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Effects of genotype identity and diversity on the invasiveness and invasibility of plant populations

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Abstract Genetic diversity within species is a potentially important, but poorly studied, determinant of plant community dynamics. Here we report experiments testing the influence of genotype identity and genotypic diversity both on the invasibility of a foundation, matrix-forming species (Kentucky bluegrass, *Poa pratensis*), and on the invasiveness of a colonizing species (dandelion, *Taraxacum officinale*). Genotypes of Kentucky bluegrass in monoculture showed significant variation in productivity and resistance to dandelion invasion, but the productivity and invasion resistance of genotypic mixtures were not significantly different from those of genotypic monocultures. Indirect evidence suggested temporal shifts in the genotypic composition of mixtures. Dandelion genotypes in monoculture showed striking and significant variation in productivity and seed production, but there was no significant tendency for these variables in mixtures to deviate from null expectations based on monocultures. However, productivity and seed production of dandelion mixtures were consistently greater than those of the two least productive genotypes, and statistically indistinguishable from those of the three most productive genotypes, suggesting the possibility of greater invasiveness of genotypically diverse populations in

the long run due to dominance by highly productive genotypes. In both experiments, the identity of genotypes was far more important than genetic diversity per se.

Introduction

Genetic diversity within species provides the basis for evolutionary change, but may also have important ecological consequences within even a single generation (Hughes et al. 2008). The vast majority of theoretical models in community ecology implicitly treat species as genetically invariant, which may produce faulty predictions if the outcome of species interactions depends on the genetic composition and diversity of the interacting populations (Yoshida et al. 2007; Vellend 2006; Fridley et al. 2007). Some recent studies have demonstrated important effects of genotype identity and genetic diversity on variables such as population productivity, recovery from stress or disturbance, and the composition and diversity of the associated insect community on plants (Hughes and Stachowicz 2004; Reusch et al. 2005; Johnson et al. 2009; Crutsinger et al. 2006; Agashe 2009). There have been relatively few such studies, especially on the consequences of genetic diversity for interactions between species at the same trophic level (but see Booth and Grime 2003; Fridley et al. 2007; Crutsinger et al. 2008; De Meester et al. 2007).

Current interest in the ecological consequences of genetic diversity stems in part from the vast literature and intense debate on the role of species composition and diversity in determining community and ecosystem properties such as productivity, nutrient retention, and resistance to

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invasion (Loreau et al. 2002; Srivastava and Vellend 2005). Genetic diversity within species can influence the same variables via many of the same processes, with the magnitude of effects surprisingly large in some cases relative to effects of species diversity (Hughes et al. 2008). Of particular interest in this paper are the hypotheses that diversity within a resident community or population can enhance its resistance to invasion (Elton 1958), and that genetic variation within an invading population can have important consequences for its success (Dlugosch and Parker 2007).

In a single growing season or generation, a variable such as invasion resistance or productivity may be higher or lower in a diverse mixture of genotypes than in monocultures due to two main classes of process. First, the productivity (or other property) of each genotype relative to its initial input or abundance may be greater in mixtures than monocultures due to complementary resource use or to other positive genotype–genotype interactions. This class of process has been referred to as "complementarity" (e.g. Loreau and Hector 2001). Second, if genotypes with high (or low) monoculture productivity dominate mixtures, total productivity of the mixtures may be greater (or less than) the average monoculture. These have been referred to as positive (or negative) "selection effects" (Loreau and Hector 2001). Separating complementarity and selection requires data not just at the plot level, but on each species or genotype in the mixture; this is straightforward for different species, but presents a challenge for genotypes that are difficult or impossible to distinguish morphologically. Both complementarity and selection effects appear to be prevalent in species mixtures across many different systems (Cardinale et al. 2006, 2007), and both may occur in genotype mixtures (e.g. Reusch et al. 2005), though too few studies have been conducted at the genetic level to assess their general prevalence.

Here we present a study of how genotype identity and genotypic diversity influence the interaction between two perennial plant species, Kentucky bluegrass (*Poa pratensis*) and dandelion (*Taraxacum officinale*). Both species are native to Europe, currently have widespread distributions throughout the temperate zone, and commonly co-occur in open and disturbed habitats such as lawns and pastures. Kentucky bluegrass is a rhizomatous grass, and often a desired dominant species of lawns and fields, with many commercial cultivars sold for this purpose. Dandelions are notorious weeds of lawns and agricultural fields, with non-clonal growth from a taproot, and highly dispersive wind-blown seeds. As such, we consider Kentucky bluegrass to be the foundation or matrix-forming species in this experimental two-species community, whose invasibility was assessed with respect to the success of invading dandelions. Manipulation of genotypic identity and diversity was greatly facilitated by the fact that both species produce seed

asexually via apomixis, allowing us to easily generate many replicate plants of different genotypes via seed. We conducted two main experiments to test for: (1) effects of Kentucky bluegrass genotype and genetic diversity on invasibility, and (2) effects of dandelion genotype and genetic diversity on invasiveness. The size and seed production of dandelion plants in small experimental populations were used to assess both bluegrass invasibility and dandelion invasiveness. This is the first study to look at the consequences of genetic diversity for both the resistance of one species to invasion, and also the success of the invading species.

Materials and methods

Study system

We used commercial Kentucky bluegrass cultivars as "genotypes" in our experiments. This species is highly, though not obligately, apomictic; each cultivar represents a distinct and extremely narrow genetic stock, and can therefore be meaningfully considered a genotype (Lickfeldt et al. 2002). Candidate cultivars were selected with the goal of including genotypes showing as much potential ecological differentiation as possible. To this end we used data from the National Turfgrass Evaluation Program (NTEP), in which qualitative characters (e.g. leaf colour, leaf texture, percent cover) are scored for hundreds of cultivars under standardized conditions (http://www.ntep.org). For the experiments reported here, we selected five cultivars (Alpine, Jewel, Langara, Merit and NuGlade) representing both the range of variation in characters measured in a pilot greenhouse experiment (leaf width, shoot density), and the range of variation in the NTEP data (see Table S1; Figs. S1-2). These variables used in cultivar selection include some that have clear potential relevance to lawn invasibility (e.g. density, cover), and others (e.g. leaf characters) that we interpret as potentially indicative of more general ecological differentiation.

In its native Europe, *T. officinale* occurs both as diploid and triploid individuals, but only the asexual triploids have been found in North America (King 1993). Several studies have demonstrated that dandelion populations contain multiple genotypes (Solbrig 1971; Vavrek 1998; Vellend et al. 2009), and genotypes have been shown to vary in a number of traits, including the timing of flower production, competitive ability, and tolerance of disturbance (Solbrig 1971; Ford 1981; Vavrek et al. 1996; Vavrek 1998; Vellend et al. 2009).

To identify and select dandelion genotypes for this experiment, we first grew replicate plants from 30 seed heads collected from the Vancouver area (British Columbia,

Canada) in a greenhouse, and for six of these that covered the full range of trait space (based on leaf measurements), their genetic distinctness was confirmed using microsatellite DNA markers (see Vellend et al. 2009). Five of these six genotypes were used in the diversity experiments (genotypes 2, 9, 16, 24 and 64), and these genotypes showed more than a tenfold variation in fitness when grown at our field site (described below) in a common garden (Vellend et al. 2009). Based on the microsatellite analysis, we initially believed we had seven distinct genotypes identified, but after subsequent experiments had already begun we discovered a genotyping error such that one of the genotypes (genotype 16) ended up overrepresented twofold in the following experiments. This had essentially no impact on our ability to draw inferences on our questions of interest.

Genotypic diversity experiments

Our experiments were conducted at Totem Field, a 12-ha field on the University of British Columbia campus (Vancouver). In each experimental unit, we simulated the establishment of a Kentucky bluegrass lawn that is subsequently invaded by dandelions—a very common sequence of events in the north-temperate zone. We established two parallel field experiments—one to test the effects of genotype and genotypic diversity in Kentucky bluegrass on the suppression of dandelions, and the other to test the effects of genotype and genotypic diversity in dandelions on their invasion success. In both experiments, Kentucky bluegrass lawns were first established from seed in raised beds, after which dandelion populations consisting of 12 seedlings were planted in each plot. The number of genotypes per population was manipulated in different ways in the two experiments (described below). We established seedlings of the five dandelion genotypes in a growth chamber in autumn 2006 from seeds collected in the greenhouse. Sixty-eight wooden raised beds, 47 cm × 51 cm and 20 cm high, were placed on bare soil at Totem Field in June 2006 and filled with a soil composed of peat, sand and subsoil (silt and fines) from Richmond, British Columbia (Kutny's Richmond Soils, Richmond, B.C.). Each plot was amended with 125 g of Osmocote Pro slow-release fertilizer (N:P:K = 19:5:9, 12–14 month release; Scotts, Ohio).

Experiment I—consequences of genetic diversity in Kentucky bluegrass

Each of 30 raised beds ("plots") was assigned randomly to one of six treatments with five replicates each. Each Kentucky bluegrass cultivar was grown alone, giving five one-genotype treatments, and all five were grown together in a single five-genotype treatment. We recognize that we have only one combination of five genotypes in the high genetic diversity treatment (in both experiments), but previous studies indicate that results for mixtures of the full genotype or species pool (for which there is, by definition, only one combination of genotypes or species) are highly consistent with different combinations of multiple genotypes or species (e.g. Tilman et al. 1996; Reusch et al. 2005). Each plot received 2.7 g of seed, with the seed lot for the five-genotype treatment created by combining equal seed weights of the five cultivars. Seedlings began to emerge within a week of seed sowing, and productivity of the Kentucky bluegrass in each plot was measured both before and after dandelion invasion. Regular mowing (typical of habitats where bluegrass and dandelions coexist) was simulated by clipping at 5.1 cm approximately once per month during the growing season. The dry mass of the grass clippings was used to measure productivity.

In April 2007, the spring following bluegrass establishment, 12 dandelion seedlings were planted in a 4 × 3 grid in the centre of each plot, with 5-cm spacing between plants, which corresponds to the upper end of dandelion densities observed in the field (M. V. personal observation). Each dandelion population comprised five genotypes, with genotype 16 represented by four individuals and all other genotypes by two individuals, with identical randomly determined positions of genotypes within each 4 × 3 grid. Plants that died within 6 weeks of planting (<5%) were replaced.

To assess the performance of the dandelions, we estimated individual plant size and reproduction throughout the experiment. Total leaf area of each plant was estimated approximately once per month from May to October 2007. Leaf area (LA; cm^2) on each plant was estimated using a parameterized regression model based on the total number of leaves >4 cm long (n), and for the longest leaf, its length (L), and the maximum distance from the central leaf vein to a leaf lobe tip (maximum "half width"; W). The model was LA = 0.221 × n × L × 2W (r^2 = 0.95 based on 56 field-collected plants). To minimize mortality during establishment, dandelions were not clipped during summer 2007. Aboveground vegetative biomass (>4 cm) of dandelions was clipped, dried, and weighed in September 2007, and all aboveground dandelion biomass was harvested in late May 2008 (there was substantial growth between the two harvests). After the final aboveground biomass harvest, we extracted dandelion taproots, drying and weighing the portion down to 9-cm depth (the maximum depth to which we could reliably retrieve the entire tap root). Throughout the experiment we regularly monitored dandelion reproduction, counting and removing all seed heads shortly before opening. We report data on seed head production, and also seed production, with the latter calculated using the mean number of seeds per head estimated in a common garden experiment (Vellend et al. 2009). In April–May 2008 we were

unable to assign flowering heads to particular plants given a high degree of entanglement between plants, so these data were collected at the plot level.

To investigate potential processes underlying differences among Kentucky bluegrass cultivars in their resistance to dandelion invasion, we estimated soil nutrient availability during the initial stage of dandelion invasion—when we considered nutrient draw-down by bluegrass to be most likely to influence dandelions. We were specifically interested in K, as uptake of K by competing species has been shown to suppress dandelions (Tilman et al. 1999). Two soil cores, 6 cm diameter and 10 cm deep were taken in June 2007 from opposite corners of each plot, ∼5 cm from plot edges, and combined into a single composite sample. Soil samples were air dried, and extractable NH_4^+–N, NO_3^-–N, P, and K were estimated on each sample using standard techniques (Lavkulich 1978).

To test whether bluegrass productivity, soil nutrient availability, or dandelion size and seed production in five-bluegrass-genotype plots (Y_O) differed from the null expectation based on the same variables measured in bluegrass monocultures (Y_E), we conducted one-sample t-tests assessing deviations of the "net biodiversity effect" ($\Delta Y = Y_O - Y_E$) from zero [method described in Loreau and Hector (2001)]. With perfect balance in the representation of genotypes in monocultures versus polycultures this is equivalent to testing the hypothesis that the mean across polycultures is greater than the mean across monocultures, but the ΔY method provides a simple means of accounting for any imbalance in genotype representation, such as the overrepresentation of genotype 16 in mixtures in experiment II. Values of ΔY were square-root transformed retaining the initial sign of each value (Loreau and Hector 2001). To test for differences among the five one-bluegrass-genotype treatments, we conducted two mixed-model repeated-measures analyses (described below), one on Kentucky bluegrass biomass production, estimated 11 times, and one on dandelion leaf area or biomass, estimated 6 times. To facilitate interpretation and graphical display of the repeated measures analyses, and also to allow dandelion leaf area and biomass measurements (both estimates of total plant size) to be used in the same analysis, we first converted these square-root transformed data to standardized mean differences (i.e. z-scores using the estimated mean and SD) across all plots within time periods (raw data are available in Table S2). We used total aboveground plus belowground biomass as the final measurement, which gave essentially the same results as either above- or below-ground biomass alone (results not shown). For the repeated-measures analyses, we employed restricted maximum likelihood using Proc Mixed in SAS version 9.1 (SAS Institute, Cary, N.C.), with genotype, time, and genotype × time as fixed effects. The spatial-power variance–covariance

structure was chosen for both analyses as the best descriptor of the observed variance–covariance matrix, and for the bluegrass biomass analysis plot was included as a random effect to account for high variability among replicates within treatments. Standard one-way ANOVAs were conducted on each individual size variable for both Kentucky bluegrass and dandelions, on total dandelion seed-head production, and on the availability of each soil nutrient.

Since we did not have precise data on the genotypic composition of the five-bluegrass-genotype plots (allozyme analyses failed to distinguish different genotypes), we assessed this indirectly by calculating correlations of biomass z-scores in different windows of time between the mixture treatment mean and each single-genotype treatment mean. If the pattern of temporal variation in biomass production in mixtures mirrors the pattern found for a particular genotypic monoculture, this provides indirect, qualitative evidence that the mixtures contained a high abundance of that genotype. We conducted two analyses of this type. First, correlations were calculated from the first time point to all possible end points with a minimum of four time points included (i.e. time periods 1–4, 1–5,…, 1–11). Second, correlations were calculated from all possible start points up to the final time period, again with a minimum of four time points included (i.e. time periods 1–11, 2–11,…, 8–11).

Experiment II–consequences of genetic diversity in dandelions

Each of 38 raised beds was sown in June 2006 with the same five-genotype mix of Kentucky bluegrass seeds as described for experiment I. Productivity of Kentucky bluegrass was estimated on approximately the same schedule as experiment I. Dandelion seedlings were planted concurrently with experiment I in spring 2007, using identical methods. The dandelion population in each plot comprised either 12 individuals of the same genotype, or two individuals of the genotypes 2, 9, 24 and 64 plus four individuals of genotype 16, with treatments randomized across plots. Eight plots received the five-dandelion-genotype mixture, and the position of genotypes within the 4 × 3 grid was randomized in each plot. The remaining 30 plots were planted with dandelion genotype monocultures, with five plots per genotype (ten plots of genotype 16). Dandelion size and seed production were assessed as in experiment I.

Between November 2007 and March 2008 all but a few of the dandelions were destroyed in 16 of the 38 plots, more or less evenly spread across treatments. The cause was not determined, but root herbivory by insects or small mammals and possible removal of weakened plants by crows was suspected. Thus, we terminated the experiments in

spring 2008, and analyses of final measurements were restricted to the 22 remaining plots.
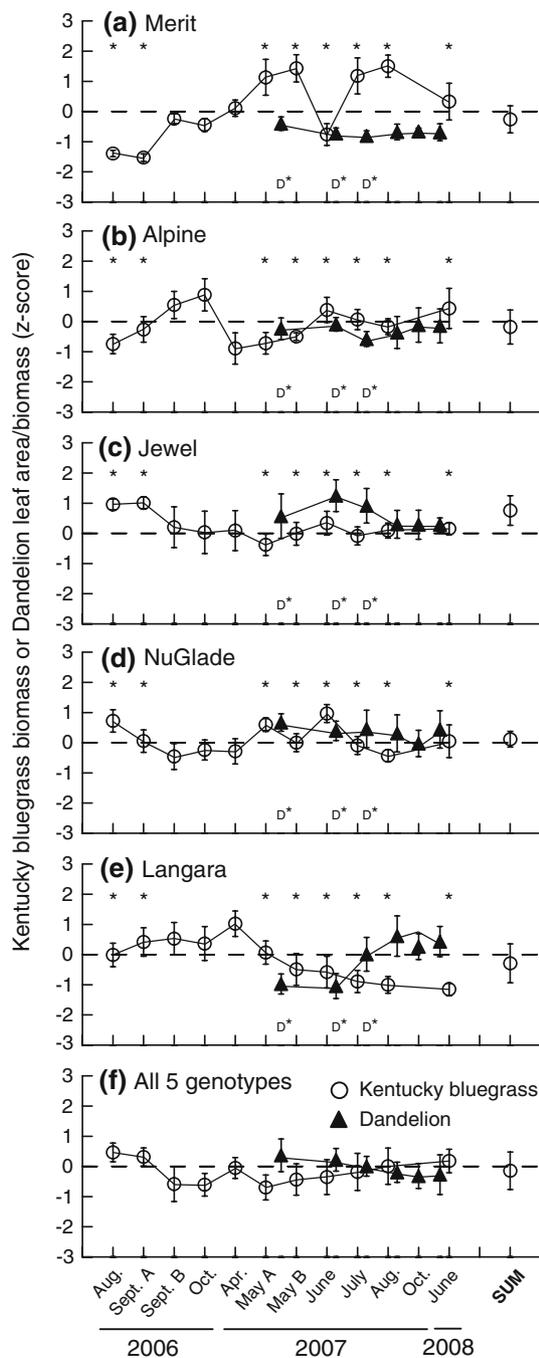
For variables characterizing plot-level dandelion leaf area, biomass, and seed head production, we tested for a significant deviation of five-genotype plots from the expectation based on the one-genotype plots as described above. When we had data for individual plants in each mixture plot, we also calculated the additive components of ΔY using the methods of Loreau and Hector (2001), which quantifies effects of complementarity and selection. Our inability to collect seed head data at the individual level in spring 2008 prevented us from decomposing ΔY for seed head production, or from calculating seed production in the five-genotype plots.

To test for differences in productivity among dandelion genotypes grown in monoculture, we first conducted a mixed-model repeated-measures analysis on z-scores of the size measurements taken at 6 times, as described for experiment I but with an ante-dependence variance–covariance structure (raw data are available in Table S3). We then conducted separate one-way ANOVAs on each dandelion size measurement separately, and also the total number of seed heads, and the estimated total number of seeds produced. We used the summed biomass of Kentucky bluegrass in May–June 2007 (shortly after planting dandelions) as a covariate in the one-way analyses, as it was found to be negatively related to many variables, presumably due to negative effects of bluegrass growth on dandelions during their initial establishment and growth.

Results

Experiment I—Kentucky bluegrass

Productivity of the five-genotype mixtures of Kentucky bluegrass did not differ significantly ($P > 0.05$) from the mean productivity across monocultures for either the cumulative sum, or at any of the individual time periods (Fig. 1; t-tests for ΔY shown in Table S4). Bluegrass genotypes in monoculture varied significantly in productivity during most time periods (Table 1), and in the temporal pattern of productivity (significant time × genotype interaction; Fig. 1; Table 1), but not in cumulative productivity over the 2 years (Table 1). Each bluegrass genotype was the top biomass producer in at least one time period (Fig. 1). The five-bluegrass-genotype plots also did not differ significantly from the mean across monocultures for dandelion total leaf area, biomass, or seed-head production (Table S4). Kentucky bluegrass genotypes initially showed significant differences in their resistance to dandelion invasion, in terms of dandelion plant size and seed production, but these

Fig. 1 z-scores for productivity and growth of Kentucky bluegrass and dandelions in monoculture plots of five different Kentucky bluegrass genotypes (**a**–**e**) and plots with mixtures of all five genotypes (**f**). All data points for Kentucky bluegrass (*open circles*) represent biomass harvested at >5.1 cm at a given time. Dandelion data points (*filled triangles*) represent estimated total leaf area summed across all plants, except in September 2007 (point between August and October, which represents aboveground biomass) and in May 2008 (point just before June, which represents total biomass). Data points represent means ± 1 SE. *Asterisks* indicate significant differences ($P < 0.05$) among genotypes for Kentucky bluegrass biomass. *D** significant differences among bluegrass genotypes for dandelion size or biomass at particular time periods

Table 1 Results of ANOVA and repeated-measures ANOVAs on variables measured in diversity experiment I on Kentucky bluegrass

Variable	Transformation	Effect	F	P	df
Kentucky bluegrass					
Biomass, August 2006	Sqrt	Genotype	16.21	**<0.0001**	4, 20
Biomass, September 2006a	Sqrt	Genotype	10.22	**0.0001**	4, 20
Biomass, September 2006b	Sqrt	Genotype	1.11	0.3788	4, 20
Biomass, October 2006	Sqrt	Genotype	1.34	0.2886	4, 20
Biomass, April 2007	Sqrt	Genotype	2.72	0.0585	4, 20
Biomass, May 2007a	Sqrt	Genotype	4.34	**0.0109**	4, 20
Biomass, May 2007b	Sqrt	Genotype	5.10	**0.0053**	4, 20
Biomass, June 2007	Sqrt	Genotype	4.14	**0.0133**	4, 20
Biomass, July 2007	Sqrt	Genotype	4.69	**0.0078**	4, 20
Biomass, August 2007	Sqrt	Genotype	14.22	**<0.0001**	4, 20
Biomass, June 2008	Sqrt	Genotype	3.04	**0.0412**	4, 20
Biomass, Sum	Sqrt	Genotype	0.98	0.4403	4, 20
Biomass (repeated measures)	z-score of sqrts	Genotype	0.70	0.6022	4, 20
		Time	0.31	0.9785	10, 160
		Time × Genotype	5.26	**<0.0001**	40, 167
Dandelions					
Leaf area, May 2007	Sqrt	Genotype	3.58	**0.0235**	4, 20
Leaf area, June 2007	Sqrt	Genotype	8.81	**0.0003**	4, 20
Leaf area, July 2007	Sqrt	Genotype	3.11	**0.0384**	4, 20
Aboveground biomass, September 2007	Sqrt	Genotype	1.41	0.2682	4, 20
Leaf area, October 2007	Sqrt	Genotype	1.57	0.2200	4, 20
Total biomass, May 2008	Sqrt	Genotype	1.30	0.3052	4, 19
Seed head production	Sqrt	Genotype	2.00	0.1349	4, 19
Leaf area/biomass (repeated measures)	z-score of sqrts	Genotype	2.78	**0.0468**	4, 27
		Time	0.15	0.9796	5, 96
		Time × Genotype	2.48	**0.0018**	20, 96
Soil nutrients					
NH_4^+–N	Sqrt	Genotype	0.61	0.6618	4, 20
NO_3^-–N	Sqrt	Genotype	0.48	0.7513	4, 20
Sum N	Sqrt	Genotype	0.56	0.6918	4, 20
P	Sqrt	Genotype	0.26	0.9012	4, 20
K	Sqrt	Genotype	0.57	0.6877	4, 20

Sqrt Square root

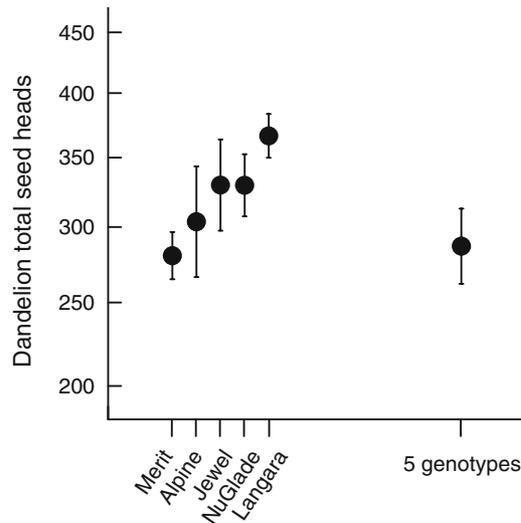Significant tests ($P < 0.05$) are indicated in *bold*

differences dissipated later on (Table 1; Fig. 1), such that there were no significant differences among bluegrass genotypes either in final dandelion biomass or total seed head production (Fig. 2). Temporal change in the dandelion populations varied significantly among Kentucky bluegrass genotypes (significant time × genotype interaction; Fig. 1; Table 1). Nutrient availability in mixture plots did not differ from the mean across monocultures (see Table S4), nor were there significant differences among bluegrass genotypes for any of the nutrients measured (Table 1).

The two most productive bluegrass genotypes early on, Jewel and NuGlade, had temporal patterns of productivity that showed the strongest correlations with the early temporal pattern of productivity in the five-genotype plots (Fig. 3a). The strength of these correlations diminished over time, and during the final four to five measurement periods the five-genotype plots showed temporal patterns of productivity most correlated with those in the Alpine and Merit plots (Fig. 3b), which by that time were the most productive and resistant to dandelion invasion (Fig. 1).

Diversity experiment II—dandelions

Neither the raw differences between dandelion genotype mixtures and the null expectation based on monoculture plots (ΔY), nor the complementarity or selection components

Fig. 2 Total dandelion seed head production (mean ± 1 SE) in five Kentucky bluegrass genotype monocultures and mixture. There were no significant differences among bluegrass genotypes

of these differences (which can potentially cancel each other out in ΔY), were significantly different from zero (Figs. 4, 5; statistics in Table S5). However, dandelion plant size and seed head production in five-genotype plots were consistently greater than those of the two poorest performing genotypes (64 and 24), and not statistically different from those of the three best performing genotypes (16, 2, and 9; Figs. 4, 5a).
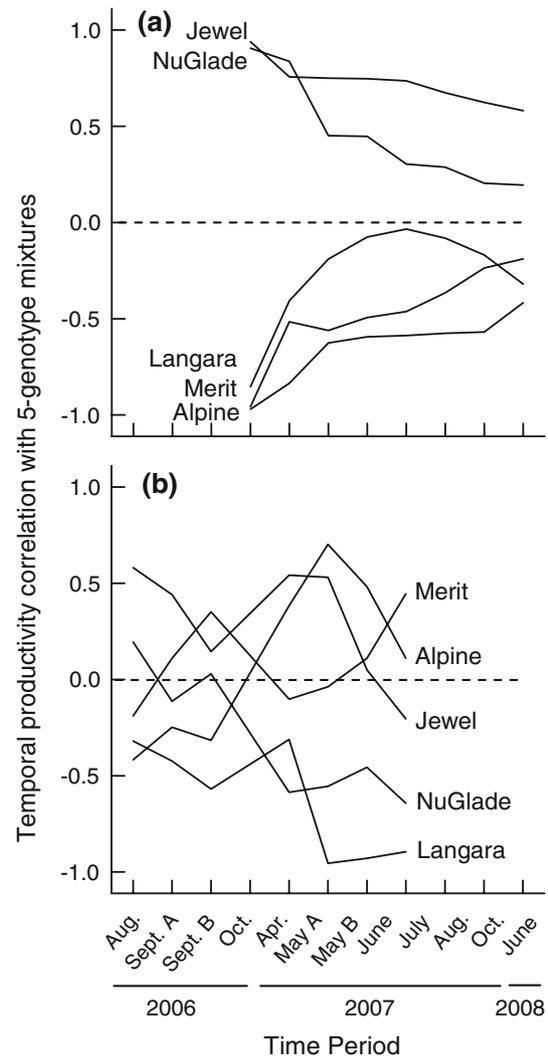
Dandelion monocultures varied markedly among genotypes for all measures of size and reproductive output (Figs. 4, 5). Size differences were established early on, and largely maintained and magnified during the course of the experiment (Fig. 4; Table 2). Total seed head production corresponded closely with plant size across genotypes (Fig. 5).

Discussion

Both experiments revealed significant and large variation among genotypes for virtually all measurements, but no statistically significant deviation of mixtures from expectations based on the monocultures. Genotypic identity was far more important than genotypic diversity, and there were some intriguing temporal trends and differences between Kentucky bluegrass and dandelions with respect to the consequences of genetic diversity.
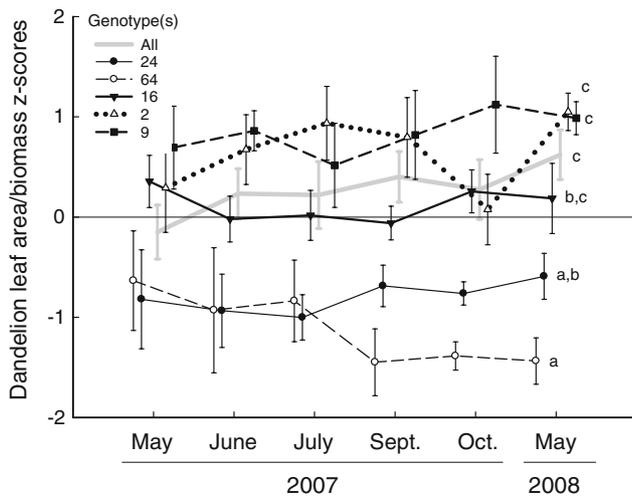
Genetic diversity in Kentucky bluegrass

Kentucky bluegrass genotype identity had a substantial influence on the temporal pattern of productivity, and the resistance to early invasion by dandelions. The number of

Fig. 3 Correlations between productivity *z*-scores in Kentucky bluegrass mixtures over time, with each of the bluegrass genotypes in monoculture. **a** Correlations using same start point and different end points. **b** Correlations calculated using different starting time points continuing until the end of the experiment
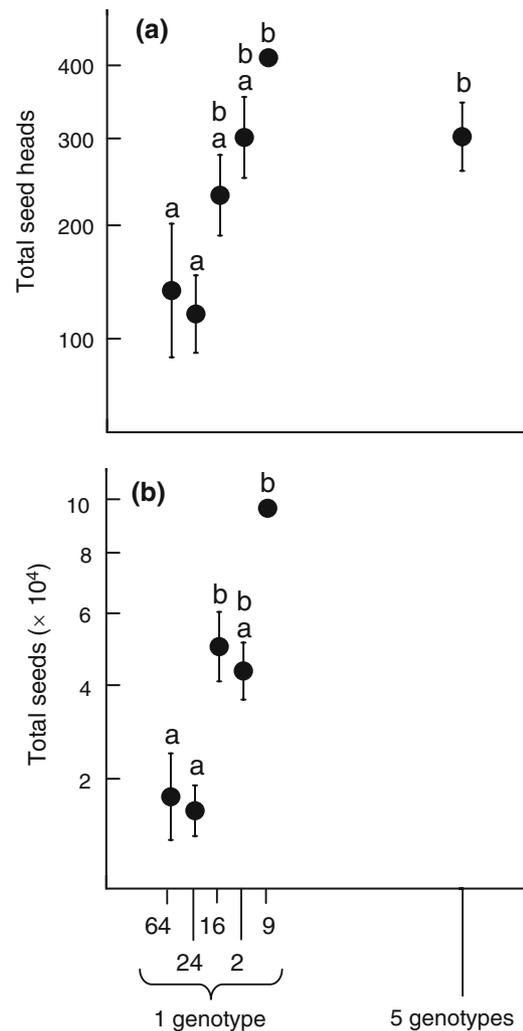
genotypes per se made little if any difference. This is in contrast to recent studies with the seagrass, *Zostera marina* (Hughes and Stachowicz 2004; Reusch et al. 2005) and goldenrod, *Solidago altissima* (Crutsinger et al. 2006), in which the productivity of mixtures exceeded the mean across monocultures. However, in the two seagrass studies the differences were only observed after severe herbivory (Hughes and Stachowicz 2004) or heat stress (Reusch et al. 2005), suggesting that diversity effects may be revealed largely following disturbance or stress, or are at least environment dependent. In the case of goldenrod, the more productive mixtures also suppressed invasion by other species (Crutsinger et al. 2008), while in contrast, Weltzin et al. (2003) found no effect of the number of *Arabidopsis thaliana* genotypes on invasion success of *Arabidopsis suecica* in a greenhouse. Crop trials with intraspecific

Fig. 4 Total leaf area or biomass *z*-scores of dandelion genotype monocultures or mixtures measured over time. Data were square-root transformed prior to calculating *z*-scores. Each data point represents the mean ± 1 SE. Data points represent estimated total leaf area summed across all plants, except in September 2007 (aboveground biomass) and in May 2008 (total biomass). *Different letters* indicate significant differences (*P* < 0.05, Tukey–Kramer test) for the final measurement. Data points within time periods are offset slightly for ease of presentation

monocultures versus mixtures give highly variable results, with mixtures outyielding monocultures in some but certainly not all cases (Smithson and Lenné 1996). Overall, the effects of genotypic diversity on productivity and invasion resistance appear highly variable across systems, while a far more general result appears to be that genotypic identity is a strong determinant of population performance.

Significant variation among bluegrass genotypes in their suppression of dandelions occurred during the first few months following dandelion invasion, with differences dissipating later on (Table 1). A likely explanation involves vertical rooting zonation: Kentucky bluegrass roots are concentrated in the upper 10–15 cm of soil (Reader et al. 1993; personal observation), while mature dandelion taproots can extend to at least 40 cm (personal observation). Upon initial invasion, dandelion roots occupy the same vertical zone as Kentucky bluegrass roots, such that any differences among Kentucky bluegrass genotypes with respect to belowground suppression of dandelions should be expressed at this time. Once dandelion roots extend beyond those of Kentucky bluegrass, dandelion performance should become increasingly independent of the grass matrix. Although we did not find any evidence that bluegrass genotypes had drawn down the availability of key soil nutrients to different degrees (Table 1), the most productive genotype during the period of dandelion presence (Merit) was also the most resistant to invasion (Fig. 1a), and the least productive genotype during this time period (Langara) was the least resistant (Fig. 1e). In addition, there

Fig. 5 Reproductive performance of dandelion genotype monocultures (*1 genotype*) and mixtures (*5 genotypes*). **a** Total seed heads; **b** total number of seeds produced. Data points represent means ± 1 SE. *Different letters* indicate significant differences (*P* < 0.05, Tukey–Kramer test)

was a perfect, positive rank-order correlation across genotype means for P availability and dandelion leaf area at the time when dandelion performance varied most among bluegrass genotypes (June 2007, same time as soil sampling; data not shown). This is at least suggestive of possible belowground competition. The presence of bluegrass genotype differences in resistance to dandelion invasion early but not later in the experiment also suggests that these effects may have been magnified, and possibly longer lasting, had we planted seeds rather than seedlings. (Dandelion seedlings were used to ensure a known genotypic identity of each plant, with no way to distinguish experimental from volunteer germinants in the field.)

Productivity and invasion resistance of Kentucky bluegrass genotype mixtures showed no tendency to deviate from monoculture averages, and were just as likely to be

Table 2 Results of ANOVA and repeated-measures ANOVAs on variables measured in diversity experiment II on dandelions

Variable	Transformation	Effect	F	p	df
Leaf area, May 2007	Sqrt	Genotype	2.53	0.0668	4, 24
Leaf area, June 2007	Sqrt	Genotype	7.80	**0.0004**	4, 24
Leaf area, July 2007	Sqrt	Genotype	5.54	**0.0026**	4, 24
Aboveground biomass, September 2007	Sqrt	Genotype	9.41	**0.0001**	4, 24
Leaf area, October 2007	Sqrt	Genotype	9.55	**<0.0001**	4, 24
Total biomass, May 2008	Sqrt	Genotype	12.40	**0.0005**	4, 11
Seed head production	Sqrt	Genotype	6.07	**0.0079**	4, 11
Seed production	Sqrt	Genotype	16.47	**0.0001**	4, 11
Leaf area/biomass (repeated measures)	z-score of sqrts	Genotype	8.49	**0.0002**	4, 26
		Time	0.12	0.9727	4, 40
		Time × genotype	2.51	**0.0053**	16, 59

Kentucky bluegrass productivity in May–June 2007 was used as a covariate in all analyses except the repeated-measures ANOVA. Significant tests ($P < 0.05$) are indicated in *bold*

most similar to the most productive or least productive monocultures (or somewhere in between) at a given time (Fig. 1). The similarity of temporal patterns between bluegrass mixtures and different monocultures (Fig. 3) indicated that mixtures were likely dominated initially by genotypes that were most productive early in the experiment (Jewel and NuGlade), as one would expect. However, these initially productive bluegrass genotypes were not the most productive or resistant to dandelion invasion in the longer term (Fig. 1). Indeed, the indirect evidence (Fig. 3) suggests a shift in the genotypic composition of mixtures later in the experiment, possibly due to the substantial temporal changes in which genotypes were most productive (Fig. 1). However, despite the potential for bluegrass genotype mixtures to respond to temporally variable selection, the results show that any such responses (if present) did not lead to high productivity or invasion resistance (Fig. 1), nor to reduced temporal variance in productivity ($P > 0.15$ for ANOVAs comparing mixtures versus monocultures for either the SD or coefficient of variation over time of raw biomass or biomass z-scores). We can speculate that the relatively slow rate of ramet turnover in dense vegetation (most ramets live for a year or more; Tamm et al. 2002) constrained the rate at which bluegrass mixtures could respond to selection. This is in marked contrast to systems with very rapid turnover of individuals, such as aquatic invertebrates or microbes, in which genotype compositional changes can keep pace with rapidly changing selection pressures (e.g. Yoshida et al. 2007). This interpretation is speculative, but sufficiently intriguing to warrant further experimentation.

Finally, the fact that we used seeds of bluegrass cultivars purchased directly from suppliers has two consequences worth noting. First, it is possible that some differences among Kentucky bluegrass genotypes were attributable to maternal effects. This seems plausible for early establishment and growth, but less so for later differences, so we doubt that our results are due entirely to non-genetic variation, although we can not rule out some contribution. Second, we cannot draw inferences about the natural Kentucky bluegrass populations. Rather, our results can be considered as coming from a model system in which we have addressed the fundamental issue of how genetic diversity can have ecological consequences, and also as practically relevant to the many managed habitats where grass seed mixtures are created in much the same way as was done here (including the potential manifestation of maternal effects).

Genetic diversity in dandelions

Dandelion genotypes showed striking differences in size and reproductive traits, with the relative size of individual plants consistent between the experiments reported here and in a separate common garden experiment (Vellend et al. 2009). Genotypes 64 and 24 were always relatively small, and genotypes 16, 2 and 9 always relatively large. Unlike bluegrass, the relative differences among dandelion genotypes were consistent over time. However, the performance of dandelion genotype mixtures did not deviate significantly from the expectation based on monocultures. On one hand, this may not be unexpected. Although dandelions can grow at high densities where strong intraspecific competition would be expected, individual plants are often found with no conspecifics as immediate neighbours. As such, in contrast to habitat-forming species such as seagrasses or goldenrods, which typically grow in dense stands, past selection for dandelion genotypes that interact in complementary ways may have been weak or non-existent.

However, with upwards of tenfold variation among genotypes in productivity and fitness as individual plants (Vellend et al. 2009) or as monoculture populations (Fig. 5b), we expected to find enhanced productivity via selection effects in dandelion mixtures.

Two lines of evidence suggest the possibility that such selection effects may be manifested over the long term. First, the difference between final dandelion mixture biomass and the null expectation (albeit not statistically significant) was 28%—similar to that in comparable studies. For seagrasses, Hughes and Stachowicz (2004) found a 35% increase in shoot density in eight-genotype mixtures compared to monocultures, and Reusch et al. (2005) found 26 and 34% increases in biomass and shoot density, respectively, in six-genotype mixtures relative to monocultures. In a study of goldenrod, six-genotype and 12-genotype mixtures produced 26% and 36% more biomass, respectively, than monocultures (Crutsinger et al. 2006). Our replication of the high genotypic richness treatment ($n = 8$) was comparable to that in other studies ($n = 9$, 12, and 7 in the three studies above), suggesting that high, unexplained within-treatment variance may have limited our power to detect a difference. Second, the size and reproductive output of dandelions in mixtures were consistently greater than those of the poorest performing monocultures, and statistically indistinguishable from those of the most productive monocultures (Figs. 4, 5), also consistent with comparable studies on genetic diversity (Hughes and Stachowicz 2004; Reusch et al. 2005; Crutsinger et al. 2006), and species diversity (Cardinale et al. 2006, 2007). With evidence to suggest that germination and establishment differences among genotypes would magnify rather than equalize fitness variation (Vellend et al. 2009; E. Drummond, unpublished data), it is possible that longer term dynamics would lead to increasing dominance of mixtures by genotypes 16, 2 and 9, and ultimately greater productivity than monocultures.

In sum, just as effects on ecosystem properties with declines in species diversity depend greatly on which species are lost (Srivastava and Vellend 2005), our results emphasize that the ecological consequences of losing genetic diversity should likewise depend greatly on which genotypes are lost. For dandelions, losing genotypes 64 or 24 would make little difference, but it would make a big difference if these were the only two genotypes remaining in a population. Both of our experiments showed that genotype identity had tremendous population-level consequences, while the number of genotypes per se had little if any effect, although for dandelions it seems possible that selection effects in the long term may confer an advantage to genotype mixtures.

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