ARE INVASIVES BIGGER? A GLOBAL STUDY OF SEED SIZE VARIATION IN TWO INVASIVE SHRUBS

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Abstract. We explored the spatial structure of seed size variation and tested whether seed size differed between native and exotic populations in two invasive species. Seed of *Cytisus scoparius* (Scotch broom) is significantly heavier in its exotic range, whereas seed of *Ulex europaeus* (European gorse) is no different between ranges. This result suggests that seed size in *C. scoparius* is either adaptively or phenotypically responsive to conditions in its exotic range or that plants with large seeds were preferentially introduced. We found that modern ornamental broom seed was no bigger than seed from natural or naturalized populations, suggesting that large seed size in the exotic range is not due to preferential introduction of ornamental varieties with large seeds. Most previous studies of trait differences between native and exotic ranges in invasive species have not taken variation throughout the ranges into account. This is the most comprehensive survey of seed size variation in any species, and the first time that variation in a trait of an invasive species has been studied from individual plant level up to global ranges. Demographic rates can be affected by seed attributes making this study an important first step in understanding how population processes may differ between native and exotic ranges.

Key words: Cytisus scoparius; *evolutionary change; invasive plants; linear mixed effects models; phenotypic plasticity; seed size variation;* Ulex europaeus.

INTRODUCTION

Allocation of resources to growth or defense within a plant has been suggested to differ between native and exotic ranges (Blossey and Nötzold 1995) and such differences could lead to changes in population dynamics and ''weediness.'' Understanding how demographic rates change between native and exotic ranges is critical for understanding the dynamics of invasive species and for formulating successful management strategies. Characteristics of invasive plants in their native and exotic ranges differ, although the pattern is not consistent (Thébaud and Simberloff 2001). Invasive plants have been reported to grow taller (Blossey and Nötzold 1995), produce more seeds (Noble 1989), and live longer (Rees and Paynter 1997) in their exotic range when compared with native range. However, none of these studies examined trait variation over a

wide area of the species' range, making it difficult to place differences in context. We studied seed size as it is highly correlated with maternal and offspring fitness through attributes such as dispersal, dormancy, and resource storage (Harper et al. 1970). Seed size is also the least variable of reproductive characters (Harper et al. 1970), making small changes between ranges easier to detect. We tested the null hypothesis that seed size does not differ between native and exotic ranges.

Abiotic causes

Differences in plant traits between native and exotic ranges are often explained as phenotypically plastic responses to a new environment with different abiotic conditions, fewer competitors, and fewer species-specific herbivores (Willis et al. 2000). Seed size has been reported to change in response to abiotic conditions (Wulff 1986). We tested whether latitude and elevation had any affect on seed size, as these variables are easily measured, globally comparable, and represent large-scale differences among sites.

Genetic causes

Possible causes of genetic differences between plant species in native and exotic ranges are founder effects (Amsellem et al. 2000) and post-invasion evolutionary change (Blossey and Nötzold 1995), although little evidence of evolutionary change exists (Willis et al. 2000). Many species such as *Cytisus scoparius* (Scotch broom) were introduced for ornamental purposes; thus, differences in seed size between ranges could be due to founder effects if ornamental varieties have different seed sizes than natural populations. We tested whether seed size of modern ornamental broom varieties differed from seed from natural or naturalized populations.

Substantial seed size variation has been documented within and between plants (Howe and Richter 1982, Michaels et al. 1988), and occasionally between populations (Telenius and Torstensson 1999). There is however little or no evidence of variation among sites or countries as few studies have been done at a wider geographic scale. Variation at different spatial scales is due to different processes; for example, differences in seed size within the same plant result from positional effects within the plant or fruit (Harper et al. 1970), genotypic variation due to different male parents (Bingham 1966), novel recombinations and mutations, and phenotypic variation within each of the genotypes produced (Roach and Wulff 1987). Variation at broader spatial scales is due to phenotypic response to abiotic differences such as climate, latitude, and elevation, or genetic differences such as local adaptation, drift, and founder effects (Amsellem et al. 2000). The processes that cause variation in seed size at different spatial scales could differ between ranges, which led us to test a second null hypothesis: patterns of variation in seed size at different spatial scales do not differ between native and exotic ranges. We test this hypothesis by comparing statistical models of variation between native and exotic ranges.

Previous studies of seed size variation have either concentrated on comparative cross-species analyses (Leishman et al. 1995, Rees 1996), or for a single species, these analyses have been confined to a single ecoregion (Telenius and Torstensson 1999). Previous tests of trait differences between ranges have been limited by a lack of sampling rigor. For example, Blossey and Nötzold (1995) compared just one exotic population with one native population of *Lythrum salicaria*; thus interpopulation differences were confounded with range effects. Adequate tests of our hypotheses therefore required extensive sampling throughout the native and exotic ranges. Sampling in a fully random manner across continents was impossible; therefore we made use of a hierarchical sampling regime and statistics that account for correlation between data points at different spatial scales in order to correctly partition variation in seed size. Failure to account for lack of independence

of data points inflates the error degrees of freedom leading to an increased chance of making a Type I error.

The finest scale of sampling was within individual plants, which were nested within populations; populations were nested within sites chosen to differ in their latitude and elevation; sites were nested within countries; and finally countries were grouped into native or exotic ranges. Countries were included in the analysis because introductions, and therefore genetic history, might be expected to follow trading routes, rather than natural dispersal. We used two closely related and ecologically similar invasive shrubs with comparable global distributions and exotic introduction histories, *Ulex europaeus* L. and *Cytisus scoparius* (L.) Link (Fabaceae). By minimizing differences between the species, we hoped to minimize the number of potential causes of any between-species differences in the trait studied.

METHODS

Species

Both *C. scoparius* and *U. europaeus* are polycarpic perennial shrubs found on all continents except Antarctica. *Cytisus scoparius* (Scotch broom) and *U. europaeus* (European gorse) are both native to Europe; see Peterson and Prasad (1998) and Holm et al. (1997) for native and exotic distributions. Both species were introduced to all countries in their exotic ranges in the early to mid 1800s (Hosking et al. 1996, Richardson and Hill 1998). *Cytisus scoparius* and *U. europaeus* are closely related; according to a molecular phylogeny, both species are in the same monophyletic tribe, Genisteae, within the Papilionoideae (Käss and Wink 1997). They occupy similar habitats in both the native and exotic ranges although *U. europaeus* is typically found on drier sites (Clements et al. 2001).

Both species produce seeds in pods with *U. europaeus* producing 1–6 seeds per pod (Richardson and Hill 1998) and *C. scoparius* producing up to 22 seeds per pod, but more commonly 5–8 seeds (Smith and Harlen 1991). Total seed production per plant is extremely variable from year to year (Hosking et al. 1996) in both species. Both *U. europaeus* and *C. scoparius* seeds are dispersed ballistically up to 5 m from the parent plant, although most seeds fall within 1 m; seeds can be dispersed longer distances by ants, water, animals, and through human activities (Hosking et al. 1996, Richardson and Hill 1998). *Cytisus scoparius* produces seed once a year in late summer or autumn (Hosking et al. 1996) whereas *U. europaeus* often produces seed in both spring and autumn in both its native and exotic ranges (Richardson and Hill 1998). See Rees and Hill (2001) and Rees and Paynter (1997) for reviews of biology and population dynamics of these species.

Sampling and statistics

Seeds were collected from 10 countries or islands associated with 5 continents in summer or early autumn

REPORTS

TABLE 1. The country and site origin of seed samples for two invasive species.

Range and country	Site	Species† (No. populations)	Collection date	Elevation (m)	Latitude
Exotic					
Australia	Barrington Tops	C (4)	Feb. 2000	1180	31.8° S
	Shoalhaven	C (4)	Dec. 1999	300	35.8° S
New Zealand	Lake Taupo	C (3)	Jan. 2001	480	38.7° S
	Canterbury	U (1)	Dec. 1999	20	43.6° S
	Auckland	U (3)	Dec. 1999	60	36.3° S
	Otago	U (3)	Dec. 1999	140	45.9° S
USA	California	C (5), U (2)	Jul. 2000	1000	38.0° N
Chile	Achao	U (5)	Jan. 2000	30	42.5° S
	Arauco	U (5)	Feb. 2000	70	37.2° S
	Carillanca	C (1)	Feb. 2000	200	38.7° S
	Chacao	C (5), U (5)	Jan. 2000	15	41.8° S
	Collipulli	U (3)	Feb. 2000	100	37.9° S
	Contulmo	C (5)	Feb. 2000	25	38.0° S
	Curanilahue	C (5)	Feb. 2000	150	37.5° S
	Dalcahue	C (5), U (5)	Jan. 2000	50	42.3° S
	Lebu	U (5)	Feb. 2000	150	37.6° S
	Loncoche	C (5), U (5)	Jan. 2000	115	39.3° S
	Puerto Montt	C (5), U (5)	Jan. 2000	30	41.5° S
	Valdivia	C (5), U (5)	Jan. 2000	10	39.8° S
Sri Lanka	N. Elizabeth	U (1)	Mar. 2000	1850	6.9° N
Native					
England	Berkshire	C (4), U (5)	Jul. 1999	30	51.5° N
	Bristol	C (2), U (1)	Jul. 2000	70	51.5° N
Scotland	Banchory	U (3)	Aug. 2000	75	57.1° N
	Stirling	C (3), U(3)	Aug. 2000	50	50.0° N
France	Cevennes	C (3)	Jun. 2000	300	44.0° N
	P. Orientales	C (5)	Jun. 2000	20	42.5° N
Corsica	Corsica	C (5)	Jul. 2000	1000	42.0° N
Germany	Black Forest	C (1)	Aug. 2000	810	47.0° N
Switzerland	Bergell	C (2)	Aug. 2000	1000	46.4° N

† C = *C. scoparius* and U = *U. europaeus.*

in each hemisphere between July 1999 and January 2001. A hierarchical sampling regime was used in order to partition variance in seed mass according to the following structure: among 30 seeds within the same plant, among 15 plants within populations, among up to 5 populations within sites, among up to 8 sites within countries, and among countries (see Table 1 for details). The Chilean sample did not have seed from individual plants kept separately, so within and among plant variance could not be estimated for this country. Therefore, we tested whether seed size differed between ranges using the data including Chile, but excluded Chile from analyses where variance was partitioned at all spatial scales.

The spatial scales used in the sampling were chosen in order to capture variation at increasing distances. A population was arbitrarily defined as a group of plants more than 200 m away from the next population sampled; plants within 200 m of each other may be more similar in seed size through genetic relatedness or local variation in abiotic conditions than plants at greater distances. Sites, defined as geographically continuous areas within countries, were chosen to differ in two covariates (i.e., latitude and elevation). We retained country in the analysis as the provenance of introduced populations may reflect political or cultural differences.

Approximately 15 seedpods were collected from individual plants when the pods were brown and dry at the end of the fruiting season. Seeds were kept in paper bags in cool dry conditions until January 2001 when they were cleaned and weighed. The order in which the samples were weighed was fully randomized to eliminate the effects of changing humidity during weighing. Thirty seeds per individual were weighed, one seed at a time, using a Sartorius "Handy" electronic scale sensitive to 0.1 mg (Sartorius, Goettingen, Germany); a total of 10 521 seeds of *U. europaeus* and 17 301 seeds of *C. scoparius* were weighed. Samples of seed from commercial seed producers were acquired for both the UK (John Chambers Wild Flower Seeds, Northamptonshire, UK) and the USA (Chiltern Seeds, Ulverton, Cumbria, UK). Thirty seeds of each of these commercial varieties were weighed, one seed at a time, and a *t* test was used to compare ornamental seed with seed collected from natural or naturalized populations in the same country.

We used hierarchical (also known as multi-level) linear mixed effects (LME) models to combine the estimation of fixed effects (exotic or native range) while allowing for variation in sample sizes and multiple levels of nested random effects (Pinheiro and Bates 2000). The multilevel LME model is described in detail by

TABLE 2. Mean seed mass for each species within each country sampled in the native and exotic ranges.

Range and country	Cytisus scoparius		Ulex europaeus	
	No. seeds	Mean mass (1 SE)	No. seeds	Mean mass (1 SE)
Exotic (totals)	7995	9.26 (0.70)[a]	5373	6.31 (0.17)[a]
Australia	3569	9.30 (1.00)		
New Zealand	1352	9.25 (1.43)	2764	7.21 (0.42)
USA (California)	1994	9.18 (1.40)	869	6.11 (0.57)
Chile	1080	9.88 (0.5)	1290	6.28 (0.18)
Sri Lanka			450	5.78 (0.61)
Native (totals)	9306	7.08 (0.44)[b]	5148	6.47 (0.30)[a]
England	2548	7.77 (1.01)	2508	6.61 (0.41)
Scotland	1350	8.29 (1.43)	2640	6.34 (0.39)
France	3049	7.25 (1.00)		
Corsica	1895	5.25 (1.40)		
Germany	219	5.89 (1.55)		
Switzerland	245	7.03 (1.46)		

Notes: Identical superscripts beside a species total for mean mass indicate a lack of significant difference. Different superscripts indicate a significant difference between the ranges. Mean seed mass for each country is shown to demonstrate the similarity of seed size within the extent of the range sampled.

Pinheiro and Bates (2000:60–61); a brief description is given here. A mean value is estimated for each level of the fixed effect (in this case, range), whereas the random effects are regarded as additional error terms to account for correlation among observations within the same group. A variance is predicted for each random effect. The random effects and within group error term are assumed to be normally distributed, and the random effects are assumed to be independent of each other. We used random effects to model the covariance structure introduced by grouping the data according to our hierarchical sampling regime. The spatial autocorrelation between plants within the same scale is therefore accounted for, and exploited in order to more sensitively test differences between fixed effects. All analyses were carried out in R 1.3.1 (Ihaka and Gentleman 1996, [available online])[11] using the LME procedure available within the "nlme" package.

The significance of each scale in the spatial hierarchy was determined by comparing models with each scale individually deleted while preserving the nested structure. Maximum likelihood tends to underestimate the random effects (Pinheiro and Bates 2000:75–76). We therefore tested the significance of random effects using restricted maximum-likelihood (REML), whereas the significance of range (native or exotic) as a fixed effect was tested using maximum-likelihood (ML). For a variance term to be estimated there must be replication within the grouping level of the random effects term. However, some of our data (e.g., *C. scoparius* in Germany and the United States) lack replication at the scale of population or site. For these countries, no variance could be estimated for the missing levels. However, these samples were retained in the analysis as

they provide information on the variance at other scales (e.g., plant within population).

Variance at each scale in the sampling hierarchy was converted to a percentage of the total variance to allow informal comparison between species. Diagnostic plots (as described in Pinheiro and Bates 2000:174–196) were used to validate the assumptions of normality of residuals and random effects; no deviations from assumptions were detected. Means and standard errors (REML estimates) for seed mass were obtained from the model including range or country as a fixed effect. Effects of elevation and latitude on seed size were tested using site means of seed size for each species and the elevations and latitudes of the sites (Table 1). As latitude and elevation differed only at the level of sites, general linear models were used to determine the effects of elevation, latitude, range, and their interactions on seed mass.

RESULTS

Hypothesis 1: Seed size does not differ between the native and exotic ranges

This hypothesis was rejected for *Cytisus scoparius*; seeds were significantly heavier in the exotic than in the native range ($LR_{1,6} = 13.97$, $P = 0.002$). The same test for *U. europaeus* showed no difference ($LR_{1,6} = 0.22$, $P = 0.64$). These results hold throughout the extent of the native and exotic ranges sampled (Table 2). Neither latitude, elevation, nor their interactions with range were significant for *C. scoparius* (latitude $F_{1,15} = 0.24$, $P = 0.63$; elevation $F_{1,15} = 0.19$, $P = 0.67$). Neither elevation nor range were significant for *U. europaeus* ($F_{1,16} = 3.69$, $P = 0.07$ and $F_{1,16} = 2.82$, $P = 0.11$, respectively). Latitude was significant ($F_{1,16} = 5.75$, $P = 0.03$). However this was due to high leverage of the Sri Lankan sample; without these data
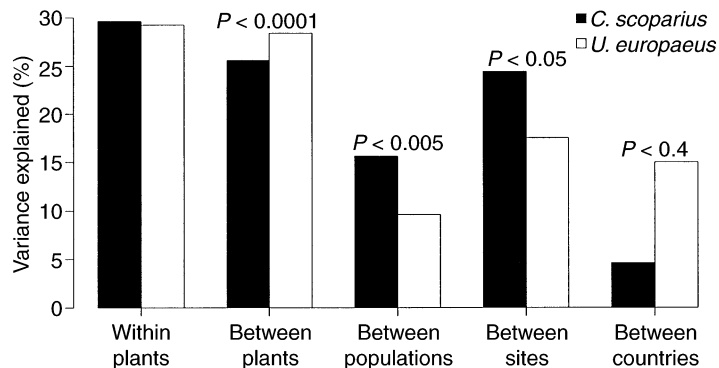
Fig. 1. Variance in seed mass as a percentage of the total variance of the random effects for each level in the sampling hierarchy (native and exotic ranges combined). Significance values for each element of the sampling hierarchy are given above the bars and are the same for both species.

the relationship was not significant ($F_{1,15} = 1.01$, $P = 0.33$). Commercially produced seeds of *C. scoparius* in both the United Kingdom and the United States were not significantly different from seeds from natural or naturalized populations in the same countries (UK $t = -0.09$, df = 29, $P > 0.9$; USA $t = 0.26$, df = 29, $P > 0.8$).

Hypothesis 2: Variance partitioning does not differ between ranges

For both species, we accepted the null hypothesis; we found the same pattern of significant variation for both the native and exotic ranges (Fig. 1). Within and between plant variation was significant ($P < 0.0001$) and accounted for most of the variation in seed size (~ 55–60%); there was also significant variation between populations and sites. Variation at the country scale was not significant for both species. In the native range, seed of *C. scoparius* was more variable than *U. europaeus* (coefficient of variation = 30% and 19%, respectively).

DISCUSSION

Seeds of *C. scoparius* were heavier in the exotic range compared with the native range, whereas seeds of *U. europaeus* showed no difference between ranges. For both species, most variation in seed size occurred within and between individual plants, although there was also significant variation at the population and site level. These results are crucial first steps in working toward the answers to more general questions, such as why variation exists at different scales, and the demographic and evolutionary consequences of seed size variation. The expression of seed size is often under conflicting selection pressures arising from predation (Moegenburg 1996), dispersal (Kigel 1992), and competition (Rees and Westoby 1997). In addition, parental and offspring optima may not coincide (Shaanker et al. 1988). Overlain on these genotypic causes of variation are phenotypic realizations of seed size. The pattern of variation at different spatial scales allows us to draw some conclusions about processes affecting seed size.

Variation at different spatial scales

Variation in seed size was greatest within and between plants in both species; these results are commonly found in studies of seed size variation. At these spatial scales, seed size can be affected both by the abiotic environment (Wulff 1986) and by pollination effects (Wolfe 1995). Seed size is also sensitive to maternal effects (Schmid and Dolt 1994) mediated by the level of herbivory on female parents (Agrawal 2001) and plant density (Mazer and Wolfe 1992). There are no data available on how seed size varies from year to year in these species. We know that seed production is variable from year to year (Hosking et al. 1996), and if correlated with variation in seed size sampling for one year only might lead us to underestimate variation in seed size. For *C. scoparius*, we can discount seasonality affecting within plant or within population variation in this study, because all plants within populations were sampled at the same time. However, as *U. europaeus* produces seed twice a year, we may have underestimated variation by only sampling during one season.

Populations were defined as being at least 200 m apart; this distance is likely to be insufficient to prevent gene flow between groups of plants. Bees are known to pollinate *C. scoparius* and can fly considerable distances (Parker 1997). The relatively small amount of interpopulation variation (~ 10–15%) is therefore indicative of similar environmental conditions affecting populations within a site and/or gene flow between populations as we defined them.

Intersite variation is the third most important source of variation in *C. scoparius* and *U. europaeus*. It is significant and represents $\sim 25\%$ and 17% of the total variance in *C. scoparius* and *U. europaeus*, respectively. Variation in seed size at the site level has not been found previously due to a lack of studies at this spatial scale. The occurrence of variation at this spatial scale indicates that plants are adapted to or are phenotypically affected by broad-scale environmental differences. This variability cannot be accounted for by broad scale differences in latitude or elevation; thus it

may be caused by other factors not linearly correlated with latitude or elevation that differ from site to site, such as rainfall, soil type, or the surrounding ecological community. The proportionally less variable seed mass at the site scale in *Ulex europaeus* compared with *C. scoparius* suggests a smaller amount of genetic variation available for adaptation to new environments in *U. europaeus*, or a smaller amount of phenotypic plasticity in seed development. *Ulex europaeus* also exhibits less variation in seed size both overall and in its native range than *C. scoparius*. If there is a genetic component to this difference, then it could explain why *U. europaeus* seeds do not show an increase in seed size under very similar conditions compared to the more variable *C. scoparius*.

Countries such as Chile and Australia have different colonial histories that could have resulted in seeds being introduced from different sources. For this reason, we were interested in the possibility that differences in seed size could occur at the country level. However, there was no significant variation among countries, which suggests that founder differences are relatively unimportant. Due to the paucity of accurate historical records of introductions and the possibility of multiple introductions, the only way of reconstructing relationships between populations and tracing the origins of introduced populations is through analysis of isozymes or genetic sequence data (Amsellem et al. 2000).

Differences between native and exotic range

Lack of significance indicates that the larger mean seed mass in the exotic samples of *C. scoparius* is not related to elevation or latitude. It is also unlikely that *C. scoparius* transported to different countries at multiple times was derived from the same source of plants with large seeds. This is supported by our results showing that modern seed produced for ornamental purposes was no heavier than seed collected from wild populations. This suggests that some post-introduction increase in seed size has occurred in *C. scoparius*. There are two hypotheses that could account for the differences in seed size between the ranges. First, larger seed size in the exotic range is caused by the absence of specialist herbivores; in the native range these herbivores affect seed size either through reduced vigor of the parent plants and consequent maternal effects (Agrawal 2001) or through selection against large seeds (Moegenburg 1996). The insect fauna of *C. scoparius* differs in guild composition between native and exotic ranges (Memmott et al. 2000); in particular, specialist herbivores are much less common in the exotic range. A second hypothesis is that there has been selection for larger seeds of *C. scoparius* in the exotic range in response to increased intraspecific seedling competition. Seedling densities are higher in the exotic range (Rees and Paynter 1997) causing higher intraspecific seedling competition. Studies on a variety of species have shown that seed size influences early growth and

survival of seedlings (Howe and Richter 1982, Eriksson 1999) although this is habitat and species specific (Paz et al. 1999). If seed size is heritable and if larger seeds are better able to grow or survive in a highly competitive environment, all else being equal, the result would be selection for larger seed sizes. Note that because plants in the exotic range may be larger (Rees and Paynter 1997), this increase in seed size might not result in a decrease in per capita fecundity relative to plants in the native range (Venable 1992). The effects of seed size, competition, and country of origin on subsequent seedling and adult performance are currently being investigated using an experimental approach. Likewise, tests of the heritability of seed size are currently underway.

We cannot expect all invasive plant species to share the same response as *C. scoparius* in seed size; indeed the closely related and ecologically similar *U. europaeus* does not show a similar response. We can however expect invasive plants to exhibit a range of changes in traits (one of which is seed size) due to changes in abiotic conditions, competition, and/or the lack of specialist herbivores with potentially important consequences for population dynamics. By using hierarchically structured sampling, we are more likely to identify real differences due to greater sensitivity of tests of fixed effects and less likely to report spurious differences due to confounding within-species variation with variation between ranges.

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