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Ecological Differentiation among Genotypes of Dandelions (*Taraxacum officinale*)

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We tested for ecological differences among apomictic dandelion genotypes in Vancouver, British Columbia, Canada, in order to establish a basis for predicting potential ecological consequences of genetic variation in invading populations. A greenhouse experiment on 30 potential clonal families revealed significant among-family variation for leaf morphological traits, and molecular analyses confirmed the presence of multiple genotypes. In a field common-garden experiment on six confirmed genotypes, plant size and seed production both varied over an order of magnitude among genotypes, suggesting great potential for selection among genotypes during invasion. Genotypes also varied significantly in the timing of reproduction, which may indicate differences in the timing of resource use that could promote population performance of genotype mixtures. There was no evidence of a trade-off between adult plant fitness and seed dispersal or regeneration traits. Genetic variation in dandelion populations appears to have great potential for influencing their invasive success.
Nomenclature: Dandelion, *Taraxacum officinale* Weber in Wiggers.
Key words: Exotic species, fitness, genetic variation, genetic diversity, plant invasion, seed production.

Ecological models typically make the implicit assumption that individuals within a species are genetically identical (Hughes et al. 2008; Vellend 2006). Although this may be a reasonable simplifying assumption in many cases, there is growing evidence that genetic variation within species can have important ecological consequences beyond the obvious requirement for genetic variation in adaptive evolution (Hughes et al. 2008). For example, the structure and diversity of insect communities can depend in large part on the genetic variation in their host plants (Johnson et al. 2006), and the outcome of competition between plant species can hinge on which genotypes are represented within each species (Fridley et al. 2007; Vavrek 1998). The degree to which genetic variation will have important ecological consequences depends to a large degree on which particular traits are genetically variable, and the magnitude of this variation (Hughes et al. 2008).

Exotic weeds have been the focus of many studies of genetic variation, particularly with respect to population bottlenecks during the process of introduction to a new continent (Novak and Mack 2005) and identification of original source populations (Nissen et al. 1995). Somewhat less attention has been paid to the consequences of genetic variation in ecologically important traits within plant species for their invasion success in particular localities (Dlugosch and Parker 2007). In one example, genetic variation in reed canarygrass (*Phalaris arundinacea* L.) in North America appears to have been elevated by interbreeding among individuals from multiple source populations in Europe as well as native North American populations, and this genetic variation has permitted adaptation via increased colonization success and phenotypic plasticity (Lavergne and Molofsky 2007). Other studies have demonstrated adaptation of exotic species to the novel conditions of their introduced range, such as a paucity of natural enemies, or different climatic conditions (Dlugosch and Parker 2007; Vellend et al. 2007). As such, the particular genotypes that invade a site may be an important determinant of the dynamics of local weed invasion.

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In this study, we tested for differentiation among genotypes of a widespread exotic weed, the dandelion, in the Vancouver area of British Columbia, Canada. Our goals were (1) to test for the presence of genetic variation in ecologically relevant traits, such as fitness and the timing of reproduction; and (2) to assess potential trade-offs among genotypes between adult-plant fitness and regeneration traits, such as seed-dispersal potential and germinability. As part of a broader long-term research program, the motivation behind our first goal was to establish a basis for making predictions concerning possible mechanisms by which genetically diverse dandelion populations might behave differently than genetically depauperate populations. Two types of traits were of particular interest in this context. First, large differences among genotypes in productivity or fitness traits suggest possible selection effects (Loreau and Hector 2001), such that genetically diverse populations may have increased productivity or fitness via the increased probability of containing highly productive genotypes. Second, traits that are indicative of differences in resource-use strategies suggest possible niche differentiation and consequently the potential for complementarity (Loreau and Hector 2001) among genotypes. Based on a previous study with dandelions (Vavrek et al. 1996), we focused here on flowering phenology differences as indicative of possible differences in the timing of resource use.

Materials and Methods

Study System. Dandelions are notorious weeds of lawns and agricultural fields in North America, with growth of one or more rosettes of leaves from a taproot, and highly dispersive wind-blown seeds (Stewart-Wade et al. 2002). In their native Europe, dandelions occur both as diploid and asexual triploid individuals, but only the obligately apomictic triploids have been found in North America (Lyman and Ellstrand 1984). Several studies from other regions have demonstrated that apomictic dandelion populations are often comprised of multiple genotypes (Lyman and Ellstrand 1984; Solbrig and Simpson 1974; Vavrek 1998), and genotypes have been shown to vary in a number of traits, including the timing of flower production, competitive ability, and tolerance of disturbance (Ford 1981; Solbrig and Simpson 1974; Vavrek 1998; Vavrek et al. 1996, 1997). We conducted several

experiments to test for the presence of different genotypes locally, and ecological differentiation among them.

Dandelion Genotype Selection and Pilot Experiment. Our goal in field collection of dandelion seeds and an initial greenhouse experiment was ultimately to identify at least five distinct genotypes representing a range of genetic characteristics present in our local area for further study, and to generate seeds for these experiments from plants grown in a common environment. During summer 2005 we collected single, ripe seed heads from 30 dandelion plants in the Vancouver area. We refer to these collections as clonal families; only after demonstrating molecular–genetic differences (see below) do we refer to genotypes. Plants were selected haphazardly from as wide a variety of habitats and areas of the city as possible, with a concentration of samples within ~5 km of the University of British Columbia (UBC) campus. Habitats included mown lawns with varying degrees of irrigation and shade, lawn–fence edges where mowing appeared to be infrequent or absent, sidewalk cracks, fallow fields, bare soil in landscaped areas, and gardens. The sampling area furthest from the UBC campus was 20 km away, in Ladner, BC.

In the initial pilot experiment, we planted 5–10 seeds of each of the 30 clonal families in each of eight 15-cm-diam pots in the UBC Horticulture Greenhouse on October 27, 2005. Half the pots were filled with a sterilized sandy loam collected from the field at UBC campus farm, and the other half with a bedding plant potting mix[1] (75% peat, 25% perlite, with a "starter charge" of N–P–K and Fe plus granular micronutrients). Two soil types were used only to test whether potting soil would be adequate for growth of dandelions in the greenhouse for production of seeds to use in future field experiments. Pots were randomly distributed on a flood bench,[2] with dilute fertilizer application twice per week (N–P–K 15–5–15, ~100 ppm). Random pot positions were shuffled once per month, and seedlings were thinned to one.

Following Vavrek et al. (1997), we measured several leaf traits to assess morphological differences among clonal families that may be indicative of different genotypes, and potentially of variation in ecologically important traits in the field. We collected the two largest leaves from each plant on January 26, 2006, and on each flattened leaf we measured the following: length, width at the midpoint between the base and tip, the length of the longest lobe or tooth, and total area (with the use of a LI-COR LI-3100C leaf area meter[3]). We collected four small hole-punch leaf discs from the upper portion of the leaf lamina for assessment of specific leaf area (SLA: leaf area per dry mass). For each variable, each plant was characterized by the mean across the two leaves. We also collected leaf samples from each plant for molecular–genetic analysis, as well as seeds from surviving plants for subsequent field experiments. Flowering began in March 2007, and continued until the experiment was terminated in July.

Sixty-eight of the original 240 plants were lost because of greenhouse pests (white flies and aphids). For 16 clonal families with at least three replicate plants surviving in each soil type, we tested for variation in each variable among clonal families with the use of general linear models (PROC GLM, SAS version 9.1[4]), with soil type as a fixed factor and clonal family as a random factor. We characterized multivariate variation among clonal families with the use of principal-component analysis (PCA). Leaf area correlated strongly ($r > 0.75$) with all variables except lobe size ($r = 0.48$) and SLA ($r = -0.04$); the weakest remaining correlation for leaf area was with the midpoint width ($r = 0.78$). As such, we conducted the PCA on clonal-family means for four variables: leaf area, midpoint width, lobe size, and SLA. This analysis included 165 plants of 25 clonal families with at least three surviving plants (regardless of soil type).

Microsatellite DNA Genotyping. We used microsatellite DNA markers developed for *Taraxacum* (Falque et al. 1998; Vašut et al. 2004) with the hope of identifying distinct genotypes representing the range of multivariate space defined by PCA axes 1 and 2 from the greenhouse experiment. Because of the apomictic reproductive system in dandelions, some (possibly many) of our "clonal families" may have in fact been genetically identical. Because the common-garden experiment (see below) was aimed at assessing *genetic* variation in the field, it was essential to use clonal families that were genetically distinct (i.e., "genotypes").

DNA was extracted from three to four plants of each of the 25 clonal families in the PCA, with the use of a modification of the CTAB protocol of Doyle and Doyle (1990) to include RNAse A and Proteinase K incubations. PCR was attempted on the following microsatellite loci: msta53, msta85, and msta60 from Falque et al. (1998), and msta143, msta101, and msta105 from Vašut et al. (2004). Because of difficulties with amplification of DNA from some plants, we ultimately took a strategic, stepwise approach, in which genotyping efforts continued until we had identified seven putative genotypes covering the range of multivariate space in the PCA. We focused on loci msta53, msta85, and msta143, for which PCR was most successful. We used IRDye labeled primers from LI-COR[5], and 10-μl amplification reactions: 5.65 μl double-distilled H_2O, 1 μl 10× buffer, 0.3 μl $MgCl_2$ (50 mM), 0.2 μl deoxyribonucleotide triphosphate (10 mM), 1.5 μl forward primer (1 μM), 0.15 μl reverse primer (10 μM), 0.2 μl Taq DNA polymerase (5 U μl^{-1}), and 1 μl template DNA (0.3 ng μl^{-1}) Genotyping was carried out on a LI-COR 4300.[6]

After subsequent experiments were already underway we discovered a gel interpretation error, such that two clonal families initially classified as genetically different in fact had identical multilocus microsatellite genotypes. These two clonal families occupied dissimilar positions on axis 2 of the PCA, although this axis was mainly defined by SLA, which did not vary significantly among clonal families (see Results). The lack of statistical differences for morphological characters between these two clonal families in the field common-garden experiment, and the fact that all confirmed genotypes were highly significantly different for multiple morphological or fitness traits (see Results), confirmed the ability of our microsatellite analysis to distinguish genotypes. In addition, identical multilocus genotypes were confirmed for three to four separate offspring from the same seed head for each genotype.

One of our genotypes (64) had reddish achenes, which some authors classify as a different species [*T. laevigatum* (Willd.) DC.], although genetic evidence indicates that plants with red seeds are part of the same evolutionary lineage, and thus are part of *T. officinale* (King 1993; see also Taylor 1987).

Common-Garden Experiment. The common-garden experiment was aimed as assessing genetic variation among confirmed dandelion genotypes for traits related to fitness in an open-field environment and traits related to regeneration via seed. For this experiment we established dandelion seedlings in a growth chamber starting on October 5, 2006. Seed lots were created for each of the six confirmed genotypes by combining seeds from 30 to 40 seed heads collected in the greenhouse experiment. We planted 5 to 10 seeds of each genotype in 1-in. Rootrainer cells ("fives" style[7]) filled with a commercial lawn mix soil comprised of peat, sand, and subsoil (silt and fines) from Richmond, BC.[8] By dry weight the mix is 10% peat, 70% sand, and 20% subsoil, which corresponds to ~10% sand by volume. A Conviron E15 growth chamber[9] was set to mimic relatively warm autumn conditions in Vancouver: 10 C for 8 h, ramping up to 18 C for about 5 h, followed by 5 h at 18 C, and decreasing back to 10 C to complete a 24-h cycle. Incandescent and fluorescent lights (~600 mmol m^{-2} s^{-1}) were on for 11 h 40 min per day, starting with the initial temperature increase. The soil was thoroughly watered prior to planting, and kept moist with misting during seedling establishment. Seedlings began to emerge 5 d after seed planting, with most cells containing some seedlings after 2 wk. We thinned seedlings to one, and added a light fertilizer application (Miracle Gro Liquid All Purpose Plant Food, N–P–K 12–4–8) three times before moving seedlings outdoors on November 13. Seedlings were allowed to acclimatize over the winter prior to being transplanted into the common garden.

The common garden was established at Totem Field, a 12-hectare field on flat ground on the UBC campus with loamy-sand soil formed from glacial till (Guthrie and Bomke 1980). On 1 May 2007, in a freshly plowed area of Totem Field, we planted 10 seedlings of each genotype in random positions within four rows of plants, with 50 cm between plants and 1 m between rows. Any plants dying during the first 2 wk were replaced, and wood-chip mulch was added around plants to a distance of ~25 cm. Fertilizer (Miracle Gro Liquid All Purpose Plant Food) was applied twice during the first month of establishment, and seedlings were watered during dry periods during summer 2007. We periodically weeded and mowed between rows in the common-garden area. Fifteen plants died during 2007, and were removed from all analyses.

On each plant in this experiment we estimated total leaf area three times, July 16, 2007, May 29, 2008, and June 30, 2008 (there was substantial leaf turnover in early June 2008). Total plant leaf area (LA) was estimated with the use of a parameterized regression model based on the total number of leaves > 4 cm long (N), the length of the longest leaf (L), and the maximum distance from the central leaf vein to a leaf lobe tip (maximum half width, W). The model was $LA = 0.221 \times N \times L \times 2W$ ($r^2 = 0.95$ based on 56 field-collected plants, with total leaf area measured on a LI-COR LI-3100C leaf area meter[3]). We counted and removed all fruiting heads prior to opening and release of seeds, once during July 2007, and every 1 to 3 wk during the main flowering periods of April through May and August through November 2008. Heads were collected after flowers had closed and petals dried and withered, which indicates that head reopening and seed release is imminent (M. Vellend, personal observation).

On a sample of 10 seed heads per genotype collected in September 2008, we counted the number of seeds per head. For five fully ripe seed heads per genotype we measured pappus radius (described below) on five seeds, and weighed a sample of 40 air-dried seeds with the pappus removed. Pappus radius was measured as a key determinant of seed dispersal potential (Sheldon and Burrows 1973) by first scanning seeds at 400 dots per inch, and subsequently tracing and measuring the length of two pappus hairs per seed head with the use of ImageJ.[10] We calculated the mean across the two hairs per seed, and then the mean across the five seeds per seed head as a single data point. We assessed seed germination in all genotypes except 53 (which was not included in subsequent and ongoing field experiments) by placing four replicate petri plates per genotype with 20 seeds on moistened filter paper in a growth chamber set to 16 h in the light at 20 C and 8 h in the darkness at 15 C, conditions that maximize germination of dandelion seeds (Mezynski and Cole 1974). Germination was recorded over 3 wk, with no additional germination occurring for 2 mo after that. Although these measurements were based only on autumn-collected seeds, differences among genotypes were consistent with separate germination and seedling emergence trials of spring-collected seeds (E.B.M. Drummond, unpublished data) and with our qualitative visual observations of seeds per head and pappus dimensions in the spring.

For the three leaf area measurements we tested for genotype differences with the use of a repeated-measures ANOVA. We conducted one-way ANOVAs on each individual leaf-area estimate as well, and on each of the variables described above, as well as two variables characterizing the timing of flowering, which occurred in distinct spring and autumn periods. We analyzed the proportion of 2008 seeds produced in spring (April to May), and the proportion of spring seeds produced in April (the rest were produced in May). Flower numbers were converted to seed numbers with the use of each genotype's mean for seeds per head. Variables were transformed as appropriate to meet statistical assumptions. Because seed-related traits were assessed only on subsets of plants and all size and seed production variables were positively correlated, we did not conduct multivariate analyses across multiple traits simultaneously.

Results and Discussion

Pilot Greenhouse Experiment and Microsatellites. We found significant variation among clonal families for all variables measured, except specific leaf area (Table 1). Leaves were slightly wider on plants grown in field soil than in potting soil (mean 2.3 cm vs. 2.0 cm), but there were no other main effects of soil type, and there was no significant interaction between clonal family and soil type in determining any of the leaf variables (Table 1). In the PCA, axes 1 and 2 accounted for 58.5 and 27.3% of the variance, respectively, with leaf area, midpoint width, and lobe size loading positively on axis 1, and SLA loading positively on axis 2 (Figure 1). This experiment suggested the existence of genetic variation in the dandelions of our region, and allowed us to generate seeds for the field common-garden experiment in which genotype identity was not confounded by the environment where maternal plants were growing. The microsatellite analysis confirmed the presence of multiple genotypes within the initial set of clonal families (Table 2). The position in the PCA of each of the six confirmed genotypes is shown in Figure 1, and their microsatellite genotypes and collection locations are shown in Table 2.

Table 1. Mixed-effects general linear models testing for variation among dandelion clonal families and effects of soil type on leaf measurements made in a greenhouse on three to four plants per soil type in each of 16 clonal families.

Variable	Transformation	Effect	*F*	P	df
Leaf length	None	Family	3.12	0.0174	15,15
		Soil	0.13	0.7190	1,15.025
		Family × soil	1.56	0.1007	15,95
Width at leaf midpoint	None	Family	7.78	0.0001	15,15
		Soil	11.06	0.0046	1,15.038
		Family × soil	1.03	0.4291	15,95
Lobe/tooth length	Log	Family	4.07	0.0050	15,15
		Soil	3.33	0.0878	1,15.038
		Family × soil	1.03	0.4335	15,95
Leaf area (one leaf)	None	Family	2.54	0.0402	15,15
		Soil	4.31	0.0553	1,15.09
		Family × soil	0.81	0.6605	15,94
Specific leaf area	None	Family	1.31	0.3041	15,15
		Soil	0.47	0.5055	1,15.038
		Family × soil	1.04	0.4240	15,95

Common Garden Experiment. *Vegetative Growth and Seed Production*. Dandelion genotypes varied significantly in all of the traits we measured in the field common-garden experiment, except seed mass (Table 3). Whole-plant leaf area varied more than 20-fold across genotypes in May 2008, and differences among genotypes were fairly consistent across time, with the exception of genotype 64, which was initially of average size and later the smallest of the five (Figure 2). As such, the repeated-measures ANOVA for whole-plant leaf area showed a significant interaction between genotype and time ($F = 13.0$, $P < 0.0001$), as well as significant main effects of genotype ($F = 48.9$, $P < 0.0001$) and time ($F = 29.6$, $P < 0.0001$). Seed-head production varied > 5-fold among genotypes, and genotypes producing more seed heads also tended to produce more seeds per head, thus creating > 10-fold variation among genotypes in estimated total seed production (Figure 3). Genotypes with larger plants tended to produce more seeds, although the relationship was not perfect, for example with genotype 16 producing more seeds than genotype 2, despite its smaller size (Figures 2 and 3).

The simple presence of genetic variation in dandelions is not surprising given the widespread occurrence of heritable genetic variation for life-history, functional, and morphological traits across a wide variety of plants (Geber and Griffen 2003), including dandelions (Ford 1981; Solbrig and Simpson 1974; Vavrek 1998; Vavrek et al. 1996, 1997). However, the magnitude of fitness variation among genotypes in the field experiment was striking, especially given the relatively subtle differences observed among genotypes in the greenhouse, and comparatively modest variation in fitness among dandelion genotypes observed in other regions (Solbrig and Simpson 1974; Vavrek et al. 1996).

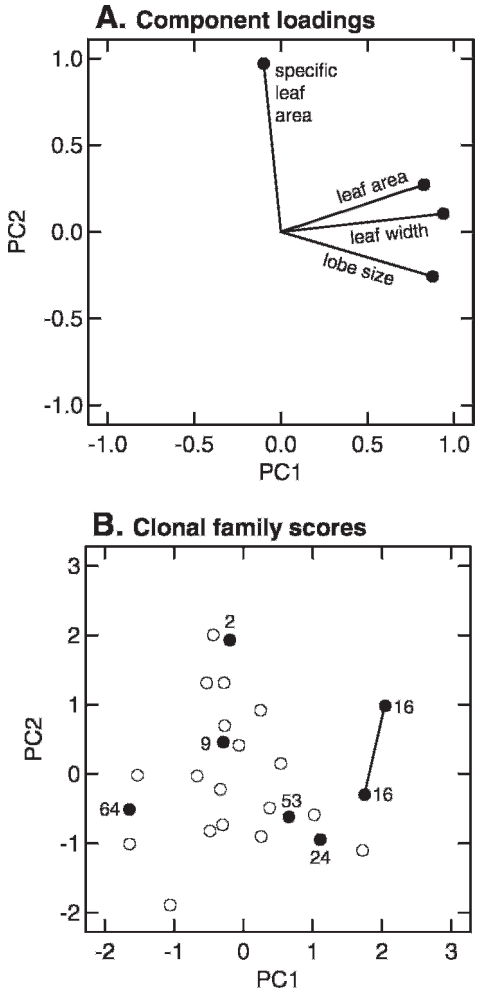

Figure 1. Component loadings and clonal family scores from a principal-components analysis of dandelion clonal family means for four traits measured in a greenhouse: leaf area of a single leaf, the width at the midpoint of the leaf (leaf width), the length of the longest tooth or lobe (lobe size), and specific leaf area (SLA). Clonal families represented by filled circles were confirmed as distinct genotypes with microsatellite DNA markers; the two families connected by the line represent the same multilocus genotype.

With respect to the potential consequences of genotype identity and genotypic diversity for local dandelion populations, our results indicate that if the initial pool of genotypes in an invading population is limited, plant fitness, and therefore quite likely the dynamics of invasion, should be strongly influenced by which genotypes are present. The results also provide a basis for predicting possible consequences of genetic diversity per se (Hughes et al. 2008; Smithson and Lenne 1996) in populations of competing

Table 2. Microsatellite alleles and location of seed-head collection for six dandelion genotypes in the Vancouver area of British Columbia, Canada. Locus names and primer sequences are from Falque et al. (1998) and Vašut et al. (2004). *N* is the number of individuals genotyped. Totem Field is the field site on the University of British Columbia campus where experiments were conducted.

	Locus: msta53		Locus: msta85		Locus: msta143		
Genotype	Alleles (bp)	*N*	Alleles (bp)	*N*	Alleles (bp)	*N*	Habitat and location of seed-head collection
2	204, 208	3	182, 190	3	222, 236, 238	4	Fence–lawn edge in Chaldecott Park, Vancouver (49°14′59″N, 123°11′36″W)
9	200, 204	4	182	4	236, 238, 242	4	Lawn adjacent to Spanish Banks beach, Vancouver (49°16′43″N, 123°14′4″W)
16	204, 208	3	178, 182	3	232, 234	4	Disturbed soil with tomato plants, Totem Field (49°15′24″N, 123°15′0″W)
24	208, 228	3	184, 186	3	234, 238, 242	4	Disturbed soil under isolated alder tree, Totem Field (49°15′21″N, 123°15′2″W)
53	200, 204, 212	3	182	4	238, 240, 246	3	Lawn–garden edge, Quilchena Park, Vancouver (49°14′36″N, 123°8′51″W)
64	202, 204	3	174, 182, 186	3	232, 234	3	Roadside vegetation, Ladner (49°6′14″N, 123°4′45″W)

Table 3. One-way ANOVAs for variables measured on dandelion plants or seeds from the common garden experiment.

Variable	Transformation	*F*	df	P
Leaf area, July 2007	Log	10.8	5,49	< 0.0001
Leaf area, May 2008	Log	34.2	5,49	< 0.0001
Leaf area, June 2008	Log	40.1	5,49	< 0.0001
Total seed-head production	Square root	25.7	5,49	< 0.0001
Seeds per head	None	56.6	5,54	< 0.0001
Total seed production	Square root	50.6	5,49	< 0.0001
Seed mass	None	2.2	5,24	0.092
Pappus radius	None	2.9	5,24	0.036
Seed germination	Arcsin–square root	35.6	4,15	< 0.0001
Prop. 2008 seeds spring[a]	Arcsin–square root	13.3	5,49	< 0.0001
Prop. spring seeds Apr.[b]	Arcsin–square root	37.9	5,49	< 0.0001

[a] Proportion of 2008 seeds produced in spring (April–May).
[b] Proportion of spring seeds produced in April.

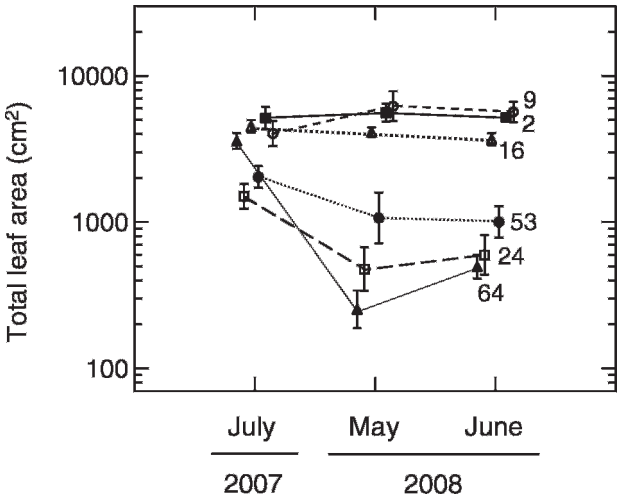

Figure 2. Total leaf area of individual plants of six dandelion genotypes measured at three times in a common garden. Sample sizes for genotypes 64, 24, 53, 16, 2, and 9 were 9, 8, 8, 15, 7, and 8, respectively. Genotype means are presented ± 1 standard error of the mean. Points are offset slightly on the *x*-axis for visual clarity.

dandelions: are more genetically diverse populations likely to have greater invasion success than genetically depauperate populations? So-called ''selection effects'' (Loreau and Hector 2001) arise if genotypes with inherently high productivity come to dominate populations that are initially genetically diverse, thereby leading to average productivity of these mixture populations that is greater than the average of monoculture populations of the different genotypes. Given the huge productivity differences among genotypes we observed, we can predict the likely manifestation of selection effects in genetically diverse populations, with genotypes 9, 16, and 2 likely to dominate over the others in this environment.

Seed and Pappus Characteristics. Genotypes did not vary significantly in seed mass (Figure 3). There was significant variation, though of relatively modest magnitude, among genotypes for pappus radius (Figure 3; Table 3), but no tendency for genotypes producing fewer seeds to have seeds with greater dispersal potential. The ratio of pappus radius to seed mass, which is a close proxy for seed terminal velocity and therefore potential dispersal distance (Sheldon and Burrows 1973), did not vary significantly among genotypes ($P > 0.25$; data not shown). Seed germination varied significantly among genotypes, with genotypes producing larger plants also tending to have higher germination (Figure 3).

With no tendency for genotypes with smaller plants and lower seed production to show greater mass per seed, dispersal potential, germination, or seedling emergence in field trials (E.B.M. Drummond, unpublished data), these results do not indicate a trade-off between adult-plant fitness components and aspects of regeneration via seed. Such trade-offs are

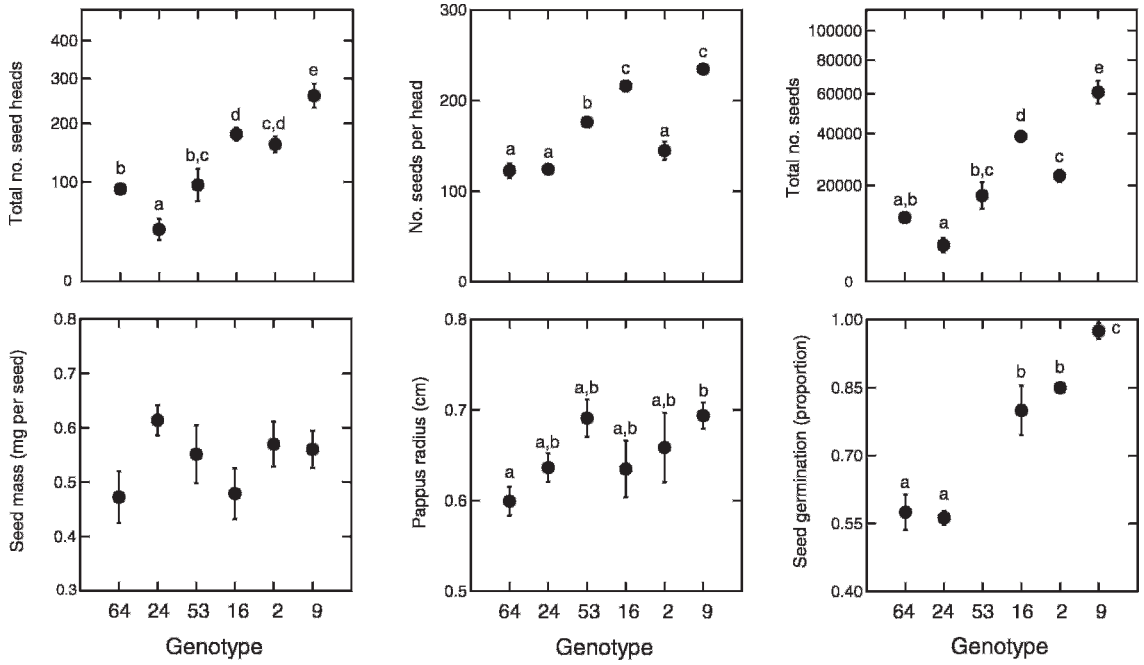

Figure 3. Dandelion genotype means ± 1 standard error for variables measured on plants or seeds from the common garden experiment. Genotypes are ordered from those producing the smallest plants based on total leaf area (left) to those producing the largest plants (right). Different letters indicate significant pairwise differences ($P < 0.05$, Tukey-Kramer test).

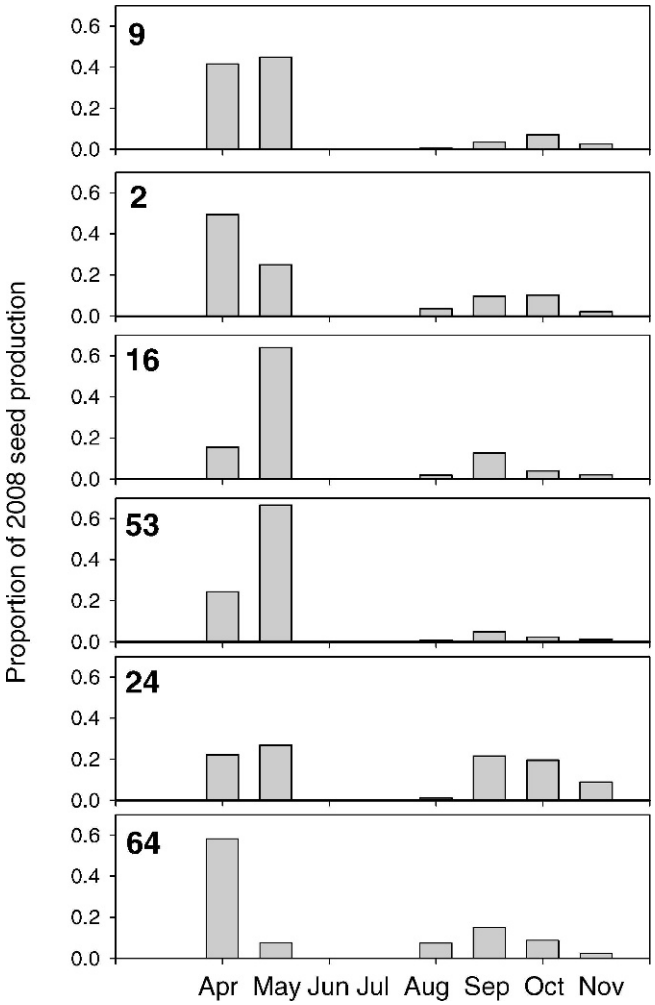

Figure 4. The timing of seed production among dandelion genotypes, showing the proportion of seeds produced during each month of 2008. See Table 3 for statistical comparisons among genotypes for proportion of seeds produced at different times.

ecologically important in that they can potentially promote the stable coexistence of different genotypes or species (Tilman 1994). Our result is in contrast to the study of Solbrig and Simpson (1974), in which a trade-off between vegetative growth in competition and seed production was found for two dandelion genotypes in Michigan. As such, we have to look elsewhere for mechanisms that maintain coexistence among these dandelion genotypes in the Vancouver area. Given the wide range of habitats in which dandelions grow, spatially variable selection (i.e., genotype-by-environment interactions) seems a likely candidate (see also Solbrig and Simpson 1974), although we cannot address this issue at present as our experiment was conducted in only one environment. There was no obvious tendency for the highly productive genotypes (2, 9, 16) to come from habitats more similar to the plowed-field environment of the common garden than the other genotypes (see Table 2), but a much broader analysis of genotype-habitat relationships will be necessary to test this possibility. Future common-garden experiments in multiple environments are needed as well.

The Timing of Reproduction. Genotypes also varied significantly in the timing of seed production (Table 3; Figure 4). All genotypes except 24 produced the large majority of their seeds in the spring, and within the spring flowering period some genotypes produced most of their seeds early (64, 2), others produced most of their seeds later (16, 53), and still others (24, 9) produced equal numbers of seeds in April and May (Figure 4).

This result may have implications for potential ''complementarity'' among genotypes (Loreau and Hector 2001), whereby complementary resource-use strategies among genotypes leads most or all genotypes to be more productive in mixtures than in monoculture. In this study, we were particularly interested in possible temporal resource partitioning, given the findings of Vavrek et al. (1996) on dandelions in West Virginia, where genotypic niche partitioning with respect to the temporal pattern of growth and reproduction appeared to contribute to the maintenance of genetic diversity. We found similar variation among Vancouver dandelion genotypes in the temporal pattern of flowering (Figure 4), and if these differences are indicative of the timing of resource use, increased invasion success in genetically diverse dandelion populations via complementarity is also a possibility.

In sum, in this study we found marked variation among dandelion genotypes for a variety of traits, including key components of fitness, which likely have important consequences for the dynamics of dandelion populations.

Sources of Materials

[1] Potting mix, West Creek Farms Ltd., Suite C-25044 River, Langley, BC, Canada.

[2] Flood bench, Prins Greenhouses, 38900 No. 4 Road, Abbotsford, BC V3G 2G2, Canada.

[3] LI-COR LI-3100C leaf area meter, LI-COR Biosciences, Li-Cor Inc., 4421 Superior Street, Lincoln, NE 68504.

[4] PROC GLM, SAS version 9.1, SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513-2414.

[5] Primers, LI-COR Biosciences, Li-Cor Inc., 4421 Superior Street, Lincoln, NE 68504.

[6] LI-COR 4300, LI-COR Biosciences, Li-Cor Inc., 4421 Superior Street, Lincoln, NE 68504.

[7] Rootrainer cells,Spencer-Lemaire Industries, Ltd., 11406 119th Street, Edmonton, AB T5G 2X6, Canada.

[8] Lawn mix, Kutny's Richmond Soils, 9811 No. 6 Road, Richmond, BC V6W 1E5, Canada.

[9] Growth chamber, Conviron, 590 Berry Street, Winnipeg, MB R3H 0R9, Canada.

[10] ImageJ, Image Processing and Analysis in Java, http://rsb.info.nih.gov/ij/.

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