Genetic variation in *Bromus tectorum* (Poaceae): comparison between native and introduced populations

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The amount and distribution of genetic variation in 51 native (Eurasian and northern African) populations of *Bromus tectorum* were assessed at 25 loci using starch gel electrophoresis and were compared with our previous results for introduced (North American) populations of this predominantly cleistogamous grass. More alleles and variable loci were detected across populations in the native range than in North American populations. Within populations, however, the level of polymorphism is higher in the introduced range than in the native range. Deviation from Hardy–Weinberg expectation among native populations is almost as severe as for introduced populations. Eurasian populations exhibit greater genetic differentiation than those in North America; populations from Southwest Asia are the most genetically differentiated. Comparison of single-locus genotypes suggests possible source populations in both Europe and Southwest Asia for the populations now so prominent in western North America. Genetic differences between introduced and native populations of *B. tectorum* stem from two opposing factors: the reduction in genetic variability across populations produced by founder effects combined with an increase in the within-population component of genetic variation from multiple introductions.

Keywords: *B. tectorum*, genetic variation, introduced populations, native populations.

Introduction

Severe reductions in the size of populations, either through population bottlenecks or founder events, can cause rapid alteration or loss of genetic variation (Baker & Stebbins, 1965; Brown & Marshall, 1981; Clegg & Brown, 1983). Theoretical results emphasize the influence of the size of a founder population, the number of times a founder event occurs and the severity of a population bottleneck on the level of genetic variation within subsequent generations (Nei *et al.*, 1975; Watterson, 1984; Maruyama & Fuerst, 1985; Goodnight, 1987, 1988). For example, genetic diversity within founder populations will probably increase as more colonizations stem from the source population(s) (Wade & McCauley, 1988; Barrett & Husband, 1990; Whitlock & McCauley, 1990). Unfortunately, empirical confirmation of these predictions is tenuous; few experiments have assessed directly the effects of population bottlenecks (Bryant *et al.*, 1986a, b; Polans & Allard, 1989; McCommas & Bryant, 1990).

Our knowledge of the impact of founder effects on a population's genetic variation is more extensive and has been derived almost entirely from invasive plant and animal species (Brown & Marshall, 1981; Clegg & Brown, 1983; Barrett & Husband, 1990). Most introduced species in their new ranges do indeed possess little or no genetic variability (Barrett & Richardson, 1986; Gray, 1986; Barrett & Shore, 1989), although exceptions have been reported (Brown & Marshall, 1981). Lack of satisfactory explanation for these exceptions (as well as proper quantification of the general cases) persists in part because the genetics of invading species have almost always been studied in the species' introduced range alone. Assessment of the impact of founder events on introduced species should ideally include comparison of populations from both the introduced and native ranges, thereby giving a relevant gauge of a species' genetic variation in its new range. Few studies have, however, provided this requisite comparison (but see Brown & Marshall, 1981; Clegg & Brown, 1983; Barrett & Husband, 1989).

Bromus tectorum (cheatgrass) is a diploid ($2n = 14$), predominantly cleistogamous, annual grass with wide

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distribution in temperate grasslands (Upadhyaya et al., 1986). Its native range encompasses most of Europe, the arid northern rim of Africa, plus Southwest (SW) Asia and extends to Tibet, Kashmir and southern Pakistan (Pierson & Mack, 1990). The grass has been inadvertently introduced into Japan, Australia, New Zealand, temperate South America and North America (Upadhyaya et al., 1986). Bromus tectorum was probably introduced directly into North America from Eurasia as a contaminant of grain seed or packing material (Mack, 1981). The early collection history of the species suggests that it was introduced at several widely-separated sites and that range expansion occurred rapidly through a merging of isolated foci. Its subsequent spread occurred in discarded livestock bedstraw along railroad sidings, through adulterated grain seed and via livestock (Mack, 1981). Seed of B. tectorum possess a long, rigid awn (12–14 mm) that aids in its attachment to fur (La Tourrette et al., 1971), machinery and clothing. In the century since this alien grass was introduced into the Intermountain West of North America it has become one of the region's most abundant vascular plant species (Mack, 1981; Upadhyaya et al., 1986).

As part of our general assessment of the evolution of B. tectorum since its arrival in North America (Novak, 1990; Novak et al., 1991; S. J. Novak et al., unpublished data), we investigated the level of genetic variation of this grass in its native range. We asked: (1) how does the genetic variation of B. tectorum in Eurasia compare with the variation previously detected in North America? (2) does the distribution of genetic variation across, within and among populations differ between the native and introduced populations? and

(3) can we identify the source populations from which populations in the introduced range have been derived (or at least eliminate some native populations as sources)?

Materials and methods

Fifty-one populations from the native range of B. tectorum were analysed and assigned to two geographical regions: Europe (including one population from Morocco) and SW Asia (Fig. 1 and Table 1). Three categories of plant material were used: the panicles from 10 to 40 plants collected individually from populations in the field, bulk-harvested panicles from field populations and accessions from the USDA Western Region Plant Introduction Laboratory, Pullman, WA (USA). Accessions from the Plant Introduction Laboratory were the product of an unknown number of grow-outs since they were first collected.

Seeds of B. tectorum were germinated and starch gel electrophoresis was conducted with seedlings as previously described (Novak et al., 1991). The same 15 enzymes employed with North American populations were used. The genetic basis of all observed allozymic variation was easily inferred based on the known subunit structure and compartmentalization of the enzymes used (Gottlieb, 1982; Weeden & Wendel, 1989). When more than one locus was detected for an enzyme, loci were numbered sequentially; the most anodally migrating isozyme was designated 1. Different alleles at a locus were identified using letters, with the most anodal allozyme designated a, the next b and so on.
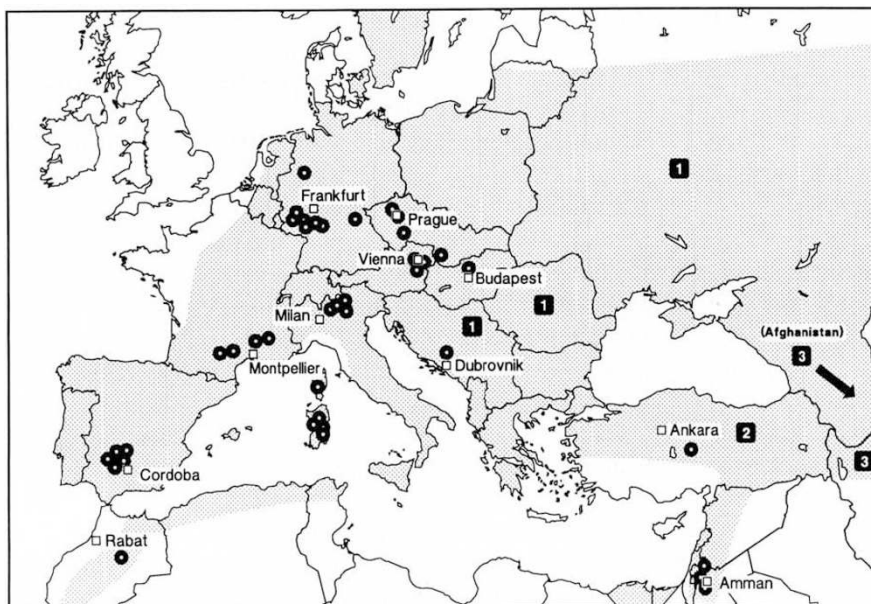

Fig. 1 Location of Eurasian and North African B. tectorum populations analysed. The number of populations from USDA accessions known only to country of origin are denoted in squares. Stippled area denotes the western native range of this grass. From Hulten & Fries (1986).

Table 1 Genetic variability statistics for European (including Morocco) and SW Asian populations of *B. tectorum*. Summarized results for North American populations† and all populations are also provided

Region	Population	N	A	$\% P$	Expected genetic diversity, H_e
Europe	Conquerac, France	40	1.00	0.0	0.000
	Anduze, France‡	50	1.00	0.0	0.000
	Moureze, France‡	50	1.00	0.0	0.000
	Tarassac, France‡	50	1.04	4.0	0.003
	Corsica, France‡	50	1.00	0.0	0.000
	Puerto Calarano, Spain	30	1.04	4.0	0.005
	Pozoblanco, Spain	28	1.04	4.0	0.018
	Belmez, Spain	24	1.04	4.0	0.009
	Hinojosa, Spain	23	1.08	8.0	0.015
	Espiel, Spain	14	1.04	4.0	0.013
	Touna Station, Morocco	27	1.12	12.0	0.057
	Arzano, Italy	29	1.00	0.0	0.000
	Gonari, Italy	26	1.00	0.0	0.000
	Mt. Orlobene, Italy	30	1.00	0.0	0.000
	Sarule, Italy	30	1.00	0.0	0.000
	Sonico, Italy	20	1.00	0.0	0.000
	Breno, Italy	19	1.00	0.0	0.000
	Tirano, Italy	30	1.00	0.0	0.000
	Grosio, Italy	29	1.00	0.0	0.000
	Cermerno, Yugoslavia	29	1.00	0.0	0.000
	Yugoslavia-2§	50	1.00	0.0	0.000
	Griesheim, Germany	30	1.00	0.0	0.000
	Lorch, Germany	30	1.00	0.0	0.000
	Russelsheim, Germany	29	1.00	0.0	0.000
	Rudesheim, Germany	30	1.00	0.0	0.000
	Ingelheim, Germany	33	1.00	0.0	0.000
	Mainz, Germany	30	1.00	0.0	0.000
	Brilon, Germany	22	1.00	0.0	0.000
	Bayreuth, Germany	12	1.00	0.0	0.000
	Vienna–Landstrasse, Austria	30	1.04	4.0	0.018
	Vienna–First District, Austria	31	1.00	0.0	0.000
	Baden, Austria	31	1.00	0.0	0.000
	Libochovice, Czech Republic	27	1.04	4.0	0.014
	Prague, Czech Republic	26	1.00	0.0	0.000
	Tabor, Czech Republic	29	1.00	0.0	0.000
	Bratislava, Slovakia	28	1.08	8.0	0.006
	Vac, Hungary‡	50	1.08	8.0	0.032
	Romania§	50	1.00	0.0	0.000
	Soviet Union§	50	1.00	0.0	0.000
SW Asia	DeGoreme, Turkey	25	1.00	4.0	0.008
	Turkey-2§	50	1.00	0.0	0.000
	Turkey-3§	50	1.00	0.0	0.000
	Madaba, Jordan	12	1.00	0.0	0.000
	Amman, Jordan	20	1.00	0.0	0.000
	Algada, Jordan	27	1.00	0.0	0.000
	Iran-1§	50	1.20	20.0	0.012
	Iran-2§	50	1.00	4.0	0.002
	Iran-3§	50	1.00	4.0	0.006
	Afghanistan-1§	50	1.00	0.0	0.000
	Afghanistan-2§	50	1.00	0.0	0.000
	Afghanistan-3§	50	1.12	12.0	0.029

Table 1 *Continued*

Region	Population	N	A	$\% P$	Expected genetic diversity, H_e
	Eurasian populations	1726	1.01	2.12	0.005
			(0.01)	(0.31)	(0.004)
	North American populations	2146	1.05	4.60	0.012
			(0.02)	(0.48)	(0.009)
	All populations	3872	1.03	3.46	0.009
			(0.01)	(0.18)	(0.007)

SE for populations appear in parentheses.
†Novak *et al.* (1991).
‡Populations collected as bulk harvested samples.
§Accessions of the USDA Western Regional Plant Introduction Station, Pullman, Washington.

Table 2 Total number of alleles and polymorphic loci for native and introduced populations of *B. tectorum*

Range	Number of populations	Number of individuals	Number of alleles	Mean number of alleles	Number of polymorphic loci	Polymorphic loci (%)
Native	51	1726	43	1.64	13	52
Introduced	60	2141	33	1.32	7	28

Electrophoretic data were analysed using BIOSYS-1 (Swofford & Selander, 1981). Intrapopulational genetic variability statistics, including the mean number of alleles per locus (A), the percentage polymorphic loci per population ($\% P$) and the expected genetic diversity (H_e) were averaged over all loci for each population: $H_e = 1 - \Sigma p_i^2$; where p_i is the frequency of the *i*th allele at any given locus. Wright's (1965) fixation index (F), was calculated for each polymorphic locus in a population. The significance of deviations of observed from expected genotype frequencies was determined for each polymorphic locus and assessed using a Chi-square test (Workman & Niswander, 1970). Gene diversity statistics were calculated according to Nei (1973, 1977) and genetic identity (I) was calculated following Nei (1978). Genetic identity values were averaged for all populations within and among populations of two regions in the native range and four regions in the introduced range. The unweighted pair-group method with arithmetic averaging (UPGMA) algorithm was employed to generate a phenogram of Nei's genetic identity values (Swofford & Selander, 1981).

Results

A total of 1726 individuals from 51 native populations of *B. tectorum* was analysed. All scored enzyme bands

migrated anodally; the 15 enzymes analysed were coded by the same 25 loci detected in North American populations (Novak *et al.*, 1991). Across all native populations 13 variable loci were detected (Table 2): *Adh, Got-1, Got-3, Got-4, Idh, Lap, Mdh-2, Mdh-3, Pgi-2, Pgm-1, Pgm-2, Skdh* and *Tpi-1*.

A comparison (Table 2) of native and introduced populations reveals fewer alleles in North American populations (33) compared with native populations (43). Across all populations, 13 variable loci (52 per cent) were detected in the native range; seven variable loci (28 per cent) were found in the introduced range. The number of loci that maintain more than two alleles was also higher in native (three) compared with the introduced populations (one). More alleles and polymorphic loci were detected in native populations even though fewer individuals were examined compared with the introduced range.

Genetic variation within populations

Thirty-five of the 51 (69 per cent) native populations we analysed are monomorphic for the 25 loci examined (Table 1). For all Eurasian populations A is very low (1.01) with little difference between populations from Europe and SW Asia (1.01 and 1.03, respectively). Eleven of 39 populations from Europe are polymorphic, with a mean value of $\% P$ for all

European populations of 1.64 per cent; the Touna Station, Morocco population has the highest level of polymorphism (12.0 per cent). Populations from SW Asia show a twofold greater % *P* (3.67 per cent) compared with European populations. Iran-1 had the highest % *P* (20.0 per cent), Afghanistan-3 was next highest (12.0 per cent).

Mean expected genetic diversity (H_e) for all Eurasian populations was 0.005, with little difference between populations from Europe (0.006 per cent) and SW Asia (0.005) (Table 1). The Touna Station population has the highest value of H_e, 0.057, reflecting both a relatively high % *P* (12.0 per cent) and an equal distribution of alleles at polymorphic loci. The Afghanistan-3 population has the highest H_e value of any population analysed from SW Asia (0.029). Intrapopulational genetic variability statistics reveal three areas in the native range of *B. tectorum* with populations displaying allelic variability: the western Mediterranean, central Europe and Iran–Afghanistan (Table 1).

Large differences were seen in % *P* and H_e (Table 1) although the number of alleles per locus differs little between Eurasian and North American populations. The values of % *P* and H_e for North American populations are more than twofold greater than values calculated for Eurasian populations (4.60 and 0.012 and 2.12 and 0.005, respectively). On a regional basis, populations from east of the Rocky Mountains (1.14 per cent) and Europe (1.64 per cent) had the lowest % *P*, whereas populations from British Columbia displayed the highest level of polymorphism (8.40 per cent). Populations from the remaining three regions, SW Asia (3.67 per cent), Intermountain West (4.73 per cent) and Nevada–California (5.14 per cent), possess intermediate values for % *P* (data not shown). The level of polymorphism in populations in western North America was greater than that seen for any region of the native range. For all 111 *B. tectorum* populations analysed *A* is 1.03, % *P* is 3.46 per cent and H_e is 0.009 (Table 1).

Conformance to Hardy–Weinberg expectations

The test of deviation from Hardy–Weinberg expectations at individual loci reveals substantial heterozygote deficiencies at 24 of 27 loci (Table 3). The fixation index at *Got-3* in the Touna Station and *Got-4* in the Vienna–Landstrasse population are 0.922 and 0.927, respectively ($P < 0.001$), indicating a significant deviation for the number of heterozygotes expected despite the presence of a single heterozygous individual in each population. Non-significant deviations from Hardy–Weinberg expectations were observed at *Got-4* and *Idh* in the Iran-1 population (fixation indices for

Table 3 Fixation indices (F) for each polymorphic locus in populations of *B. tectorum* from Eurasia indicating deviation from Hardy–Weinberg expectations

Population	Locus	F^*
Tarassac, France	*Pgi-2*	1.0
Puerto Calatrano, Spain	*Pgi-2*	1.0
Pozoblanco, Spain	*Got-3*	1.0
Belmez, Spain	*Pgi-2*	1.0
Hinojosa, Spain	*Got-3*	1.0
	Pgi-2	−0.022 ns
Espiel, Spain	*Pgi-2*	1.0
Touna Station, Morocco	*Got-3*	0.922
	Pgi-2	1.0
	Skdh	1.0
Vienna, Landstrasse, Austria	*Got-4*	0.927
Libochovice, Czech Republic	*Got-4*	1.0
Bratislava, Slovakia	*Pgm-1*	1.0
	Pgm-2	1.0
Vac, Hungary	*Pgm-1*	1.0
	Pgm-2	1.0
DeGoreme, Turkey	*Adh*	1.0
Iran-1	*Got-4*	−0.010 ns
	Idh	−0.010 ns
	Pgi-2	1.0
	Pgm-1	1.0
	Pgm-2	1.0
Iran-2	*Tpi-1*	1.0
Iran-3	*Pgi-2*	1.0
Afghanistan-3	*Mdh-2*	1.0
	Mdh-3	1.0
	Skdh	1.0

*All values are significant at the 0.001 level unless otherwise indicated.

these two loci were both −0.010 and at *Pgi-2* in the Hinojosa, Spain population −0.022, indicating slight heterozygote excesses. These are the only three loci that conformed to Hardy–Weinberg expectations among plants we sampled in either the native or introduced range of *B. tectorum* (Novak *et al.*, 1991).

Population differentiation

The mean value of G_{ST} for all polymorphic loci is 0.754 (i.e. 75.4 per cent of the total allelic variability occurs among populations) whereas 24.6 per cent of the diversity is located within populations (Table 4). Hierarchical analysis of the total allelic diversity (H_T) in the native populations reveals 80.7 per cent can be attributed to regional differentiation. Within the component of regional differentiation, 75.2 per cent of the allelic diversity is accounted for by differentiation among populations within regions; the remainder (5.5

Table 4 Nei's gene diversity statistics for all Eurasian populations of *B. tectorum*. Summarized gene diversity statistics for North American populations are also provided†

Locus	H_T	H_S	D_{ST}	G_{ST}	Among populations within regions	Among regions
Adh	0.005	0.004	0.000	0.100	0.097	0.003
Got-1	0.075	0.000	0.075	1.000	1.000	0.000
Got-3	0.066	0.025	0.041	0.616	0.621	0.000
Got-4	0.143	0.016	0.127	0.886	0.884	0.019
Idh	0.075	0.000	0.075	0.995	0.994	0.097
Lap	0.237	0.000	0.237	1.000	1.000	0.315
Mdh-2	0.044	0.005	0.039	0.891	0.886	0.041
Mdh-3	0.044	0.005	0.039	0.891	0.886	0.041
Pgi-2	0.173	0.032	0.141	0.816	0.817	0.000
Pgm-1	0.086	0.010	0.076	0.882	0.873	0.071
Pgm-2	0.086	0.010	0.076	0.882	0.873	0.071
Skdh	0.091	0.015	0.076	0.839	0.830	0.056
Tpi-1	0.001	0.001	0.000	0.010	0.009	0.001
Eurasian populations	0.087	0.009	0.077	0.754	0.752	0.055
North American populations	0.115	0.046	0.069	0.478	0.453	0.026

†From Novak *et al.* (1991).

per cent) is attributable to populations among regions. Consequently, the level of allelic differentiation detected within regions in the native populations is approximately 14-fold larger than the among-region component.

In contrast to results for other genetic parameters, major differences occur between native and introduced ranges in the distribution of genetic variation between populations (Table 4). The value for total gene diversity for introduced populations is greater than for native populations (0.115 compared with 0.087); the among-population component (D_{ST}) is much higher in the native range. The value for G_{ST}, therefore, is much higher in native compared with introduced populations (0.754 and 0.478, respectively). There is apparently more population differentiation in the native range (Table 4). The within-population component for introduced populations (0.522) is twofold larger than that calculated for native populations (0.246). Most genetic variability in the native populations is apparently partitioned among populations whereas total genetic variability in the introduced populations is evenly partitioned among and within populations.

Nei's unbiased genetic identity (I) coefficients were computed for all possible pairwise comparisons among the native populations. This coefficient was also averaged within and between each region in the native and introduced ranges (Table 5). Mean values of I for native and introduced populations are 0.930 and 0.980, respectively. The value of I for all comparisons of native populations with introduced populations is 0.966 and for all populations of *B. tectorum* is 0.969. The lowest mean genetic identity value occurs for the within-region comparison of SW Asian populations (0.899) (Table 5). Furthermore, inter-regional comparisons between the SW Asian populations and populations from all other regions are consistently lower than all other comparisons (Table 5).

A cluster diagram of populations from all six regions of the native and introduced ranges, based on Nei's (1978) genetic identity values, reveals that populations from SW Asia are the most genetically differentiated (Fig. 2). The genetic identity value for populations from this region with the other regions (0.927) would have been even lower had not populations from Turkey and Jordan possessed the most common genotype of *B. tectorum*. Populations from Europe fall into an intermediate position among introduced populations. Populations east of the Rocky Mountains were differentiated from other populations of the introduced range whereas populations from western North America are more genetically similar to each other than to populations from other regions.

Table 5 Nei's genetic identity for populations of *B. tectorum* within and between regions of Eurasia and North America†

Region	N	Europe	SW Asia	East	Nevada and California	Intermountain West	British Columbia
Europe	39	0.982 (0.896–1.000)					
SW Asia	12	0.930 (0.694–1.000)	0.899 (0.680–1.000)				
East of Rocky Mountains	14	0.978 (0.855–1.000)	0.928 (0.760–1.000)	0.975 (0.890–1.000)			
Nevada and California	14	0.980 (0.896–1.000)	0.927 (0.738–1.000)	0.975 (0.880–1.000)	0.983 (0.951–1.000)		
Intermountain West	22	0.979 (0.896–1.000)	0.927 (0.758–1.000)	0.975 (0.880–1.000)	0.986 (0.951–1.000)	0.989 (0.960–1.000)	
British Columbia	10	0.976 (0.883–1.000)	0.927 (0.765–0.999)	0.976 (0.898–1.000)	0.980 (0.908–1.000)	0.983 (0.908–1.000)	0.979 (0.924–1.000)

†From Novak *et al.* (1991).
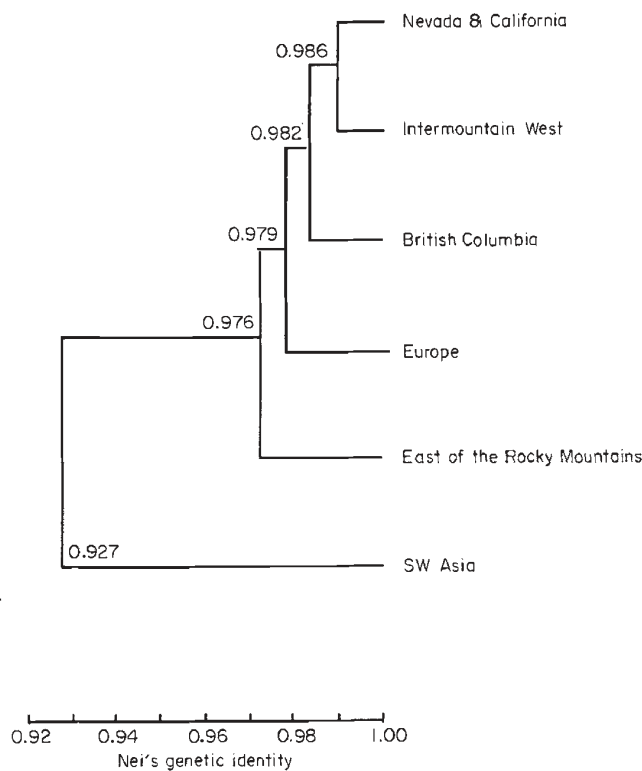
Fig. 2 Cluster phenogram of Nei's genetic identity values for populations from all native and introduced regions of *B. tectorum*.

Discussion

Genetic variation within populations

The level of genetic variation in the native populations of *B. tectorum* we examined is low and is consistent with reports for other predominantly selfing plant species (Brown, 1979; Hamrick & Godt, 1990). Conclusions based on our results on whether genetic variation in this species was reduced coincident with its introduction in North America (founder effects) depend, however, on the level of population structure being examined. We detected more alleles and variable loci across native populations (41 and 52 per cent, respectively) than for introduced populations (33 and 28 per cent). Within populations the level of polymorphism [% P and $H(\exp)$] appears higher in North American populations (4.60 per cent to 2.72 per cent and 0.012 per cent to 0.006 per cent). In addition, native and introduced populations differ in the distribution of genetic variation. Most total gene diversity in Eurasian populations is partitioned among populations whereas North American populations display an even distribution of allelic diversity among and within populations.

Our assessment of the level of genetic variability for *B. tectorum* in its native range is similar to that reported earlier for 25 European populations using four enzyme systems (Krzakowa & Kraupe, 1981). Krzakowa and Kraupe detected two enzyme phenotypes for the enzyme glutamate oxalate transaminase (GOT). Esterase (EST) was the most polymorphic enzyme they detected: nine enzyme phenotypes were observed and 11 of 25 (44 per cent) populations were polymorphic. We were unable to resolve EST for all our populations; however, our partial results for this enzyme also indicated a high level of polymorphism.

Maruyama & Fuerst (1985), Nei *et al.* (1975) and Watterson (1984) predicted on theoretical grounds a decrease in alleles per locus, following a founder event, through the loss of low-frequency alleles. Our findings

generally agree with these predictions. Rare alleles in the native populations were apparently not included in the genetic sampling associated with emigration (Table 2). Statistics for intrapopulational genetic variability (Table 1), however, show that populations in North America contain more alleles and polymorphic loci than Eurasian populations. This difference probably results from introductions of *B. tectorum* at widely separated sites in North America (S. J. Novak *et al.*, unpublished data). Our interpretation is consistent with the theoretical models of Wade & McCauley (1988) and Whitlock & McCauley (1990) and illustrates the importance of multiple immigrations in establishing genetic diversity within populations of an alien species (Barrett & Husband, 1990).

Population differentiation

The large within-population component of genetic variation in *B. tectorum* in North America is probably the result of multiple immigrations of the grass into this new range (Mack, 1981; S. J. Novak *et al.*, unpublished data). For example, in North American populations *Got-4* is the most variable locus (Novak *et al.*, 1991); 36 of 60 populations (60 per cent) analysed are polymorphic (possessing both *Got-4b* and *c*). In contrast, only two populations from the native range are polymorphic at *Got-4* (Libochovice, Czech Republic and Iran-1) and the Bayreuth (Germany) population is fixed for *Got-4c*. Multiple introductions may have collectively offset the loss in genetic variation associated with founder events, i.e. both the number of alleles and the level of polymorphism within these introduced populations have increased, with an apparent increase in the within-population component of genetic diversity (S. J. Novak *et al.*, unpublished data).

Identification of source populations

Genetic and chemotaxonomic markers have been used repeatedly to identify potential sources within an alien species' native range (Singh & Jain, 1971; Clegg & Allard, 1972; Rodman, 1974, 1976). Using single-locus gene distributions we identified several distinct populations or localities in the western Mediterranean, central Europe and SW Asia as potential sources of *B. tectorum* in North America. The allele *Pgi-2b* was found in eight western Mediterranean populations from France, Spain and Morocco and a single population from Iran; among North American populations only those near Reno, NV possess this allele (Novak, 1990; Novak *et al.*, 1991). Such correspondence is probably more than coincidental given the early prominence of Spanish settlers in California (and later

Nevada) (Burcham, 1957). One of the most common alleles in naturalized populations (*Got-4c*) is shared with only two central European populations that are within 200 km of each other: Bayreuth, Germany and Libochovice, Czech Republic. The absence of this allele in other native populations, especially those in the west of Germany and to the east in Austria and the Czech and Slovak Republics, places some geographical boundaries on the area from which founder populations could have been drawn. *Got-4d*, which we found in the native range only in Vienna (Landstrasse) has been detected in North America only at Provo, UT and Dubois, ID. *Mdh-1b* and *Mdh-2b* were both detected in two populations in Nevada (Emigrant Pass and Taber Creek) and four populations in eastern Washington (Ritzville, Rattlesnake Springs, Hodges Ranch and Tonasket); these alleles were also detected in the populations Afghanistan-2 and Afghanistan-3 but are absent from the European populations.

Populations from Vac, Hungary, Bratislava, Slovakia and one population each from Iran and Afghanistan display the alleles *Pgm-1a* and *Pgm-2a* that are found in widely separated populations in Kentucky, Oklahoma, British Columbia and north-central Washington. The scattered geographic distribution of these alleles among native and introduced populations suggests a potentially far more complicated pattern of migration than can be resolved with our data. For instance, these occurrences suggest the immigration of populations from either SW Asia or central Europe into eastern North America and subsequent spread to the West. Alternatively, genetic sampling could have occurred repeatedly in the native range with separate introductions in eastern US and western North America.

Detection of other alleles of *B. tectorum* only in its native range suggests that much of the grasses' genetic diversity in Eurasia is unrepresented in western North America. For example, the three alleles *Got-3b, Pgi-2a* and *Skdha*, found in Moroccan and Spanish populations, have not been detected in North America. Such examples further illustrate the stochasticity of genetic sampling in the native range in which unpredictable events probably determine whether one population (and its genome) contributed immigrants compared with others close by. In contrast, the origin of similarity between some North American populations and those in Iran and Afghanistan (e.g. the correspondence of *Mdh-2b* and *Mdh-3b* in Nevada and Washington and populations Afghanistan-2 and -3) is exceptionally problematic and probably reflects the indecipherable migration history of many colonizing species across Eurasia (Baker & Stebbins, 1965).

Our results indicate *B. tectorum* has probably experienced many population fluctuations that have led to major and complex modifications of its genome. Whether this resultant genome has enhanced the species' weediness is an open and vexing question (Baker, 1972). By analysing Eurasian populations of *B. tectorum* we have, however, detected genetic consequences of its introduction into North America. In addition, identifying potential source populations now allows assessment of the direction of and constraints on natural selection for these populations (Brown & Marshall, 1981; Barrett & Husband, 1990).

Acknowledgements

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