habitats.

Acknowledgments Thanks to Julie Maniecki, Erin Leclair, Greg Baute, Paul Kron, Sarah Baldwin, Tannis Slimmon, Mike Mucci, Pedro Tognetti, Enrique Chaneton, Walter Martin, Karl Fiander, Jennifer Firn, Hafiz Maherali, Merritt Turetsky, John Klironomos, and Rieger-Hoffmann. Seed importation and the destruction of plant material at the end of the experiment followed the guidelines of the Canadian Food Inspection Agency. Funding provided by NSERC (Canada), the European Union through the European Regional Development Fund (Estonian Center of Excellence FIBIR) (Estonia), FCEyN and CONICET (Argentina), the International Bureau of the Federal Ministry for Education and Research (Germany), and by the New Zealand Foundation for Research, Science and Technology grant C09X0502.

References

- Ainouche ML, Fortune PM, Salmon A, Parisod C, Grandbastien M-A, Fukunaga K, Ricou M, Misset M-T (2009) Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). *Biol Invas* 11:1159–1173
- Bennett MD, Smith JB (1976) Nuclear DNA amounts in angiosperms. *Philos Trans R Soc Lond B* 274:227–274
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *J Ecol* 83:887–889
- Bosdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144:1–11
- Bretagnolle F, Thompson JD (2001) Phenotypic plasticity in sympatric diploid and autotetraploid *Dactylis glomerata*. *Int J Plant Sci* 162:309–316
- Callaway RM, Thelen GC, Rodriguez A, Holben W (2004) Release from inhibitory soil biota in Europe may promote exotic plant invasion in North America. *Nature* 427:731–733
- Casler MD, Fales SL, McElroy AR, Hall MH, Hoffman LD, Leath KT (2000) Genetic progress from 40 years of orchard grass breeding in North America measured under hay management. *Crop Sci* 40:1019–1025
- Chapin FS, Mooney HA, Matson PA (2002) Principles of terrestrial ecosystem ecology. Springer, Toronto
- Colautti RI, Maron JL, Barrett SCH (2009) Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evol Appl* 2:187–199
- Creber H, Daview MS, Francis D, Walker HD (1994) Variation in DNA C value in natural populations of *Dactylis glomerata* L. *New Phytol* 128:555–561
- D'Antonio C, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmill NJ (2005) Are invasive species the drivers of ecological change? *Trends Ecol Evol* 20:470–474
- Dolezel J, Binarová P, Lucretti S (1989) Analysis of nuclear DNA content in plant cells by flow cytometry. *Biol Plant* 31:113–120
- Firn J, MacDougall AS, Schmidt S, Buckley YM (2010) Early emergence and resource availability can competitively favour natives over a functionally similar invader. *Oecologia* 163:775–784
- Firn J, Moore JL, MacDougall AS, Borer ET, Seabloom EW et al (2011) Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecol Lett* 14:274–281
- Gaskin JF, Schaal BA (2002) Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proc Nat Acad Sci USA* 99:11256–11259
- Gauthier P, Lumaret R, Bedecarrats A (1998) Ecotype differentiation and coexistence of two parapatric tetraploid subspecies of cocksfoot (*Dactylis glomerata*) in the Alps. *New Phytol* 139: 741–750
- Goldberg DE, Landa K (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J Ecol* 79:1013–1030
- Harnden J, MacDougall AS, Sikes B (2011) Field-based effects of allelopathy in invaded tallgrass prairie. *Botany* 89:227–234
- Harpole WS, Tilman D (2005) Non-neutral patterns of species abundance in grassland communities. *Ecol Lett* 9:15–23
- Henery ML, Bowman G, Mráz P, Treier UA, Gex-Fabr E, Schaffner U, Müller-Schrer H (2010) Evidence for a combination of pre-adapted traits and rapid adaptive change in the invasive plant *Centaurea stoebe*. *J Ecol* 98:800–813
- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *J Ecol* 93:800–813
- Hierro JL, Eren Ö, Khetsuriani L, Diaconu A, Török K et al (2009) Germination responses of an invasive species in native and non-native ranges. *Oikos* 118:529–538
- HilleRisLambers J, Yelenik SG, Colman BP, Levine JM (2010) California annual grass invaders: the passengers, not drivers, of change. *J Ecol* 98:1147–1156
- Küster EC, Kühn I, Bruelheide H, Klotz S (2008) Trait interactions help explain plant invasion success in the German flora. *J Ecol* 96:860–868
- Lambdon PW (2008) Why is habitat breadth correlated strongly with range size? Trends amongst the alien and native floras of Mediterranean islands. *J Biogeogr* 35:1095–1105
- Lindner R, Lema M, García A (1999) Ecotypic differences and performance of the genetic resources of cocksfoot (*Dactylis glomerata* L.) in northwest Spain. *Grass Forage Sci* 54:336–346
- Lolicato S, Rumball W (1994) Past and present improvement of cocksfoot (*Dactylis glomerata* L.) in Australia and New Zealand. *NZ J Agr Res* 37:379–390
- Lortie CJ, Munshaw M, Zikovitz A, Hierro J (2009) Cage matching: head to head competition experiments of an invasive plant species from different regions as a means to test for differentiation. *PLoS One* 4:e4823
- Lumaret R (1988) Cytology, genetics and evolution in the genus *Dactylis*. *Crit Rev Plant Sci* 7:55–91
- MacDougall AS, Turkington R (2004) Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *J Ecol* 92:422–434
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55
- MacDougall AS, Beckwith B, Maslovat C (2004) Defining conservation strategies with historical perspectives: a case study from a degraded oak ecosystem. *Conserv Biol* 18:455–465
- MacDougall AS, Rillig M, Klironomos J (2011) Weak conspecific feedbacks and exotic dominance in a species-rich savanna. *Proc R Soc Lond B* 278:2939–2945

- Maceira NO, Jacquard P, Lumaret R (1993) Competition between diploid and derivative autotetraploid *Dactylis glomerata* L. from Galicia: implications for the establishment of novel polyploid populations. *New Phytol* 124:321–328
- Mack RN, Pyke DA (1983) The demography of *Bromus tectorum*: variation in time and space. *J Ecol* 71:69–93
- Mason RAB, Cooke J, Moles AT, Leishman MR (2008) Reproductive output of invasive versus native plants. *Glob Ecol Biogeogr* 17:633–664
- Norton DA (2009) Species invasions and the limits to restoration: learning from the New Zealand experience. *Science* 325:569–571
- Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climate niche shifts are rare among terrestrial plant invaders. *Science* 335:1344–1347
- Ramette A (2007) Multivariate analyses in microbial ecology. *FEMS Microb Ecol* 62:142–160
- Ricklefs RE, Guo Q, Qian H (2008) Growth form and distribution of introduced plants in their native and non-native ranges in Eastern Asia and North America. *Divers Distrib* 14:381–386
- Rout ME, Callaway RM (2009) An invasive plant paradox. *Science* 324:734–735
- Sax D, Brown J (2000) The paradox of invasion. *Divers Distrib* 14:381–386
- Schepers JS, Francis DD, Vigil M, Below FE (1992) Comparison of corn leaf nitrogen and chlorophyll meter readings. *Comm Soil Sci Plant Anal* 23:2173–2187
- Seabloom EW, Harpole WS, Reichman OJ, Tilman D (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc Nat Acad Sci USA* 100:13384–13389
- Simpson GM (2007) Seed dormancy in grasses, 2nd edn. Cambridge University Press, New York
- Stebbins GL (1985) Polyploidy, hybridization, and the invasion of new habitats. *Ann Miss Bot Gard* 72:824–832
- Suda J, Trávníček P (2006) Reliable DNA ploidy determination in dehydrated tissues of vascular plants by DAPI flow cytometry—new prospects for plant research. *Cytometry* 69:273–280
- Sugiyama S (2003) Geographical distribution and phenotype differentiation in populations of *Dactylis glomerata* L. in Japan. *Plant Ecol* 169:295–305
- Thebaud C, Simberloff D (2001) Are plants really larger in their introduced ranges? *Am Nat* 157:231–236
- Thebaud A, Gillet F, Müller-Schärer H, Buttler A (2011) Polyploidy and invasion success: trait trade-offs in native and introduced cytotypes of two Asteraceae species. *Plant Ecol* 212:315–325
- Tilman D (1988) Plant strategies and the dynamics of plant communities. Princeton University Press, Princeton
- Tuna M, Khadka DK, Shrestha MK, Arumuganathan K, Golan-Goldhirsh A (2004) Characterization of natural orchardgrass (*Dactylis glomerata* L.) populations of the Thrace Region of Turkey based on ploidy and DNA polymorphisms. *Euphytica* 135:39–46
- van Kleunen M, Dawson W, Schlaepfer DR, Jeschke JM, Fischer M (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecol Lett* 13:947–958
- Vilhar B, Vidie T, Jogan N, Dermastia M (2002) Genome size and the nucleolar number as estimators of ploidy level in *Dactylis glomerata* in the Slovenian Alps. *Plant Syst Evol* 234:1–13
- Zohary D (1959) Natural triploids in the orchard grass, *Dactylis glomerata* L., polyploid complex and their significance for gene flow from diploid to tetraploid levels. *Evolution* 13:311–317