

# Chapter 4

## Mating System, Introduction and Genetic Diversity of *Bromus tectorum* in North America, the Most Notorious Product of Evolution Within *Bromus* Section *Genea*

Stephen J. Novak and Richard N. Mack

**Abstract** The genus *Bromus* (Poaceae) consists of approximately 150–160 species that occur in temperate regions worldwide. Members of section *Genea* in *Bromus* are native to Eurasia, and most are invasive in North America (NA). Most environmentally and economically important among these species is *Bromus tectorum*, which along with *Bromus rubens* and *B. diandrus* are some of the most destructive invasive grasses in the Western United States (USA). Members of section *Genea* form a polyploid series. Molecular data suggest a reticulate speciation pattern (a netlike pattern of diversification) for the polyploid members of *Genea*. Seed set, floral characteristics, sex allocation patterns, and genetic markers reveal that *B. tectorum* is predominately self-pollinating. Historical records and genetic data indicate that *B. tectorum* entered repeatedly into NA and that its current distribution can be attributed to multiple phenomena, including direct introduction from its native range and multidirectional range expansion. Across invasive populations of *B. tectorum*, overall genetic diversity (e.g., allelic richness and number of polymorphic loci) is lower compared to the diversity among native populations. Conversely, invasive populations of *B. tectorum* exhibit, on average, higher within-population genetic diversity than found in native populations, suggesting that multiple introductions have partially offset founder effects within invasive populations. Additionally, invasive populations appear to be genetic admixtures composed of two or more independently derived native genotypes. These admixtures have produced invasive populations with generally less genetic differentiation than native populations. The genetic consequences of multiple introductions have implications for the management of invasive populations of *B. tectorum*, especially in Western NA.

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## 4.1 Introduction

Some members of the Poaceae rank among the worst plant invaders, especially in steppe, shrub-steppe, and savannas (Holm et al. 1977; Mack 1989); furthermore, some invasive grasses have become prominent where the forest canopy has been removed, including low-elevation coniferous forest (Summers and Archibold 2007; D'Antonio et al. 2011). The array of grasses that have become invasive (or at least extensively naturalized) defies straightforward taxonomic classification, but multiple species in *Avena*, *Brachiaria*, *Eragrostis*, *Nassella*, *Pennisetum*, and *Poa* have become major pests in their new ranges (Holm et al. 1977; Parsons and Cuthbertson 1992; Bromilow 1995). Whether outcompeting native species or causing devastating alterations of the fire cycle within invaded communities (D'Antonio and Vitousek 1992), these grass immigrants collectively cause enormous environmental and economic damage worldwide (Pimentel et al. 2005). Among any list of destructive grasses, few genera match the ecological breadth and resulting spread seen for many members of the genus *Bromus* L. (Germino et al. 2015; Brooks et al. 2015).

The introduction and range expansion of species in the genus *Bromus* (brome-grasses) across Western North America (NA) provide abundant examples of the negative consequences of plant invaders. For example, *Bromus rubens* L. (red brome) is the dominant invasive brome-grass in the Southwestern United States (USA) (Beatley 1966; Brooks 1999a, b; Salo 2005), and *Bromus diandrus* Roth. (ripgut brome) and *Bromus hordeaceus* L. (soft brome or chess) are invasive in California, especially the Central Valley (Dyer and Rice 1999; Gerlach and Rice 2003; Keeley et al. 2006; Brooks et al. 2015). In addition, the invasion of *B. tectorum* L. in sagebrush-steppe habitats of the Intermountain West (the Columbia Basin, especially the Snake River Plains, Basin and Range Province, and the Colorado Plateau) has contributed to the loss of native species diversity and community structure, modified ecosystem processes, such as nutrient cycling and productivity patterns, and altered disturbance regimes, especially the frequency, extent, and intensity of rangeland fires (Stewart and Hull 1949; Hulbert 1955; D'Antonio and Vitousek 1992; Knaap 1996; Sperry et al. 2006; Chambers et al. 2007; Mack 2011; Germino et al. 2015).

Three of the four species listed above, *B. diandrus*, *B. rubens*, and *B. tectorum*, as well as several other brome-grasses invasive in NA, occur in section *Genea* of the genus *Bromus* (Sales 1993, 1994). Consequently, we begin this chapter by describing evolutionary relationships among species in section *Genea*, which includes a polyploid series with diploid, tetraploid, hexaploid, and octoploid species. *Bromus*

*tectorum* (cheatgrass, downy brome) will however be our main focus, given its enormous impacts as an invasive species in temperate grasslands in NA. We (1) describe the mating system of *B. tectorum*, based on seed set, floral characteristics, sex allocation patterns, and genetic markers, (2) present historical and genetic data to reconstruct the introduction and pattern of range expansion of *B. tectorum* in NA, and (3) assess the genetic consequences of these events by summarizing studies describing the level and structure of genetic diversity within and among native and invasive populations of *B. tectorum*. The results discussed here indicate that invasive populations of *B. tectorum* throughout much of NA have, on average, higher levels of genetic diversity than native populations, due to multiple introductions. Furthermore, the genetic consequences of multiple introductions have implications for the management of invasive populations of *B. tectorum*, especially in Western NA.

## 4.2 Evolutionary Relationships among Species in Section *Genea*

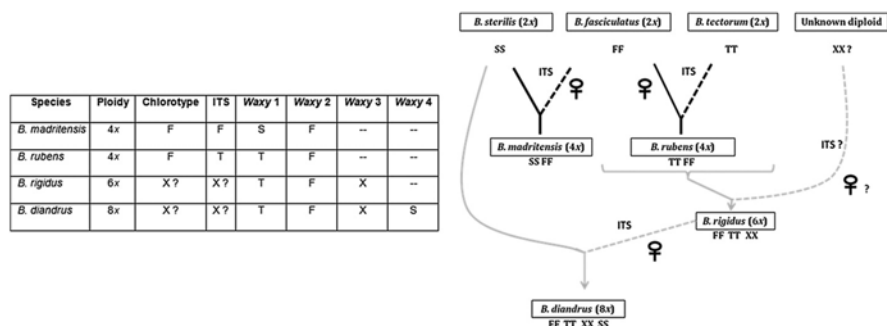
A context for assessing life history traits, ecology, and the potential for invasiveness of *B. tectorum*, and other species within section *Genea*, is provided by considering the species' evolutionary history, phylogenetic relationships, and patterns of speciation (see Prinzing et al. 2002 for an interesting discussion of these issues). Such an assessment is particularly useful for the study of diploid species within this section and their roles in the origins of the polyploid taxa of this section.

Within the Poaceae, *Bromus* is classified in the tribe *Bromeae*, which is part of subfamily Pooideae (Catalan et al. 1997; Kellog 2001; Bouchenak-Khelladi et al. 2008; Schneider et al. 2009; Atkinson and Brown 2015). The genus *Bromus* consists of approximately 150–160 annual and perennial species; these species collectively have a worldwide distribution (Smith 1970; Acedo and Liamas 2001; Fortune et al. 2008). Smith (1970) assigned the species of *Bromus* to six sections, *Bromus*, *Ceratochloa* (P. Beauv.) Griseb., *Genea* Dumort., *Neobromus* Shear., *Nevskiella* V. Krecz and Vvevd., and *Pnigma* Dumort. Species within section *Genea* are hypothesized to have originated in the Middle East and the Mediterranean Region (Sales 1993, 1994), where they likely evolved concomitantly with the emergence of agriculture and human disturbance (Balfourier et al. 1998). In addition, these species exhibit much morphological variation, phenotypic plasticity, and polyploidy (Sales 1993, 1994). Seven species that form a polyploid series are recognized in section *Genea*: the diploids *B. fasciculatus* Presl., *B. sterilis* L., and *B. tectorum*, the tetraploids *B. madritensis* L. and *B. rubens*, the hexaploid *B. rigidus* Roth., and the octoploid *B. diandrus* Roth. (Smith 1970; Sales 1993, 1994; Acedo and Liamas 2001; Fortune et al. 2008). These species are native to Eurasia; all are invasive in the USA, with the exception of *B. fasciculatus*.

Fortune et al. (2008) elegantly assessed evolutionary relationships and patterns of speciation among these seven species. DNA sequence data from three gene regions were employed: the low copy nuclear gene *Waxy*, nuclear ribosomal DNA

(rDNA) regions ITS1 and ITS2, and the chloroplast spacer regions *trnT-trnL* and *trnL-trnF*. Results from nuclear ITS regions and chloroplast DNA indicate that section *Genea* is monophyletic. The phylogenetic tree based on nucleotide sequence data from *Waxy* however indicates that section *Genea* is paraphyletic because this clade also includes species from section *Bromus* (Fortune et al. 2008). Two of the diploid species within section *Genea*, *B. sterilis* and *B. tectorum*, are sister species (i.e., they are more closely related to each other than any other species in this section); *B. fasciculatus* is more distantly related. Based on chloroplast DNA data, *B. fasciculatus* appears to have served as the maternal parent for the hybridization that produced the tetraploids *B. madritensis* and *B. rubens*, whereas the paternal parents for the two tetraploids appear to be *B. sterilis* and *B. tectorum*, respectively (Fig. 4.1). The hexaploid *B. rigidus* may have originated from a hybridization event involving *B. rubens* and an unknown diploid species, which served as the maternal parent (Fig. 4.1). The octoploid *B. diandrus* appears to have originated from a crossing event involving *B. rigidus* and *B. sterilis* as the maternal and paternal parents, respectively (Fig. 4.1).

The above summarized results point to the reticulate (i.e., a netlike pattern of diversification) origins of the polyploid species in section *Genea* (Fortune et al. 2008). In addition, these data indicate that all seven species in this section have unique evolutionary histories. Thus, all four polyploid species in section *Genea* (*B. madritensis*, *B. rubens*, *B. rigidus*, and *B. diandrus*) are appropriately recognized as distinct, separate species. With the exception of *B. fasciculatus*, which is listed as endangered on Mediterranean islands (Fortune et al. 2008), the remaining six species in section *Genea* are considered weeds across much of their native range



**Fig. 4.1** Depiction of hypothesized origins of the polyploid species in section *Genea* of the genus *Bromus*, reproduced from Fortune et al. (2008). Molecular markers used in this analysis are listed in the table and include chlorotype (chloroplast spacer regions *trnT-trnL* and *trnL-trnF*), ITS (nuclear rDNA regions ITS1 and ITS2), and four *Waxy* (a low copy nuclear gene) nucleotide sequences. The table provides the identity of the genomes (F, S, T, and X) detected in the polyploid taxa based on different hybridization events. F=*B. fasciculatus*, S=*B. sterilis*, T=*B. tectorum*, and X=an unknown diploid species. The maternal parent in each cross is indicated (female symbol). See the text for a summary of the results shown in this figure

(Smith 1980). Traits that contributed to their weediness in the native range likely served as preadaptations (*sensu* Futuyma 2005), contributing to their establishment and subsequent invasions, especially in Western NA.

### 4.3 Mating Systems

In his classic paper “The evolution of weeds,” Baker (1974) described the characteristics of the “ideal weed,” and whereas no weed species exhibits all these characteristics, *B. tectorum* displays many. We concentrate here on the fifth characteristic in Baker’s list, which describes a weed’s potential mating system, “Self-compatible but not completely autogamous or apomictic.” The mating system (how much outcrossing versus self-pollination occurs) has a large influence on the biology and genetics of plant populations. The outcome of reproduction is directly associated with the mating system; plants with high rates of self-pollination (hereafter referred to as selfing) typically have greater seed set compared with plants with an outcrossing mating system (Harmon-Threatt et al. 2009; Eckert et al. 2010). In addition, plants with a selfing mating system have lower levels of gene flow, through the movement of pollen, within and among populations. Thus, plant mating systems govern the spatial and temporal fluctuation of genotypes within and among populations: populations with high rates of selfing typically contain few individuals with heterozygous genotypes and many individuals with homozygous genotypes, compared to populations with high rates of outcrossing (Stebbins 1957; Allard et al. 1968; Barrett et al. 2008). Furthermore, species with high rates of selfing have lower levels of genetic diversity within populations and higher levels of genetic differentiation among populations, compared to species with high rates of outcrossing (Brown and Burdon 1987; Slatkin and Barton 1989; Ellstrand and Elam 1993; Sork et al. 1999).

#### 4.3.1 Mating System of *Bromus tectorum*: Seed Set, Floral Characteristics, and Sex Allocation Pattern

McKone (1985, 1987, 1989) compared the mating systems of five *Bromus* species: *B. inermis* Leyss., *B. latiglumis* (Shear) Hitchc., *B. ciliatus* L., *B. kalmii* A. Gray, and *B. tectorum*. These grasses encompass a range of characteristics; they include species that are native and introduced in NA, perennials and annuals, rhizomatous and non-rhizomatous species, and species with diploid and polyploid cytotypes (see McKone 1985). In order to determine self-fertility, McKone (1985) measured the seed set of bagged inflorescences of all five species. He also documented floral characteristics, including the manner in which the florets of each species opened and the extent to which anthers were exerted. Both the bagged and open-pollinated inflorescences of *B. tectorum* had the highest seed set (McKone 1985). These results

are consistent with previous reports for highly selfing plant species (Stebbins 1957) and indicate that *B. tectorum* is self-compatible and highly selfing. In addition, McKone (1985) made observations on floral characteristics of all five *Bromus* species and found that the florets of *B. tectorum* "...rarely (if ever) opened..." (p. 1336), and he "...never found anthers completely exerted from the florets" (p. 1335). These results indicate that *B. tectorum* produces cleistogamous flowers (i.e., they rarely open), which is associated with the production of progeny almost exclusively through selfing (see Campbell et al. 1983).

Sex allocation theory predicts equal paternal (pollen production) and maternal investment (seed production) for hermaphroditic plants (Charlesworth and Charlesworth 1981; Brunet 1992; Campbell 2000). McKone (1987) determined the relative paternal and maternal investment among the same five *Bromus* species listed above by measuring the ratio of pollen to seed production. He also determined the species' absolute paternal and maternal investment by measuring the caloric energy and mineral content (nitrogen, phosphorous, potassium, magnesium, and calcium) of their reproductive structures. Of the five species, *B. tectorum* has the shortest anther length (0.65 mm), smallest pollen diameter (32.43  $\mu\text{m}$ ), least volume of pollen per floret ( $\text{cm}^3 \times 10^{-6}$ ), intermediate seed weight (1.99 mg), largest value for percent seed set per floret (79.0 %), and smallest ln (ratio of pollen volume to seed weight per floret) (2.28), compared with values for the obligate outcrosser *B. inermis* (4.02 mm, 41.61  $\mu\text{m}$ , 424.1  $\text{cm}^3 \times 10^{-6}$ , 2.32 mg, 29.9 %, and 6.31, respectively) (McKone 1987). Estimates of sex allocation based on caloric energy and mineral content show that the paternal investment of *B. tectorum* was < 2 %, compared to approximately 50 % for *B. inermis*. Additionally, the cleistogamous flowers of *B. tectorum* produce less pollen relative to number of seeds produced, especially compared to *B. inermis* (McKone 1989). *Bromus tectorum* invests little in pollen production, results that are consistent with the ratio of paternal to maternal investment expected for a highly selfing plant species (Brunet 1992; Campbell 2000).

#### 4.3.2 *Mating System of Bromus tectorum: Genetic Markers and Outcrossing Rates*

A species' mating system can also be estimated using molecular markers that are expressed through codominance, such as allozymes (enzyme electrophoresis) or microsatellite DNA (Avisé 2004; Schlotterer 2004). Using codominant genetic markers, individuals with homozygous and heterozygous genotypes can be clearly identified based on their banding or chromatogram phenotypes (i.e., patterns). Two methods are commonly used to estimate mating system parameters using molecular data: progeny array analysis and Wright's Coefficient of Inbreeding (Wright 1931; Clegg 1980; Brown 1990; Dudash and Fenster 2001). With progeny array analyses, the genotypes of 10–20 seeds from a maternal plant are determined; mating system parameters (outcrossing rate  $t$  and selfing rate  $s$ ) are estimated from these data,

**Table 4.1** Summary of genetic diversity for *Bromus tectorum* populations in the introduced range in North America and the native range in Europe and Southwest Asia

Region	Number of pops.	$N$	$A$	% $P$	$H_{exp}$	$H_{obs}$	$H_T$	$G_{ST}$
Eastern USA <sup>a</sup>	38	1248	1.01	1.05	0.002	0.0000	0.075	0.560
Central USA <sup>b</sup>	60	1905	1.05	4.73	0.014	0.00003	0.187	0.582
Mid-continent USA <sup>c</sup>	54	1624	1.04	4.07	0.009	0.0002	0.084	0.290
Intermountain West USA <sup>d</sup>	26	961	1.05	4.31	0.011	0.0000	0.119	0.241
Nevada and California <sup>d</sup>	14	546	1.05	5.14	0.014	0.0000	0.192	0.500
California and American Southwest <sup>e</sup>	60	1974	1.03	3.27	0.007	0.000017	0.057	0.277
Eastern Canada <sup>f</sup>	16	495	1.05	5.00	0.013	0.0003	0.265	0.447
Western Canada <sup>f</sup>	44	1397	1.04	3.91	0.012	0.00005	0.131	0.316
Europe <sup>g</sup>	39	1246	1.01	1.64	0.006	0.0001	0.069	0.656
SW Asia <sup>g</sup>	12	484	1.03	3.67	0.005	0.002	0.201	0.735

$N$  is number of individuals analyzed in each region,  $A$  is number of alleles per locus, % $P$  is percent polymorphic loci,  $H_{exp}$  is expected mean heterozygosity,  $H_{obs}$  is mean observed heterozygosity,  $H_T$  is mean total gene diversity, and  $G_{ST}$  is proportion of total gene diversity partitioned among populations

<sup>a</sup>Bartlett et al. (2002); <sup>b</sup>Huttanus et al. (2011); <sup>c</sup>Schachner et al. (2008); <sup>d</sup>Novak et al. (1991); <sup>e</sup>Pawlak et al. (2015); <sup>f</sup>Valliant et al. (2007); <sup>g</sup>Novak and Mack (1993) as cited in Huttanus et al. (2011)

typically using a mixed mating system model that assumes both outcrossing and selfing are occurring (Ritland 2002). The Coefficient of Inbreeding,  $F$ , can be calculated from population genetic data based on the ratio of mean observed heterozygosity ( $H_{obs}$ ) to expected mean heterozygosity ( $H_{exp}$ ), using the equation  $F = 1 - H_{obs}/H_{exp}$  (Wright 1931; Dudash and Fenster 2001). The outcrossing rate is calculated as  $t_f = (1 - F)/(1 + F)$ , and the selfing rate is calculated as  $t_s = 1 - t_f$ .

Along with our students, we have assessed the genetic diversity within and among populations of *B. tectorum*, using enzyme electrophoresis (Novak et al. 1991; Novak and Mack 1993; Bartlett et al. 2002; Valliant et al. 2007; Schachner et al. 2008; Huttanus et al. 2011; Pawlak et al. 2015). To date, we have analyzed 10,150 individuals from 312 naturalized or invasive populations in NA and 1730 individuals from 51 native populations in Eurasia (Table 4.1), with the genetic diversity of each individual assayed at 25 putative enzyme loci. Heterozygous individuals have been detected (reported as  $H_{obs}$  values) within populations from the Central USA, the mid-continent USA, California and the American Southwest, Eastern Canada, Western Canada, Europe, and Southwest Asia (Table 4.1).

Using data from these population genetic surveys, we have estimated mating system parameters (outcrossing rate,  $t_f$ , and selfing rate,  $t_s$ ) for populations of *B. tectorum*, employing Wright's Coefficient of Inbreeding (Table 4.2). These results indicate that for six of the seven regions analyzed, the average outcrossing rate per population ranged from 0.11 % to 1.17 %, and the average selfing rate per population ranged from 98.83 % to 99.89 % (Table 4.2). Estimates of the mating system parameters for

**Table 4.2** Percent outcrossing and selfing among populations of *Bromus tectorum* calculated using the Coefficient of Inbreeding ( $F$ ) method (Wright 1931; Dudash and Fenster 2001). Rates of outcrossing are low for populations from most regions, with the exception of Southwestern Asia

Region	Number of pops.	$H_{\text{exp}}$	$H_{\text{obs}}$	$F$	$t_i$ , outcrossing rate (%)	$t_s$ , selfing rate (%)
Central USA <sup>a</sup>	60	0.014	0.00003	0.998	0.11	99.89
Mid-continent USA <sup>b</sup>	54	0.009	0.0002	0.978	1.12	98.88
California and American Southwest <sup>c</sup>	60	0.007	0.000017	0.998	0.12	99.88
Eastern Canada <sup>d</sup>	16	0.013	0.0003	0.977	1.17	98.83
Western Canada <sup>d</sup>	44	0.012	0.00005	0.996	0.21	99.79
Europe <sup>e</sup>	39	0.006	0.0001	0.983	0.84	99.16
SW Asia <sup>e</sup>	12	0.005	0.002	0.600	25.00	75.00

$H_{\text{exp}}$  is expected mean heterozygosity, and  $H_{\text{obs}}$  is mean observed heterozygosity.

<sup>a</sup>Huttanus et al. (2011); <sup>b</sup>Schachner et al. (2008); <sup>c</sup>Pawlak et al. (2015); <sup>d</sup>Valliant et al. (2007);

<sup>e</sup>Novak and Mack (1993) as cited in Huttanus et al. (2011)

populations from Southwest Asia are in striking contrast; populations from this region had an outcrossing rate of 25 % and a selfing rate of 75 %. This outcome probably arose because low-frequency alleles were only detected in individuals with heterozygous genotypes in several populations in Southwest Asia (Novak and Mack 1993); this result increased the value of  $H_{\text{obs}}$  relative to that of  $H_{\text{exp}}$ .

The estimated outcrossing rates ( $t$ ) published by Meyer et al. (2013) are remarkably similar to the rates reported for six of the seven regions listed in Table 4.2. Meyer et al. (2013) estimated outcrossing rates for four “wild” populations of *B. tectorum* from the Western USA, which ranged from 0.0027 to 0.0133 (i.e., 0.27 % to 1.33 %, with selfing rates that ranged from 98.67 % to 99.73 %). Similar results ( $t=0.0082$ , or 0.82 %) were obtained with analysis of individuals grown in a common garden (Meyer et al. 2013). The values of  $H_{\text{obs}}$  reported in Table 4.2 are generally consistent with observed heterozygosity values previously reported for *B. tectorum* by Ramakrishnan et al. (2006), Kao et al. (2008), Leger et al. (2009), and Scott et al. (2010). In contrast, the high levels of observed heterozygosity reported by Ashley and Longland (2007, 2009) in two of four populations of *B. tectorum* from Northern Nevada are inconsistent with the values reported by other investigators. For instance, using seven microsatellite DNA loci, Ashley and Longland (2009) report an observed heterozygosity value of 0.06 for the Peavine Mountain population. This value is approximately 35- to 54-fold larger than values reported by Meyer et al. (2013) for the Lower Peavine (0.0017) and Upper Peavine (0.0011) populations, even though Meyer et al. (2013) used a more polymorphic marker system, 91–93 single nucleotide polymorphisms (SNPs). This wide discrepancy among these results for populations of *B. tectorum* from a similar locality (Peavine Mountain) remains unresolved.

The preponderance of data indicates that *B. tectorum* reproduction is predominantly through selfing (as reported by McKone 1985); outcrossing rarely occurs within populations from NA. High selfing rates also appear to occur in European populations



of *B. tectorum* (Table 4.2); consequently, this trait may form a preadaptation that has contributed to the establishment and invasion of *B. tectorum* in NA. Rare outcrossing events in populations that are comprised of genetic admixtures may generate novel, recombinant genotypes (Novak 2007). Such events may indicate post-immigration evolution (Maron et al. 2004; Lavergne and Molofsky 2007; Schierenbeck and Ellstrand 2009; Xu et al. 2010). Reproductive plasticity in *B. tectorum* (see Meyer et al. 2013) could in turn enhance the species' invasion in NA (Huttanus et al. 2011). Whether or not post-immigration evolution is occurring within populations of invasive species is not solely an intriguing theoretical question; it also holds important implications for the management of invasions (Allendorf and Lundquist 2003; Sakai et al. 2001; Muller-Scharer et al. 2004; Le Roux and Wiczorek 2009).

#### 4.4 Biological Invasions: Propagule Pressure, Preadaptation, and Post-immigration Evolution

Invasive species can have profoundly negative ecological, conservation, economic, and health consequences (D'Antonio and Vitousek 1992; Mack et al. 2000; Sala et al. 2000; Pimentel et al. 2005; Mack and Smith 2011) and have consequently been a focus of much deserved research. Identifying which species will become invasive and which communities are susceptible to invasion however remains elusive (Novak 2007), and our ability to predict which introduced species will become established (and potentially invasive) will likely be facilitated by gaining a better understanding of the invasion process (Estoup and Guillemaud 2010). Consequently, propagule pressure, defined as the number of individuals transported to and introduced into a new range (Lockwood et al. 2005), has emerged as one predictor of naturalization and the likelihood of invasion (Kolar and Lodge 2001; Lockwood et al. 2005; Colautti and MacIsaac 2004; von Holle and Simberloff 2005; Colautti et al. 2006; Simberloff 2009; Ricciardi et al. 2011). Simberloff (2009) described three components of propagule pressure: (1) propagule size, the number of founder individuals in a propagule; (2) propagule number, the rate at which propagules arrive per unit time; and (3) both propagule size and propagule number. Humans' pervasive role as dispersal agents certainly increases the probability of high propagule pressure. With high propagule pressure, alien species are buffered from negative stochastic events during all phases of an invasion (Mack 2000), and large founder populations or multiple introduction events or both could characterize the release of an alien species in a new range.

Propagule pressure also has genetic consequences (Simberloff 2009; Huttanus et al. 2011): with high propagule pressure (e.g., multiple introductions), the overall genetic and phenotypic diversity of a species would likely be increased in its new range, and the potential for severe founder effects would likely decrease (Novak and Mack 2005; Wares et al. 2005; Durka et al. 2005; Lavergne and Molofsky 2007; Dlugosch and Parker 2008). In addition, high propagule pressure may lead to the formation of introduced populations that are admixtures, i.e., introduced populations

containing the genetic information of multiple native populations (Kolbe et al. 2007). Propagule pressure can also influence the likelihood of an invasion through the introduction of preadapted genotypes and by increasing the potential for post-immigration evolution.

Preadaptation during invasion involves the chance sampling of genotypes (and phenotypes) in one environment and their subsequent release into a new environment where they contribute to fitness (Futuyma 2005). Increased propagule pressure increases the likelihood of preadapted genotypes arriving in a new range, thus increasing the potential for invasion. The introduction of preadapted genotypes is likely to be the main mechanism leading to the invasion of some plant species, especially species that exhibit uniparental reproduction such as apomixis, vegetative reproduction, and selfing. The introduction of preadapted genotypes is implicated in the invasions of *Capsella bursa-pastoris* (Neuffer and Hurka 1999) in North America, the colonization of *Hypericum canariense* (Dlugosch and Parker 2007) in the Canary Islands, and the invasion of *Chondrilla juncea* (Gaskin et al. 2013) across three continents.

Post-immigration evolution is now widely recognized as an important contributor to invasion. Post-immigration evolution results from multiple introductions; the descendants conjointly produce genetic admixtures, outcrossing or hybridization among individuals with different genotypes, genetic reshuffling or recombination, and generation of novel genotypes, leading to subsequent natural selection (Lee 2002; Cox 2004; Facon et al. 2006; Novak 2007; Suarez and Tsutsui 2008; Prentis et al. 2008; Schierenbeck and Ellstrand 2009). Post-immigration evolution has been demonstrated repeatedly (e.g., Brown and Marshall 1981; Sexton et al. 2002; Leger and Rice 2003; Maron et al. 2004; Blair and Wolfe 2004; Brown and Eckert 2004; Lavergne and Molofsky 2007; Cano et al. 2008; Xu et al. 2010). Sufficient genetic diversity (especially additive genetic variance) within introduced populations is a prerequisite for post-immigration adaptive evolution. High propagule pressure increases the likelihood for high levels of genetic diversity and can set the stage for an increase in invasiveness through post-immigration evolution (Novak and Mack 2005; Wares et al. 2005). The multiple facets of evolution in an invasion suggest that it may be difficult to predict whether an invasion will occur because invasions unfold over widely varying periods of time (Novak 2007).

#### **4.5 Introduction of *B. tectorum* in North America: Historical Information and Genetic Data**

As pointed out above, assessing the propagule pressure of a biological invasion requires the number of founder individuals (founder population size), the rate at which propagules arrive (the number of discrete founder events), or both (Lockwood et al. 2005; Simberloff 2009). Such detailed demographic information is usually unavailable, especially for accidentally introduced plants, such as *B. tectorum*. As a result, attempts to determine patterns of introduction and range expansion for an

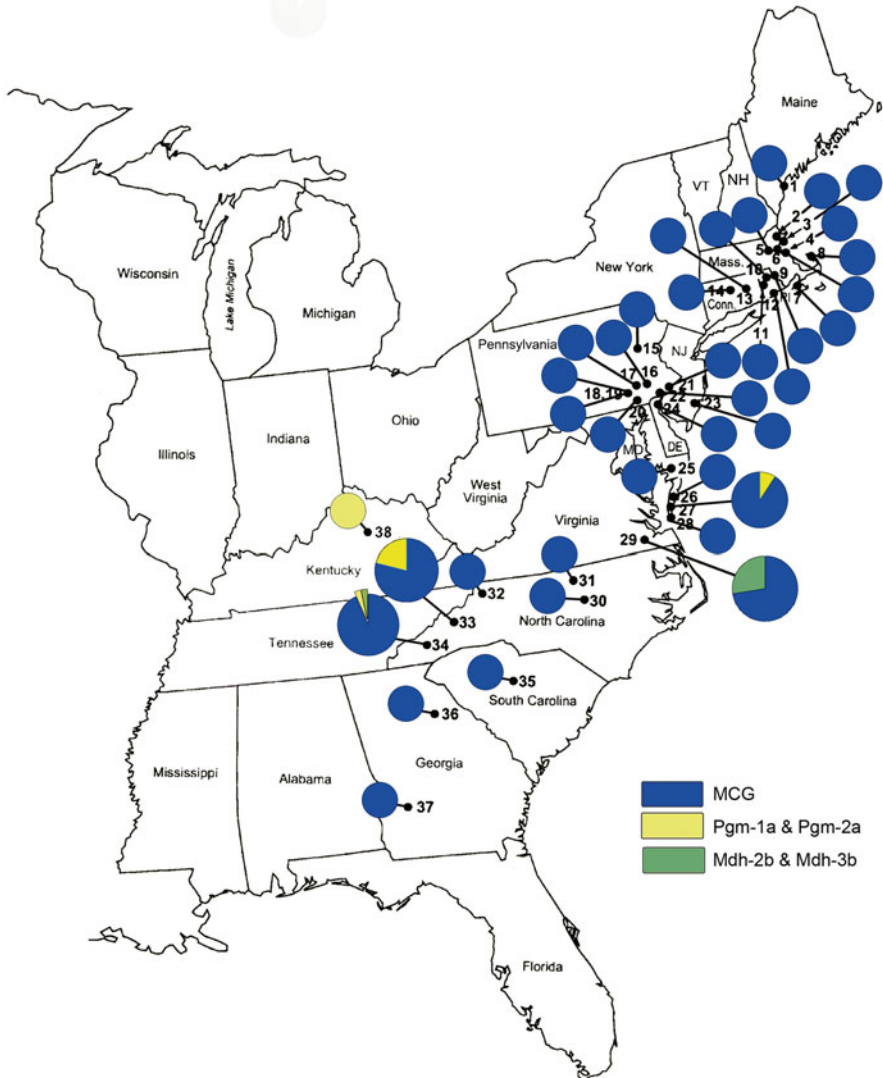
invasive species (its propagule pressure) are almost always constructed retrospectively (Mack 2005). These investigations require multiple sources of data, including historical records and genetic analyses (Estoup and Guillemaud 2010; Estoup et al. 2010; Lombaert et al. 2011; Novak 2011; Gaskin et al. 2013).

We have attempted to reconstruct the introduction history and the concatenation in the range expansion for *B. tectorum* into and across NA by combining reliable historical sources (herbarium specimens and published accounts) with the results of molecular genetic analyses that employ enzyme electrophoresis (allozymes) (Novak et al. 1991, 1993; Novak and Mack 1993, 2001; Bartlett et al. 2002; Valliant et al. 2007; Schachner et al. 2008; Huttanus et al. 2011; Pawlak et al. 2015). Other studies assessing the genetic diversity of *B. tectorum* in NA using molecular markers either have analyzed only 2–10 populations from a limited geographic area (1–2 states) (Ramakrishnan et al. 2004; Ashley and Longland 2007, 2009; Kao et al. 2008; Leger et al. 2009; Scott et al. 2010) or have analyzed larger numbers of populations from across a portion of Western NA (Ramakrishnan et al. 2006; Merrill et al. 2012). Our reconstruction has been assembled through the analysis of 10,150 individuals from 312 populations distributed across NA (the USA and Canada). The main results of these studies are summarized here.

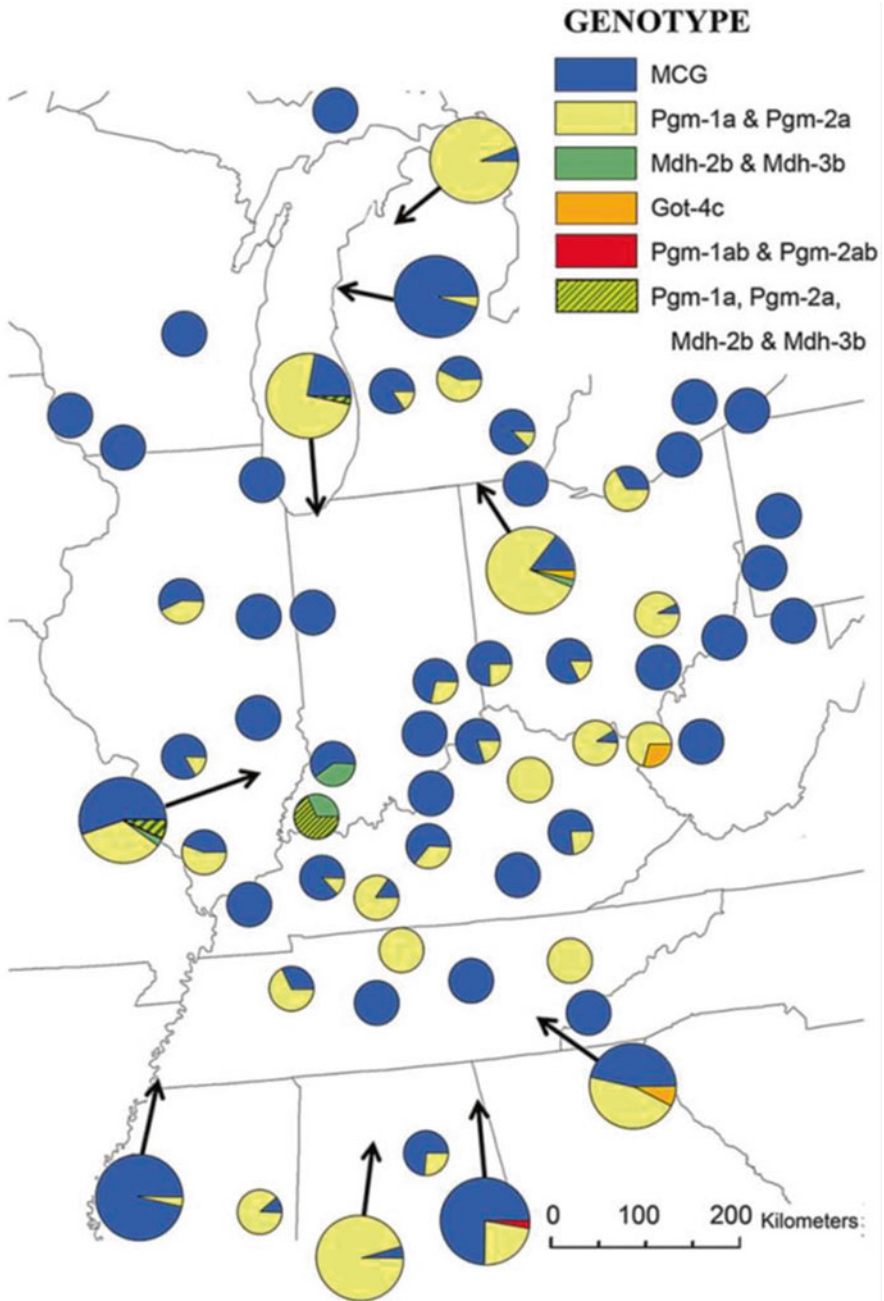
The earliest record of *B. tectorum* in NA of which we are aware is from Lancaster County, Pennsylvania, where the grass was collected no later than 1790 (Muhlenberg 1793). Unfortunately, Muhlenberg's identification cannot be verified because his herbarium specimen has been lost, although he probably employed a European voucher specimen with which to identify the grass (Bartlett et al. 2002). The species was not reported again in the Eastern USA until a specimen was collected approx. 80 km east of Lancaster in West Chester, Pennsylvania, in 1859. This gap in detection could have arisen because populations of the plant were small and overlooked or the populations Muhlenberg saw went extinct and the species' detection in the nineteenth century stems from reintroductions. In any event, the frequency of its collection in the Eastern USA increased markedly after 1860 (see Table 7, Bartlett et al. 2002). Although the geographic spread of these records (1860–1880) suggests that multiple introductions occurred, these data alone do not demonstrate this scenario.

We determined the distribution of multilocus genotypes (MLGs) and genetic diversity among 38 populations of *B. tectorum* from the Eastern USA to assess the grass' pattern of introduction and regional spread (Bartlett et al. 2002). All 25 populations sampled at localities extending from Maine to Delaware are fixed for what we have termed the Most Common Genotype (MCG) (Fig. 4.2). The MCG occurs most frequently in populations from the native and introduced ranges of *B. tectorum* and refers to the most common combination of alleles at the 25 scored loci (Novak et al. 1991; Novak and Mack 1993; Bartlett et al. 2002; Valliant et al. 2007; Schachner et al. 2008; Huttanus et al. 2011; Pawlak et al. 2015). The *Pgm-1a* & *Pgm-2a* MLG occurs in four Eastern US populations included in this analysis, and we also detected the *Mdh-2b* & *Mdh-3b* MLG in two populations (Fig. 4.2). Consequently, Eastern US populations of *B. tectorum* appear to have arisen from a minimum of two to three separate introductions. Additional introductions may have taken place but remain undetected because of the preponderance of the MCG in

East Coast populations. The distribution of *B. tectorum* across NA suggests that the grass could have spread westward with European settlers. Alternatively, the species' occurrence throughout NA may stem from separate introductions. These two hypotheses were tested through genetic analysis of populations of *B. tectorum* across the USA and Canada.



**Fig. 4.2** Multilocus genotypes for 38 populations of *Bromus tectorum* in the Eastern USA. Pie diagrams illustrate the proportions of each multilocus genotype in each population. (Sizes of the pie diagrams and any offset segments here and in Figs. 4.3–4.8 vary only to enhance legibility.) Lines accompanying pie diagrams indicate locations of the populations. Numbers are population designations from Bartlett et al. (2002)



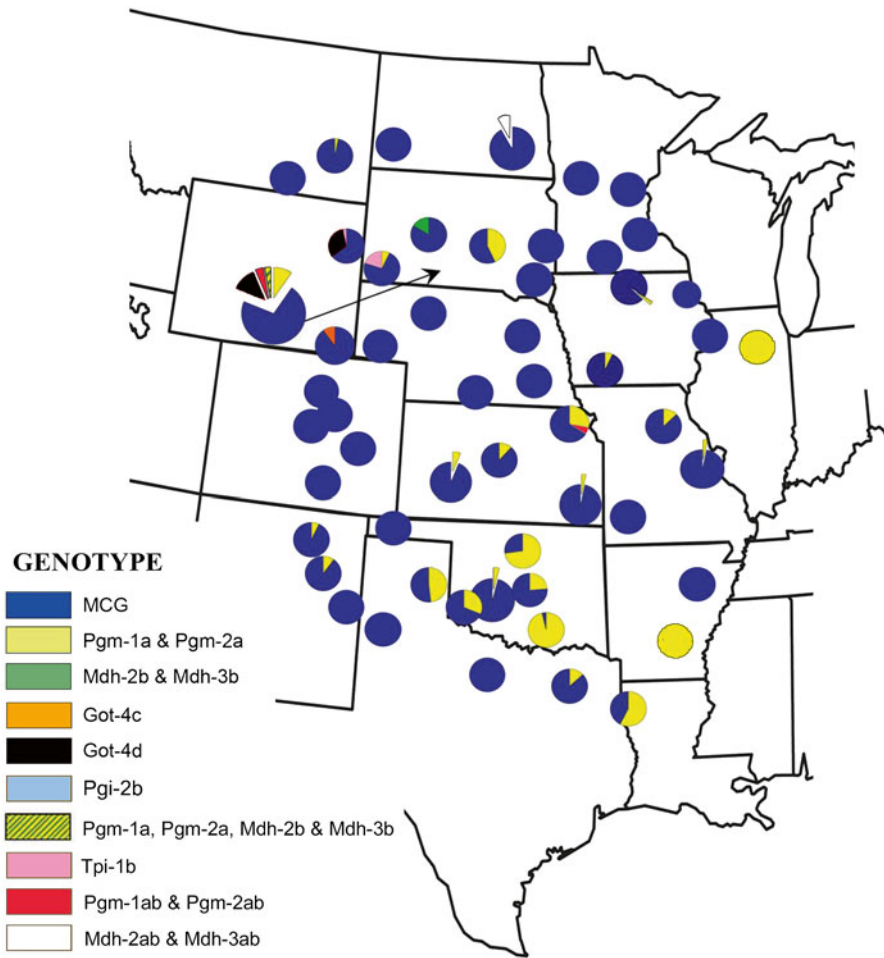
**Fig. 4.3** Multilocus genotypes for 60 populations of *Bromus tectorum* in the Central USA. Pie diagrams illustrate the proportions of each multilocus genotype in each population. (See caption for Fig. 4.2 for further explanation of the pie diagrams.) Data are from Huttanus et al. (2011)

The earliest collections of *B. tectorum* in the Central USA were made in the late 1880s and early 1890s (Mack 2011), 20–30 years after collections of the plant were being made with increasing frequency in the Eastern USA (Bartlett et al. 2002). If the species arrived in the Central USA with settlers that migrated westward, we predict that the same MLGs detected in Eastern US populations (or a subset of these genotypes) would also be detected among Central US populations. Alternatively, if the species arrived in this region through direct introduction(s) from the native range or from another region in NA, we would detect MLGs not found in the Eastern USA.

We analyzed 60 populations of *B. tectorum* from the Central USA using enzyme electrophoresis (Huttanus et al. 2011); six MLGs were detected (Fig. 4.3). Three of these genotypes (MCG, *Pgm-1a* & *Pgm-2a*, and *Mdh-2b* & *Mdh-3b*) match genotypes detected within Eastern US populations. This finding supports the hypothesis that *B. tectorum* was introduced into the Central USA as settlers from the East traveled westward. The MCG occurs in high frequency in the Central USA, the *Pgm-1a* & *Pgm-2a* MLG was detected in 34 of 60 populations, and the *Mdh-2b* & *Mdh-3b* genotype occurred at low frequency (four of 60 populations).

Three other MLGs were also detected at low frequency in populations in the Central USA: *Got-4c*, *Pgm-1ab* & *Pgm-2ab*, and *Pgm-1a*, *Pgm-2a*, *Mdh-2b* & *Mdh-3b* (Fig. 4.3). Only a single individual from the Valley Head, Alabama population displayed the *Pgm-1ab* & *Pgm-2ab* genotype; as a heterozygous genotype, it appears to be the product of a rare outcrossing event (Huttanus et al. 2011). The *Pgm-1a*, *Pgm-2a*, *Mdh-2b* & *Mdh-3b* MLG was detected in three populations and also occurs in a single individual collected in Martin, South Dakota (Fig. 4.4). This MLG may be a novel, recombinant genotype that arose *in situ* wherever plants with the *Pgm-1a* & *Pgm-2a* and *Mdh-2b* & *Mdh-3b* MLGs co-occurred (Huttanus et al. 2011). Alternatively, this genotype may have been introduced directly into the USA (e.g., near Daylight/Earle, Indiana, where it occurs at its highest frequency among sampled populations) and subsequently spread. This MLG has not been reported among native populations analyzed thus far (Novak and Mack 1993, 2001); its detection in the native range would be unlikely if indeed it is a novel, recombinant genotype. Only analysis of additional native populations will allow us to resolve this issue.

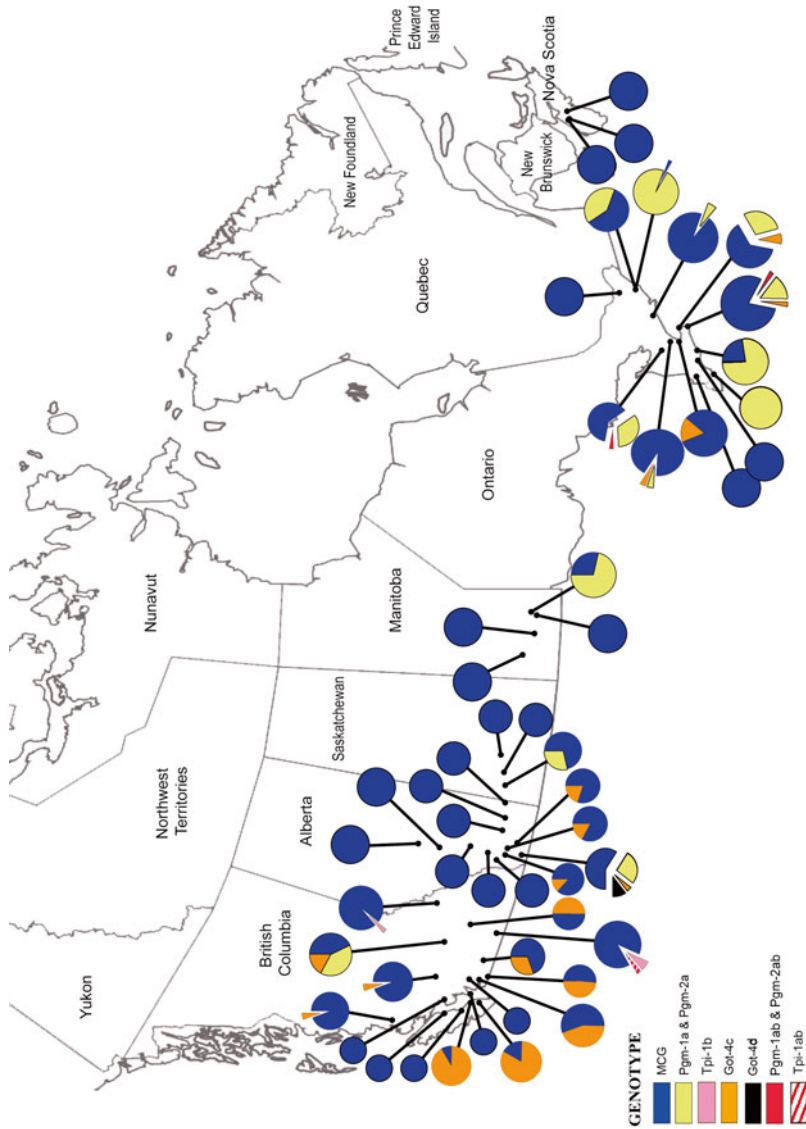
The occurrence of the *Got-4c* MLG in three populations in the Central USA is intriguing because this genotype was undetected among Eastern US populations (Fig. 4.2); the closest US population with this genotype is far to the west in Laramie, Wyoming (Fig. 4.4). Consequently, at least two scenarios explain the occurrence of the *Got-4c* MLG in the Central USA. It may have been introduced directly from the native range. Alternatively, the *Got-4c* genotype may have spread from Eastern Canada, where it has been detected in four of 13 populations in Southern Ontario (Fig. 4.5). Great Lakes commerce and shipping between the Central USA and Southeastern Canada predates 1800, and *B. tectorum* may have been dispersed by this traffic (Huttanus et al. 2011). This same traffic may provide an alternative explanation for the occurrence of the *Pgm-1a* & *Pgm-2a* MLG in the Central USA; this genotype was detected in nine of 13 populations from Southern Ontario



**Fig. 4.4** Multilocus genotypes for 60 populations of *Bromus tectorum* in the mid-continent USA. Pie diagrams illustrate the proportions of each multilocus genotype in each population. (See caption for Fig. 4.2 for further explanation of the pie diagrams.) Data are from Schachner et al. (2008)

(Fig. 4.5). Thirty-two of the 60 populations (53.3 %) from the Central USA are genetically polymorphic (i.e., genetic admixtures).

The earliest herbarium specimens of *B. tectorum* from the northern portion of the mid-continent USA were collected in the 1890s, whereas the earliest specimens from the southern portion of this vast region were collected in the 1920s. These sizeable differences in the apparent timing of the entry of *B. tectorum* in the mid-continent USA may reflect different patterns of introduction, patterns that can also be detected through genetic analysis. Among the 54 mid-continent US populations of *B. tectorum* analyzed by Schachner et al. (2008), nine MLGs were detected: the MCG, *Pgm-1a* & *Pgm-2a*, *Mdh-2b* & *Mdh-3b*, *Got-4c*, *Got-4d*, *Tpi-1b*, *Pgm-1a*,



**Fig. 4.5** Multilocus genotypes for 51 populations of *Bromus tectorum* in Canada. This figure does not include nine population of *B. tectorum* from central British Columbia (see Fig. 4.8). These nine populations were omitted only to increase the readability of the figure. Pie diagrams illustrate the proportions of each multilocus genotype in each population. (See caption for Fig. 4.2 for further explanation of the pie diagrams.) Data are from Valliant et al. (2007)

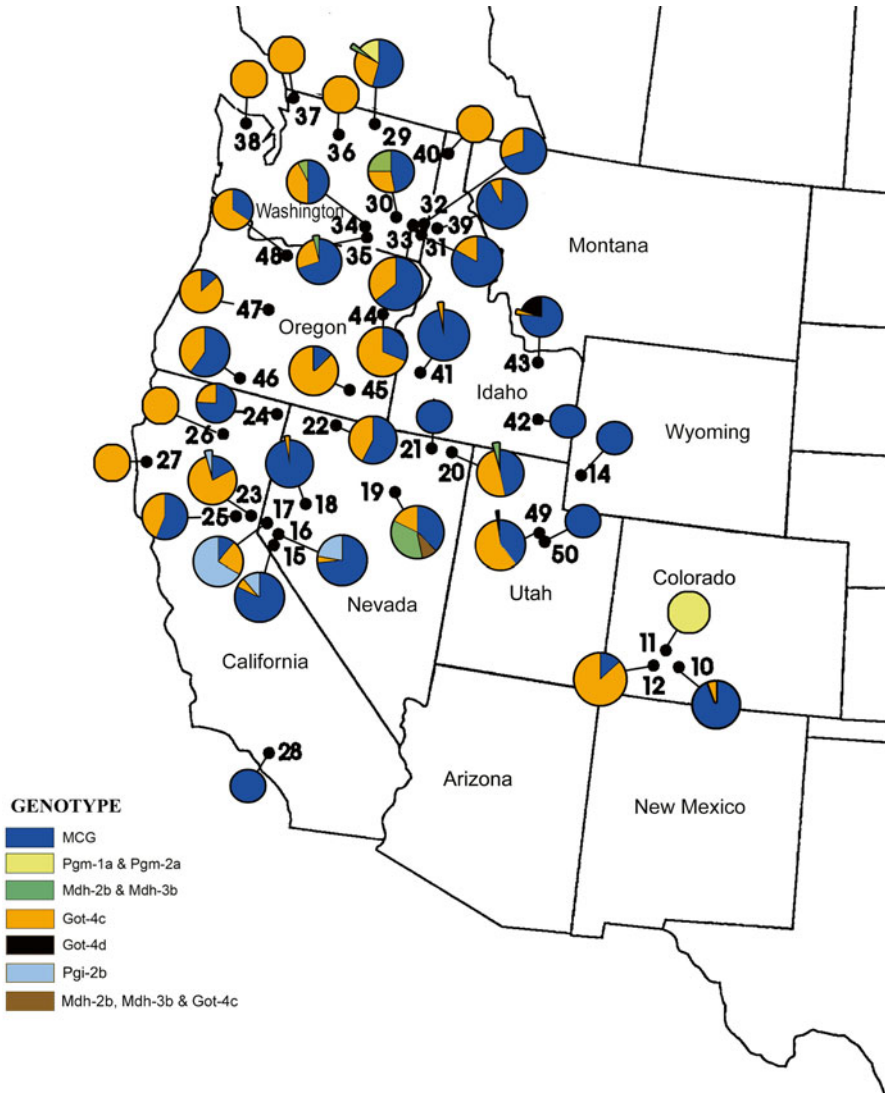


*Pgm-2a*, *Mdh-2b* & *Mdh-3b*, *Pgm-1ab* & *Pgm-2ab*, and *Mdh-2ab* & *Mdh-3ab* (Fig. 4.4). Approximately one-half of the populations in the mid-continent USA (26 of 54) are genetic admixtures, i.e., they consist of two or more genotypes previously detected among native Eurasian populations (Novak and Mack 1993). The MCG occurs at high frequency (52 of 54 populations) in the mid-continent USA. The *Pgm-1a* & *Pgm-2a* MLG occurs in 24 of 54 populations from the mid-continent USA: 17 of these populations occur in the eight states in the region's southern portion. Only three MLGs (MCG, *Pgm-1a* & *Pgm-2a*, and *Pgm-1ab* & *Pgm-2ab*) were detected in the eight states in this southern portion, whereas all nine MLGs found within the mid-continent USA were detected in populations from the eight states in the region's northern portion (Fig. 4.4). These patterns of genotype distributions indicate that events leading to the establishment of *B. tectorum* in the northern and southern portions of the mid-continent USA arose via different scenarios.

The MCG is clearly prominent within the 26 widespread populations we sampled in the northern portion of the mid-continent USA. The *Pgm-1a* & *Pgm-2a* MLG is a distant second in prominence with detection in seven populations (Fig. 4.4). Other MLGs however have more restricted distributions. For instance, the *Mdh-2b* & *Mdh-3b* MLG, the *Got-4d*, and the *Tpi-1b* genotypes were found in two populations each. The *Got-4c* genotype was detected in a single population. All populations with these MLGs are located in either South Dakota or Eastern Wyoming. The seemingly scattered occurrence of populations with these MLGs indicates additional sampling is warranted to improve estimates of the regional genetic diversity of populations. In addition, field experimentation with *B. tectorum* populations could be conducted to determine whether this genetic diversity has contributed to greater invasiveness.

Five heterozygous individuals were encountered within three populations in the mid-continent USA (Fig. 4.4). The *Pgm-1ab* & *Pgm-2ab* heterozygous MLG was detected in two individuals from the Oskaloosa, Kansas, population and one individual from the Martin, South Dakota, population. Two individuals from the Colfax, North Dakota, population had the *Mdh-2ab* & *Mdh-3ab* genotype. These heterozygous individuals were the product of outcrossing events. The *Pgm-1a*, *Pgm-2a*, *Mdh-2b* & *Mdh-3b* genotype was observed in a single individual from the Martin, South Dakota population, and as discussed above, several mechanisms potentially explain its occurrence.

Several non-mutually exclusive scenarios potentially explain the occurrence of different MLGs among *B. tectorum* populations in the mid-continent USA, especially those in the region's northern portion. European settlers migrating from the east may have dispersed some of these genotypes (e.g., the MCG, *Pgm-1a* & *Pgm-2a*, and *Mdh-2b* & *Mdh-3b*), some genotypes (e.g., *Got-4c*, *Got-4d*, and *Tpi-1b*) may have arrived from the Western USA, where they also occur (Fig. 4.6), and some may have been introduced directly from the native range. Ascertaining the role, if any, of these scenarios in the regional occurrence of genotypes will require a molecular marker with greater resolving power (e.g., microsatellite DNA or SNPs) than allozymes (Avisé 2004; Schlotterer 2004; Estoup et al. 2010; Lombaert et al. 2011).



**Fig. 4.6** Multilocus genotypes for 40 populations of *Bromus tectorum* in the Western USA. Pie diagrams illustrate the proportions of each multilocus genotype in each population. (See caption for Fig. 4.2 for further explanation of the pie diagrams.) Numbers are the population designations from Novak et al. (1991)

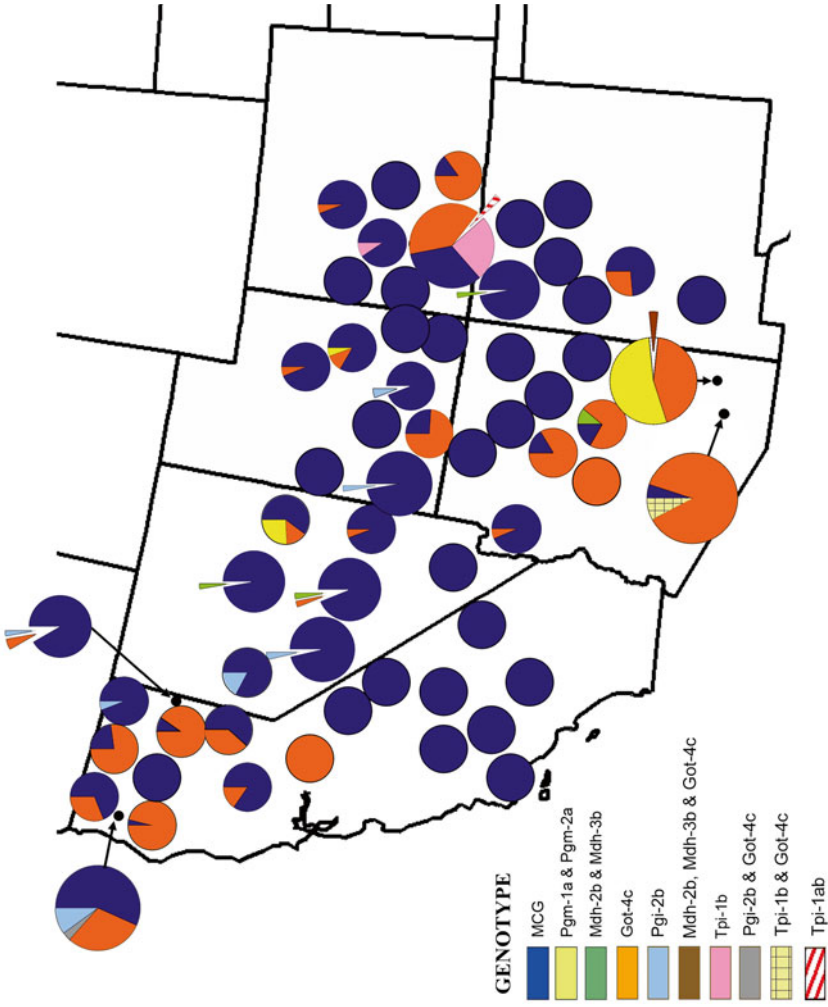
The collection history of *B. tectorum* in the Intermountain West of NA is well documented (Mack 1981). The grass was first collected at Spences Bridge, British Columbia, in 1889; Ritzville, Washington, in 1893; Provo, Utah, in 1894; Pullman, Washington, in 1897, Eastern Colorado in 1897, Boise, Idaho, in 1899, and the Klamath Valley of Oregon in 1902. Similar to the introduction of *B. tectorum* in the

Eastern USA, the chronology in the West suggests multiple introductions. Analysis of 40 populations from this region (which includes 26 populations from the Intermountain West and 14 populations from Nevada and California, see Table 4.1), using enzyme electrophoresis largely confirms this hypothesis (Novak et al. 1991).

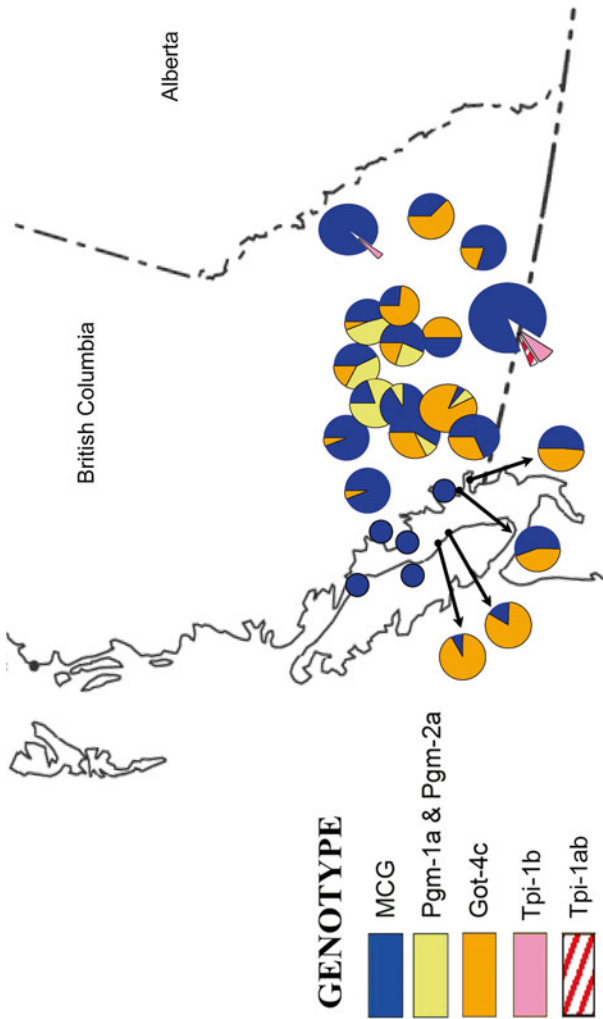
Seven MLGs were identified among Western US populations: the MCG, *Pgm-1a* & *Pgm-2a*, *Mdh-2b* & *Mdh-3b*, *Got-4c*, *Got-4d*, *Pgi-2b*, and *Got-4c*, *Mdh-2b* & *Mdh-3b* (Fig. 4.6). Unlike the prominence of genotypes elsewhere in the USA, the MCG and the *Got-4c* genotype are equally common in the West. The *Got-4c* genotype occurs in 34 of 40 populations and is the only genotype (i.e., it is “fixed”) in six of these populations. The MCG occurs in 33 of 40 populations and is also fixed in six populations. Other MLGs occur at lower frequency: *Mdh-2b* & *Mdh-3b* occurs in six populations (four from Eastern Washington and two from Northern Nevada); *Pgm-1a* & *Pgm-2a* was detected in two populations (Gunnison, Colorado, and Tonasket, Washington), and *Got-4d* was detected in the populations from Provo, Utah, and Dubois, Idaho (Fig. 4.6). The *Got-4c*, *Mdh-2b* & *Mdh-3b* MLG was found only in the population at Emigrant Pass, Nevada, and appears to be a novel, recombinant genotype. The *Pgi-2b* MLG was detected in three populations near Reno, Nevada, and among several individuals in the population at Truckee, California (Fig. 4.6). In addition, this genotype has been also found at low frequency in seven populations from California and the American Southwest (the Southwestern USA) (Fig. 4.7). No heterozygous individuals were detected among the individuals from the 40 mostly Intermountain West populations we analyzed (Table 4.1). Among these 40 populations, most (28) were genetically polymorphic (i.e., genetic admixtures).

Several scenarios potentially explain the occurrence of different MLGs among *B. tectorum* populations from the Western USA. The *Got-4d* genotype may have been introduced through long distance dispersal into Provo, Utah, an early collection site for *B. tectorum* in the West (Mack 1981). Other genotypes may have arrived from elsewhere in NA. For instance, the occurrence of plants with the *Pgm-1a* & *Pgm-2a* genotype at Gunnison, Colorado, may be the result of dispersal from mid-continent US populations, and the occurrence of this genotype in a population at Tonasket, Washington, may reflect spread from populations in nearby British Columbia. The *Pgm-1a* & *Pgm-2a* MLG has a high frequency of occurrence within populations in the southern portion of the mid-continent USA (Fig. 4.4) and in central British Columbia (Fig. 4.8).

The earliest collection of *B. tectorum* in California of which we are aware was made in Siskiyou County in 1899 (Pawlak et al. 2015). Over the next 20 years, other collections were made in northern counties in California (Siskiyou, Shasta, and Humboldt). The conspicuous absence of any collection records well into the twentieth century in the San Francisco Bay area, a locale of intense plant collecting, strongly suggests that ships arriving in San Francisco Bay played no role in its introduction (Pawlak et al. 2015). The earliest collections in Southern California occurred in 1902 in Santa Cruz, Santa Barbara, and Ventura counties. Earliest collections in both northern and southern parts of Nevada were made in the early 1900s (Pawlak et al. 2015). The earliest collection in Arizona was in Coconino County in 1901. The collection record of *B. tectorum* in the rest of the American Southwest is



**Fig. 4.7** Multilocus genotypes for 60 populations of *Bromus tectorum* in California and the American Southwest. Pie diagrams illustrate the proportions of each multilocus genotype in each population. (See caption for Fig. 4.2 for further explanation of the pie diagrams.) Data are from Pawlak et al. (2015)



**Fig. 4.8** Multilocus genotypes for 25 populations of *Bromus tectorum* in British Columbia. This figure includes nine population of *B. tectorum* from central British Columbia previously reported in Novak et al. (1991). Pie diagrams illustrate the proportions of each multilocus genotype in each population. (See caption for Fig. 4.2 for further explanation of the pie diagrams.) Data are from Valliant et al. (2007)

exceptionally sparse, especially for Colorado and New Mexico. As indicated above, the earliest collection in Utah (1894) occurred in Provo.

Ten MLGs were detected among the 60 populations of *B. tectorum* from California and the American Southwest analyzed by Pawlak et al. (2015). Two MLGs are conspicuous in California and the American Southwest; the MCG occurs in 57 of 60 populations and is predominant in many, whereas the *Got-4c* genotype has a high frequency of occurrence within populations in Northern California and Southern Arizona (Fig. 4.6). The *Pgi-2b* genotype occurs at relatively low frequency in seven populations, three from Northern California, two from Nevada, and two from Utah. The *Pgm-1a* & *Pgm-2a* and *Mdh-2b* & *Mdh-3b* MLGs sporadically occur across the region, within three and four populations, respectively. Two populations in southeastern Colorado (Olathe and Hermosa) contain the *Tpi-1b* MLG. The only heterozygous individual we detected in this region (*Tpi-1ab*) was collected at Hermosa, Colorado. Three MLGs believed to be novel, recombinant genotypes may have arisen *in situ* among regional populations: *Mdh-2b*, *Mdh-3b* & *Got-4c* and *Tpi-1b* & *Got-4c* occur in populations in Southern Arizona (Turkey Flat and Mount Lemmon, respectively), and the *Pgi-2b* & *Got-4c* MLG was detected in a population from Northern California (Orleans).

The collection record and genetic analysis of *B. tectorum* populations from California and the American Southwest indicate that the introduction and regional spread of the grass were rapid and multidirectional and resulted in 31 of 60 (52 %) populations being comprised of genetic admixtures (i.e., polymorphic at one or more loci). For instance, the high frequency of *Got-4c* MLG in Northern California (Fig. 4.7) likely arose through the spread of *B. tectorum* southward from the Pacific Northwest; evidence for this pathway is provided by the high frequency of the *Got-4c* genotype among populations in Oregon (Fig. 4.6). The *Got-4c* MLG also has a high frequency of occurrence within populations in the mountains of Southern Arizona (Fig. 4.7). Postfire reseedling can inadvertently introduce nonnative plant species (Keeley et al. 2006). Perhaps *B. tectorum* with the *Got-4c* genotype arrived in Southern Arizona by this mode: forests on Mount Lemmon were extensively burned in 2003, and *B. tectorum* was first detected on the mountain 2 years later (L.A. Brigham, personal communication) (Pawlak et al. 2015).

In contrast, the MCG and other genotypes appear to have spread into California and the American Southwest from populations farther east. Finally, the *Pgi-2b* MLG has only been detected in 11 populations from California, Nevada, and Utah (Figs. 4.6 and 4.7). These are the only populations of *B. tectorum* in NA with this MLG, and the restricted distribution of this genotype likely stems from direct introduction from the native range, followed by dispersal (Pawlak et al. 2015).

The collection history of *B. tectorum* in Canada was described by Valliant et al. (2007). The oldest reported herbarium specimen for the grass in Canada was collected in Kingston, Ontario, in 1886 (see Fig. 4.3, Valliant et al. 2007). Other early collection sites for *B. tectorum* in Southern Ontario are ports along the Great Lakes. In Western Canada, *B. tectorum* was first collected in 1889 from an irrigated field near Spences Bridge, British Columbia, a site more than 3000 km west of Southern Ontario. A second pre-1900 collection of the grass in Western Canada was made on

Vancouver Island. Additional collecting of *B. tectorum* in Southern Ontario in the early twentieth century appears to have lagged, while the grass was collected with increasing frequency in the arid interior of British Columbia (the Okanagan Valley) between 1901 and 1925 (Valliant et al. 2007).

As described earlier, this distinct bicoastal pattern of collection is consistent with multiple introductions for the grass. This hypothesis was tested with an enzyme electrophoresis analysis of 60 *B. tectorum* populations from across Canada (Valliant et al. 2007). In Eastern Canada, the MCG and the *Pgm-1a* & *Pgm-2a* MLG occur commonly, and two populations in Southern Ontario (Port Colborne and Alliston) contain individuals with the heterozygous genotype *Pgm-1ab* & *Pgm-2ab* (Fig. 4.5). The *Got-4c* genotype occurs in four populations in Southern Ontario. Although the frequency of this genotype in Eastern Canada is low (Fig. 4.5), it is higher than its frequency in populations in the eastern third of the USA (see Figs. 4.2 and 4.3). As observed in Eastern Canada, the MCG and the *Pgm-1a* & *Pgm-2a* genotype are commonly found within populations in Western Canada (Fig. 4.5). The *Pgm-1a* & *Pgm-2a* genotype was detected in populations from Manitoba, Saskatchewan, Alberta, and British Columbia. But its highest frequency (seven populations) occurs in central British Columbia (Fig. 4.8). Several genotypes were found in populations in Western Canada: the *Tpi-1b* MLG in two populations in British Columbia (Golden and Osoyoos) and the *Tpi-1ab* heterozygous genotype in a population at Osoyoos (Fig. 4.8). In Western Canada, the *Got-4d* genotype has been detected only in a population at Waterton, Alberta. In the Western USA, this same genotype had been previously reported from populations in Provo, Utah, and Dubois, Idaho (Fig. 4.6) (Novak et al. 1991, 1993). The area around Waterton, Alberta, was settled by people from Utah at the end of the nineteenth century, and their route to Alberta took them near Dubois, Idaho (Valliant et al. 2007). Whether *B. tectorum* with this genotype may have been spread from Provo, Utah, via Dubois, Idaho, to Waterton, Alberta, by these settlers remains an intriguing hypothesis.

## 4.6 Source Populations

Although the patterns described above are consistent with multiple introductions, definitive test of such introductions requires detecting the same genotype within native populations. We have conducted an enzyme electrophoresis analysis of 1730 individuals from 51 native population of *B. tectorum* in Eurasia (Novak and Mack 1993), and these data allow us to assess the species' pattern of introduction into NA and identify source populations (or regions) for such introductions. We are not aware of any other published reports that have assessed and compared the genetic diversity (and the distribution of genotypes) of native and invasive populations of *B. tectorum* using the same molecular marker system.

For *B. tectorum*, many of the multilocus genotypes observed in NA are widely distributed across the continent. In contrast, the same genotypes often have restricted geographic distribution among native, Eurasian populations (Novak and Mack 1993).

The exception to this general pattern is the MCG, which occurs across much of the species' native range. If native genotypes have restricted geographic distributions (i.e., geographically structured), accurate identification of the geographic origins of an invasion is facilitated (Novak and Mack 2001; Novak 2011). The *Pgm-1a* & *Pgm-2a* MLG has been detected in the native range at Bratislava, Slovakia, and Vac, Hungary (Novak and Mack 1993, 2001). The *Got-4c* MLG occurs in some populations in Eastern NA and has its highest prominence in Western NA, whereas in the native range this genotype is known only from Libochovice, Czech Republic, and Bayreuth, Germany. In the native range, we have detected the *Got-4d* genotype in a single population in Vienna, Austria. In Western NA, the *Pgi-2b* genotype has been detected in 11 populations from California, Nevada, and Utah; in the native range, this genotype occurs in populations in France, Spain, and Morocco. In contrast, no published accounts report the *Mdh-2b* & *Mdh-3b* and *Tpi-1b* genotypes among native Eurasian populations. Based on these data, the geographic origins of the invasion of *B. tectorum* in NA appear to be among populations from Central Europe and the western Mediterranean region (Novak and Mack 1993, 2001). Identification of the sources for other genotypes in NA will require analysis of additional native populations and perhaps a different genetic marker.

#### 4.7 Genetic Diversity within and among Populations of *B. tectorum*

If the above listed demographic data are unobtainable, propagule pressure can be estimated with molecular data (Ficetola et al. 2008; Ross and Shoemaker 2008; Goncalves da Silva et al. 2010; Huttanus et al. 2011). Huttanus et al. (2011) lists four patterns of genetic diversity that may reflect high propagule pressure: (1) the number of multilocus genotypes of a species across its new range would likely be large; (2) genetic admixtures, if propagule pressure results in the establishment of two or more independently derived native genotypes within invasive populations; (3) similar levels of genetic diversity within native and introduced populations and little evidence for founder effects; and (4) if genetic admixtures are common, introduced populations will have similar, or even less, genetic structure than native populations.

The detection of seven homozygous, nonrecombinant multilocus genotypes among NA populations of *B. tectorum* indicates that multiple introductions have occurred, which in turn likely reflect moderate propagule pressure. In addition, 156 of the 312 (50 %) NA populations we have analyzed are genetically diverse, the products of either direct introduction events or dispersal of genotypes among populations. These populations are genetic admixtures.

The genetic diversity of a species, or group of populations, can be hierarchically partitioned across (among) and within populations, and the amount of diversity at these two levels can be compared to assess the genetic consequences of introduction and range expansion (Novak and Mack 2005). At the 25 scored loci, NA populations of *B. tectorum* have lower allelic richness (33 vs. 43) and fewer polymorphic



loci (7 vs. 13) than native populations (Novak and Mack 1993, 2005), indicating that NA populations arose through the loss of genetic diversity by founder effects. Despite reduced genetic diversity across invasive populations, the amount of genetic diversity detected, on average, within populations from all regions in NA except one (Eastern USA) is higher than the diversity within populations in either of the major regions we denote in the grass's native range (Table 4.1). Thus, at the within-population level, populations of *B. tectorum* from NA possess more genetic diversity than native populations.

Values of  $G_{ST}$  for the populations of *B. tectorum* from all regions of NA ( $G_{ST}=0.241-0.582$ ) are lower than the values for either European populations ( $G_{ST}=0.656$ ) or populations from Southwest Asia ( $G_{ST}=0.735$ ) (Table 4.1). These data indicate that the genetic structure among populations in NA is less than the genetic structure of populations from both regions in the native range, a likely outcome of multiple introductions. The propagule pressure associated with the introduction of *B. tectorum* into NA from genetically diverse source populations and subsequent dispersal events appears to have largely offset the reduction in genetic diversity associated with transcontinental migration.

## 4.8 Management Implications

The evolutionary history of species within section *Genea*, including *B. tectorum* (Sales 1993, 1994; Balfourier et al. 1998), serves as a guide to management of brome-grasses and *B. tectorum* in particular. First, disturbances (e.g., livestock grazing, off-road vehicle use) should be minimized in habitats within which *Bromus* species do not yet occur or are not yet abundant. Although the link between disturbance and invasion is well known (Hobbs and Huenneke 1992; Hierro et al. 2006), the information presented here places the relationship between the occurrence of these species and disturbance in an evolutionary context.

Results of the genetic analysis of *B. tectorum* across NA reveal the importance of multiple introductions of MLGs from different native source populations to the subsequent spread of these genotypes among NA populations. These events have resulted in genetic admixtures: one-half (156 of 312) of NA populations are comprised of genotypes from different native populations. This diversity complicates the management of *B. tectorum* in NA because no one control prescription is likely to be effective for all genotypes, especially in all habitats. Consequently, we advocate measures that reduce propagule pressure (i.e., reduce or eliminate additional introduction events). These efforts should certainly include prevention through border inspections as well as early detection and rapid response, and eradication while the infested area remains small (Mack et al. 2000; Wittenberg and Cock 2005). In addition, gene flow should be deliberately limited (i.e., reduce propagule dispersal) among populations of *B. tectorum*; gene flow can produce populations with increased genetic diversity and bring together genotypes that have never co-occurred in the same population.

We also believe that the management of *B. tectorum* in NA can be enhanced by assessing the performance (survival, growth and reproduction) of plants with different MLGs across an array of environmental conditions. Based on this information, optimal habitat conditions for specific MLGs may be identified. If a stringent regime for genetic monitoring of *B. tectorum* populations were implemented (see below), land managers could specifically target certain MLGs for control because of the ability of plants with these genotypes to dominate a site. Such information on the performance of different MLGs could also be used to predict changes in the distribution and abundance of *B. tectorum* driven by climate change (see Hufft and Zelikova 2015).

The landscape level management of *B. tectorum* in NA by herbicides, tillage, and grazing has been largely ineffective (Mack 2011); consequently, a classical biological control program, which involves foreign exploration for natural enemies, such as insects or fungi, should be considered. Although use of classical biological control for invasive grasses has been viewed as problematic (McFadyen 1998), this method is gaining more support for particularly noxious grasses. For instance, biological control agents have been sought for *Spartina alterniflora* Loisel. in the USA (Grevstad et al. 2003; Fisher et al. 2005) and Chilean needle grass (*Nassella neesiana* (Trin. and Rupr.) Barkworth in Australia and New Zealand (Anderson et al. 2010, 2011).

The information summarized in this chapter (source populations, reconstructing the introduction and range expansion of *B. tectorum* in its new range, and an assessment of the genetic diversity of invasive populations) is requisite for development of a classical biological control program (Roderick and Navajas 2003; Novak and Sforza 2008; Gaskin et al. 2011). For instance, the overall genetic diversity of *B. tectorum* in NA is low compared with native populations of the grass; consequently, as suggested by Muller-Scharer et al. (2004), only a few highly specialized control agents may be necessary. In such cases, control agents would probably experience fast population buildup and spread as they attack the target species. With multiple introductions, genotypes from several native source populations have been detected across NA, and under these circumstances, agents from different portions of the native range would be required for control (Burdon and Marshall 1981). Furthermore, several control agents may be needed within the same locality (Muller-Scharer et al. 2004), given the high frequency of genetic admixtures among invasive populations of *B. tectorum*. Finally, the geographic origins for the invasion of *B. tectorum* into NA appear to be in Central Europe and the western Mediterranean region. The search for biological control agents that are both specific and effective should be conducted within these two regions (Goolsby et al. 2006; Gaskin et al. 2011).

## 4.9 Research Needs

The composite picture that emerges from the genetic analysis of *B. tectorum* summarized here is that multiple introductions into NA occurred, and range expansion of the grass across the continent was rapid and multidirectional. Future research

should analyze both native and invasive populations of *B. tectorum* using genetic markers with higher resolving power than enzyme electrophoresis (e.g., microsatellite DNA, SNPs) to more precisely determine the number of introductions that have occurred in NA and the location of source populations within the native range. The genetic markers listed above are considered to be neutral to selection; thus care should be exercised when attempting to infer the adaptive significance of these data (Avisé 2004). These markers can be instead used more reliably to infer demographic processes (e.g., dispersal and colonization events and the effective population size), detect population admixture, estimate mating system parameters, and assess parental (paternity) and kinship relationships (Schlotterer 2004).

Alternatively, the amount of genetic diversity within populations, especially the level of allelic richness within populations, is associated with a species' evolutionary potential (Fisher 1958; Van Kleunen et al. 2000; Vergeer et al. 2003). To more accurately estimate evolutionary potential of *B. tectorum*, efforts need to be made to determine more precisely the amount of single-locus genetic diversity (measured using genetic markers), quantitative (ecologically important) trait variation (e.g., ecophysiological traits), and phenotypic plasticity within and among native and invasive populations of the grass within the same experimental design. For example, this approach was utilized by Lavergne and Molofsky (2007) to show that invasive populations of *Phalaris arundinacea* L. possess higher single-locus allelic diversity, quantitative trait variability, and phenotypic plasticity, compared with native populations; these features increased the evolutionary potential that contributed to this species' invasion in NA.

Outcrossing events, although rare, have nonetheless led to the production of heterozygous individuals within populations of *B. tectorum* in several regions; legacies of such outcrossing events are novel, recombinant genotypes within populations in the Central USA, mid-continent USA, and California and the American Southwest. These findings suggest that post-immigration evolution is taking place, even within populations of this highly selfing species. Thus, future efforts should be taken to evaluate the extent to which these events influence the invasion of *B. tectorum* by monitoring populations using a genetic approach (see Novak and Rausch 2009). This genetic approach might first focus on marginal habitats or recently invaded sites, as described in Kao et al. (2008).

Future research could assess how the occurrence of heterozygous individuals and recombinant genotypes influence quantitative trait variation and phenotypic plasticity within invasive populations of *B. tectorum*. In the future, this effort could incorporate genomics and proteomics approaches that include DNA sequence analysis, quantitative trait loci (QTL) mapping, and microarray analysis of transcriptional regulation (Basu et al. 2004; Hudson 2008; Stinchcombe and Hoekstra 2008; Nadeau and Jiggins 2010; Eklblom and Galindo 2011). In addition, assessing the role of epigenetic variation and differentiation in the invasion of *B. tectorum* may prove especially important because epigenetic mechanisms can result in phenotypic trait variability, even in the absence of genetic variation (Bossdorf et al. 2008; Richards et al. 2010, 2012). Finally, the manner in which single-locus genetic diversity, quantitative trait variation, phenotype plasticity, and epigenetics, singly

and in combination, influences the invasion of *B. tectorum* in the USA under global climate change will need to be assessed (Reusch and Wood 2007; Salamin et al. 2010; Nicotra et al. 2010) if this most noxious member of *Bromus* section *Genea* is to be curbed.

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