GENETIC VARIATION IN *BROMUS TECTORUM* (L.) (POACEAE) IN THE

EASTERN MEDITERRANEAN REGION

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of HEATHER LYNN LINDON find it satisfactory and recommend that it be accepted.

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Chair

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Abstract

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 Bromus tectorum L. (cheatgrass) has spread from its native Eurasian range to North and South America and Australia in the past 200 years. An understanding of the level and genetic structure of populations in the native and introduced ranges is important for understanding the invasion history of cheatgrass and as an aid in its eventual control. The grass's genetic structure was analyzed in 51 populations from Cyprus, Greece (including Crete and Santorini), and Turkey using starch gel electrophoresis. The results were compared to populations in North America and elsewhere in Eurasia. The mean number of alleles and percent polymorphic loci is higher in populations in the Eastern Mediterranean region compared to either North American or other Eurasia populations, so far reported. On average, populations in the Eastern Mediterranean region have higher total genetic diversity than other Eurasian populations but lower total genetic diversity compared to populations in Canada and the Western United States. Genetic variation is distributed equally within and among populations in Eastern Mediterranean populations ($G_{ST} = 0.520$), in contrast to the predominantly among population variation in other Eurasian populations ($G_{ST} = 0.754$). No heterozygotes were detected in any of the

populations. Five novel alleles were detected at the *Mdh-2*, *Me, Pgm-2*, *Tpi-1,* and

6Pgd-1 loci and forty-one multilocus genotypes were detected overall. Thirty-one of

these multilocus genotypes have only been detected in this region. The high level of

genetic diversity in the Eastern Mediterranean region suggests this area is either close to

the origin of the species or has served as a broad conduit for genotypes across the native

range, or both. *B. tectorum* may have spread from the Asia through the Eastern

Mediterranean region to Western Europe, and then carried in commerce onward to new

ranges.

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Dedication

For Christodoulos Andronikos Foufoulides.

Without you, none of this would have been possible.

INTRODUCTION

Invasive species are routinely reported as having both native and introduced ranges (Elton, 1958; Richardson et al., 2000; Brown and Sax, 2004). Although correct in a general sense, this coarse dichotomy masks almost all the geographical and environmental detail needed to unravel the genetic and evolutionary events that have allowed the species to proliferate in its new range(s). Both donor and recipient ranges may consist of disjunct populations, long separated through chance dissemination or by physical barriers, or both (Mooney and Cleland, 2001). As a result, the emigrants rarely encompass the genetic variation of a species across its native range, (e.g., *P. radiata,* Griffin and Critchfield, 1972, Moran et al., 1987. Emigrants are instead much more likely to have been assembled, either accidentally or deliberately, within only part of the native range and thereby encompass only a small fraction of the species' genetic variation (Tsutsui et al., 2000; Sakai et al., 2001). Furthermore, immigrants often arrive repeatedly in a new range, in events that may span centuries and from radically different donor ranges (Thaman, 1974; Amsellem et al., 2000; Mack and Erneberg, 2002 and references therein). Differences in the location and date of emigration increase the likelihood that the genotypes that arrive in separate introductions are also genetically different (Maron et al., 2003).

Examination of the distribution and identity of an invader's genotypes with its native range sharpens our resolution in addressing a variety of fundamental and applied topics about these increasingly damaging species. Comparing the level of genetic variation and the genetic structure of native and introduced populations is a gauge of the rate and character of natural selection and genetic drift within known time frames (Blair

and Wolfe, 2004; Sakai et al. 2001), provides a means to detect the frequency and causes for the emergence of new genotypes, either through post-immigration evolution, including hybridization with natives in the new range (Ellstrand and Schierenbeck, 2000), and as a means to more effectively pair potential bio-control agents with a harmful invader (Müller-Schärer et al., 2004; Thrall and Burdon, 2004). Despite the multiple advantages of such comparisons, these investigations have not been extensively pursued with plants (but see Garcia et al., 1989).

Bromus tectorum L. (cheatgrass, downy brome), a small, diploid ($2n = 14$) annual grass (Hulbert, 1955; Upadhyaya et al., 1986) is a deserving candidate for a detailed investigation of its genetic variation in its native and introduced ranges. Cheatgrass is cleistogamous and almost exclusively self-fertilizing (Hulbert, 1955), though some evidence of out-crossing has been observed in introduced populations in North America (Schachner, 2005; Valliant et al., *in press*) as well as some European populations (Novak and Mack, 1993).

The putative native range of *B. tectorum* spans much of Europe, Southwest and Central Asia, the Middle East and the northern rim of Africa (Pierson and Mack, 1990; Upadhyaya et al., 1986). It has subsequently spread to North America, southern South America, Japan, South Africa, Australia, and New Zealand (Mack, 1981; Upadhyaya et al., 1986). The invasions of *B. tectorum* across temperate grasslands world-wide likely stem from a variety of features, including its phenotypic plasticity (Rice and Mack, 1991a; 1991b; 1991c), its strong competitive ability, especially as a seedling (Harris, 1967) and its highly combustible fuel (Klemmedson and Smith, 1964; Keeley and McGinnis, 2007)).

In North America persistent cheatgrass populations are reported from all U.S. states, except Florida, and across southern Canada (Valliant et al., *in press*). Its genetic variation has been examined in much of the U.S. and Canada (Novak et al., 1991; Oja, 1999; Bartlett et al., 2002; Schachner, 2005; Valliant et al., *in press*), and Western Europe (Novak et al., 1993; Novak and Mack, 1993). The almost totally obligate cleistogamy of *B. tectorum* (Valliant et al., *in press*) greatly enhances the ability to identify source populations for introduced genotypes in the naturalized ranges: introduced populations can be reliably considered as admixtures of genotypes, rather than swarms of post-immigration out-crossing.

Examination of the genetic diversity and structure of *B. tectorum* in its native range has been limited heretofore to populations in Western Europe (mainly west of Carpathian Mountains), although Novak and Mack (1993) analyzed several bulk samples of seeds from Turkish populations. Yet the genetic structure and variation of populations in the Eastern Mediterranean region deserve detailed examination because Asia Minor has likely provided land and sea conduits through which *B. tectorum* has dispersed for millennia (Perissoratis and Conispoliatis, 2003). The long history of commerce, especially by ships, in this region means that cheatgrass has had ample opportunity to move throughout the region as long as 10,000 years ago (Wachsmann, 1998). Additionally, several genotypes now in North America have had been detected in Western Europe (Schachner, 2005, Valliant et al., *in press*) – a plausible region of their emigration. Alternatively, these genotypes may have arrived in North America directly from Eastern Mediterranean populations, as ship traffic has linked this region directly to North America at least for the past 300 years (Field, 1972), and with Turkey specifically

since 1676 (Finnie, 1967). Investigation of the character of these genotypes and their locales could help resolve the origin of genotypes now found in North America.

Populations of *Bromus tectorum* from Greece, Cyprus and Turkey were analyzed in this study. Macroclimates vary across the study area; these differences are most apparent between the coastal climates in Greece and Turkey and climates in central Turkey and mountains in Cyprus (Novara, 1969). On Cyprus (925 km^2), *B. tectorum* appears to be restricted to the southern Troödos Mountains at sites above 900 m (Meikle, 1977), though historical sources indicate that it was present at least 100 years ago in the Messoria Plain (Holmboe, 1914). Within these mountains, cheatgrass occurs on roadsides, rocky slopes and in open forests characterized by *Pinus brutia* and *Cedrus libani* ssp. *brevifolia* (Meikle, 1977); the montane soils are derived from igneous rock. In contrast, cheatgrass is widely distributed and common throughout mainland Greece from sea level to 2000 m elevation, on sandy beaches, along roadsides, and in disturbed agricultural and grazed sites (Strid and Tan, 1991); it is most abundant in northeastern Greece near the Turkish border (H.L. Lindon, pers. obs.). *Bromus tectorum* occurs on some larger Aegean Islands such as Thasos, Samothraki, (Strid, 1998) Enousses Island Group near the island of Chios (Panitsa et al., 1994), Rhodes, Khalki and Tilos (Carlstrom, 1987), but populations apparently do not persist on some of the smaller islets (i.e. Theotokos, Snogerup and Snogerup, 2004). Cheatgrass is common, but not usually abundant, across much of western Turkey in treeless habitats; it is particularly associated with disturbance (Davis, 1965; R.N. Mack, pers. observ.).

I used starch gel electrophoresis to address the following questions: 1) How much genetic variation occurs in Eastern Mediterranean populations of *B. tectorum*? 2) How is

genetic variation partitioned within and among these populations? 3) How does the genetic structure in these populations in the Mediterranean region correspond to the genetic structure in populations in the introduced North American range? 4) Are there interregional differences between populations in these Mediterranean countries? 5) Could any of these populations have served as donors for populations in North America? 6) Do novel (i.e., not detected previously) genotypes occur among these Mediterranean populations?

MATERIALS AND METHODS

Plant Material: Mature caryopses from fifty-one populations were collected in spring-early summer of 2005 and 2006 within a broad swath of the Eastern Mediterranean range of *B. tectorum* (hereafter referred to as the Eastern Mediterranean region) (Table 1): 20 populations in Greece, 19 populations in Turkey and 12 populations in Cyprus. Voucher specimens from Cyprus were also collected and were deposited in the Ownbey Herbarium at Washington State University. Collecting was conducted either in a 500-m^2 area or throughout the entire population, whichever was smaller. In each population, between 20 and 40 seed-bearing plants were collected, where possible, to adequately sample the population's genetic variation; if < 30 individuals occurred at a site, then all individuals were sampled. Collecting was done either at 1-m intervals along roadsides, or haphazardly at approximately 1-3-m intervals in other sites, and the mature panicles were stored in numbered paper envelopes in the field.

Electrophoresis: Seeds were germinated on moistened filter paper in Petri dishes for approximately 10 days or until the plants were 3-10 cm tall; the resulting seedlings

were harvested. At least 30 individuals were analyzed for each population; all individuals were analyzed if fewer than 30 individuals were collected. Electrophoretic procedures followed Novak et al. (1991). Fifteen enzymes were assayed: (alcohol dehydrogenase (ADH), aldolase (ALD), glucose-6-phosphate dehydrogenase (G6PDH), glutamate dehydrogenase (GDH), glutamate oxalacetate transaminase (GOT), isocitrate dehydrogenase (IDH), lucine aminopeptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), shikimate dehydrogenase (SKDH), superoxide dismutase (SOD), and triosephosphate isomerase (TPI).

Alleles names consisted of enzyme abbreviations and, when more than one locus was observed for an enzyme, sequential numbers corresponding to the position of the locus with the most anodally migrating locus given the designation *1*. Alleles were identified with letters starting at *a* for the most anodally migrating allele, *b* for the next fastest allele etc. Nomenclature of loci and alleles followed Novak et al. (1991) and Novak and Mack (1993) except for *Mdh-2*, *Me, Pgm-2*, *Tpi-1*. The discovery of a novel *Mdh-2* fast allele in the Akseki, Turkey and Ardanio, Greece populations means that the previous *Mdh-2a* is now *Mdh-2*b and *Mdh-2b* is now *Mdh-2c*. A novel slow allele at *Me* (designated *Me-b*) was discovered in seven Turkish populations and four Greek populations. The discovery of a novel *Pgm-2* fast allele from the Paranimni, Crete population means that the previous *Pgm-2a* is now *Pgm-2b* and *Pgm-2b* is now *Pgm-2c*. The discovery of a novel *Tpi-1* fast allele in the Athens, Greece population means that the previous *Tpi-1a* is now *Tpi-1b* and *Tpi-1b* is now *Tpi-1c*.

Data analysis: The data were analyzed using the program BIOSYS-1 (Swofford and Selander, 1981) following Novak et al. (1991), Novak and Mack (1993), Bartlett et al. (2002), Schachner (2005) and Valliant et al. (*in press*). The data were entered into the program by specifying the number of individuals possessing a genotype at each of the 25 loci assayed. The data were also entered in a geographical hierarchy divided into the three countries, allowing comparisons within and between regions. Measures of genetic variability include number of alleles per locus (A), percent of polymorphic loci (%P) (using the 99% criterion where a locus is considered polymorphic if the frequency of the most common allele is 0.99), observed mean heterozygosity (H_{obs}) and expected mean heterozygosity (H_{exp}). The Direct Count Method was used to obtain the observed heterozygosity value. Nei's unbiased estimate method (1978) was used to calculate expected heterozygosity in order to account for the small population size.

Measures of allelic diversity were calculated using Nei's (1973, 1977) gene diversity statistics from the variances given in the Wright, 1978 F-statistics analysis in BIOSYS-1. Total allelic diversity (H_T) is broken down into diversity partitioned among populations (D_{ST}) and within populations (H_S) where $D_{ST} + H_S = H_T$. The proportion of among population diversity relative to the total allelic diversity (G_{ST}) is calculated using $G_{ST} = D_{ST}/H_T$. Means of Nei's gene diversity statistics were used to compare the allocation of allelic diversity in Eastern Mediterranean populations with the distribution of allelic diversity in populations of *B. tectorum* in other geographical regions. Wright's (1965) fixation index (F) was calculated where $F = 1 - (H_{obs}/H_{exp})$ to determine the deviation of H_{obs} from H_{exp} for each polymorphic locus. Wright's (1978) F-statistics (an extension of the fixation index) was also calculated.

Nei's (1978) unbiased genetic identity coefficient (*I*) was calculated for all pair-wise comparisons of the 51 Eastern Mediterranean region populations. Means of pair-wise comparisons were averaged to generate a matrix of coefficients for all the populations. The unweighted pair-group method with arithmetic averaging (UPGMA) algorithm (Swofford and Selander, 1981) was used in BIOSYS-1 to generate a phenogram for the 51 Eastern Mediterranean region populations. The values for *I* range from 0.00 to 1.00, with 1.00 denoting two genetically identical populations.

RESULTS

The results of this analysis show that the amount of total genetic diversity of populations in the Eastern Mediterranean region (H_T) is higher than the H_T among all other Eurasian populations previously analyzed. The genetic diversity of these Eastern Mediterranean populations is distributed approximately equally within and among populations. The Eastern Mediterranean populations contain more alleles, more polymorphic loci and more multilocus genotypes than have been detected within populations in any other range analyzed previously. No clear genetic pattern emerged for the dispersal of cheatgrass around the Eastern Mediterranean region or from the Eastern Mediterranean region to other parts of the world

Genetic variability: Genetic variability of *Bromus tectorum* in the Eastern Mediterranean region was determined by analyzing a total of 1503 individuals from 51 populations (Fig. 1; Table 1). A total of 45 alleles were detected at the 25 loci scored with an average of 1.06 alleles per locus. Ten of the 25 loci are variable: *Adh, Got-4, Lap, Mdh-2, Mdh-3, Me, Pgi-2, Pgm-1, Pgm-2, 6Pgdh-1* and *Tpi-1* (Table 2). Variation

at the *Adh-a* allele occurs in five populations from Turkey and Greece among the populations I analyzed. One of the Greek populations, Keramouti (populations no. 42, hereafter the population numbers will appear in parentheses), is fixed for *Adh-a,* while the other populations containing the *Adh-a* allele are polymorphic (Table 2). Populations polymorphic for *Lap* were also detected in all three countries. The population from Panteleimona, Greece (no. 40) is unusual in that it is fixed for the less common *Mdh-2c (Mdh-2b)* and *Mdh-3b* alleles (Table 2). The Ia, Greece (Santorini) (no. 51) population is fixed for the *b* allele at the *Mdh-3* locus and the *b (a)* allele at the *Mdh-2* locus. Two other populations from Greece, Ardanio (no. 44) and Ia (no. 51), are polymorphic at *Mdh-2* but fixed at the *Mdh-3* locus. Variations at the *Pgm-1* and *Pgm-2* loci have also appeared linked in other populations, however, the population from Paranimfi, Crete (no. 49) has the newly detected *Pgm-2a* allele but is also fixed for the *Pgm-1b* allele.

The mean number of alleles per locus (*A*) for all populations was 1.06 (Table 3) with low genetic variation, a likely consequence of a high level of cleistogamy. The average percent of polymorphic loci (*%P*) for all populations is 6.74 and expected heterozygosity (*H_{exp}*) is 0.020 (Table 3). No heterozygotes were detected in the Eastern Mediterranean populations, as a result, *H_{obs}* is 0.000 for all populations. Thirty-six of the 51 populations sampled were polymorphic at one or more loci. The populations from Cyprus are only polymorphic at *Lap, Tpi-1,* or both. Populations from Turkey and Greece have a higher percentage of polymorphic populations than populations from Cyprus, Turkish and Greek populations also have more polymorphic loci than Cypriot populations (Table 4). The highest *%P* is 24% and occurs in two Turkish populations,

Assos (no. 15) and Isebeyli (no. 20) (Table 3). All three countries had populations (17 total) that were polymorphic at *Tpi-1*.

Wright's fixation index (*F*) is 1.000 for all Eastern Mediterranean region populations because no heterozygotes were detected (Table 5). The F_{IT} and F_{IS} values are also all 1.00 for each locus, indicating a significant deviation from random mating. The relatively high F_{ST} values (mean = 0.602) for the polymorphic loci also indicate substantial deviation from Hardy-Weinburg expectations of random mating.

Population differentiation: Nei's gene diversity statistics (Table 6) reveals that in *B. tectorum* populations in the Eastern Mediterranean region the *Lap* locus has the highest total genetic diversity (H_T = 0.419) and the highest proportion of total genetic diversity partitioned among populations (G_{ST} = 80%). The *Me* locus has the highest within population (H_S) and among population (D_{ST}) diversity ($H_S = D_{ST} = 0.089$). The lowest H_T is at the *Pgm-1* locus (0.043), while the lowest H_S (0.011) occurs at the *Adh* locus. The locus *Got-4* has the lowest D_{ST} (0.012). Approximately half of the variable loci have more (G_{ST} >50%) of the genetic variation distributed among populations, while half of the loci have more of their genetic variation distributed within populations (G_{ST} < 50%).

Analyzing the results for each country's populations reveals that populations from Cyprus have the highest H_T (0.354) and the highest G_{ST} (65%) (Table 7). Turkey's populations have both the lowest H_T (0.095) and the lowest G_{ST} (26%). Nei's (1978) unbiased genetic identity coefficients *(I)* were calculated to compare the genetic similarity among the populations in the three countries (Table 8). The mean *I* for all pair-wise comparisons of populations is 0.971. Though numbers are not very different, some

trends can be seen. Populations within Turkey have the highest genetic identity value ($I = 0.984$). The lowest genetic identity value ($I = 0.953$) occurs for populations within Greece. Cypriot and Greek populations are genetically more similar to themselves than they are to populations in other countries. Greek populations are equally different from Turkish and Cypriot populations ($I = 0.963$) and least similar to each other. However, as the confidence intervals for these values overlap any differences can only be taken as indications of general trends.

For a more detailed picture of the genetic relationships among the populations, a UPGMA phenogram was compiled based on Nei's (1978) genetic identity values (Fig. 2). The top part of the diagram consists of monomorphic populations fixed (or nearly fixed) for the most common genotypes. No clear relationships were apparent among the polymorphic populations. Cypriot, Greek and Turkish populations do not cluster with any discernable geographic patterns. The Cretan (Greece) populations (Kamareas and Paranimfi (nos. 48 and 49)) and Santorini (Greece) populations (Perissa and Ia (nos. 51 and 51)), which one might expect to be similar because of these populations' geographic proximity to each other, do not form a cluster in the phenogram.

Multilocus genotypes: The high amount of genetic variability across multiple loci indicates there are many more multilocus genotypes for this region than previously reported anywhere else. In this study 40 multilocus genotypes were detected within the 51 populations (Table 9). Four multilocus genotypes were detected in Cypriot populations, though no novel genotypes emerged. Twenty-four multilocus genotypes were detected in populations from Greece, 15 are novel (Table 10). Twenty-six multilocus genotypes were detected in Turkish populations, 18 are novel (Table 10). The

highest number of multilocus genotypes in a single population is 11 in a population from Assos, Turkey (no. 15). The average of number of multilocus genotypes over all 51 populations is 3.04 per population. The distribution of genotypes among populations in the Eastern Mediterranean region do not show any strong patterns indicating how populations have spread or where certain genotypes may have originated (Fig. 3). The only apparent pattern is that the populations located along the Aegean Sea (i.e. the Peloponnese populations, mainland Greece populations and far western Turkish populations) have more genotypes present within a single population than populations located far from the Aegean Sea (i.e. eastern Turkish populations and populations from Cyprus).

DISCUSSION

The analysis of populations of *Bromus tectorum* from the Eastern Mediterranean region has revealed higher amounts of genetic variation in a species that has previously been characterized by low genetic variation, even within its native range (Novak and Mack, 1993; Oja 1999). The presence of a high number of novel multilocus genotypes and polymorphic populations in the Eastern Mediterranean range compared to the Western European range suggests two different scenarios for the introduction and persistence of populations within those two regions. These findings alter the perception of what constitutes the native range of *B. tectorum*.

Genetic variability: These results illustrate that sampling density can have an effect on the level of genetic diversity of a species, especially in its native range. The detection of novel genotypes, high genetic variation and novel alleles in these Eastern Mediterranean region populations could have been anticipated, given the large number of

individuals sampled (1503). Previous sampling in the native range of *B. tectorum,* mainly Western Europe*,* has been conducted over a much larger area using populations collected as families and bulk-harvested samples (Novak and Mack, 1993; Oja, 1999). Although the mean values here are lower than the average values assembled by Hamrick and Godt (1990) for selfing plant species ($A = 1.31$, *%P* $= 20.0\%$, and $H_{exp} = 0.074$), the *A* and *%P* values are significantly higher ($p < 0.001$; JMP, 2004) than values in the previous study of Eurasian populations ($A = 1.02$, *%P* $= 2.12$ and $H_{exp} = 0.005$) and North American populations ($A = 1.03$, *%P* $= 3.63$ and $H_{exp} = 0.009$) (Table 4).

The higher values for alleles per locus, percent polymorphic loci and expected heterozygosity among these populations from the Eastern Mediterranean region, compared with values reported earlier from the native range (European and Southwest Asian populations) have several explanations. Results from earlier reported populations may reflect their samplings. Seeds used by Novak and Mack (1993) from Southwest Asia were accessions from the USDA Western Regional Plant Introduction Laboratory in Pullman, WA that may have been collected as bulk-harvested samples and/or subject to multiple grow-outs after their collection (Novak, 1990). The rare alleles detected from these samples in low frequencies (e.g. *Adh-a* $= 0.120$) or that were fixed (e.g. *Idh-b*) may be products of a population bottleneck resulting from successive grow-outs (Allard, 1988). Many of these rare alleles were found in higher frequencies in populations collected from the Eastern Mediterranean region than were detected in the Southwest Asian samples. Five novel alleles were also detected among the Eastern Mediterranean populations analyzed here. Only one locus (*Adh*) in one of three Turkish populations analyzed by Novak et al. (1993) (DeGöreme) showed any polymorphism; the discrepancy

between the results of these two studies suggests that bottlenecks or sampling error, or both, may have occurred in the USDA samples analyzed. As a result, these bulk samples may not be an accurate representation of the genetic variation of these Turkish populations and almost certainly not reflective of Turkish populations as a whole.

In a similar genetic study of *B. tectorum* Oja (1999) characterized the genetic structure of populations in Western Europe, Greece, Turkey, Russia and Syria. Oja's allozymic study showed similar results to mine: low genetic variation in populations from Western Europe, in contrast to high genetic variation in populations from Turkey and Syria. Oja found six multilocus allozyme lineages (or multilocus genotypes) in 21 bulk-harvested Turkish populations; four out of twelve loci (33%) analyzed were polymorphic. The highest number of multilocus allozyme lineages detected in any country in Western Europe has been three among German populations, although eight of the ten German populations were fixed for the most common lineage. Only one multilocus allozyme lineage was detected by Oja (1999) in a Greek population, however, only one accession was analyzed.

The discovery of extensive isozyme diversity in Turkish populations and the relatively higher amount of genetic diversity detected by Novak and Mack (1993) in the bulk harvested populations from Iran and Afghanistan suggests that populations in the Eastern Mediterranean region may contain more genetic variation than that contained within any other region's populations analyzed so far. Genetic variation in Turkish populations analyzed here, where previous analysis showed none, suggests a reduction in genetic variation occurred in the bulk populations used by Novak and Mack (1993). Alternatively, the genetic variation may not have been present in these populations upon

their collection, and the grow-outs had consequently no effect on genetic variation. The Iranian and Afghani populations analyzed by Novak and Mack (1993) may have experienced a similar reduction in genetic variation due to bottlenecks after multiple grow outs, although the paucity of populations from either Turkey, Iran and Afghanistan in this earlier investigation makes resolution here problematic. Variation in the Iranian and Afghani populations, despite grow outs and bottlenecks, suggests that even more genetic variation, as yet undetected, occurs in populations from these countries. Populations of the widespread *Hordeum spontaneum* C. Koch (wild barley) also contain greater genetic variation in Southwest Asia than in other parts of the plant's introduced and native ranges (Nevo et al., 1979; 1986a; 1986b). A more thorough investigation of *B. tectorum* populations from Southwest Asia may well reveal more novel alleles and genotypes and potentially greater levels of genetic diversity

What accounts for the pattern of genetic variation across Europe and North America? *Bromus tectorum* may have been introduced into Europe from Southwest Asia. In this scenario the species expanded northward after cessation of Pleistocene glaciation (Tzedakis, 1994) or via human migration. The lower genetic variation in Europe would then be the result of a genetic bottleneck during range expansion or simply fewer of the genotypes that arose in Central Asia dispersed westward. Furthermore, the genotypes in North America may have arrived from the Eastern Mediterranean region via a stepping stone pathway via Western Europe (*sensu* Slatkin, 1985). It is unlikely that *B. tectorum* moved directly to North America from the Eastern Mediterranean region, although some direct ship commerce has operated between the two regions for about 300 years (Finnie, 1967). Though direct trade to Asia was forbidden to the colonies, merchants from

Boston, Philadelphia, Baltimore and New York traded under British flags with the ports of Iskenderun, Izmir and Istanbul for fruits, nuts, raw wool and hides (Finnie, 1967). An analysis of the genetic structure of populations in the Balkans region, northwest of Greece and Turkey, could prove informative for discerning the movement by land of *B. tectorum* into Southeast Europe and onward to the West (Gibbons, 1891).

Bromus tectorum is apparently continuing to expand its range to the northwest across Europe. Buchenau (1901) lists *B. tectorum* as rare in northwestern Germany (*e.g.* around Bremen and Oldenberg); he reports that populations in these areas only became established through accidental dispersal. Although cheatgrass is not native to the British Isles populations do occur there, although not commonly (C.L. Kinter, pers. obs.). Stace (1997) reports *B. tectorum* [which he terms *Anisantha tectorum* (L.) Nevski] as naturalized in S. Wales, the Channel Islands, and Southwest England and Southern Ireland. Tutin et al. (1980) lists *B. tectorum* as occurring in Albania, Austria, Belgium, Bulgaria, Corsica, Crete, Czechoslovakia, Denmark, France, Germany, Greece, Hungary, Italy, Luxemburg, the Netherlands, Norway, Poland, Portugal, Romania, Russia, Sardinia, Sicily, Spain, Sweden, Switzerland, Turkey, Yugoslavia, and as naturalized in Britain, Finland and the Baltic region of Russia.

The lack of heterozygotes detected in the 1503 individuals sampled here is intriguing, given the recent detection of heterozygotes in the introduced range in North America (Valliant et al., *in press*). In a predominately cleistogamous plant such as *B. tectorum* outcrossing is rare, and allelic variants are few, with the majority of individuals homozygous across all loci (Novak and Mack, 1991; Novak and Mack 1993; Bartlett, 2002; Schachner, 2005; Valliant et al., *in press*). Consequently, if outcrossing were to

occur, it would go undetected because the alleles would be the same and no heterozygote band would appear. Heretofore, only ten heterozygotes have been detected with allozymes out of the 9506 individuals sampled (0.1%), eight from the introduced range in South Dakota (Schachner, 2005) and Ontario (Valliant et al., *in press*) and two from the native range (Novak and Mack, 1993). A separate study of allozyme diversity in *B. tectorum* in Eurasia also failed to detect any heterozygotes (Oja, 1999). The occurrence of outcrossing events can vary widely from year to year (Adams and Allard, 1982) and are sometimes influenced by environmental factors, such as moisture (Brown et al., 1978). Seeds used here may have been collected in a year that did not prompt outcrossing. Alternatively, a method that uses a more variable measure of genetic diversity than isozymes, such as microsatellites or AFLPs, may detect heterozygotes more readily (Green et al., 2001, Ramakrishnan, 2004).

Population differentiation: An average value for the mean total genetic variation (H_T) among populations for selfing species is 0.334, with about 51% (G_{ST}) of the variation among populations and 49% within (Hamrick and Godt, 1990). The H_T for the populations in the Eastern Mediterranean region is 0.116, approximately twice that of populations in Eurasia as a whole ($H_T = 0.087$). Total genetic diversity of populations in the Eastern Mediterranean region may be higher than the amount found heretofore in Eurasian populations for a number of reasons. For example, populations analyzed here are a subset of all Eurasian populations, and the Eastern Mediterranean region has now been more extensively sampled than the rest of Eurasia. Furthermore, the Eastern Mediterranean region may be nearer to the center of origin for *Bromus tectorum* and consequently the populations there will contain more genetic diversity (Stebbins, 1981).

Populations in the Eastern Mediterranean region also display significantly more within population diversity ($H_S = 0.046$) than populations from Eurasia as a whole ($H_S = 0.009$), but a lower H_S than populations in Canada ($H_{S=}0.076$). The G_{ST} for this region is only 52%, whereas for populations in Eurasia as a whole H_S is 75% and in Canadian populations it is 40%.

Genetic diversity statistics for the Eastern Mediterranean populations were higher than those for both the Eastern U.S. populations (Bartlett et al., 2002) and the Midwestern U.S. populations (Schachner, 2005) but similar to the statistics for Western U.S populations (Novak et al., 1991). Genetic indices for populations in the Eastern Mediterranean region were strikingly similar to values for all 60 North American populations combined: ($H_T = 0.115$, $H_S = 0.046$, $D_{ST} = 0.069$, $G_{ST} = 0.478$ for North American populations) (Novak et al., 1990). The radically different introduction histories for *B. tectorum* among the four North American regions (i.e. Western U.S., Eastern U.S., Midwestern U.S., Canada) (Mack, 1981; Novak and Mack, 2001; Bartlett et al., 2002; Schachner, 2002; Valliant et al., *in press*) may account for the variation in H_T between the North American regions. More frequent or recent introductions, or both, could have led to a higher H_T value in the Western U.S. compared to the other North American regions.

In the introduced ranges of the Eastern and Western U.S. populations also have somewhat more diversity among than within populations (56% vs. 62% respectively). This high mean total and within population genetic diversity may be another result of multiple introductions to the same location. Alternatively, more diversity partitioned among populations is expected in introduced ranges where founder events have recently occurred due to factors, such as genetic drift and low gene flow (Brown and Marshall,

1981). Populations in both the Eastern Mediterranean region and Eurasia have more of their genetic diversity partitioned among populations rather than within populations. G_{ST} (52%) for populations in the Eastern Mediterranean region is closer to the value for the average value for selfing plants (51%) (Hamrick and Godt, 1990) than to the value among populations in Eurasia ($G_{ST} = 75\%$). The high proportion of among population variation observed in populations in Eurasia may again reflect the vast range and comparative low density of collecting so far employed in much of Europe for *B. tectorum*.

Island populations may have lower genetic diversity than their mainland counterparts due to genetic drift and genetic sampling error, as products of their introduction to the island (Frankham, 1997). Among Cypriot populations this expectation is met: only two of the twenty-five loci scored are variable with only two alleles per each variable locus, although more sampling of the island seems advisable. For example, the plains (a mix of native steppe and agricultural fields) in the Messaria region of Cyprus were reported to have cheatgrass populations in 1904 (Holmboe, 1914). These areas are today either no longer cultivated or largely inaccessible because of the current Turkish occupation. Consequently, no populations were collected in this area. Collection of *B. tectorum* in western Cyprus (if populations still persist) may reveal more genetic variation among the island's populations, the product of its different environment from that in the mountainous central part of Cyprus, the site of all my sampling.

Only two populations were collected on each of the other islands I visited, Crete and Santorini, so conclusions about the genetic structure of these islands' populations are quite tentative. For Santorini (73 km^2) the two collections do reveal several polymorphic

loci and the fixation of a rare allele (*Mdh-3b*) in the Ia population. The fixation of the

Mdh-3 locus for the *b* allele without a corresponding *Mdh-2c (Mdh-2b)* allele is unusual;

the two loci have previously been seen linked together (Novak and Mack, 1993;

Schachner, 2005)

Difficulties in visiting more remote islands, such as Corfu or Rhodes also

precluded comprehensive island sampling. Populations on these islands may provide

clues as to dispersal of *B. tectorum* between Southern Greece and Turkey, or Northern

Greece and Italy. Another Aegean island, Chios, was an important port for shipping in

the 19th and 20th centuries (Harlaftis, 1996), and consequently its *B. tectorum* populations

may reflect numerous introductions. Sampling only two islands among the

approximately 3,000 Greek islands and ten Turkish islands in the Aegean Sea likely

provides an admittedly limited picture of the genetic variation in this region. Identifying

which islands support populations of *B. tectorum* may also reveal how seeds are moved

around the Aegean Sea. Snogrup and Snogrup (2004) report the disappearance of a *B.

tectorum* population from a small islet near the larger island of Skiros. They contend that

many annuals establish only after disturbance (particularly grazing) and that annuals

often do not persist with succession of the native community.

Crete was not collected extensively, but both of the populations analyzed had

polymorphic loci. This island is 160 km south of the Greek mainland in the; its more

southerly locale may allow plants to mature earlier than their counterparts elsewhere in

the study area (Hogan, 2003). For example, by June 2006, many *B. tectorum* populations

had already matured or had been consumed entirely by livestock. Needed is a more

thorough analysis of *B. tectorum* populations on Crete to determine the level of genetic variation among the island's populations

Multiple introductions have likely resulted from the constant ship traffic to islands close to the Greek mainland for millennia (Wachsmann, 1998) and would in turn account for high levels of genetic diversity in these islands' populations. Low diversity on these islands would be surprising, given the ample opportunity for island-to-island cheatgrass dispersal since the beginning of seafaring in the Aegean in the Upper Paleolithic (approx. 10,000 y.b.p.) (Wachsmann, 1998). More thorough sampling of the islands in the Aegean Sea would provide a much better picture of the distribution and pathways of dispersal for *B. tectorum* in this region.

Interregional genetic similarity within Eurasia: Cyprus, Greece and Turkey have topographical and environmental features that vary widely. Cyprus has a forested central mountain range (annual precipitation, 500 - >1000 mm); its rocky coastal areas receive 300-500 mm annual precipitation (Novara, 1969; Meikle, 1977). The Greek islands in the eastern and southern Aegean Sea receive 400-800 mm annual rainfall (Novara, 1969), whereas the mountains in northern and western Greece mainland receive >1200 mm of precipitation per year (Strid and Tan, 1991). Turkey's Mediterranean coast supports forests of *Pinus brutia, Pinus nigra, Cedrus libani* and *Abies cilicica* that receive 600-1200 mm of rainfall per year, while the more inland Anatolian Plain supports steppe with 200-400 mm of annual precipitation (Atalay, 1994).

Comparing gene frequencies, phenotypic characteristics and environmental factors would be invaluable for understanding the relationship between genotypes and the invasion potential of *B. tectorum* (Husband and Barrett, 1996). Discovery of the same

specific genotypes in the same microhabitats across the entire region would be needed to find such a link. In this study the UPGMA phenogram (Fig. 3) does not show a segregation of populations by country, proximity to the sea, or any discernable simple clinal or environmental patterns. This lack of geographic clustering of genotypes may indicate that genotypes occur locally among habitats on a scale too fine to be detected without more specific location data. Alternatively, their distribution might be the product of continual movement of these genotypes since antiquity. These results are at variance with those of Oja (1999), who found similar multilocus allozyme lineages of *B. tectorum* in regions with similar environments, including Turkey, Syria and central Russia. In a common greenhouse experiment differences in growth characteristics (height, leaf width, tiller number at 60 days, culm diameter, vegetative biomass, panicle biomass, and days from emergence to flowering) of *B. tectorum* were due to genotypic differences and not phenotypic plasticity at the regional level (Kinter, 2003). Using seed germination (seed dormancy and smut resistance) and plant growth characteristics (vernalization, proportion flowering, weeks to flowering, and seed yield per plant) genotypic differences at the population level have also been characterized in populations from Nevada and Utah (Ramakrishnan, 2004). Nevo et al. (1979, 1986a, 1986b) suggest that genetic variation in *H. spontaneum* (wild barley) in Iran, Turkey, and Israel is correlated with environmental conditions. Factors, such as temperature and rainfall, are predictors of genetic diversity in *H. spontaneum.* Clegg and Allard (1972) found different genotypes in *Avena barbata* linked to different environments in the native and introduced ranges.

Nei's genetic identity values (Table 5) suggest that among the three countries' populations Turkish populations are most similar to each other ($I = 0.980$). These

Turkish populations were collected mainly near the Mediterranean Sea coast and from localities that receive similar amounts of rainfall. Plants in this area may be under similar selective pressures. Nei's genetic identity values for populations from Greece are least similar to each other ($I = 0.953$) – potentially a product of repeated introductions, isolation by high relief on the mainland and geographic isolation among island populations. Among the populations analyzed here, populations in Turkey and Cyprus are the most similar to each other ($I = 0.980$). This close genetic similarity likely has several sources, including similar selection regimes or extensive genetic exchange through long-standing commerce between countries that are separated by as little as 75 km of the Mediterranean Sea (Haldane, 1993; Peltenburg et al., 2001), or both.

Multilocus genotype distribution: Multilocus genotypes based on allozymes of *B. tectorum* have been used repeatedly to unravel the immigration history of the grass in its introduced range (Novak and Mack, 1991; Novak and Mack, 1993; Schachner, 2005; Valliant et al., *in press*). The same tool may also identify factors affecting the distribution of *B. tectorum* in the native range. The average number of *B. tectorum* genotypes for the Eastern Mediterranean region (3.04) is almost twice the number reported previously for populations in the native range (1.56) (Novak, 1990). Twenty-eight multilocus genotypes are novel, six were previously reported in North America (Schachner, 2005) and five were previously reported from other Eurasian populations (Novak, 1990). It is unlikely that all these multilocus genotypes arose independently via separate mutation events at either the population or country level. More likely these genotypes are the result of rare outcrossing events within a population (Hamrick and Godt, 1990) repeated introductions from other populations (Novak and Mack, 1993), or a

combination of the two. Two exact matches to multilocus genotypes previously detected in North America but not in the native range are among the Eastern Mediterranean genotypes: the *Tpi-1c* variant (Schachner, 2005; Valliant et al., *in press*) and the *Mdh-2b, Mdh-3c* variant (Schachner, 2005).

The accidental spread of seeds in ship ballast and packing materials is a classic mode of plant dispersal (Ridley, 1930; Mack, 2003), as is dispersal as seed contaminants in crop seeds (Mack and Erneberg 2002). Dispersal of *B. tectorum* in the Eastern Mediterranean region may have begun by sea, starting at least 10,000 y.b.p., if not earlier, with Cyprus acting as one link between Asia Minor and Europe and the Aegean (Wachsmann, 1998). *Bromus tectorum* is often a contaminate of seed lots of cereals (Mack, 1981), and it has played this role for millennia: remains of cheatgrass seeds have been found as a weed in wheat storage in Bronze Age (approx. 10,000 y.b.p.) archeological sites in the Balkans (Marinova, 2003). Furthermore, cities throughout the Eastern Mediterranean region such as Cyrenaica in present day Libya and Ephesus in present day Turkey engaged in commerce for wheat with Greek city-states during food shortages in Hellenistic times (Shipley, 2000). The constant need for grain combined with the relative ease of sea transportation has meant that the wheat trade in the Mediterranean has continued since ancient times. In the 16th century western countries of the Mediterranean in both Europe and Africa relied heavily on wheat producing countries with easy access to the sea such as Cyprus, Greece (including certain Aegean islands such as Patmos), Turkey, Egypt and Russia (Braudel, 1966).

Russian wheat was commonly shipped, particularly in the early 19TH century through the Eastern Mediterranean region from Odessa on the Black Sea (Harlaftis,

1996). In fact, grain shipping increased exponentially during the early 19TH century due

in part to demands created through increased European Industrialization. For example,

more than 600 million kg of grain (including wheat) was shipped from Southern Russia

in 1910. Wheat was shipped from Russian Black Sea ports to Britain, France, Holland,

Italy and Germany (Harlaftis, 1996). This commerce in grain makes it more likely that

genotypes of *B. tectorum* from the Black Sea region were introduced recently, and

repeatedly, into various countries bordering the Mediterranean Sea as well as Western

Europe.   This recent and repeated introduction in different locations may explain the

relatively low genetic variation in Western European populations compared to Eastern

Mediterranean and Southwest Asian populations.

Some alleles found previously in Europe and North America, such as the *Got-4c*

variant (Novak and Mack, 1991; Novak and Mack, 1993; Schachner, 2005; Valliant et

al., *in press*), are not present among the populations analyzed here. These alleles may be

absent because they are not well adapted to the environment of the Eastern Mediterranean

region, though this explanation is unlikely given the grass's occurrence in the U.S.

Intermountain West. Alternatively these alleles may have arisen separately in Western

Europe. Alleles found east of the Eastern Mediterranean region that were not found in

this study such as *Skdh-c* and *Idh-b* (Novak, 1990) may not be suited to this region's

environment, or may simply have been lost as *B. tectorum* migrated from the East.

Turkish populations analyzed here display only *Got-4a* and *Got-4b* alleles, while Greek

populations have *Got-4b* and *Got-4d* alleles. The *Got-4a* allele had been previously

detected only in bulk-collected samples from Iran, and the *Got-4d* allele from a

population in Bayreuth, Germany (Novak and Mack, 1993). The *Got-4d* allele has also

been reported in populations in the North American range, including populations from Waterton, Alberta (Valliant et al., *in press*), Martin, South Dakota, and Mule Creek, Wyoming (Schachner, 2005).

Among the novel genotypes found in the Eastern Mediterranean range are the *Mdh-2c (Mdh-2b)* and *Mdh-3b* (NA5) and *Tpi-1b (Tpi-1a)* (NA8), variants found in North America (Schachner, 2005, Valliant et al., *in press*) but unknown in the native range until detected in this study. The Eastern Mediterranean populations with these multilocus genotypes are from diverse geographic regions. As a result, it is currently impossible to pinpoint an origin for the introduced populations. The *Mdh-2c* (*Mdh-2b)* and *Mdh-3b* genotype is found only in four Greek populations, though it is unlikely that an introduction occurred directly from Greece to the Midwestern US. Populations polymorphic at the *Lap* locus were detected, whereas only fixation for the *a* or *b* alleles had been reported previously in the native range (Novak and Mack, 1993). The *Tpi-1c* (*Tpi-1b)* variant occurs in both Turkish and Greek populations, but again the wide distribution of the genotype suggests that seeds were not introduced directly from the Eastern Mediterranean to North America. More likely the Eastern Mediterranean region is a conduit through which genotypes have moved from the center of diversity (the Middle East) through Western Europe and into the rest of the world.

Conclusions: Although the number of individuals analyzed from the native range of *B. tectorum* is still roughly half the number analyzed from North America (Table 4), the argument made by Novak and Mack (1993) for a reduction in genetic diversity in the introduced range is strengthened by the analysis of these additional Eurasian populations. The data reported here for populations in the Eastern Mediterranean region increases the

number of detected alleles in the native range from 45 to 50 and the percent of variable

loci from 52% to 53%, still well above the introduced range (33 and 28% respectively)

(Novak et al., 1991; Schachner, 2005; Valliant et al., *in press*).

This study also addresses other questions raised by previous investigations on the

genetic diversity of *B. tectorum,* such as the geographic origins of introduced populations

(Novak et al., 1991; Bartlett et al., 2002; Schachner, 2005; Valliant et al., *in press*).

Analysis of Eastern Mediterranean populations reveals novel alleles and novel multilocus

genotypes within the grass's native range. Some of these novel multilocus genotypes

were also found in introduced populations in North America (Schachner, 2005; Valliant

et al., *in press*). Discovery of matching genotypes in Eastern Mediterranean populations

does not fully address the origin of populations in North America: other regions with

highly diverse populations (e.g. Southwest Asia, *sensu* Novak and Mack, 1993) may also

contain these genotypes and have been the ultimate source for the introduced populations.

Needed is further investigation of Western European populations to provide

comprehensive understanding of the link between Eurasia and introduced populations.

I was able here to characterize the type and amount of genetic variation in

populations of *B. tectorum* in the Eastern Mediterranean region and to describe the

partitioning of genetic variation within and among populations in this region. The

genetic structure of populations in the Eastern Mediterranean region was compared to the

genetic structure of populations from the introduced range in North America (Novak et

al. 1991; Bartlett et al., 2002; Schachner, 2005; Valliant et al., *in press*) and to previously

analyzed Eurasian populations (Novak and Mack, 1993; Oja, 1999). The results reported

here reveal that there is more genetic variation within and among populations of *B.*

tectorum in the Eastern Mediterranean region compared to populations across the European and North American ranges of this species. These results add to our understanding of how the wide-ranging dispersal of one species can hold genetic consequences far-removed from its native range.

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Fig. 1. Collection map of the 51 *Bromus tectorum* populations analyzed in the Eastern Mediterranean. The numbers correspond to populations described in Table 1.

Greece

Turkey

Cyprus

Crete
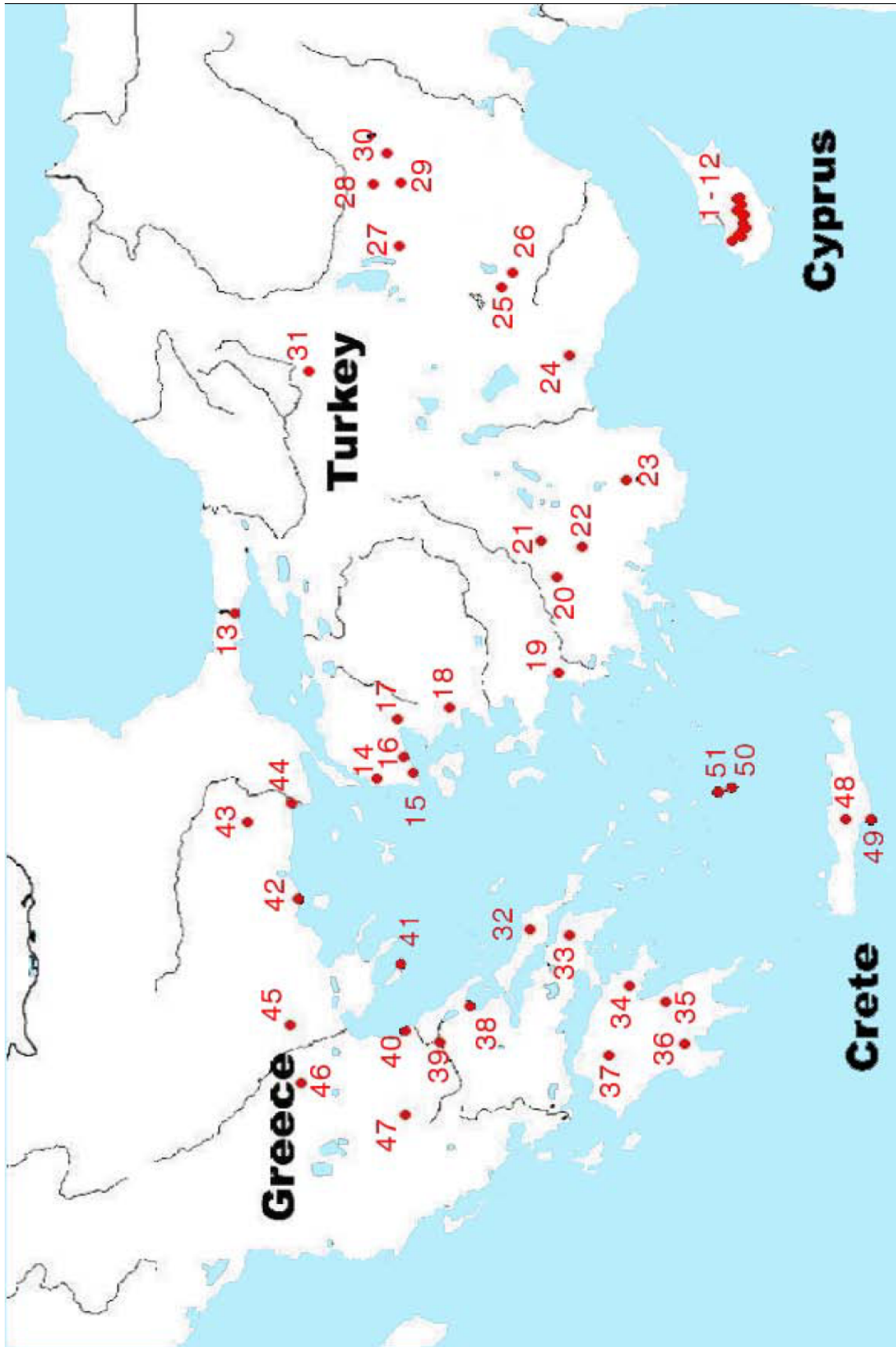
Table 1. Collection localities and habitat descriptions for the 51 *Bromus tectorum*

populations analyzed in this study. Populations were collected by the author unless

otherwise indicated.

Population	Locale
1. Tripylos, Cyprus	27 May 2005. Summit of Mt. Tripylos, in vicinity of fire lookout station. Along gravel road and surrounding rocky area. Plants ranging from immature (green tinged with purple) to mature (yellow). Associated with other grasses in a cedar forest. 1362 m ele.
2. Tripylos Road, Cyprus	27 May 2005. Plants growing mainly along road, down from the summit of Mt. Tripylos. In isolated patches, 0.5 m -15 m apart along the road, the road while not freshly dug, was well plowed, plants growing on/in/around rocks.

Table 1. continued.

Population	Locale
3. Pano Amiandos, Cyprus	28 May 2005. 2 km from Pano Amiandos. S-facing slope on roadside viewpoint above Pano Amiandos overlooking old asbestos mine. Growing on gravelly soil with other grasses and pines. Plant immature (green) to mature (purple to yellow stage). Area approx. 60 m by 20 m, 1600 m ele.
4. Spilia, Cyprus	28 May 2005. W of Spilia in abandoned gravel road and gravelly slope, E- facing slope below a house. Vegetation sparse, few other plants, adjacent to tall pine forest. Gravely road/soil. Plants almost all mature (purple or yellow stage). Approx. 1100 m. ele.
5. Palechori, Cyprus	28 May 2005. Along paved roadside, E- facing slope 1 km West of Palechori. Plants along side and steep slope of gravel hill for about 5 m and associated with other weedy species. About 1000 m ele.

Table 1. continued.

Population	Locale
6. Stavros, Cyprus	4 June 2005. 10 km N on road from Stavros and along gravelly road below main road, E-facing slope. Growing on/among igneous rock formations. Plants all mature (purple or yellow stage). Plants small and scarce, possibly due to lower altitude (900 m).
7. Moutii Kou Stavros, Cyprus	4 June 2005. E-facing slope of steep hill at E lookout point on Moutii Kou Stavros Nature Trail. Dominant on slope; plants all short and mature (yellow). 1200 m ele.
8. Kykkos, Cyprus	4 June 2005. W, NW and N side of mountain (Tomb of Makarios). On a gravel road next to and below paved road leading to tomb for about 100 m. Along roadside with other bromes and pine trees. Plants all mature (yellow), voucher specimen collected. 1300 m ele.

Table 1. continued.

Population	Locale
9. Odou, Cyprus	9 June 2005. Small road to Levadios from Odou, 1-2 km on this road next to water cistern on a gravel road. Plants abundant along gravel path and main road. WNW slope, plants all mature (yellow). Next to abandoned grape field. Area approx 20 by 50 meters. 1000 m ele.
10. Maxeras, Cyprus	9 June 2005. Just below peak of Kionia NW of Vavatsinia. Plants along road for approx 100 m to gate at A.T.H.K.CY.T.A. antenna,. Seeds fully mature. Few other plants, some pines. Dry rocky soil. 1423 m ele.
11. Chionistra, Cyprus	15 June 2005. Chionistra (or Mt. Olympus). W facing slope on dirt road below Cyprus telecommunications base. Growing with pines, low scrubby plants, and junipers. Clayey soil. Plants still unripe (green). Probably the largest area (50 x 50 m) covered by *B. tectorum* seen in Cyprus. 1951 m ele.

Table 1. continued.

Population	Locale
12. Prodromos, Cyprus	15 June 2005. Hill opposite Lemthou, on the road from Palaiomylos 2-3 km towards Prodromos on the road in the village dump. Plants fully mature (yellow). Pines and many other bromes present. Soil gray/gravelly. 1200 m ele.
13. Istanbul, Turkey*	5 June 2006. Collected by T. Ekim near Istanbul University, precise location unknown.
14. Troy, Turkey**	21 May 2005. Scattered plants in the ruins across the site. Usually only a few plants together; well past maturity and plants may have already lost some caryopses.
15. Assos, Turkey**	22 May 2005. Scattered plants in amongst the ruins of this site.

Table 1. continued.

Population	Locale
16. Kuçukkuyu, Turkey**	21 May 2005. Roadside fruit stand on steep winding road < 5 km west of Kuçukkuyu. In and around the walls and retaining wall for this fruit/honey stand. Coniferous forest surrounds the site.
17. Edremit, Turkey**	22 May 2005. Small population; in a recently disturbed area (vehicle parking area and rubble dump) next to a filling station. Site is approx. 2 km south of Edremit (Rt E-87).
18. Bergamon, Turkey**	22 May 2005. Plants amongst the ruins; scattered; no large clusters.
19. Selçuk, Turkey**	24 May 2005. Small population in a restaurant parking area and adjacent vacant lot, about 4 km south of Selçuk (Rt 550). Site is on a long sloping grade into Selçuk; on left hand side of road as one proceeds downhill; near Kusadasi.

Table 1. continued.

Population	Locale
20. Isebeyli (Nazilli), Turkey**	25 May 2005. Hamlet that merges with the larger town, Nazilli. Along roadside in disturbed ground, directly across road from a filling station-restaurant-tourist shop area.
21 Hierapolis, Turkey**	25 May 2005. Although plants did not occur in high densities here, they were all through the ruins site; often occurring at the base of the crypts (collected two populations here within 100 m of each other).
22. Aphrodisias, Turkey**	25 May 2005. Plants locally abundant here; throughout the ruins site.

Table 1. continued.

Population	Locale
23. Sogut, Turkey**	May 2005. Small scattered population at a very small village, collected in the traffic median flower bed. Some plants had been mowed a few hrs earlier; others along the roadside. Site is in the Taurus Mountains and the phenology of these plants was definitely delayed from those seen elsewhere in Turkey. Almost all the plants were green but the caryopses appeared full (doughy stage). Overstory was arboreal in the immediate vicinity.

Table 1. continued.

Population	Locale
24. Akseki, Turkey**	29 May 2005. Rt 695 5 km from Akseki at a major filling station/restaurant/tourist shops area. Scattered plants along the roadside beside this filling station. In the Taurus Mtns. Surrounding vegetation dominated by *Pinus* and *Cedrus*.
25. Konya, Turkey**	29 May 2005. Most plants collected on the grounds of the Sufi mosque downtown. The remainder collected in the driveway of the restaurant immediately beside the garden area for the mosque or in the traffic island in front of the mosque. *B. tectorum* is abundant Konya seen along the roadways and thoroughfares leading into the city.

Table 1. continued.

Population	Locale
26. Catalhuyuk, Turkey**	29 May 2005. Neolithic excavation site SSE of Konya. On the grounds of this site; very abundant here (as abundant locally as any site I saw in Turkey). The coverage of *B. tectorum* here approached 50% locally. Plants around the museum building as well as locally abundant all across the site.
27. Aksaray, Turkey**	29 May 2005. At junction of main hwy (E-90) and the road to Nevsehir (Rt 300). Across the street from a large filling station/restaurant/tourist shop area. Plants were locally abundant at roadside.
28. Göreme, Turkey**	30 May 2005. Scattered plants in the Göreme church site and down the hill immediately outside this site.
29. Uchisar, Turkey**	30 May 2005. Nevsehir area. At roadside overlooking Pigeon Valley. On slope in dumped soil. Locally abundant.

Table 1. continued.

Population	Locale
30. Urgup, Turkey**	30 May 2005. City Center, Mustafa Hotel; on hillside next to driveway. Disturbed site adjacent to hotel flowerbeds; broken tiles and rocks in the site. Anatolian Plateau in Nevsehir area.
31. Ankara, Turkey**	31 May 2005. At base of old city wall 75 m uphill from the Museum of Anatolian Civilizations, Ankara.
32. Delphi, Greece**	July 2005. Delphi, Greece. In the town on steep embankment.
33. Athens, Greece	22 May 2006. Emettos mountain overlooking Athens University, growing about halfway up the mountain along roadside on a gravel turnout.
34. Arachnea, Greece	24 May 2006. Olive grove; E of Arachnea, very abundant on rocky dirt paths. (N 37°37.167', E 22°57.147').

Table 1. continued.

Population	Locale
35. Varvitsa, Greece	25 May 2006. Roadside outside of Varvitsa. Red dirt soil, plants interspersed with many other grass/weedy species. (N 37°16.748', E 22°39.486').
36. Artemitsa, Greece	26 May 2006. Roadside between Artemitsa and Tripi, gravel road turn off after roadside tavern. (N 37°04.708', E 22°16.232').
37. Platanitsa, Greece	26 May 2006. Along roadside E of Platanitsa. (N 37°56.708', E 21°51.315').
38. Melissatika, Greece	27 May 2006. Along road and in almond grove, very spread out, packed soil. (N 39°23.631', E 22°54.698').
39. Larissa, Greece	28 May 2006. Along dirt roadside, growing with wild wheat etc. (N 39°38.354', E 22°24.139').

Table 1. continued.

Population	Locale
40. Panteleimona, Greece	28 May 2006. Along beach road next to railroad. (N 40°00.662', E 22°35.476').
41. Pefkochori, Greece	28 May 2006. Along roadside, outside Pefkochori center; also many plants growing in olive grove. (N 39°58.818', E 23°36.610').
42. Keramouti, Greece	29 May 2006. Along beach road (sandy) east of village of Keramouti, seaside. (N 40°51.381', E 24°41.587').
43. Kotronia, Greece	29 May 2006. Along roadside from Kotronia towards Alexandropoli in pine forest habitat. (N 41°07.271', E 26°10.216').
44. Ardanio, Greece	30 May 2006. Abundant along the roadside from Ardanio to Alexandropoli. (N 40°56.516', E 26°12.2981').

Table 1. continued.

Population	Locale
45. Cherso, Greece	30 May 2006. Along roadside headed E out of Cherso; growing with aspens and grasses. Common along edge. (N 41°05.685', E 22°46.361').
46. Arissa, Greece	30 May 2006. 500 m from Arissa, next to the parking lot of Avin gas station; near agricultural field. (N 40°47.361', E 21°52.694').
47. Meteora, Greece	31 May 2006. Along the road to monastery of Agia Sofia. (N 39°43.169', E 21°38.208').
48. Kamareas, Crete, Greece	4 June 2006. On road between Voriza and (closer to) Kamares at the Paradosiako tavern. (N 35°09.057', E 24°49.909').

Table 1. continued.

Population	Locale
49. Paranimfi, Crete, Greece	4 June 2006. Un-grazed enclosed field in pastureland between Paranimfi and Platanitasa. Along mountainside on dirt road between the villages. (N 34°58.514', E 25°06.820').
50. Perissa, Santorini, Greece	6 June 2006. Along the road from Perissa to the beach near abandoned wheat fields and vineyards around a construction site. (N 36.20.933', E 25.27.536').
51. Ia, Santorini, Greece	6 June 2006. Left side of the road at the top of the hill coming up from the port. (N 36°27.763', E 25°22.388').

* Collected by T. Ekim

** Collected by R. N. Mack

Table 2. Allele frequencies of populations that exhibit variability relative to the most common genotype (MCG). Numbers correspond to populations in Table 1 and Fig. 1. Numbers in parentheses correspond to sample sizes in each population. Populations not listed were fixed for the MCG.

Table 2 continued.

Locus	Allele	MCG	Populations						
			3 (27)	**4** (29)	**5** (30)	**6** (25)	**8** (22)	**9** (30)	**10** (30)
Adh	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Got-4	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lap	a	0.000	0.259	0.172	0.000	0.000	0.654	0.069	0.067
	b	1.000	0.741	0.828	1.000	1.000	0.346	0.931	0.933
Mdh-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mdh-3	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Me	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pgi-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	c	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pgm-1	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgm-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	c	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Tpi-1	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.889	0.966	0.933	0.880	0.269	0.586	0.067
	c	0.000	0.111	0.034	0.067	0.120	0.731	0.414	0.933
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6Pgd-1	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 2. continued.

Locus	Allele	MCG				Populations			
			13	14	15	16	17	18	19
			(20)	(23)	(32)	(27)	(29)	(26)	(41)
Adh	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.976
Got-4	a	0.000	0.000	0.174	0.250	0.000	0.000	0.000	0.000
	b	1.000	1.000	0.826	0.750	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lap	a	0.000	0.000	0.000	0.125	0.000	0.000	0.000	0.341
	b	1.000	1.000	1.000	0.875	1.000	1.000	1.000	0.659
Mdh-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.900	1.000	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000
Mdh-3	a	1.000	1.000	0.696	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.304	0.000	0.000	0.000	0.000	0.000
Me	a	1.000	1.000	1.000	1.000	1.000	1.000	0.115	0.195
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.885	0.805
Pgi-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000
	c	1.000	1.000	1.000	0.969	1.000	0.517	1.000	1.000
	d	0.000	0.000	0.000	0.000	0.000	0.483	0.000	0.000
Pgm-1	a	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	0.969	1.000	1.000	1.000	1.000
Pgm-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000
	c	1.000	1.000	1.000	0.969	1.000	1.000	1.000	1.000
Tpi-1	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.000	1.000	0.781	0.778	1.000	0.962	0.585
	c	0.000	0.000	0.000	0.219	0.222	0.000	0.038	0.415
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6Pgd-1	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 2. continued.

Locus	Allele	MCG	Populations						
			20	**21**	**22**	**23**	**24**	**29**	**32**
			(38)	(46)	(39)	(28)	(35)	(30)	(40)
Adh	a	0.000	0.054	0.000	0.000	0.000	0.000	0.167	0.000
	b	1.000	0.946	1.000	1.000	1.000	1.000	0.833	1.000
Got-4	a	0.000	0.243	0.087	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.757	0.826	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lap	a	0.000	0.297	0.000	0.000	0.000	0.000	0.000	0.733
	b	1.000	0.703	1.000	1.000	1.000	1.000	1.000	0.267
Mdh-2	a	0.000	0.000	0.000	0.000	0.000	0.486	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	0.514	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mdh-3	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Me	a	1.000	0.378	0.894	1.000	0.741	0.686	1.000	0.533
	b	0.000	0.622	0.106	0.000	0.259	0.314	0.000	0.467
Pgi-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.135	0.043	0.000	0.000	0.029	0.000	0.289
	c	1.000	0.865	0.957	1.000	1.000	0.971	1.000	0.711
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pgm-1	a	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	0.974	1.000	1.000	1.000	1.000
Pgm-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.000
	c	1.000	1.000	1.000	0.974	1.000	1.000	1.000	1.000
Tpi-1	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.946	1.000	1.000	0.929	1.000	1.000	1.000
	c	0.000	0.054	0.000	0.000	0.071	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6Pgd-1	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 2. continued.

Locus	Allele	MCG	Populations						
			33	**35**	**37**	**38**	**39**	**40**	**42**
			(33)	(30)	(35)	(16)	(26)	(26)	(24)
Adh	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.000
Got-4	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lap	a	0.000	0.000	0.173	0.000	0.000	0.231	0.000	0.000
	b	1.000	1.000	0.821	1.000	1.000	0.769	1.000	1.000
Mdh-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	0.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
Mdh-3	a	1.000	1.000	1.000	1.000	1.000	1.000	0.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
Me	a	1.000	1.000	0.500	1.000	0.688	1.000	1.000	1.000
	b	0.000	0.000	0.500	0.000	0.313	0.000	0.000	0.000
Pgi-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.061	0.000	0.000	0.000	0.269	0.000	0.000
	c	1.000	0.939	0.765	1.000	1.000	0.731	1.000	1.000
	d	0.000	0.000	0.250	0.000	0.000	0.000	0.000	0.000
Pgm-1	a	0.000	0.000	0.000	0.000	0.000	0.308	0.077	0.000
	b	1.000	1.000	1.000	1.000	1.000	0.692	0.923	1.000
Pgm-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.000	0.000	0.308	0.077	0.000
	c	1.000	1.000	1.000	1.000	1.000	0.692	0.923	1.000
Tpi-1	a	0.000	0.061	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.939	1.000	1.000	0.750	0.962	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.250	0.038	0.000	0.000
6Pgd-1	a	1.000	1.000	1.000	0.514	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.486	0.000	0.000	0.000	0.000

Table 2. continued.

Locus	Allele	MCG	Populations						
			43	**44**	**45**	**46**	**47**	**48**	**49**
			(30)	(29)	(27)	(30)	(26)	(30)	(24)
Adh	a	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	0.933	1.000	1.000	1.000
Got-4	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.967	0.600	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.033	0.400	0.000	0.000	0.000	0.000	0.000
Lap	a	0.000	0.000	0.800	0.000	0.000	0.962	0.000	0.000
	b	1.000	1.000	0.200	1.000	1.000	0.038	1.000	1.000
Mdh-2	a	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000
	b	1.000	0.500	0.967	1.000	1.000	0.962	0.774	1.000
	c	0.000	0.500	0.000	0.000	0.000	0.038	0.226	0.000
Mdh-3	a	1.000	0.500	1.000	1.000	1.000	0.962	0.774	1.000
	b	0.000	0.500	0.000	0.000	0.000	0.038	0.226	0.000
Me	a	1.000	0.600	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.000	0.400	0.000	0.000	0.000	0.000	0.000	0.000
Pgi-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.000	0.000	0.000	0.000	0.000	0.462	0.000	0.000
	c	1.000	1.000	1.000	1.000	0.967	0.538	1.000	1.000
	d	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000
Pgm-1	a	0.000	0.000	0.000	0.222	0.467	0.000	0.000	0.000
	b	1.000	1.000	1.000	0.778	0.533	1.000	1.000	1.000
Pgm-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.231
	b	0.000	0.000	0.000	0.222	0.467	0.000	0.000	0.000
	c	1.000	1.000	1.000	0.778	0.533	1.000	1.000	0.769
Tpi-1	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6Pgd-1	a	1.000	1.000	1.000	0.514	1.000	1.000	0.806	0.077
	b	0.000	0.000	0.000	0.486	0.000	0.000	0.194	0.923

Table 2. continued.

Locus	Allele	MCG	Populations		
			50	**51**	
			(30)	(29)	
Adh	a	0.000	0.000	0.000	
	b	1.000	1.000	1.000	
Got-4	a	0.000	0.000	0.000	
	b	1.000	1.000	1.000	
	c	0.000	0.000	0.000	
	d	0.000	0.000	0.000	
Lap	a	0.000	0.000	0.000	
	b	1.000	1.000	1.000	
Mdh-2	a	0.000	0.000	0.000	
	b	1.000	0.367	1.000	
	c	0.000	0.633	0.000	
Mdh-3	a	1.000	1.000	0.000	
	b	0.000	0.000	1.000	
Me	a	1.000	1.000	1.000	
	b	0.000	0.000	0.000	
Pgi-2	a	0.000	0.000	0.000	
	b	0.000	0.067	0.000	
	c	1.000	0.933	1.000	
	d	0.000	0.000	0.000	
Pgm-1	a	0.000	0.000	0.000	
	b	1.000	1.000	1.000	
Pgm-2	a	0.000	0.000	0.000	
	b	0.000	0.000	0.000	
	c	1.000	1.000	1.000	
Tpi-1	a	0.000	0.000	0.000	
	b	1.000	1.000	0.333	
	c	0.000	0.000	0.667	
	d	0.000	0.000	0.000	
6Pgd-1	a	1.000	1.000	1.000	
	b	0.000	0.000	0.000	

Table 3. Measures of genetic variation for 51 populations of *Bromus tectorum* collected in Cyprus, Greece and Turkey, N is the number of individuals sampled, A is the mean number of alleles per locus, %P is the percent polymorphic loci, H_{exp} is the expected mean heterozygosity and H_{obs} is the mean observed heterozygosity.

Population Number	Population	N	A	%P	H_{exp}	H_{obs}
1	Tripylos, Cyprus	30	1.0	0	0.000	0.000
2	Tripylos Road, Cyprus	30	1.0	0	0.000	0.000
3	Pano Amiandos, Cyprus	30	1.0	0	0.000	0.000
4	Spilia, Cyprus	29	1.1	8	0.014	0.000
5	Palechori, Cyprus	30	1.0	4	0.005	0.000
6	Stavros, Cyprus	25	1.0	4	0.009	0.000
7	Moutii Kou Stavros, Cyprus	30	1.0	0	0.000	0.000
8	Kykkos, Cyprus	26	1.1	8	0.035	0.000
9	Odou, Cyprus	29	1.1	8	0.025	0.000
10	Maxeras, Cyprus	30	1.0	4	0.005	0.000
11	Chionistra, Cyprus	28	1.0	0	0.000	0.000
12	Prodromos, Cyprus	24	1.0	0	0.000	0.000
13	Istanbul, Turkey	20	1.0	4	0.007	0.000
14	Troy, Turkey	23	1.1	8	0.029	0.000
15	Assos, Turkey	32	1.2	24	0.045	0.000
16	Kuçukkuyu, Turkey	27	1.0	4	0.014	0.000
17	Edremit, Turkey	29	1.0	4	0.020	0.000
18	Bergamon, Turkey	24	1.1	12	0.032	0.000
19	Selçuk, Turkey	41	1.2	16	0.053	0.000
20	Isebeyli (Nazilli), Turkey	37	1.2	24	0.069	0.000
21	Hierapolis, Turkey	46	1.2	12	0.030	0.000
22	Aphrodisias, Turkey	39	1.1	8	0.004	0.000
23	Sogut, Turkey	27	1.1	8	0.021	0.000

Table 3 continued

Population Number	Population	N	A	%P	H_{exp}	H_{obs}
24	Akseki, Turkey	35	1.1	12	0.040	0.000
25	Konya, Turkey	22	1.0	0	0.000	0.000
26	Catalhuyuk, Turkey	36	1.0	0	0.000	0.000
27	Aksaray, Turkey	28	1.0	0	0.000	0.000
28	Göreme, Turkey	29	1.0	0	0.000	0.000
29	Uchisar, Turkey	30	1.0	4	0.011	0.000
30	Urgup, Turkey	30	1.0	0	0.000	0.000
31	Ankara, Turkey	42	1.0	0	0.000	0.000
32	Delphi, Greece	45	1.1	12	0.053	0.000
33	Athens, Greece	33	1.0	4	0.005	0.000
34	Arachnea, Greece	25	1.0	0	0.000	0.000
35	Varvitsa, Greece	28	1.1	12	0.048	0.000
36	Artemitsa, Greece	30	1.0	0	0.000	0.000
37	Platanitsa, Greece	35	1.0	4	0.020	0.000
38	Melissatika, Greece	16	1.1	8	0.033	0.000
39	Larissa, Greece	26	1.2	20	0.068	0.000
40	Panteleimona, Greece	26	1.1	8	0.012	0.000
41	Pefkochori, Greece	30	1.0	0	0.000	0.000
42	Keramouti, Greece	24	1.0	0	0.000	0.000
43	Kotronia, Greece	30	1.2	16	0.063	0.000
44	Ardanio, Greece	30	1.1	12	0.035	0.000
45	Cherso, Greece	27	1.1	8	0.028	0.000
46	Arissa, Greece	30	1.2	16	0.048	0.000
47	Meteora, Greece	26	1.2	16	0.030	0.000
48	Kamareas, Crete	31	1.1	12	0.041	0.000
49	Paranimfi, Crete	13	1.1	8	0.021	0.000
50	Perissa, Santorini	30	1.1	8	0.024	0.000
51	Ia, Santorini	30	1.0	4	0.018	0.000
	MEAN	29.47	1.06	6.75	0.020	0.000

Table 4. Measure of genetic variability for *Bromus tectorum* by geographic area. (See Table 3 for abbreviations.)

Region	Populations	N	A	%P	H_{exp}	H_{obs}
Eastern Canada*	16	495	1.05	5.00	0.013	0.00030
Western Canada*	44	1397	1.03	3.90	0.012	0.00004
Canada*	60	1892	1.03	4.20	0.012	0.00010
Eastern U.S.**	38	1250	1.01	1.05	0.002	0.00000
Midwestern U.S.***	54	1624	1.04	4.07	0.009	0.00020
Western U.S. †	40	1507	1.05	4.60	0.012	0.00000
United States	132	4381	1.03	3.36	0.008	0.00009
North America (Total)	192	6273	1.03	3.63	0.009	0.00009
Cyprus††	12	341	1.03	3.00	0.008	0.00000
Turkey††	19	597	1.07	7.37	0.020	0.00000
Greece††	20	565	1.09	8.40	0.027	0.00000
Eastern Mediterranean††	51	1503	1.06	6.75	0.020	0.00000
Europe†	13	530	1.02	1.85	0.007	0.00010
SW Asia†	12	484	1.03	3.67	0.005	0.00020
Eurasia †	51	1730	1.02	2.12	0.005	0.00010
Native Range	127	4247	1.03	3.60	0.009	0.00010
All Populations	294	9506	1.04	4.39	0.012	0.00007

*Valliant 2005 (revised)

**Bartlett et al. 2002

***Schachner 2005

† Novak and Mack 1993

†† current study

Table 5. Summary of F-statistics at all polymorphic loci for populations of *Bromus tectorum* in the Western Mediterranean region. F_{IT} is the overall fixation index and measures the reduction of heterozygosity across all populations. F_{IS} is the reduction of heterozygosity within populations. F_{ST} is the amount of genetic differentiation among populations.

Locus	F_{IT}	F_{IS}	F_{ST}
Adh	1.000	1.000	0.784
Got-4	1.000	1.000	0.249
Lap	1.000	1.000	0.801
Mdh-2	1.000	1.000	0.628
Mdh-3	1.000	1.000	0.729
Me	1.000	1.000	0.510
Pgi-2	1.000	1.000	0.314
Pgm-1	1.000	1.000	0.312
Pgm-2	1.000	1.000	0.294
Tpi-1	1.000	1.000	0.499
6Pgd-1	1.000	1.000	0.693
Mean	1.000	1.000	0.607

Table 6. Nei's gene diversity statistics for the 51 populations in the Eastern
Mediterranean Region. H_T is the total gene diversity, H_S is the within-population
diversity, D_{ST} is the among-population component, and G_{ST} is the proportion of the total
genetic diversity partitioned among populations.

Locus	H_T	H_S	D_{ST}	G_{ST}
Adh	0.050	0.011	0.039	0.781
Got-4	0.049	0.037	0.012	0.237
Lap	0.419	0.085	0.334	0.798
Mdh-2	0.112	0.043	0.070	0.621
Mdh-3	0.067	0.018	0.048	0.724
Me	0.179	0.089	0.089	0.501
Pgi-2	0.081	0.056	0.025	0.303
Pgm-1	0.043	0.030	0.013	0.299
Pgm-2	0.052	0.038	0.015	0.279
Tpi-1	0.160	0.082	0.079	0.490
6Pgd-1	0.061	0.019	0.042	0.687
Mean	0.116	0.046	0.070	0.520

Table 7. Summary of Nei's gene diversity statistics for *B. tectorum* by the mean for various geographic areas. (See Table 8 for abbreviations).

Region	H_T	H_S	D_{ST}	G_{ST}
Canada *	0.158	0.076	0.083	0.405
Eastern U.S. **	0.075	0.014	0.061	0.560
Midwestern U.S. ***	0.084	0.038	0.046	0.290
Western U.S.	0.132	0.056	0.076	0.617
Cyprus	0.354	0.121	0.233	0.651
Greece	0.161	0.062	0.099	0.531
Turkey	0.095	0.055	0.040	0.262
Eastern Mediterranean	0.116	0.046	0.070	0.520
Eurasia†	0. 087	0.009	0.077	0.754

*Valliant 2005

**Bartlett et al. 2002

***Schachner 2005

† Novak and Mack 1993

Table 8. Nei's genetic identity (*I*) mean values for populations of *Bromus tectorum* within and between countries in the Western Mediterranean Region. N is the number of populations in each country. Means of all intra-country pair-wise population comparisons appear on the diagonal. The pair-wise means of inter-country comparisons are below the diagonal. The range of values for the population pairs in that sample are in parentheses.

Country	N	Cyprus	Turkey	Greece
Cyprus	12	0.979 (0.925-1.000)		
Turkey	19	0.980 (0.910-1.000)	0.984 (0.946-1.000)	
Greece	20	0.963 (0.861-1.000)	0.963 (0.849-1.000)	0.953 (0.823-1.000)

Fig 2. UPGMA phenogram of Nei's genetic identity values for 51 Western Mediterranean populations of *Bromus tectorum*. Abbreviations in parentheses are (CY) = Cyprus (GR) = Greece and (TR) = Turkey.

1 TRIPYLOS (CY)
2 TRIPYLOS ROAD (CY)
7 MOUTTI KOU (CY)
12 PRODROMOS (CY)
25 KONYA (TR)
27 ASKARAY (TR)
28 GORME (TR)
30 URGUP (TR)
31 ANKARA (TR)
36 ARTEMITSA (GR)
22 APRODISIAS (TR)
33 ATHENS (GR)
5 PALACHORI (CY)
6 STRAVOS (CY)
13 ISTANBUL (TR)
29 UCHISAR (TR)
3 PANO AMIANDOS (CY)
4 SPILIA (CY)
45 CHERSO (GR)
14 TROY (TR)
21 HIERAPOLIS (TR)
23 SOGUT (TR)
38 MELISSATIKA (GR)
9 ODOU (CY)
16 KUCUKKUYU (TR)
15 ASSOS (TR)
17 EDRERMIT (TR)
24 AKSEKI (TR)
39 LARISSA (GR)
46 ARISSA (GR)
37 PLATANITSA (GR)
49 PARANIMFI (GR)
18 BERGAMON (TR)
19 SELCUK (TR)
20 TSEBEYLII (TR)
35 VARVITSA (GR)
43 KOTRONIA (GR)
8 KYKKOS (CY)
10 MAXERAS (CY)
11 CHIONISTRA (CY)
26 CATALHUYUK (TR)
34 ARACHNEA (GR)
41 PEFKOCHORI (GR)
40 PANTELEIMONA (GR)
48 KAMAREAS (GR)
44 ARDANIO (GR)
47 METEORA (CR)
32 DELPHI (GR)
50 PERISSA (GR)
42 KERAMOUTI (GR)
51 IA (GR)

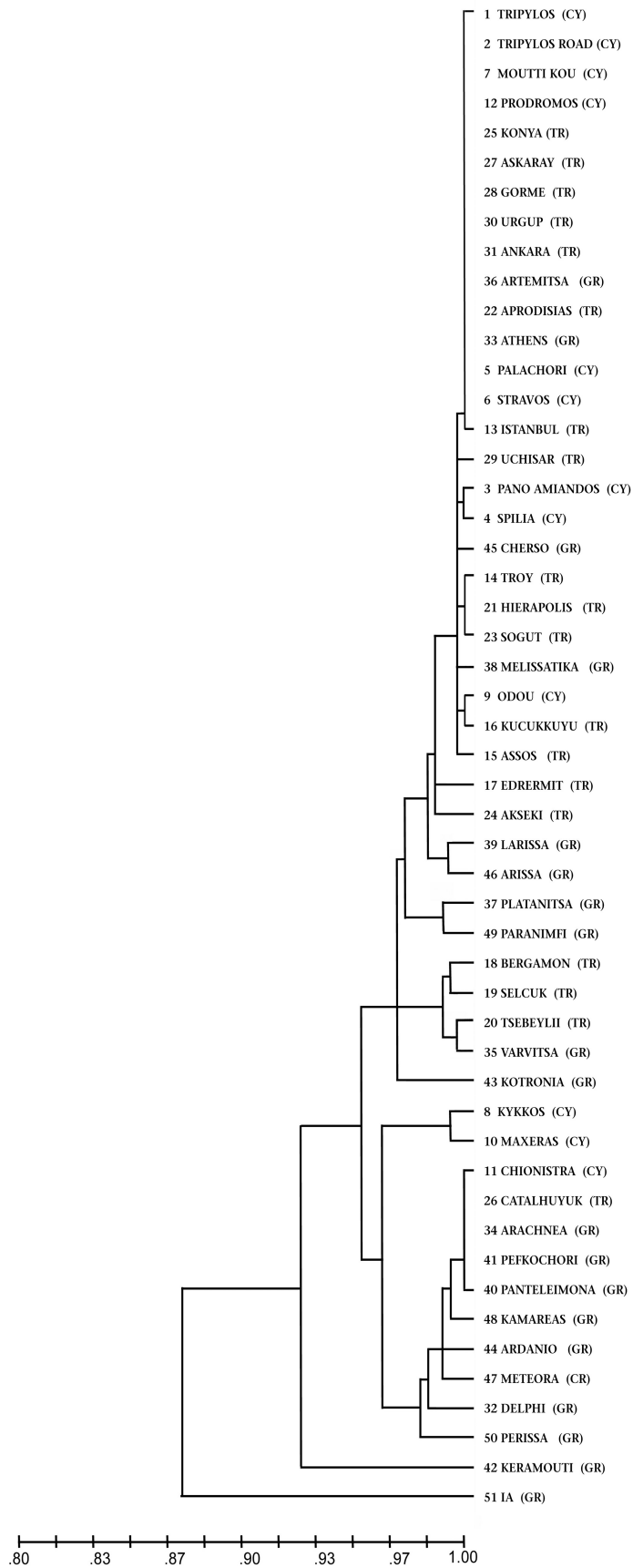.80   .83   .87   .90   .93   .97   1.00

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Table 9. Multilocus genotypes summarized for all individuals of *Bromus tectorum*

analyzed from populations in the Eastern Mediterranean Region. N is the number of

populations with the genotype analyzed in each country. The frequency is the proportion

of individuals with a certain genotype divided by the total number of individuals

analyzed within the country. MCG is the most common genotype (see text), while the

prefixes ESW refer to genotypes found by Novak (1990) in populations from Europe and

Southwest Asia, SWA is South West Asia, and NA are North American genotypes. EM

means that this genotype has only been found in populations from the Eastern

Mediterranean Region. The sequence of loci is *Adh, Got-4, Lap, Mdh-2, Mdh-3, Me,*

Pgi-2, Pgm-1, Pgm-2, Tpi-1, 6Pgd-1.

Country	N	Genotype Designation	Multilocus Genotypes	N	Frequency
Cyprus	12	MCG	22221132321	10	0.663
		ESW 11	22121131321	6	0.132
		ESW 16	22121132331	4	0.123
		NA 8	22221132331	6	0.073
Greece	20	MCG	22221132321	17	0.508
		ESW 11	22121131321	4	0.064
		ESW 2/NA 4	22221122321	4	0.017
		SWA 12	12221132321	2	0.046
		NA 2	22221131221	4	0.041
		NA 5	22232132321	4	0.037
		NA 7	24221132321	2	0.007
		NA 8	22221132331	1	0.004
		EM 6	24121132321	1	0.016
		EM 7	22111132321	1	0.002
		EM 8	22121232321	2	0.025
		EM 9	22121222321	1	0.011
		EM 11	22121122321	2	0.027
		EM 16	22221142321	2	0.014
		EM 17	22232232321	1	0.002

Table 9. continued.

Country	N	Genotype Designation	Multilocus Genotypes	N	Frequency
		EM 18	22232132331	1	0.035
		EM 19	22221232321	4	0.032
		EM 20	22221232121	1	0.007
		EM 22	22221121221	1	0.012
		EM 23	22221132121	1	0.002
		EM 24	22221132341	2	0.009
		EM 25	22231122321	1	0.002
		EM 28	22221132311	1	0.055
		EM 29	22232132322	3	0.005
		EM 30	22221132122	1	0.002
		EM 31	22221132322	1	0.002
Turkey	19	MCG	22221132321	19	0.658
		ESW 11	22121131321	2	0.013
		ESW 16	22121132331	1	0.002
		ESW 2/NA 4	22221122321	3	0.030
		SWA 12	12221132321	1	0.008
		NA 2	22221131221	1	0.002
		NA 7	24221132321	1	0.007
		NA 8	22221132331	3	0.015
		EM 1	21221132321	3	0.017
		EM 2	21121232331	1	0.003
		EM 3	21121132331	1	0.003
		EM 4	21221232321	2	0.017
		EM 5	21221132331	1	0.002
		EM 8	22121232321	4	0.037
		EM 9	22121222321	2	0.003
		EM 10	22121232331	2	0.010
		EM 11	22121122321	1	0.003
		EM 12	22211132321	1	0.017
		EM 13	22211232321	1	0.010
		EM 14	22211222321	1	0.001
		EM 15	22231132321	1	0.003
		EM 19	22221232321	8	0.107
		EM 20	22221232121	2	0.003
		EM 21	22221232331	2	0.020
		EM 26	12221232321	1	0.002
		EM 27	12221132331	1	0.003

Table 10. Locations of populations with alleles that differ from the MCG (most common genotype).

Allele	Eastern Mediterranean Population	Eurasian Population†	North America
Adh-a	Selçuk, TR	De Göreme, TR	Not Found
Got-4a	Troy, TR Assos, TR Isebeyli, TR Hierapolis, TR	Iran-1 Afghanistan-1	Not Found
Got-4d	Kotronia, GR Ardanio, GR	Vienna-Landstrasse, Austria	Waterton, AB* Martin, SD*** Mule Creek, WY*** Dubois, ID†† Provo, UT††
Lap-a	Pano Amiandos, CY Spilia, CY Kykkos, CY Odou, CY Maxeras, CY Assos, TR Selçuk, TR Isebeyli, TR Delphi, GR Varvitsa, GR Larissa, GR Ardanio, GR Meteora, GR	Soviet Union	Not Found

Table 10. continued

Allele	Eastern Mediterranean Population	Eurasian Population†	North America
Mdh-2a	Akseki, TR Ardanio, GR	Novel allele	
Mdh-2c	Istanbul, TR Panteleimona, GR Kotronia, GR Meteoria, GR Kamareas, Crete Perissa, Santorini	Afghanistan-2 Afghanistan-3	Holland, VA** Bryson City, NC** Colfax, ND*** Martin, SD*** Sturgis, SD*** 2 from Nevada†† 4 from Washington††
Mdh-3b	Troy, TR Panteleimona, GR Kotronia, GR Meteoria, GR Kamareas, Crete Ia, Santorini	Afghanistan-2 Afghanistan-3	Holland, VA** Bryson City, NC** Colfax, ND*** Martin, SD*** Sturgis, SD***
Me-b	Bergamon, TR Selçuk, TR Isbeyli, TR Hierapolis, TR Sogut, TR Akseki, TR Delphi, GR Varvitsa, GR Melissatika, GR Kotronia, GR	Novel Allele	
Pgi-2b	Assos, TR Isebeyli, TR Hierapolis, TR Akseki, TR Delphi, GR Athens, GR Larissa, GR Meteora, GR Perissa, Santorini	Thoureze, France Tarassac, France Touna Station, Morocco Puerto Calatrav, Spain Pozoblanco, Spain Belmez, Spain Hinojosa, Spain Espiel, Spain Iran-1	3 from Nevada†† Truckee, CA†† Kuna, ID†† 4 from the Canary Islands†† 2 from Chile††
Pgi-2d	Edremit, TR Varvitsa, GR Arissa, GR	Iran-3	Not Found

Table 10. continued

Allele	Eastern Mediterranean Population	Eurasian Population†	North America
Pgm-1a	Assos, TR Aphrodisias, TR Larissa, GR Panteleimona, GR Cherso, GR Arissa, GR	Vac, Hungary Bratislava, Slovakia Afghanistan-1 Iran-1	9 Ontario populations* Selkirk, MB* Maple Creek, SK* Waterton, AB* 7 British Columbia populations* Kiptopeke, VA** Burnsville, NC** Bryson City, NC** Lexington, KY** 24 Midwest populations*** Tonasket, WA†† Gunison, CO†† 3 from Argentina††
Pgm-2a	Paranimfi, Crete	Novel Allele	
Pgm-2b	Assos, TR Aphrodisias, TR Larissa, GR Panteleimona, GR Cherso, GR Arissa, GR Paranimfi, Crete	Vac, Hungary Bratislava, Slovakia Afghanistan-1 Iran-1	9 Ontario populations* Selkirk, MB* Maple Creek, SK* Waterton, AB* 7 British Columbia populations* Kiptopeke, VA** Burnsville, NC** Bryson City, NC** Lexington, KY** 24 Midwest populations*** Tonasket, WA†† Gunison, CO†† 3 from Argentina††
Tpi-1a	Athens, GR	Novel Allele	
Tpi-1c	Pano Amiandos, CY Spillia, CY Palechori, CY Stavros, CY Kykkos, CY Odou, CY Maxeras, CY Assosy, TR Kuçukkuyu, TR	Iran-2	Osoyoos, BC* Golden, BC* Hot Springs, SD*** Mule Creek, WY***

Table 10. continued

Allele	Eastern Mediterranean Population	Eurasian Population†	North America
	Bergamon, TR Selçuk, TR Isebeyli, TR Sogut, TR Ia, Santorini		
Tpi-1d	Melissatika, GR Larissa, GR	Novel Allele	
6pgd-2b	Platanitsa, GR Kamareas, Crete Paranimfi, Crete	Novel Allele	

*Valliant 2005

**Bartlett et al. 2002

***Schachner 2005

† Novak 1990

†† Novak and Mack 2001

Fig. 3. Multilocus Genotypes detected in the Eastern Mediterranean Region.

DESIGNATION	GENOTYPES	
EM 31	6PGD1b	
SWA 12	ADHa	
EM 26	ADHa/MEb	1
EM 27	ADHa/TPI1c	2
EM 1	GOT4a	
EM 2	GOT4a/LAPa/MEb/TPI1c	3
EM 3	GOT4a/LAPa/TPI1c	4
EM 4	GOT4a/MEb	
EM 5	GOT4a/TPI1c	5
NA 7	GOT4d	
EM 6	GOT4d/LAPa	6
ESW 11	LAPa	
EM 7	LAPa/MDH2a	7
EM 8	LAPa/MEb	
EM 9	LAPa/MEb/PGI2b	
EM 10	LAPa/MEb/TPI1c	
EM 11	LAPa/PGI2b	
ESW 16	LAPa/TPI1c	
MCG	MCG	
EM 12	MDH2a	8
EM 13	MDH2a/MEb	9
EM 14	MDH2a/MEb/PGI2b	
EM 15	MDH2c	
NA 5	MDH2c/MDH3b	
EM 29	MDH2c/MDH3b/6PGD1	10
EM 17	MDH2c/MDH3b/MEb	11
EM 18	MDH2c/MDH3b/TPI1c	12
ESW 2/NA 4	MDH2c/PGI2b	13
EM 19	MEb	
EM 20	MEb/PGI2b	14
EM 21	MEb/TPI1c	
ESW 2/NA 4	PGI2b	
EM 22	PGI2b/PGM1a/PGM2b	15
ESW 2/NA 4	PGI2d	
NA 2	PGM1a/PGM2b	
EM 23	PGM2a	16
EM 30	PGM2a/6PGD1b	17
EM 28	TPI1a	18
NA 8	TPI1c	
EM 24	TPI1d	