Guidelines for Native Seed Production and Grassland Restoration

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Edited by

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CHAPTER ONE:

NATIVE SEED PRODUCTION AND GRASSLAND RESTORATION

INTRODUCTION

KATHRIN KIEHL, ANITA KIRMER,
NANCY SHAW AND SABINE TISCHEW

During recent decades, the degradation and destruction of both natural and traditionally used semi-natural ecosystems has increased drastically world-wide due to industrialization, large-scale land-use changes, the spread of invasive species and climate change (MEA 2005, Nelleman & Corcoran 2010). As a result there is an increasing need for the restoration of ecosystems, including their biodiversity and ecosystem functions (SER 2004, van Andel & Aronson 2012). This need has been recognized and included in national and international political strategies, e.g. by the CBD Conference of the Parties (Louw et al. 2012, Aronson & Alexander 2013), the United Nations (Nelleman & Corcoran 2010), the European Commission (2011 & 2013) and the United States (USDI & USDA 2002).

Parallel to the increase in practical restoration projects led by local and regional authorities, NGOs and private initiatives, restoration ecology has established itself as a scientific discipline "bridging the gap between theory and practice" (Temperton et al. 2004, Roberts et al. 2009, van Andel & Aronson 2012). To successfully restore target ecosystems, both scientific investigations and practical experience from restoration at the landscape scale are necessary to develop, test and evaluate methods for the improvement of abiotic and biotic conditions (Bradshaw 1987, SER 2004). The necessity for and levels of intervention in ecological restoration depend on disturbance severity, productivity of restoration sites, regional biodiversity and the predictability of successional trajectories (Prach & Hobbs 2008, Walker et al. 2014).

Worldwide, many studies have shown that the successful restoration of grasslands and related ecosystems of open landscapes can be limited by unsuitable abiotic conditions (e.g. high nutrient loads) favouring common weed species or invasive exotic species, seed limitation of native target species and/or by unsuitable management (Bakker & Berendse 1999, Walker et al. 2004, Bakker et al. 2012, Galatowitsch 2012). Recent reviews indicate, however, that the lack of target species in the seed bank of restoration sites and dispersal limitation in fragmented landscapes can be overcome successfully by measures of species introduction, e.g. seeding, application of seed-containing plant or soil material or planting (Monsen et al. 2004, Hedberg & Kotowski 2010, Kiehl et al. 2010, Hölzel et al. 2012).

The transfer of seed-containing chaff from hay barns in order to restore grasslands for agricultural use was described by Columella in Roman times (Lange 1976) and was a common local practice of European farmers until the 20th century (Duffey et al. 1971). Since the 1950s land use intensification led to a strong increase in the use of cultivars of productive grass species in agriculturally improved grasslands. This resulted in decreasing plant and animal species richness in grassland biocoenoses (Lesica & DeLuca 1996, Henderson and Naeth 2005, Tischew et al. 2010, Wesche et al. 2012). The first grassland restoration projects with the aim of restoring diverse grassland ecosystems on degraded sites by using native plants were initiated in the 1930s in the US (Curtis Prairie, Jordan III et al. 1987) and in the 1970s in the United Kingdom. T.C. Wells restored species-rich grasslands in the UK by seeding site-specific seed mixtures or by introduction of seed-containing plant material (Wells et al. 1986).

The importance of seed and plant material provenance has been understood in forestry for more than 100 years (e.g. Engler 1908, Zon 1913, Baldwin 1933). However, it was largely neglected in grassland restoration until the 1990s. Since then, knowledge from studies on ecotypic differentiation and regional adaptation of plants has been used in the context of ecological restoration to a greater extent (e.g. van Andel 1998, Hufford & Mazer 2003, Johnson et al. 2004). Although the use of seeds and plant material of local or regional provenance is recommended (e.g. Johnson et al. 2010, Vander Mijnsbrugge et al. 2010), debates continue as to “how local is local” (McKay et al. 2005), and to what extent genetic and phenotypic differences among plants of different origins are relevant in ecological restoration (e.g. Bischoff et al. 2006 & 2010, Leger 2008, Leimu & Fischer 2008).

Available commercial seed mixtures of non-native species and genetically uniform cultivars and varieties threaten local species diversity (e.g. Lesica & DeLuca 1996, Tischew et al. 2010). Consequently, efforts to develop native seed sources are receiving considerable attention

(Tischew et al. 2011). Moreover, practice-oriented seed transfer guidelines for the use of native seeds in ecological restoration are still missing in most countries. Therefore, the aim of this book is to summarize current scientific knowledge and to derive recommendations for the restoration of grassland and sagebrush steppe ecosystems in different parts of Europe and North America.

For the long-term establishment of native target species, not only is the creation of suitable microsites for seedling recruitment during the initial restoration phase important, but also appropriate management to suppress undesirable weeds or exotic species and to maintain high species diversity (Monsen et al. 2004, Kirmer & Tischew 2006, Scotton et al. 2012). Although restoration approaches to overcome limiting factors can be generalized to a certain extent, the examples in this book show that restoration goals differ among studies and restoration measures must always be adapted to the local situation and to problems that may occur during the restoration process.

From 9 to 14 September 2012 the ***8th European Conference on Ecological Restoration*** was held in České Budějovice, Czech Republic. During this conference with the main theme *Near-natural restoration* we organized a ***Special Session*** on ***Native Seed Production and Use in Restoration Projects*** with contributions from different parts of Europe and the United States. Part I of this session focused on guidelines for native seed harvest and production with special emphasis on genetic and ecological aspects of seed provenance selection and on implications for the development of seed zones and standards for seed production. Part II of the session addressed guidelines for grassland restoration using native seed mixtures by comparing results of scientific experiments and practical experiences as well as large-scale restorations at the landscape level.

In this book ***Chapter 2*** compiles actual knowledge on ***Ecological and Genetic Aspects of Seed Propagation and Species Introduction***. In *Chapter 2.1* Leger & Baughman ask *"What can natural selection tell us about restoration?"* Using the Great Basin (USA) as an example, they show how native species can evolve in response to invasive species and heavily altered disturbance regimes. Based on results from genetic and phenotypic trait analyses they conclude that native plants surviving in disturbed and invaded systems may provide valuable information on adaptive traits in altered systems, and may also serve as valuable seed sources of local or regional origin for restoration of similar environments.

The literature review of Bischoff in *Chapter 2.2* shows that *"Local populations do not always perform better"* than non-local ones as environmental distances between habitats of different ecotypes of a species may be more important than geographical distances. Nevertheless he recommends the use of local seed and plant material in ecological restoration because increasing genetic diversity by mixing local and non-local populations may increase the risks of intraspecific hybridisation and cryptic invasions. Implications of genetic analyses for the development of seed zones for the propagation of native seeds are presented by Jørgensen et al. in *Chapter 2.3 Use of molecular markers for defining site specific seed material for restoration in Norway*. These authors suggest a protocol for analyses of genetic diversity in order to provide a scientific base for choosing local material to be used in development of site-specific seed mixtures for restoration projects.

Chapter 3 deals with ***Native seed production in practice***. In *Chapter 3.1 Native seed production in Norway* Aamlid et al. summarize results from the research projects MOUNTAIN SEED and ECONADA, which aimed to provide seed for near-natural restoration in alpine areas of Norway by developing techniques for the production of native seeds. Furthermore, they evaluate the use of native seed in comparison to commercial non-regional seed mixtures and natural re-vegetation in restoration projects. In contrast to Norway, seed zones in Germany have been derived from analyses of regional climatic and geological conditions. In *Chapter 3.2* Rieger et al. describe techniques for the *Agricultural propagation of native seeds and development of a certification procedure in Germany*. They point out that certification and independent control is necessary to ensure the regional provenance and to maintain high predefined quality standards.

Chapter 4 presents a broad range of results from recent studies on ***Restoration of plant communities using native seed material***. In *Chapter 4.1* Kirmer and Tischew give an overview of the *Conversion of arable land to lowland hay meadows* and analyse the factors that influence restoration success. Based on scientific results and practical experiences they give detailed guidelines on how to overcome the various obstacles that limit restoration success. In *Chapter 4.2 The challenge of using native plant materials for sagebrush steppe restoration in the Great Basin, USA,* Shaw and Jensen present results from restoration projects that aim to restore native communities on semi-arid lands. They conclude that restoration strategies have to take into account recent research on seed zones and native seed production, interactions of native and invasive species, and technologies for reestablishing native communities in order to enhance restoration success. Jaunatre et al. *(Chapter 4.3)* review the state of the art in *Restoring species-rich Mediterranean dry grassland in France using different species-transfer methods.* They summarize results from different restoration projects that have been conducted in The Crau, Southern France, after different types of disturbance in order to restore species-rich dry grassland communities. They recommend combining different restoration approaches including the restoration of appropriate abiotic conditions, species introduction by soil or hay transfer and transplantation of perennial dominant species that provide structure in the reference herbaceous plant community. Török et al. *(Chapter 4.4)* studied the *Recovery of alkaline grasslands using native seed mixtures in the Hortobágy National Park (Hungary).* Their results indicate that it is possible to restore grasslands by seeding low-diversity mixtures of native species but that the suppression of arable weed species, which are still present in the seed bank, is necessary. Because of this issue, they stress that a long-term post-restoration management program is essential for sustaining restored grassland biodiversity. In *Chapter 4.5* Jongepierová and Prach summarize results from several long-term studies on *Grassland restoration in the Czech Republic.* Their study region, the Bílé Karpaty Protected Landscape Area and Biosphere Reserve, is the only region in the Czech Republic where species-rich mixtures of regionally propagated native grasses and herbs or direct harvest (by combine harvester or brush harvester) have been sown on a large scale. They found that spontaneous succession and sowing of commercial seed mixtures lead to the establishment of mesic grassland vegetation whereas dry grassland vegetation with higher proportions of rare species developed after sowing regional seed mixtures. Similar restoration approaches were used in Great Britain, where Twiston-Davies et al. *(Chapter 4.6)* studied the *Restoration of species rich grasslands in the Stonehenge World Heritage Site, UK.* In this region more than 500 ha of grasslands have been restored in order to re-connect formerly isolated fragments of ancient chalk grassland. In this study the evaluation of restoration success included not only vegetation analyses but also analyses of butterfly and bumblebee diversity. Kiehl et al. *(Chapter 4.7)* present results from a recent project on *Restoration of species-rich field margins and fringe communities by seeding native seed mixtures,* which was carried out in two German study regions with different climatic and geological conditions. They define criteria for the development of regionally adapted site-specific seed mixtures and study the effects of different soil preparation and management measures on the establishment of target communities. In *Chapter 4.8 The parable of the sower: Using native plant material in urban areas* Scott describes the development of native plant use for creative conservation projects in the United Kingdom. He links restoration practices not only to ecological issues but also to social messaging, arts projects and human welfare.

Chapter 5 Planning and implementation of restoration projects using native seed and plant material gives a synthesis of the main findings of all contributions in Chapters 2, 3 and 4. We summarize major aspects of restoration project planning and implementation with a focus on the use of native seed and plant material and present a decision tree for the successful implementation of restoration projects.

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Chapter Two:

Ecological and Genetic Aspects of Seed Propagation and Species Introduction

CHAPTER 2.1

WHAT CAN NATURAL SELECTION TELL US ABOUT RESTORATION? FINDING THE BEST SEED SOURCES FOR USE IN DISTURBED SYSTEMS

ELIZABETH A. LEGER
AND OWEN W. BAUGHMAN

Abstract

Plant populations can be adapted to local environments, and it is presumed that a combination of climatic, soil, and biological factors contribute to patterns of local adaptation observed in the wild. The invasion of new species or changes in local disturbance regimes has the potential to drastically change the selective environment for plants in altered systems. In these situations, traits that confer local adaptation may radically change over small scales, based on the presence or absence of a new selective agent. A challenge for restoration will be to continue to match traits of transplanted material with local adaptive optima, recognizing that the degree of contemporary disturbance may affect plant fitness as much as historical evolutionary relationships with local environmental conditions. Evolutionary changes within populations of native plants may help them persist in altered environments, and taking advantage of these evolutionary changes may allow for more effective restoration. Here, we discuss how native species can evolve in response to invasive species and altered disturbance regimes. Secondly, we present a survey of traits that have been considered desirable in the selection of restoration material currently used in the Great Basin, USA, and examine whether traits are selected to increase agronomic suitability or performance in restorations. Next, we discuss how natural selection may be useful for identifying strategies that can increase plant establishment under disturbed or modified field

conditions. Finally, we present an example of an experimental framework that can be used to determine the degree of adaptation of restoration seeds to particular sites during restoration activities, with the goal of identifying traits that increase plant establishment. Viewing restorations as evolutionary experiments could increase our ability to match adaptive traits with particular environments, leading to increased plant establishment during restoration, as well as increased our understanding of the role of natural selection in shaping population differentiation.

Introduction

"If you can look into the seeds of time,
And say which grain will grow and which will not,
Speak then to me" Shakespeare (Macbeth 3.1.3)

The fate of most seeds is to die, a state of affairs true for seeds produced by plants in the wild as well as for seeds planted as part of many wildland restorations (Clark et al. 2007, Hardegree et al. 2011). Seeds can fail to turn into adult plants because they never germinate, germinate but fail to emerge from the soil surface, or die along the many steps it takes to go from an emergent seedling to reproductive adult (e.g. Chambers & MacMahon 1994). Causes of death range from herbivory, disease, abiotic stress caused by climate or soil conditions or from biotic stress imposed by competitive interactions with other plants.

When death occurs without respect to inherited traits of the plant (that is, when a seed fails to become an adult plant simply by being in the wrong place at the wrong time), it affects population genetic structure through genetic drift (Futuyma 2005). This occurs when seed and seedling death is random with respect to plant traits. Gene frequencies can change in response to loss of individuals, but the resultant genetic change in the population is also random. If, on the other hand, death is non-random, and survival is affected by the expression of particular traits under genetic control (traits such as germination timing, drought tolerance, phenotypic plasticity, root allocation, etc.), population genetic structure is affected by selection, and change in gene frequencies is directly related to performance (Futyma 2005). Selection pressures can be natural, in the case of plants growing in the wild, or artificial, in the case of human selection of traits for restoration. Natural and artificial selection can result in adaptation to particular environmental conditions. Many studies have demonstrated that plant populations can be adapted to local environments (Leimu & Fischer 2008), and it is presumed that a combination of climatic, soil, and biological factors contribute to patterns of local adaptation observed in the wild (Figure 2.1-1a).

The invasion of new species or change in local disturbance regimes has the potential to drastically change the selective environment for plants in altered systems (Figure 2.1-1b). In these situations, traits that confer a fitness advantage may change based on the presence or absence of a new selective agent, such as invasive species, disease, altered grazing regimes, or climate changes (Wilkinson 2001, Rice & Emery 2003). A challenge for restoration will be to continue to match traits of planted material with local adaptive optima, recognizing that the degree of contemporary disturbance may affect plant fitness as much as historical evolutionary relationships with local environmental conditions.

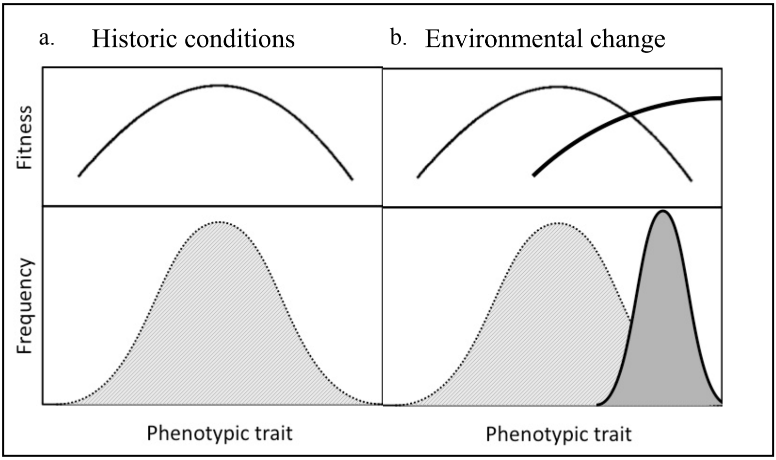

Figure 2.1-1. Local adaptation within a species occurs when phenotypes (observable characteristics) with the highest fitness in a particular location become the most abundant in a population. In this simple single trait example, in a), the trait value that corresponds to the highest fitness (top panel) is the most commonly observed phenotype in the population (bottom panel); individuals that possess the optimal value of this trait are best able to survive and reproduce in a particular environment, and that phenotype becomes the most frequently observed trait value in the population. In b), as the environment changes, the optimal phenotype changes (bold line, top panel). Shifts in the frequency of traits in a population in the direction of the new optimum (bottom panel) represent adaptation to the new environment.

Evolutionary changes within populations of native plants may help them persist in altered environments (Strauss et al. 2006, Carroll 2007), and taking advantage of these evolutionary changes may allow for more effective restoration (Leger 2008). When selective agents are strong, there is variation within a population in response to these agents, and that has a genetic basis, adaptive evolution can occur rapidly (Strauss et al. 2006). There are now many examples of native species evolving in response to the introduction of other species. Many of these examples are interactions across trophic levels, such as insects evolving to colonize new host plants, or evolution in response to diseases or parasites, but there is also a growing body of work showing that under some conditions, native plants can evolve in response to invasive competitors (e.g. Callaway et al. 2005, Lau 2006, Mealor and Hild 2007, Cipollini & Hurley 2008, Leger 2008, Ferrero-Serrano et al. 2011, Goergen et al. 2011, Rowe & Leger 2011).

It is important to note that multiple environmental factors can change at the same time, when, for example, populations experience both climate change and alteration of disturbance regimes. The presence of multiple new selective agents presents additional challenges to wild populations. Theoretical and experimental evidence indicates that population responses to multiple selection agents can be complex, and the ability to adapt depends on the strength of selection and the genetic nature of the traits under selection (Falconer & Mackay 1996). Factors such as the location of important genes on the same or different chromosomes, the number of genes involved in the expression of particular traits, and the effect of genes under selection on multiple traits all affect how populations evolve.

Researchers are making advances towards understanding these dynamics in natural populations (e.g. Etterson 2004, Hellmann & Pineda-Krch 2007), but because responses to selection are highly dependent on the genetics of individual species and populations, this complexity is unlikely to be resolved for most wild organisms. This means restorationists are unlikely to have a clear picture of the genetic basis of important traits in particular species they want to restore, and won't be able to predict how species can respond adaptively to multiple environmental changes.

What is a restorationist to do? First, don't despair, as there are ways to use evolution to our advantage in restoration, even if we don't know the genetic basis of important traits. In the rest of this chapter, we will outline ways that awareness of variation in adaptive traits within a species and evolution via natural selection can improve restoration success, focusing primarily on restoration in the Great Basin, USA. First, we will describe traits that are emphasized in the restoration seeds most commonly used in this region. Secondly, we will look at what wild systems can tell us about traits that increase fitness in changing systems. Finally, we will look at how restorations themselves can be used to determine which traits are most suitable for particular species in particular environments. In all sections, we are primarily considering variation in traits below the species level, addressing how particular populations are chosen to be the source used to restore a particular species.

I. What traits have been favoured in restoration?

In the Great Basin, tens of millions of hectares of essentially continuous vegetation communities exist across a topographically and climatically heterogeneous landscape that is sparsely populated. While much of this area contains intact native communities with little need of restoration, rapidly increasing portions have been highly degraded by a combination of land use and invasive species, as well as associated changes in landscape-scale disturbances such as wildfire (see Shaw and Jensen, this volume). When attempting to reestablish desirable vegetation at these large scales, three of the most important aspects of plant material (by which we mean any seeds collected or produced for restoration) bound for restoration are site appropriateness, agronomic suitability, and performance in the field (Figure 2.1-2).

In our view, site appropriate species include native species planted within their contemporary range, species beneficial to native biodiversity (including other plants and animals), and species that are successionally suitable. In our region, agronomic suitability is important because much of the seed destined for restoration is grown in farmed settings, rather than sown directly from wildland collections, and seed volume and production costs must be appropriate for large-scale restoration efforts. This consideration affects both the species used for restoration (some are difficult to farm efficiently) and the particular populations selected for increase (due to variation in traits like plant height, seed morphology, etc., some populations are more amenable to harvest than others).

Finally, a seed's ability to survive and thrive in the restoration environment is essential for restoration success. In areas that have not undergone substantial environmental change, selecting species that are site appropriate may be sufficient to ensure establishment in restorations, but in areas that have been highly, and potentially irrevocably disturbed, additional steps (outlined in sections II and III below) may be needed to ensure that seeds survive in restorations.

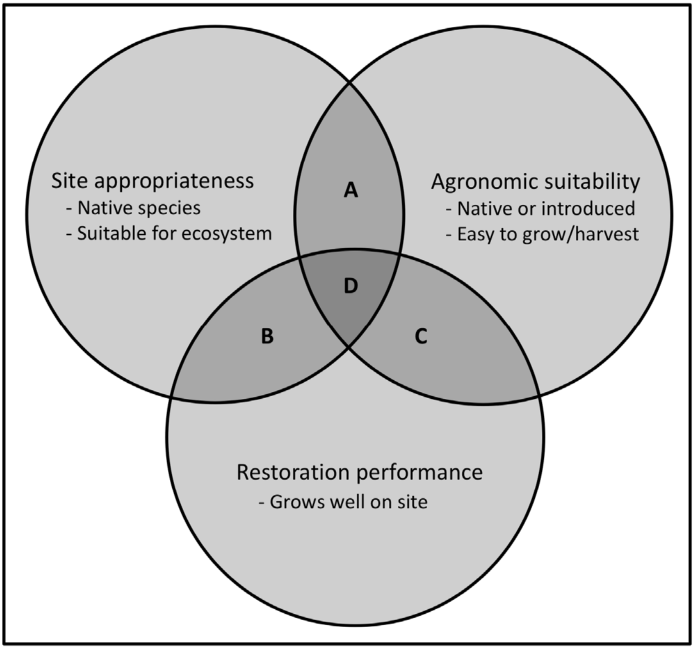

Figure 2.1-2. Plant materials development must balance multiple considerations to achieve the best and most efficiently-produced restoration seed. Here we present three considerations of primary importance: site appropriateness (species are native and suited to local environments), agronomic suitability (potential for high-volume and low-cost production of seeds as a farmed crop), and restoration performance (the ability of seeds to establish in field settings). Only a portion of appropriate species are also suitable for cultivation (A) or likely to establish well with current techniques (B), and even fewer satisfy all three considerations (D). Likewise, not all species that are easy to farm are site appropriate (A) or consistently successful in restorations (C). Restoration strategies focusing on wild collected materials (B) may improve efficiency by producing some material agriculturally, while regions that use non-native species or species with little contribution to ecosystem functioning (C) may achieve more desirable results by incorporating site appropriate species.

Agronomic suitability has long been a priority for seed development in our region, with a heavy focus on grasses (not necessarily native species), and the history of cooperation between federal research agencies (who collect, select, and develop particular varieties) and commercial seed growers (who increase materials as row crops and sell them to management agencies or other practitioners). This has generated a great deal of infrastructure and experience with respect to cultivating and producing restoration material of a desired quality (Booth & Jones 2001). Recently, however, there has been substantial progress toward improving the site appropriateness of materials in the western United States, with a strong focus on native species, including forbs as well as grasses, and increasing research on seed transfer zones (Executive Order 13112, McKay et al. 2005, Shaw et al. 2012). Although there is an active effort to reduce the agronomic focus of Great Basin restoration (Johnson et al. 2010), the current state of restoration practice is largely a result of this structure.

Low establishment of native plants in restoration efforts is still all too common in our region (James & Svejcar 2010, Davies et al. 2011, Kulpa et al. 2012) despite our efforts to select and develop regionally appropriate materials (e.g. Asay et al. 2003, Jones & Larson 2005). What are we doing wrong? Choices about which populations to increase may affect how well species perform in restoration. Are we selecting populations with the suite of traits most associated with successful field establishment, or are traits associated with agronomic performance more commonly valued?

To investigate this question, we surveyed published literature that describes native materials produced by development programs that are suitable for the Great Basin. We confined our search to grass species that are commonly planted in the drier parts of the semi-arid landscapes of the Great Basin. Our survey included 26 plant materials, ranging from cultivars to pre-variety germplasms and wild-collected accessions of eight native perennial grass species (most species had multiple materials). We quantified which traits were described as valuable in these materials. Species included *Achnatherum hymenoides* (Roem. & Schult.) Barkworth, *Elymus elymoides* (Raf.) Swezey, *E. trachycaulus* (Link) Gould ex Shinners, *E. wawawaiensis* J. Carlson & Barkworth, *Leymus cinereus* (Scribn. & Merr.) Á. Löve, *Pascopyrum smithii* (Rydb.) Á. Löve, *Poa secunda* J. Presl, and *Pseudoroegneria spicata* (Pursh) Á. Löve.

For each plant material, we noted all traits that were mentioned as criteria for selecting particular materials, as well as any traits of the final product that were highlighted as contributing to its quality as restoration material. It was often not clear whether a trait was specifically selected or if it was simply being noted by the developer, but we assumed that if a trait was presented in the short description, it was considered important. Traits were grouped together when they shared a larger purpose. For example, reduced awn mass, determinant disarticulation, reduced glaucousness, and increased mature seed retention are traits selected to improve seed harvestability in agronomic settings, and were grouped together for presentation.

Traits related to high seedling vigor were the most frequently highlighted (Figure 2.1-3). Additionally, drought tolerance and high seed yield traits were commonly mentioned. Traits associated with increased establishment and persistence, high biomass production, high/fast germination, increased plant height, and improved seed harvestability were also often discussed. Other traits mentioned as valuable in more than one plant material were related to competitiveness with exotic species, phenology of heading (i.e., the timing of flower and seed production), increased seed mass, high genetic diversity, and large adapted range.

Some of these traits are clearly important for restoration success, such as seedling vigor and high establishment and persistence, though in many cases, it was not clear that these traits had been evaluated in restoration settings, and may only represent performance in agricultural settings. Increased competitive ability with exotic invaders and drought tolerance are traits likely to be linked to restoration success in our arid, highly invaded field settings. Competitive ability was only noted for four plant materials; drought tolerance was more commonly discussed (Figure 2.1-3). Other traits are clearly associated with making native species more croplike and agronomically suitable, such as high seed yield, seed harvestability, and phenological traits. Traits such as greater seed mass, high/fast germination, plant height, and biomass production could be desirable in both agronomic and wildland settings. Agronomically, larger plants would be likely to produce larger yields, and in wildland settings, large size could be valued for forage production or because of an assumption that these traits increase competitive ability. Whatever their intended purpose, the effects that many of these traits have on fitness and survival are often context dependent and complex.

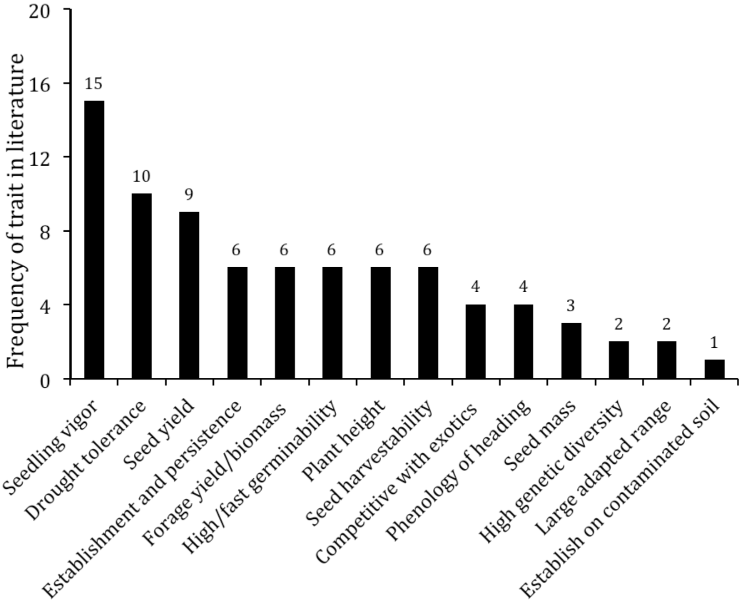

Figure 2.1-3. An analysis of traits currently valued in plant material development. Published release notices and descriptions of 26 plant materials of eight of the most commonly seeded grass species in the Great Basin (*Achnatherum hymenoides, Elymus elymoides, E. trachycaulus, E. wawawaiensis, Leymus cinereus, Pascopyrum smithii, Poa secunda*, and *Pseudoroegneria spicata*) were examined for positive references to traits desirable for restoration (based on references in Appendix A). Vertical bars represent the number of plant materials in which each trait or trait group was mentioned as a selection criteria or positive attribute of the material.

Large plants are often more competitive than smaller plants, but this is not always the case in limited resource environments (e.g. Hendrix et al. 1991, Casper 1996). Early emergence time may provide a competitive advantage to seedlings, but there is much temporal, spatial and phylogenetic variability in this relationship (Verdú & Traveset 2005). Larger seed mass is also typically considered to increase fitness, but, as described in more detail below, smaller seeded, less fecund individuals of *E. elymoides* had increased survival in our region during restoration (Kulpa & Leger 2013), though others have found opposite results in the Great Basin (Benard & Toft 2007) and elsewhere (Metz et al. 2010).