THESIS

DEVELOPMENT AND USE OF A DATABASE WITH INFORMATION ABOUT *BROMUS* SPECIES FOR RESEARCH ON INVASIONS

Submitted by

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ABSTRACT

DEVELOPMENT AND USE OF A DATABASE WITH INFORMATION ABOUT *BROMUS* SPECIES FOR RESEARCH ON INVASIONS

Invasive plants are a serious problem worldwide. Plant invasions cause damage to agricultural and natural ecosystems, and contribute to loss of biological diversity. They are difficult to predict, prevent, and control. The Poaceae or grass family contains many species that have been introduced into areas outside of their native ranges and have become invasive. Brome grasses are a group of C3 grasses that grow primarily in temperate regions. A number of brome grasses have been introduced into the North America, sometimes accidentally, and sometimes for use as hay and forage, or for other purposes. Introduced brome grasses display varying levels of invasiveness.

In conjunction with a research project focusing on invasive brome grasses in the western United States, I developed a database that contains information about traits of brome grasses, and about their interactions with biotic and abiotic features of their native and introduced ranges. The database contains information about over 150 species and is designed both to support research into the causes and effects of plant invasions, and to provide information useful for anyone dealing with the use, management, and control of brome grasses. It is hosted on the Great Basin Research and Management Project website at http://greatbasin.wr.usgs.gov/GBRMP/bromus/bromus.html.

I used the data in the database to look for patterns of invasion. Correlations were found between invasiveness (defined as wide distribution outside of the native range combined with weediness), and taxonomic section, seed awn length, polyploidy, human use and availability of cultivars. Annual brome grasses have been widely introduced into new regions around the world and have a high probability of being destructive agricultural, ruderal, and environmental weeds. Long awn length is correlated with invasiveness, especially in annual species. Perennial brome grasses generally remain confined to their native regions unless they are cultivated for hay, forage, or revegetation. Once introduced, perennial bromes can escape cultivation and damage natural communities. The few invasive perennial species are polyploid, while invasive annual species may be diploid or polyploid. Invasiveness in brome species is associated with human activities including habitat disruption, agriculture, grazing, and use for revegetation. Climate change and habitat disruption are likely to change the way brome grasses invade. Most research on brome grasses focuses on highly invasive species, and information about less-invasive and non-invasive species is limited. Collection of information about all brome species in a central location facilitates

comparisons among species, and provides data that can be used for modeling, prediction, management and control of brome grass invasions.

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Introduction

Humans have moved plants from one area to another since before recorded history. In some cases, humans have accidentally introduced plants into new ranges when seeds or other plant parts have travelled as contaminants in grain or hay, ship bilge water, soil, and other materials. Other plants have been introduced into new areas for a variety of purposes. Most of our food crops and garden ornamentals are plants that we grow far from their native ranges. Many introduced plants remain limited to our fields and gardens. Others move out into disturbed areas and natural communities. A few negatively affect native plant populations. As humans continue to accidentally or purposefully introduce species into new areas far from their native ranges, some of these species become invasive.

Invasive plants cause severe environmental damage as they replace native species, alter or destroy existing ecosystem interactions, and change biotic and abiotic environmental conditions. They may affect soil water availability, change nutrient cycling, produce allelopathic chemicals, alter fire cycles, carry diseases, or simply crowd out native plants. Invasive plants are a serious problem in agricultural systems, and can greatly reduce productivity of crops and of rangelands. Economic costs associated with plant invasions are enormous. It has been estimated that weeds cost $24 billion U.S. dollars in crop losses and $1 billion dollars in forage losses each year in the United States. Control on pastures and rangelands costs another $5 billion dollars (Pimentel et al. 2005). Invasive species damage natural and semi-natural ecosystems and can contribute to the extinction of native species. Sharma et al. (2005, p 726) believe the invasion of exotic species to be "among the most important global scale problems experienced by natural ecosystems". An assessment by the U.S. Congress Office of Technology considers habitat destruction and alien species invasions to be the two leading causes of loss of biodiversity (1993, cited by Clout and De Poorter 2005). Climate change adds a new dimension to the evaluation and management of plant invasions, causing some invasive species become less of a threat and encouraging invasive behavior by other species (Bradley et al. 2010; Diez et al 2012). Plant introductions are increasing as the global economy expands (McNeely 2006; Ward et al. 2008). Essl et al. (2011) have suggested that there is likely to be a significant “invasion debt” related to species that have already been introduced but not yet recognized as invasive.

As concerns about the negative effects of plant invasions mount, international and national organizations are seeking ways to prevent or limit new invasions and to manage existing ones. A few countries such as Australia and New Zealand now screen all plant introductions (Pheleung 1999; Keller et al. 2007). In 1999, President Clinton issued an executive order mandating that a management plan for invasive species be created and implemented for the United States (Reichard 2004). A National Invasive Species Council (NISC) was created, and management plans were produced (NISC 2008). The Convention on the Conservation of European Wildlife and Habitats (Bern Convention) has released a European strategy on invasive alien species, which was adopted in 1993 (Genovesi and Shine 2004; Clout and De Poorter 2005). In 1997, a number of international organizations including the Scientific Committee on Problems of the Environment, the United Nations, the World Conservation Union, and CAB International, started the Global Invasive Species Program (GISP) (Clout and De Poorter 2005). GISP has recommended that all species being considered for introduction into new regions be evaluated, that the scientific basis for prediction of invasive potential be improved, that pathways for unplanned introductions be better controlled, and that management techniques for control of invasions be improved (McNeely 2006).

Definitions of Terms

The terms “invasion” and “invasive” are widely used in both scientific and popular literature to describe organisms that grow in large numbers outside of their native ranges and/or communities, with the possible additional meaning that their presence is considered to be undesirable or destructive. Other terms are often also used to describe plants and other organisms that are considered to be growing in places where they are not expected or wanted, including “alien”, “exotic”, “non-native”, “non-indigenous”, “weed” and “weedy”, “pest”, “introduced”, “adventive”, and “naturalized”. A number of authors have tried to provide clearer definitions of terms commonly used to describe the spread and impact of plants and other organisms (Davis and Thompson 2000; Richardson et al. 2000; Pyšek et al. 2004).

Difficulty with the terminology of invasion and invasive plants begins with the concept of “native” or “indigenous” species. The areas in which plants grow naturally change over time as a result of a great many factors, including climate, ecological factors, interactions with other organisms, disturbance, and chance. Generally the terms “native” or “indigenous” are used to mean that a plant originated and evolved in the region to which it is native and was not purposefully or accidentally introduced into an area by human activities. Pyšek et al. (2004, p 135) define native plants as those “that have originated in a given area without human involvement or that have arrived there without intentional or unintentional intervention by humans from an area where they are native”. In Europe, species often considered to be native are usually those present before the beginning of the Neolithic period. Plants introduced into Europe before the discovery of America in 1492 (or before 1500) are called “archeophytes”, and plants introduced since are called “neophytes”. In the western hemisphere, plants are typically considered to be native if they were present before the beginning of European exploration. In some regions of the Pacific, plants are considered to be native if they were present before Polynesian settlement (Pyšek 1995; Pyšek et al. 2004; Bean 2007). It can be very difficult to determine whether a species of plant is native to a given region. Bean (2007) suggests that a number of criteria should be used including historical records, phenotypic and genetic diversity, presence in unmodified communities, and associations with a wide range of pests and diseases.

Plants that are not native to a given area are often said to be “introduced”, “alien” or “exotic” with “alien” and “exotic” having somewhat more negative connotations. These terms are generally used to mean that the plant was accidentally or intentionally moved to the area by human activity. A “casual” alien is one that is present in a given region where it is not native, but which not developed a stable or increasing self-sustaining population. If a plant reproduces itself and establishes a stable or increasing population over a period of time, it is said to be “naturalized”. The term “adventive” tends to imply that a plant is present in a region but is not fully established. It may imply that the plant is reproducing but has not formed a stable population or that the plant is present due to introductions, but has not become naturalized (Pyšek 1995; Richardson et al. 2000).

A “weed” is a plant that grows in places where it is not wanted or where it causes some type of harm. The term weed has generally been used to describe unwanted plants growing in agricultural crops, gardens, or in disturbed or waste areas. A “ruderal weed” is a plant that grows in areas where vegetation is frequently and severely disturbed, often by human activities, including roadsides, waste areas, and areas that are frequently flooded (Grime 1977). The term “environmental weed” is commonly used today to describe a non-native species that grows in and harms natural communities (Richardson et al. 2000). “Noxious weeds” are those that are difficult to exterminate or those which affect the growth and reproduction of other plants (Baker 1974). The use of this term in some countries such as the United States, Australia, and New Zealand may indicate that control or eradication is mandated (Hulme 2012). The term “weed” does not imply that a plant is an alien. Native plants may be considered to be weeds if they damage crop yields, are inconvenient, or need to be controlled or eradicated. Many authors use the term “invasive” to describe species that have become widely naturalized outside of their native region and that have the potential to spread over a large area. Some authors also use the term “invasive” to imply that the spread of the plant into new regions has negative effects of some type, especially damage to natural communities. Therefore, the term “invasive” has two interlinked meanings – widely naturalized outside of the native region, and destructive. Because of the confusion that this creates, Richardson et al. (2000) have suggested that the term "invasive" be used only to describe a plant that is widely naturalized and that has the potential to spread into large areas. In contrast, Davis and Thompson (2000) developed a classification of eight types of plant colonizers based on dispersal distance, uniqueness of the species to a new region, and impact on the environment of the new region. They concluded that only two of the eight classifications, those for novel species with a large impact on the environment, warranted the use of the word "invader".

The term "transformer" is used to describe species that have strong impacts on natural communities. Transformers may change the composition of natural communities by affecting resources, stabilizing or destabilizing soils, promoting or suppressing fire, carrying diseases or pests, or by simply displacing other species (Rejmánek et al. 2005).

While many plants are introduced outside of their native ranges, most remain casual aliens. A fairly small number of species become naturalized and form stable and self-sustaining populations. Many of these remain confined to fields, roadsides, waste ground and disturbed areas. Alien weeds of crops, old fields, overgrazed rangeland, waste ground and disturbed areas can cause considerable economic damage. Relatively few species form large self-sustaining populations in natural areas but those that do can cause serious ecological damage and are a serious concern for biodiversity. A few species have caused extreme environment damage, displacing or destroying natural communities over large regions, and sometimes producing large areas of monoculture.

Patterns of Invasiveness and Invasion

Researchers have investigated a number of types of issues involving plant invasions including questions about what types of plants become invaders, what factors may predispose communities to invasion, how invasions occur, how invasions affect ecosystems and human activities, and how they can be prevented, managed, or controlled. Not all plants introduced into new regions become invasive. Williamson and Fitter (1996b) estimated that one in ten species of animals and plants imported into Britain will escape into the wild, one in ten of those will establish and one in ten established species will become a pest. Plant invasions involve interactions between potentially invasive species, habitats and communities that are susceptible to invasion, and stochastic factors such as method, timing, and number of introductions (Chong et al. 2006; Huttanus et al 2011; Catford et al. 2012). Propagules must be present for an invasion to occur. The invading species must be able to grow and reproduce under existing environmental conditions. In some cases, alien species may be introduced into environments that meet their specific requirements. However, some alien species are generalists that have the ability to grow and reproduce under a wide variety of environment conditions (plasticity) and thus may be able to invade a wide variety of habitats. Moderate environments may be more vulnerable to invasion by generalists than extreme environments where successful plants need to develop special adaptations to cope with difficult conditions (Rejmánek et al. 2005). Alien species may also evolve over time to grow and reproduce effectively in new environments. In some cases, introduced species may be able to hybridize with native species and gain genes that help them to better adapt to the new environment (Abbot 1992). Researchers hypothesize that plant species introduced into alien environments may be released from the need to defend against specialized herbivorous or pathogenic organisms living in their native communities. This may allow an alien plant species to reallocate resources in ways that help it to outcompete native species (Blossey and Notzold 1995). Alien species may be more likely to invade new habitats that do not contain closely related natives, as they are less likely to be susceptible to native herbivores and pathogens (Rejmánek et al. 2005).

Communities may become susceptible to invasion intermittently because of surges in resource availability due to factors such as climate variation, population fluctuations or disturbance. Alien species may also have an advantage when they are introduced into communities where they can make use of niches that are empty due to community composition factors or to disturbances (Rejmánek et al. 2005; Holzmuller and Jose 2011; Pearson et al. 2012). Disturbance also favors the growth and reproduction of annual plant species that can germinate on open ground, grow and reproduce quickly, and produce large easily dispersed seeds and maintain persistent seed banks (Lososová et al. 2006). Transformer species may alter communities in ways that are beneficial to themselves and to other alien species by changing environmental factors such as fire or water cycles, by manipulating light, nutrients or other factors or by producing allelopathic chemicals that inhibit growth of competing species (Ehrenfeld 2010; Holzmueller and Jose 2011). This has lead to the idea of invasion meltdown where invasion by one species leads to additional invasions by other species in a positive feedback loop (Simberloff and Von Holle 1999).

Researchers have also studied introduction factors and the invasion process to better understand plant invasions. An invasion by a non-indigenous species takes place in a series of steps or transitions. The plant must be transported to a new environment either accidentally or purposefully. The plant must then be released into a new environment where it can grow and reproduce. A self-sustaining population must be created as the plant establishes itself. Finally, it must spread into new environments. Traits that help a plant through one transition may not be useful for the other transitions (Kolar and Lodge 2001). In some cases, plants that are transported to a new environment may encounter a genetic bottleneck if the initial population is very small or if the initial population contains only a small fraction of the genetic diversity present in the population of the native range. This can limit the ability of some species to adapt to the new environment but does not always prevent invasion (Bartlett et al. 2002; Poulin et al. 2005; Uller and Leimu 2011). Other species may be able to tolerate a wide range of environment conditions in spite of limited genetic diversity (Poulin et al. 2007). Evolutionary change may also occur relatively quickly in populations of invading species and may involve change in traits which are associated with invasiveness (Whitney and Gabler 2008). Researchers have noticed that longer residence times in new areas are associated with invasion in that area (Rejmánek 2000). This may be based to some extent on increased adaptation to the new environment. Once new species have established a reproducing population in a new region, it is common for the population to remain relatively small and stable for a period of time. In the case of invasive species, this "lag time" may last for many years (Mack et al. 2000; Simberloff 2011). A number of explanations for this type of delay in population growth are possible. Invasions may begin slowly and not be noticed immediately, populations may begin to grow rapidly as the result of new adaptations, or population growth may accelerate due to some environmental factor or factors favoring the invasive species. Because many invading species have long lag periods, it may be difficult for observers to identify early stages of an invasion and to predict which introduced species are likely to cause serious environmental impacts in a new region (Mack et al. 2000).

Two other factors that increase the likelihood of invasive behavior are large initial population size and repeated introductions. Multiple introductions increase the probability of a new species surviving the early stages of introduction and becoming established (Mack et al. 2000; Rejmánek 2000). Introductions of species from different areas in the native region can also bring together individuals with widely varying genotypes. Crossbreeding between plants of the same species with different traits may produce plants with new adaptations (Uller and Leimu 2011).

Changes in plant populations and ecological communities clearly occur naturally and no ecosystem is ever static. However, human activities have greatly accelerated the movement of species from one area to another, and many invasive plants are also highly associated with human activities. A number of weeds have evolved with agricultural crops, and agriculture continues to be an important pathway for transportation of weedy species (Ellstrand et al. 2010; Pyšek et al. 2011). Ornamental horticulture has become another important pathway for the introduction of species into new areas and has been the source of many seriously invasive plants (Reichard and

White 2001; Dehnen-Schmutz 2011). Areas that have been disturbed by human activities such as old fields, roadsides, and waste areas are generally heavily invaded. Grazing land is likely to contain large numbers of invasive species and some invaders may persist long after grazing is discontinued (Sinkins and Otfinowski 2012).

While it is clear that stochastic events play an important role in invasions, an understanding of taxonomy, invasion history, species traits, growth requirements, environmental factors and community relationships can help researchers and managers to make better assessments of the likelihood of invasive behavior.

Research into Factors Associated with Plant Invasions

General Approaches

Rejmánek (2000) described five general categories of ways to study invasiveness in order to exclude species likely to become invasive or to detect, control, and manage invasions. Stochastic approaches focus on introduction factors such as the type, timing, and number of introduction events. Evaluation of the invasion history of a specific taxon provides a second approach. A third approach is to evaluate biological traits such as life span and phenology, reproduction methods, genetic characteristics, and growth patterns and requirements to predict whether specific groups or species of plants are likely to become invasive when introduced into new environments. A fourth approach attempts to evaluate factors that make a given type of habitat susceptible to invasion, and to attempt to match species that might be invasive with habitats that are invasible. A fifth approach uses experimentation to test predications based on the other four.

Comparative Studies

A large number of studies have done comparisons of invasive and non-invasive species to identify traits that are associated with invasiveness. Pyšek and Richardson (2007) have reviewed a number of comparative studies. Some of these studies compared alien species with different levels of invasiveness in a specific region. For example, Hamilton et al. (2005) compared species introduced to eastern Australia by using herbaria records. They evaluated specific leaf area, plant height, seed mass, and residence time across both regional and continental scales. Llorett et al. (2004) constructed a database of alien plants on eight Mediterranean islands, and evaluated traits including stem height, growth form, and dispersal mode. Other studies have compared the traits of invasive aliens with those of natives in an invaded habitat. Williamson and Fitter (1996a) used the Ecological Flora Database of Plants of Great Britain to compare 26 traits of native and non-native species and found plant size and characteristics that relate to propagule pressure associated with human activities to correlate with invasiveness. Godoy et al. (2009) compared flowering times of native and introduced species in three Mediterranean-type ecosystems, and found that alien plants from temperate areas tended to bloom earlier than natives, while those from Mediterranean areas bloomed around the same time, and those from tropical areas bloomed later. Smith and Knapp (2001) found higher specific leaf areas in alien species introduced into a Kansas tall grass prairie habitat relative to native species, but did not find much difference in other growth related traits.

Pyšek and Richardson (2007) have reported a number of patterns based on their evaluation of multiple comparative studies. For example, invading species are often taller, have longer flowering periods, are either more extreme R-strategists or more extreme K-strategists than native species, and may have high specific leaf area. These types of studies have provided much information about the nature of invasions and the traits that help plants invade. However, the information that studies comparing plants of diverse taxa provide is often too general to be useful for prediction.

Kolar and Lodge (2002, pp 1233-1234) have suggested that pessimism about the possibility of predicting invasions has emerged from “searching for characteristics that apply generally to all taxonomic groups and in all ecosystems", and state that such characteristics do not exist. Lodge (1993) pointed out that different taxonomic groups may have different characteristics that are associated with invasiveness. Studies focusing on specific plant families or genera may better identify traits that can help to predict whether a given species is likely to become invasive (Burns 2004; Simberloff 2005; Pyšek and Richardson 2007). These types of studies are typically done in two ways. One approach is to compare two confamilial or congeneric species that display differing levels of invasiveness. Goodwin et al. (1999) compared life form, stem height, and flowering period of pairs of species where one species was a successful European invader in New Brunswick and the other was a non-invasive European member of the same genus. They also evaluated the number of geographic regions in the native range and concluded that having a native range containing high numbers of geographic regions was more predictive of invasiveness than the biological traits that they studied. Grotkopp and Rejmánek (2007) paired woody species considered invasive in Mediterranean regions with phylogenetically related less-invasive or non-invasive species. They evaluated seedling relative growth rate, and specific leaf area, and concluded that high values for both of these traits are associated with invasiveness. Another approach is to compare a number of plants in the same family or genus and identify traits that differ between the two groups. Comparative studies have been done on pines (Grotkopp et al. 2002; Richardson and

Rejmánek 2004; Richardson 2006) and on a number of plants in the Asteraceae family including *Centaurea* (Gerlach and Rice 2003; Muth and Pigliucci 2006), *Crepis* (Muth and Pigliucci 2006), and *Senecio* (Radford and Cousens 2000). Other studies have focused on a specific topic, including photosynthesis in *Rubus* (McDowell 2002), self-fertilization in congeneric pairs in the Iridaceae family (van Kleunen et al. 2008), climatic and latitudinal ranges of cordgrass (*Spartina* spp.) (Daehler and Strong 1996), relative growth rates across nutrient gradients for plants in two genera of the Commelinaceae family (Burns 2004), and seed and inflorescence characteristics based on herbarium records of introduced *Crotolaria* species in Taiwan (Wu et al. 2005).

Discussion

Introduction of plants and other biological organisms into new areas have been common throughout history, but have increased as humans have developed more efficient methods of transportation. While many biological introductions do not create problems either for human activities or for natural systems, a significant minority of introduced organisms establish, spread, and cause serious ecological and economic problems. Invasions have become the focus of much research. However, uncertainty remains about the causes, processes and impacts of biological invasions. Possibly because invasions are not yet well understood, the terminology used by invasion researchers has not always been well defined, and this has added to the difficulty of research on invasions.

Many of the approaches that have been used by researchers to study biological invasions use comparisons between organisms that have spread extensively and caused serious damage in new areas, and those that have not. Because of the complexity of biological systems, comparative studies will probably never provide enough information to allow researchers to determine with complete certainty whether a plant or other organisms will become invasive. Comparative studies can, however, lead to better understanding of the causes and effects of biological invasions. This type of knowledge can be combined with more detailed information about the traits, growth requirements and environmental interactions of specific plants to improve prediction, prevention, and management of plant invasions.

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CHAPTER 2: DEVELOPMENT OF A DATABASE OF INFORMATION ABOUT BROME GRASSES

Introduction

The identification of species with the potential to become invasive has become an important area of research. It has become increasingly clear that there is no easy way to identify species with a potential for invasiveness. The National Research Council has stated that while a "conceptual basis exists for understanding invasions" (2002, p. 9), there are "no known broad scientific principles or reliable procedures for identifying the invasive potential of plants, plant pests, or biological control agents in new geographical ranges" (2002, p. 9). Nevertheless, the high level of damage to natural and agricultural systems has made research into the prediction and management of invasions imperative.

A number of risk assessment systems have been developed to evaluate the likelihood that a plant will eventually become invasive, and to estimate the possible effects on natural and agricultural systems that could result. Risk assessment systems typically use multiple approaches to evaluate an organism's potential for invasiveness. One approach is to determine if an organism has a history of invasiveness. Another uses traits or characteristics that are associated with invasiveness. A third approach is to examine ways that a species might interact with biotic and abiotic environmental factors. This can help to determine if a species is likely to be invasive in specific types of habitats. Risk assessment systems may also evaluate the likelihood of introduction of a species, and the potential damage that may result from an introduction (Reichard and Hamilton 1997; Pheloung et al. 1999; Jian et al. 2008)

Use of Databases for Research into Invasiveness and Invasion

Comparative studies and risk assessment require the collection and analysis of large amounts of data. Collection and organization of data are labor intensive and time consuming. The development of databases with information about species descriptions and distribution, plant traits, genetic data, research resources, and environmental factors has been valuable for researchers. Databases can give researchers and managers quick and easy access to diverse types of data collected over many years by researchers around the world, and can help to reduce bias in the selection and evaluation of data (Cadotte et al. 2006). Databases provide tools that can allow users to view information in new and varied ways. This can help researchers to generate new questions and ideas. When researchers with different viewpoints can look at a set of data from different perspectives and use multiple analytical approaches, informative and useful patterns may emerge. Researchers, land managers, modelers and others can use the information in databases to make better predictions about which species of plants have the potential to become invasive, and about ways in which a given species may interact with environmental factors in a specific habitat. Databases can also provide information about management and control of existing invasions.

Many databases with information that could be useful for studies of plant invasiveness are now available on the internet. Biodiversity Information Standards (formerly The Taxonomic Database Working Group), an international nonprofit organization that develops standards and protocols for sharing biodiversity data, maintains a website (http://www.tdwg.org) that lists over 600 biodiversity projects and online databases. Table 2.1 lists some examples of the many databases available on the Internet that may be useful for research on plant invasiveness. Many of these databases contain information about species of plants found in a specific country or region of the globe, while others focus on specific taxa.

Regional databases have proved to be valuable for research. A number of regional floras are now available on line. The eFloras.org project provides online floras and partial floras for regions or countries including China, Pakistan, Chile, and North America (Song). Floras or partial floras are also available online for Great Britain (Peat and Fitter), New Zealand (Landcare Research), Israel (Danin 2006+), and Australia (Australia Department of Sustainability, Environment, Water, Population and Communities), while the USDA Plants database provides distribution maps and other types of information for plants of the United States and its territories. Data in the BiolFlor (Hemholtz-Centre for Environmental Research, Bundesamt für Naturschutz) database, which contains information about biological and ecological traits of plants found in Germany, has been used for a number of projects. These include a study correlating traits with naturalization success of introduced ornamentals in Germany (Hanspach et al. 2008), an evaluation of plant traits associated with annual vegetation in man-made habitats in Central Europe (Lososová et al. 2006), and a study of the effects of self-compatibility on the distribution of European plants in North America (van Kleunen and Johnson 2007). Regional databases contain a wealth of information. However, regional databases may not help to identify plants with invasive potential that have not yet been introduced into a specific region. Researchers who are interested in a particular species of plant must try to find and combine diverse types of information from various regional databases, and may find it difficult to make comparisons. Databases with information about specific taxa are also available. Several useful online databases of information on grasses, include the GrassBase database (Clayton et al.) available on the Kew Gardens website, the

Table 2.1: A sample of databases that have useful information about invasive plants and are available on the internet.

Database Name	Website URL	Authors/Organizations	Focus of Database	Database Content
African Flowering Plants Database	http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php	South African National Biodiversity Institute, Conservatoire et Jardin Botaniques de la Ville de Genève, Tela Botanica.	African flower plants	Database of plants with ecology, status and distribution information
APASD - Asian-Pacific Invasive Species Database	http://apasd-niaes.dc.affrc.go.jp	National Institute for Agro-Environmental Sciences Working group for the APASD	Invasive alien species in Asian and Pacific countries	Database of invasive species and associated information
BIOLFLOR	http://www2.ufz.de/biolflor/index.jsp	Helmholtz Centre for Environmental Research (UFZ), Bundesamt für Naturschutz	Vascular plants in Germany	Database of native and established alien plants with biological and ecological trait information
BioDiversity Information Standards	http://www.tdwg.org	Biodiversity Information Standards (TDWG) - formerly the Taxonomic Database Working Group	Global biodiversity projects and databases	Databases of biodiversity information projects, biodiversity information networks, and biodiversity informatics events
DAISIE	http://www.europe-aliens.org	DAISIE (Delivering Alien Species in Europe) Program of the European Commission	Alien species in Europe	Database of alien species with description, distribution, introduction, impact, and management information
Ecological Flora Database of Plants of Great Britain	http://www.ecoflora.co.uk	Dr Helen Peat and Professor Alastair Fitter at the University of York, with financial support from the British Ecological Society and the Natural Environment Research Council.	Plants in Great Britain	Database of plants of Great Britain with description, distribution in Great Britain and Europe, and ecological information
Global Compendium of Weeds	http://www.hear.org/gcw	R. Randall, Hawaiian Ecosystems at Risk, Department of Agriculture and Food, Western Australia	Global invasive plants	Listing of 18,000 plant taxa that have been cited as invasive in specific references
Global Invasive Species Database	http://www.issg.org/database/welcome	Invasive Species Specialist Group (part of the World Conservation Union)	Global invasive species	Database of invasive organisms with description, distribution, introduction, ecology, impact, and management information
GrassBase	http://www.rbgkew.org.uk/data/grasses-db.html	W.D. Clayton, K.T. Harman, and H. Williamson, Royal Botanic Gardens, Kew, Great Britain	Global grasses	Database with detailed descriptions, distribution information, and an interactive key
GrassPortal	http://www.grassportal.org	Osborne CP, Visser V, Chapman S, Barker A, Freckleton RP, Salamin N, Simpson D, Uren V.	Global grasses	Project that synthesizes information from large datasets to provide information on taxonomy, ecology, geography and evolution
Plants Database	http://plants.usda.gov	United States Department of Agriculture	Plants in the United States	Database with images, biological and ecological traits, noxious weed classification, and other information

Manual of North American Grasses (Barkworth et al.) provided by Utah State University, and Ausgrass2 (Simon and Alfonso 2011). The GrassPortal project (Osborne et al. 2011) which was developed as a result of collaboration between the University of Sheffield, the Royal Botanic Gardens (Kew), Knowledge Now Limited, and the University of Lausanne allows users to combine morphologic data and synonymy from GrassBase (Clayton et al.), distribution data from the Global Biodiversity Information Facility (GBIF 2012) and phylogenic data from the GrassWeb database (University of Lausanne, Swiss Institute of Bioinformatics) with environmental data from NASA and other sources.

There are also some excellent databases that contain information about invasive species around the world such as the The Global Invasive Species Database (Invasive Species Specialist Group). These often do not contain data about non-invasive species, which is essential for identifying how invasive species differ, and some do not have enough depth for many types of research.

Focus on Poaceae

An alternative approach is to create a database with information about a specific taxonomic group of organisms that is designed to be used for research on invasion. It is known that some plant families have high numbers of invasive species. One of these families is the grass family (Poaceae). Pyšek (1998) used the proportion of invasive species to evaluate the invasiveness of plants in angiosperm families. He included the Poaceae family in his list of seven families that contain high numbers of invasive species, and suggested that the highly evolved inflorescences and successful dispersal systems of grasses contribute to their ability to become invasive. Daehler (1998) showed that the Poaceae family contains higher than expected numbers both of agricultural weeds and natural area invaders relative to the number of species in the family.

Invasive grasses cause serious economic loss and environmental degradation in many parts of the world. *Sorghum halepense* (L.) Pers. (Johnsongrass) is an agricultural weed that can reduce yields of many crops including cotton, corn, sorghum, soybeans, and sugarcane (Chao et al. 2005), resulting in serious crop losses and significant economic impact (Griffin et al. 2006; Gunes et al. 2008). It is found around the globe in warm climate areas and has extended its range as far north as southern Canada (Newman 1993). Scientists in Australia, New Zealand, California, and other coastal areas, are concerned about damage to coastal habitats by *Ammophila arenaria* (L.) Link, a beach grass native to Europe and North Africa that has been used for dune stabilization. *Ammophila* *arenaria* displaces native plant species, alters habitats in ways that affect other organisms, and changes dune formation patterns (Beckstead and Parker 2003; Hilton et al. 2006).

Members of the Global Invasions Network, a U.S. National Science Foundation funded research coordination network, suggested that an invasion focused database of information about species in the family Poaceae would be a valuable tool for research into the ecology and evolutionary biology of invasion. A database with information about species in the Poaceae family would provide a central location for information that could be used by researchers both to investigate invasion by Poaceae species and to address fundamental questions regarding mechanisms of plant invasions. It would allow researchers to compare and contrast data for different species of grasses, and to examine data from many types of research studies. By providing researchers with multiple ways to query data, the database would help researchers detect patterns and develop a deeper understanding of plant invasions. It would facilitate communication and provide information to land managers and others involved with the practical aspects of controlling current invasions by invasive grasses. However, a database about with information about grass species world wide would be a massive project.

Brome Grasses

A number of grasses in the tribe Bromeae have been widely introduced into areas outside of their native ranges and have caused serious problems in the western United States. The Eurasian species *Bromus tectorum* L. is a crop pest of winter cereals, a common weed of disturbed areas, and an environmental weed that has invaded enormous tracts of land across the western United States, where it disrupts communities, often forms monocultures, and changes fire cycles (Leopold 1949; Mack 1981; Davies et al. 2011; Pierson et al. 2011). *Bromus rubens* L. (*Bromus madritensis* ssp. *rubens* (L.) Husn.) is an invader and transformer species in desert areas of the southwestern United States and has also affected fire cycles (Salo 2004; Salo 2005; Salo et al. 2005; Brooks and Berry 2006; Abella et al. 2012, Brooks 2012). Other brome species such as *Bromus secalinus* L. and *Bromus sterilis* L. are weeds both within and outside of their native ranges (Tsvelev1984; Cussans et al. 1994, Koscelny et al. 1990; Andersson et al. 2002; Milberg and Andersson 2006; Behre 2008). *Bromus inermis* Leyss. and *Bromus catharticus* Vahl have been introduced to many areas of the world as forage grasses and are now invasive in some regions (Otfinowski et al. 2007; Dillemuth et al. 2009; Sinkins and Otfinowski 2012). However, many other brome grasses grow only in their native ranges and are not considered to be weedy.

In conjunction with a USDA supported REENet research project focusing on brome grasses in the western United States, I have developed a database and website of information about that is designed to support research on invasion and invasiveness, while also providing a central location for information about brome grasses. The database includes data for species of brome grasses around the world, and gives researchers, land managers, students, and others the ability to quickly find information, and to compare traits of invasive and non-invasive species. By providing researchers with multiple ways to query data, the database can help researchers detect patterns and develop a deeper understanding of plant invasions. It facilitates communication and provides information to land managers and others involved with the practical aspects of controlling current invasions by invasive brome grasses.

Methods

I began development of a database by creating and documenting requirements. To determine the kinds of information that should be included in the database, I read and evaluated a number of papers listing plant traits and other factors associated with weediness and invasiveness (Baker 1974; Roy 1990, Rejmánek 2000; Rejmánek et al. 2005; Pyšek and Richardson 2007; Whitney and Gabler 2008). I then compiled a list of factors commonly associated with invasiveness, and identified data types that could be used for information about these factors. See Table 2.2. I used a traditional (or waterfall) design and development lifecycle including development of requirements and creation of a requirements document, a design document, a table relationship diagram, and a data dictionary. See Figure 2.1. Microsoft Access 2007 was selected for the database software because of its wide availability. I designed the database to include both categorical and textual data. The categorical data facilitates searches and species comparisons, while the textual data provides more context and detail. The database was designed so that it can easily be expanded to include more kinds of information and additional taxa. To populate the database, I collected distribution and trait data from a wide variety of sources including regional floras and manuals, online databases, papers in peer-reviewed journals, government documents, dissertations and theses. To determine which bromes to include in the database as valid species, I used the Kew Gardens GrassBase database of global grass species (Clayton et al.) and the Integrated Taxonomy Information System database of North American species (ITIS). Brome grasses not listed in either of these databases were not considered to be valid species and were listed as synonyms of valid species. Population of the database began in 2010 and is ongoing. A web interface and online search algorithms were created using SQL and Microsoft ASP.NET by personnel at the USGS Snake River Field Station in Boise, Idaho.

Table 2.2: Data types included in the database are based on factors commonly listed in research papers as contributing to plant invasions.

Factors Affecting Invasiveness	**Citations**	**Associated Information in Database**
Short-lived / Long-lived	Pyšek and Richardson (2007)	Life Span (annual, winter annual, biennial, short-lived perennial, perennial)
Rapid growth and short generation time	Baker (1974); Roy (1990); Rejmánek (2000); Rejmánek et al. (2005); Pyšek and Richardson (2007); Whitney and Gabler (2008)	Specific Leaf Area, Genome Size
Self-compatibility (especially with some crossing)	Baker (1974); Roy (1990); Rejmánek (2000); Rejmánek et al. (2005); Whitney and Gabler (2008)	Mating System (selfing only, mostly selfing, selfing and outcrossing, mostly outcrossing, outcrossing only)
Generalist genotypes / plasticity – growing and reproducing under a wide range of environmental conditions	Baker (1974); Roy (1990); Rejmánek (2000); Rejmánek et al. (2005); Whitney and Gabler (2008)	Number of Global Biomes, Minimim and Maximum Temperature, Minimum and Maximum pH Latitudinal Range Information
Small seeds / Large seeds	Pyšek and Richardson (2007)	Seed Weight
Continuous, long or prolific seed output	Baker (1974); Roy (1990); Pyšek and Richardson (2007); Whitney and Gabler (2008)	Seeds per Shoot/ Ramet
Effective seed dispersal, adaptations for short-and long distance seed dispersal	Baker (1974); Roy (1990); Pyšek and Richardson (2007); Whitney and Gabler (2008)	Seed Weight, Maximum and Minimum Awn Length
Seed dispersal by vertebrates	Rejmánek (2000); Rejmánek et al. (2005); Whitney and Gabler (2008)	Seed Weight, Maximum and Minimum Awn Length
Vegetative reproduction	Baker (1974); Roy (1990); Rejmánek (2000); Rejmánek et al. (2005); Pyšek and Richardson (2007)	Vegetative Reproduction (rhizomes, no rhizomes)
Hybridization	Rejmánek (1996); Whitney and Gabler (2008)	Hybridization (Known to hybridize, no known hybridization, is a hybrid) + text field
Polyploidy	Roy (1990)	Ploidy Level (diploid, polyploid), Chromosome Count
Large native range	Rejmánek (2000); Rejmánek et al. (2005)	Native Distribution Information
High interspecific competitive ability	Baker (1974); Roy (1990); Rejmánek et al. (2005); Whitney and Gabler (2008)	Root to Shoot Ratio, Vegetative Reproduction (rhizomes, no rhizomes), Impact (text)
Characteristics favoring dispersal by humans	Rejmánek (2000); Rejmánek et al. (2005); Pyšek and Richardson (2007)	Human Uses (hay, forage, revegetation, horticulture, others) Availability of Cultivars Grazing Value
No specialized germination requirements /germination in many environments	Baker (1974); Roy (1990); Whitney and Gabler (2008)	Management Information (text)
Effective defenses against enemies, resistence to herbivory	Pyšek and Richardson (2007); Whitney and Gabler (2008)	Maximum and Minimum Awn Length
Seed longevity / discontinuous germination	Baker (1974); Roy (1990); Pyšek and Richardson (2007)	Seed Bank (transient, short-term persistent, long-term persistent)
Tolerance of burning	Pyšek and Richardson (2007)	Association with fire, Impact (text), Management (text)
Time since Multiple introductions	Rejmánek et al. (2005)	Introduction Information
Release from predators or pathogens	Rejmánek (2000); Rejmánek et al. (2005)	Interactions with Other Organisms

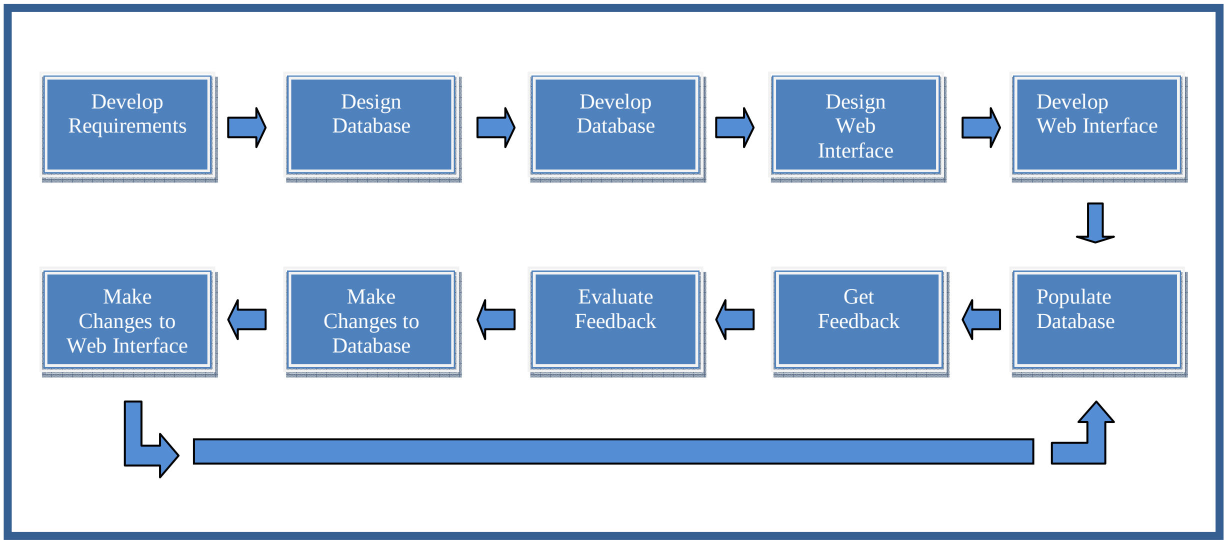

Figure 2.1: A traditional waterfall lifecycle used for the design and development of the database, including a process for evaluating and responding to feedback.

The database contains records for 150 species in genus *Bromus*, four species in genus *Littledalea*, and one species in genus *Boissiera*. Species records include commonly used synonyms, common names, distribution and introduction information by country, and information about plant traits, growth requirements, human associations and management. There are also links to images available on the Internet for over 50 species. References are provided throughout the database for specific data items so that users can find and refer to the original data sources. The database includes an extensive searchable bibliography and a list of other websites that provide useful information about *Bromus* species and invasions.

The web interface provides users with the ability to search for species records by scientific name or by country. It shows maps (by country) of native and introduced distributions, along with some detailed information for individual countries. Distribution maps by state and province are also shown for the United States and Canada. Advanced search options allow users to search for species that have specific categorical trait values or combinations of categorical trait values. A simple reference search allows users to search for references by keyword. A more advanced bibliographic search allows users to search for terms in specific combinations of reference record fields and to search for research papers that focus on specific topics.

The database and web interface are hosted on the Great Basin Research and Management Partnership website, and are part of the *Bromus* Research, Education, and Extension (REENet) project which coordinates networking and facilitates research on exotic and invasive grass species of the genus *Bromus* that have been introduced to the western United States. The web interface can be accessed at http://greatbasin.wr.usgs.gov/GBRMP/bromus/bromus.html.

Discussion

Databases provide a useful way to organize data and to make it widely available. However, some caution must be used when data that has been collected in this type of database is used to investigate ecological topics such as invasiveness and invasion. Availability of information and decisions about what information to include and how to combine and format the data inevitably introduce bias. The amount of available information for some species (such as *Bromus tectorum*) is overwhelming, while almost no information exists for other valid species. Information that would be useful to researchers is unavailable for many species or may be too inconsistent to use. Data is inevitably presented using many different units of measurement and in many different formats. When it is added to the database, it often needs to be converted and reformatted. Available information often conflicts, and some sources are more reliable than others. And while a focus on a specific taxon may have implications for a broader understanding of invasiveness, any specific patterns observed apply only to the taxon group studied. The evaluation of data collected in databases is clearly observational, and data analysis can show correlations, but not cause and effect. However, many of these same caveats also apply with other sources of information.

The types of information needed to make assessments of invasion potential for plants must generally be gathered from many sources. Collection of data into a central location simplifies this process and supports use of evaluation tools at the national and state or provincial levels, and also at much more local levels where plant trait and growth requirement data can be matched to characteristics of specific habitats and communities. Advanced search options can be used to facilitate comparisons between species and can help to reveal patterns that suggest additional avenues for research.

Collection of data in a central location can also reveal gaps in data. A majority of the information found in journal articles and on the Internet focuses on *Bromus tectorum*, an annual species that causes serious ecological damage in western North America. Information on other species of annual bromes that grow in Europe and North America is also fairly extensive and can be found on the Internet. Less information is available for annual bromes that grow in other areas of the world. Information is also limited for perennial *Bromus* species with the exception of those that are used extensively for hay and forage. The information that is available is often in printed floras and other sources, and is less easily accessed by researchers. Language barriers can make information difficult to find and use. Much more information is available for brome species that are used by humans or that are perceived to be invasive or destructive than for species that have limited human associations. There are a number of species for which almost no information exists. These species tend to have limited ranges and some may be endangered or extinct.

Many types of information that would be useful for prediction, management, and control of invasions are currently limited or unavailable. More information on growth requirements such as temperature range and soil pH would be especially valuable for modeling. Projects like the GrassPortal may help to make this type of information available in the future. GrassPortal combines data from the Kew Gardens GrassBase Database, the GrassWeb phylogeny database, the GBIF species occurrence database, with climate and habitat information from NASA and other sources (Osborne et al. 2011), and may be used in the future to provide information for the *Bromus* database.

As research on plant invasion continues, the collection and organization of data will become increasingly important. This database was designed to examine a possible approach to the collection and analysis of data about a specific taxa of invasive grasses, and to evaluate the value of this type of data collection both for management of brome grasses and for the development of a better understanding of plant invasion.

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CHAPTER 3: LOOKING FOR PATTERNS OF INVASIVENESS AND INVASION IN BROME GRASSES

Introduction

Humans have long been concerned with the negative impacts created by plants that grow in places where they are not wanted. Many of the concerns about invasive plants have focused on financial costs and damage associated with agricultural, horticultural, and rangeland weeds (Wyse 1994; Sheley et al. 1998; Brunson and Tanaka 2011; Davies and Johnson 2011). The effects of plant invasions on natural ecosystems have also become a serious concern (Pimentel et al. 2005; Simberloff 2005; Davies et al. 2011). Invasive plants displace native species, change the way that communities function, and reduce species diversity (United States Congress Office of Technology 1993 cited by Clout and Poorter 2005; Sharma et al. 2005; Simberloff 2005).

Many researchers have searched for ways to evaluate plant species in order to identify the plants that are most likely to become invasive and to predict where invasions are likely to occur. Most people who have studied plant invasions now believe that there are no consistent and easily used sets of traits or factors that apply to all plants and can be used to identify species that will become invasive. In a study of 49 annual species in Britain, Perrins et al. (1992) were unable to identify characters that could be used to separate weeds from non-weedy plants. A more recent study of alien angiosperm plants in the Mediterranean region failed to find evidence of a phylogenetic component to invasiveness (Lambdon et al. 2008). The taxonomic groups of species included in theses past studies may be too broad for particular traits associated with invasive species to emerge. Studies focusing on specific plant families or genera could better identify factors that can help to predict whether a given species is likely to become invasive (Perrins et al. 1991; Burns 2004; Simberloff 2005; Pyšek and Richardson 2007). They may also help to identify communities that are likely to be damaged by a particular invasive species. Studies that focus on invasive traits and ecological interactions of species in a given family or genus may help researchers make more accurate risk assessments at national or regional scales, and at smaller scales for habitats of concern. They can also provide information that can help managers to respond to invasions and to select appropriate management techniques.

The grass family (Poaceae) contains higher numbers of weedy and invasive species than expected relative to the number of species (Daehler 1998, Pyšek 1998). A number of brome grasses in the subfamily Pooideae and the tribe Bromeae have been widely introduced into the United States, and some are considered invasive (Clayton and Renvoize 1986). The subfamily Pooideae is an important group of grasses that have adaptations to temperate zone climates and often to dry winter climates typically found around the Mediterranean Sea. Pooideae are C3 grasses with large chromosomes (Renvoize and Clayton 1992). Morphologically, bromes appear similar to grasses in the genus *Festuca* of the tribe Poeae, but are considered to be most closely related to grasses in the tribe Triticeae, which includes wheat, barley, and rye (Clayton and Renvoize 1986). Grasses in tribes Bromeae and Triticeae have simple rounded starch grains rather than the compound starch grains found in the *Festuca* L. and most other grasses (Renvoize and Clayton 1992, Grass Phylogeny Working Group 2001). The Grass Phylogeny Working Group (2003) showed brome grasses to be closely related to grasses in the genus *Triticum* L. (wheat) and also to grasses in the genera *Avena L.* (oats) and *Brachypodium* P. Beauv (false brome). Most brome grasses grow in the temperate zones of the world with a few species found at high elevations in the tropics.

The largest genus in the tribe Bromeae is the genus *Bromus* L. *Bromus* grasses are annual, biennial, or perennial with culms ranging from 5-190 cm. in height, sheaths closed to near the top, membranous ligules, erect or nodding panicles or racemes with up to 30 fertile florets, unequal glumes shorter than the spikelets, lower lemmas usually with a subapical awn (or with three awns in a few species), with disarticulation above the glumes. The tribe Bromeae also contains the genera *Boissiera* Steud. with one annual species which is found in central Asia and Africa and *Littledalea* Hemsley, a genus with large papery lemmas that contains four species in central Asia (Tsvelev 1984, Clayton and Renvoize 1999; Asghari-Sakaria 2007; Pavlick and Anderton 2007; Clayton et al.). Many brome grasses have multiple synonyms and species may be difficult to differentiate on the basis of morphological characteristics (Saarela et al 2007; Fortune et al. 2008). Some sources list more than 400 species, but about 150 species are widely accepted as valid (Soderstrom and Beaman 1968 cited by Saarela et al. 2007; Clayton et al.).

Taxonomists have divided the brome grasses into a number of subgroups based on characteristics such as the number of nerves in the glumes, the shape of the spikelets, and features of the lemmas. In a 1970 paper, Smith reviewed earlier classifications of *Bromus* species and proposed a classification based on morphology and serology which separates species in the genus *Bromus* into sections*.* Stebbens (1981) evaluated chromosome morphology and pairing of chromosomes in interspecific hybrids, and suggested the use of subgenera. Sections are typically based on only one or two characteristics, and species in separate sections may be quite similar. The use of subgenera implies that there is more difference between groups (Stebbins 1981). Stebbins commented that there are greater differences between some *Bromus* subgenera than between genera in many other plant taxa. Tsvelev (1984) separated the bromes even more completely by breaking them into multiple genera. Today, the systems suggested by Smith, Stebbins, and Tsvelev are all in use. All three systems are similar with the same species grouped together.

See Table 3.1. A number of researchers are now using protein and DNA analyses to study phylogenetic relationships of brome grasses (Anouche and Bayer 1997; Oja 2002; Oja and Paal 2005; Oja 2007; Saarela et al. 2007; Fortune et al. 2008). Saarela et al. (2007) compared nuclear and chloroplast DNA sequences in 46 species of brome grasses and concluded that most sections are monophyletic, but that section *Bromopsis* contains several lineages.

Table 3.1: Taxonomy of Tribe Bromeae - Three systems of taxonomy are commonly in use today. P. Smith (1970) divided genus *Bromus* into six sections. L. Stebbins (1981) divided genus *Bromus* into seven subgenera (with *Boissiera* now moved to genus status). Tsvelev (1984) divided genus *Bromus* into separate genera. In addition, *Triniusia* is occasionally used for species with three lemma awns (Scholz 1998), and Keng used section *Sinobromus* for five Asian species (Liu et al. 2006).

Genus	**Subgroups**	**Life Span**	**No. Species**	**Ploidy**	**Native Distribution**
	Genus *Bromus* Linneaus Section *Bromus* Subgenus *Bromus*	annual, occ. biennial	ca. 30	diploid, polyploid	Asia, Europe, Africa
	Section *Triniusia* (Steudel) Nevski	annual	2-3	diploid	Asia, Europe
	Genus *Bromopsis* (Dumortier) Fourreau Section *Bromopsis* Dumortier or *Pnigma* Dumortier or *Festucoides* Cosson & Durieu Subgenus *Festucaria* Link	perennial, 1 annual	70-90	diploid, polyploid	Asia, Europe, Africa, Australia, North America, South America,
	Section *Sinobromus* Keng	perennial	5		Asia
	Genus *Ceratochloa* Beauvois Section *Ceratochloa* (Beauv.) Grisebach Subgenus *Ceratochloa* (Beauv.) Hackel	annual, biennial, short-lived perennial, perennial	ca. 20	polyploid	North America, South America
	Genus *Anisantha* (C. Koch) Section *Genea* Dumortier Subgenus *Stenobromus* Hackel	annual	5-8	diploid, polyploid	Europe, North Africa, and Western Asia, especially around the Mediterranean
	Genus *Nevskiella* Kreczetovich & Vvedensky Section *Nevskiella* (Krecz. & Vved.) Tournay Subgenus *Nevskiella* (Krecz. & Vved.) Krecz. & Vved.	annual	1	diploid	Western and Central Asia
	Genus *Trisetobromus* Nevski Section *Neobromus* (Shear) Hitchcock Subgenus *Neobromus* Shear	annual (or perennial)	2	polyploid	South America (Chile)
Genus *Boissiera* Hochstetter ex Steudel		annual	1	diploid, polyploid	Eastern Mediterranean, Asia
Genus *Littledalea* Hemsley		perennial	4	?	Western China, Central Asia

The species in three sections of the genus *Bromus* – *Bromus* (a section in genus *Bromus*), *Genea*, and *Nevskiella* - are annuals or occasionally biennials, while the species in the largest section, *Bromopsis*, are (with one exception) all perennials. The section *Ceratochloa* includes annuals, bienniels, short-lived perennials, and perennials. The descriptions of life spans of individual species in section *Ceratochloa* and also section *Neobromus* may vary depending on the source.

The two annual sections contain large numbers of weedy and invasive species (Roy et al. 1991; Oja 2002, Oja and Paal 2007). Some of the most serious brome invaders in western North America, including downy brome (*Bromus tectorum* L.), red brome (*Bromus rubens* L. or *Bromus madritensis* ssp. *rubens* (L.) Husn.) and ripgut brome (*Bromus diandrus* Roth), are members of the relatively small section *Genea*. Many species in section *Bromus* are widely distributed around the world and commonly grow in agricultural or disturbed areas. However, some perennial species in sections *Bromopsis* and *Ceratochloa* are also invasive.

Brome species have been the focus of several studies comparing plant traits and invasiveness. Hulbert (1955) evaluated characteristics and behavior of ten annual brome species introduced to the western United States and suggested that winter hardiness, ability to germinate at lower temperatures, rapid and deep root growth and spring maturation, and high seed output all contibute to the invasion success of one species, *Bromus tectorum,* in semi-arid areas of the western North America. Roy and his colleagues evaluated physiological, genetic, and demographic characteristics of annual brome species with varying levels of invasiveness (Roy et al. 1991). They found a positive relationship between the number of climatic zones in the native distribution area, and the number of regions with a Mediterranean climate occupied worldwide, but did not see other clear differences between invasive and non-invasive species (Roy 1990, Roy et al. 1991).

In conjunction with a USDA supported REENet research project focusing on brome grasses in the western United States, I have developed a database of information about brome grasses that is designed to support research on invasion and invasiveness, while also providing a central location for information about brome grasses and the control and management of brome invasions. The database includes data for species of brome grasses around the world, and gives researchers, land managers, students, and others the ability to quickly find information, and to compare traits of invasive and non-invasive species. The database also includes an extensive reference and bibliography section, and provides links to other web-based information sources. I used the database to investigate patterns of invasiveness and invasion, and to develop and examine hypotheses about invasiveness in brome grasses. See Table 3.2.

Table 3.2: The hypotheses evaluated were based on factors that are commonly listed as contributing to invasiveness in research papers (Baker 1974; Roy 1990; Rejmánek 2000; Rejmánek et al. 2005; Pyšek and Richardson 2007); Whitney and Gabler 2008). Availability of data for many *Bromus* species was a consideration in choosing the factors to use for analyses.

	Factor	**Associated Data**	**Hypothesis**
1	Taxa	Section	Invasiveness is correlated with taxonomic section, with species in sections *Genea* and *Bromus* more likely to be invasive than species in sections *Ceratochloa* and *Bromopsis*.
2	Life Span	Short, Medium, Long	Shorter life spans are correlated with invasiveness.
3	Effective seed distribution	Maximum lemma awn length	Long lemma awns are correlated with invasiveness.
4	Effective seed distribution	Average seed weight	Low average seed weight is correlated with invasiveness.
5	Ploidy level	Mostly diploid, Mostly polyploid, Both	Polyploid chromosome counts are correlated with invasiveness.
6	Human Use	Use for hay, forage, and/or revegetation	Use by humans for forage, hay, and revegetation is correlated with invasiveness.
7	Human Use	Availability of cultivars	Availability of cultivars is correlated with invasiveness.

Hypotheses 1 and 2 are based on the many references in the literature to the high incidence of weediness in annual brome species in sections *Bromus* and *Genea* (Stebbins 1981; Ainouche, et al. 1995; Barkworth et al. 2007, Saarela et al. 2007). Hypotheses 3 and 4 relate to the often cited role of effective methods of seed dispersal in plant invasions. Hypothesis 3, species with long seed awns are more likely to be invasive, is based on the observation that humans are effective dispersers of long-awned *Bromus tectorum* seeds which adhere in large numbers to the socks and boots, and on the assumption that other vertebrate species are also likely to move long-awned seeds into new areas. Hypothesis 4 is based on the assumption that lighter seeds of species such as brome grasses may be more easily moved than heavier seeds. Small seed weight or mass is sometimes cited as a possible factor associated with invasiveness. Rejmánek et al. (2005) have associated invasiveness of woody plants in disturbed areas with small seed mass based on a study of invasiveness in pine species. However, Roy (1990) found seed weight to be of no value for the prediction of invasiveness in brome grasses. Hypothesis 5 states that polyploidy species are more likely to be invasive, as polyploidy may pre-adapt plants to grow in new habitats, support adaptation, and facilitate both sexual and asexual reproduction under certain conditions (te Beest et al. 2012). Hypotheses 6 and 7 are related to human use of brome species, and are based on information in the literature about the use of some *Bromus* species for forage, hay, and revegetation in the western United States, and on observation of the widespread presence of smooth brome (*Bromus inermis* Leyss.) along highways in the North American West.

Methods

Creation and Population of the Database

I created the database using Microsoft Access 2007 and populated it using a wide variety of sources including regional floras and manuals, online databases, papers in peer-reviewed journals, government documents, dissertations and theses. I then looked for patterns of similarities and differences between *Bromus* species that are invasive and those that are not. I identified factors for which I was able to collect the most information, and created hypothesis for these factors based on scientific literature about plant traits and invasion. Population of the database is ongoing, and the statistical analyses in this paper are based on the data present in the database in September of 2012. See Appendix Table A1.

To identify invasive species, I looked first at how widely each species is naturalized outside of its native range, and whether it is considered to be a weed. I used a 0-5 scale based on the number of biogeographic realms included in a species' current range relative to its native range to to measure how widely brome species are distributed. The eight biogeographic realms are Palearctic, Nearctic, Afrotropic, Neotropic, Indo-Malay, Australasia, Oceania and Antarctic (Udvardy 1975, Olson and Dinerstein 2002). The scale is based on biogeographic realms rather than continents, because they map better to typical brome native ranges. Species were assigned a distribution score of 4 or 5 if they are found in 2 or more biogeographic realms outside of the native range. These species were classified as widely distributed. See Table 3.3.

I then evaluated information on species that are considered to be destructive by using three classifications of weed type: crop weeds, ruderal weeds, and environmental weeds. Crop weeds grow in agricultural systems, ruderal weeds grow in disturbed or waste areas, and environmental weeds grow in and harm natural and semi-natural communities. A species could be assigned to one, two, or all three weed categories. Species that were described only as naturalized and that did not fit into a specific weed category were not recorded as weedy. For this study, I considered species that are both widely distributed and assigned to at least one weed category to be invasive.

Table 3.3: Scale used to evaluate distribution outside of native range.

Distribution Code	Definition	Associated Terminology
0	Undetermined	
1	Restricted to one or a few locations within a limited area, or believed to be extinct in the wild	Limited distribution
2	Restricted to a moderate to large native range	Limited distribution
3	Found outside of native range in native biogeographic realms or in no more than one additional biogeographic realm	Moderate distribution outside of native range
4	Naturalized in two biogeographic realms outside of native range	Wide distribution outside of native range
5	Naturalized in three or more biogeographic realms outside of native range	Wide distribution outside of native range

I used three values for life span: short for annual species, medium for species described as biennial or short-lived perennial, and long for perennial species. Species sometimes described as annual and sometimes as perennial were also classified has having a medium life span.

Seeds of brome grasses have lemma awns of various lengths from zero to over 40 millimeters. The values for the high end of the awn length range in the species descriptions on the Kew Gardens GrassBase database (Clayton et al. accessed 3/2012) were used for all but one species. I collected seed weight values for 64 species using the weight of 1000 seeds in grams. Seed weight values came from a variety of sources, including the USDA ARS Germplasm Resource Information Network (GRIN) database and the Kew Gardens Seed Information Database. Seed weight values from all sources were averaged for each species.

Chromosome counts were collected from a wide variety of sources. I categorized species as diploid, polyploid, or both diploid and polyploid, based on evaluation of chromosome count and ploidy level data and also on information in the literature. These categories were non-overlapping. Species were categorized as diploid if all or almost all records of ploidy level found were 2N (having 14 chromosomes) and if the literature indicated that the species is normally considered to be diploid. Other species were categorized as polyploid if all or almost all records of ploidy level were found were 4N or higher and if the literature indicated that the species is normally considered to be polyploid. All species in Section *Ceratochloa* were categorized as polyploid, as this is a characteristic of the section.

I also evaluated information about *Bromus* species that are currently used for hay, forage, or revegetation or have been used for these purposes in the past, and species for which named cultivars are available (where cultivars are named varieties intentionally breed or selected for cultivation). Other human uses of *Bromus* species were not included in the analyses.

Statistical Analysis

I used SAS version 9.2 to calculate Pearson's Correlation Coefficient (r) to examine relationships between wide distribution outside of the native range, crop weed status, ruderal weed status, and environmental weed status for 152 species in sections *Bromus, Genea, Ceratochloa, Bromopsis, Nevskiella* and *Neobromus.* I then ran logistic regressions with SAS 9.2 to analyze relationships between high distribution and the following individual factors: section, life span, average seed weight, maximum awn length, ploidy levels (diploid, polyploid, both diploid and polyploid), human use (for forage, hay or revegetation), and availability of cultivars. I repeated the logistic regressions for each weed category. For the logistic regressions, I used 148 species in sections *Bromus*, *Genea*, *Ceratochloa*, and *Bromopsis*. The three species in sections *Neobromus* and *Nevskiell*a were not used because the small size of these sections. I eliminated one additional species, *Bromus andringitrensis* A. Camus, which was collected in Madagascar in 1922 (Camus 1956). This species is listed as valid in Kew Gardens GrassBase, but information about it is very limited.

I ran a multivariate logistic regression with 56 species for which multifactor data were available and used a backward stepwise reduction with the following factors: average seed weight, maximum awn length, ploidy level (diploid, polyploid, or both), human use (forage, hay, revegetation), and availability of cultivars.

After running analyses on the species in the four largest sections, I separated these species into three groups, sections *Bromus* and *Genea* (with mostly annual life spans), section *Ceratochloa* (with annual to perennial life spans), and section *Bromopsis* (with perennial life spans). I combined the sections *Bromus* and *Genea* together because species in these sections have similar mostly annual life spans, and because there is a relatively small number of species in section *Genea*. I repeated the logistic regressions with the species in each of the three groups, and also created histograms showing species counts for maximum awn length (using 5 mm. intervals), average seed weight (using 2 mg. intervals), ploidy level, use by humans for forage, hay, and revegetation, and availability of cultivars.

Results

I identified 24 species in the genus *Bromus* as widely distributed outside of the native range, and 18 more as moderately distributed outside of the native range, and categorized 33 species as crop weeds, 34 species as ruderal weeds, and 23 species as environmental weeds. These categories are not exclusive; 15 species were categorized as widely distributed outside of the native range, and also included in all three weed categories.

The Pearson's Correlation Coefficient (r) analysis showed significant correlation between wide distribution outside of the native range and weed status. Values of r were 0.623 for the relationship between wide distribution and environmental weed status, 0.647 for the relationship between wide distribution and crop weed status, and 0.677 for the relationship between wide distribution and ruderal weed status. All but two of the 24 species in the genus *Bromus* classified as widely distributed outside of the native range (naturalized in two or more biogeographic realms outside of the native range) were also classified as weedy. Species classified as moderately distributed outside of the native range are somewhat less likely to be weedy with 10 of 18 moderately distributed species falling into at least one weed category. Of the 110 species restricted to their native ranges, only nine species were classified as weedy. The Pearson's Correlation Coefficient analysis also showed high levels of correlation between the crop weed, ruderal weed, and environmental weed status. Out of the 41 species listed as weedy, 18 were included in all three weed categories. The highest correlation was between crop weed status and ruderal weed status (r = 0.75127). See Figure 3.1 and Appendix Table A2.

The logistic regressions showed taxonomic section, life span, high maximum awn length, use for hay forage and revegetation, and availability of cultivars all to be significantly correlated with wide distribution outside of the native range and with all three weed categories. Ploidy level was also significantly correlated with wide distribution outside of the native range and with crop weed and ruderal weed status, but not with environmental weed status. Polyploid species were more likely to be widely distributed and weedy. Average seed weight showed no significant correlation with either wide distribution or with weediness. The multivariate logistic regressions showed significant correlations between long maximum awn length and wide distribution, and between long maximum awn length and weed status for all three weed categories.

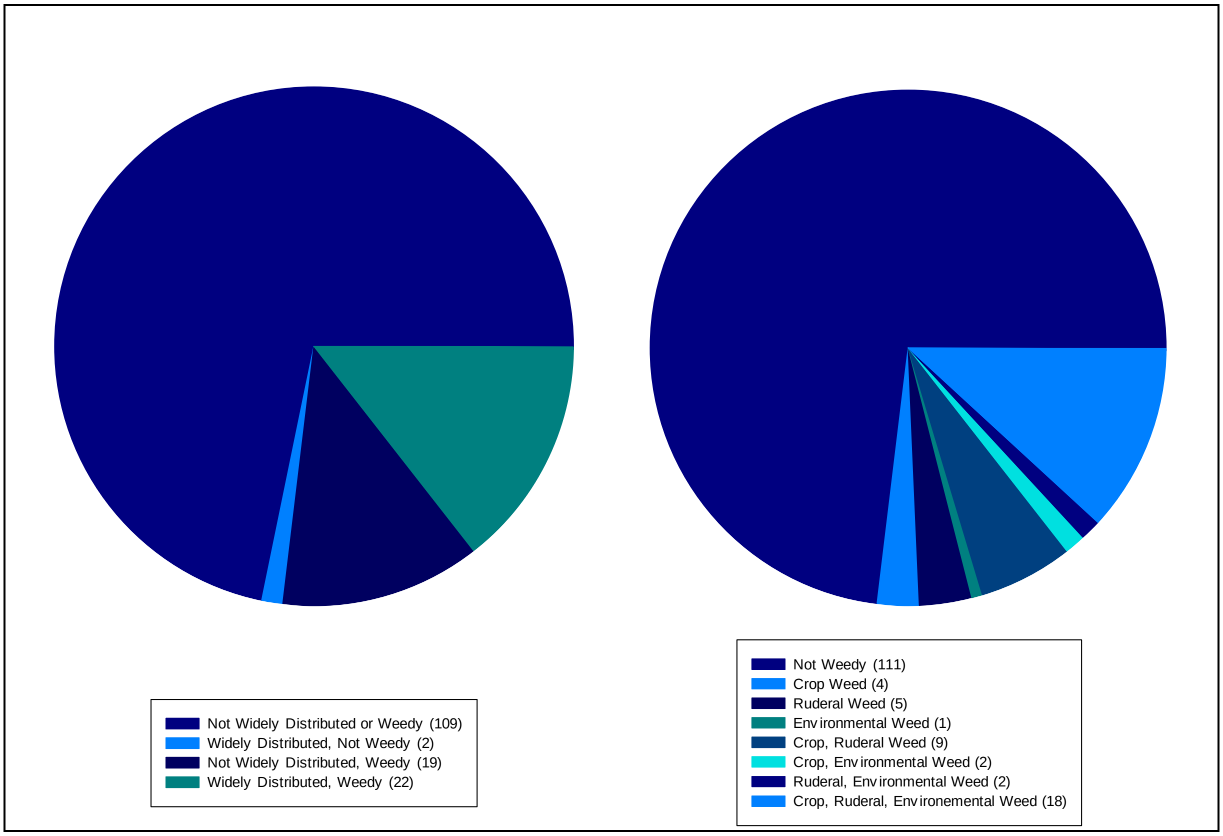

Figure 3.1: These charts include 152 species in the six sections of genus Bromus: *Bromus*, *Genea*, *Ceratochloa*, *Bromopsis*, *Nevskiella*, and *Neobromus*. The chart on the left shows combinations of values for distribution outside of the native range and listing as a weed. The chart on the right shows numbers of species that are listed as one .or more type of weed (crop, ruderal, and environmental).

Cultivar availability was also significantly correlated with high distribution and with ruderal and environmental weed status, but not with crop weed status. See Tables 3.4, 3.5 and Appendix Tables A3.1a and b.

When species were broken into three groups (sections *Bromus* and *Genea*, section *Bromopsis*, and section *Ceratochloa*), logistic regressions showed few significant correlations due to issues with quasi-separation of data points and loss of power. However, the histograms show clear differences between groups.

Discussion

Taxonomy and Life Span (Hypotheses 1 and 2)

Many researchers have commented that the annual species of brome grasses in sections *Bromus* and *Genea* are likely to be weedy and that many have been widely introduced around the world (Stebbins 1981; Ainouche, et al. 1995; Barkworth et al. 2007, Saarela et al. 2007). My hypotheses 1 and 2, that short-lived species in sections *Bromus* and *Genea* are likely to be invasive, were based on these comments. The information in the database and

Table 3.4: Relationships between factors from which logistic regressions (α = 0.05) produced statistically significant results . Species used for logistic regressions belonged to the four largest sections - *Bromus, Genea, Ceratochloa* and *Bromopsis*.

Factor	Widely Distributed Outside of Native Range	Crop Weed	Ruderal Weed	Environmental Weed	Comments
Section	Yes	Yes	Yes	Yes	Species in section *Genea* were the most widely distributed and weedy, and species in section *Bromopsis* were the least.
Life Span	Yes	Yes	Yes	Yes	Shorter life spans were correlated with wide distribution and weediness.
Maximum Awn Length	Yes	Yes	Yes	Yes	Longer maximum awn length was correlated with wide distribution and weediness
Average Seed Weight	No	No	No	No	No significant correlations were found.
Ploidy	Yes	Yes	Yes	No	Polyploidy was correlated with wide distribution and weediness, but this pattern was much weaker for annual species than for perennials.
Human Use (Forage, Hay, Revegetation)	Yes	Yes	Yes	Yes	Human use was correlated witih wide distribution and with weediness
Availability of Cultivars	Yes	Yes	Yes	Yes	Availability of cultivars was correlated with wide distribution and with weediness

Table 3.5: Multivariate logistic regressions with stepwise reductions (α = 0.05) found only maximum awn length and availability of cultivars to be statistically significant.

Factor	**Widely Introduced**	**Crop Weed**	**Ruderal Weed**	**Environmental Weed**	Comments
Maximum Awn Length	Yes	Yes	Yes	Yes	
Average Seed Weight	No	No	No	No	
Ploidy	No	No	No	No	
Human Use (Forage, Hay, Revegetation)	No	No	No	No	
Availability of Cultivars	Yes	No	Yes	Yes	

the results of the analyses supported these hypotheses. See Figure 3.2. Section *Genea* has only 8 species, but 6 are widely naturalized, and are destructive crop weeds, ruderal weeds and environmental weeds (Andersson et al. 2002; Kleeman and Gill 2006; Fortune et al. 2008; Williams et al. 2011). This section includes the seriously invasive species *Bromus tectorum* and *Bromus rubens*. Out of 32 species in the section *Bromus*, at least 18 species now grow in two or more biogeographical realms outside of the native range, 11 (or more) are crop weeds, 11 (or more) are ruderal weeds, and at least 8 are environmental weeds. The other sections of brome grasses contain fewer invasive species. Out of eighty-nine species in the section *Bromopsis* (which are all perennial with the exception of

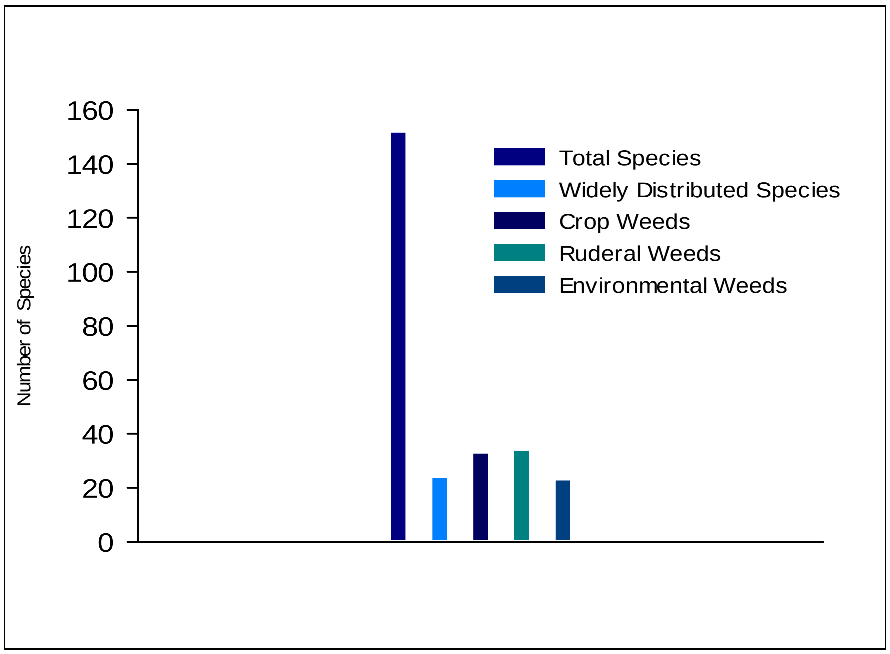

Figure 3.2: The number of species in four sections considered to be widely distributed, crop weeds, ruderal weeds, and/or environmental weeds. Four species in genus *Bromus* are not included in the logistic regression analyses and the histograms – two species in section *Neobromus*, one species in section *Nevskiella*, and one additional species from Madagascar. Of these four species, only Chilean brome, *Bromus berteroanus* Colla (formerly *Bromus trinii* E. Desv.) is classified as weedy. Chilean brome has spread from southern South America into western North America.

Bromus texensis (Shear) Hitchc.), only *Bromus inermis* Leyss. and *Bromus erectus* Huds. fit the criteria for invasiveness used in this study. The species in section *Ceratachloa* include annual, biennial and perennial species, and are somewhat more likely to be invasive than the species in section *Bromopsis*, but less so than the species in sections *Bromus* and *Genea*. See Figure 3.3.

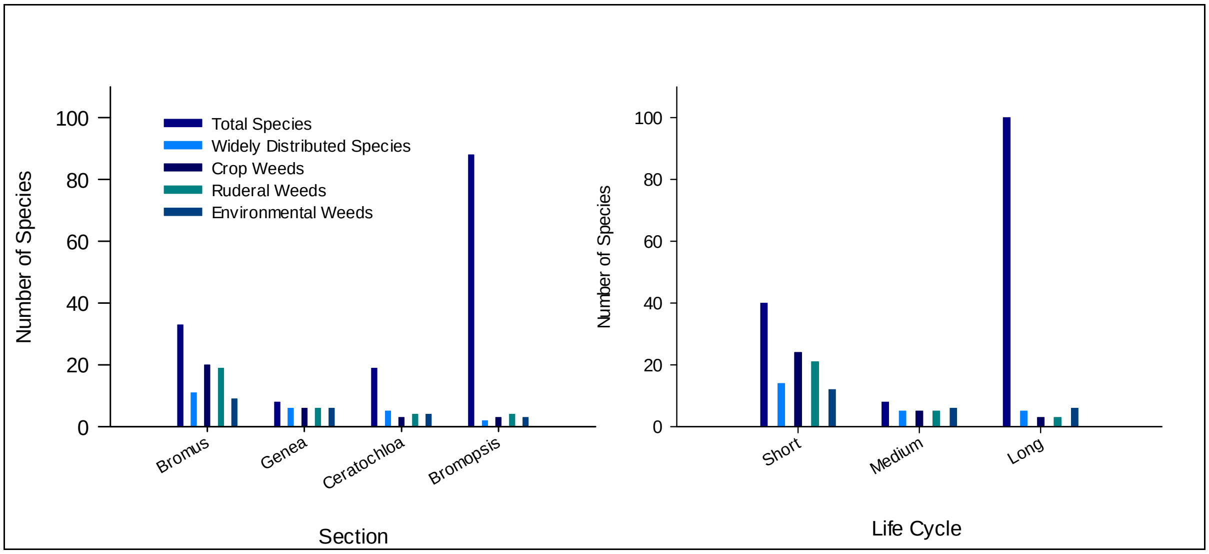

Figure 3.3: Annual sections *Bromus* and *Genea* have much higher percentages of widely distributed species and weedy species. Perennial section *Bromopsis* has relatively few species that are widely distributed, weedy or both. Species in section *Ceratochloa* tend to have intermediate or variable life spans.

Stebbins (1981) believed that the genus *Bromus* evolved in Eurasia, along with grassland ungulates including wild cattle, bison, and sheep, and that sections *Bromopsis* (subgenus *Festucaria)*, *Ceratochloa*, and *Neobromus* differentiated during the Pliocene. He suggested that bromes in sections *Ceratochloa* and *Neobromus* reached North America and eventually South America by the end of the Pliocene, with diploid and tetraploid *Ceratochloa* and *Neobromus* species eventually becoming extinct, and only New World species with higher ploidy levels remaining extant. Grasses in section *Bromopsis* also spread to Africa and the Americas during the Pliocene. The species in sections *Bromus* and *Genea* (subgenera *Bromus* and *Stenobromus)* probably developed from different early species of Central Asian *Bromopsis* during the Pleistocene. They differentiated and spread into Europe in conjunction with human activities including agricultural and livestock herding. The *Genea* species, especially, have seeds with long awns and other features that facilitate distribution by grazing animals, while some species in the section *Bromus* are associated with specific crops and others grow primarily in areas disturbed by other human activities. *Bromus secalinus* L., or rye brome, in section *Bromus* is a seed mimic in winter cereals that was frequently harvested and eaten along with more desirable grains by Neolithic Europeans (Behre 2008), and a number of other species in section *Bromus* are crop weeds. The evolutionary association of the annual species in the sections *Bromus* and *Genea* with grazing and agriculture in Europe and Asia suggests that they have developed adaptations that are likely to make them highly competitive weeds globally in areas heavily affected by human activities.

Reproduction (Hypotheses 3 and 4)

I hypothesized that long seed awns and low seed weight would both be correlated with invasiveness because they would lead to more effective seed dispersal. I found that long maximum seed awn length was significantly correlated both with wide distribution outside of the native range, and with all three types of weediness. However, low average seed weight was not correlated with either wide distribution outside of the native range or with weediness. See Figures 3.4 and 3.5.

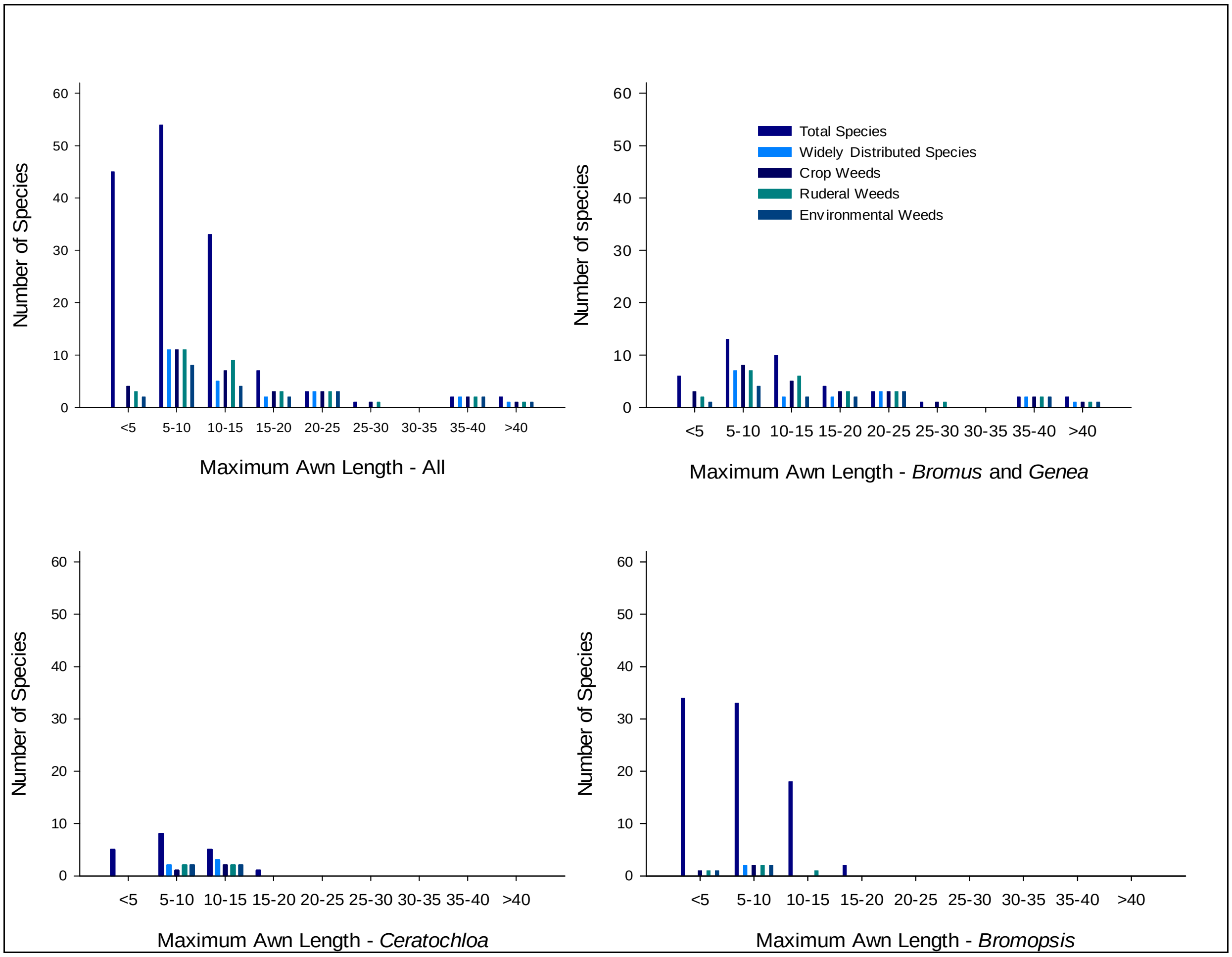

Figure 3.4: Maximum awn length is significantly correlated with both wide distribution and weediness. Analyses using median awn length produced similar results. Species in section *Genea* have the longest awns. Long awns that stick in wool or fur may facilitate distribution by grazing animals, and the awns of some species may injure livestock and wildlife, discouraging grazing once seeds have formed.

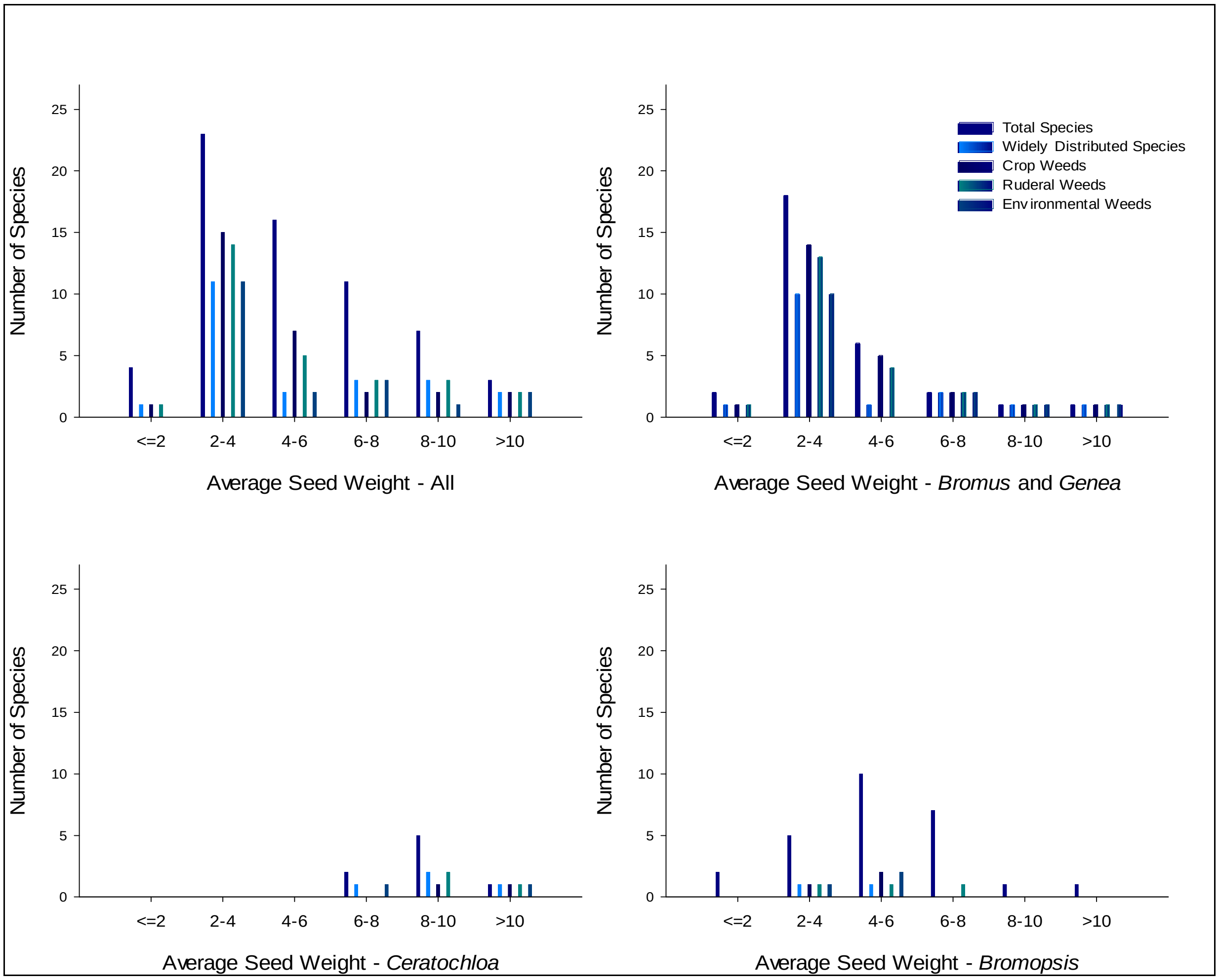

Figure 3.5: Average seed weight is not correlated with either wide distribution or with weediness. Many species with light seeds are invasive, but species with heavy seeds are also likely to invade. *Bromus* seeds are distributed in a variety of ways, and this may explain the lack any obvious relationship between seed weight and invasiveness. Seed weights are more likely to be available for widely distributed and weedy species than for those that have a limited distribution and are not weedy.

Many of the traits that researchers have suggested may lead to invasiveness in plants are reproductive traits that help plants rapidly spread and become established. These include the ability to self-pollinate, use of generalist species and wind for cross pollination, production of small light seeds, adaptations for vertebrate seed dispersal, heavy seed output, seed longevity, and vegetative reproduction. While the database includes information on these traits for many species, much of the data for these traits remains incomplete. One feature of the bromes that stands out, however, is the presence of short to long subapical lemma awns that can help the seeds stick in animal fur or wool and that also may discourage grazing. Some species have awns that are long and stiff enough to cause damage to livestock and wildlife. Downy brome, *Bromus tectorum*, is a useful forage grass early in the season, but the dried awns can injure the mouths of grazing animals later in the summer (Reid et al. 2008) and *Bromus diandrus* has earned the common name of ripgut brome because of its long stiff awns which can penetrate skin, eyes, intestines and feet of livestock (New South Wales Department of Primary Industries and Murrumbidgee Catchment Management Authority 2008). Of the bromes in the annual sections, *Genea* species have medium to long awns, while those of species in section *Bromus* range from short to medium. The awns of the longer-lived species in sections *Bromopsis* and *Ceratochloa* are also short to medium in length. While six of the species in long awned section *Genea* are invasive, two other species including *Bromus sericeus*, which has very long awns, are not widely distributed outside of the native range. Long awns aid with vertebrate distribution and discourage herbivory during part of the year, but other factors are clearly also important in determining which brome species become invasive.

Low seed weight (or mass) is sometimes included in lists of traits that help plants spread rapidly into new areas. However, I did not see associations between low seed weight and either wide distribution or weediness. In a discussion of factors associated with invasiveness in pines, Rejmánek (1996) suggested that small seed weight might be associated with high number of seeds, better dispersal, high initial germinability, and shorter required chilling period. Baker (1974) commented that smaller seeds can be more easily dispersed, while larger seeds may produce seedlings that are better able to compete. Invasive (and non-invasive) brome species have a wide range of seed weights. Annual species in sections *Bromus* and *Genea* have seeds that range from light to heavy. The perennial *Bromopsis* species have relatively light seeds, and *Ceratochloa* species have heavy seeds. Many of the annual species in sections *Bromus* and *Genea* that have light seeds are crop and ruderal weeds. A somewhat smaller number are also environmental weeds. Species with heavier seeds are often successful invaders too. Some of the invasive species that have heavier seeds also have long awns, and may depend on vertebrates to move seeds around. Others are crop seed mimics or hay species that rely on human activities for dispersal. One observation is that the highly invasive species *Bromus tectorum* and *Bromus rubens* both have a fairly light seeds and moderately long awns. This combination may facilitate dispersal in rangelands and other open habitats (Sales 2004). Seed weight information may be useful in evaluation of invasive potential if it is used in association with better understanding of methods used for seed dispersal by specific plant taxa.

Ploidy Level (Hypothesis 5)

I hypothesized that polyploid brome grasses would be more likely to be invasive than diploid species. Statistical analysis of the entire Bromus genus showed polyploid species to be more widely distributed and also more likely to be weedy. However, other patterns are visible in the histograms for individual sections. Among the short-lived species in sections Bromus and Genea, diploid species, polyploid species, and species with both diploid and polyploid chromosome counts are all likely to be invasive, while in perennial section Bromopsis, all of the invasive species are either polyploid or both diploid and polyploid See Figure 3.6.

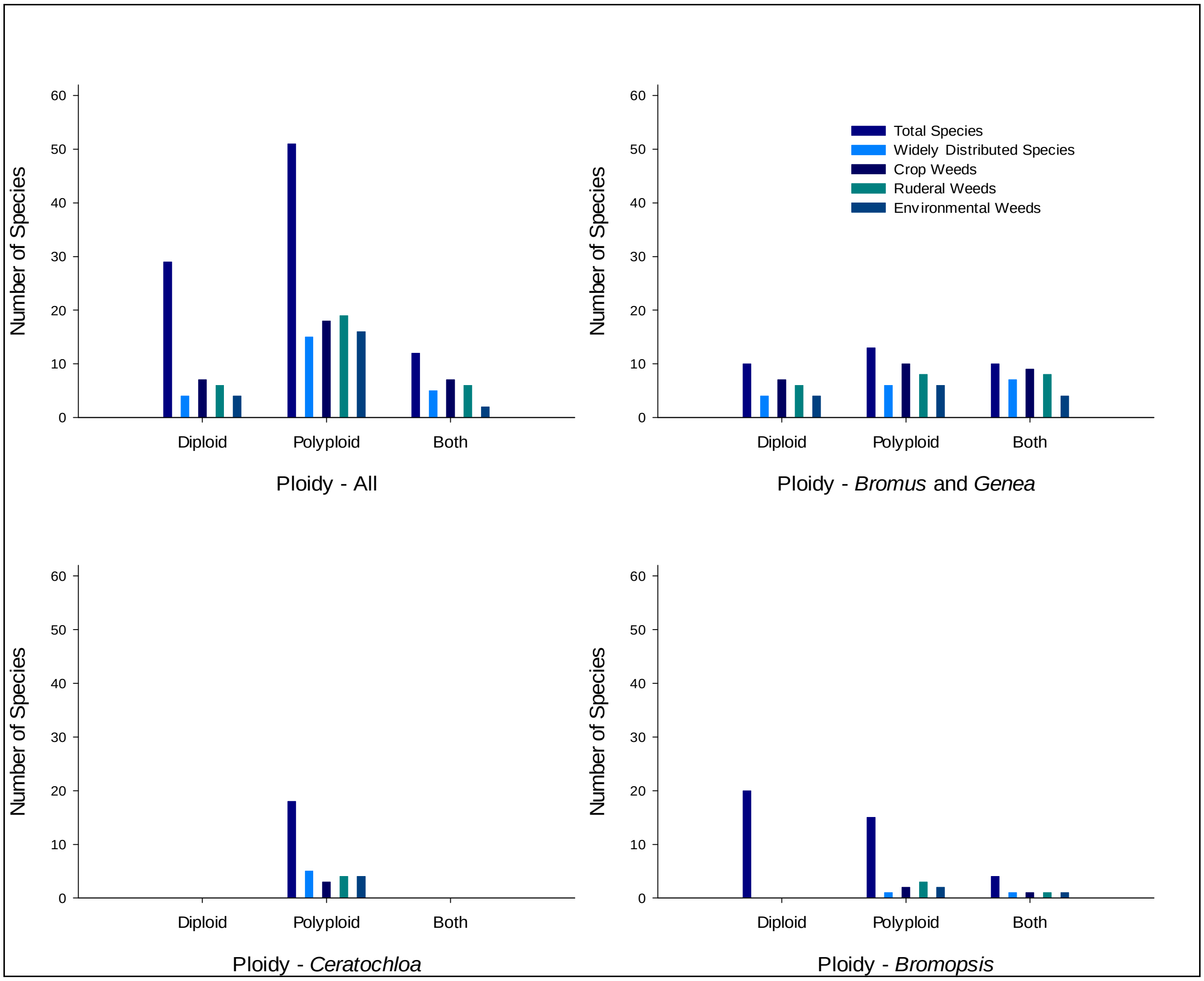

Figure 3.6: Inclusion of polyploid individuals in a species is correlated with wide distribution and invasiveness in the genus *Bromus* but this pattern is related to the absence of invasive diploid species in section *Bromopsis* and the polyploid section *Ceratochloa*. In the annual sections *Bromus* and *Genea*, some diploid species are invasive and there is less of a relationship between polyploidy and invasiveness.

Brome species may be either diploid or polyploid. In a number of species, some individuals are diploid, while other individuals in the same species have varying levels of polyploidy. The species in section *Ceratochloa* are all polyploid with ploidy levels ranging from 6x to 12x (Stebbins 1981; Stebbins and Tobgy 1944). Both diploid and polyploid chromosome counts may provide advantages that help species invade new environments. Diploid species are likely to have smaller genome sizes and are able to quickly complete mitosis and meiosis, to rapidly grow, and to reproduce more quickly than polyploid species (Monty et al. 2010). However, Bennett and Smith (1972) showed that while polyploid species tend to take longer to complete meiosis and to produce pollen than diploid species, these processes speed up somewhat as ploidy level increases. Polyploid plants may have higher levels of variation and may be better able to adapt to new and fluctuating environmental conditions. In addition, polyploidy may affect plant physiology and morphology, producing a number of effects including slower growth rates, larger flowers and seeds, more robust plants, delayed or prolonged reproduction, greater tolerance to stress, and better winter survival (Rejmánik 1996; Monty et al. 2010; te Beest et al. 2012). Stebbins (1956) commented that diploid species are likely to be better adapted to the original habitat in which they evolved than polyploids, but polyploidy allows plants to better deal with novel environmental conditions, especially when it is combined with hybridization. Roy (1990) suggested that the absence of a relationship between ploidy level and invasiveness in annual bromes might be related to the recent development of both polyploidizaton and invasions. The relationship between polyploidy and invasiveness in the species of perennial section *Bromopsis* may be due to extensive use of polyploid species for hay, forage, and revegetation and for development of cultivars.

The species in the section *Ceratochloa* are all polyploid. South American species are generally hexaploid. Most North American species are octaploid and may have developed the higher chromosome counts as a result of hybridization with species in section *Bromopsis* (subgenus *Festucaria*) (Stebbins 1981). The most invasive species in section *Ceratochloa* is *Bromus catharticus*, or rescue grass, a South American species that is used for hay and grazing. Invasiveness in this section seems to be more related to human use than to ploidy level.

Human Use (Hypotheses 6 and 7)

Hypotheses 6 and 7 state that species that are used for hay, forage, and revegetation are more likely to be invasive than those that are not, and that development of named cultivars is correlated with invasiveness. The logistic regressions supported both of these hypotheses. Use by humans and availability of cultivars is associated with invasiveness especially in perennial species. See Figures 3.7 and 3.8.

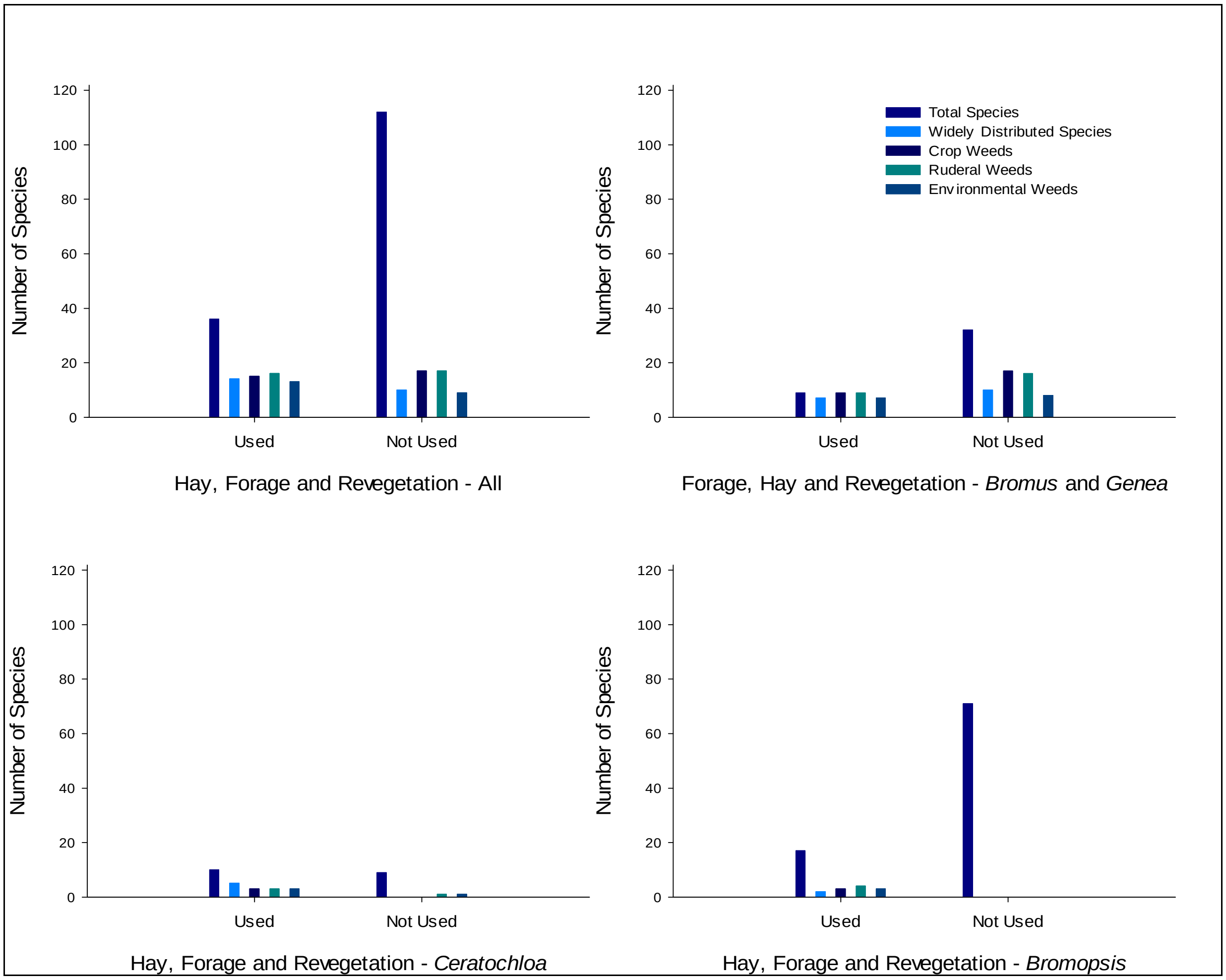

Figure 3.7: Human use is correlated with wide distribution outside of the native range and with weediness. Most bromes in cultivation today are perennial species. In the 1800s and 1900s, annual species such as *Bromus tectorum* were evaluated and often recommended for use as forage and sometimes for hay. *Bromus tectorum* is still extensively used for early season forage in parts of the American West.

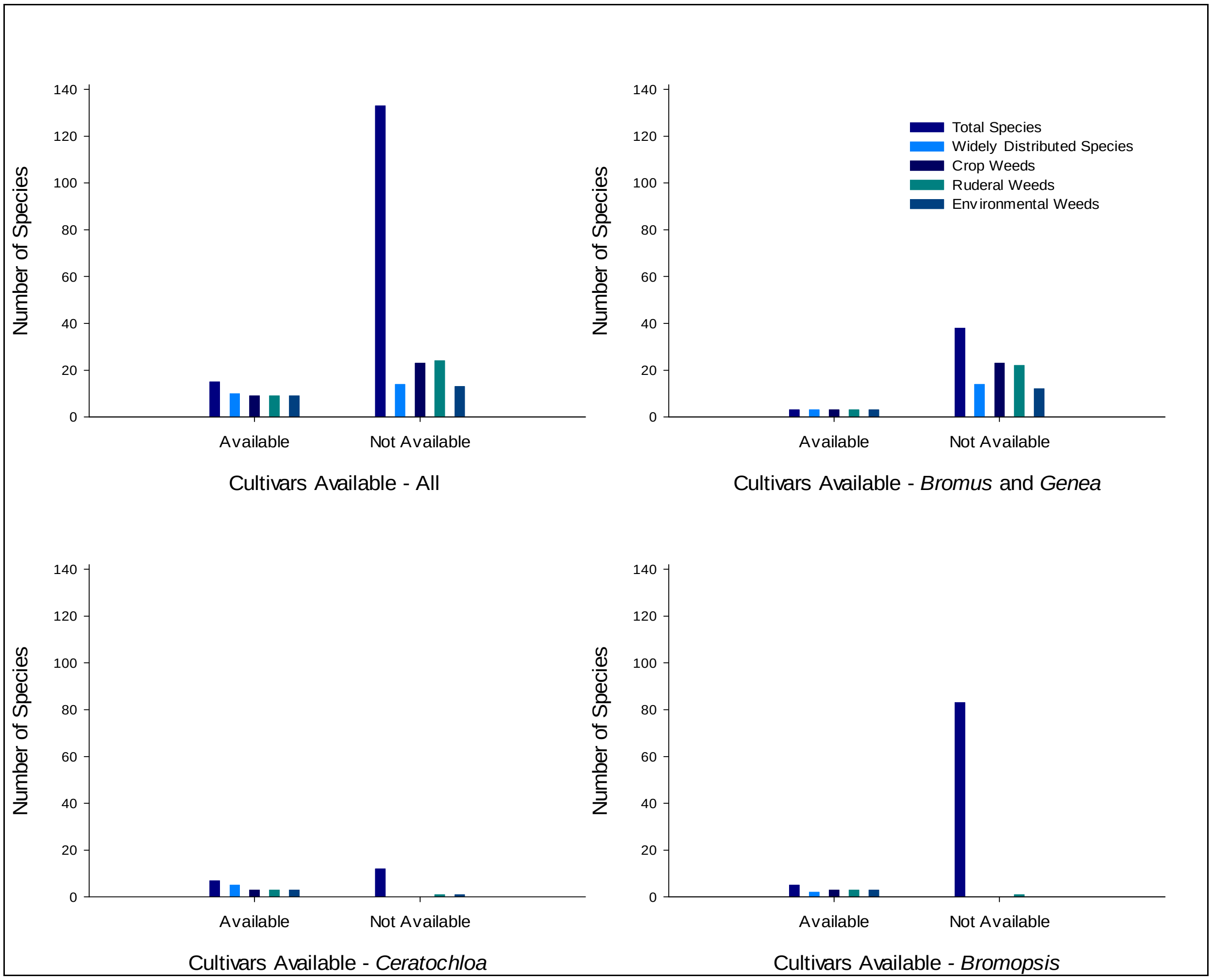

Figure 3.8: Cultivars of some perennial species in sections *Bromopsis* and *Ceratochloa* are widely used in many regions. Use of annual cultivars is much more limited. Availability of cultivars is correlated with wide distribution outside of the native range in perennial bromes, and some widely used species have escaped cultivation and are causing serious environmental impacts.

Bromus inermis Leyss., in section *Bromopsis*, is widely grown for hay and forage, and has been used for revegetation of roadsides, ditches, mine tailings and other disturbed areas in North America (Weintraub 1953; Otfinowski et al. 2007; Lass and Prather 2007; Dillemuth et al. 2009; Brown et al. 2010). Many cultivars of *Bromus inermis* are available. These are typically grouped into northern meadow types based on strains introduced from relatively wet temperate regions in Eastern Europe and Russia, southern steppe types based on strains probably introduced from Hungary, and intermediate types (Williams et al. 2011; Smoliak et al., accessed 7/12/2012). Cultivar “Polar” is a hybrid of *Bromus inermis* and *Bromus pumpellianus* Scribn. *Bromus pumpellianus* is native across both North America and Asia and is sometimes to be considered a subspecies of *Bromus inermis*. For this reason, *Bromus inermis* is often listed as native in North America. However, *Bromus inermis* ssp. *inermis* was introduced from Eurasia in the 1880s and has interbred with and often replaced *Bromus pumpellianus* (Elliot 1949). *Bromus inermis* grows for many miles along highways in western North America and is invading natural areas including parts of the pothole prairie region of the North Central United States where it is changing distribution patterns of native cordgrass (Dillemuth et al. 2009). It is considered invasive in a number of national parks throughout the western United States (Invasive Plant Atlas of the United States).

Another species in section *Bromopsis*, *Bromus erectus*, is a pasture and hay grass in Europe (Jongepierova et al. 2007). It is introduced in North America where it grows in disturbed areas in the eastern United States and Canada, and is listed as a crop weed and a weed of the natural environment in Australia (Barkworth et al. 2007; Randall 2007). Two other species in section *Bromopsis,* the closely related (or conspecific) *Bromus biebersteinii* Roem. & Schult. and *Bromus riparius* Rehmann have also been introduced into North America for hay and forage and are only occasionally reported as being weedy (Lass and Prather 2007; Williams et al. 2011). *Bromus riparius* is sometimes suggested for use as a less aggressive alternative to *Bromus inermis*, and the two species hybridize (Williams et al. 2011). Several other species in section *Bromopsis*, including *Bromus leptoclados* Nees in Africa, and *Bromus auleticus* Trin. ex Nees in South America are used for hay or forage, but have not been widely introduced into new regions.

Bromus catharticus Vahl, or rescue brome, is a South American species in the section *Ceratochloa*. The taxonomy of *Bromus catharticus* is difficult, and a number of *Ceratochloa* grasses are now often considered to be conspecific with *Bromus catharticus*. These include *Bromus stamineus* E. Desv. (grazing brome), *Bromus valdivianus* Phil., *Bromus unioloides* Kunth, *Bromus tunicatus* Phil. and *Bromus mango* E. Desv. Rescue grass varieties are used for forage in hay in North America, Australia, New Zealand, and Europe and cultivars are available (Stewart 1996; Williams et al. 2011). Grasses in the *Bromus catharticus* complex have escaped from cultivation in a number of areas around the world and have become roadside weeds and invaders of natural environments (Randall 2007; Wu et al. 2009). North American *Ceratochloa* species including *Bromus carinatus* Hook & Arn. (California brome), and the closely related or conspecific *Bromus marginatus* Nees ex Steudel (mountain brome*)* are used in North America for fodder and revegetation (Tilley et al. 2006, Williams et al. 2011). *Bromus carinatus* can be used as a cover crop, but can also be an agricultural weed (Darris 2007, USDA National Resources Conservation Service 2007). It is now found in some parts of Europe and is occasionally grown for fodder (Stace et al. 2005). *Bromus carinatus* is susceptible to bacterial wilt and this may have prevented widespread use (Stebbins and Tobgy 1944; Samson et al. 1983; Stewart 1996).

A few cultivars of annual brome species have been developed. *Bromus rubens* L. “Panoche” was developed in California for soil stabilization. A cultivar of *Bromus mollis* L. (*Bromus hordeaceus* L.), also developed in California, is used as a cover crop, and for range reseeding and burn rehabilitation. *Bromus arvensis* L. “Dos” is a Russian cultivar (Williams et al. 2011). *Bromus rubens*, *Bromus hordeaceus*, and *Bromus arvensis* are all considered to be weedy and invasive both in North America and in other parts of the world, although *Bromus arvensis* has become less common in some parts of Europe (Ainouche and Bayer 1997, Stace et al. 2005).

Humans do also use annual brome grasses, including species that are clearly invasive such as *Bromus tectorum* which is used extensively as early season forage in many parts of western North America (Upadhyaya et al. 1986). Introduction and distribution of annual bromes for forage, hay, and other uses occurred during the 1800s and 1900s, and current invasions by annual bromes in the western United States are to a large extent, a legacy of earlier agricultural introductions and practices.

Patterns of Invasiveness

While most invasive species of brome grasses are annuals, perennial species may also create serious problems as crop, ruderal, and environmental weeds. However, causes of invasiveness seem to differ between annual and perennial species. Annual bromes in the sections *Bromus* and *Genea* have long been associated with human habitation, and have adapted to grow and reproduce effectively in association with crops and ruderal areas (Stebbins 1981). In some cases, humans have purposely introduced annual species to new areas. A number of annual bromes were introduced to the United States in the 1800s and sold to farmers as forage grasses. One species, *Bromus briziformis* Fisch. & C. A. Mey. was sold for use in dried flower arrangements (Mack 1991). However, annual brome species are also often introduced and spread by grain contamination, grazing animals, and vehicles (Mack 1981; Salo 2005).

Species in sections *Bromus* and *Genea* may all pose some risk of invasion. Six of the eight species in the annual section *Genea* are widely distributed and are included in all three categories of weeds. The other two, *Bromus fasciculatus* C. Presl and *Bromus sericeus* Drobow, are limited to their native range and not generally listed as weeds. *Bromus fasciculatus* is found around the Mediterranean. Like other *Genea* species, it has seeds that are adapted for vertebrate dispersal, but it has been described as relatively rare and populations in some areas appear to be decreasing (Sales 1994; Acedo and Llamas 2001; Oja 2002; Fortune, et al. 2008). *Bromus sericeus*, a Middle Eastern species, is sometimes considered to be a subspecies of *Bromus tectorum*. *Bromus sericeus* grows in xeric environments, has a relatively limited range (Sales 1994) and is listed as an obligate natural on the Flora of Israel website (Danin 2006+). A number of species in section *Bromus* also are listed as both widely distributed and weedy, and some species in this section fall into all three weed categories. *Bromus japonicus* Thunb. ex Murr. is a serious crop weed in the north central section of the United States that is invading natural environments (O'Connor et al. 1991; Haferkamp et al. 1997). A number of species in section *Bromus* are weeds in winter cereal crops, and some also grow in other types of agricultural systems such as vineyards (Tsvelev 1984; Cussans et al. 1994; Connor et al. 1991; Walters 2011). *Bromus* crop weeds cause economic damage by reducing yields, and increasing control costs, but also because many countries have restrictions limiting imports of commodities that contain propagules of some species (Cowbrough et al. 2007; Walters 2011). Changes in agricultural methods may be reducing populations of some species in section *Bromus*. *Bromus secalinus* L., or rye brome, is a crop mimic that falls into all three weed categories, but is primarily a crop weed (Cowbrough et al. 2007). It is reported to be decreasing in abundance in many areas, probably because of improved seed cleaning techniques and other methods of control (Darbyshire 2003; Luneva 2003-2009; Stace, et al. 2005). Several species in section *Bromus* are associated with crops that are no longer commonly grown and have almost disappeared. *Bromus interruptus* (Hack.) Druce grew in sainfoin fields in Britain and *Bromus bromoideus* (Lej.) Crep. was found primarily in or near fields of spelt wheat in the Ardennes of Belgium and France. Both are probably extinct in the wild (Ainouche and Bayer 1997; Rich and Lockton 2002; Bilz 2011, Gigot 2011).

Only a few perennial bromes in section *Bromopsis* are weedy or invasive. Taxonomists have suggested that species in this section fall into two groups. The first group is a mostly polyploid Eurasian group with large anthers and small chromosomes and a rhizomatous or densely tufted growth pattern. This group includes *Bromus inermis* Leyss., *Bromus pumpellianus* Scribn., *Bromus erectus* Huds., *Bromus riparius* Rehmann, *Bromus cappadocicus* Boiss. and Balansa, *Bromus variegatus* M. Bieberstein, *Bromus biebersteinii* Roem. & Schult., and possibly South American species *Bromus auleticus* Trin. ex Nees. Grasses in this group often cross pollinate. The second group contains mostly self-pollinating American species. These have small anthers and large chromosomes and are less densely tufted and non-rhizomatous. Some Eurasian species of *Bromopsis,* including *Bromus ramosus* Huds. and *Bromus benekenii* (Lange) Trimen are more similar to North American species (Stebbins 1981; Armstrong 1983;

Saarela 2001; Saarela et al. 2007; Sutkowska and Mitka 2008). The species with small chromosomes in the Eurasian group have traits that suggest that they may pose more of a risk than the species in the American group. Rhizomes facilitate spread of plants introduced into new environments, and rhizomatous species like *Bromus inermis* may cause more serious damage in natural and semi-natural communities because they often exclude other species and form monocultures (Otfinowski et al. 2007; Otfinowski and Kenkel 2008; Sinkins and Otfinowski 2012). The denser growth patterns of grasses in the Eurasian group also make them useful for hay and for revegetation.

The species in the section *Ceratochloa* seem to fall somewhere in the middle. They may behave as crop weeds and ruderal weeds under some circumstances. However, the *Ceratochloa* species of most concern, *Bromus catharticus* Vahl, is a valuable forage species with many cultivars. It has spread into new areas as a result of purposeful introduction and cultivation, and escaped into natural environments in some areas.

As with many other invasive species, invasiveness in brome grasses is strongly related to human activities and influences. Annual brome species are well adapted to grow in association with human activities such as agriculture, sheep-herding, cattle grazing, road building, and other forms of environmental disturbance. Most of the few perennial species that are invasive have been purposely introduced and are used for hay, forage, and revegetation.

Opportunities for Additional Research

The factors discussed in this paper are clearly only a subset of factors that could influence invasiveness in brome grasses. Collection of more information about both invasive and non-invasive species of brome grasses could help to identify species that pose a serious risk of invasion. Additonal data about temperature, pH, water use and nutrient use, response to elevated $C0_2$ levels, latitudinal range, seed bank persistance, mating strategies, and fire survival could all be valuable and may be particularly useful for researchers and managers who are dealing with land use issues related to climate change. Expansion of a database of this type to include additional genera within the family Poaceae could also help researchers identify factors and patterns that influence grass invasions.

Bromus tectorum, in section *Genea*, has caused widespread damage to communities over large areas of the western United States and has been the focus of much of the research into invasion by brome grasses. It is also naturalized in other regions of the world, but has not been associated with the severe damage to communities seen in the western United States (Stohlgren, et al. 2011). Kinter and Mack (2004) have suggested that differences in levels of fitness in founder population sources might be responsible for differences in behavior in the two regions. This would be an interesting and important topic for additional study.

A large amount of research has been done on *Bromus tectorum*, but less research has focused on other species in section *Genea*. Six of the eight species this section is present in the United States and are considered weedy or invasive in native and introduced ranges. The other two species, *Bromus fasciculatus* (C. Presl) and *Bromus sericeus* (Dobrow), seem to be confined to their native ranges and may be adapted to specific types of environments. *Bromus sericeus* is often considered to be a subspecies of *Bromus tectorum* (*Bromus tectorum* ssp. *lucidus* Sales) and it grows in xeric environments (Sales 1991; Sales 1994). There is less information available for these two species than for other species in section *Genea*, and it would be interesting to better understand the factors that have limited their distribution, and to further evaluate them for invasive potential. While *Bromus tectorum* is found throughout much of the United States and southern Canada, some species in section *Genea* are primarily found in along the West Coast and in southwestern states . Others are more widely distributed, but their populations remain relatively limited in size. Six of the eight species in section *Genea* are serious crop, ruderal, and environmental weeds. It would be useful to have a good understanding of factors that limit or encourage growth and spread of all species in section *Genea*, and to further evaluate possible effects of climate change and land use patterns on their distribution and on their agricultural and environmental impacts.

Additional information about growth requirements and possible effects of environmental and climate change would also be useful for species in section *Bromus*, many of which are widely distributed worldwide as crop and ruderal weeds. Species in this section can also damage natural environments. *Bromus hordeaceus* L. is one of the annual grasses that have replaced native bunchgrass species in much of California. A number of other species section *Bromus* are present in North America and in many other regions outside of their native ranges. It is possible that changes in climate and rainfall patterns could effect the distribution and growth of species in this section.

Several species included by taxonomists in section *Bromus* may be hybrids between grasses in sections *Bromus* and *Genea*. One of these is *Bromus pectinatus* Thunb., which is probably closely related to *Genea* species *Bromus diandrus* Roth (Saarela et al. 2007). *Bromus pectinatus* is native to Africa and to Asia as far east as Tibet and is a crop weed in Africa (Wilcox 1986, Taa 2004), but is not known to be present in North America. Australian brome, *Bromus arenarius* Labill., is closely related to *Bromus pectinatus* and is also sometimes thought to be a hybrid between grasses in sections *Bromus* and *Genea* (Stebbins 1956; Stebbins 1981; Ainouche and Bayer 1997;

Oja 2007; Saarela 2007). *Bromus arenarius* currently grows in dry, sandy, and disturbed areas in California, and other parts of the western United States and has been collected as far north as coastal Washington (Barkworth et al. 2007; Rocky Mountain Herbarium Specimen Database). Further study and evaluation of these species would be valuable.

It would be useful to see more data and research on the relationship between invasion and human cultivation of hay and forage both for brome grasses and for other grass taxa. Two factors correlated with wide distribution, weediness and environmental damage are use by human beings for hay, forage, and revegetation, and the development of cultivars. That these factors would be correlated with wide distribution is clearly expected. Humans move species that are useful to new areas. Of more concern is the association of human use and cultivar development with environmental damage. Correlations do not imply cause and effect. The factors that help species to move into new areas and establish large populations may also make them useful for hay, forage, and revegetation. However, human cultivation and development of cultivars suited to a variety of environments may give introduced plants an advantage over native species. A study of introduction pathways of plants in the Czech republic showed that plants that were purposely released or escaped from cultivation have a higher level of invasion success than those introduced accidentally (Pyšek et al. 2011). Ellstrand et al. (2010) pointed out that both crop plants and weeds often grow in disturbed environments as monocultures. Another concern is that hybridization between domesticated varieties and closely related natives may introduce new variation into natural populations (De Wet and Harlan 1975). More information about the relationship between invasion and the use of cultivars could help to encourage and support the development of varieties that are less likely to escape from cultivation and damage natural environments. The history of *Bromus inermis* in North America would make an interesting case study.

Finally, while there are a large number of *Bromus* species that have become invasive, some species are endangered and others are likely to be threatened by habitat loss and climate change. A number of *Bromus* species grow in limited areas, sometimes at high elevations or in areas with extreme environmental conditions. Information about these species is difficult to find, and their current status unknown.

Conclusion

An important goal of invasion science has been to develop a better understanding of characteristics of invasive plants. Researchers have identified general factors and traits that are associated with invasiveness. Using more detailed data about the ways that plants in specific families, genera, and species grow, reproduce, and interact with their environment can add to understanding of the causes of plant invasions. The collection of many types of data for plants in groups that are known to have relatively high numbers of invasive species can facilitate comparisons, highlight knowledge gaps, and help researchers see overall patterns that may not be obvious in data from more focused studies. Comparisons of closely related species with differing records of invasion provide researchers with opportunities to examine similarities and differences that can help to explain why plants become invasive and how they invade. Collection of data for plants in taxa with high numbers of invasives can also be used to identify species that may warrant additional evaluation and monitoring, and can provide a central location where researchers and land managers can find basic information and additional resources. Understanding of plant invasions may be facilitated by combining a broad understanding of the factors associated with plant invasions with detailed information about how these factors relate to the behavior of plants at family, genus and species levels.

The differences in numbers of invasive species in the different sections of brome grasses suggests that the combination of a broad understanding of the factors associated with plant invasions with more detailed information about how these factors relate to the behavior of plants in specific taxa may be helpful for the study of invasiveness, especially as increasing availability of molecular data provides researchers with a better understanding of phylogenic relationships and evolutionary history. The brome grasses also highlight the relationship between invasion and human activity. *Bromus* species that grow primarily in undisturbed natural habitats are unlikely to be invasive when introduced into new areas. The *Bromus* species that invade are those that take advantage of human activities and habitat disruption, and those that humans purposely distribute and cultivate.

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APPENDIX

Table A1: Data collected for 152 Bromus species in sections *Bromus*, *Genea*, *Ceratochloa*, *Bromopsis*, *Nevskiella*, and *Neobromus*.

Species	Section	Distrib.	Crop Weed	Rud. Weed	Environ. Weed	Life Span	Avg. Seed Weight	Max Awn Length	Ploidy	Human Use	Cultivars
aegyptiacus	Bromus	2	0	0	0	Short	5	11	Diploid	0	0
aleutensis	Ceratochloa	2	0	0	0	Long		10	Polyploid	0	0
alopecuros	Bromus	5	1	1	0	Short	3.46	20	Both	0	0
andringtrensis		1	0	0	0					0	0
anomalus	Bromopsis	2	0	0	0	Long	3.08	4	Both	1	0
araucanus	Bromopsis	2	0	0	0	Long	6.49	5		0	0
arenarius	Bromus	3	0	1	1	Medium	2.7	15	Polyploid	0	0
aristatus	Bromopsis	2	0	0	0	Long		7		0	0
arizonicus	Ceratochloa	2	1	0	1	Short		15	Polyploid	1	1
armenus	Bromopsis	2	0	0	0	Long		8		0	0
arvensis	Bromus	5	1	1	1	Short	2.4	10	Diploid	1	1
attenuatus	Bromopsis	1	0	0	0	Long		3		0	0
auleticus	Bromopsis	2	0	0	0	Long	6.82	6	Polyploid	1	0
ayacuchensis	Ceratochloa	1	0	0	0	Long		5.5	Polyploid	0	0
benekenii	Bromopsis	2	0	0	0	Long	4.55	8	Polyploid	0	0
berteroanus	Neobromus	3	1	1	1	Medium		15	Polyploid	1	0
biebersteinii	Bromopsis	3	1	0	1	Long	5.13	4	Polyploid	1	1
bikfayensis	Bromopsis	2	0	0	0	Long		8		0	0
bonariensis	Ceratochloa	1	0	0	0	Long		5	Polyploid	0	0
borianus	Bromopsis	1	0	0	0	Long		12		0	0
brachyanthera	Bromopsis	2	0	1	0	Long		12	Polyploid	1	0
brachystachys	Bromus	2	0	0	0	Short	2.31	7	Diploid	0	0
briziformis	Bromus	3	1	1	1	Short	3.18	1	Diploid	0	0
bromoideus	Bromus	1	0	0	0	Short	2.83	12	Polyploid	0	0
cabrerensis	Bromus	2	0	0	0	Short		8	Polyploid	0	0
cappadocicus	Bromopsis	2	0	0	0	Long	5.14	6	Polyploid	0	0
carinatus	Ceratochloa	4	1	1	0	Medium	8.25	15	Polyploid	1	1
catharticus	Ceratochloa	5	1	1	1	Medium	11.05	9	Polyploid	1	1

Species	Section	Distrib.	Crop Weed	Rud. Weed	Environ. Weed	Life Span	Avg. Seed Weight	Max Awn Length	Ploidy	Human Use	Cultivars
cebadilla	Ceratochloa	4	0	0	1	Long	6.99	12	Polyploid	1	1
ceramicus	Bromopsis	1	0	0	0	Long		6		0	0
chrysopogon	Bromus	2	0	1	0	Short		14		0	0
ciliatus	Bromopsis	3	0	0	0	Long	4.38	3.5	Diploid	1	0
coloratus	Ceratochloa	3	0	0	0	Long	8.15	8	Polyploid	1	1
commutatus	Bromus	5	1	1	0	Short	4.1	10	Both	0	0
condensatus	Bromopsis	2	0	0	0	Long	1.92			0	0
confinis	Bromopsis	2	0	0	0	Long		6		0	0
danthoniae	Bromus	3	1	1	0	Short	4.07	15	Diploid	0	0
densus	Bromopsis	1	0	0	0	Long		1.5		0	0
diandrus	Genea	5	1	1	1	Short	8.79	75	Polyploid	0	0
dolichocarpus	Bromopsis	2	0	0	0	Long		11	Polyploid	0	0
epilus	Bromopsis	1	0	0	0	Long		14		0	0
erectus	Bromopsis	4	1	1	1	Long	4.35	8	Both	1	1
exaltatus	Bromopsis	2	0	0	0	Long		4	Diploid	0	0
fasciculatus	Genea	2	0	0	0	Short	1.79	18	Diploid	0	0
firmior	Bromopsis	1	0	0	0	Long		12		0	0
flexuosus	Bromopsis	2	0	0	0	Long		8		0	0
formosanus	Bromopsis	1	0	0	0	Long		7		0	0
frigidus	Bromopsis	1	0	0	0	Long		6		0	0
frondosus	Bromopsis	2	0	0	0	Long		4	Diploid	0	0
gracillimus	Nevskiella	2	0	0	0	Short		19	Diploid	1	0
grandis	Bromopsis	2	0	0	0	Long		7	Diploid	0	0
grossus	Bromus	1	1	0	0	Short	4.6	12	Polyploid	0	0
gunckelli	Neobromus	1	0	0	0	Medium			Polyploid	0	0
hallii	Bromopsis	2	0	0	0	Long		7		0	0
himalaicus	Bromopsis	2	0	0	0	Long		12	Diploid	0	0
hordeaceus	Bromus	5	1	1	1	Medium	2.71	10	Polyploid	1	1
induratus	Bromopsis	2	0	0	0	Long		11		0	0
inermis	Bromopsis	5	1	1	1	Long	3.33	10	Polyploid	1	1
insignis	Bromopsis	2	0	0	0	Long		8.5		0	0
intermedius	Bromus	2	1	0	0	Short		0.75	Both	0	0
interruptus	Bromus	1	1	0	0	Short	3.17	8	Polyploid	0	0

Species	Section	Distrib.	Crop Weed	Rud. Weed	Environ. Weed	Life Span	Avg. Seed Weight	Max Awn Length	Ploidy	Human Use	Cultivars
japonicus	Bromus	5	1	1	1	Short	3.86	16	Diploid	1	0
kalmii	Bromopsis	3	0	0	0	Long	2.6	3	Diploid	0	0
koeieanus	Bromopsis	1	0	0	0	Long		4		0	0
kopetdagensis	Bromopsis	1	0	0	0	Long		5		0	0
laevipes	Bromopsis	2	0	0	0	Long	4.49	6	Diploid	0	0
lanatipes	Bromopsis	2	0	0	0	Long		4	Polyploid	0	0
lanatus	Bromopsis	2	0	0	0	Long		4		1	0
lanceolatus	Bromus	4	1	1	1	Short	3.48	12	Both	0	0
latiglumis	Bromopsis	2	0	0	0	Long	3.2	5	Diploid	0	0
lepidus	Bromus	4	0	0	0	Short		7	Polyploid	0	0
leptoclados	Bromopsis	2	0	0	0	Long	14.88	12	Polyploid	1	0
lithobius	Ceratochloa	3	0	1	1	Long		6	Polyploid	0	0
luzonensis	Ceratochloa	2	0	0	0	Long		15	Polyploid	0	0
macrocladus	Bromus	1	0	0	0	Short		13		0	0
madritensis	Genea	5	1	1	1	Short	2.42	23	Polyploid	0	0
magnus	Bromopsis	2	0	0	0	Long		8		0	0
mairei	Bromopsis	2	0	0	0	Long		20		0	0
mango	Ceratochloa	3	0	0	0	Long	8.86	1	Polyploid	1	0
marginatus	Ceratochloa	4	0	0	0	Long		7	Polyploid	1	1
maritimus	Ceratochloa	2	0	0	0	Long	7.69	7	Polyploid	0	0
maroccanus	Bromopsis	1	0	0	0	Long		3		0	0
meyeri	Bromopsis	2	0	0	0	Long		1		0	0
modestus	Bromopsis	2	0	0	0	Long		4		0	0
moellendorffianus	Bromopsis	1	0	0	0	Long		9	Diploid	0	0
moesiacus	Bromopsis	1	0	0	0	Long	1.76	7	Diploid	0	0
morrisonensis	Bromopsis	2	0	0	0	Long		5		0	0
mucroglumis	Bromopsis	2	0	0	0	Long		5	Polyploid	0	0
natalensis	Bromopsis	2	0	0	0	Long		15		0	0
nepalensis	Bromopsis	1	0	0	0	Long		12		0	0
nervosus	Bromus	1	0	0	0	Short		6.5		0	0
nottowayanus	Bromopsis	2	0	0	0	Long		8	Diploid	0	0
orcuttianus	Bromopsis	2	0	0	0	Long	6.55	8	Diploid	0	0
oxyodon	Bromus	3	1	1	0	Short	5.08	30	Polyploid	1	0

Species	Section	Distrib.	Crop Weed	Rud. Weed	Environ. Weed	Life Span	Avg. Seed Weight	Max Awn Length	Ploidy	Human Use	Cultivars
pacificus	Bromopsis	2	0	0	0	Long		11	Polyploid	0	0
pannonicus	Bromopsis	2	0	0	0	Long	4.22	8		0	0
parodii	Ceratochloa	2	0	0	0	Long		3	Polyploid	1	0
paulsenii	Bromopsis	2	0	0	0	Long		5		1	0
pectinatus	Bromus	3	1	1	1	Short		17	Polyploid	1	0
pellitus	Bromopsis	2	0	0	0	Long		4		0	0
pindicus	Bromopsis	1	0	0	0	Long		10		0	0
pitensis	Ceratochloa	2	0	0	0	Long		5	Polyploid	0	0
plurinodis	Bromopsis	2	0	0	0	Long		15		0	0
polyanthus	Ceratochloa	2	0	0	0	Long	8.85	6	Polyploid	1	0
porphyranthos	Bromopsis	2	0	0	0	Long		18		0	0
porteri	Bromopsis	2	0	0	0	Long		3.5	Diploid	0	0
psammophilus	Bromus	1	0	0	0	Short		0		0	0
pseudobrachystachys	Bromus	2	0	0	0	Short		5		0	0
pseudodanthoniae	Bromus	3	1	1	0	Short	3.27	15	Both	0	0
pseudolaevipes	Bromopsis	2	0	0	0	Long		5	Diploid	0	0
pseudoramosus	Bromopsis	2	0	0	0	Long		14		0	0
pseudosecalinus	Bromus	1	1	0	0	Short	2.96	6	Diploid	0	0
pubescens	Bromopsis	3	0	0	0	Long	4.62	8	Diploid	0	0
pumpellianus	Bromopsis	2	0	1	0	Long	6.2	3	Polyploid	1	1
racemosus	Bromus	5	1	1	1	Short	3.28	10	Polyploid	1	0
ramosus	Bromopsis	3	0	0	0	Long		11	Both	0	0
remotiflorus	Bromopsis	2	0	0	0	Long		12	Diploid	0	0
richardsonii	Bromopsis	2	0	0	0	Long		5	Polyploid	0	0
rigidus	Genea	5	1	1	1	Medium	10.15	40	Polyploid	0	0
riparius	Bromopsis	3	0	0	0	Long	5.52	8	Polyploid	1	1
rubens	Genea	5	1	1	1	Short	2.56	23	Both	1	1
scoparius	Bromus	5	1	1	0	Short	1.51	10	Both	0	0
secalinus	Bromus	5	1	1	1	Short	7.4	8	Both	0	0
segetum	Bromopsis	2	0	0	0	Long		9		0	0
sericeus	Genea	2	0	0	0	Short	3.69	45	Both	0	0
setifolius	Bromopsis	2	0	0	0	Long	9.16	4		1	0
sewerzowii	Bromus	3	1	1	0	Short	4.06	4	Polyploid	0	0

Species	Section	Distrib.	Crop Weed	Rud. Weed	Environ. Weed	Life Span	Avg. Seed Weight	Max Awn Length	Ploidy	Human Use	Cultivars
sinensis	Bromopsis	2	0	0	0	Long		14		1	0
sipyleus	Bromopsis	2	0	0	0	Long		9		0	0
sitchensis	Ceratochloa	4	0	1	0	Long	9.89	12	Polyploid	1	1
speciosus	Bromopsis	1	0	0	0	Long		6		0	0
squarrosus	Bromus	5	1	1	0	Short	2.54	11	Diploid	1	0
staintonii	Bromopsis	2	0	0	0	Long		5		0	0
stenostachyus	Bromopsis	2	0	0	0	Long		3.5	Diploid	0	0
sterilis	Genea	5	1	1	1	Medium	6.5	40	Both	0	0
striatus	Ceratochloa	2	0	0	0	Short		18	Polyploid	0	0
suksdorfii	Bromopsis	2	0	0	0	Long		4	Diploid	0	0
sundaicus	Bromopsis	1	0	0	0	Long		10		0	0
syriacus	Bromopsis	2	0	0	0	Long	6.1	5		0	0
tectorum	Genea	5	1	1	1	Short	2.94	25	Diploid	1	0
texensis	Bromopsis	1	0	0	0	Short		10	Polyploid	0	0
thysanoglottis	Bromopsis	1	0	0	0	Medium		4.5		0	0
timorensis	Bromopsis	1	0	0	0	Medium		10.5		0	0
tomentellus	Bromopsis	3	0	0	0	Long	7.06	15	Both	1	0
tomentosus	Bromopsis	2	0	0	0	Long	3.86	3		0	0
tunicatus	Ceratochloa	2	0	0	0	Long		2	Polyploid	0	0
turcomanicus	Bromus	1	0	0	0	Short		4		0	0
tytthanthus	Bromus	2	0	1	0	Short		8		0	0
tyttholepis	Bromopsis	2	0	0	0	Long		3		0	0
variegatus	Bromopsis	2	0	0	0	Long	5.93	9	Diploid	1	0
villosissimus	Bromopsis	2	0	0	0	Long		3		0	0
vulgaris	Bromopsis	2	0	0	0	Long	6.72	8	Diploid	1	0

Table A2: Pearson's Correlation Coefficients and prob > |r| under H0: Rho=0 for 152 Bromus species in sections *Bromus*, *Genea*, *Ceratochloa*, *Bromopsis*, *Nevskiella*, and *Neobromus*.

	Wide Distribution outside of native range	**Crop weed**	**Ruderal weed**	**Environmental weed**
Wide distribution outside of native range	1.00000	0.647 <.0001	0.677 <.0001	0.623 <.0001
Crop weed	0.647 <.0001	1.00000	0.751 <.0001	0.668 <.0001
Ruderal weed	0.677 <.0001	0.751 <.0001	1.00000	0.654 <.0001
Environmental weed	0.623 <.0001	0.668 <.0001	0.654 <.0001	1.00000

Table: A3.1a: Results of single factor logistic regressions using species in sections *Bromus*, *Genea*, *Ceratochloa*, and *Bromopsis*. Sections *Nevskiella* and *Neobromus* contain only three species and were not used because species in these sections all associated with a number of factors producing quasi-separation of data points.

Factor	**Number of Species Used**	**Comparisons of Categorical Factors**	**High Distribution**			**Crop Weed**			**Ruderal Weed**			**Environmental Weed**		
			Wald Chi Sq.	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**
Section	148		22.2011	<.0001		37.4323	<.0001		35.2080	<.0001		21.3987	<.0001	
		Bromus vs. Bromopsis			21.500 (4.439-104.145)			43.590 (11.339 - 167.568)			28.496 (8.433 - 96.289)			10.625 (2.665-42.358)
		Ceratochloa vs. Bromopsis			15.357 (2.711-87.004)			5.312 (0.983 - 28.707)			5.599 (1.261 - 24.864)			7.556 (1.534-37.214)
		Genea vs. Bromopsis			129.000 (15.368->999.999)			85.000 (11.837 - 610.397)			62.990 (9.529 - 416.384)			85.000 (11.837-610.397)
		Bromus vs. Ceratochloa			1.400 (0.400-4.894)			8.205 (1.989-33.847)			5.089 (1.385-18.696)			1.406 (0.367-5.386)
		Bromus vs. Genea			0.167 (0.029-0.965)			0.513 (0.089-2.939)			0.452 (0.079-2.585)			0.125 (0.021-0.737)
		Ceratochloa vs. Genea			0.11 (0.018-0.795)			0.063 (0.008-0.471)			0.089 (0.013-0.621)			0.089 (0.013-0.621)
Life Span	148		23.0111	<.0001		35.3027	<.0001		34.9289	<.0001		20.6887	<.0001	
		Medium vs. Long			31.66 (5.841-171.685			53.889 (8.598 - 337.772			46.999 (7.764 - 284.489)			31.661 (5.840-171.656)
		Short vs. Long			10.231 (3.374-31.026			48.500 (13.066-180.033)			17.316 (6.166 - 48.627)			8.143 (2.643-25.086)
Avg. Seed Weight	64		0.0014	0.9698	0.996 (0.820-1.211)	2.3444	0.1257	0.850 (0.691-1.046)	0.6474	0.4210	.923 (0.760-1.220)	0.1063	0.7444	0.966 (0.784 - 1.190

Factor	Number of Species Used	Comparisons of Categorical Factors	High Distribution			Crop Weed			Ruderal Weed			Environmental Weed		
			Wald Chi Sq.	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**
Max. Awn Length	147		11.7471	0.0006	1.123 (1.051-1.200)	12.0101	0.0005	1.126 (1.053-1.205	13.5333	0.0002	1.146 (1.066 - 1.232)	10.7564	0.0010	1.110 (1.043-1.181)
Ploidy	92		8.3911	0.0151		8.7683	0.0125		7.5467	0.023		3.0221	0.2207	
		Both vs. Diploid			8.666 (1.948 - 38.562)			8.214 (1.955-34.510)			7.200 (1.753-29.567)			3.611 (0.792-16.472)
		Both vs. Polyploid			4 (1.153-13.876)			5.5 (1.483 -20.391)			3.600 (1.034 - 12.529)			1.496 (0.422-5.300)
		Polyploid vs. Diploid			2.167 (0.628 - 7.479)			1.494 (0.526 - 4.239)			2.000 (0.681-5.873)			2.414 (0.706-8.261)
Human Use	148		15.4326	0.0001	6.491 (2.553-16.503)	10.4336	0.0012	3.992(1.723 -9.245)	12.3320	0.0004	4.471 (1.938-10.312)	14.4497	0.0001	6.469 (2.470-16.938)
Availability of Cultivars	150		21.1326	<.0001	16.999 (5.079-56.887)	11.7496	0.0006	7.171 (2.325-22.121)	11.201	0.0008	6.811 (2.214-20.948)	19.0239	<.0001	13.846 (4.251-45.101)

Table A3.1b: Results of a multiple factor logistic regression with stepwise reduction using species in sections *Bromus*, *Genea*, *Ceratochloa*, and *Bromopsis.* Factors included in the stepwise reduction were average seed weight, maximum awn length, ploidy, human use (for forage/hay/revegetation), and availability of cultivars. Only max awn length and availability of cultivars produced significant results. Availability of cultivars was eliminated in the stepwise reduction for crop weeds.

Factor	**Number of Species Used**	**High Distribution**			**Crop Weed**			**Ruderal Weed**			**Environmental Weed**		
		Wald Chi Sq.	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est**
Max. Awn Length	58	6.668	0.0098	1.110 (1.025-1.201)	3.8573	0.0495	1.078 (1.00-1.161)	5.4306	0.0198	1.105 (1.016-1.202	5.5568	0.0184	1.080 (1.013-1.152)
Availability of Cultivars	58	8.7244	0.0031	8.903 (2.087 -37.985				4.1051	0.0428	4.156 (1.048 16.491)	7.8158	0.0052	7.404 (1.819-30.128)

Table: A3.2: Results of single factor logistic regression analysis using species in sections *Bromus* and *Genea* . Species in these sections have similar annual life spans with many winter annuals. Species in sections *Bromus* and *Genea* probably evolved in association with human activity. “S-QSDP” indicates “Semi-quasi Separation of Data Points”.

Factor	**Number of Species Used**	**Comparison of Categorical Factors**	**High Distribution**			**Crop Weed**			**Ruderal Weed**			**Environmental Weed**		
			Wald Chi Sq.	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**
Avg. Seed Weight	30		1.0950	0.2954	0.797 (0.521 - 1.219)	1.2212	0.2691	1.605 (0.694 - 3.714)	0.9410	0.3320	1.334 (0.745 - 2.390)	1.8847	0.1698	1.364 (0.876 – 2.126)
Max. Awn Length	41		3.3067	0.0690	1.061 (0.995-1.132)	1.4918	0.2219	1.042 (0.975-1.113)	2.9319	0.0868	1.076 (0.989-1.171)	3.7246	0.0536	1.065 (0.999-1.136)
Ploidy			2.1818	0.3359		1.3130	0.5187		1.0021	0.6059		0.3328	0.8467	
		Both vs. Diploid			3.500 (0.549 - 22.340)			3.856 (0.326 - 45.550)			2.66 (0.361 - 19.712)			1.0 (0.167 – 5.985)
		Both vs. Polyploid			3.111 (0.559 - 17.330)			3.599 (0.337 - 38.460)			2.222 (0.334 - 14.803)			0.667 (0.129-3.446)
		Polyploid vs. Diploid			1.125 (0.216-5.855)	1.125 (0.216-5.855)		1.071 (0.180 - 6.363)			1.200 (0.225-6.388)			1.500 (0.290 – 7.753)
Human Use	41		5.2854	0.0215	7.700 (1.351-43.878)	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	6.8299	0.0090	10.500 (1.800-61.241)
Availability of Cultivars	41		S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP

Table: A3.3: Results of single factor logistic regressions using species in section *Ceratochloa*. Species in this section have varying life spans ranging from annual to perennial. Ploidy was not evaluated for this section as all *Ceratochloa* species are polyploid. “S-QSDP” indicates “Semi-quasi Separation of Data Points”.

Factor	**Number of Species Used**	**Comparison of Categorical Factors**	**High Distribution**			**Crop Weed**			**Ruderal Weed**			**Environmental Weed**		
			Wald Chi Sq.	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**
Avg. Seed Weight	8		0.5637	0.4528	0.611 (0.169-2.213)	1.3260	0.2495	2.525 (0.522-12.221)	1.8853	0.1697	6.079 (0.462-79.919)	0.1686	0.6814	1.318 (0.353-4.925)
Max. Awn Length	19		1.7429	0.1868	1.169 (0.927-1.474)	2.5512	0.1102	1.299 (0.942-1.791)	0.8663	0.3520	1.119 (0.883-1.419)	0.8663	0.3520	1.119 (0.8831 - 1.419)
Human Use	19		S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	0.9481	0.3302	3.428 0.287 - 40.943)	0.9481	0.3302	3.428 (0.287-40.943
Availability of Cultivars	19		S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	2.6597	0.1029	8.250 (0.653 - 104.195)	2.6597	0.1029	8.250 (0.653 - 104.195)

Table: A3.4: Results of single factor logistic regressions using species in section *Bromopsis.* Species in section *Bromopsis* are perennial with the exception of *Bromus texensis*. "S-QSDP" indicates "Semi-quasi Separation of Data Points".

Factor	**Number of Species Used**	**Comparisons of Categorical Factors**	**High Distribution**			**Crop Weed**			**Ruderal Weed**			**Environmental Weed**		
			Wald Chi Sq.	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**	**Wald Chi Sq.**	**Pr > Chi Sq.**	**Odds Ratio Point Est.**
Avg. Seed Weight	26		0.8402	0.3594	1.551 (0.607 - 3.964)	0.5876	0.4434	0.760 (0. 0.377-1.533)	0.2417	0.6230	0.857 (0. 465-1.583)	0.5876	0.4434	0.760 (0.377-1.533)
Max. Awn Length	87		0.2999	0.5840	1.095 (0.792-1.513)	0.0066	0.9350	0.987 (0.728-1.339)	0.1532	0.6955	1.050 (0.822-1.341)	0.0066	0.9350	0.987 (0.728-1.339)
Ploidy	39		S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP
Human Use	88		S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP
Availability of Cultivars	88		S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	S-QSDP	12.5477	0.0004	122.998 (8.581->999.999)	S-QSDP	S-QSDP	S-QSDP