Title

Ecological Genetics of Stipa pulchra in Environmental Restoration

Permalink

https://escholarship.org/uc/item/97d392j2

Author

Rassbach, Kathleen Ida

Publication Date

2019

Ecological Genetics of *Stipa pulchra* in Environmental Restoration

By

Kathleen Ida Rassbach

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Wildland Resource Science

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Lynn Huntsinger, Chair
Professor James Bartolome
Professor Ellen Simms

Summer 2019

Abstract

Ecological Genetics of *Stipa pulchra* in Environmental Restoration

by

Kathleen Ida Rassbach

Doctor of Philosophy in Wildland Resource Science

University of California, Berkeley

Professor Lynn Huntsinger, Chair

Ecological restoration has become a large enterprise driven by regulatory policies and by public and private initiatives. Regulatory agencies and ecologists call for use of propagules that are adapted to project sites, compatible with other species, and genetically diverse. This project uses a native California grass, *Stipa pulchra*, to ask whether the cost-management practice of collecting seeds from dense stands of target species can have unintended selective effects on species used in restoration. Absolute cover, standing biomass, species composition, and *S. pulchra* density and culm count were recorded on plots in three central California sites. *S. pulchra* seeds from these plots were sown in pots allocated to two watering groups and three temporal blocks.

Pot-study plants grown from seed collected from plots with greater *S. pulchra* density and absolute cover had significantly higher basal diameters, tiller counts, and root: shoot ratios. Plants derived from less-competitive plots set seeds earlier and gave rise to more culms. These results indicate that distribution of *S. pulchra* genotypes in the field may reflect a competition: colonization pattern, with more fecund *S. pulchra* plants inhabiting less-competitive patches than those occupied by their more-competitive conspecifics. Other aspects of pot-study plant growth appeared to correlate with background vegetation of the field plots. Although plants grown from seeds collected at the three sites were significantly different, there was no evidence that ecological distance reflected geographic distance. Plants receiving more water had relatively greater aboveground growth and lower root: shoot ratios. Statistical interactions of blocking and watering treatments with site may reflect plant adaptation to climate and soil at the various sites. Implications of these results apply to environmental restoration and extend to ecological research, where nonrandomly collected propagules are often used to represent genetic characteristics of entire populations.

Table of Contents

List of Tables

List of Figures

Acknowledgements

This dissertation was possible only with the help of a sizeable assortment of people and institutions. The members of my dissertation committee, Drs. Lynn Huntsinger, James Bartolome and Ellen Simms, provided their advice, encouragement and suggestions, and plowed through two very different versions of the end result. Dr. Greg Biging provided invaluable help on how to clarify my statistical approach. Dr. Robert Raabe and Dr. James Vlamis provided helpful information and suggestions during the common-garden study. Ed Kleiner of Comstock Seed, Gardnerville, Nevada provided perspectives on commercial seed collection. A number of able assistants, including Josephine Burns, Carla Jo, Jennifer Lo, Keith McLamb, Jean Oh, Gabriela Owens, Julie Shortidge, Ana Tighe, Thuy Binh Truong, Nick Tucker, Heiman (Camas) Tung and Herman Yee, provided help weighing seeds, and taking and inputting data for the field and common-garden studies. Dorothy Duff Brown helped me understand how to organize and present this research in a readable fashion. Dr. Peter Hopkinson offered a welcoming smile and a listening ear over the years when I stopped by the Range Lab. Administrative staff members of the Department of Environmental Science, Policy, and Management helped guide me through the wildlands of University policy.

Access to field sites was provided through the generosity of Kathleen Kraft and the Ocean Song Farm and Wilderness Center, Sonoma County, California, and the University of California Richmond Field Station. The Chevron-Texaco Corporation, who owns the Pt. Molate site (and who didn't know I was there) has perhaps inadvertently allowed plant enthusiasts and a number of UC Berkeley researchers access to a convenient, biologically diverse, and lovely site. The common-garden study was conducted at The Oxford Tract Research Facility, College of Natural Resources, University of California at Berkeley, with liberal help from its staff.

The Environmental Sciences, Policy, and Management Department, University of California at Berkeley, generously supported my graduate studies and work towards this dissertation through a Block Grant Fellowship in 1996–1997; the Frank Myers Scholarship in Forestry, Howard William Siggins Fellowship, and Arthur H. and Karen Nelson Fund for 1998–1999; and Graduate Student Research appointments for 1999–2000 and 2002–2003. Additional support and encouragement came from Theresa Fields and the California Health and Human Services Agency.

Finally, I thank and thank again my husband, Peter Deibler. This project took a very long time, and could not have been started and certainly not completed without his patient support and faith in me. I dedicate this dissertation to him, and to my daughter Maria for her sparkle.

Chapter 1. Introduction

Every year, thousands of seed-company workers, public-agency employees, volunteers, and enthusiasts fan out across American wildlands to collect native seed. Their goal is the restoration of habitat in places ranging from roadsides and urban streambanks to vast areas devastated by fires, mining, flood-control projects, and development. Restoration projects require huge and growing amounts of seeds at substantial cost. The questions of whether seed collection costs and convenience directly and unavoidably impinge on capturing the genetic variability of wild populations, and whether this results in nonadaptive genetic selection, prompted this project. While this study focuses on seeds, many of the issues discussed apply to cuttings and other propagule types as well.

Little information is available on quantities of native seed used nationally, but a few figures may provide a sense of scale. The ecological restoration industry employs an estimated 126,000 workers and generates nearly $10 billion in economic output annually in the United States alone (BenDor et al. 2015). In the western United States, the largest revegetation need is post-fire rehabilitation, where action required on short notice often leaves little opportunity to prepare ahead. In 1999, at least 1.7 million acres of land burned in the Great Basin (BLM 1999). Over five million pounds of seed were dispersed over burnt rangelands in Nevada, nearly a third of which came from native plant species (Christensen 2000). The 2007 Murphy Fire complex in Idaho and Nevada charred 650,000 acres, requiring an estimated 1.4 million pounds to reseed a third of the area. Hundreds of volunteers were sent into the desert to collect part of the seed, despite the drought-induced reduction in seed availability (J. Miller 2007). In Utah, reseeding 25,000 acres of the 47,000-acre Wood Hollow Fire restoration area required 352,000 pounds of seed at a cost of $3.2 million (Prettyman 2012). An examination of over 1200 USDA Forest Service Burned Area Emergency Response reports taken in the western US during four decades (1970s–2000s) found that the area burned annually by wildfire increased several-fold over this time, and that the rate of increase accelerated after 1990 (Robichaud et al. 2014). From 1997 to 2012, the total area of US land that burned annually continued to increase, to over nine million acres (Bracmort 2013). In recent years, the US Bureau of Land Management (BLM) has purchased an annual average of 1.4 million kg of seed annually, mostly for post-fire use, and has often needed much more (Oldfield & Olwell 2015).

Native seed is costly, ranging from $10 to over $4000 per pound (Olwell 2002; Agrecol Native Nursery 2015). Source-identified[1] grass seed costs roughly $15-40 per pound for species such as *Elymus glaucus* and *Danthonia californica*, to as much as $800 per pound for *Calamagrostis canadensis* (Earth-Source, Inc. 2013; Heritage Seedlings, Inc. 2015). During the period 2000 to 2007, Forest Service emergency seeding expenditures increased 192 percent compared to the average during the previous 30 years (Peppin et al. 2010). The BLM native plant program budget has experienced similar increases (Figure 1). An average of 21 percent of burned area was seeded in the 1970s, compared to only four percent between 2000 and 2007.

---

[1] Seed identified as to species and location of the parental population.

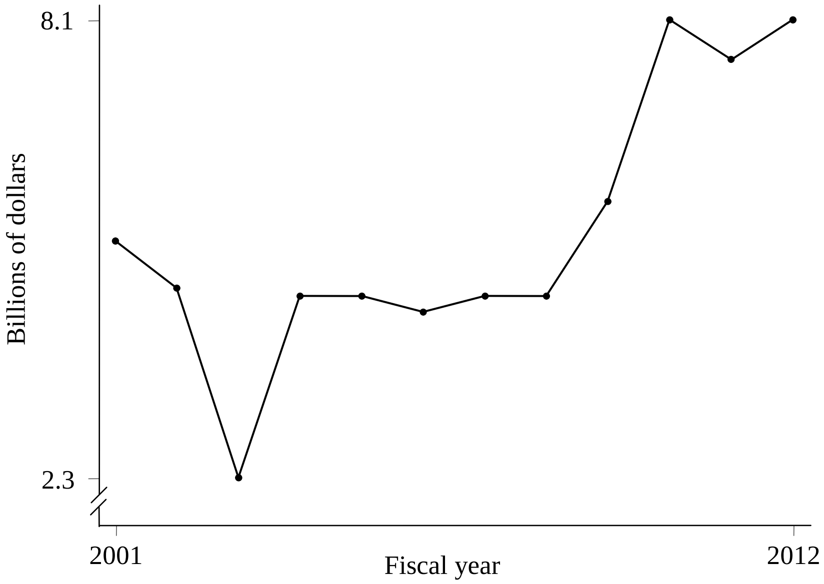

Figure 1.
US Bureau of Land Management Native Plant Program Budget 2001–2012

Data from Olwell 2012

The increased per-acre seeding cost likely reflects increased use of native species and sterile hybrids (Peppin et al. 2010).

The business of providing seeds and plants for restoration has grown rapidly. Dozens of companies, most of them small businesses, market native plants through revegetation trade journals and on the Internet (A. White et al. 2017). Native-seed producers are steadily expanding production (Strategic Marketing Services 2002); one seed-collection and contract-growing company, Bitterroot Restoration, reported 40% per year growth for 10 years (Fitzsimmons 2002). Unscrupulous or poorly informed seed harvesters have been caught harvesting hundreds of pounds of seeds illegally from public lands (Bragg 2000; Stark 2009). Seed companies often buy seeds from many individuals and have to depend on the collectors' integrity and knowledge, thus taking the potentially ruinous risk of selling mislabeled seeds. As a result, some seed companies actively avoid local-ecotype seed (S. Smith et al. 2007).

Against this backdrop, concerns have been raised about native herb and shrub germplasm that is transferred from one location to another (Handel et al. 1994; Helenurm & Parsons 1997;

Hufford & Mazer 2003; Knapp & Rice 1996 and 1997; Montalvo & Ellstrand 2000; S. Williams & Davis 1996). Gustafson et al. (2004a and 2004b), for example, found that restored grass populations established with presumably local seeds shared greater genetic resemblance with one another than with nearby remnant populations, and that populations spread over 200 km that had been restored by the same restoration practitioner were genetically more similar to each other than to nearby populations. Y-Y Li et al. (2005) found that artificial populations of the endangered dawn redwood (*Metasequoia glyptostroboides*) were more similar to one another than to remnant wild populations. The limited genetic variation in these restored populations has resulted in reduced seed mass and germination rates (Y-Y Li et al. 2012).

The debate continues today, indeed, the number of scholarly journal articles about restoration genetics has increased exponentially (Mijangos et al. 2015). Issues discussed in the literature include maladaptation to abiotic factors such as fire (Falk 2006), soil (Bakker & Berendse 1999; Mahieu et al. 2013; Ohsowski et al. 2012), and climate (Johnson et al. 2010); and biotic factors such as arthropod consumers, mutualists, pollinators, and pathogens (Cox et al. 2013; Dixon et al. 2009; Gibbs et al. 2008; Halpern et al. 2007; Kardol & Wardle 2010; Ritchie & Johnson 2009). Insufficient genetic variation may lead to poor long-term adaptation of a restored population (Hufford & Mazer 2003; Kettenring et al. 2014). Where basic adaptation can be assured, there remain concerns about genetic compatibility, including introduction of invasive genotypes and genetic inundation of small local populations by larger introduced ones (Byrne et al. 2011; Millar et al. 2012). The potential for inbreeding depression, which can affect outcrossing species, must be balanced against potential outbreeding depression, an issue for inbred species that may not become apparent until the F2 or subsequent generations (Bowles et al. 2015; Edmands 2007; Frankham et al. 2011; Lloyd et al. 2012). Critics worry that fitness of existing local populations can be reduced by germplasm introductions, through breakup of adaptive gene complexes (Hufford & Mazer 2003; Pélabon et al. 2005); genetic swamping (Byrne et al. 2011; Handel et al. 1994; Hufford & Mazer 2003; K. Rice 1995); differing flowering phenology (Montalvo et al. 1997), and mismatched ploidy in species with multiple ploidy levels (Delaney & Baack 2012; Hufford & Mazer 2003). Ample disagreement exists on these topics (e.g., Cronn et al. 2003; Frankham et al. 2011; Larson et al. 2001).

Population genetic data is lacking for many wild species. Critical factors such as mating system, gene flow, and ploidy may vary among subpopulations of a species in time and space, limiting the applicability of available research (Booy et al. 2000; Coates et al. 2013; Delaney & Baack 2012; Etterson et al. 2016; Gehring & Linhart 1992; Knapp & Rice 1996; Liston 2003; McArthur & Tausch 1995; Severns & Liston 2008). Inbred species in particular show variation among populations in allele diversity and effective neighborhood size (Schoen & Brown 1991). Natural plant populations frequently feature small-scale genetic differentiation in a wide range of characters, often reflecting limited gene dispersal and spatial heterogeneity in environmental characteristics (Lara-Romero et al. 2014; Linhart & Grant 1996; McLeod et al. 2012; Vekemans & Hardy 2004). Genotypes can be extraordinarily localized, even differing over a few meters (Bennington et al. 2012; Bockelmann et al. 2003; Knapp & Rice 1998; Krauss et al. 2013; Y.C. Li et al. 2000; Linhart 1988).

Data available to guide restoration practitioners and policy makers is limited. Conservation genetics studies generally focus on rare or threatened species, which, because of factors related to their rarity, may have population genetic characteristics quite different from the community dominants commonly used in restoration programs (Aguilar et al. 2008; Cole 2003; Honnay & Jacquemyn 2007). Rare plants, moreover, may not contribute substantially to ecosystem productivity, while the diversity of community dominants, including genetic diversity within species, may regulate ecosystem function and composition (Barbour et al. 2009; Grime 1998; Gustafson et al. 2004b; Seliskar et al. 2002; Whitham et al. 2006).

The genetic unknowns interact with the practical elements of restoration, which include who is carrying out the restoration and why, applicable regulations, and funding. Public and private agencies often ask producers to meet specific requirements in collection, agronomic seed production, and handling of propagules based on limited information about genetic characteristics of individual species and populations, all of which can affect the genetic characteristics of restoration plantings (Clewell & Rieger 1997; Dorner undated*;* Knapp & Rice 1994, 1996, and 1997; Lippitt et al. 1994; Montalvo et al. 1997; S. Smith et al. 2007). Seed-source requirements in turn may increase restoration project cost and complexity (Mustoe 2014; Richards et al. 1998; Scianna 2003; Strategic Marketing Services 2002). While many native-plant seed companies and nurseries claim to provide seeds for specific, site-appropriate ecotypes, source population and genetic background of planting stock is often unknown (Cronn et al. 2003; Gehring & Linhart 1992; Gibbs et al. 2012; Gustafson et al. 2004a). At worst, seeds are sometimes of the wrong species or are interspecific hybrids (Dunwiddie & Delvin 2006; Gibbs et al. 2012; Pendleton et al. 2008).

The cost and viability of seed may depend on how it is harvested or otherwise produced for planting. Commercial seed collectors are paid based on the amount of seed collected, and may be motivated to collect when and where it is easiest. Contract growers grow out, or "increase," wild-collected, sometimes site-specific seeds and cuttings. Cultivars of native species have been developed for restoration and revegetation. Growing native plants under agronomic conditions, however, may allow selection, drift, and inadvertent cross-pollination with other genotypes to shift the means and variances of plant genetic characteristics (A. Dyer et al. 2016; Ferdinandez et al. 2005; Montalvo et al. 1997; Schröder et al. 2013; Soleri & Smith 1995).

Intent of This Study

Little data apparently exists on actual among-microhabitat collection practices for native herb and shrub germplasm. The need for cost control may prompt harvesters to seek out and harvest from patches containing relatively high densities of target plants, which greatly simplifies and speeds collection of herb and grass seed. This study asks whether this practice may affect the genetic characteristics of collected seeds. If subpopulation differentiation can occur in the absence of obvious abiotic environmental variation, it may be wholly unapparent to seed collectors. If adaptive genetic differentiation can occur at the subpopulation level, and if some subpopulations are inherently difficult, unpleasant, or time-consuming to harvest, harvesters may encounter substantial difficulties capturing adaptive differentiation within the practical limitations of seed collection.

This research question emerged from a seed collection trip I took with a reputable commercial seed supplier that allowed me to observe some aspects of the economic forces in seed collection. Early in the trip, we examined a site that included the target species *Danthonia californica* mixed with the undesirable species *Bromus tectorum*, each at roughly 40% relative dominance. The culms of both grass species were erect, ripe, and about the same height. As we collected a few ounces of seed, I quickly found that *Danthonia* seeds had to be harvested stem by stem with careful attention to species identification to avoid collecting *Bromus*. The seed contractor rejected the site as too "weedy" for economical harvesting. We later visited one of his work crews camped out nearby. The contractor gave them a sample of the *Danthonia* seeds, and instructed them to look out for dense *Danthonia* patches to harvest. *Danthonia* was a new product for this contractor, and I later learned that he missed an important factor: *Danthonia* carries much of its seed as cleistogenes at the base of its culms, and restoration harvesters generally take whole culms to winnow later (Kathleen Kraft 2002, *pers. comm.*). This illustrates another issue in commercial seed collection: seed suppliers don't always have the luxury of adequate information. Their workers, moreover, are by no means professional botanists. The camping-out crew members were indigents recruited from city streets, and other harvesters we visited included the children of local ranchers.[2] Like the seed contractor, all of these harvesters were paid by the pound. Seed harvesters need to meet purity requirements, which ensures they avoid weed species, but they may have little financial incentive to harvest from a wide range of subpopulations within a collection area, and substantial motivation to collect large quantities of seed as quickly as possible. If subpopulations vary in their genetic characteristics, then the understandable human tendency to collect seed where doing so is easy and efficient may produce unintended selection among genotypes.

This study examines inherited differences between *Stipa pulchra* (purple needlegrass) plants originating in relatively dense patches versus conspecifics growing sparsely intermixed among other species, and focuses on traits that might affect plant performance in restoration projects. The contrast of dense versus sparse patches may bring to light cost-driven, unintended selection by seed harvesters among genetically different subpopulations. This study assumes there may be unintended impacts from translocation of inappropriate genetic material in the effort to produce new populations or augment existing ones. The study species is the most widespread native California grass species today, and is therefore relatively well-studied and often used in revegetation projects (Corbin et al. 2004). The study sites are natural populations in the San Francisco Bay Area that evidently have not been substantially disturbed for at least 20 years.

Chapter 2 explores population genetics theory as it applies to this study. Chapter 3 discusses seed collection and production for restoration in light of concerns about restoration

---

[2] Some restoration projects, including seed collection, are carried out by specially-trained prison inmates (Carl Elliott 2016, *pers. comm*). Mr. Elliott is Conservation Nursery Manager of the Sustainability in Prisons Project (http://sustainabilityinprisons.org).

genetics, and Chapter 4 discusses regulatory approaches to these concerns. Chapter 5 describes the study context and the challenge of restoring California grasslands, and presents the study hypothesis. The study sites and experimental methods, including field observations, seed collection, and a common-garden study, are described in Chapter 6. Chapters 7 and 8 present the detailed results of the field and common garden study. The implications of the study results, both for ecological theory and environmental restoration, are presented in Chapter 9.

Chapter 2. Role of Population Genetics in Ecological Restoration

Ecological restoration is the effort to produce natural ecosystems by artificial means, in order to secure ecosystem services such as erosion control and water filtration, ensure habitat for rare species, and maintain wildland species out of respect and appreciation. Restoration efforts are thus controlled both by human preferences and the exigencies of nature. This chapter reviews scientific efforts to define what is needed and what is best avoided in providing plants that are genetically adapted to restoration sites. Key restoration-genetics goals that may sometimes come into conflict are local adaptation, adequate genetic diversity, and ability of restored populations to adjust to altered conditions such as climate change. The second part discusses how patchiness in populations may be reflected in their genetic composition.

Defining Restoration

Environmental restoration may be defined as manipulation of natural processes of ecological succession to create self-organizing native ecosystems, including viable populations of native species that are well-adapted to current conditions and possess enough genetic variation for continued evolution (Bradshaw 1996; Hobbs & Norton 1996; Knapp & Rice 1994). The BLM *Integrated Vegetation Management Handbook* defines restoration as "implementation of a set of actions that promotes plant community diversity and structure that allows plant communities to be more resilient to disturbance and invasive species over the long term" (BLM 2008, p. 3-12). While this definition does not specify indigenous species, BLM policy and practice, as discussed in Chapter 4, have increasingly emphasized native species. The Society for Ecological Restoration (SER) describes an ecosystem as successfully restored "when it contains sufficient biotic and abiotic resources to continue its development without further assistance or subsidy," can "sustain itself structurally and functionally," and will "demonstrate resilience to normal ranges of environmental stress and disturbance" (SER 2004, p. 3). The SER *Primer* specifies that the restored ecosystem will be comprised mostly or entirely of indigenous species.

Other forms of revegetation do not make a goal of recreating the original ecosystem. BLM, for example, defines post-fire rehabilitation as the "repair" of a wildland fire area using native or nonnative plant species to obtain a stable plant community that will protect the burned area from erosion and invasion by weeds; and defines "revegetation" as establishing desirable plants in areas where they are absent or of inadequate density. The US Department of the Interior (DOI) defines "reclamation" as the process of reconverting disturbed land to its former or other productive uses, a definition commonly applied in the context of mined lands (DOI 2013). DOI notes that the definition of "restoration" and similar terms varies among authorizing and implementing agencies. Stahl et al. (2006) observe that definitions of ecological restoration and land reclamation have become more similar since the 1970s, perhaps due to the recognition that disturbed sites cannot often be restored to pre-disturbance conditions, and due to legal requirements for remediation of planned disturbances that increasingly call for use of native species and reestablishment of certain levels of diversity.

The effort and expense required for restoration ranges from limited management of relatively unmodified sites, to "building of ecosystems from bare ground" on devastated places such as mines (Montalvo et al. 1997). The aim in all cases is to develop a sustainable, essentially natural system within limitations of time and budget. Physical site restoration is sometimes enough to allow establishment of native species from the soil seed-pool or through immigration from nearby populations (Hobbs & Norton 1996). Native plants, however, may be seed- or recruitment-limited, or prevented from site dominance by invasive species (Kettenring & Galatowitsch 2011). Where disturbance is more severe or native species cannot return on their own, restoration extends to planting seeds, cuttings, or other germplasm of one or more species. The long-term goal is creation of self-sustaining communities that will support ecosystem functions and processes in turn requires plants that are well-adapted to current and future site conditions, and will thrive without damaging surrounding ecosystems (Lesica & Allendorf 1999). In sum, restorationists need germplasm that is genetically appropriate and fits within project budgets.

The Call for Local Germplasm

Restoration researchers and practitioners have generally preferred local genotypes for restoration purposes (Bischoff et al. 2010; Hancock & Hughes 2012; Hufford & Mazer 2012; Johnson et al. 2010; Jones 2013; Krauss et al. 2013). Restoration guidelines often call for seed collected near the restoration site to avoid negative impacts of maladaptation, inbreeding and outbreeding depression, and spatial genetic homogenization or genetic swamping (Krauss & He 2006; McKay et al. 2005; Mortlock 2000). Preference for local germplasm reflects a substantial body of research demonstrating that plants are commonly adapted to their habitat of origin. This "home-site" advantage is particularly apparent in reciprocal transplant experiments where the sites used differ in important environmental characteristics such as climate regime, and where experiments have continued for a number of years, allowing differences among plants to become more apparent (J. Anderson et al. 2011; Bennington et al. 2012; Hufford & Mazer 2012; Ishizuka & Goto 2011; K. Rice & Knapp 2008; Vander Mijnsbrugge et al. 2010; Verhoeven et al. 2011).

Using local germplasm may reduce risk of restoration-project failure, and can help conserve the genetic diversity represented among populations (Sackville-Hamilton 2001). Local seed may be most important for species with high degrees of population differentiation, such as species characterized by short lifespans, small dispersal areas, and self-pollination (L. Garnier et al. 2002; Handel 1985; Krauss & He 2006; Levin and Kerster 1971; Loveless & Hamrick 1984; C. Williams 1994). Where a species has limited gene flow, its populations may have long genetic memories of initial colonization patterns and subsequent site variations such as climate or disturbance (Loveless & Hamrick 1984); Schmitt 2007).

Use of local germplasm can help ensure compatibility among species on a restoration site. An ecosystem is not truly restored unless it supports a normal complement of reference-system species in full interaction with one another and their environment. As restorationists can only plant a subset of an ecosystem's component species, success of a restoration may depend in part on genetic compatibility between the restored species and other suitable species that are already in place or are likely to colonize from adjacent areas. Vandegehuchte et al. (2012) studied arthropods living on local and introduced genotypes of the beach grass *Ammophila arenaria*, and found that the diversity of the invertebrate community decreased with increasing geographical distance from the plants' location of origin. Longcore (2003), working in California coastal sage scrub, found that while plant diversity, percent cover, and structural complexity did not differ between undisturbed sites and sites restored 15 years earlier, arthropod diversity remained lower at restoration sites than at undisturbed or even disturbed sites. Longcore et al. (1997), citing unpublished data showing that non-local ecotypes of otherwise local plant species may fail to support local insect species, comment that, "a restoration is not successful if the plants kill the organisms that depend on them."

How local is local enough? The value of using local germplasm varies among species, populations, and restoration projects; it also varies among the differing perspectives of restoration researchers. Adaptation can vary sharply, even over a few hundred meters in areas with strong contrasts in edaphic conditions or effective climate regime, such as salt-marsh salinity gradients, or snow fields as they ascend to windy ridgetops (Bennington et al. 2012; Bockelmann et al. 2003; Lara-Romero et al. 2014). Plants growing along such gradients can vary in flowering phenology, and hybrids derived even from closely spaced populations could miss the pollination window (Lara-Romero et al. 2014). Individual traits may vary in spatial genetic structure; for example, traits controlling seedling size may be correlated with temperature regime, while root growth may correlate with moisture availability (O'Brien et al. 2007; St. Clair & Johnson 2004).

Restoration using nonlocal genotypes can produce mixed populations that can replace distinctive populations with hybrids, a process called genetic swamping (Todesco et al. 2016). Hybrid populations may be unusually vigorous and unduly competitive (Gustafson et al. 2004a and 2004b; Schierenbeck & Ellstrand 2009). Conversely, even where population mixing increases fitness via heterosis in the F1 generation, chromosomal recombination may disrupt intrinsic coadapted gene complexes (positive epistatic interactions), potentially reducing fitness in the F2 generation and beyond (Keller et al. 2000; Tallmon et al. 2004). Fenster and Galloway (2000) found that in some species, making crosses among populations separated by only hundreds of meters can result in disruption of fitness components across all phases of life history. Finding no linear effect of distance between populations in the extent of hybrid breakdown, they state that as much differentiation occurs between populations at the local level as at higher levels. The issue is complicated by studies that demonstrate elements of both heterosis and outbreeding depression, sometimes at different life stages (Bowles et al. 2015; Edmands 2007). Some of the few studies that follow organisms into F2 and later generations find that initial heterosis in the F1 generation may be followed by poorer performance in the F2 and F3 generations attributed to breakup of adapted complexes, which in turn may or may not be followed by rebounding performance in the F6 or later generations (Erickson & Fenster 2006; Johansen-Morris & Latta 2006; Kramer & Havens 2009). Where hybridization of indigenous and outside genotypes is unlikely, for example, due to differing flowering phenology, the introduced population may simply overwhelm the indigenous plants through greater competitiveness or fecundity (Holmstrom et al. 2010).

Optimal maximum distances for seed transfer may be species- or even population-specific, based on the degree of outcrossing and dispersal of each species (Hufford & Mazer 2003; McCann 2014). Many conifer species, for example, disperse their genes over wide areas (Johnson et al. 2004), but for some conifers, natural gene flow would limit seed collection zones to less than 1 km across (Govindaraju 1990; St. Clair & Johnson 2004). Some restorationists call for developing seed-transfer prescriptions based on species- and population-specific data regarding ploidy levels, lifespan, mating system, and other factors (Knapp and Rice 1996). Because detailed data is unavailable for many species, using propagules from the immediate vicinity or nearby populations in matching habitats may entail fewer risks than obtaining germplasm from a regional seed-transfer zone (O'Brien & Krauss 2010; Vander Mijnsbrugge et al. 2010). The California Native Plant Society (CNPS) recommends planting germplasm from within the same watershed and the same altitude as the project site (CNPS 1995 and 2001); and the National Park Service has specified plants from within the same watershed for Golden Gate National Recreation Area (McCann 2014). Where genetic data is lacking, Linhart (1995) recommends collecting within areas of probable genetic similarity, e.g., within 100 m for herbs and 1 km for trees, distances that may not often be practicable.

Why local may not always be best. Although restorationists commonly prefer locally-sourced germplasm (Hancock & Hughes 2012), a number of researchers have questioned the local-is-best dictum. Local populations are not always better adapted to a site than populations from other, matched provenances (Jones 2013; Leimu & Fischer 2008). Fragmentation, maladaptive drift, genetic impoverishment, and inbreeding can reduce the value of local populations, particularly small ones, as seed sources (Broadhurst et al. 2008; Honnay & Jacquemyn 2007; Kettenring et al. 2014; McKay et al. 2005). The alleles needed to adapt to changing environments may also be low-frequency alleles, which are the most easily lost from small populations. Where microclimatic or soil conditions vary sharply, plants from nearby populations may be poorly adapted to a restoration site, and plants from similar environments may provide a better match (Jones 2013; Lawrence & Kaye 2011; Whalley et al. 2013). Extreme disturbance or contamination, such as is often found at abandoned mine sites, may also preclude compatibility of local germplasm (Johnson et al. 2010; Lesica & Allendorf 1999). Where adaptation of local and nearby populations to a restoration site are not at issue, local germplasm may remain problematic due to the potential impacts of overharvesting seeds from source populations (Broadhurst et al. 2008; Meissen et al. 2015; Mortlock 2000; S. Smith et al. 2007). From a practical standpoint, a large number of restoration projects, each with its own local germplasm sources, would lead to many small collection zones (versus a few large ones), in turn translating into higher costs and operational complexities for both resource managers and commercial seed producers (Cronn et al. 2003; Mustoe 2014).

The Need for Genetic Diversity

Artificial populations need to contain adequate genetic diversity in order to thrive. Concerns about restoration germplasm relate to both the genetic mean and variance of a restored population, that is, whether newly established populations will be adapted to conditions currently normal to a site and also be able to adapt to environmental changes over time. While local germplasm is commonly recommended, local populations may not exist. Of particular concern is the potentially limited genetic diversity of some source populations. As a result, the goals of near-term adaptation and long-term adaptability can come into conflict.

Populations originating from a small number of genotypes may suffer founder effects and greater vulnerability to environmental change (Wise et al. 2002). Loss of genetic variation can also increase likelihood of inbreeding depression, as well as reduced fecundity through loss of self-incompatibility alleles (Frankham 2005; Frankham et al. 2011). The capacity to adapt will become increasingly important as mean climate conditions shift and climate variability increases in the wake of global warming (Booy et al. 2000; Jump & Peñuelas 2005).

Experiments suggest that genetic variability in restoration plantings can result in better survival, denser restored populations, greater invasion resistance, greater interspecific diversity, and improved provision of ecosystem services (Crawford & Rudgers 2012 & 2013; Crawford & Whitney 2010; Crutsinger, Souza & Sanders 2008; Forsman & Wennersten 2015; Hughes et al. 2008; Maschinski et al. 2012; Reynolds et al. 2012; Vellend 2006). Much as species diversity can increase ecosystem productivity, including productivity of planted communities (Brooker et al. 2008; Callaway et al. 2003; Grime 1998; Guo 2007), genetic diversity within species can similarly influence population fitness and productivity (Bischoff et al. 2010; Crawford & Whitney 2010; Crutsinger, Souza & Sanders 2008; Forsman & Wennersten 2015, Hughes et al. 2008). Populations with high levels of heterozygosity may have greater ecological amplitude (Procaccini & Piazzi 2001), attributable to the higher fitness of heterozygous individuals under some circumstances, and the greater genetic diversity often present in populations with high levels of heterozygosity (Booy et al. 2000). Genetic diversity in plant populations provides for spatial and temporal variation in disease-resistance traits, promoting both individual and population fitness (Booy et al. 2000; Linhart 1991; Lively 2010). In eelgrass (*Zostera marina*) this diversity leads to greater shoot density and patch expansion, greater biomass production, more flowering, higher percent seed germination, greater faunal abundance, and greater tolerance of high water temperatures and other disturbances (Hughes & Stachowicz 2011; Reusch et al. 2005; S. Williams 2001). Some authors attribute increased population performance and biomass production in genetically diverse populations to niche partitioning and facilitation (Drummond & Vellend 2012; Ennos 1985; Hughes et al. 2008). Others note that research in this area generally focuses on short-term plantings with limited numbers of genotypes, and caution that sampling effects of including one or more high-yielding genotypes in mixtures may result in increased productivity, which in turn may prove transient (Münzbergová et al. 2009).

Interspecific effects of within-species genetic diversity. Genetic variation within component species may influence community species diversity and ecosystem functions (Ehlers et al. 2016; Gibson et al. 2012; Proffitt et al. 2005; Seliskar et al. 2002). Violle et al. (2012)

contrast three theories that address the relationship of inter- and intraspecific diversity within ecosystems.

- In niche-based theory, the range of resources used by each species (niche width) must become narrower as the number of species increases; as species richness increases, therefore, intraspecific variation decreases.
- In neutral theory of biodiversity, intraspecific variation in a community is unpredictable and is not related to species diversity.
- In individual-variation theories, high levels of intraspecific variation help maintain interspecific diversity: "high diversity is possible because species differ in so many ways" (J. Clark 2010).

Modeling studies of single functional groups or trophic levels can generate highly variable and context-dependent predictions of the effect of genetic diversity on species diversity. Some models indicate that increased intraspecific variation would result in competitive exclusion of species, while others support the idea that "diversity begets diversity," an effect enhanced by the sessile character of plants.

Observational studies reveal that species diversity and intraspecific genetic diversity are often correlated (Vellend & Geber 2005). This is particularly true of studies using discrete sampling units such as islands or lakes, versus studies using non-discrete sampling units such as equal-area plots (Vellend et al. 2014). Possible mechanisms for this relationship include species diversity fostering genetic diversity (Adams & Vellend 2011), or genetic diversity fostering species diversity (Booth & Grime 2003). It is possible, however, that the correlation stems simply from parallel processes acting in a similar manner on both levels of diversity. Causation is difficult to assign in observational studies, in that factors that influence species diversity, such as habitat area, environmental heterogeneity, and migration, similarly influence genetic diversity within species (Vellend & Geber 2005).

Experimental work generally reveals positive correlations between intraspecific and interspecific diversity (Whitlock 2014). Booth and Grime (2003), for example, assembled experimental grassland communities of 11 component species using one to four genotypes of each species. Over the next several years, genetically depauperate assemblages lost more species diversity (though not significantly) compared to richer communities, and had significantly less-predictable and less-consistent canopy structure and proportional species composition. Crawford and Rudgers (2012), working with *Ammophila breviligulata* (American beachgrass) as the dominant species in a dune system, manipulated three types of diversity: genetic diversity of *Ammophila* alone; species diversity alone; and species diversity simultaneously with genetic diversity in *Ammophila*. As genetic diversity within *Ammophila* increased, the relationship between species diversity and community-level biomass shifted from negative to positive.

Interactions between interspecific coadaptation and genetic diversity. Where changes in one taxon shift selection pressures in another, the evolution of the two taxa may come to be partly dependent on each other (Begon et al. 1990). This reciprocal relationship operates on an individual basis, where the specific genotype of one individual acts on the specific genotype of the other. Experimental studies have found that interactions between plants of different species can vary on a genotype-by-genotype basis. Taylor and Aarssen (1990), studying perennial grasses in a Canadian hayfield, found that certain genotypes of a competitively inferior species may outcompete some genotypes of other species that are usually competitively superior. Fridley et al. (2007) grew assemblages of *Koeleria macrantha, Carex caryophyllea*, and *Campanula rotundifolia* under differing conditions of soil fertility and simulated grazing. Each genotype of the grass performed best next to a different genotype of the sedge, and the identity of the highest-performing genotype pairings varied with environment. Kelley and Clay (1987) found that co-occurring genotypes of two perennial bunchgrasses, *Anthoxanthum odoratum* and *Danthonia spicata*, differed in interspecific competitive performance; the competitive performance of a specific genotype of one species often depended on the genotypic identity of the other species. Aarssen & Turkington (1985), found that *Rhizobium* and *Lolium* that are neighbors in the field, when combined, disproportionately increase yield of *Trifolium* when compared to unassociated *Rhizobium*/*Lolium* pairings; this relationship exists regardless of *Trifolium* genotype, and is apparently mediated by *Rhizobium* interaction with *Lolium* (see also Chanway et al. 1989). Specific genotypes of dominant plant species can influence establishment and tissue allocation of specific genotypes of heterospecific neighbors (Genung et al. 2012; Gustafson et al. 2014).

Where local populations of interacting species have coevolved, genetic variation particularly within keystone or dominant species may support species richness in other trophic or functional groups (J. Bailey et al. 2009). Conversely, introduced populations may fail to interact compatibly with their new neighbors. In the case of invasive species, release from enemies, indeed release from community complexity (Strauss 2014), can contribute to their ability to invade. In the case of restored species, introduced populations may not only fail to thrive, but may also fail to support other species in the community (Longcore 2003; Severns 2011).

The relatively new field of community genetics addresses genetic interactions that occur between species in complex communities (Whitham et al. 2006). Most studies to date have focused on the effects on arthropod communities of genetic variation in dominant plant species, particularly effects mediated by plant secondary metabolites. Crawford and Rudgers (2013) found that genetic diversity in *Ammophila breviligulata* can influence arthropod communities more strongly than does plant species diversity, with arthropod richness and abundance peaking at high levels of *Ammophila* genetic diversity. Genotypic diversity in tall goldenrod (*Solidago altissima*) can have strong effects on diversity and composition of foliage-consuming arthropods, although effects on litter-based arthropods may be smaller (Crutsinger, Reynolds et al. 2008). Whitham et al. (2003) have studied how resistance in pinyon pine (*Pinus edulis*) to a stem-boring moth cascades through multiple trophic levels. Stem-borer damage affects pine tree morphology and seed production, and genetic variation in resistance therefore influences competition between rodents and birds for seeds, in turn influencing dispersal distance of pinyon seeds. The stem-borer resistance factors also influence soil microbes. In another tri-trophic study, Poelman et al. (2013) found that parasitoid wasps may be more attracted to plants that, when damaged by herbivores, release relatively large amounts of volatile compounds, a genetic trait; the volatile compounds can indicate when the wasps' prey is eating from the plants in question.

In *Populus* and *Eucalyptus* hybridizing systems, variation in composition of chemical defenses such as tannins and phenolic glycosides differentially affects viability of a wide range of herbivores and pathogens, resulting in a very high level of agreement between tree pedigree and arthropod community composition on individual trees (Whitham et al. 2003). The breadth of tree genotypes thus determines the potential breadth of arthropod community diversity. Again, these effects can cascade through multiple trophic levels. Variation in *Populus* (aspen) affects aphid populations, thus affecting their ant mutualists, in turn affecting the predator and parasite species specifically dependent on ant-aphid mutualism. Varying concentrations of inducible tannins in *Populus* leaves also explain a large portion of variation in decomposition rates and N mineralization. Müller et al. (2006) found that chickadees' preference or rejection of gypsy moth caterpillars (*Lymantria dispar*) correlated with genetically-based variation in secondary-compound content in the caterpillars' *Populus tremuloides* foliage diet.

Plant adaptations that improve fitness with regard to one co-occurring species may reduce fitness vis-à-vis others; for example, plant toxins that discourage generalist herbivores may stimulate herbivory by specialists (Linhart 1991; Simms 1990). These interspecific genetic effects can vary at fine spatial scales. Prentice and Cramer (1990) found significant correlations between electrophoretic variation in *Gypsophila fastigiata* (fastigiate gypsophila) and fine-scale gradient change (on the order of 1 m^2) in community composition.

Restoration requires the full suite of community organisms, including nitrogen-fixers, mycorrhizae, decomposers, pollinators, seed-dispersers, and so forth, which must be able to colonize a restored habitat for restoration to succeed (Handel et al. 1994; Hobbs & Norton 1996). Evidence of genotype-by-genotype adaptation among species within communities raises the question of compatibility of genotypes of different species potentially collected from several source ecosystems. For example, Ji et al. (2010) and Weinbaum et al. (1996) found evidence that mycorrhizae matched with their host and soil of origin display greater survival and enhancement of plant growth when compared with mycorrhizae grown with exotic hosts and soil. Introduction of alien mycorrhizae in restoration, agronomy, and forestry is troubling to some researchers (e.g., Schwartz et al. 2006) and has been implicated in soil-carbon losses associated with carbon-offset pine plantations (Chapela et al. 2001). Many restoration practitioners apply commercial mycorrhizae claimed to be appropriate for a wide range of ecosystems (e.g., Pawnee Butte Seeds 2013); apparently only a minority collect soil as well as seeds in order to propagate native mycorrhizae along with coadapted plants (e.g., Recon Native Plants 2013). Perhaps restoration practitioners should transplant whole suites of potentially coadapted species to create well-functioning ecosystems.

Maximizing genetic diversity with alternative provenancing. Concerns about genetic diversity in restoration projects have led to the development of a range of alternative seed-sourcing strategies that aim to capture diverse genotypes and allow evolutionary processes to generate new, locally adapted populations. Some authors recommend that each individual restoration project use seeds from a single large, genetically diverse population to retain natural genetic structures and avoid potential outbreeding depression, while still providing the diversity needed for restored populations to evolve to match site conditions (Krauss & He 2006; Pickup et al. 2012). Others recommend using propagules from a wide range of source populations growing in environments edaphically and climatically matched to the restoration site, in order to improve the likelihood of including highly-functioning ecotypes and of ensuring resource capture through niche partitioning (Kettenring et al. 2014; Whalley et al. 2013). Still others suggest, in contrast, that hybrids between populations, or mixtures of genotypes from different, ecologically distinct populations covering a substantial part of a species' range, may be the best approach for highly disturbed, altered, or invaded areas, because the conditions to which local genotypes were adapted may no longer exist. They propose that a mixture of genotypes may reduce problems of hybrid failure stemming from environmental incompatibility (Cronn et al. 2003; Johnson et al. 2010; Lesica & Allendorf 1999). Frankham et al. (2011) suggest that germplasm from multiple populations can be mixed safely without fear of breaking up adaptive complexes if there are no fixed chromosome differences, and if the populations diverged less than 500 years ago.

The question of where to collect germplasm also hinges on the issue of climate change. While ecological restoration commonly refers to recreating the community that existed before disturbance, long-lived plants may have recruited under conditions that already no longer exist. Attempts to create permanent communities may fail given shifting precipitation and temperature patterns. Effective restoration may now mean planting species and genotypes from environments that match predicted future climate rather than current conditions (Harris et al. 2006; McLachlan et al. 2007). Sgrò et al. (2011) call for "predictive provenancing," the planting of genotypes experimentally determined to be adapted to projected site conditions, and suggest matching seed stock with 2050 climate projections. Thomas et al. (2011) and Weeks et al. (2011) provide decision-making frameworks addressing which species to move. These approaches would require accurate climate projections as well as more-detailed adaptation data than is available for most species. Broadhurst et al. (2008) recommend "composite provenancing," the mixture of seed from populations at a range of distances in an attempt to mimic natural gene flow. Where the data required for predictive or composite provenancing is unavailable, Breed et al. (2012) suggest "admixture provenancing," the planting of seed collected from multiple large populations "with no spatial bias towards the revegetation site."

Outside the context of restoring disturbed habitats, some authors have suggested transporting species to communities where the translocated species do not currently exist but might persist in a changed climate, a form of preemptive restoration (McLachlan et al. 2007; Weeks et al. 2011). Other authorities point to evidence that assisted migration may fail or may have serious unintended consequences such as hybridization, invasiveness, and disruption of *in situ* populations (Pelini et al. 2009; Ricciardi & Simberloff 2009). Survey data from Australia indicates that while both restoration practitioners and researchers believe that climate change may require translocations, they also believe that the information needed to carry out translocations in relative safety remains insufficient (Hancock & Gallagher 2014; Hancock & Hughes 2012). Ensuring habitat connectivity can increase the ability of species to migrate on their own; US Department of Interior Secretarial Order No. 3289 calls for ensuring habitat corridors to provide climate-driven migration opportunities, but does not call for active translocation of species (Salazar 2009).

Patchiness and Genetic Variation

Restoration researchers may debate where propagules should be collected, but they agree on the need for of genetic variation in restored communities. Gathering a full range of genotypes may require sampling across the whole of a population. Abiotic factors giving rise to subpopulation differentiation can follow gradual clines (such as rainfall) and sharp discontinuities (such as localized soil types) that physically separate individuals adapted to different regimes (Knapp & Rice 1998; Linhart & Grant 1996; Monson et al. 1992; Owuor et al. 1999). The biotic environment, in contrast, presents a shifting array of selective pressures exerted by a patchy, overlapping mosaic of mutualists, competitors, predators, and pathogens, resulting in individuals with contrasting adaptations intermixed within a small area (Linhart & Grant 1996). Indeed, in diversifying and frequency-dependent selection, genotypes are favored merely because they are unusual within a population; examples include host resistance to pathogens and gametophytic self-incompatibility (Antonovics & Ellstrand 1984; Hartl & Clark 1997; Kelley 1984). Some species display significant genetic structuring among subpopulations despite high levels of gene flow (Gehring and Linhart 1992). Capturing genetic variation requires appropriate sampling methods to ensure seed collection across subpopulations, even across genetically differentiated patches within a larger population.

Variations in density of a species can be both an effect and a cause of microsite differences (Beckman & Mitton 1984; Eviner 2004). A patch containing unusually high or low density of a given plant species may initially develop due to abiotic conditions, such as soil nutrient or water availability, or may simply reflect stochastic factors such as seed dispersal. Clonal growth patterns naturally lend themselves to patch formation.

Patch density and competitive regimes. A dense stand may reflect unusually high site quality for the species found there, resulting in some degree of competitive exclusion of other species. These conditions might also select for strong competitors among successful colonists, leading to more competitive offspring. Conversely, even without variation among microsites, a dense stand could potentially result from appearance of a genotype that is unusually competitive and able to exclude other species.

Patchiness of inter- versus intraspecific interactions. Plants surrounded mostly by conspecifics and plants growing in mixed neighborhoods may face different selection regimes, potentially leading to genetic differences. Plants growing in small, dense patches mostly among conspecifics would likely experience a narrower range of microenvironments than an equal number of conspecifics spread out over larger areas might encounter (L. Huntsinger 2005 *pers. comm.*). Some studies have demonstrated genetic trade-offs between intra- and interspecific competitive ability, in some cases correlated with dense versus dispersed distribution of conspecifics (Lankau 2008; Linhart 1988; Semchenko et al. 2013; R. Shaw et al. 1995). Under certain circumstances, plant populations may differentiate into subpopulations with distinct inter- and intraspecific competitive abilities (Linhart 1988; Linhart & Grant 1996).

Patchiness and facilitation. A patch may reflect biotic factors that result in positive feedbacks. Self-organized patchiness has been studied particularly in arid systems, where interplay between facilitation over short distances and competition over longer ones can result in characteristic patterns in plant cover (Deblauwe et al. 2011; Kéfi et al. 2016; Rietkerk et al. 2004; Sheffer et al. 2013). These patterns, in some places nicknamed tiger bush or leopard bush for their striped or spotted appearance, develop where vegetation allows for greater infiltration of water and nutrients, creating patches of relative fertility within a low-resource environment. Plants extend their roots under adjacent bare spaces, further decreasing soil resources and seedling survival between vegetated patches. Similar feedback-driven patterning has been found in a wide range of environments, including peat bogs, salt marshes, mussel beds, and ribbon forests (Rietkerk & van de Koppel 2008; van de Koppel et al. 2008; Weerman et al. 2012).[3]

California native perennial grasses can also create zones of resource depletion around themselves and form elongated patches parallel to hill contours, which may increase ability to harvest water and nutrients (Fehmi et al. 2008; Parker et al. 2012). In addition, many California grassland species are highly dependent on mycorrhizal fungi, whereas exotic species are not. This may produce in a positive feedback in which initial dominance of exotic species reduces presence of mycorrhizae, thus excluding natives, and initial dominance of natives results in high densities of mycorrhizal fungi and sustained dominance of native species (Vogelsang & Bever 2009).

Researchers have generally assumed that facilitation occurs where there is little niche overlap (Maestre et al. 2009), and that intraspecific facilitation would be limited to interactions between different life stages, such as adult trees providing nurse effects (Fajardo & McIntire 2011). A few studies have uncovered same-age intraspecific facilitation, primarily among seedlings or young plants. Chu et al. (2008) planted *Elymus nutans* in a stressful alpine meadow at a range of densities, and found that both individual mean biomass and total mean biomass reached a maximum at intermediate densities. Fajardo and McIntire (2011) planted two-year-old lenga beech trees (*Nothofagus pumilio*) singly and in close-planted groups along a transect spanning a forest interior, forest edge, and stressful wind-swept prairie. They found that tree seedlings in groups had better survival than singletons in the windy prairie, while in the forest the opposite was true. Leicht-Young et al. (2011) found that seedling lianas had greater survival without reduced height growth under high-density versus low density conditions. In a nutrient-limited outdoor pot study employing multiple seed and seedling densities, Sheley and James (2014) found that while bottlebrush squirreltail (*Elymus elymoides*) and medusahead (*Taeniatherum caputmedusae*) reduced each other's growth, both species, in particular squirreltail, facilitated their conspecifics.

Intraspecific facilitation can shift selection pressures and genotype composition over time. Cohorts establishing at different times may have different adaptations, particularly where the pioneer generation alters growing conditions (Linhart & Grant 1996). Beckman and Mitton (1984), for example, found that ponderosa pines (*Pinus ponderosa*) that were early grassland colonists differ genetically from later-establishing conspecifics in adaptation to xeric grassland conditions versus the more mesic conditions produced by the initial pioneers. Facilitation among

---

[3] Equidistant planting of trees and shrubs is common in mine reclamation. In addition to giving revegetated areas the aesthetics of orchards rather than that of wildlands, this practice assumes purely competitive relationships and may reduce the opportunity for intraspecific facilitation.

conspecifics would support formation of dense groups of related plants (Dudley et al. 2013; Fajardo et al. 2016; Karban & Shiojiri 2010; Kigathi et al. 2013; Lepik et al. 2012).

Effects of intra- versus interspecific patch density on mating system. Plants growing in sparse distributions of conspecifics may experience mating conditions that differ from those encountered by plants growing in dense conspecific patches. Self-incompatible plants can suffer reduced seed-set in dispersed populations because isolated plants may receive limited conspecific pollen (Ghazoul 2005). While sparse distributions might select for self-compatibility (Loveless & Hamrick 1984; Stebbins 1957), self-compatible plants can also have reduced reproductive success at low density (Ghazoul 2005). The effect of high density on mating is further influenced by plant size and growth form; flowers within large, dense patches receive proportionately little pollen from other conspecific plants, again favoring self-compatibility, while closely-interdigitated neighboring plants of a guerrilla[4] species can freely trade pollen (Handel 1985; Heywood 1991; Loveless & Hamrick 1984).

Patchy distributions can lead to genetic differentiation of subpopulations through isolation by distance (Wright 1943). Giles et al. (1998), working with the dioecious herb *Silene dioica*, compared genetic differentiation among island populations to differentiation among patches separated by tens of meters on the same islands; they found that differences among patches were greater than differences among islands, likely due to highly localized pollination and seed dispersal. Distance between mates can affect offspring fitness; in *Ipomopsis aggregata* (scarlet gilia), higher seed set per flower, and greater survival and fecundity of offspring, occur at intermediate pollination distances (10 m) compared to 1-m and 100-m pollination distances (Waser & Price 1989; Waser et al. 2000).

In sum, plants in dense patches may differ genetically from conspecifics in sparse distributions for a number of reasons, including intrinsic microsite differences, mating system, successional changes, competition, and facilitation, all exerting selective pressures. Restoration prescriptions often call for seed collection from a full range of subpopulations and maintenance of the seed's genetic characteristics during agronomic increase. If the economics of seed collection require bypassing sparse patches, and if plants from sparse patches differ genetically from plants in dense patches, there may be an unavoidable conflict between cost control and genetic goals in environmental restoration. This study therefore asks whether density variation may correlate with important adaptive differences.

---

[4] Lovett Doust (1981) originated the growth-form descriptor "phalanx" to denote clonal expansion via short rhizomes or stolons, versus "guerrilla" to denote penetration of the surrounding neighborhood via long rhizomes or stolons.

Chapter 3. Seed Production for Restoration Plantings

Successful restoration depends on use of appropriate germplasm, as discussed in Chapter 2. Seed production for restoration, however, must balance reasonable project economy and practicality against the need for germplasm that is well adapted to present and potential site conditions, can coexist with other restored or endemic species, and will not damage the ecological functioning of the site. The need in many restoration projects to plant tons of seed often means that the planted seeds are not themselves gathered from wildland plants, but instead are field-propagated from seeds or cuttings collected in the wild. Genetic shifts and losses can occur at any stage of the reintroduction process, including propagule harvest from wild plants, seed bulking and storage, and propagation. Inadvertent selection can be especially problematic where rare species or fragmented populations are concerned (Krauss et al. 2002). This chapter first discusses genetic issues entailed by seed propagation. The basis for all restoration planting, however, is germplasm collected from wild populations, and the conclusion of this chapter discusses the potential for inadvertent selection during seed harvesting from natural populations.

Agronomic Increase of Wild-collected Seed

Commercial growers provide most restoration seeds. To produce site-specific seeds, a grower typically needs a minimum of three years to collect wild seeds, plant them in a production field, and harvest a crop (Majerus 2005). As a result, agronomic increase of site-specific seeds is limited to planned restoration projects. Commercial growers also cultivate native plants for restoration outside of planned projects, for example, in preparation for post-fire seeding. The latter category includes seeds originating as US Department of Agriculture Natural Resources Conservation Service (NRCS) Plant Materials Center germplasm releases, which are discussed further below.

Wild species are more difficult to grow than domesticated crops, because of greater seed dormancy, longer life cycles, lesser seed output, narrower climate and soil adaptations, and often limited information about their original habitat (A. Brown et al. 1997; Scianna 2003). Surveys conducted on the market for native seed have found that impediments to planting diverse, local, source-identified seeds include cost, limited availability, and lack of information (S. Smith et al. 2007; Strategic Marketing Services 2002). Growers face many impediments, including time needed for stands to come to reproductive age, labor and equipment investments, scarcity of appropriate local-origin start-up seeds, variable demand, and market competition from cultivars.

Despite these hindrances, agronomic increase can greatly improve seed availability. The amount of seed required per acre for rapid revegetation is roughly similar to the amount needed for plantation establishment (Pacific Northwest Natives 2005). For *Elymus glaucus*, ten to 15 pounds per acre of wild-collected grass seed may be needed to establish a plantation that will yield 100-1000 pounds per acre within one or two years (Archibald et al. 2000; D. Dyer 2001; Winslow 2002a and 2002b). The cost of the resulting seed ranges from \$8-25 per pound Kaiser et al. 2003).

Evolution under agronomic conditions. While agronomic increase can improve cost and availability of native seed, it can also shift genetic characteristics significantly within as little as one generation (A. Dyer et al. 2016; Espeland et al. 2016; Ferdinandez et al. 2005; Humphrey & Schupp 2002; Knapp & Rice 1994; K. Rice 1995; Rogers 2004; Soleri & Smith 1995). Agronomic conditions tend to select for high relative growth rate and select against seed-dormancy adaptations and other traits that are important to fitness in stressful environments (Schröder & Prasse 2013a). Monoculture production, with its concomitant competitive conditions, is more common than mixed-species production (Archibald et al. 2000; D. Dyer 2001; Strategic Marketing Services 2002; Winslow 2002a and 2002b[5]). Some increase operations use clonal propagules rather than seeds to establish plantations, significantly restricting genetic variation. To overcome selection and drift, seed growers often "refresh" the genetics of their crop species by collecting new wild seeds, but the frequency of refreshing is not standardized, and guidance for seed growers in the scientific literature is limited (S. Smith et al. 2007). Growers of local-ecotype seed also face the constant risk of unintended and undetected hybridization of their crop (S. Smith et al. 2007). Conversely, Dunwiddie & Delvin (2006) note that storing and growing out seed collections can help correct for errors made in collection, such as confusion of similar taxa.

Propagation of field-increase and source-identified seeds often entails intensive management, which can affect genetic diversity in wild plants (Borders 2009; A. Dyer et al. 2016; Kölliker et al. 1998). Wild-collected seeds may be mechanically cleaned and de-awned, refrigerated, subjected to germination treatments such as scarification and stratification, and established in a greenhouse before being planted in tilled plots. The plots may be ripped and disked, fumigated and fertilized, seeded with groundcovers such as perennial rye, and treated with herbicides, insecticides, and fungicides both before and during growth of the target plants (Flessner & Trindle 2007). Plot borders may be mowed, and young plants irrigated (Archibald et al. 2000; D. Dyer 2001; Navarrete-Tindall & Erickson 2002; Winslow 2002a and 2002b). The harvested seeds may in turn be mechanically cleaned or removed from seed pods, sometimes through use of a modified meat grinders or hammer mills, then heat-dried, treated with insecticides or fungicides, and subsequently refrigerated or frozen (Ailstock & Shafer 2006; Archibald et al. 2000; D. Dyer 2001; Laverack et al. 2006; Lippitt et al. 1994; Winslow 2002a and 2002b), which may result in differential selection in storage (Goodwin 1994; M. Hamilton 1994). Small seeds may be less vulnerable to mechanical damage than larger seeds of the same species (Stanton 1985), although they may be less able to survive storage or seedling competition. Despite concerns regarding genetic shifts, some observers believe that large-scale propagation programs entailing dedicated seed production areas are needed to meet global restoration demand (Nevill et al. 2016).

Pre-varietal releases and cultivars. Because project-specific agronomic production of locally adapted seed is impractical for many revegetation projects (Larson et al. 2001), restoration projects often employ large quantities of commercial native-species cultivar seeds,

---

[5] See also the many propagation protocols available on the United States Department of Agriculture Native Plant Network, https://npn.rngr.net/npn/propagation/protocols.

which are relatively inexpensive and readily available (Baer et al. 2002; Cronn et al. 2003; Gustafson et al. 2004a). The Association of Official Seed Certification Agencies (AOSCA), which promulgates testing methods and standards for seed quality, has created a "natural track" appropriate for seeds destined for conservation planting that is distinct from the "manipulated track" of traditional plant breeding (Young et al. 2003). Both natural-track and manipulated-track plants may be released as cultivars after undergoing several generations of selection and evaluation in comparative trials. Unlike traditional cultivars, natural-track cultivars are not hybridized across source populations, and efforts are made to limit directional selection during cultivar development.

Native plant species require 10-20 years to develop as cultivars (BLM undated a). Plant lines that have not undergone enough generations of testing to become full-fledged cultivars can be certified as "pre-varietal releases." Natural-track pre-varietal releases include

- Source-Identified or "yellow-tag" seeds, which are unevaluated germplasm identified in terms of species and location of their wild ancestors,
- Selected Class or "green-tag" seeds, which have been selected either within or among accessions as potentially having desirable inherited traits, and
- Tested Class or "blue-tag" seed, which have proven to have inherited desirable traits.

The BLM *Integrated Vegetation Management Handbook* recommends wild-collected or yellow-tag seeds for restoration planting (BLM 2008).

Natural Resources Conservation Service native plant development. The NRCS Plant Materials Program[6] has developed and released over 600 varieties of conservation plants, predominately grasses and including both native and introduced species, for commercial producers to use as planting stock (NRCS 2007). NRCS staff also processes and grows out seeds collected from national parks for restoration in the parks, thus assuring local genetic sources (NRCS undated b). Many NRCS varieties predate by several decades the existence of the natural-track designation, but few have undergone intentional genetic manipulation (NRCS undated a). The recent desire for broader-based germplasm and more native materials has led the NRCS to focus on explicitly "natural-track" native species and adopt the pre-varietal release concept for many of its native-plant releases (S. Lambert 1997). Seed-labeling rules for natural-track seeds typically limit agronomic increase to five or fewer generations.

Cultivar controversies. Even though natural-track cultivars have been developed specifically for revegetation, use of cultivars is controversial. Some researchers in this area work with conservation cultivars that have been in production for many decades (Gibson et al. 2013; Gustafson et al. 2014; Klopf & Baer 2011; A. Lambert et al. 2011; Mutegi et al. 2013), and some with more recently developed pre-varietal germplasm releases (Baughman 2014; Herget, Hufford, Mummey, Mealor & Shreading 2015). In either case, these researchers raise questions regarding appropriate use of cultivars. In an article supporting use of "restoration-appropriate" cultivars, Jones and Robins (2011) summarized the common objections to using cultivars for restoration:

---

[6] The USDA Soil Conservation Service, founded in reaction to the Dust Bowl of the 1930s, was renamed the Natural Resources Conservation Service in 1994.

- they do not reflect natural phylogeographic patterns,
- they induce outbreeding depression upon hybridization with remnant indigenous material,
- they may themselves be subject to outbreeding depression,
- they are excessively competitive or potentially invasive,
- they are poorly adapted and lacking in fitness,
- they possess too much genetic variation as a result of hybridization, and
- they possess too little genetic variation as a result of selection.

Cultivars are grown and tested largely in monoculture conditions, and important concerns about their role in restoration involve potential interactions with other species. While cultivars may be quite vigorous when grown in monoculture, their performance may suffer under interspecific competitive conditions (Baughman 2014; Herget, Hufford, Mummey, Mealor & and Shreading 2015; Herget, Hufford, Mummey, & Shreading 2015). Use of cultivars can shift the genetic and species composition of other plants in the restored area and in nearby remnant native populations (Gustafson et al. 2014; Mutegi et al. 2013). Cultivars may have faster and more abundant germination than noncultivars, but can experience greatly reduced fitness under weather extremes (Schröder & Prasse 2013a and 2013b). Some researchers who might otherwise prefer wild-collected seeds are comfortable with use of cultivars for restoration in specific circumstances, such as planting tolerant cultivars on soil contaminated with heavy metals, or in small, highly disturbed areas where native genotypes may be poorly adapted (Bugg et al. 1997; Handel et al. 1994; Humphrey & Schupp 2002; Lesica & Allendorf 1999).

Collecting Wild Seed: Cost Versus Diversity

Collection of germplasm from the wild is the starting point for all restoration plantings, whether propagules are planted directly or increased via cultivation. Any inadvertent selection during the initial wild-population harvest may be reflected in subsequent generations. The remainder of this chapter focuses on wild-collected seed as the basis for all native-species restoration.

An optimal seed-collection site, from a collector’s standpoint, would be flat, weed-free, and thickly covered with dense stands of the target species; and would have fruiting phenology geared to generous, simultaneous seed ripening, characteristics not especially typical of remnant natural communities. Density or dominance of the target species, and presence of weed species, can limit seed collection areas. Sites must be accessible, lawful to harvest, and fruitful enough to warrant harvesting.

Harvesters can collect seeds from wild stands by hand, through use of equipment such as vacuums and brush harvesters, or through collection of seed-containing donor soil or wild hay. Hand harvesting is generally the most costly method per pound of seed; one estimate suggests wild-collected seed can cost 10 to 100 times more than commercially available seed (S. Smith et al. 2007). In the case of *Elymus glaucus,* which has relatively large seeds, a person can collect anywhere from less than 100 to over 1000 grams of clean seed in an hour from a wild stand (Winslow 2002a and 2002b). Mechanical harvesting is often limited to flat areas near roads that have high densities of target species and no weed seeds. Stevenson et al. (1997) compared manual collection of mixed-species grassland seeds versus mechanical harvesting using a 100-kg, 11-hp vacuum machine. Hand collection yielded about 1 kg per 40 hours of collection, versus more than 1 kg per 8 hours using the vacuum. Percent viability of hand-collected seed was 13.7, versus 8.5 for vacuum harvested and 56.1 for commercially-grown native seed.

As discussed in Chapter 1, manual collection from herbaceous plants is far more efficient in dense stands. For herbaceous species, manual collection is generally necessary, because target species rarely grow in pure stands, and topography prevents use of machinery (Lippitt et al. 1994). Collecting even small amounts of plant material can be physically challenging. Where disturbance has eliminated easily accessible populations, restorationists may need to collect seeds from locations such as cliff faces (Powell 1994; P. Shaw 2014). Some seagrass restoration projects require divers to collect vegetative material from underwater populations. The divers can generally cover only small areas, and some source populations have little genetic diversity; both factors can reduce genetic diversity in these restorations (Montalvo et al. 1997; S. Williams 2001). Where seagrass seeds are collected, storms can eliminate collection sites, limiting seed harvests to protected coves (Ailstock & Shafer 2006).

Suitability of collected seeds depends not only on which site is chosen for harvesting, but also on how seeds are collected within a site. Collection procedures may skew the proportions of genotypes collected (Gustafson et al. 2004a and 2004b; Y.C. Li et al. 2005). Avoiding inadvertent selection means taking seed from many individuals in a random or at least representative fashion (Hufford & Mazer 2003). Articles in the refereed literature recommend optimal collection processes for herbaceous species, such as harvesting seed randomly across the full extent of the population or along transects perpendicular to wind or other dispersal direction, taking equal amounts of seed from all harvested plants, and including the full range both of spatial microenvironments and of seed-ripening times through repeated collections (DeBolt & Spurrier 2004; Knapp & Rice 1994). Collection guidelines aimed at practitioners suggest harvesting across all microhabitats and at multiple collection times, but rarely provide much information on spatial randomization, which may increase the likelihood that "random" collection is merely haphazard. Some guides include no randomization method (Ailstock & Shafer 2006; Florabank undated a & b), while others suggest only that seed be collected from widely-spaced individuals (Basey et al. 2015; Dumroese et al. 2008; Florabank undated c). A few guidelines suggest informal transects, for example, collecting at intervals of three paces (ENSCONET 2009; Houseal 2009). The BLM's 39-page *Seeds of Success* technical protocol for seed collection and conservation calls for randomized collection across the full range of a population without providing guidance on randomization methods (BLM 2008 and 2015b). Seed harvesting prescriptions historically have varied on how to respond to phenotypic characteristics in the field that may indicate genetic variation, for example, whether to harvest only from healthy, presumably disease-resistant plants (Dumroese et al. 2008; Lippitt et al. 1994), or to harvest as well from "scrawny" or unusual-looking plants to ensure genetic diversity (Basey et al. 2015; Dorner undated; Houseal 2009).

Seed collection guidelines commonly suggest that collecting seed from at least 30 to 50 individuals selected randomly and evenly from throughout a population will capture 95% or more of the genetic diversity of a plant population (e.g., BLM 2015b). Some researchers believe these guidelines may not reflect sample sizes needed to capture multiple alleles at multiple loci. If the goal is capturing the full range of genetic variation in the source population, hundreds or thousands of plants may be needed to sample rare alleles (DeBolt & Spurrier 2004; M. Hamilton 1994; Knapp & Rice 1994). Crossa et al. (1993) and Crossa and Venscovsky (2011) present a statistical-genetics approach that indicates sample sizes of 160 to 250 plants of a random-mating population would be needed to ensure a 90-95% likelihood of capturing at least one copy each of alleles that are present at allele frequencies of 0.05 or higher at each of 150 loci. Based on a range of theoretical and empirical evidence, Frankham et al. (2014) indicate that, at minimum, an effective population size $Ne = 1000$ is required to maintain long-term evolutionary potential in naturally outbreeding species; in smaller populations the ability to evolve will erode with time. Converting Ne into mean adult census population size (N) requires information on the Ne/N ratio, which is available for few species. Average measured Ne/N is 0.10–0.14; but may vary tremendously among species or even populations. Based on this, Frankham et al. (2014) suggest that the minimum viable population size (N) for long-term persistence is of the order of several thousand individuals. An additional factor is clonality, in that populations of clonal organisms may contain relatively few genetic individuals (Vallejo-Marín et al. 2010), and what appears to be many parental plants may represent far fewer genetic individuals.

Optimal seed harvesting from hundreds or even thousands of rigorously randomized parent plants may be practically and economically unfeasible. Commercial seed suppliers must control seed collection costs while adhering to purity standards and narrow limits on percent weed contamination. Land managers often view requirements for using specific species and seed sources as barriers to planting native seed, because these requirements increase project cost and complexity (Jones & Johnson 1998; Mustoe 2014; Richards et al. 1998). Cheaper species are more readily used than expensive ones, resulting in the common cost-control practice of using a minimal number of vigorous, generalist species (Richards et al. 1998). If propagules of less-prolific or specialist species are neither planted nor present in the soil, these species may be indefinitely excluded (Grime 1998; Pywell et al. 2003). Ironically, rare and specialist species are often those most in need of restoration.

If planting a full range of species is too costly, presumably ensuring a full genetic range within all those species would be costlier still. Where portions of a population cannot be sampled easily or efficiently, the need to preserve genetic variation may conflict directly with the need for cost control. Under such circumstances, it seems likely that genetic variation will suffer. An obvious example is location of part of a population on steep, unstable slopes or other areas that are physically hard to reach; such locations may correspond to differing selective regimes and genetic composition.

Differential distribution of genetic variation within an otherwise fairly uniform environment would be less apparent but may be important. Manual collection of seed entails pulling or cutting off seed heads, or sometimes harvesting whole plants. If the plants are growing in clumps, seeds can be harvested by the handful. If target plants are intermixed with undesirable species, however, collectors may need to harvest stem by stem. Practical and economic considerations thus conspire to push seed collectors onto dense patches of the target species, where they can harvest far more seeds per hour while more easily avoiding weeds. This study explores whether this practice results in unconscious selection between genetically differentiated subpopulations. The relative ease and efficiency of harvesting seeds from high-density patches means that seed collection may be biased with regard to genetic variation tied to patch density. This study examines the potential relationship between intraspecific patch density and genotype.

Chapter 4. Ecological Restoration Policy

Large-scale restoration projects in the United States commonly take place on public lands or in response to regulatory requirements, and as a result the restoration process is substantially driven and controlled by state and especially by federal legislation and regulation. Government policies affect which seeds are planted, through definitions of appropriate germplasm sources and through assignment of restoration responsibilities and costs. Policies and practice regarding planting native species on public land reflect both the social purposes of restoration and scientific perspectives on how best to revegetate disturbed ecosystems (Richards et al. 1998). Key concerns include preservation of at-risk species and their critical habitats, control of introduced species, and the maintenance or restoration of native ecosystems.

The federal government owns about 640 million acres, or about 28 percent of US land area, mostly in the western states and Alaska. Four agencies administer 609 million acres of this land.

- The US Department of Agriculture Forest Service (USFS) manages 193 million acres; in FY 2013, the Forest Service "sustained or restored" almost 880,000 acres of forest and grassland and restored 987 miles of stream habitat (USFS 2014).
- The Bureau of Land Management (BLM), which is part of the Department of the Interior (DOI), manages 247 million acres, almost all in the western states and Alaska, and administers about 700 million acres of federal subsurface mineral property (Vincent et al. 2014).
- The DOI Fish and Wildlife Service (FWS) administers over 150 million acres of federal land, and through partnerships with other organizations helps manage and conserve a much larger area of non-federal land (FWS 2014).
- The National Park Service (NPS), also part of DOI, manages about 80 million acres.

The Interior Department targeted over 1.1 million acres of land and 879 riparian miles for restoration between 2011 and 2016 (DOI 2012).

While the bulk of this chapter focuses on BLM and USFS, a number of other agencies participate in restoration-related activities. The US Department of Defense (DOD) manages over 14 million acres of federal land (Vincent et al. 2014). Limited development and restricted public access on some military lands has prevented large-scale habitat loss and protected threatened or endangered species, including over 70 species found only on military lands (DOD 2013). The 1960 Sikes Act directs the Interior and Defense Departments to work with each other and with state agencies to maintain wildlife resources on US military reservations (FWS undated). The DOD Strategic Environmental Research and Development Program has supported native-plant research projects geared to producing wear- and weed-resistant native plant genotypes and cultivars for use on military bases, including cultivars that have been released commercially for use in revegetation (Hild 2004; Palazzo et al. 2003; T. Smith & Hild 2011; USACE 2005).

On non-federal lands, the DOD Army Corps of Engineers carries out a wide range of projects and regulatory activities involving water resources, including conservation projects, and has begun addressing the need for "genetic diversity and genetic integrity" in reservoir, wetland,

and estuary projects (P. Bailey & Martin 2007; Streever & Perkins 2000). In the Interior Department, FWS works with other government agencies and private groups in conservation of non-federal lands and on administration of the Endangered Species Act; indeed, by far most of the habitats managed by FWS are on non-federal lands. The agency recently targeted almost 600,000 non-DOI acres for restoration (DOI 2012). The DOI Bureau of Indian Affairs provides funds for restoration-related programs including the return of bison to Native American homelands, tribal wetland rehabilitation projects, and watershed restoration efforts (DOI 2012). The USDA Farm Services Agency's Conservation Reserve and Conservation Reserve Enhancement Programs provide 10- to 15-year rental contracts with farmers in exchange for retiring environmentally-sensitive marginal farm land and for planting species, particularly natives, to prevent erosion, improve water quality, and conserve wildlife habitat. As of September 2015, 24 million acres and over 170,000 stream miles with riparian forest and grass buffers were protected under these programs (USDA 2015). The USDA Natural Resources Conservation Service (NRCS) offers easement programs and assistance to landowners who want to protect and restore privately-owned wetlands and forest (NRCS undated c). The NRCS Working Lands for Wildlife (WLFW) program helps ranchers and farmers create and restore habitat of targeted declining species (NRCS undated d). Ranchers and other partners working with the Sage Grouse Initiative, part of WLFW, have improved habitat conditions on 4.4 million acres (NRCS 2015). The NRCS also operates the Plant Materials Program, which develops plants releases for conservation and restoration.

Evolution of Forest Service and Bureau of Land Management Native Species Policies

The dominant agencies in US native seed policy are the Forest Service and BLM. Indeed, BLM is the largest seed buyer in the Western Hemisphere (BLM 2009). Within these agencies, policies affecting native-species management have evolved in broadly parallel manners, in both cases reflecting opposing pressures to conserve natural habitats and to use land for economic production.

Early 20th-century federal land policies resulted in the vast expansion of national parks, creation of the first federal wildlife refuges, and the development of science-based natural resource management (MacCleery 2008). Following World War II, increased affluence, greater mechanization, and improved transportation increased the demand for natural resources and the capacity to extract them. At the same time, demand for outdoor recreation also increased. As public interest in conservation grew in the 1960s, Forest Service and BLM budgets also grew, new agency staff introduced greater expertise in wildlife biology, soil science, archaeology, and other fields, and legislation shifted the agencies' roles.

The Multiple Use Sustained Yield Act (MUSY) of 1960 and the Classification and Multiple Use Act (CMUA) of 1964 required the Forest Service and BLM, respectively, to manage agency lands not just for economic purposes such grazing, timber, and mining, but also for recreation and wildlife habitat (Richards et al. 1998). In 1965, emblematic of its changing role, BLM replaced its old insignia, which depicted a logger, cowboy, oil driller and surveyor, with an image of a river winding from a snowcapped peak across a grassland (Muhn & Stuart

1988). In 1976, Congress passed the National Forest Management Act and the Federal Land Policy and Management Act, which substantially ended land transfer into private hands and mandated the Forest Service and BLM, respectively, to develop in-depth plans for managing and preserving agency lands (MacCleery 2008; Muhn & Stuart 1988).

The changes in agency policy and culture were reflected in what the agencies planted on degraded lands and after wildfires. During the 1950s, range revegetation projects focused on soil stabilization and forage production, often emphasizing widely adapted introduced species. These introduced plants, such as *Agropyron* species, were used because they compete effectively against undesirable nonnative species; however, they can preempt some native species from planting sites (Richards et al. 1998). Since the 1980s, widespread use of nonnative species in range revegetation has become politically and scientifically controversial (Richards et al. 1998; Morris & Rowe 2014; G. Williams 2005). While SUMY, CMUA and the 1976 management acts supported increased use of native species, field-level native plant polices and manuals took years to appear. Shifting pressures from constituencies supporting or opposing use of native species, vague legislative language, potential legal challenges, land managers' discretionary interpretations of policies, limited budgets, and limited expertise resulted in erratic implementation of native-species policies (Richards et al. 1998).

In 1994, several federal agencies announced joint policies affecting native-species management (FWS 1994). In January, the USFS, FWS, BLM, NPS, and the Commerce Department National Marine Fisheries Service (NMFS) issued a memorandum of understanding to improve cooperation in protection of declining species not yet listed as threatened or endangered. In July, FSW and NMFS jointly issued several policies calling for better species-protection planning and implementation via greater cooperation among stakeholders, application of multispecies and ecosystems approaches, and increased use of scientific expertise. In September, USFS, FWS, BLM, NPS, NMFS and several other federal agencies issued an MOU pledging cooperation in protecting listed species. In May 1994 and most directly affecting native plant policy, the USFS, NPS, BLM, FWS and several other federal agencies entered into an MOU to link resources and expertise and develop a coordinated national approach to plant conservation. This effort evolved into the Plant Conservation Alliance (PCA), a collaborative partnership including 12 federal agency Members and over 300 non-federal Cooperators (BLM 2014b and 2014d). In 2015, the PCA Federal Committee, chaired by BLM, issued the *National Seed Strategy for Rehabilitation and Restoration 2015-2020*, again aimed at a more coordinated approach to ecological restoration (PCA 2015). The Strategy entails cooperation among BLM, 11 other federal agencies, and tribal, state, local, and private entities, including commercial growers, to ensure availability of genetically appropriate seed for restoration.

In 2001, Congress created the Native Plant Materials Development Program (NPMDP) to foster a stable, economical supply of genetically appropriate native plant materials for restoration of public lands, "the first program to coordinate native plant materials development on a national scale" (BLM 2015c). The program, administered by BLM, seeks to expand seed collection, curation, and storage capacity, and to develop seed transfer guidelines. In the same year, BLM joined with the Millennium Seed Bank Project[7] of the Royal Botanic Gardens, Kew, to found Seeds of Success (SOS), which is discussed further below.

In 2006, the Forest Service published a framework for restoration and management of lands managed by the agency (USFS 2006). The framework describes increased threats to forest and grassland health (fire, disease, insects, invasive species, loss of open space, unmanaged outdoor recreation, and climate change) and insufficient Forest Service response due to internal agency limitations (limited understanding of ecological restoration, a focus on individual programs, and inadequate planning, budgeting, and management). The framework recommends development of a national policy on restoration, greater emphasis on restoration planning, and better integration across the agency and its stakeholders. In 2008, the Chief of the Forest Service issued a national ecological restoration policy for Forest Service lands aimed at consistent, cohesive agency approach, incorporated in Chapter 2020 of the *Forest Service Manual*. The policy was administered under an interim directive that was reissued several times, and was made permanent in 2016 (USFS 2013, 2015a, and 2016). The policy set a goal of management for ecological resilience in the context of uncertainty and climate change, and describes the adaptive capacity of ecosystems as including within-species genetic diversity, biodiversity within ecosystems, and heterogeneous ecosystem mosaics within landscapes and biomes. While these policies give all USFS resource-management programs restoration responsibilities, the Forest Service continues to support economic activities such as energy development, recreation use, grazing, and timber production.

Vast amounts of "local" seed. BLM obtains seed for revegetation and restoration from private seed collectors and growers, often in response to wildfire. In 1999, BLM purchased 6.5 million pounds of seeds, of which 70% was non-native. In 2007, following the establishment of the Native Plant Materials Development Program, BLM purchased nearly 7.5 million pounds of seeds, over half of which were native species. In 2009, however, BLM purchased less than 0.5 million pounds (BLM 2011; Christensen 2000). In years with extensive range fires, demand drives seed prices up; for example, in 2012, the price of bluebunch wheatgrass seed increased from $4–5 a pound to $20 per pound (Dickie 2015). To help reduce market fluctuations stemming from unpredictable wildfire events, BLM has proposed to buy about 3 million pound of seeds annually (BLM 2011). DOI's Rangeland Fire Initiative began creating a national network of seed-storage facilities. By 2015, three facilities in Idaho and Nevada could store up to two million pounds of seed, far more than the 800,000 pounds housed in the Boise facility in 2010 (Dickie 2015).

Seeds of Success. BLM established Seeds of Success (SOS) in 2001 to collect wildland native seed for research, development, germplasm conservation, and ecosystem restoration, as the first step of the NPMDP (BLM 2014c and 2014e). SOS quickly came to include many partners, including federal agencies and non-federal organizations committed to employing a

---

[7] The Millennium Seed Bank Partnership, based in the United Kingdom, is the world's largest *ex situ* plant conservation program, and works with a network of partners across 80 countries to conserve the germplasm of a substantial percentage of at-risk plant species.

common protocol for coordinating seed-collection and species-targeting efforts. As of 2014, SOS had garnered over 14,800 native seed collections for its National Collection.

The USFS Seed Extractory in Bend, Oregon cleans most of the seeds collected by BLM workers. The first 6,000 seeds in each collection are preserved in cold storage, half at the USDA's National Center for Genetic Resources Preservation in Fort Collins, Colorado, and half at the Western Regional Plant Introduction Station in Pullman, Washington.[8] Remaining seeds are used for restoration, native-plant materials development by USDA-NRCS and other entities, common-garden studies, and seed-increase protocol establishment (BLM 2014c and 2014e). SOS set a goal of amassing 10 to 20 collections of each target species across its range in order to develop genetically appropriate ecotypes.

Development of Seed Zones

Regulatory approaches to delineating appropriate seed-source zones have varied among and within agencies and have evolved over time. During the mid-20th century, concern about seed origins of commercial trees arose from observations that conifer plantations established using nonlocal seeds sometimes failed following severe weather or outbreaks of insects and disease, while adjacent, naturally regenerated stands survived. Plantation failure often followed decades of healthy growth (St. Clair & Johnson 2004). In 1970, the USFS established roughly 85 conifer tree zones in California incorporating genetic clines and environmental gradients to ensure that conifer seeds were planted in appropriate environs; other timber-producing states and British Columbia developed similar tree-seed zones (Alden 1991; Johnson et al. 2004; Kitzmiller 1990). Keeping tree-seed transfer within the same zone and the same 500' elevation band was meant to ensure adaptation of seed stock to planting sites. The regional seed zones now used by most federal authorities for herbaceous and shrub species broadly follow the model of seed zones used for commercial conifers (Johnson et al. 2004; Knapp & Rice 1996).

The size and delineation of nonconifer seed zones has continued to evolve. USFS has developed a mapping system for stratifying the earth into progressively smaller areas of increasingly uniform ecological potential, as determined by vegetation, soils, lithography, geomorphology, and climate. In 1976, an initial map divided the US into ecoregions and subregions (R. Bailey 1976). The Bailey map was followed by development of section and subsection maps and descriptions (ECOMAP 2007). USFS delineated California into 19 sections and 222 subsections (Miles & Goudey 1997).

Beginning in the 1990s, individual USFS and BLM offices defined "local" germplasm in terms of tree seed zones or ecological subsections (Lowe 1994; USFS Eastern Region 2004). BLM's California office called for germplasm to originate in the same USFS ecological subregion, vegetation series, and general soil type within 500' elevation of the project site; further tailoring could be based on research regarding individual species (Hastey 1996). Other BLM offices had differing policies (BLM undated b and c). BLM additionally put forward plans to develop seed-transfer zones for 250 restoration "workhorse" species (BLM 2009).

---

[8] In the first ten years of SOS, portions of seeds collected from specified species (the "Kew list") were sent to the Royal Botanic Garden, Kew, for long-term storage in the Millennium Seed Bank.

The BLM has its own seed-zone system. The *Integrated Vegetation Management Handbook* defines "local" in terms of Omernik Level III ecoregions, at least as a starting point in lieu of species-specific data (BLM 2008).[9] These ecoregions are based on maps developed by the US Environmental Protection Agency in collaboration with other federal and state agencies, and denote areas within which ecosystems have broadly similar geology, soils, climate, hydrology, wildlife, and vegetation. While the Omernik and Bailey systems are conceptually similar, the resulting maps differ in detail. The Omernik Level III map divides the continental United States into 105 ecoregions. California is divided into eleven Level III ecoregions and Nevada into three (EPA 2016; USGS 2016).

Seed transfer within Omernik Level III subregions may be most appropriate for widespread plants living in areas with limited environmental gradients. They may be less appropriate in areas with strong variations in climate, soils, or topography, and where small, isolated populations may differ from one another genetically (S. Miller et al. 2011). Level III land segments can be further subdivided into Omernik Level IV ecoregions, or by overlaying the Level III map with another land-segmentation system (Johnson et al. 2010). For example, the USFS Western Wildland Environmental Threat Assessment Center (WWETAC) has developed generalized provisional seed zones based on climate indices including mean monthly maximum and minimum temperatures and an aridity index calculated as a function of mean annual precipitation and mean annual temperature. The intersection of temperature and aridity bands results in the delineation of 64 regions of relative climatic similarity (Bower et al. 2014). (This method does not appear to distinguish zones that differ in seasonality of precipitation.) Superimposing Omernik's level III ecoregions over these climate zones can help to distinguish areas that are similar climatically yet different ecologically. WWETAC has indicated that these zones are only a starting point for guiding seed transfer, and should be used in conjunction with species-specific information and local knowledge of microsite differences. Empirical seed zones have been developed for a handful of species, primarily western-state grasses, via common-garden studies assessing production, morphology, phenology, and physiological traits. Genetic variation is linked with collection-location environments by means of regression models, and the results extended to delineate seed zones (WWETAC undated).

Another approach is represented in focal-point models that account for biogeoclimatic features of the landscape, such as climate, aspect, and soil characteristics. A model developed by Hargrove and Hoffman (2004), for example, does not rely on predefined boundaries. Instead, it relies on degrees of similarity between source and potential planting sites in different dimensions of a statistically-generated multivariate space incorporating as many as 25 factors at fine resolution, including elevation, temperature, precipitation, soil characteristics, and solar inputs. Depending on model specifications, this method can easily divide the United States into thousands or even millions of cells — which may well ensure precise ecological matching of seeds to restoration sites, but may not be very practical for the massive and often unpredictable germplasm needs of agencies like BLM.

---

[9] The Omernik ecoregions are modified from Omernik 1987.

Assigning Costs and Responsibility

On public lands, post-fire rehabilitation and mining reclamation cover the largest land areas and have substantially different goals and methods (Richards et al. 1998). Wildfire protection and post-fire treatment are increasingly important for both the Forest Service and BLM, and post-fire planting is the largest federal use of native seeds. The proportion of USFS budget spent on wildfire suppression increased from 13% to over 40% between 2004 and 2014 (USFS 2104).

In the 1970s, Congress directed federal agencies with wildland fire protection responsibilities to overcome historical inefficiencies. Catastrophic fires in the late 1980s and 1990s spurred efforts to develop a more comprehensive wildland fire strategy. In 2002, the Secretaries of Agriculture and the Interior established the Wildland Fire Leadership Council to support a more unified federal approach to wildfire preparedness, suppression, and post-fire rehabilitation. As of 2016, the council included the US Fire Administration (part of the Homeland Security Department), with representation of state, tribal, county, and municipal government officials (Forests and Rangelands 2015). In 2009, Congress passed the Federal Land Assistance, Management, and Enhancement (FLAME) Act, which provided separate funding for emergency wildfire suppression to reduce transfers from other programs; and required DOI and USFS to develop a cohesive strategy to address wildland fire problems (DOI-OPA 2012).

Wildfires are treated as emergencies under the National Environmental Protection Act (Richards et al. 1998). Post-fire planting has historically focused on immediate watershed protection, and secondarily on the need for wildlife habitat, forage production, and preventing spread of invasive species. In the 1990s, USFS emergency fire procedures called for reseeding to establish immediate-term cover to protect watersheds, life, and property, but not to improve wildlife habitat or other ecosystem functions. In contrast, BLM was directed to reseed burned areas with species, including native plants, that would also provide wildlife habitat (Richards et al. 1998). These agencies now have more unified policies calling for natural revegetation or planting of "genetically local" native species when possible, using non-invasive introduced species only as needed for stabilization (USFS 2015b).

The second largest revegetation need after fire is mine reclamation (Richards et al. 1998). There are 14,000 active mines in the US, including about 1,700 coal mines, 11,000 quarries and sand or gravel mines, and 1,200 metal and non-metal mines; over 90% of the total are surface mines (CDC 2015). Where a single large party is responsible for damage to publicly owned resources, as is common in the case of mining, cost of restoration can be assigned. Depending on the nature and location of the mineral resource, public-lands mine reclamation is administered by BLM, USFS, or state authorities. These agencies generally require the mine operator to seek establishment a plant community that will support designated post-mining land uses, typically a native ecosystem capable of natural successional processes (30 CFR; 36 CFR; Richards et al. 1998; USFS 2008). Costs are often assigned through bonds that can be used to pay for restoration if the responsible party defaults on its commitment to restore the ecosystem to some specified condition. The value of restoration bonds have unfortunately not always been sufficient to pay for reclamation, and in some cases it has been more attractive to default (GAO 2011; Holl & Howarth 2000).

There are about 5,200 abandoned coal mines and 39,000 known and an estimated 100,000 – 500,000 unidentified or uncharacterized abandoned hardrock mines in the US, including over 47,000 in California (BLM 2015c; CA-AMLU 2000). These mines mostly date from before imposition of mine closure and revegetation standards. Reclaiming these sites can be costly; for example, a single abandoned mine site, the Pleasant View Project in Hopkins County, Kentucky covered 250 acres and required 10 tons of seed for revegetation (OSMRE 2002). DOI's Office of Surface Mining Reclamation and Enforcement (OSMRE) administers the Surface Mining Control and Reclamation Act and manages reclamation of abandoned coal mines, substantially via grants to states and tribes with approved programs. In 2016, OSMRE recently set a goal of reclaiming 14,000 acres degraded by past coal mining (OSMRE 2016).

Reclamation of abandoned hardrock and uranium mines falls within the purview of several agencies, in particular BLM's Abandoned Mine Lands program and its partners. The primary focus in reclamation of abandoned mines is managing safety and health hazards, such as open shafts and toxic runoff; however, many of these sites are revegetated with native species (BLM 2014a). Reclamation of abandoned mines has faced challenges due to unclear jurisdiction, differing agency approaches, and inadequate funding (EPA 2010). A per-ton fee on coal helps pay for reclamation of abandoned coal mines, but no similar funding source exists for abandoned hardrock mines, which are reclaimed using other agency funding (DOI 2012; GAO 2012). Abandoned sand, gravel, and clay pits and quarries are not addressed by federal programs and are managed at state and local levels (BLM 2014a).

There are also over 800,000 active and as many as three million abandoned oil and gas wells in the US (A.R. Brandt et al. 2014a and 2014b; Kang et al. 2014). Active oil sites are supposed to be revegetated at the oil company's cost, generally with native species, as part of closure operations (DOI & USDA 2007). The cost of closing abandoned oil and gas sites falls on state agencies, whose focus is on capping and safety.[10]

Where damage has already occurred, recovering restoration costs via fines can be difficult, especially if the responsible party cannot be identified or made to pay; if the disturbance resulted from the activities of many small parties, such as pollution in urban streams; or if there is no responsible party, as in the case of exotic species in California grasslands. Under these circumstances, restoration costs may be paid through taxation, including excise taxes related to environmental disturbance, much like taxes on coal to reclaim abandoned mined lands. Paying for restoration through general taxation can be justified by the provision of ecosystem services to society as a whole and/or removal of damages such as those caused by wildfires (Holl & Howarth 2000).

Compensatory Mitigation: Restoration as Replacement

In circumstances not governed by mining law, unavoidable habitat damage may fall under requirements of the National Environmental Policy Act (NEPA, 1969), the Clean Water

---

[10] Abandoned oil and gas wells notably leak large amounts of methane, a potent greenhouse gas (Kang et al. 2014).

Act (1972), or the Endangered Species Act (1973) (Holl & Howarth 2000; Zedler & Callaway 1999). The US and several other countries nominally employ a mitigation hierarchy of: (1) avoiding impacts, (2) minimizing impacts; and (3) offsetting or compensating for residual impacts as an option of last resort. In practice, however, avoidance is ignored more often than it is implemented (Clare et al. 2011).

Compensatory mitigation can entail generating or sometimes preserving replacement habitat of a size similar or larger to land slated for development, with the underlying assumption that acreage is a reasonable surrogate for function (USACE 2002). Biodiversity offsets are thus intended as a means of balancing development and conservation goals. Under the Clean Water Act, options for compensatory mitigation, in order of preference, are

- mitigation banks, which are large sites where habitat is created, restored, or preserved, thus creating mitigation credits that can be sold to permittees required to provide compensatory mitigation;
- in-lieu fee programs, which allow for funds to be paid to governmental or non-profit natural resources management entities to satisfy compensatory mitigation requirements, and transfer the responsibility of providing compensatory mitigation to the in-lieu program sponsors; and
- permittee-responsible mitigation, in which the permittee retains full responsibility for establishing, restoring, or preserving compensatory habitat (EPA undated).

Mitigation banks have advantages compared to individual mitigation projects, in that they result in larger (albeit fewer) conservation sites, consolidate economic, planning, and scientific resources, and improve economies of scale (Mack & Micacchion 2006). Generating a single large mitigation site in lieu of many smaller sites, however, increases the biological cost if the single site fails (Maron et al. 2012; Moilanen et al. 2009). As of 2011, at least 45 mitigation programs existed around the world, and at least 27 programs were under development, underpinning a multibillion-dollar mitigation market (Madsen et al. 2011). The majority of mitigation credits in the US, however, are still provided through permittee-responsible mitigation (Madsen et al. 2011).

Since 1980, federal law has required compensatory mitigation for wetland losses, often through wetland creation or restoration (BenDor 2009), making wetland mitigation perhaps the oldest offset program (McKenney & Kiesecker 2010). Wetland mitigation in the US can therefore illustrate the underlying issues for many other habitat offsets. In 1987, the US adopted a "no net loss" policy requiring full replacement of impacted wetlands in terms of acreage and functionality (BenDor 2009). Mitigation policies call for offsetting activities to be in place before allowing project impacts, thus requiring developers to anticipate project impacts and finance up-front costs (McKenney & Kiesecker 2010). US wetland mitigation policy allows for offset-credit releases as project milestones are reached, such as securing a site, developing plans, and planting vegetation. An estimated 90 percent of US wetland banks sell some credits before achieving any performance standard (McKenney & Kiesecker 2010). In some cases, as much as 100 percent of offset credits have been released once adequate hydrology was established but before any planting occurred (Mack & Micacchion 2006).

If replacement habitat is of lower quality, acre-for-acre mitigation means a net loss of habitat. Although US offset policy calls for no net loss of wetland function, the ecological function and quality of a compensation site may not match that of the impact site. Mitigation ratios are used to account for these differences; thus an impact site of 10 acres might be replaced by a 30-acre mitigation site of lower per-acre quality. Less clear is how to calculate a ratio that will ensure the mitigation site at least matches the ecological function of the impact site (Moilanen et al. 2009; Maron et al. 2012). The law allows for offset transactions based on land area alone; for example, Ohio’s ratio is 1-to-1 for wetlands restoration and 2-to-1 for preservation.

A number of observers have questioned the adequacy of such ratios. Mack & Micacchion (2006) examined the 12 oldest of Ohio's 25 wetland mitigation banks, and found that only three of them successfully met restoration criteria, five passed in some areas, and four functioned as shallow unvegetated ponds rather than as wetlands. None of the mitigation banks provided adequate amphibian habitat. Site monitoring by the Army Corps and EPA had not resulted in amelioration of the mitigation-bank failures. Similarly limited success has been reported for a wide range of restoration and mitigation projects (Moreno-Mateos et al. 2012; Rey Benayas et al. 2009; Suding 2011), implying that mitigation ratios now in use are inadequate.

Methods suggested to improve compensatory mitigation would multiply its costs. BenDor (2009) recommends lengthening the time developers are responsible for mitigation-site monitoring, encouraging mitigation methods that have significant lead times (such as banking) to reduce time lags, enforcing the use of viable compensation sites, and raising mitigation ratios. Moilanen et al. (2009) propose "robustly fair offset ratios" to incorporate the uncertainties of effective restoration and time discounting, and demonstrate that even moderate estimates of time lags, potential for failure, and discount rates can result in offset ratios that are one or even two orders of magnitude larger than current ratios. Curran et al. (2014) conducted a meta-analysis of 108 studies to estimate the time required for a disturbed, restored ecosystem to converge on the species diversity of undisturbed habitat. They found that disturbed ecosystems can eventually recover, and that recovery time is significantly shortened by active restoration; nevertheless, large, unavoidable lag times and uncertainty of success make reasonable compensation ratios range from 20: 1 to 100: 1. One can easily imagine that developers might find the resulting mitigation costs to be unacceptable.

Shifting Political Sands

This chapter has described efforts by government, in particular at the federal level, to balance competing demands for consumption and use of natural resources against care and protection of ecosystems. During most of the last several decades, governmental policies have moved largely in the direction of maintaining natural systems. Federal restoration policy, however, continues to shift in response to political mood swings.

In January 2017, Donald Trump assumed the US presidency. The administration's proposed 2018 budget included deep cuts in environmental programs, including major initiatives that incorporate ecosystem restoration in the Great Lakes, Chesapeake Bay, South Florida, and the San Francisco Bay delta. As of June 2017, information on the BLM website regarding the Seeds of Success program had been severely truncated, and a number of program documents appeared to be no longer available. Environmentalists have of course been profoundly dismayed at the shift towards resource extraction and away from valuing natural systems for their own sake. Elimination and reduction of ecological restoration programs will also displace many workers. The 126,000 people employed in restoration considerably exceed the number employed in coal mining, and restoration indirectly supports an estimated additional 95,000 jobs (BenDor 2015). For growers who have taken on the challenge of growing native-plant seed for use in restoration, moreover, policy shifts away from planting native seeds could devastate their investments.

Chapter 5. Study Area and Problem Description

Study Area

This project takes place in the context of California grasslands, which are the subject of many restoration efforts. Grasslands and oak woodlands now cover respectively about 4.4 million and 1.7 million hectares on the coast and in the foothills surrounding the central valleys of California (CDF-FRAP 2003). California grasslands receive limited precipitation, ranging from about 12 cm per year in the southern San Joaquin Valley to nearly 200 cm per year near the Oregon border, with considerable year-to-year variation (Heady et al. 1992). Nearly all this precipitation falls between November and April. For perennial species, rapid early growth may be of critical importance to allow plants to grow large and deep-rooted enough to endure the long summer drought (A. Dyer et al. 2000; Dyer & Rice 1999).

California's native perennial grasses are mostly bunchgrasses (Heady et al. 1992). Studies of *S. pulchra* in pre-Columbian grassland conjecture a range of one to seven plants per m^2, with basal area comprising up to 10% of total plant cover and foliar cover up to 25% (Bartolome et al. 2013; Heady et al. 1992; K. White 1967). Space between clumps of perennial grasses probably featured annual grasses and forbs (A. Dyer & Rice 1997; Heady et al. 1992). Many of the perennial grasses are long-lived, and may have always recruited episodically, particularly if conditions supporting successful recruitment, such as reduced competition and adequate rainfall, were infrequent (J. Hamilton et al. 1999).

The historical composition and extent of California native grasslands is uncertain. Clements (1934) observed *Stipa pulchra*-dominated associations growing along railroad rights-of-way, and suggested that California's grasslands were once dominated by this species. Phytolith evidence, however, supports the contention that much of what is now annual grassland did not predominantly support native perennial grasses (Evett & Bartolome 2013). Parts of California's current grasslands may have been dominated by woody vegetation (J. Hamilton 1997), coastal scrub (Hopkinson & Huntsinger 2005), or forbs (Solomeschch and Barbour 2004).

Loss of native prairie. California prairies underwent extensive floristic changes beginning around 1775 with European exploration and settlement. Introduced annual plants such as *Avena*, *Bromus*, and *Erodium* species invaded and substantially replaced the native species (Bartolome et al. 2013; Heady et al. 1992). This change is one of the most extreme examples of community invasion over a large area and a short time (J. Hamilton et al. 1999). The resulting California annual grassland type consists mainly of introduced species, some 400 of which have been recorded (McNaughton 1968). Species introductions continue to the present, and introduced perennial grasses are increasingly common near the coast (Corbin & D'Antonio 2010).

Native grasses are now less visible and in many places absent from their original range, remaining most common in areas of relatively greater precipitation, such as near the coast (Jackson 1985), and inland on serpentine soils (McNaughton 1968). Introduced grasses now typically comprise 80-97% of foliar cover, and define most California grasslands (Heady 1956; Heady et al. 1992). Where the introduced annual grasses originated, they are ruderal species adapted to colonizing grazed or cultivated sites. Because the introduced plants are largely annual, the floristic composition of the grassland changes from year to year in response to environmental fluctuations such as fire, grazing, and climate variations (Bartolome 1979; Bartolome et al. 1980; McNaughton 1968). This year-to-year variation in annual cover, coupled with the long life and infrequent recruitment of the perennial species, creates difficulty in determining whether native species are still decreasing, stable, or increasing (J. Hamilton et al. 1999).

The factors causing the destruction of native grasslands are not fully understood. Explanations for grassland conversion include introduction of farming and livestock grazing, changes in fire regime, and competitive suppression by introduced species (Heady et al. 1992). These factors overlap in space and time over the whole of California grasslands, making them difficult to untangle (Corbin et al. 2004).

Agriculture and grazing. Soil cultivation physically destroys many perennial forbs and grasses, which may subsequently fail to reestablish. Stromberg and Griffin (1996) found that several native plant species, including *S. pulchra*, *Poa secunda*, and *Chlorogalum pomeridianum*, occur only on land with no history of cultivation. *S. pulchra* only slowly recolonizes previously disturbed areas.

Grazing is often cited as an important factor in floristic change (Jackson 1985). Livestock were introduced to California in 1769, and within a century had expanded into the available rangeland, devastating the range during the drought of 1862-64 (Kosco & Bartolome 1981). Some studies associate grazing by domestic livestock with reduced species richness and increased soil exposure (Stromberg & Griffin 1996), while others examine potential benefits of grazing treatments to reduce competition from annual grasses (Bartolome et al. 2004; Corbin et al. 2004; Dyer 2002). Grazing and grazing-removal studies in California grasslands have shown inconsistent benefits to populations of native perennial grasses (Bartolome et al. 2004; Corbin et al. 2004; HilleRisLambers et al. 2010; Hull & Muller 1977; Seabloom et al. 2003).

Fire regime. Lightening-related fires are rare in most of California, making fire an infrequent prehuman event in the present study area. In oak woodlands, Native Americans sometimes ignited fires to discourage insect pests, make acorn-gathering easier, and promote the abundance of herbaceous food plants (M. Anderson 2007). The Gold Rush and agriculture resulted in continued burning up to about 1900, followed by fire suppression. Fire has varying effects on native and introduced grassland species, depending on factors such as season (Larios et al. 2013), and has been studied as a means of decreasing annual species (Bartolome et al. 2004; Dyer 2002; Hatch et al. 1991; Seabloom et al. 2003). Changes in fire patterns may have contributed to reduced prevalence of natives.

Competitive suppression. The introduced annual species that began arriving with early European explorers and continued during Spanish settlement are mainly of Mediterranean origin and preadapted to California’s climate (Hatch et al. 1991; Jackson 1985). These species come from a genetically rich, ecologically wide-ranging part of the world, and had survived millennia of selection under Old-World anthropogenic conditions including species introductions, livestock grazing, and cultivation. Variation among these species in phenology and climate adaptation allows different suites of exotics to dominate from year to year across the many habitats of California grassland (Bartolome 1979; Bartolome et al. 1980; Gulmon 1979).

The introduced grasses are mostly winter annuals that evade rather than endure the long summer drought, by growing rapidly, setting seed, and senescing before water in the upper soil is gone. These species are adapted to colonizing disturbed sites and in some cases to low nutrient availability (Jackson 1985), and may benefit from ongoing disturbance by gophers (Heady et al. 1992; Seabloom et al. 2003; Stromberg & Griffin 1996). The annuals produce large numbers of seeds (Larios et al. 2013); the resulting large seed pool may compensate for high mortality when growing conditions are poor (Aarssen 2000; Bartolome 1979). The relatively large seeds and rapid germination of some introduced annuals give them a head start on growth and competition (Hull & Muller 1977; Jackson 1985; Stromberg & Griffin 1996). They extensively exploit the upper soil to 50 cm depth, and during early spring they are able to reduce moisture levels in the upper 30 cm of soil more rapidly than perennials (Holmes & Rice 1996; Seabloom et al. 2003). Their relatively high allocation to shoot biomass allows for rapid photosynthetic assimilation and growth, followed by generous seed set. Annual grasses can reduce light levels near the soil surface through their continuous, dense cover and accumulation of dead biomass, potentially suppressing native forbs and reducing species diversity (Molinari & D'Antonio 2014). In contrast, native perennial species allocate more biomass to roots, grow more slowly, and develop deeper roots than annuals (Holmes & Rice 1996), which allows them to tap deep soil resources and maintain green tissue long after the annuals have senesced. The competitive nature of the introduced species may have been a primary factor in the elimination of native plants from much of their range, and may be the greatest impediment to grassland restoration.

The competitive environment natives now experience may be very different from the one in which they evolved. Rather than competing with a few large bunchgrasses, native grass and forb seedlings now must cope with many small annual plants (Dyer & Rice 1997). Failure of perennial bunchgrasses to return to dominance with reduction of grazing, difficulties establishing stands via seeding, and competition experiments all point to interference by introduced species. Coexistence between annual and perennial grasses may be based on the ability of perennials to gain access to resources of deeper soil zones, thus compensating for their slower aboveground growth (Seabloom et al. 2003).

The relative importance of disturbance versus competition in grassland conversion may have differed across California climates and ecosystems. In the hotter, drier interior grasslands, exotic annual grasses clearly suppress both seedling and adult native grasses (Bartolome & Gemmill 1981; A. Dyer & Rice 1997). In the coastal prairie (within 100 km of the coast), native grasses compete more effectively with annuals (Seabloom et al. 2003), indicating that grassland conversion there may have required widespread disturbance or stress (Corbin & D'Antonio 2004). In a coastal-prairie study, Corbin and D'Antonio (2004) found that exotic annual grasses suppress natives in the first growing season, while natives have no effect on exotics; in subsequent seasons, the natives suppress the annual grasses, and the effect of the annual exotics on native-species productivity becomes smaller over time. They concluded that where the experience of summer drought is modified by maritime influences, native grasses may have an incumbency advantage starting with their second year. The introduced perennial grasses that are becoming more prevalent in the coastal grasslands function similarly to native perennials, but in some cases can outcompete the natives (Corbin & D'Antonio 2010).

Seabloom et al. (2003) suggest that loss of native grasslands was likely due to heavy grazing reducing the number of native plants, and the resulting loss of seed production and impaired recruitment led to continued dominance by introduced annuals. Perennial grasses can take decades to invade and increase in numbers because of limited seed dispersal (Stromberg & Griffin 1996). Dispersal limitation combined with prodigious seed production on the part of introduced annuals means that severe disturbance, such as combined drought and fire, can tip the balance in favor of introduced annuals (Larios et al. 2013). Observing that a mixture of native perennial grasses seeded at 2500 seeds/m^2 was able to establish effectively and suppress productivity of annual grasses, Seabloom et al. (2003) concluded that restoration of perennial grasses in some areas would only require direct seeding.[11]

Restoration of California Grasslands: Limited Prospects

Complete restoration of California's grasslands to pre-Columbian conditions would require permanent removal of competitive introduced species, which makes full restoration effectively impossible. Instead, native grassland restoration efforts focus on seeding, transplanting, or increasing stands of native species and reducing cover of exotics (Corbin et al. 2004; Huntsinger et al. 1996) to produce a mixed annual-perennial grassland. "In essence we are attempting to establish a new set of ecological processes that will create and maintain a visual appearance that mimics California's native prairie" (Hatch et al. 1991, p. 346).

Even if complete restoration cannot be accomplished, there are reasons to pursue partial grassland restoration via introduction of native species. In situations such as roadside planting, the consistent year-to-year soil cover and extensive, persistent root systems of native shrubs and perennials make these species useful for weed suppression and erosion protection (Bugg et al. 1997; Cione et al. 2002; Holmes & Rice 1996). The perennial species tap deep soil moisture, extending seasonal productivity and potentially removing resources that might otherwise be available to invasive summer annuals (Holmes & Rice 1996; K. Rice et al. 1993; Tilman 1997). Several of the native grasses, including *S. pulchra*, are valuable as forage due to their palatability (Hatch et al. 1991). Adding perennials to the existing annual grasslands may increase cover, productivity, and stability of ecosystem functions through greater species diversity (Schwartz et al. 2000; Tilman 1997 and 2004; Tilman et al. 1996). Where cultivation or disturbance has reduced pools of soil carbon, grassland restoration may be more effective than natural succession in hastening recovery of soil carbon (Baer et al. 2002). Restoration of native grasses may improve habitat for oaks (K. Rice et al. 1993) and for native annual forbs that have become rare in the wake of invading annuals, so long as populations of the invading species are drastically curtailed (C. Brown & Bugg 2001; Carlsen et al. 2000). Native grasses may also improve habitat

---

[11] This seeding rate may be compared with the present study's estimate of natural seed production, which averaged about 400 seeds/m^2 where *S. pulchra* was present at low density, and about 2000 seeds/m^2 where *S. pulchra* density was high.

and resource availability for native animal species (Lesica & Allendorf 1999). Finally, restoration of California's native species may be desirable for aesthetic reasons and for the intrinsic worth of native ecosystems (Holl & Howarth 2000).

Stipa pulchra

This study uses *Stipa pulchra* to examine potential subpopulation differentiation in relationship to environmental restoration. One of the species commonly used in California grassland restoration, *S. pulchra* is currently the most widely distributed native perennial grass. It grows naturally in a variety of soil types and on all slope aspects from the coast to the Sierra Nevada foothills, in habitats receiving from 56 to over 127 cm annual precipitation and at elevations ranging from near sea level (in the present study) to 890 m (Bartolome & Gemmill 1981; Knapp & Rice 1998). Estimated longevity of *S. pulchra* individuals is in excess of 100 years (J. Hamilton et al. 1999 citing unpublished data).

Several researchers have described *S. pulchra* as the dominant perennial grass in California prior to European settlement (Heady 1977; Heady et al. 1992). Some of its characteristics, however, indicate that *S. pulchra* may have acted as a colonist of disturbed sites. *S. pulchra* germinates under all but the most severe moisture stress, and establishes more easily on bare ground than under mulch (Bartolome & Gemmill 1981). It is often found growing in disturbed areas, such as roadcuts adjacent to undisturbed grasslands (Heady et al. 1992; also observed during the present study), and thrives after competitors are removed by fire and grazing (Bartolome & Gemmill 1981; but see Larios et al. 2013). It self-pollinates, allowing reproduction at low densities that might occur after long-distance dispersal or disturbance (Aarssen 2000; Larson et al. 2001; Stebbins 1957). Much like introduced annuals, *S. pulchra* produces copious, relatively large seeds, and germinates rapidly, but in most circumstances its seedlings do not effectively compete with introduced annual seedlings (Bartolome & Gemmill 1981; Larson et al. 2001).

Competition from introduced annuals affects both seedling and adult *S. pulchra*, although the ecological impact of competition may be greatest at seedling and recruitment stages (Howard & Goldberg 2001) and varies according to site conditions. *S. pulchra* germinates and leafs out more slowly than introduced annuals, reaching peak density later and suffering greater mortality than the introduced annuals during the growing season (Bartolome & Gemmill 1981; Stromberg & Griffin 1996). Bartolome and Gemmill (1981) found that *S. pulchra* seeds planted in pots with seeds of the introduced annuals *Bromus hordeaceus* and *Festuca myuros* germinated more slowly and attained lower density with high densities of the annual species, even though *S. pulchra* emergence may be accelerated in the presence of specific introduced species and its total germination is not affected (Dyer et al. 2000). *S. pulchra* seedling mortality is high during the spring peak growth period for annuals (Bartolome & Gemmill 1981). Survivorship of *S. pulchra* seedlings is low (roughly 1 percent, even on undisturbed soil), and as few as 0.01 percent of *S. pulchra* seedlings planted into annual grassland survive into their fourth year (Stromberg & Griffin 1996).

Mature *S. pulchra* plants have as much as 94–98 percent year-to-year survival rate in the presence of annuals, but their growth and fecundity is commonly reduced by competition (A. Dyer & Rice 1999). In a multiyear study of weeding, grazing, and burning treatments, A. Dyer and Rice (1997) found that the rapid growth and strong intraspecific competitive effect of *S. pulchra* in weeded plots was not apparent on unweeded plots, indicating that diffuse competition from annuals had an overriding effect. Dennis (1989) found that weeding *S. pulchra* plots in mid-December tripled tiller number and somewhat increased flowering. J. Hamilton et al. (1999) found that *S. pulchra* is water-limited in the presence of annuals, and that removal of annuals increased *S. pulchra* performance to the same degree as watering without weeding.

Overview of This Research Project

This study uses *S. pulchra* to ask whether economic considerations of seed collection conflict directly with restoration goals of capturing genetic variation and establishing well-adapted new populations. Do *S. pulchra* plants in sparse patches, where seeds would be difficult to collect, differ genetically from plants in dense patches, where seed collection would be most efficient? Would seed harvesting on dense patches alone lead to omission of genotypes found in sparse patches? Seed collectors paid on a product-weight basis may be driven to bypass sparse stands. If plant genetic charcteristics differ according to patch density, harvesting solely from dense patches might skew the genetic composition of collected seed and affect the range of microenvironments to which the collected seeds may be adapted.

This study focuses on patches where a great deal of seed is readily available, which I call "thick" patches, in comparison to "thin" patches where there is little seed of the target species. While "thick" and "thin" correspond roughly to dense and sparse relative cover of *S. pulchra*, the correspondence is far from exact, and patches were selected for study based on apparent availability of seed prior to any cover measurements. Thus for experimental methods and results reported herein, *S. pulchra* culm density, rather than *S. pulchra* cover, more accurately reflects the study approach.

The experimental hypothesis (H1) underlying this study is that plants grown from seeds collected from thick patches differ genetically from plants grown from thin-patch seeds, with divergence potentially including

- emergence time and growth rate;
- reproductive timing and allocation;
- morphological characters such as leaf length and width, number of tillers, and below- versus aboveground biomass; and
- differential response to watering treatments.

The corresponding null hypothesis (H0) is that plants from thick patches do not differ from plants originating in thin distributions. Rejection of the null hypotheses would follow detection in a common garden setting of consistent, significant differences between plants correlated with intraspecific density in the field

This study employs *S. pulchra* from three sites. Concerns regarding genetic variation among plants from different sites are well incorporated in restoration literature. Use of multiple sites is intended here to address whether differences between plants from thick versus thin plots are consistent among sites, and to compare variation among populations to variation within populations.

The study approach entailed characterizing patches (plots) with differing amounts of available *S. pulchra* seeds, collecting seeds from these plots, and planting them in a common garden. Effects on soil moisture mediated through competition are often cited as an important impact of introduced grass species in California (A. Dyer & Rice 1997; Holmes & Rice 1996), and unusually dry or wet winters may improve competitive outcome for *S. pulchra* by, respectively, desiccating annual seedlings or relieving water shortage (J. Hamilton et al. 1999). The common garden experiment therefore included two watering treatments to explore differential moisture response among plants from different sites and plot types.

Chapter 6. Methods

Field Study

As described in Chapter 1, this project focuses on differences in plants from "thick" patches of *Stipa pulchra*, where large amounts of seed would make seed collection relatively quick and easy, versus "thin" patches, where scarcity would render seed collection more difficult and time-consuming. In addition, it addresses potential variation in plants correlated with other field variations such as absolute cover and species diversity. Seeds collected during the field study were used in the common-garden study discussed later in this chapter, and patch characteristics measured in the field study were used in analysis of common-garden measurements.

Time and place of field study. Field observations took place during the spring and summer of 2000 and 2001. Overall weather in the study area was cooler and drier in the months preceding the second field season compared to the first (Table 1). The study patches were in three sites in the San Francisco Bay Area that represent a range of soil and climate conditions, had experienced little or no disturbance for two or more decades prior to this study, and contain areas of variable *S. pulchra* density (Figure 2)

. ***Point Molate*** (37° 58'N, 122° 25'W) is a rocky hillside northwest of the former Pt. Molate naval refueling station that overlooks San Francisco to the southwest and San Pablo Bay to the north. The site is in the *Ecological Subregions of California* (Miles & Goudey 1997) subsection 261Ad (Central California Coast East Bay Terraces and Alluvium). The hillside, while privately owned, is unfenced and used by hikers and others as *de facto* open space. The plots were on the west-facing part of the hillside in relatively steep terrain.

At the National Climatic Data Center cooperative weather station in Richmond, about six km southeast of Pt. Molate, the average annual daily minimum temperature between 1981 and

Table 1
Climate Conditions During Field Study Years (October 1 to September 30)

Location	Date range	Total precipitation (cm)	Mean temperature (degrees C)
Richmond	1999 – 2000	59.2	13.6
	2000 – 2001	36.4	12.5
Graton	1999 – 2000	104.7	14.1
	2000 – 2001	65.7	13.7

Western Regional Climate Center. http://www.wrcc.dri.edu. Accessed March 10, 2015.

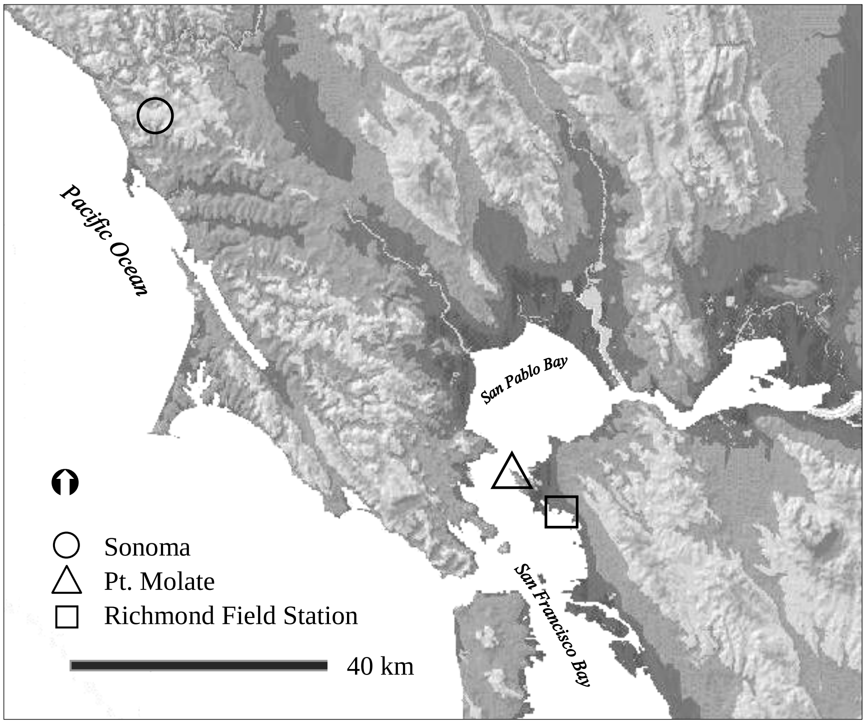

Figure 2.
Map of Study Area

Adapted from California Department of Fish and Game 2005.

2010 was 10.2°C, with an average daily low temperature of 6.1°C in January, the coldest month (Western Regional Climate Center 2015). Average annual daily maximum temperature was 19.3°C, with average daily high temperatures of 23.4°C in September, the warmest month. Total annual precipitation in those years averaged 63.3 cm, reaching its maximum in midwinter with an average of 12.3 cm of rain falling in January, and diminishing to less than 1 cm during the summer months. Observations indicate that Pt. Molate has the shortest growing season of the three sites, with grass foliage senescing a few weeks earlier in spring than at the other sites.

Soil at Pt. Molate is Millsholm Loam, a loamy, mixed, thermic Lithic Xerochrepts in the Los Osos/Millholms series, a well-drained upland soil formed from interbedded shale and finegrained sandstone (Welch 1977). This soil is medium-tan in color and rocky. Occasional rock outcrops indicate that soil is underlain in some areas with shallow bedrock.

Richmond Field Station (RFS; 37° 55'N, 122° 20'W) is adjacent to San Francisco Bay, and is owned by the University of California at Berkeley. Like Pt. Molate, RFS is in the ecological subregion and subsection 261Ad (Miles & Goudey 1997). Richmond Field Station is about four km from the National Climatic Data Center cooperative weather station in Richmond, and about nine km from Pt. Molate. Precipitation and temperature regimes at Richmond Field Station and Pt. Molate are broadly similar.

The RFS grasslands were probably once used for grazing and harvesting hay. Available evidence, including the presence of *Stipa pulchra*, *Elymus glaucus*, and *Wyethia angustifolia*, implies that the site was not severely disturbed prior to 1910. In about 1910, the area was subdivided into parcels, roads were graded, and a sidewalk system was installed, but no permanent structures were built. Aerial photographs taken in 1939, 1946, and 1953 may indicate past irrigation but show no development or uniform cultivation (David Amme Associates 1993).

Soil at the Richmond Field Station is a fine, montmorrillonitic, thermic Typic Pelloxererts belonging to the Clear Lake Series of the Clear Lake-Cropley Association. Formed from fine-textured alluvial deposits, this is a dark-gray clay soil (David Amme Associates 1993; Welch 1977). The soil is poorly drained, and the site has less than one percent slope, so that water stands in wet swales for days at a time in the rainy season. During the summer, the soil shrinks, becomes very hard, and sometimes cracks. RFS includes the only coastal prairie grassland on lowland clay soils in the greater East Bay area.

Ocean Song Farm and Wilderness Center, Sonoma County (Sonoma; 38° 24'N, 123° 1'W) is a former ranch in a rolling landscape about 8.5 km west of Occidental in Sonoma County (Kathleen Kraft *pers. comm.* 2001). The *Ecological Subregions of California* (Miles & Goudey 1997) places this site in Section 263A: Northern California Coast, near the boundary between subsections 263Ag and 263Aj (respectively the Coastal Franciscan and the Coastal Hills–Santa Rosa Plain subsections). The site is currently operated as a private not-for-profit learning center (Ocean Song 2014).

The Sonoma site is the most mesic and has the widest annual and diurnal temperature range of the sites. At the National Climatic Data Center cooperative weather station in Graton, about 13 km east of Ocean Song, the average annual daily minimum temperature from 1981 to 2010 was 5.8°C, with an average daily minimum temperature in December, the coldest month, of 1.9°C (Western Regional Climate Center 2015). The average annual daily maximum temperature was 22.3°C, with an average daily high temperature of 28.6°C in July, the warmest month. Total annual precipitation averaged 107.4 cm, reaching its maximum in midwinter with an average of 21.3 cm falling in January and less than two cm during the summer months. During the field observations in summers of 2000 and 2001, the study area was often cloaked with heavy ground-level fog in the mornings, which would lift gradually before noon and return around sunset. Ground and plant surfaces were sometimes wet with condensation until midmorning. In contrast, RFS and Pt. Molate sometimes had overcast skies but no ground fog.

Soil at the Sonoma site is in the Yorkville-Laughlin association of sandy-clay and clay loams (ArcGIS 2014; V.C. Miller 1972). Surface soil in the study patches is intermediate between Pt. Molate and RFS soils in rockiness. Yorkville soils are derived in part from serpentinized igneous rocks, and the Ocean Song area includes some patches of serpentine soil. *S. pulchra* is better able than most introduced grasses to grow well on serpentine soil (McNaughton 1968), and *S. pulchra* originating on serpentine soil may differ genetically and phenotypically from other *S. pulchra* ecotypes (Huntsinger et al. 1996). The plots at the Sonoma site all contain vigorously-growing introduced grasses, which implies they are sited on non-serpentine soil.

Plot selection. At each site, patches containing relatively large numbers of seed-bearing *S. pulchra* culms were designated as "thick," and represent stands that might attract a person seeking efficient collection of seeds. Each thick patch was matched at the same site to a "thin" patch with broadly similar slope, aspect, general composition of forb, legume and grass species, and overall appearance, but with far fewer *S. pulchra* culms. Plots were loosely paired in terms of background vegetation to avoid, for example, having all thin plots at a given site dominated by *Bromus* while thick plots were dominated by *Avena*. The core factor in designating patches as thick or thin was apparency of *S. pulchra* culms, rather than density or percent cover of *S. pulchra*. In practice, thick patches had disproportionately higher density of *S. pulchra* than thin patches. Study patches were large enough to accommodate a 2 × 3 meter plot area with a buffer at least one meter wide of similar *S. pulchra* culm frequency.

A total of 14 plots were established, in seven plot pairs distributed among the three sites (Table 2). The plots were spread out across the site at Pt. Molate, such that the members of each thick-thin plot pair were not paired in space. Plots were also unpaired in space at RFS, but because the site is smaller than the other two, all the plots were relatively closely spaced. At Ocean Song in Sonoma, each thick plot was within a few meters of its paired thin plot, with the two pairs spread farther apart.

Table 2
Distribution of Field Plots Among Sites, Plot Pairs, and Plot Types

Hierarchal Level							
Site	Pt. Molate			RFS		Sonoma	
Plot Pair	PtM1	PtM2	PtM3	RFS1	RFS2	Son1	Son2
Plot Type:							
Thick ("K")	P1K	P2K	P3K	R1K	R2K	S1K	S2K
Thin ("N")	P1N	P2N	P3N	R1N	R2N	S1N	S2N

As *Stipa* seed and pollen are wind-distributed, plants are apt to be more closely related to individuals located directly up- or downwind than to those located perpendicularly across the prevailing wind. To reduce the likely degree of genetic relatedness among plants in each plot, plots were oriented perpendicular to prevailing wind patterns as indicated by the lodging pattern of the grasses at Pt. Molate and RFS. At Ocean Song, the prevailing wind is from the northwest, but is not strong enough at ground level to result in a consistent lodging pattern in the grasses, so the plots in one pair were oriented roughly north-south and the others east-west.

Plot characterization and seed collection. A 2-meter × 3-meter plot was established in each of the selected thick and thin patches at the three sites. Fieldwork on these plots included collecting seeds for common-garden planting, and characterizing the plots by measuring

- percent absolute cover,
- percent relative cover of *S. pulchra* and of other species,
- number of *S. pulchra* culms per m^2,
- number of seeds per culm, and
- height of *S. pulchra* culms.

As described later in this chapter, field methods evolved during the first weeks of the 2000 season, particularly affecting data collection on the first four plots at Pt. Molate.

Plot subdivision. Division of the plots into smaller units allowed data collection at different scales and supported subsampling within each plot. Each 2 × 3 meter plot was divided into six meter-square subplots, and subplot corners were marked with survey flags that remained in place through both years of fieldwork. Each meter-square subplot was further divided into 10 cm × 10 cm cells using a grid system (Fehmi & Bartolome 2001) made by weaving yardsticks through the grass at 10 cm intervals. The grid was used in subsampling, as described below.

Absolute and relative cover. Cover was visually estimated at the meter-square subplot scale, including

- absolute cover to a maximum of 100 percent,
- relative cover of individual species to a maximum of 100 percent, and
- area of soil covered with recent gopher tailings, versus soil that was unvegetated for other reasons, in 2001 only.

Culm count. All *S. pulchra culms* were counted each 10 cm × 10 cm cell, omitting culms that were not open enough to be sure of species or that appeared sterile. Some culms produced only pale, unfilled seeds, and others were affected by a blight that replaced the entire panicle with dark-brown spores initially enclosed by the sheath. If seed had dehisced, there was no way to determine whether the released seed was viable or not; culms were recorded as viable unless they clearly were not. Culms that might have developed or opened after plot characterization were also omitted; this would have most strongly affected plots at Pt. Molate that were sampled before the end of the growing season in 2000.

Seed collection. The common-garden study described later in this chapter required collecting sufficient seeds from across each plot, ideally in sibships (i.e., seeds from the same culm). During each field season, four 10 cm × 10 cm cells in each meter-square subplot (totaling 24 cells per plot) were chosen at random for seed collection. All ripe seeds in these randomly selected plot cells were collected, with each culm's seed put into a separate, labeled envelope identifying the culm. In 2000, the panicle was collected as well in order to count florets. On thin plots, the limited number of culms led to collection of seed from plot cells adjacent to the random cells, or from all culms with enough seeds for purposes of the common garden study. To ensure having sufficient seed, additional seed was harvested in bulk from all plots, generally from culms that lacked sufficient ripe seed to represent a sibship (i.e., fewer than six seeds). To the extent practicable, seeds were bulk-collected in small groups; for example, a seed envelope might contain seeds taken from several culms growing inside one 10 cm × 10 cm plot cell. As a result, some envelopes of bulk-collected seeds may have represented single parent plants. Bulk-collected seeds were riper in some cases than seeds from single culms, particularly for seeds collected in 2000 from Pt. Molate plots.

Culm heights in the field. The same randomly selected 10 cm × 10 cm cells used for seed collection were also used for measuring *S. pulchra* culms. Height was measured from the soil surface to the bottom of the highest glume on each culm. This meant omitting closed culms, which may not have been fully elongated, and culms with blight. Culm heights were not measured on the first four Pt. Molate plots in 2000.

Where possible, four plot cells per subplot (24 per plot) were used for height measurements. If there were not enough *S. pulchra* culms in four cells to produce adequate samples (about 20 culms per subplot), four or eight more random cells per subplot were added to the sample. In practice, getting a reasonable sample often required more cells than anticipated, particularly on thin plots. Moving across a subplot breaks the culms, so it was not possible to increase sample size from a subplot after initial sampling. Instead, if the first subplot sampled in a plot provided a skimpy sample of culms, subsequent subplot sampling was adjusted by adding more random cells. As a result, the number of plots cells used sometimes varied from one subplot to the next within a plot, as the original estimate of number of plot cells needed for adequate sampling met reality. In several thin plots, height measurements were taken from all mature, unbroken culms.

***S. pulchra* culm collection for seed counting.** The randomly selected 10 cm × 10 cm cells were also used to collect panicles for seed-production estimates. *S. pulchra* bears one seed per spikelet, so each pair of glumes remaining on a culm after seed drop represents a seed. In 2000, all *S. pulchra* culms from the randomly selected 10 cm × 10 cm cells were bagged, and florets (i.e., pairs of glumes) were later counted in the lab. As described above, the number of plot cells sampled varied depending on the frequency of culms, and all open culms were collected from some thin plots. Where the resulting sample contained too many culms to reasonably count florets, culms were randomly subsampled within subplot in the lab. Collecting culms for floret counts was added to the sampling protocol after fieldwork began, so on four Pt. Molate plots, culms were collected in 30 cm strips along the north, east, and south edges of these plots for floret counting.

Aboveground biomass production in the field. In 2001, biomass samples were collected from the field plots to determine aboveground production. From each of the random cells initially selected that year for seed collection and culm counts, aboveground plant material was clipped to approximately 1 cm above soil level and placed in an individually labeled bag. Some of the selected plot cells had no visible aboveground biomass; these cells were counted as having zero biomass. Where recent gopher activity produced bare soil, gopher mounds may have hidden current-year growth.

Most of the biomass samples contained some material remaining from the prior year's growing season. In the lab, each bag's contents were separated into material from 2001 and 2000 based on appearance. Material that was largely intact and mostly golden-yellow to reddish-brown was assumed to be current-year growth, whereas material that was dull, friable, and gray or black from weathering was assumed to be left over from 2000. The 2001 material was rebagged separately from the 2000 material, dried at 65^{o}C for 24 to 48 hours, and weighed. Because samples were collected after most seeds of all species had fallen, mass of seed production was not captured. The separation of material from Sonoma County into 2001 and 2000 origin was complicated by the collection of these samples in September. By this time, the frequent heavy fog and dampness had begun the weathering process, so that some materials in these samples were not unambiguously separable by year of growth.

Summary of fieldwork. The products of seed collection and plot characterization included

- seeds collected and labeled by sibship (culm), plus bulk-collected seed
- number of *S. pulchra* culms
- culm characteristics (height and number of florets), and
- plot characteristics: "snapshot" estimates of percent live cover, species composition, and aboveground biomass production.

Common Garden Study

The common-garden pot study examined differences among *S. pulchra* plants grown from the field-collected seeds. The central question was whether variation among plants in the common garden would correlate with the biotic environment of maternal plants, in particular whether systematic differences would exist between plants from thick and thin plots. The steps in the common garden study were

- weighing seeds and allocating them among block and treatment groups,
- taking measurements during plant emergence and growth, and
- harvesting the plants for further measurements.

Seed weighing. Seeds were weighed to determine initial biomass, which may reflect maternal environmental effects (Roach & Wulff 1987) and is critical in plant establishment and early competition. Seed collection in the field centered on obtaining enough seeds from each plot for common-garden planting rather than on determining differences among plots in mean seed weight. As a result, inferences cannot be drawn about the sites based on weight of field-collected seeds. Seed collection in the field was not wholly random, because the amount of ripe seed available varied considerably among plots and between years.

Awns were removed before the seeds were weighed. Seeds that were very green and small, damaged, or hollow were discarded as nonviable; these seeds generally weighed very little, 1.0 mg or less. Remaining seeds were weighed on a Sartorius BP 201 S analytic balance, nominally to the nearest 0.1 mg, although observations indicate precision was not better than 0.3 mg.

As described above, seeds were collected into envelopes, with each envelope representing a single culm or small bulked group of seeds. Scrutiny of weights of seeds collected in 2000 revealed that a number had been misweighed. The misweights generally occurred in groups, so that most or all seed weights from a sibship or bulk-collected group would be wrong. Suggested possible causes included poor scale calibration, static electricity buildup in the plastic weigh-boat, and air currents in the room. To correct these problems, the scale was moved to a windowless room, the plastic weigh-boat was replaced with a paper weigh-boat or no weigh-boat, and scale-calibration frequency was increased. In order to identify misweighed batches, several seeds from each culm or bulk-collected group were reweighed; where misweighed seeds were found, the whole group was reweighed. Weight checks of seeds collected in 2001 revealed no errors.

Data from an earlier greenhouse planting indicated that

- mature seeds (generally mouse-gray in color) had a higher emergence percentage than green seeds;
- small seeds had lower percent germination, e.g., seeds weighing less than 2.2 mg had a germination rate of less than 20 percent, compared to 77 percent for seeds heavier than 2.2 mg; and
- for a given weight, small green seeds had lower emergence rates than small mature seeds.

To improve percent emergence, the common-garden study excluded seeds weighing less than 2.4 mg, and excluded green seeds where mature ones were available.

Seed allocation. Sibships were chosen for planting from culms distributed across each source plot, limiting use of seeds harvested from culms growing near one another. Sibships and seeds within sibships were otherwise selected at random for planting, within restrictions of seed availability and quality. Exceptions to the preferred distribution of seeds and sibships occurred where there were not enough mature seeds of 2.4 mg or more from enough culms in a given plot. Thin plots, particularly at Pt. Molate, contained far fewer culms relative to thick plots, and thus provided fewer culms having six or more ripe seeds. To compensate, small sibships, e.g., two sibships of three seeds each, were combined and distributed among treatments in the same manner as sibships. Bulk-collected seeds were planted where the number of small sibships was insufficient. The number of small families and bulk seeds planted varied significantly by plot type, site, and collection year.

Equal numbers of seeds from each plot and year were allocated between two watering treatments and three temporal planting blocks, which are described under "Growing Conditions" below. A total of 1008 seeds, i.e., 36 seeds per plot per seed-collection year, were used in the pot study. Sibships (or combined sibships) were allocated orthogonally to block and watering treatments to render within-family variance independent of variance due to treatments (Mead 1988). One seed per sibship (i.e., culm) was allocated to each block × treatment combination (as amended by the need to use small sibships and bulk-collected seeds), for a total of 12 sibships per plot:

$$1008 \text{ seeds} = 2 \text{ treatments} \times 3 \text{ blocks} \times 14 \text{ plots} \times 2 \text{ years} \times 6 \text{ sibships/ (year} \times \text{plot)}$$

The thin plot in plot pair PtM2 produced insufficient seed for the common-garden study. To compensate, seeds collected up to 60 cm east of this plot were planted, and a similarly sized area from the western part of the plot was omitted from planting. The added area was part of this plot during the initial, more ambitious 3 m × 3 m field-plot layout, and there were no differences in common-garden results between the original and added areas of this plot.

Planting procedures. Seeds were planted in "Deepots" (Stuewe and Sons, Corvallis, Oregon, USA), which are tapered black plastic pots approximately 6.4 cm (2.5") in diameter and 25 cm (10") tall. The Deepots (hereafter "pots") fit into plastic collars that each hold 20 pots in staggered rows, which provides for hexagonal close-packing of approximately 215 pots per square meter, or 20 per square foot. Most of the pots were previously used, and had been sterilized with bleach solution before use in a related pot study not reported here. These pots were reused without washing for the current pot study. All pots were filled with "UC Berkeley" potting mix provided by the Oxford Tract Greenhouse, which consisted of 0.56 m^3 fine sand per m^3 peat moss, contained no fertilizer, and had relatively poor drainage. The potting mix was autoclaved prior to use.

Before planting, each group of 20 pots sharing a collar was assigned to a block × treatment group, and the individual pots in each collar were randomly allocated to a specific plot and year. Seeds were randomly distributed to the pots designated for that plot and year in each block × treatment group. Seeds were planted singly, each in the center of its own pot, stipe-end down so that the distal end of each seed was about five mm below the surface of the potting mix. Planting took place over a four-week period. To synchronize emergence, the planted pots remained dry and under cover until their initial watering.

Growing conditions. The common-garden plants grew outdoors for about 20 weeks from initial watering to harvest. The plants grew on two wooden tables in the UCB Oxford Tract parking lot, with each table's plants assigned to a watering treatment described below. The tables ran lengthwise east-west about two meters south of a lathhouse. The growing period for the common garden, March to August, differed from the natural growing season for *S. pulchra*. The asphalt of the parking lot radiated considerable heat during the summer. Fans in a nearby greenhouse periodically discharged warm, humid air intermittently through the lathhouse and over the collar array. As a result, the common-garden seedlings experienced a warmer environment than is common for *Stipa pulchra* in the wild.

Temporal blocks. The logistics of planting, growing, monitoring and harvesting large numbers of individual plants dictated dividing the study into three equal temporal blocks set one week apart. While this division was purely practical, it had substantial effects on growth of the plants. The influence of blocks likely stemmed from increasing temperatures during the common-garden study (Figure 3).

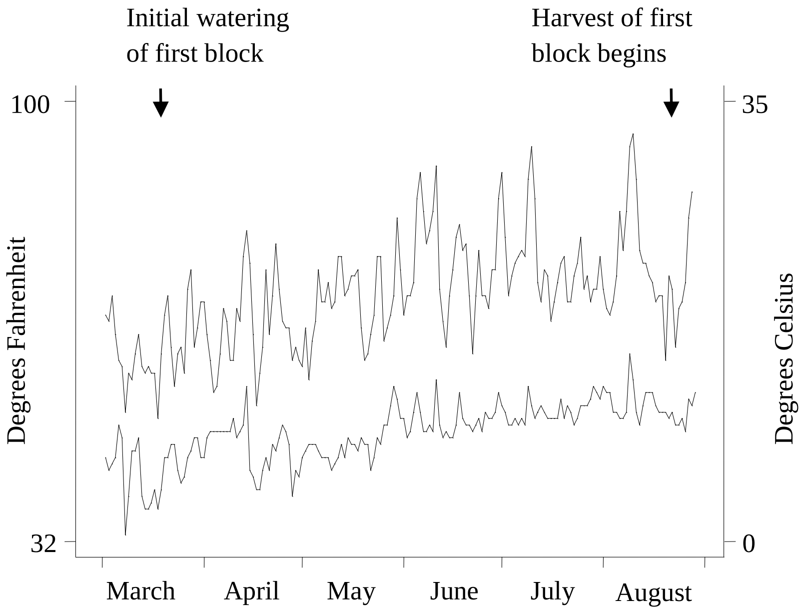

Figure 3.
Daily Maximum and Minimum Temperatures During Common-Garden Pot Study

Data from NOAA 2014

On March 8, the first block of planted pots was moved onto the tables and watered. The next two blocks followed at one-week intervals, and the new sets of pots in their collars were interspersed among others in the same watering group. When all blocks had been moved to the tables, each table held 27 collars in two rows. A 28th collar with pots containing unplanted potting mix was placed in the southwest corner of each array of collars to make two rows of 14 collars each.

To minimize temperature fluctuations, collars were pushed together on the tables so that the interior pots were in hexagonal close-packing array. During the first two weeks, wooden boards were leaned against the south-facing side of each array to reduce solar heat gain. When all three blocks were on the tables, the boards were removed, the exterior pot surfaces of each array were covered with aluminum foil crimped to the tops of the pots, and boards were then placed against the collars on all four sides of each array. The boards came to about four cm of the tops of the pots. The pots and boards remained in place until the end of the experiment.

Watering treatments. Moisture is a critical limiting factor in California grasslands, and potentially interacts with inter- versus intraspecific competition. Watering was geared to keeping one set of pots quite moist, and the other somewhat dry. The watering scheme evolved during the course of the study. All three temporal bocks experienced the shifts in watering simultaneously, which resulted in some variation among blocks in watering treatment.

On the day each block was moved to the tables, it received its first watering. Pots in the "wet" group were again watered the next day. Thereafter for the first several weeks, the wet group was watered three times per week at 2- and 3-day intervals, and the "dry" group was watered twice per week at 3- and 4-day intervals. This schedule was shifted as needed in response to rain, which sometimes resulted in slightly longer or shorter intervals between soil wetting times. Greenhouse staff initially applied diluted fertilizer to all plants once per week as part of the plants' watering schedule, using approximately 450 g "Plantex" fertilizer (Plantco, Inc.) diluted in 338 liters (80 gallons) tap water (Table 3). Otherwise, ordinary tap water was used for watering.

For both watering treatments, watering was initially geared to saturating the soil at each watering. In the initial weeks of the experiment, soil in the dry group dried to a finger's depth (about five cm) between waterings in warm weather while remaining moist at the bottom; in very

Table 3.
Constituents of Plantex Fertilizer

Constituent	Percent
Nitrogen	20
Phosphorus	20
Potassium	20
Boron	0.02
Copper	0.05
Iron	0.10
Manganese	0.05
Molybdenum	0.0005
Zinc	0.05
EDTA	1.0
Chlorine (max)	0.3

warm weather, soil in the wet group also dried to a finger's depth. Starting June 1, to sharpen the difference between treatments, the watering schedule was shifted to an 8-day schedule in which the wet plants were watered to saturation every other day, and the dry group was watered to saturation every four days. Once per eight days, all plants received diluted Plantex, leaving the potting mix saturated.

On June 7, rolled leaves were apparent on several recently watered plants. By this time, many of the plants had roots growing out of the bottom of the pots and spreading laterally on the surface of the wooden tables. In the case of the plants with rolled leaves, the extending roots were brown and decomposed-looking, indicating they suffered from root rot, probably *Pythium* species (Robert Raabe, *pers. comm.* 2002). As the potting soil had been autoclaved prior to use, likely sources of infection included the tables, which had seen many years of service, and pathogens present in the seeds. Not surprisingly, most of the affected plants were in the more frequently watered group. The majority were localized in a few collars, which may have reflected sources of infection on the tables, or areas on the tables where water formed puddles under the pots. On June 14, to reduce further damage, watering to saturation was replaced with timed watering (a set number of minutes moving back and forth over the plants with a sprinkler wand), which reduced the amount of water used roughly by half. To reduce the stress this put on the dry group, all plants were watered every other day, with the plants in the dry group receiving half as much water as the plants in the wet group. From late June through late July, watering times were incrementally reduced to gradually dry down the plants, eventually reaching about one-third the watering levels of mid-June. During this time, the amount of fertilizer was proportionately reduced, and the wet and dry groups continued to receive the same amount of fertilizer.

Herbivore control. Plastic bird netting draped over the pots during the early weeks of growth protected the plants from birds. After a snail injured several seedlings, snail bait was placed around but not in the pots to prevent further snail and slug damage. The damaged plants were omitted from statistical analyses of data collected after the damage occurred.

Measurements. The data collection schedule followed the same intervals as the original blocking schedule, so that a given measurement took place for each block at the same number of weeks from initial watering (Table 4). Measurements of growth and reproduction taken during emergence, growth, and harvest were aimed at identifying systematic differences among plants from different plots. Of particular interest were functional traits important in differential adaptation to competitive versus disturbed or (to a lesser extent) stressful environments (Dietz et al. 1998; Grime 1988; McIntyre et al. 1999; Weiher et al. 1999).

Emergence. For eight weeks, the array was checked daily for seedling emergence. During the first few days for each block, a few seeds were dislodged by watering, and were re-embedded or covered with a pinch of soil. A number of seedlings later emerged markedly off-center in their pots, indicating seed movement due to watering.

Early growth and morphology. At seven and 13 weeks after initial watering of each block, each plant's tillers were counted, and its height was measured as the taller of leaf length or culm height. In early July, about 16 weeks after initial watering of the first block, width of the

Table 4.
Common Garden Measurements

Measurement	What measurement may reflect
Seedling emergence time	Establishment success in competitive conditions
Tiller number	Space acquisition Clonality Longevity
Aboveground biomass at harvest	Competitive ability Growth rate
Belowground biomass at harvest*	Competitive ability Stress tolerance Growth rate
Height	Competitive ability Seed dispersal distance
Leaf width*	Stress tolerance
Flowering phenology	Short-term fecundity
Number of culms and seeds	Short-term fecundity
Weight of offspring seeds	Parental investment Potential establishment success of offspring

*Measured for a subset of plants.

widest leaf was measured on 59 percent of the plants. At this point, some plants displayed moisture stress, especially on the south-facing side of the planting array, which made accurate measurement difficult; thus, leaf width measurements focused on plants on the north-facing side.

Reproduction and seed collection. Culms became apparent on a few plants in the last days of May, and were counted weekly thereafter until harvest. Culms were counted as they became mature enough that awns had become visible. Once seeds began ripening, seeds were collected every three to four days by stroking the panicle over an envelope or by picking individual seeds. Indications of seed ripeness included opening glumes, bent awns, and easy dehiscence. Where possible, seeds were collected multiple times from individual plants. All seeds collected from an individual plant were put into an individual labeled envelope. Seed collection initially focused on ripe seed and (towards the end) on seeds from plants due to be harvested, whether ripe or not.

A heat wave in early July caused the majority of culms on the dry-treatment plants to turn yellow and at least partly dry out. Most of the visible seeds on these plants appeared to stop developing, and dead, very immature seeds clung to these culms afterward. Later inspection uncovered a few filled seeds within the culm sheaths. (A similar phenomenon occurs in the field: filled, viable-looking seeds appear enclosed within culm sheaths near the bottom of otherwise dried-out panicles.) All the plants remained green at least at the base, though few of the yellowed plants subsequently formed new culms.

It was not possible to collect ripe seeds from all plants. Some never produced any seeds, and because ripe seeds dehisce rapidly, the few seeds that were produced on some plants escaped collection. Seeds collected from some plants appeared to have been damaged by the July hot spell. Maturity and color formation of these seeds may have been compromised by drying-out of plants as seeds developed, that is, seeds not yet of mature color or size may have developed bent awns, open glumes, and easy dehiscence through plant dehydration alone. Many of the seeds removed from fully open culms, while filled, were green in color.

Harvest procedures. Vegetation harvesting began on July 22, with one block harvested per week. Measurements taken on each plant during harvest included

- length of longest leaf, and height of tallest culm in reproductive plants;
- basal diameter, measured twice in perpendicular directions;
- number of tillers; and
- proportion of green versus senesced foliage

Aboveground biomass was harvested by cutting plants about 1 cm above the soil level, bagging the tops in individual paper sacks, and allowing them to air-dry for several weeks. The roots remained in their pots, wrapped and kept dry with heavy plastic, for several months.

Estimation of seed production in the common garden. Seed production was estimated by counting florets (i.e., glume pairs). For each plant, the culm having the median number of florets was used for counting. Where a plant had an even number of culms, the larger of the two median culms was used. A regression comparing the number of florets on the median culm to the mean number of florets per culm on the same plant was conducted for a subsample of plants consisting of one collar of plants (20 pots) for each block × treatment combination, or about 1/9 of the total plants. In this subsample, florets from all partly-open to fully-open culms were counted. The regression estimated the mean number of florets per culm from the number of florets on the median culm as

$$\text{mean} = 0.8528 \times \text{median} + 2.766$$

This yielded an R^2 of 0.9122 when calculated using the subsample of plants.

All open and partly-open culms from each aboveground biomass sample were separated out and the sheaths opened up to expose hidden florets. The panicles were sorted by estimated number of florets, and the median culm chosen by appearance. Where panicles were broken, the broken-off top was mated with the bottom that seemed the closest match. All florets on the median culm were counted, including immature florets and those affected by the July heat wave, but ignoring any wispy, apparently sterile florets.

Offspring seed weight measurement. During floret counting, all remaining seeds were stripped from the panicles and placed in identifying envelopes. Because some loose seeds bagged with the panicles may have fallen from adjacent plants before harvest, only seeds that were still attached to the panicles were retained. Except for some seeds that had remained on the panicle and enclosed by the sheath, seeds taken from the bagged biomass samples were not wholly ripe. Seeds at apparently comparable maturity had been collected from 24 plants both before harvest and from bagged panicles, allowing for a comparison. Seeds harvested from growing plants were on average six percent heavier than seeds from the same plants in the same maturity class that were harvested from bagged panicles, but this difference was not statistically significant. For 18 plants from which no seeds were collected prior to harvest, seeds collected from the bagged panicles were substituted for seed weighing.

Prior to weighing, seeds were de-awned, and extremely green, unfilled, damaged, brittle, and distorted seeds were discarded. Where seeds remaining in a seed sample varied substantially in color, they were grouped by apparent ripeness:

- mature: medium to dark gray in color with no greenish color, or
- immature: gray-green to yellow-green.

From each common-garden plant, the most mature-looking group of seeds (i.e., one seed-color group) was weighed as a group to the nearest 0.1 mg on a Sartorius BP 210 S scale.

Biomass weights. To finish preparing aboveground biomass samples for weighing, any potting mix and remaining seeds were removed, and each sample was dried in a paper bag at 65^{o}C for at least 36 hours prior to weighing. Roots were subsampled to examine belowground biomass. The subsample consisted of the plants in the first two blocks from six of the field plots (one plot pair from each site), excluding plants affected by root rot or snails. To harvest the roots, each plant was taken from its pot, remaining leaf stubble was cut down to the crown, and potting mix washed off. The roots were fragile and some small roots were lost. The washed roots were dried in individual paper bags at 65°C for at least two days for storage, then again oven-dried at 65°C prior to weighing. Aboveground and belowground biomass samples were weighed to the nearest 0.01 g on Mettler PM600 and Mettler PE3600 scales.

Summary of common garden measurements. The completed inventory of common-garden data included

- planted seed weight and seedling emergence time,
- plant height and tiller count at three growth stages,
- leaf width for a subset of plants,
- basal area at harvest ,
- aboveground biomass at harvest,
- belowground biomass for a subset of plants,
- number of culms per plant

- number of seeds on each reproductive plant's median culm, and
- weight of seeds

Statistical Analysis

This study sets $p \leq 0.05$ as statistically significant and $p > 0.5$ but ≤ 0.10 as marginally significant. All analyses were conducted with Stata 6.0 (StataCorp 1999). Statistical methods employed herein include analysis of variance and covariance (ANOVA and ANCOVA), regression and logistic regression, and chi-square analysis. Some of the regressions employ the "cluster" option provided by Stata, which groups non-independent observations into clusters and calculates robust standard errors to account for lack of independence.

Group variables were employed in some situations, in particular logistic regressions. In the common garden, for example, Pt. Molate seeds had significantly lower emergence rates than did seeds from the other sites; the other sites do not differ from one another. The logistic regression examining emergence percentages therefore retains the group variable "Pt. Molate (vs. the other sites)" as a significant factor.

Data transformation. Few of the response variables had normal distributions. Statistical tables and graphs using transformed data in this study note what transformation was applied. Data transformation methods to improve distributions and correct heteroskedasticity included

- natural-log transform,
- square-root transform,
- Box-Cox transform provided by Stata,[12] which uses an iterative procedure to estimate the value of a constant λ used to create a more normally distributed variable:

$$\text{transformed } y = (y^{\lambda} - 1)/\lambda$$

- logit transformation, where $0 < y < 1$:

$$\text{transformed } y = \ln(y/1 - y)$$

- rank transform.

For some natural-log and Box-Cox transformations, a constant was included in the transformation formula in order to avoid undefined quantities such as ln(0), or to reduce skewness; in the latter case, Stata calculated the constant. In a few cases, data transformation entailed multiple steps (e.g., the square root of logit-transformed data might be used).

Rank transformation served where other transformations were unable to render normal distributions. The use of ranked data in this study follows Conover (1980), who notes that most nonparametric tests are essentially parametric methods applied to ranked data. He recommends

---

[12] G.E.P. Box and D.R Cox. 1964. An analysis of transformations. *Journal of the Royal Statistical Society*, Series B 26: 211-243. Cited in StataCorp 1999.

applying ANOVA and other parametric tests to ranked data and states that while this procedure is only conditionally distribution-free, it is "robust" in that the true level of significance is usually fairly close to the approximate level of significance derived from the test, no matter what the underlying population distribution might be.

Correlated variables. Several explanatory variables in this study's statistical analyses are intercorrelated. Site, for example, correlates with absolute cover. Either variable or both might be statistically significant in a given statistical test; thus, aboveground biomass in the field varied significantly by both site and absolute cover. Multicollinearity can reduce the precision of statistical inference and hinder determining which variables really matter. Where two or more intercorrelated variables were statistically significant, the variable that better explained the variance was retained, and other variables were eliminated if it appeared they did not contribute uniquely to the analysis and if eliminating them did not substantially reduce R^2. Variance-inflation factors were also calculated, and interactions that had variance-inflation factors in excess of 10 were generally eliminated. Finally, for common-garden results, univariate analyses were performed for comparison with multivariate tests; results of both univariate and multivariate tests are summarized in Tables 57-62 near the end of Chapter 8.

Implications of hierarchical data structure. Each seed planted in the common garden had a hierarchy of origin including site and plot pair, which complicates interpretation of results. Nested ANOVA requires that experimental units in the nested level be randomly selected. Although the plots were broadly typical of their sites except for the density of *S. pulchra*, the process of selecting and matching them in pairs meant that the plot pairs did not represent a random sample from each site. Nesting plot pairs within site in ANOVA would therefore not be methodologically rigorous. If plot pairs were treated as nested within site, F for site would be calculated as

$$\text{mean square } (\textit{site}) \, / \, \text{mean square } (\textit{plot pair})$$

The multivariate ANOVAs and ANCOVAs herein, however, do not nest plot pair within site. F for site is calculated as

$$\text{mean square } (\textit{site}) \, / \, \text{error mean square}$$

which has the effect of changing, usually increasing, the likelihood of site being judged significant. This arrangement complicates determination of how within-site variation compares to between-site variation. Where the multivariate test indicates significance at both site and plot-pair levels, a simple nested ANOVA was performed for comparison purposes only; results of these simple ANOVAs are provided along with multivariate results in the next chapters.

Means separation. *A-posteriori* means-comparison tests presuppose that for any α, the likelihood of falsely rejecting the null hypothesis for at least one comparison increases for each additional comparison. If n is the number of comparisons, the chance of committing at least one Type I error is $1-(1-\alpha)^n$. Means-comparison tests seek to correct this by shifting α downward to reflect the number of comparisons. In the Bonferroni adjustment, if α is set at 0.05, α for means separation becomes 0.05/*n*. In a study comparing four treatments and producing four means, for example, the six possible comparisons between means would yield an α of 0.05/6 = 0.0083. From a practical standpoint, the results of means separation tests are commonly reported by multiplying the *p*-value by the number of tests and comparing the adjusted *p* with the nominal α (e.g., 0.05).

In this study, where statistical analysis indicates significance at both the site and plot-pair levels, the Bonferroni adjustment is adapted by setting α in a manner that reflects both levels:

(1) whether sites differ:
    2 levels × 3 between-site comparisons → $\alpha = 0.05/6$
(2) whether plot pairs within sites differ:
    Sonoma and RFS, with two plot pairs each:
        2 levels × 3 sites × 1 within-site comparison → $\alpha = 0.05/6$
    Pt. Molate, with three plot pairs:
        2 levels × 3 sites × 3 within-site comparisons → $\alpha = 0.05/18$

For ease of interpretation, *p* values are adjusted in the text to reflect the shifted α, that is, if α = 0.05/6, *p* was multiplied by 6. Where variation at a given hierarchical level (e.g., among sites) was not significant in the multivariate test, only the remaining levels were subject to means comparisons, and *p* was accordingly adjusted. For frequency data, α and *p* values were adjusted in the same manner.

Pseudo-R^2 in logistic regression. There have been a number of efforts to develop a statistic for logistic regression that is comparable to R^2 as calculated in linear regression. Unfortunately none of these efforts has produced a statistic that is wholly comparable to R^2, and the various pseudo-R^2 methods have differing results (UCLA Statistical Consulting Group 2011). Stata provides McFadden's pseudo-R^2, calculated as

$$\text{pseudo-}R^2 = 1 - [\ln \hat{L}(M_{Full})] / [\ln \hat{L}(M_{Intercept})]$$

where M_{full} = Model with predictors, $M_{intercept}$ = Model without predictors, and $\hat{L}$ = estimated likelihood. McFadden's pseudo-R^2 is provided here in logistic-regression tables, but should be interpreted with caution.

Results: A Prelude

The field study revealed few significant differences between thick and thin plots other than in seed production, and to a limited extent in absolute cover and species diversity. The common-garden study revealed a number of significant differences in growth, morphology, and reproduction that correlated with measurements taken in the field, in particular with culm count and absolute cover on field plots. The following chapter provides a detailed description of field-study and common-garden results, and Chapter 9 discusses some implications of these results.

Chapter 7. Results of Field Study

Overview

This study explores inherited aspects of *Stipa pulchra* growth and reproduction as they correlate with patch characteristics, in particular with cover of *S. pulchra* and other species. The data can be divided into field and common-garden components. Field work, which took place at three sites during the spring and summer of 2000 and 2001, examined differences among plots and provided information on the seeds collected in the field (Table 5). Field observations included cover and composition estimates, weight of aboveground biomass, number and height of *S. pulchra* culms, and count of florets on a sample of *S. pulchra* culms (Table 6). The common-garden study, which is discussed in the following chapter, measured growth and reproduction of *S. pulchra* plants grown from the collected seeds.

Notes on variables, figures, and tables. Tables and graphs indicate the plot pairs by site and number; e.g., PtM1, PtM2, and PtM3 are the three plot pairs at Pt. Molate. The letters K and

Table 5.
Field Study Explanatory Variables: Time and Place of Field Work

Variable	Description
Site	Three sites • Pt. Molate • Richmond Field Station (RFS) • Ocean Song, Sonoma County (Sonoma)
Plot pair	Two to three pairs of plots on each site • PtM1, PtM2, PtM3 • RFS1, RFS2 • Son1, Son2
Year	Year of field work (2000 or 2001)
Date	Date of field observations • in 2000, between 4/21 and 7/13 • in 2001, between 7/10 and 9/19

N respectively indicate thick and thin plot type; thus P1K denotes the thick plot in the pair PtM1. The statistical analyses presented here used culms/m^2 in the field as a covariate, and the thick-versus-thin designation was used primarily in depicting the data. Most of the response variables required transformation for statistical analysis; the transformation used for each statistical test may be found in the table or graph presenting the analysis. The data displayed in graphs is raw (untransformed) data except where noted.

Table 6.
Field Study Results Variables: Field Measurements

Variable	Description
Count of *Stipa pulchra* culms	Culms per m^2 on each plot in each year
Absolute cover of • All species combined • *S. pulchra* • Native perennial grasses other than *S. pulchra*	Visual estimate on each plot in each year
Aboveground biomass	Oven-dry weight of biomass clipped in 2001
Species richness	Count of species on each plot in each year
Simpson's index	Simpson's index D on each plot in each year, calculated as $D = 1/\sum p_i^2$ where p_i is the estimated relative cover of each species (Begon et al. 1990)
Species evenness	Simpson's index D/species richness
S. pulchra culm height	Heights of culms on plots in both years
Seed production per culm	Floret count on culms sampled by plot in 2000

Results

Count of *S. pulchra* culms in the field. Culms/m^2 ranged from six to 149 (Tables 7 and 8). As discussed in Chapter 6, plots were selected in pairs, each including a "thin" member with relatively few *S. pulchra* culms/m^2, and a "thick" member with relatively many. In practice, the number of culms/m^2 varied considerably within plot type, as well as among sites (Figure 4). If plot type or another factor indicating *S. pulchra* density is not included in the ANCOVA, the number of culms/m^2 of plot area does not vary significantly by site, plot pair, year, or date of data collection as main effects. These factors are also nonsignificant in univariate analysis, although RFS plots had a higher culm count per square meter than did plots at the other sites. If absolute cover of *S. pulchra* is included in the ANCOVA, site becomes significant in interaction with year, in that *S. pulchra* cover increased at RFS and Sonoma in the second year, while culm counts dropped at Sonoma.

Cover of *S. pulchra*. Absolute cover of *S. pulchra* ranged from about one to 37 percent (Figure 5). *S. pulchra* made up nearly 70 percent of native perennial grass cover overall. Absolute cover of *S. pulchra* did not vary significantly with site, plot pair, absolute cover, date, or year in univariate or multivariate analysis. Relative cover of *S. pulchra* was higher at Pt. Molate than at the other sites, reflecting the generally lower absolute cover of all species at Pt. Molate. One plot at Pt. Molate had particularly dense cover of *S. pulchra*.

Relationship of culm count to *S. pulchra* cover. The relationship between culm count and cover of *S. pulchra* was not linear. A simplified model of this relationship,

$$\ln(\textit{culm count}) = 2.49 + [0.64 \times \ln(\textit{absolute cover of S. pulchra})]$$

($R^2 = 0.7277$; $p > 0.0001$) indicates that as *S. pulchra* cover increased, the number of culms

Table 7.
***Stipa pulchra* Culms/m^2 and Absolute Cover of *S. pulchra* on Field Plots by Site**

Site	*n*	Culms/m^2 (95% confidence range)	Percent *S. pulchra* cover (95% confidence range)
Pt. Molate	12	37 (19–45)	10.9 (2.6–11.8)
RFS	8	82 (31–128)	10.1 (2.5–16.9)
Sonoma	8	47 (11–74)	9.1 (1.4–16.1)

Means are arithmetic and weighted by year. Confidence ranges are back-calculated from confidence limits for natural-log transformed data.

Table 8.
ANCOVA of *Stipa pulchra* Culms/m^2 Plot Area

$N = 28$
$R^2 = 0.9595$
Adjusted $R^2 = 0.9425$

Source	Sum of Squares	*df*	Mean square	*F*	*p*
Model	21.991	8	2.749	56.35	<0.0001
Site	0.340	2	0.170	3.48	0.0514
Year	1.863	1	1.863	38.20	<0.0001
Absolute cover of *S. pulchra)*	15.955	1	15.955	327.08	<0.0001
Site × year	1.447	2	0.723	14.83	0.0001
Site × *S. pulchra* cover	0.535	2	0.267	5.48	0.0132
Residual	0.927	19	0.049		
Total	22.9174	27	0.849		

Data transformation: ln(*culm count*); absolute cover of *S. pulchra* is also natural-log transformed. **[13]**

relative to the area of cover decreased (Figures 6 and 7). In every plot pair, the thin plot had more culms per unit area of *S. pulchra* cover than the thick plot.

The ratio of culms to *S. pulchra* cover decreased at all three sites between 2000 and 2001, particularly at Sonoma compared to Pt. Molate. In 11 of the 14 plots, the ratio of culms to cover of *S. pulchra* diminished between 2000 and 2001. This shift may have occurred in response to generally cooler, moister conditions in the second field year.

---

[13] In the presentation of common-garden results, culm count in the field is transformed differently for conducting logistic regression. The transformation used for logistic regression produces a somewhat better distribution; however, the natural-log transformations used here produce very similar results in ANCOVA and result in an intuitively clearer relationship between culms/m^2 plot area and culms/m^2 *S. pulchra* cover.

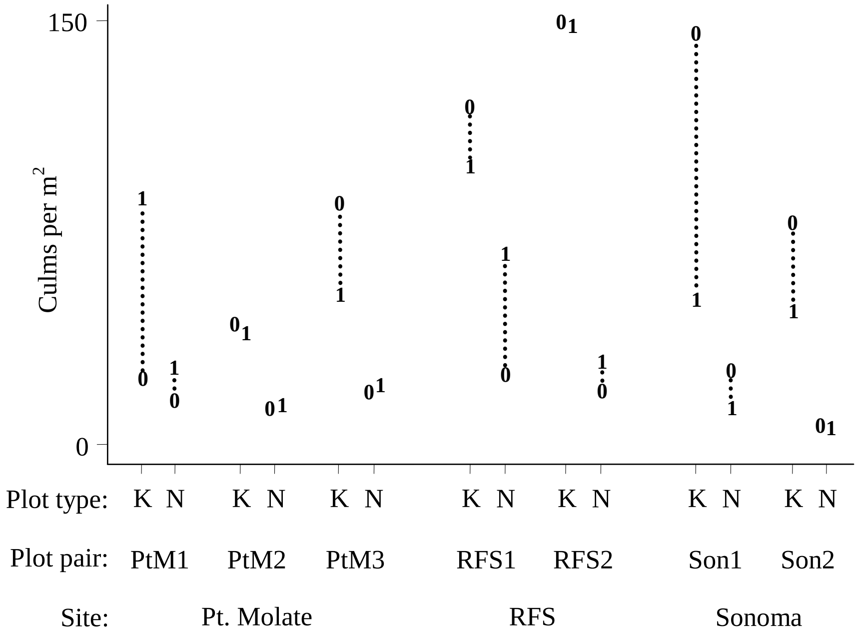

Figure 4.
***Stipa pulchra* Culms per m^2 of Plot Area in Field**

K = thick plot; N = thin plot; 0 indicates 2000 field season; 1 indicates 2001. *N* = 28.

Absolute cover on field plots. Absolute cover of all species combined varied significantly by site ($p < 0.0001$, $R^2 = 0.5962$).[14] Factors other than site were not significant. Pt. Molate had less cover overall than either of the other sites ($p = 0.001$; Figure 8). Each thin plot at Pt. Molate had lower absolute cover than its corresponding thick plot, but the site × culm count interaction was not significant in the ANCOVA.

---

[14] Absolute cover is transformed in the ANCOVA as

$$\left[\left(\frac{\ln(\mathit{absolute\ cover}/100.01}{\left[1 - (\frac{\mathit{absolute\ cover}}{100.01})\right]}\right)+1.3\right]^{0.5}$$

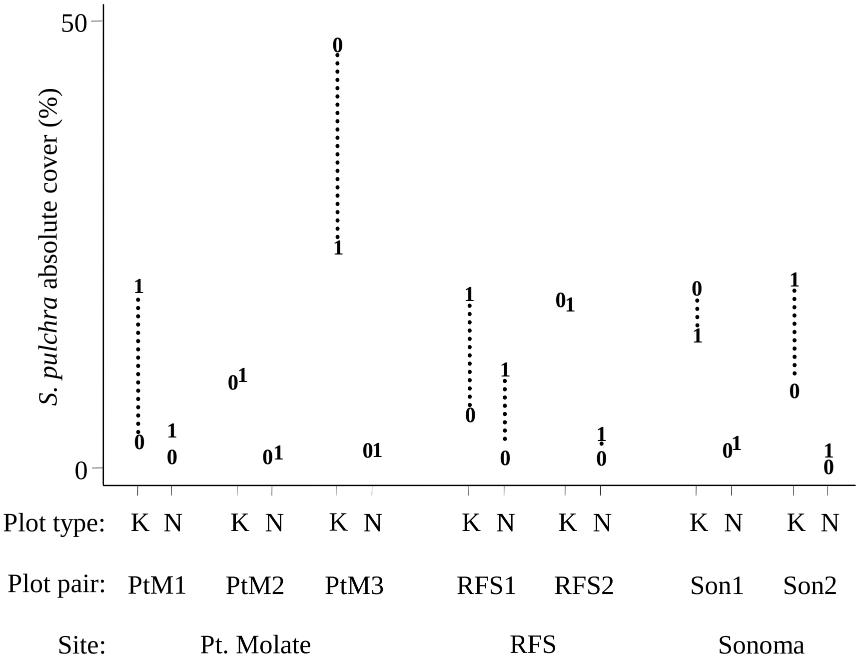

Figure 5.
Absolute Cover of *Stipa pulchra*

K = thick plot; N = thin plot; 0 indicates 2000 field season;
1 indicates 2001. *N* = 28.

Species composition of field plots. Grass species prevalent at all three sites included *Avena barbata* (especially at Pt. Molate), *Bromus diandrus*, *B. hordeaceous*, *Festuca perennis*, *F. myuros*, and *Aira caryophyllea (*Tables 9 and 10).[15] Other species common on field plots at Pt. Molate included *Erodium* species, *Chlorogalum pomeridianum*, *Carpobrotus edulis*, *Rumex* species, and *Eriogonum* species. At RFS, *Phalaris aquatica*, *Vicia* species, *Dipsacus*, *Convolvulus arvensis*, and *Wyethia* species were relatively common, and at Sonoma, common

---

[15] Nomenclature for species encountered in fieldwork for this study follows Jepson Flora Project (eds.) 2017. *Jepson eFlora*, http://ucjeps.berkeley.edu/eflora, accessed on April 7, 2017.

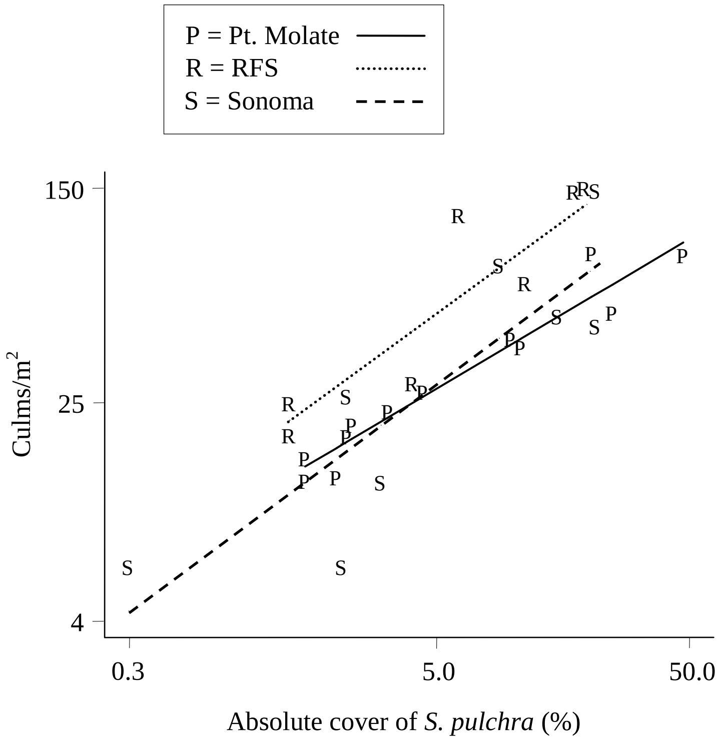

Figure 6.
Culms/m^2 Versus Absolute Cover of *Stipa pulchra*

Double log scale. Regression lines shown here were calculated separately for each site. *N* = 28.

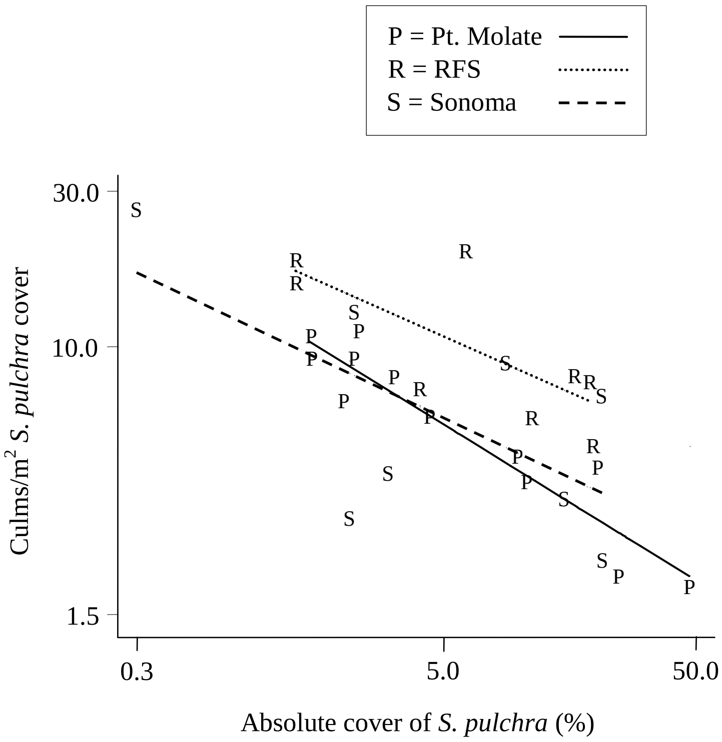

Figure 7.
Culms/m^2 *Stipa pulchra* Cover Versus Percent Cover of *S. pulchra*

Double log scale. Regression lines shown here were calculated separately for each site. *N* = 28.

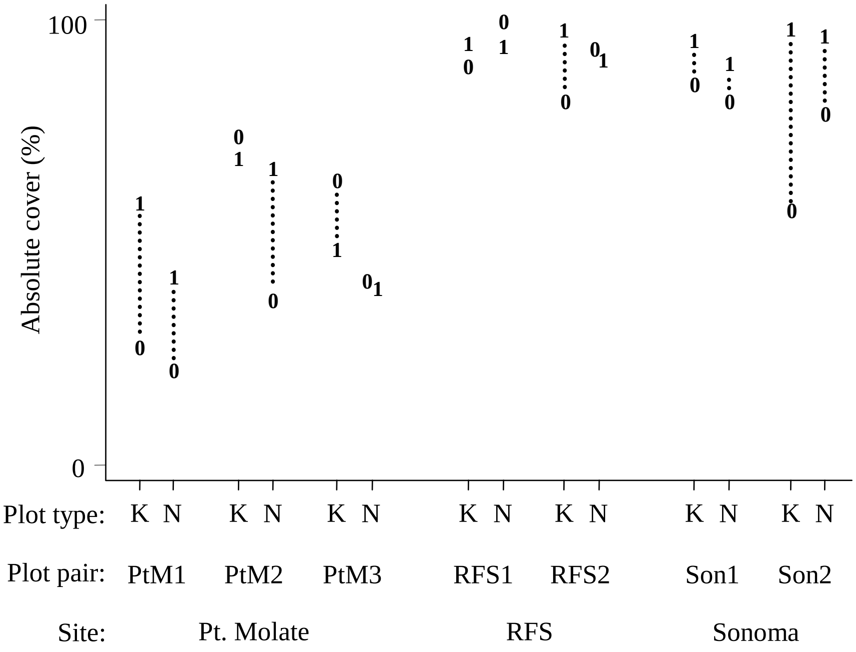

Figure 8.
Absolute Cover of All Species

K = thick plot; N = thin plot; 0 indicates 2000 field season; 1 indicates 2001. *N* = 28.

species included *Holcus lanatus*, *Rumex acetosella*, *Linum* species, and several compositae, in particular *Cirsium vulgare* and *Sonchus oleraceus*.

Native perennial grass species other than *S. pulchra* included *Stipa lepida*, *Danthonia californica*, and small amounts of *Elymus glaucus*. In multivariate regression, combined absolute cover of these grasses correlated positively with absolute cover of all species combined (Table 11); however, in simpler models this was significant only at Pt. Molate. Cover of these grass species was less at RFS than at the other sites ($p < 0.05$; Figure 9). Notably, neither *S. pulchra* cover nor *S. pulchra* culm count correlated significantly with cover of other native grasses in univariate or multivariate analyses. If the analysis is cast to include plot type,

Table 9.
Absolute Cover and Relative Cover by Species on Field Plots in 2000

Site	Pt. Molate						Richmond Field Station				Sonoma			
Plot pair	PtM1		PtM2		PtM3		RFS1		RFS2		Son1		Son2	
Plot	P1K	P1N	P2K	P2N	P3K	P3N	R1K	R1N	R2K	R2N	S1K	S1N	S2K	S2N
Date of observation	4/25	4/23	4/30	4/29	5/29	5/26	6/3	5/28	6/9	6/6	7/7	7/13	6/27	6/26
Absolute cover (%)	27	22	47	37	64	42	90	100	82	94	86	82	58	79
Relative cover (%):														
CA perennial grass total	51	7	56	4	83	13	7	1	23	2	29	10	21	2
Stipa pulchra	12	7	13	4	74	5	7	1	23	1	24	3	15	<1
Stipa lepida	39	0	42	0	1	3	0	0	0	0	0	0	0	0
Danthonia californica	0	0	0	0	0	0	0	0	0	0	3	4	3	1
Alien perennial grass total	0	0	0	0	0	0	0	0	6	2	1	0	0	0
All perennial grass total	51	7	56	4	83	13	7	1	29	4	30	10	21	2
Annual grass total	40	68	13	72	3	57	89	96	63	87	52	70	66	75
Avena spp.	0	33	2	9	1	45	1	2	1	0	1	1	0	1
Bromus diandrus	39	34	7	59	1	6	5	3	1	1	1	1	0	0
Bromus hordeaceous	0	0	1	3	1	6	3	3	2	4	2	20	2	3
Festuca perennis	0	0	0	0	0	0	39	86	25	63	4	0	42	18
Festuca myuros	0	1	2	1	0	0	41	2	34	19	38	44	12	29
All grass total	92	75	68	76	86	70	96	97	92	91	82	79	87	77
Total forbs and legumes	8	25	32	25	13	30	4	3	8	9	17	20	13	18
Shrubs	0	0	0	0	0	0	0	0	0	0	1	0	0	5
Ferns and mosses	0	0	0	0	1	1	0	0	0	0	0	0	0	0

Table 10.
Absolute Cover and Relative Cover by Species on Field Plots in 2001

Site	Pt. Molate						Richmond Field Station				Sonoma			
Plot pair	PtM1		PtM2		PtM3		RFS1		RFS2		Son1		Son2	
Plot	P1K	P1N	P2K	P2N	P3K	P3N	R1K	R1N	R2K	R2N	S1K	S1N	S2K	S2N
Date of observation	7/17	7/10	7/20	7/11	7/18	7/14	7/27	8/20	8/24	8/21	9/13	9/14	9/18	9/19
Absolute cover (%)	59	43	69	67	49	40	95	94	98	91	96	91	98	97
Relative cover (%):														
CA perennial grass total	71	10	48	5	52	9	21	13	19	5	26	9	37	4
Stipa pulchra	35	10	16	3	51	6	21	12	19	4	16	3	22	2
Stipa lepida	36	0	33	0	0	2	0	0	0	0	0	0	0	0
Danthonia californica	0	0	0	0	0	0	0	1	0	0	2	2	14	1
Alien perennial grass total	0	0	0	0	0	0	0	0	10	9	1	0	0	0
All perennial grass total	71	10	48	5	52	9	21	13	29	14	27	9	37	4
Annual grass total	12	65	41	83	34	55	65	73	63	66	65	89	59	89
Avena spp.	6	57	15	71	23	53	2	4	0	1	1	1	0	1
Bromus diandrus	4	8	4	6	4	1	17	31	5	17	2	1	0	4
Bromus hordeaceous	1	0	3	3	2	1	8	11	20	9	12	24	8	3
Festuca perennis	0	0	0	0	0	0	20	22	16	17	0	0	32	24
Festuca myuros	1	0	17	2	0	0	18	5	22	20	47	61	15	52
All grass total	83	76	89	88	86	64	86	86	92	80	92	98	96	93
Total forbs and legumes	13	24	11	12	14	36	14	13	7	14	5	2	34	4
Shrubs	4	0	0	0	0	0	0	0	0	0	3	0	<1	4
Ferns and mosses	0	0	0	0	0	0	0	2	1	6	0	0	0	0

Table 11.
ANCOVA of Absolute Cover on Field Plots of Native Grass Species Other Than *Stipa pulchra*

$N = 28$
$R^2 = 0.5554$
Adjusted $R^2 = 0.4998$

Source	Sum of Squares	df	Mean Square	F	p
Model	991.350	3	330.449	9.99	0.0002
Site	991.222	2	495.112	14.99	0.0001
Absolute cover of all species	311.129	1	311.129	9.41	0.0053
Residual	739.652	24	33.069		
Total	1785.000	27	66.111		

Data transformation: ranks of absolute cover of native species other than *S. pulchra*

however, plot type and its interaction with site are significant, an artifact largely stemming from large amounts of *S. lepida* on two thick plots at Pt. Molate that in turn resulted from the resemblance of the two *Stipa* species, especially in early springtime, to the inexperienced researcher marking out research plots. No native perennial grasses other than *S. pulchra* were observed on five plots in 2000, nor on three plots in 2001.

Plot disturbance. Recent gopher tailings covered an average of 1.7 percent of plot area in 2001. Plots at Pt. Molate had more gopher disturbance than plots at RFS and Sonoma ($p < 0.005$). There was no other disturbance apparent on the field plots.

Species richness and evenness. Species diversity entails both the number of species and the evenness of distribution of individuals among these species (Hurlbert 1971). A total of 43 species appeared on the field plots, along with five categories not identified to species, such as ferns. Over the two years of field work, a total of 29 species were observed on Pt. Molate plots, and 24 species each on RFS and Sonoma plots. The average number of species observed per individual plot was very slightly greater for Sonoma than for the other sites ($R^2 = 0.0230$; $p < 0.05$). There was limited consistency among plot pairs or between years in observed species richness, however, particularly on Pt. Molate plots.

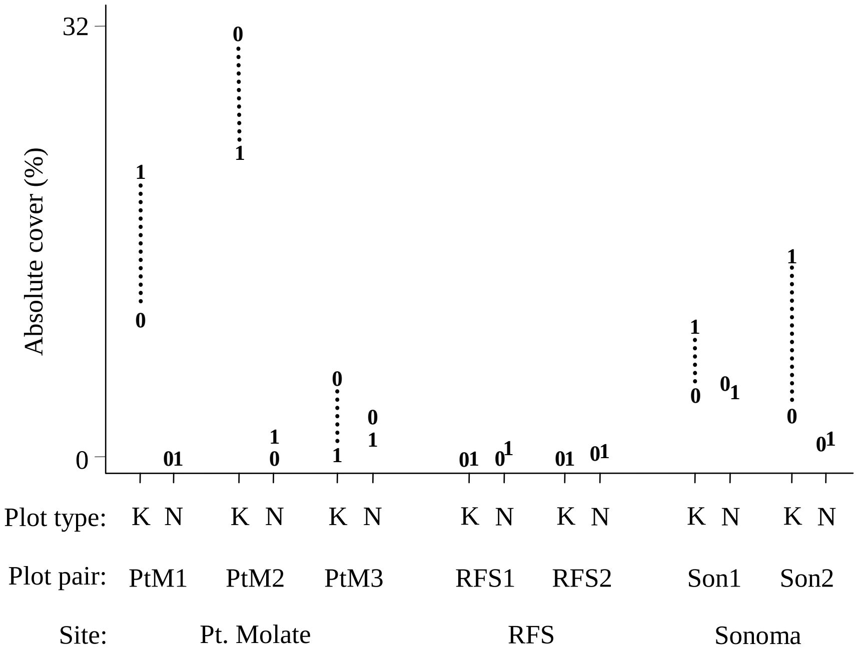

Figure 9.
Absolute Cover of Native Perennial Grasses Other Than *Stipa pulchra*

K = thick plot; N = thin plot; 0 indicates 2000 field season; 1 indicates 2001. *N* = 28.

Species richness and evenness can be described together in terms of Simpson's index D (Begon et al. 1990). The index was calculated as

$$D = 1/\sum p_i^2$$

with p_i equal to the proportional fractional relative cover of each species. Simpson's index increased substantially in 2001 on RFS plots while decreasing somewhat overall at the other sites (Table 12; Figure 10); this may be due in part to the seasonally later 2001 field work.

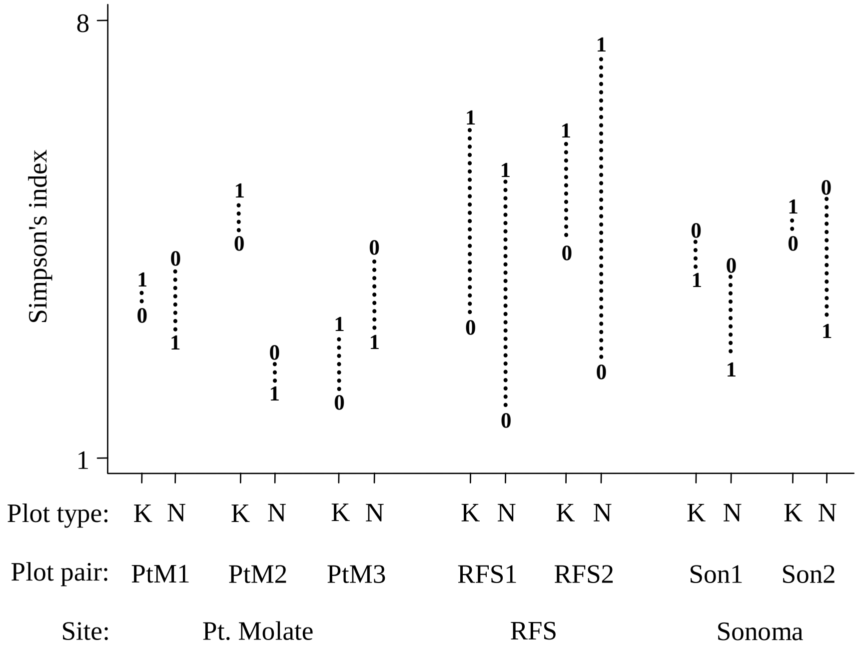

Figure 10.
Simpson's Index by Site, Plot Pair, Plot Type, and Year

K = thick plot; N = thin plot; 0 indicates 2000 field season; 1 indicates 2001. *N* = 28

Simpson's index *D* reaches its maximum when species distribution is perfectly even. Simpson's index divided by total number of species (i.e., *D*/richness) therefore provides an index of species evenness (Begon et al. 1990). In ANCOVA, species evenness was a function of the interactions between site, year, and culm density, with no significant main effects.

Aboveground biomass production. Aboveground biomass production on field plots in 2001 varied by the cube of absolute cover ($p < 0.0001$, $R^2 = 0.8208$).[16] This substantially reflects

---

[16] Field biomass was not normally distributed and was marginally heteroskedastic in regression; results are nearly identical using logit- or rank-transformed data.

Table 12.
ANCOVA of Simpson's Index *D* on Field Plots

$N = 28$
$R^2 = 0.5523$
Adjusted $R^2 = 0.4506$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	7.037	5	1.407	5.43	0.0021
Site	1.183	2	0.592	2.28	0.1257
Year	0.850	1	0.850	3.28	0.0839
Site × year	5.248	2	2.624	10.12	0.0008
Residual	5.704	22	0.260		
Total	12.741	27	0.472		

Data transformation: $(\text{Simpson's index}^{0.4199} - 1) / 0.4119$

the variation in cover among sites; however, ANOVA of variation of biomass among sites explains less of the variance. RFS and Sonoma plots were more productive than Pt. Molate plots (Figure 11).

Height of *S. pulchra* culms. Culm heights were measured on each plot in each year, excepting the four Pt. Molate plots where culms were not measured in 2000; a total of 3309 culms were measured. Calculating mean culm heights by plot and year yielded 24 data points. Mean culm height was less at Pt. Molate than at the other sites in both years ($p \leq 0.01$); culm height did not differ between RFS or Sonoma in either year. Between 2000 and 2001, mean culm height declined an average of almost 17 percent on those plots for which there are two years' data (Table 13; Figure 12).

Cooler, drier weather preceding the 2001 field season may have induced production of shorter culms. Another possibility is that the between-year difference may reflect experimental artifacts stemming from measuring culm heights later in the field season during 2001 than 2000. First, *S. pulchra* may produce relatively short culms late in the growing season, though these likely are a small fraction of total culms. Second, culms that had been broken by wind (typically the taller ones) were omitted from height measurement. As culms were measured later in the 2001 field season than in 2000, greater cumulative wind damage in 2001 may have contributed to the height difference between years. If wind damage was the reason for culm height reduction

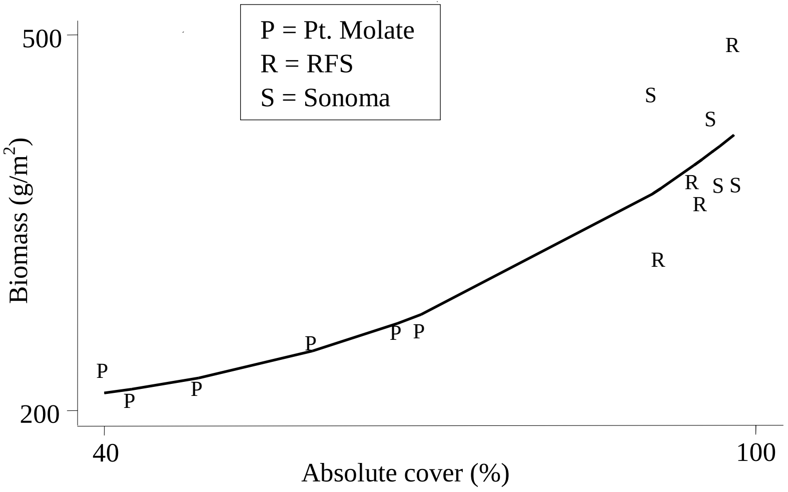

Figure 11.
Biomass per m^2 and Absolute Cover in Field, 2001

N = 28.

Table 13.
Cluster Regression of *Stipa pulchra* Culm Height in Field

N = 3309, in 14 clusters (one cluster per plot)
R^2 = 0.2732

Source	Coefficient	Standard Error	*t*	*p*
RFS (vs. the other sites)	25.48	3.47	7.35	<0.001
Sonoma (vs. the other sites)	25.83	2.03	12.74	<0.001
Year	-4.53	1.59	-2.85	0.014
Sonoma × year	-9.03	2.14	-4.21	0.001
RFS × year	-14.51	2.82	-5.14	<0.001
Constant	53.16	0.01	4841.16	<0.001

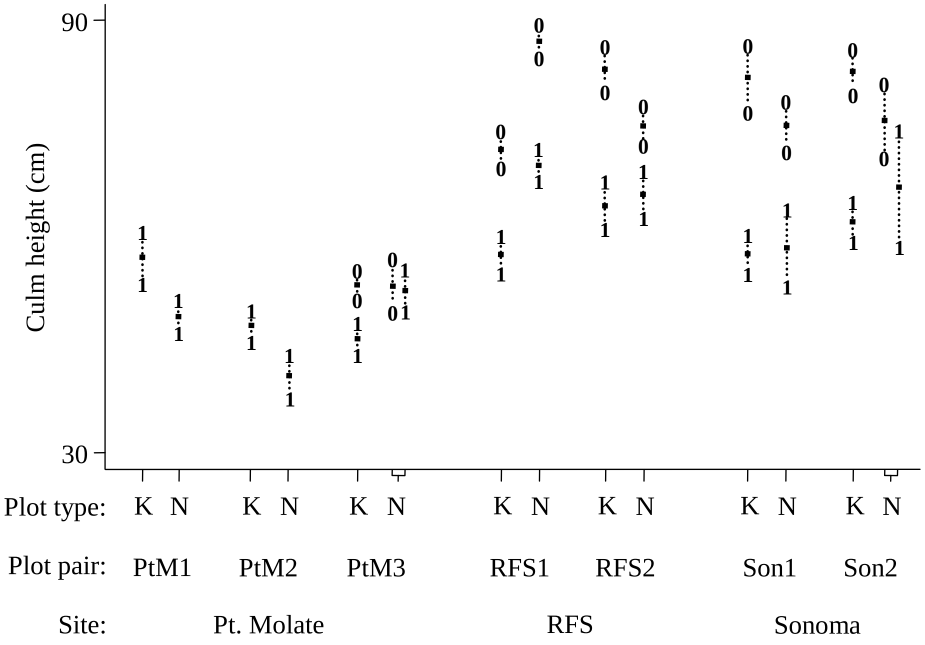

Figure 12.
***Stipa pulchra* Culm Height in Field**

K = thick plot; N = thin plot; 0 indicates 2000 field season; 1 indicates 2001.
Filled squares indicate means; dotted lines indicate 95% confidence ranges.
N = 3309.

between years, however, it seems likely that the height difference between years would be larger for the taller percentiles of culms than for the shorter, and this is not the case (Table 14).

Seed production per culm. *S. pulchra* produces one seed per spikelet, so seed production is easily estimated after seed drop by counting glume pairs on the remaining panicles.[17] There was an average of 23 florets per panicle (ranging from four to 87 florets) on culms collected in 2000. If the 915 floret counts used for estimating seed production are

---

[17] As noted in Methods, for four plots on Pt. Molate estimates of seeds per culm are based on counts from panicles harvested from narrow strips adjacent to the plots. This estimate is weighted based on number of culms sampled in each strip.

Table 14.
Height of *Stipa pulchra* Culms in Field by Year and Site

		Plot × year averages (cm)		Raw data (cm)			
					Percentiles		
Year	Place	*n*	Mean (95% CI)	*n*	10	50	90
2000	PtM3*	2	53.2 (53.0–53.4)	298	31	54	73
	RFS	4	79.5 (68.4–90.7)	594	55	78	103
	Sonoma	4	79.1 (72.8–85.4)	284	55	81	100
2001	Pt. Molate*	6	48.7 (42.7–54.6)	816	28	48	70
	PtM3	2	49.1 (6.5–91.7)	310	27	49	68
	RFS	4	64.4 (56.1–72.7)	827	35	65	92
	Sonoma	4	61.2 (54.6–67.7)	490	32	62	86

* Heights were measured on one plot pair only at Pt. Molate in 2000; heights were measured on all plots in 2001. Culm heights averaged over plot × year.

pooled into plot-wise averages, no statistical tests of the pooled data against any of the applicable study factors (site, plot pair, absolute cover, culm count, or Simpson's index) yields significant results, although culms from thick plots at Pt. Molate produced relatively small numbers of seeds (Table 15). Culms that provided seeds for the common garden study had a higher average number of florets than did culms used to estimate seed production in the field.

Seed production per m^2 plot area. The large variation in seed production among *S. pulchra* culms results in substantial uncertainty in estimates of seed production per m^2 in the field. Thick plots, which produced more culms per unit area, presumably also produced more seeds. Because thin plots produced more culms per m^2 of *S. pulchra* cover, they may also have produced a larger number of seeds than thick plots relative to the area occupied by *S. pulchra*. A graphic approximation calculated as

$$\text{seeds/m}^2 = (\text{florets/culm}) \times (\text{culms/m}^2)$$

calculated for each plot implies that the difference between thick and thin plots in seed production may have been greater at RFS and Sonoma than at Pt. Molate in 2000 (Figure 13).

Table 15.
Florets per *Stipa pulchra* Culm in Field Samples

		Mean florets per culm by plot type	
Site	Plot pair	Thick	Thin
Pt. Molate	PtM1	19	25
	PtM2	18	20
	PtM3	17	30
RFS	RFS1	22	29
	RFS2	29	20
Sonoma	Son1	27	21
	Son2	21	15

For PtM1 and PtM2, culms harvested adjacent to plots were used for floret counts. *N* = 14.

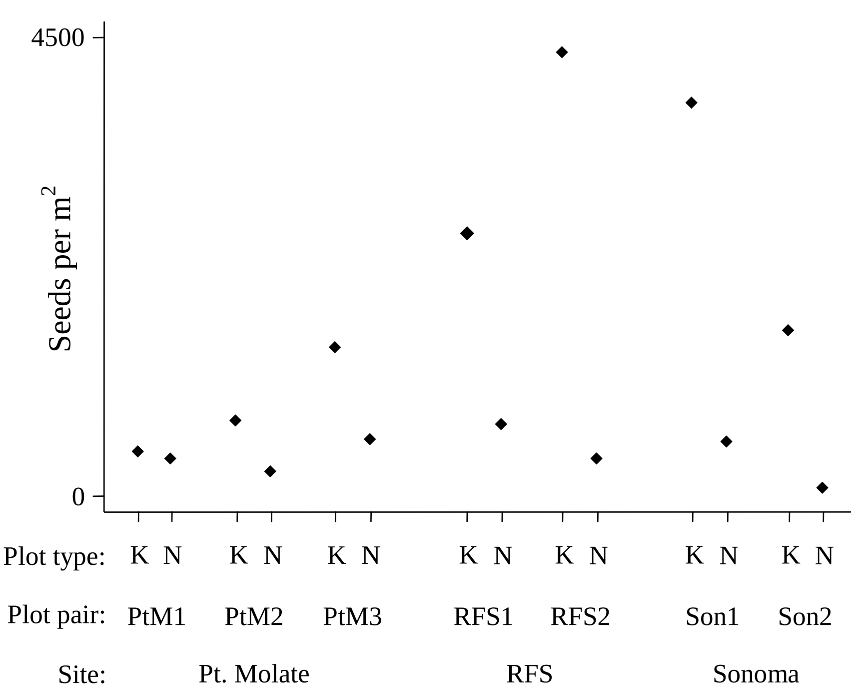

Figure 13.
Approximate *Stipa pulchra* Seed Production per m^2 on Field Plots in 2000

K = thick plot; N = thin plot. *N* = 14.

Chapter 8. Results of Common-Garden Study

Overview

S. pulchra plants grown in the common garden from seeds collected on the field plots were observed from seedling emergence through reproduction. The first part of this chapter describes common-garden plant growth and morphology, including allocation ratios that can reflect ecological strategies. The second part provides data on reproduction by seed of common-garden plants. The end of this chapter summarizes these results and discusses effect sizes of explanatory variables. The results show substantial variation among the common-garden plants reflecting experimental growing conditions and factors measured in the field. Implications of these results are discussed in Chapter 9.

Tables 5 and 6 in Chapter 7 and Tables 16-20 on the following pages list the variables used in the text, tables, and graphs in this chapter. Some of the response variables also act as explanatory variables. The response variable emergence time, for example, was affected by seed-source site and weight of the planted seed, and as an explanatory variable in turn affected several later measurements, such as aboveground biomass of common-garden plants.

Table 16.
Explanatory Variables in Common-Garden Results:
Factors Stemming from Plot-Level Field Conditions

Variable Name	Description
Absolute cover	Absolute cover of all species on each field plot in each year
Count of *Stipa pulchra* culms	Number of culms per m^2 on each field plot in each year
Simpson's index	Simpson's index *D* of each field plot in each year
S. pulchra culm height in the field	Mean height of tallest 10% of culms on each field plot in 2001

During the field study, the presence of *S. pulchra* was measured both as cover of *S. pulchra* and as number of *S. pulchra* culms per m^2. Culm count in the field, rather than *S. pulchra* cover, is used as an explanatory variable in this chapter because culm density was precisely measured in the field (by counting) rather than visually estimated as was *S. pulchra* cover, and because culm density is the factor that would influence seed collectors. Results of statistical analyses were generally similar whichever measure of *S. pulchra* was used.

Table 17.
Explanatory Variables in Common-Garden Results:
Factors Stemming from Common Garden Experimental Conditions

Variable	Description
Block	Three planting blocks spaced at one-week intervals
Watering	Two groups varying in amount of water they received
Planted seed weight	Weight of each field-collected seed planted in the common garden
Seed ripeness	Ripeness of planted seeds, based on color
Measurement period	Three measurement periods for tiller count and plant height
Seed harvest	Whether common-garden offspring seeds were harvested from live plants or from plants that had been harvested

Seedling Emergence

Weight of planted seeds. Seed collection during fieldwork focused on obtaining enough seed from each plot for the common-garden experiment. Sufficient ripe seed was not always available on plots with low culm density, resulting in occasional collection of unripe, less well-filled seed. The common-garden experiment omitted planting of damaged seeds and seeds weighing less than 2.4 mg. Variation in common-garden seed weights therefore likely differs from the variation in weight of seeds in the field (Table 21).

Seeds planted in the common garden had a mean weight of 4.6 mg. Seeds were classified as appearing fully ripe (gray-brown in color) or partly ripe (gray-green). Ripe seeds (845 of the 1008 planted) were about nine percent heavier on average than unripe seeds. Seeds collected in 2001 were about 10 percent heavier than seeds gathered in 2000. Seeds from Pt. Molate were about 10 percent heavier than seeds from the other sites ($p < 0.005$), and the difference between the two RFS plot pairs was marginally significant in means separation. Weight of planted seeds correlated positively with field culm count for Pt. Molate and RFS, but negatively for Sonoma. The significance of field culm count in the multivariate ANCOVA depends on this interaction; in univariate regression, field culm count had no significant effect on seed weight. Significant two- and three-way interactions of site plot pair, year, culm density, and seed ripeness may reflect effects stemming from variation in seed-collection conditions among individual plots during each year.

Table 18.
Response Variables in Common-Garden Results:
Emergence, Growth, and Morphology

Variable Name	Description
Percent emergence	Which seeds produced seedlings
Emergence time*	Days to emergence from first watering
Tiller count*	Total number of tillers (vegetative tillers plus culms) per plant measured at • 7 weeks from first watering • 13 weeks from first watering • 19 weeks from first watering
Plant height	Height of tallest part of plant measured at • 7 weeks from first watering • 13 weeks from first watering • 19 weeks from first watering
Culm height	Tallest culm at harvest
Foliage height	Tallest point on foliage at harvest
Leaf width	Width of widest leaf (subsample of plants)
Basal area	Basal area at harvest, calculated from two perpendicular basal diameters
Aboveground biomass*	Oven-dry weight of aboveground portion of common-garden plant, minus seeds
Belowground biomass	Oven-dry weight of washed roots and crown (subsample of plants)
Total biomass	Sum of aboveground-and belowground biomass (subsample of plants)

* Variable also appears as an explanatory variable.

Table 19.
Response Variables in Common-Garden Results: Sexual Reproduction

Variable	Description
Percent reproduction*	Whether plants produced flowers (i.e., visible awns)
Weeks to first reproduction*	Number of weeks until awns became visible in reproductive plants
Common-garden culm count*	Number of culms on each flowering plant at harvest in the common garden
Seeds per culm	Count of florets on median culms of common-garden plants
Seed color*	Color of common-garden offspring seed as estimate of ripeness (2 levels)
Offspring seed weight	Mean weight per plant of individual seeds produced by common garden plants

* Variable also acts as an explanatory variable.

Percent emergence. A total of 870 seedlings emerged from 1008 planted seeds (Table 22). Emergent seeds had a mean weight of 4.7 mg. The smallest emergent seed weighted 2.4 mg, and among seeds weighing less than 4.7 mg, larger seeds had a higher likelihood of emergence. Above 4.7 mg, seed weight had no effect on percent emergence. Seeds in the third block had roughly five percent lower emergence than seeds planted in the other blocks, possibly due to increasing temperatures during the initial weeks of the experiment. Seeds collected in 2000 had an 82 percent emergence rate, versus 91 percent for seeds collected in 2001; this was due in part to the slightly smaller size of seeds collected in 2000. In addition, among seeds weighing less than 3.8 mg, the older seeds had substantially lower emergence rates. (Above this weight the age difference was not significant.) Seeds from Pt. Molate had an emergence rate roughly 11 percent less than that of the other sites. Seeds collected in 2000 from the first plot characterized at Pt. Molate had a particularly low emergence rate, about 46 percent that of other seeds collected that year. The poor quality of these seeds likely reflects the experimenter's seed-collection expertise and the paucity of seeds on that plot rather than substantive differences among seed sources, and may explain some difference among sites and plot pairs and between years. Neither seed ripeness nor watering treatment affected percent emergence.

Table 20.
Response Variables in Common-Garden Results: Ratios

Variable	Description
Aboveground relative growth rate (RGR)	Incremental aboveground rate of growth in common-garden plants, calculated as $\ln\left(\frac{aboveground\ biomass}{planted\ seed\ weight}\right)/growing\ days$ where "growing days" is counted from time of emergence to harvest
Belowground relative growth rate	Incremental rate of root growth in common-garden plants, calculated for a subsample of plants as $\ln\left(\frac{belowground\ biomass}{planted\ seed\ weight}\right)/growing\ days$
Root: shoot ratio	Ratio of belowground biomass to aboveground biomass in common-garden plants (subsample of plants)
Ratio of flowering to vegetative tillers	Ratio of number of culms to number of vegetative tillers at harvest in common-garden plants that flowered

Time to emergence. Seedling emergence occurred within four to 27 days, with an average of 9.9 days.[18] Temporal block had the largest effect on emergence times; seedlings in the first block, which experienced cooler germination temperatures, took more than three days longer on average to emerge than seedlings in the other blocks (Table 23; all differences between blocks were significant at $p < 0.001$). For the first two blocks, seeds that received more water emerged about a half-day earlier than seeds receiving less. While Pt. Molate seedlings on average emerged more quickly than those from the other sites, the differences between plot pairs within the sites are larger than differences among sites (Figure 14), and site is not significant in simple nested ANOVA. Within sites, the difference in emergence time is significant between

---

[18] Four plants emerged after the period during which emergence was recorded; these plants are omitted from analyses that include emergence time as a factor. All four were from thick plots, one from RFS, the other three from Sonoma. Except in the unlikely case that these four plants took at least 76 days to emerge, the average emergence time of thick-plot seedlings would remain shorter than the average for thin-plot plants.

Sonoma plot pairs ($p < 0.01$) and marginally so between RFS plot pairs ($p = 0.07$). Seeds from field plots having greater species diversity and from plots with a lower culm count had slightly greater emergence time. In univariate regression, Simpson's index remains significant ($p < 0.05$), but culm count does not. Heavier seeds emerged faster than lighter ones; seed ripeness had no effect.

Table 21.
ANCOVA of Weight of Seeds Planted in Common Garden

$N = 1008$
$R^2 = 0.1662$
Adjusted $R^2 = 0.1432$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	5.099	27	0.189	7.23	<0.0001
Site	0.196	2	0.098	3.74	0.0240
Plot pair	0.342	4	0.085	3.27	0.0112
Seed collection year	0.310	1	0.310	11.89	0.0006
Culm count in field	0.254	1	0.254	9.72	0.0019
Seed color	0.155	1	0.155	5.94	0.0150
Site × culm count	0.200	2	0.100	3.82	0.0222
Plot pair × year	1.075	6	0.179	6.86	<0.0001
Plot pair × seed color	0.635	6	0.106	4.06	0.0005
Year × seed color	0.187	1	0.187	7.15	0.0076
Site × year × culm count	0.227	3	0.076	2.89	0.0344
Residual	25.589	980	0.026		
Total	30.688	1007	0.030		

Data transformation: ln(*seed weight* + 1.3215)

Table 22.
Logistic Regression of Seedling Emergence versus Nonemergence in the Common Garden

$N = 1008$
Log likelihood = -298.05
Likelihood Ratio Chi-Square (8) = 208.90 ($p < 0.0001$)
Pseudo-$R^2 = 0.2595$

Source	Odds Ratio	Standard Error	z	p
Block 3 (vs. blocks 1 & 2)	0.552	0.122	-2.696	0.007
Pt. Molate (vs. the other sites)	0.123	0.049	-5.271	<0.001
PtM1 (vs. PtM2 & PtM3)	0.403	0.144	-2.537	0.011
PtM2 (vs. PtM1 & PtM3)	2.951	1.261	2.533	0.011
Seed collection year	2.630	6.285	3.296	0.001
Planted seed weight	15.486	17.162	8.706	<0.001
Pt. Molate × year	6.512	3.052	3.997	<0.001
Year × seed weight	0.008	0.011	-3.320	0.001

Seed weight is natural-log transformed.

Unplanned Experimental Factors

Snail damage. Not long after seedling emergence, a snail damaged 19 plants before its abrupt demise. The damage set these plants back, and their subsequent size and fecundity cannot be regarded as depending either on seed source or on planned experimental conditions. These plants were omitted from analyses of data gathered subsequent to the damage.

Root rot. As described in Chapter 6, a few weeks after seedling emergence a number of plants displayed inward-rolling leaf margins, symptomatic of water stress, which appeared to stem from root rot. About eight percent of the plants eventually showed rolled leaves when recently watered; these plants were omitted from analyses of data recorded after the stress was observed. Plants from one Sonoma plot pair had over twice the average incidence of root rot (Table 24). If absolute cover is included in the logistic regression, however, statistical analysis instead indicates that plants from RFS had lower incidence of root-rot compared to plants from

Table 23.
ANCOVA of Days to Emergence in Common Garden

$N = 866$
$R^2 = 0.5151$
Adjusted $R^2 = 0.4940$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	42.653	36	1.185	24.460	<0.0001
Block	8.355	2	4.178	86.250	<0.0001
Watering	0.577	1	0.577	11.910	0.0006
Site	1.025	2	0.513	10.580	<0.0001
Plot pair	1.742	4	0.435	8.990	<0.0001
Seed collection year	0.434	1	0.434	8.950	0.0029
Culm count in field	0.523	1	0.523	10.810	0.0011
Simpson's index	0.136	1	0.136	2.800	0.0947
Planted seed weight	0.898	1	0.898	18.530	<0.0001
Block × water	0.912	2	0.456	9.410	0.0001
Block × site	1.621	4	0.405	8.370	<0.0001
Block × plot pair	1.436	8	0.179	3.710	0.0003
Block × culm count	0.609	2	0.304	6.280	0.0020
Water × plot pair	0.603	6	0.100	2.070	0.0540
Culm count × seed weight	0.240	1	0.240	4.950	0.0263
Residual	40.156	829	0.048		
Total	82.809	865	0.096		

Data transformation: = ln(*emergence time* – 0.4336)

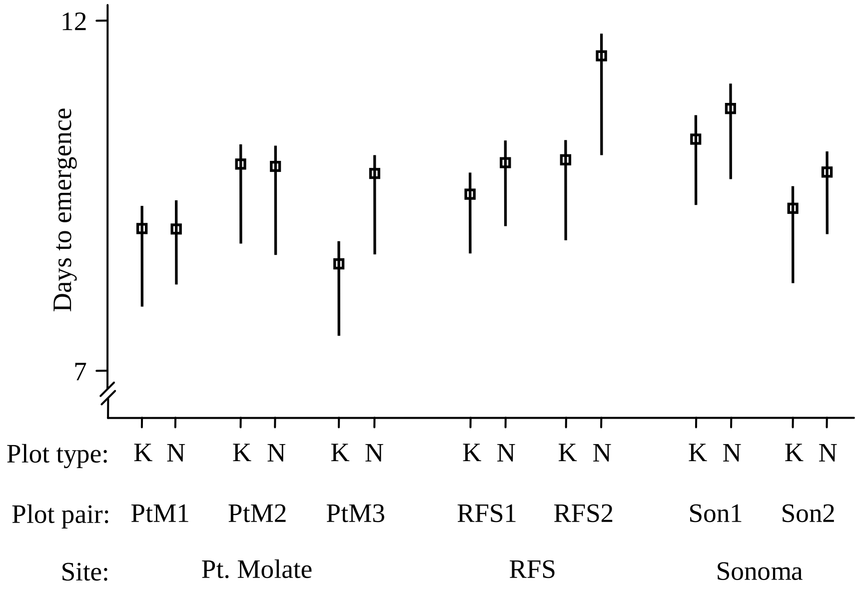

Figure 14.
Days to Emergence in the Common Garden

Squares are arithmetic means; lines are 95% confidence intervals back-calculated from natural-log transformed data. K = thick plot; N = thin plot. *N* = 866.

the other sites, and that plants originating from seeds collected on plots with greater absolute cover and with higher culm counts were more likely to develop symptoms. Differences in likelihood of root rot associated with seed-source location may have resulted from intrinsic susceptibility in these plants or from pathogens present in the seeds. If susceptibility to root rot reflects autecological differences among plants, the loss of the diseased plants from this study potentially biases later results.

At the end of the growing period, root preparation for biomass weighing revealed that about 10 percent of the remaining plants had unusually weak, fragile roots. Most of these were in the heavily watered group. The root: shoot ratio of these plants was less than that of other

Table 24.
Logistic Regression of Root-Rot Incidence in the Common Garden

$N = 870$
Log likelihood = -208.175
Likelihood Ratio Chi-Square (5) = 45.90 ($p < 0.0001$)
Pseudo-$R^2 = 0.0993$

Source	Odds Ratio	Standard Error	z	p
Watering	3.842	1.179	4.385	<0.001
Pt. Molate (vs. the other sites)	4.517	2.553	2.668	0.008
Sonoma (vs. the other sites)	5.334	2.131	4.191	<0.001
Absolute cover in field	2.730	1.011	2.713	0.007
Culm count in field	1.730	0.385	2.462	0.014

Absolute cover is transformed as

$$\ln\left(1.30 + \ln\left[\frac{\textit{absolute cover}/100.01}{1 - (\textit{absolute cover}/100.01)}\right]\right)$$

Culm count in the field is transformed as

$$\ln\left(3.85 + \ln\left[\frac{\textit{culm count}/150}{1 - (\textit{culm count}/150)}\right]\right)$$

common-garden plants. Some of these fragile-rooted plants had grown adjacent to plants that had already been eliminated due to root rot. It seems likely that the fragile roots stemmed from mild root rot. These plants were omitted from analyses involving root biomass data.

Growth and Morphology

Measurements reflecting overall growth and morphology of common-garden plants included

- height and number of tillers at seven, 13, and 19 weeks after initial watering,
- width of the widest leaf at about 16 weeks (subset of plants),
- basal area at harvest, and
- weight of oven-dry above- and belowground biomass at harvest.

Plant height. The first height measurement took place before any culms were visible. The second measurement recorded the tallest part of each plant, whether culm or foliage.[19] At harvest, when the third height measurement was taken, 655 of the 756 plants recorded had culms with visible awns, and for 466 of these plants the tallest part of the plant was a culm. At harvest, the highest point of foliage was measured, and the tallest culm as well in reproductive plants.

Average plant height increased from 113 mm at seven weeks to 542 mm at 19 weeks, when plants were harvested. Plant heights across the three measurement periods were trimodally distributed, and within each period the height distribution was slightly right-skewed (Table 25; Figure 15). In order to compare plant heights over three measurement periods, height data were transformed by

1. taking the square root of each height observation to improve the distribution of data within each measurement period;
2. standardizing each measurement period's square-root transformed observations to a mean of 0 and standard deviation of 1;
3. combining the standardized observations into one dataset containing three observations for each plant (Figure 16; Table 26); and
4. analyzing the standardized, transformed data using Stata's cluster-regression function, treating measurement period as a continuous variable.

In the first measurement period, plants in the first block were shortest and those in the third were tallest (Table 27). By the last measurement period, plants in the third block were about 10 percent shorter than those in the other blocks. A large part of the difference among blocks stems from the lesser proportion of plants setting seed in the third block, because mature *S. pulchra* culms are taller than the foliage. If the comparison is limited to reproductive plants, however, those in the third block nevertheless were shorter at the last measurement than those in the other blocks. The generally higher temperatures experienced by plants in the third block may have encouraged initial rapid growth, then reduced growth as the weather became even warmer and watering was reduced. In the first measurement period, plants receiving more water were taller than those receiving less, became relatively shorter at the second measurement, and then became taller again by harvest.

At each measurement period, Pt. Molate plants were taller than RFS and Sonoma plants (significantly so in the first two periods; $p < 0.005$), and RFS plants were shorter than those from the other sites (significantly so in the second and third period; $p < 0.005$). Conversely, Pt. Molate plants were the shortest in the field and RFS plants the tallest. Plot pairs within site changed rank order with regard to common-garden plant height from one period to the next

---

[19] The second and third height measurements and tiller counts took place after the appearance of root rot, so these later measurements include fewer plants. During the first measurement period, plants that eventually developed root rot did not differ in height or tiller count from those that remained healthy. Plants that later developed root rot were omitted from cluster regressions of height and tiller count.

Table 25.
Mean Height of Plants by Planting Block and Measurement Period

Block	*n*	Period	Height (mm)
1	270	1	94
		2	287
		3	552
2	262	1	120
		2	360
		3	569
3	252	1	127
		2	364
		3	503

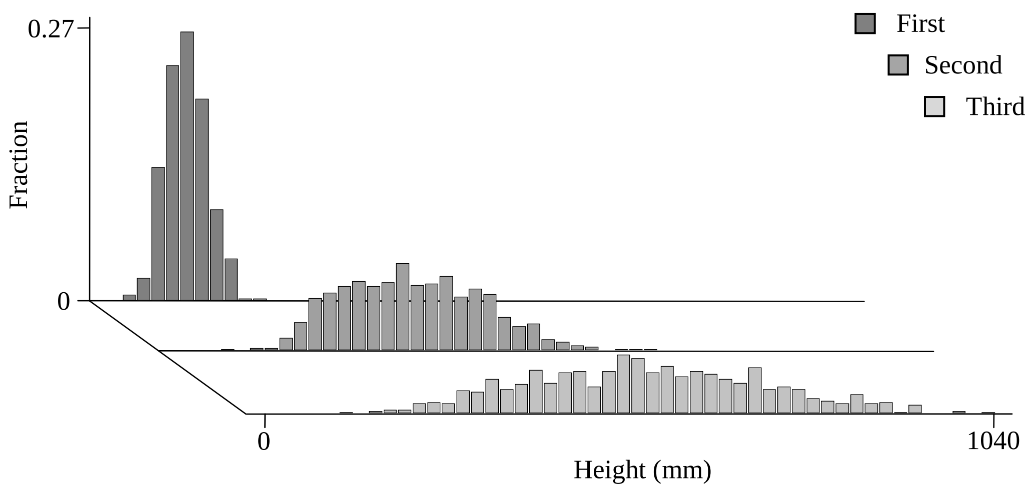

Figure 15.
Distribution of Untransformed Common-Garden Plant Heights at First, Second, and Third Measurement Periods

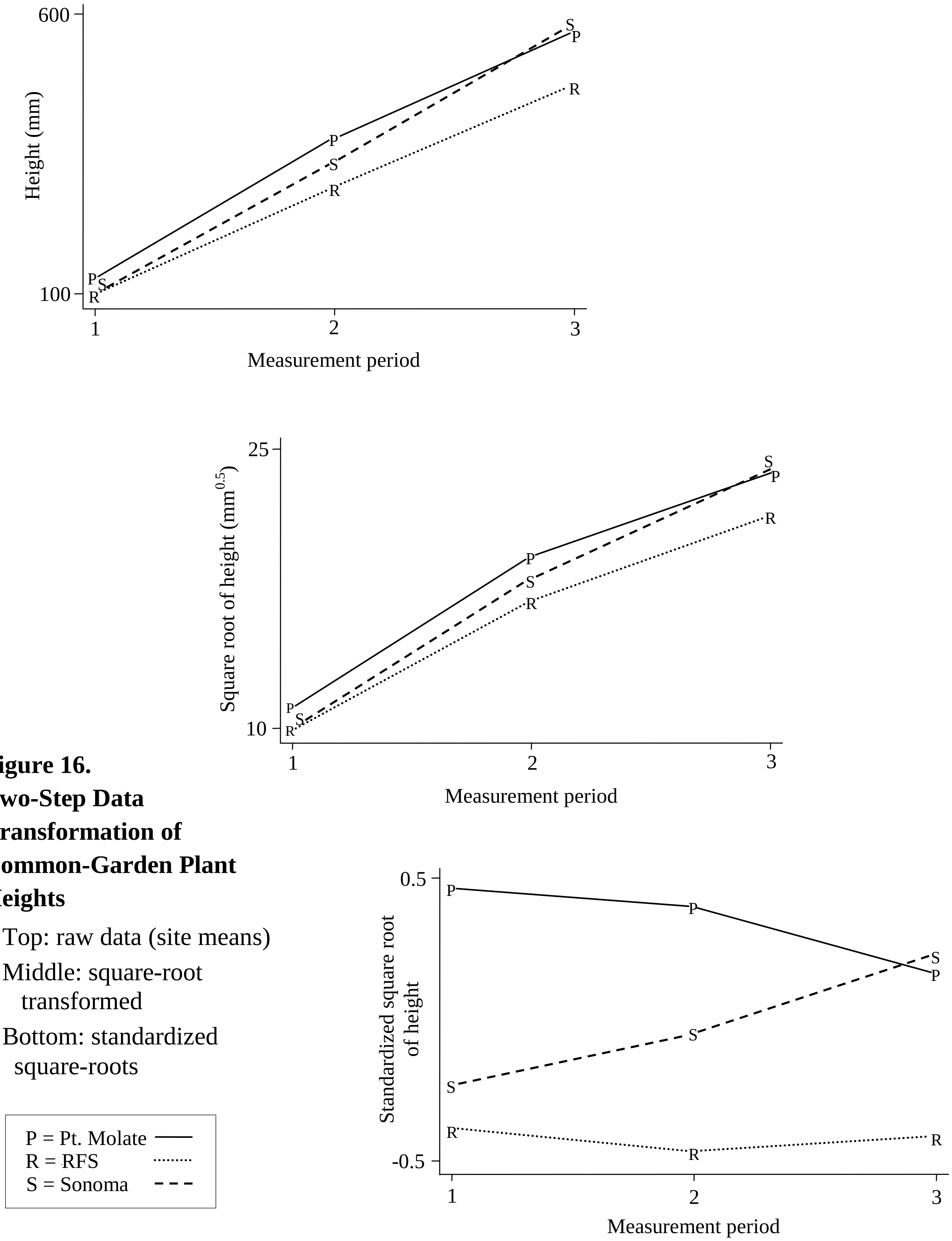

Figure 16.
Two-Step Data Transformation of Common-Garden Plant Heights

Top: raw data (site means)

Middle: square-root transformed

Bottom: standardized square-roots

Table 26.
Mean Plant Height in Common Garden:
Comparison of Raw, Square-Root Transformed, and Standardized Data:
Means by Site and Measurement Period

	Data transformation								
	Raw data (mm)			Square root			Standardized square root		
Period	1	2	3	1	2	3	1	2	3
Site									
Pt. Molate (*n* = 315)	127	375	566	11.2	19.2	23.6	0.467	0.393	0.165
RFS (*n* = 248)	102	290	471	10.0	16.9	21.4	-0.389	-0.463	-0.414
Sonoma (*n* = 222*)	106	333	587	10.2	18.0	23.8	-0.228	-0.040	0.228

* For period 1, *n* = 221.

(Figure 17; Table 28), and heights varied significantly between plot pairs for all three sites by the third measurement. In simple ANOVA, site is not significant if plot pair is nested within site.[20] The height of the tallest decile of culms measured in the field did not correlate significantly with common-garden plant height in the multivariate cluster regression.[21]

Across sites, the correlation of plant height in the common garden with culm count in the field became increasingly negative from one measurement to the next. This pattern in part reflects the lesser likelihood of seed-set in plants originating in plots with high culm counts (as discussed later in this chapter), but the pattern exists for both reproductive and nonreproductive common-garden plants. When first measured, the height of common-garden plants correlated positively with culm count in the field for RFS plants, and negatively for Sonoma plants. At the second measurement, this correlation was negative for both RFS and Sonoma, and became increasingly negative at the third measurement. Height of Pt. Molate plants in the common garden correlated positively with field culm count throughout, although the correlation became

---

[20] As discussed in Chapter 6, nested ANOVA is used here for descriptive purposes only, not as formal analysis.

[21] The correlation of the heights of the tallest 10 percent of culms versus all culms in the field exceeded 95 percent.

Table 27.
Cluster Regression of Common-Garden Plant Height over Three Measurement Periods

N = 2346
Number of clusters (i.e., plants) = 782
F (21, 781) = 101.88
R^2 = 0.5283

	Coefficient	Standard Error	*t*	*p*
Block 2 (vs. 1 and 3)	1.024	0.112	9.128	<0.001
Block 3 (vs. 1 and 2)	1.604	0.121	13.225	<0.001
Watering	0.055	0.068	0.799	0.425
Measurement period	-0.776	0.046	-16.828	<0.001
Pt. Molate (vs. the other sites)	0.734	0.155	4.726	<0.001
RFS (vs. other the other sites)	-0.141	0.057	-2.464	0.014
PtM1 (vs. PtM2 and PtM3)	0.349	0.073	4.795	<0.001
Son2 (vs. Son1)	0.389	0.068	5.735	<0.001
Culm count in field	-0.002	0.001	-3.383	0.001
Plant height in field	-0.007	0.004	-1.857	0.064
Planted seed weight	0.112	0.019	6.058	<0.001
Emergence time	-0.070	0.007	-9.301	<0.001
Reproduction	-1.159	0.104	-11.104	<0.001
Block 3 × water	-0.190	0.077	-2.466	0.014
Block 1 × period	0.433	0.037	11.811	<0.001
Block 3 × period	-0.251	0.037	-6.746	<0.001
Block 1 × reproduction	-0.167	0.094	-1.779	0.076
Watering × period	0.089	0.031	2.916	0.004
Period × Pt. Molate	-0.342	0.032	-10.800	<0.001
Period × reproduction	0.958	0.042	22.619	<0.001
Pt. Molate × culm count	0.006	0.001	4.122	<0.001
Constant	0.577	0.375	1.540	0.124

Data transformation: $height^{0.5}$ standardized within period to mean = 0 and standard deviation = 1.

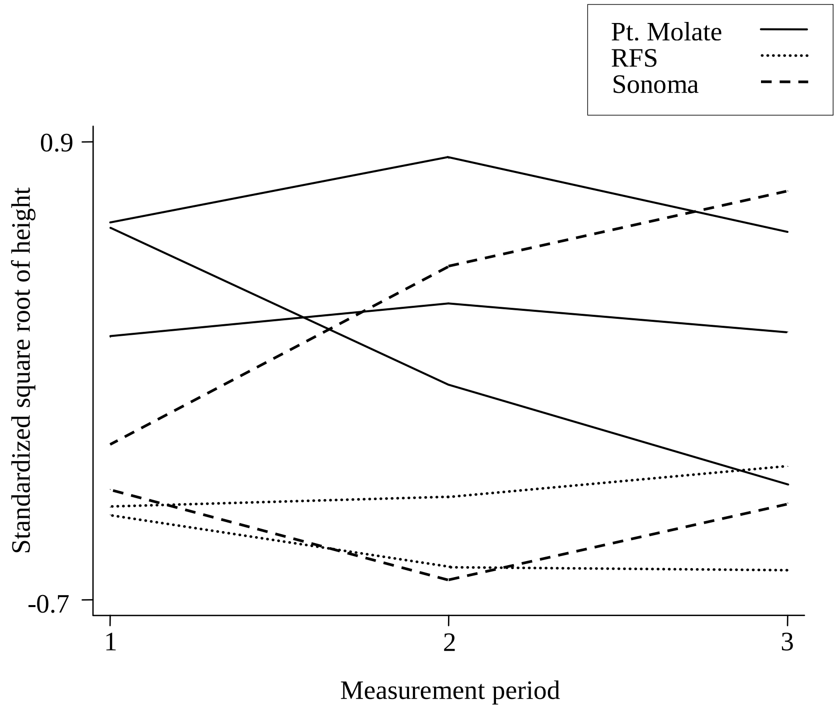

Figure 17.
Plant Height in Common Garden by Plot Pair and Measurement Period

Data transformed as standardized square root of height. *N* = 2346 (782 observations per measurement period).

weaker from one measurement period to the next. Height of common-garden plants overall correlated positively with planted seed weight and negatively with emergence time throughout the common-garden pot study; in both cases the correlations became weaker from one measurement period to the next.

Foliage height at harvest. The highest part of plant leaves averaged 451 mm in dry-treatment plants and 486 mm in plants receiving more water (Table 29).[22] Plants in the second block had taller foliage than those in the other blocks. Sonoma plants had the tallest foliage, and RFS plants the shortest; all between-sites means comparisons are significant at $p \leq 0.005$. Pt. Molate plants responded least and Sonoma plants most to higher levels of watering. Variation

---

[22] Foliage height was not recorded for the first 24 plants harvested.

among plot pairs within sites was greater than variation between sites, however, and site was not significant in simple nested ANOVA (Figure 18). All comparisons of means between plot pairs within site were at least marginally significant. Plants grown from seeds collected in 2001 grew about one percent taller in foliage height and displayed a larger response to more water than did

Table 28.
Common-Garden Plant Heights by Period, Site, and Plot Pair:
Means and 95% Confidence Intervals

		Mean height (confidence interval) (cm)					
Site and plot pair	*n*	Period 1		Period 2		Period 3	
Pt. Molate	315	127	(122–129)	375	(359–379)	567	(541–573)
PtM1	95	132	(125–136)	421	(405–432)	640	(611–659)
PtM2	106	131	(123–136)	338	(319–349)	485	(457–501)
PtM3	114	120	(112–124)	371	(344–383)	580	(540–599)
RFS	248	102	(97–103)	290	(274–294)	471	(442–478)
RFS1	124	102	(97–104)	300	(282–309)	497	(466–512)
RFS2	124	102	(95–105)	279	(259–288)	445	(404–459)
Sonoma*	222	106	(102–108)	333	(311–339)	587	(541–596)
Son1**	102	103	(98–107)	274	(253–284)	487	(432–506)
Son2	120	108	(102–111)	384	(358–396)	671	(629–692)

Means are arithmetic; 95% confidence intervals are back-calculated from square-root transformed data.

*****n = 221 in period 1.
** n = 101 in period 1.

Table 29.
Ancova of Foliage Height at Harvest in the Common Garden

$N = 756$
$R^2 = 0.5527$
Adjusted $R^2 = 0.5405$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	5.691×10^6	20	2.846×10^5	45.41	<0.0001
Block	1.624×10^5	2	8.120×10^4	12.96	<0.0001
Watering	2.383×10^5	1	2.383×10^5	38.02	<0.0001
Site	4.795×10^5	2	2.397×10^5	38.25	<0.0001
Plot pair	2.880×10^5	4	7.201×10^4	11.49	<0.0001
Seed collection year	7.397×10^2	1	7.397×10^2	0.12	0.7313
Emergence time	3.019×10^4	1	3.019×10^4	4.82	0.0285
Reproduction	5.422×10^5	1	5.422×10^5	86.51	<0.0001
Block × water	4.673×10^4	2	2.336×10^4	3.73	0.0245
Water × site	9.071×10^4	2	4.536×10^4	7.24	0.0008
Water × year	2.474×10^4	1	2.474×10^4	3.95	0.0473
Site × reproduction	1.011×10^5	2	5.055×10^4	8.07	0.0003
Emergence time × reproduction	5.896×10^4	1	5.896×10^4	9.41	0.0022
Residual	4.606×10^6	735	6.267×10^3		
Total	1.030×10^7	755	1.364×10^4		

plants from seeds collected in 2000. Foliage of reproductive plants was nearly 60 percent taller than foliage of nonreproductive plants, largely due to elongation of stem internodes in tillers that produced culms; that is, the leaf blades were not necessarily longer but were simply higher above the soil surface. Emergence time and leaf length correlated negatively in plants that reproduced, and were uncorrelated in nonreproductive plants.

Culm height at harvest. The tallest culms of reproductive plants averaged 582 mm in height (Table 30). Plants from block 3 had significantly shorter culms than plants in the other

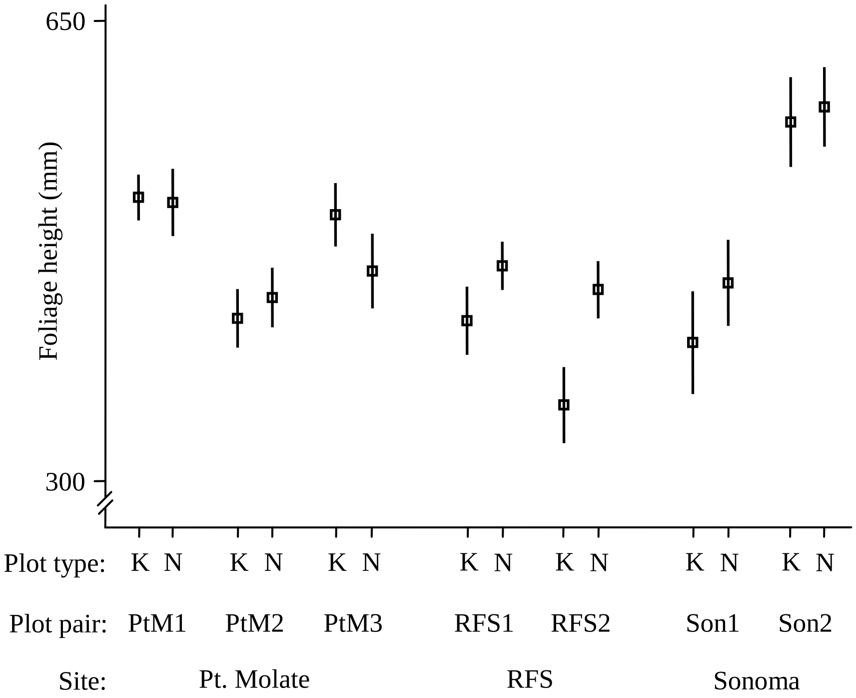

Figure 18.
Foliage Height at Harvest in the Common Garden

Means and 95% confidence intervals. K = thick plot; N = thin plot.
N = 760.

blocks ($p < 0.001$). Plants receiving more water had culms about 22 percent taller than those receiving less; this difference was greater for plants in block 3 than in the other blocks. Plants from Sonoma had the tallest culms at a mean of 665 mm, and at 508 mm RFS plants had the shortest ($p \leq 0.005$ for all between-site differences). RFS plants responded most strongly and Pt. Molate plants least to watering treatment. Two of three possible means separations between Pt. Molate plot pairs within site were significant ($p < 0.01$). In simple nested ANOVA of plot pair within site, site is not significant. Plants from larger seeds and plants that emerged faster had taller culms.

Table 30.
ANCOVA of Culm Height in the Common Garden at Harvest

$N = 640$
$R^2 = 0.4150$
Adjusted $R^2 = 0.3990$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	6.743×10^5	17	3.967×10^4	25.96	<0.0001
Block	6.569×10^4	2	3.285×10^4	21.50	<0.0001
Watering	2.152×10^5	1	2.152×10^5	140.83	<0.0001
Site	1.322×10^5	2	6.611×10^4	43.27	<0.0001
Plot pair	7.780×10^4	4	1.945×10^4	12.73	<0.0001
Planted seed weight	8.383×10^3	1	8.383×10^3	5.49	0.0195
Emergence time	1.956×10^4	1	1.956×10^4	12.80	0.0004
Block × site	1.591×10^4	4	3.978×10^3	2.60	0.0350
Water × site	1.194×10^4	2	5.971×10^3	3.91	0.0206
Residual	9.504×10^5	622	1.528×10^3		
Total	1.625×10^6	639	2.543×10^3		

Data transformation: $[(\textit{culm height})^{0.8257} - 1]/\ 0.8257$

Tiller counts. Like plant height, the number of tillers (including both vegetative and sexually reproductive tillers) was trimodally distributed over the three measurement periods (Table 31). Tiller counts were adapted for statistical analysis by

1. standardizing tiller counts within measurement periods to a mean of 0 and standard deviation of 1;
2. combining the standardized observations into one dataset containing three observations for each plant;
3. transforming the pooled observations as $(\textit{tillers} + 5)^{0.8}$; and
4. analyzing the standardized, transformed data using Stata's cluster-regression function, treating measurement period as a continuous variable.[23]

---

[23] Plants that developed root rot after the first tiller count were omitted from the cluster regression.

Table 31.
Tiller Counts by Site and Measurement Period in the Common Garden

	Tiller count: mean and standard deviation		
Period	1	2	3
Site			
Pt. Molate (*n* =315)	7.0 (1.9)	21.1 (6.4)	34.5 (8.1)
RFS (*n* = 248)	7.2 (2.1)	24.4 (5.6)	41.3 (7.9)
Sonoma (*n* = 222*)	6.8 (1.8)	21.8 (5.0)	34.0 (7.0)

Plants that developed root rot after the first measurement are omitted.
* For period 1, *n* = 221.

Plants in the third block initially had more tillers than those in other blocks, but this difference had disappeared by the third measurement period (Table 32). Plants in the well-watered group had almost one more tiller each than plants in the dry group at the first and third measurements; this fractional tiller gave wet-treatment plants a nine percent higher tiller count in the first measurement period, which declined to about two percent at the last measurement. The slight increase in tiller count with more water was smallest in Pt. Molate plants.

Plants from RFS had larger numbers of tillers than plants from the other sites at the second and third measurements ($p < 0.001$; Figure 19). Plot pairs varied marginally within site for RFS plants in the first measurement period, and in the third period for Pt. Molate plants (both $p \leq 0.10$). Common-garden tiller count correlated positively with culm count in the field; the strength of this correlation, while remaining small (particularly for Pt. Molate), increased over the three measurement periods, and was significant in univariate regressions within measurement period. The correlation of common-garden tiller count with absolute cover, while also small, became larger from one measurement period to the next, and had a small but significant effect on tiller counts in univariate regressions within measurement period. When first counted, the number of tillers correlated positively with planted seed weight, but by the last observation the correlation had become negative; planted seed weight was not significant in the cluster regression. Tiller count correlated negatively with emergence time, but this relationship also became weaker over time.

Leaf width. Leaf width, measured once on the widest leaf of each of a subsample of plants, averaged 3.8 mm. Greater watering (particularly in the second block) and heavier planted seeds correlated with wider leaves (Table 33). Sonoma plants had the widest leaves and RFS plants the narrowest; all differences between sites were significant ($p < 0.001$). Within sites, leaf

Table 32.
Cluster Regression of Common-Garden Tiller Count over Three Measurement Periods

$N = 2346$
Number of clusters (i.e., plants) = 782
$F\ (17, 781) = 108.86$
$R^2 = 0.3917$

Factor	Coefficient	Standard Error	t	p
Block 2 (vs. other blocks)	0.991	0.048	20.677	<0.001
Block 3 (vs. other blocks)	1.357	0.050	27.173	<0.001
Watering	0.196	0.041	4.795	<0.001
Measurement period	0.380	0.022	16.970	<0.001
Pt. Molate (vs. other sites)	0.309	0.087	3.568	<0.001
RFS (vs. other sites)	0.157	0.037	4.210	<0.001
PtM3 (vs. PtM1 & PtM2)	0.175	0.048	3.619	<0.001
RFS2 (vs. RFS1)	0.085	0.041	2.082	0.038
Absolute cover in field	0.003	0.001	2.919	0.004
Culm count in field	0.001	0.000	4.207	<0.001
Emergence time	-0.052	0.004	-11.527	<0.001
Block 2 × period	-0.416	0.025	-16.985	<0.001
Block 3 × period	-0.496	0.025	-19.528	<0.001
Water × period	-0.070	0.020	-3.522	<0.001
Water × Pt. Molate	-0.087	0.051	-1.708	0.088
Period × Pt. Molate	-0.119	0.020	-5.848	<0.001
Pt. Molate × culm count	-0.005	0.001	-5.147	<0.001
Constant	2.792	0.114	24.525	<0.001

Data were standardized within measurement period to a mean of 0 and standard deviation of 1. The three sets of data were pooled, then retransformed as $(tillers + 5)^{0.8}$.

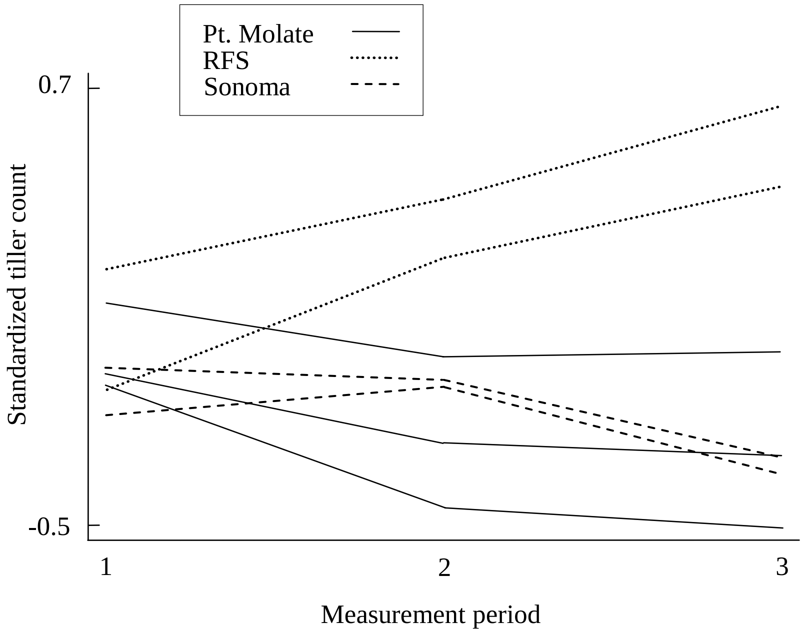

Figure 19.
Tiller Count in Common Garden by Plot Pair and Measurement Period

Tiller counts standardized within measurement period to mean = 0 and standard deviation = 1. *N* = 2346.

width correlated positively with culm frequency in the field, significantly so for Pt. Molate and nonsignificantly for the other sites. Conversely, the culm-frequency: leaf-width correlation was negative across sites (Table 34). Block was a marginally significant factor in the multivariate ANCOVA, but its significance stemmed from interactions with watering treatment and site.

Basal area at harvest. Mean basal area at harvest was 306 mm^2 for well-watered plants and 231 mm^2 for plants receiving less water (Table 35; Figure 20). Plants in the first block had mean basal area about 20 percent smaller than that of plants in the other blocks ($p < 0.001$). Basal area differed between plot pairs within site among Pt. Molate and Sonoma plants ($p < 0.01$); differences among plot pairs within these sites were larger than those between sites. Basal area in the common garden correlated positively with culm count in the field. Although the ANCOVA indicates that absolute cover in the field and common-garden basal area were positively correlated, examination of the data indicates this was the case for Pt. Molate and Sonoma only. Plants grown from larger seeds and early-emerging plants had larger basal area.

Table 33.
ANCOVA of Leaf Width of Common Garden Plants (Subsample of Plants)

$N = 438$
$R^2 = 0.4904$
Adjusted $R^2 = 0.4724$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	6.707	15	0.447	27.20	<0.0001
Block	0.077	2	0.038	2.34	0.0976
Watering	0.543	1	0.543	33.02	<0.0001
Site	2.048	2	1.024	62.29	<0.0001
Culm count in field	0.189	1	0.189	11.51	0.0008
Planted seed weight	0.141	1	0.141	8.59	0.0036
Block × water	0.223	2	0.112	6.78	0.0013
Block × site	0.227	4	0.057	3.45	0.0087
Site × culm count	0.203	2	0.101	6.17	0.0023
Residual	6.970	424	0.016		
Total	13.678	439	0.031		

Data transformation: $(\mathit{leaf\ width}^{0.1694} - 1) / 0.1694$)

Aboveground biomass. Oven-dry aboveground biomass averaged 1.79 g per dry-treatment plant, and 2.63 g for plants receiving more water (Table 36). Plants from the third temporal block had about eight percent less aboveground biomass at harvest than plants from the other blocks ($p < 0.05$), potentially because hotter, drier conditions in June and particularly July reduced growth. Plants grown from RFS seeds produced less aboveground biomass overall than plants from the other sites (Figure 21); however, because of the substantial difference in aboveground biomass between Sonoma plot pairs ($p < 0.01$), site is not significant in simple nested ANOVA. Aboveground biomass of common-garden plants correlated positively with culm count in the field for Pt. Molate plants and negatively for Sonoma plants. Plants grown from larger seeds and plants that emerged rapidly had greater aboveground biomass at harvest.

Table 34.
Correlation between Culm Count on Field Plots and Leaf Width in Common Garden Among and Within Sites

Site	Mean culms/m^2 in field	Leaf width* (mm)	Leaf width: culm count correlation (*r*)
Pt. Molate (*n* = 175)	37.9	3.7 (3.7–3.8)	0.2524
RFS (*n* = 126)	82.5	3.4 (3.3–3.5)	0.0146
Sonoma (*n* = 139)	46.0	4.3 (4.2–4.3)	0.0708
Across sites (*N* = 440)	54.3	3.8 (3.7–3.8)	-0.1289

* Arithmetic mean of leaf widths, and 95% confidence limits back-calculated from confidence limits for $(leaf\ width^{0.1694} - 1)/0.1694$. For Pt. Molate plants, univariate regression of leaf width over culm count is significant at p <0.01; for RFS and Sonoma plants the relationship is not significant in univariate regression

Belowground biomass. Root biomass was determined for plants from one plot pair per site (PtM1, RFS2, and Son1) for the first two planting blocks only, a total of 186 plants. Mean root biomass was 1.24 g per plant. Root biomass of plants that received more water averaged about nine percent greater than that of dry-treatment plants, but the difference between wet- and dry- treatment groups was not significant in multivariate ANCOVA or in univariate ANOVA. Greater belowground biomass correlated with higher culm counts in the field (Table 37).

Root biomass correlated positively with planted seed weight and negatively with days to emergence for plants in the first temporal block only. While the multivariate ANCOVA implies that absolute cover and emergence time influenced common-garden root biomass, their significance depends on their interaction; neither of these factors is significant in univariate regression. (The correlation between belowground biomass and absolute cover is more positive for slow-emerging plants; the correlation between belowground biomass and emergence time is more negative for plants from plots with relatively low absolute cover.)

Total biomass. Total biomass, calculated as the sum of above- and belowground biomass for the subsample of plants with weighed roots, averaged 4.08 g in heavily watered plants and 3.04 g in those receiving less water (Table 38). While significant in the multivariate ANCOVA, block was not significant in univariate tests. Plants grown from larger seeds and from

Table 35.
ANCOVA of Basal Area of Common Garden Plants

$N = 780$
$R^2 = 0.4795$
Adjusted $R^2 = 0.4707$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	20.068	13	1.544	54.28	<0.0001
Block	0.869	2	0.435	15.28	<0.0001
Water	8.022	1	8.022	282.10	<0.0001
Plot pair	2.672	6	0.445	15.66	<0.0001
Absolute cover in field	0.131	1	0.131	4.60	0.0322
Culm count in field	1.242	1	1.242	43.68	<0.0001
Planted seed weight	0.176	1	0.176	6.20	0.0130
Emergence time	0.945	1	0.945	33.22	<0.0001
Residual	21.783	766	0.028		
Total	41.850	779	0.054		

Data transformation: ln(*basal area* + 77.435)

seedlings that emerged faster had significantly greater total biomass. Culm count in the field, which correlated negatively with aboveground biomass and positively with root biomass, did not influence total biomass.

Green foliage at harvest. The estimated fraction of aboveground foliage that remained green at harvest varied from five to 95 percent, with a mean of 64 percent. Watering treatment was by far the most influential factor, with heavily-watered plants averaging 74 percent green foliage versus 53 percent for dry-treatment plants (Table 39)[24]. Sonoma plants had about 14 percent more green foliage than plants from the other sites; most of the difference among sites was concentrated in the heavily-watered group. The difference for Sonoma plot pairs in percent

---

[24] Percent green foliage was not recorded for the first 30 plants harvested. To correct for skewness and kurtosis, a two-step data transformation was applied. Data were first logit transformed, then transformed again using the Box-Cox transformation. This resulted in nonsignificant skewness and significant but much improved kurtosis of 2.65. Results of ANCOVA of this doubly-transformed data are not substantially different than results of ANCOVA of the same data rank-transformed or squared.

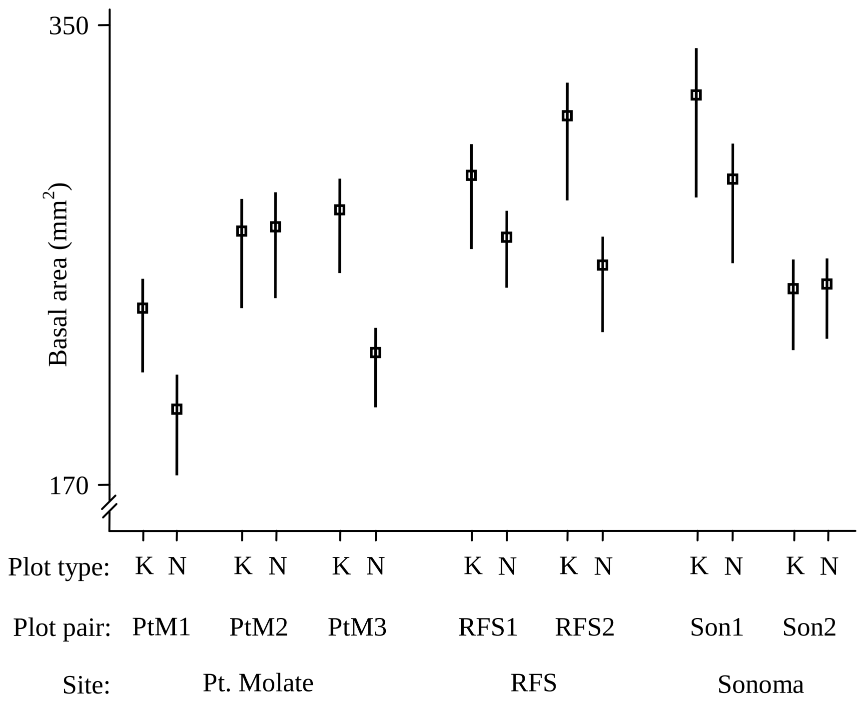

Figure 20.
Basal Area at Harvest in the Common Garden

Squares are arithmetic means; lines are 95% confidence intervals back-calculated from ln(*basal area* + 77.435). K = thick plot; N = thin plot. *N* = 784.

green foliage at harvest exceeded differences between sites, however, and in simple nested ANOVA plot pair was significant and site was not. In the multivariate ANCOVA, percent green foliage correlated marginally with Simpson's index and with culm count in the field, but neither culm count nor Simpson's index correlated with percent green tissue in simple regression. Aboveground biomass interacted with plot pair for Pt. Molate and RFS plants. Plants that emerged faster had lower average percent green foliage at harvest.

The relationship between percent green foliage and plant size at harvest was complex. For all plants combined, plants with greater aboveground biomass were greener (in particular, if

Table 36.
ANCOVA of Aboveground Biomass of Common-Garden Plants

N = 781
R^2 = 0.4016
Adjusted R^2 = 0.3906

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	21.600	14	1.543	36.71	<0.0001
Block	1.192	2	0.596	14.19	<0.0001
Watering	13.623	1	13.623	324.17	<0.0001
Site	2.827	2	1.413	33.63	<0.0001
Plot pair	0.909	4	0.227	5.41	0.0003
Culm count in field	0.127	1	0.127	3.03	0.0823
Planted seed weight	0.238	1	0.238	5.66	0.0176
Emergence time	0.877	1	0.877	20.88	<0.0001
Site × culm count	0.663	2	0.331	7.88	0.0004
Residual	32.192	766	0.042		
Total	53.792	780	0.069		

Data transformation: ln(*aboveground biomass* + 0.711)

they came from plots with high Simpson's index). This stems from watering treatment, in that well-watered plants were both greener and larger. Within the well-watered group, however, percent green foliage was negatively correlated with aboveground biomass; this correlation became increasingly negative from one block to the next. There was little correlation between aboveground biomass and percent green foliage in the dry group. This could imply that large size led to greater water stress and senescence of leaves when watering was reduced in plants accustomed to plenty of water. If percent green foliage is instead compared to root: shoot ratio, however, it appears that a larger root: shoot ratio is associated significantly if weakly with a lower percentage of green foliage for both wet-treatment plants (R^2 =0.1613; $p < 0.0005$ in univariate regression) and dry-treatment plants (R^2 =0.0697; $p < 0.01$). This may indicate the plants increased root biomass as they became water-stressed.

Aboveground relative growth rate. Relative growth rate (RGR) is the percentage increase in a plant's dry weight per unit time. Over the growth of a plant, small differences in

RGR can result in considerable differences in size. Aboveground RGR was calculated in this study as

$$\ln\left(\frac{aboveground\ biomass}{planted\ seed\ weight}\right)/growing\ days$$

where the term "growing days" means the time between seedling emergence and harvest.[25]

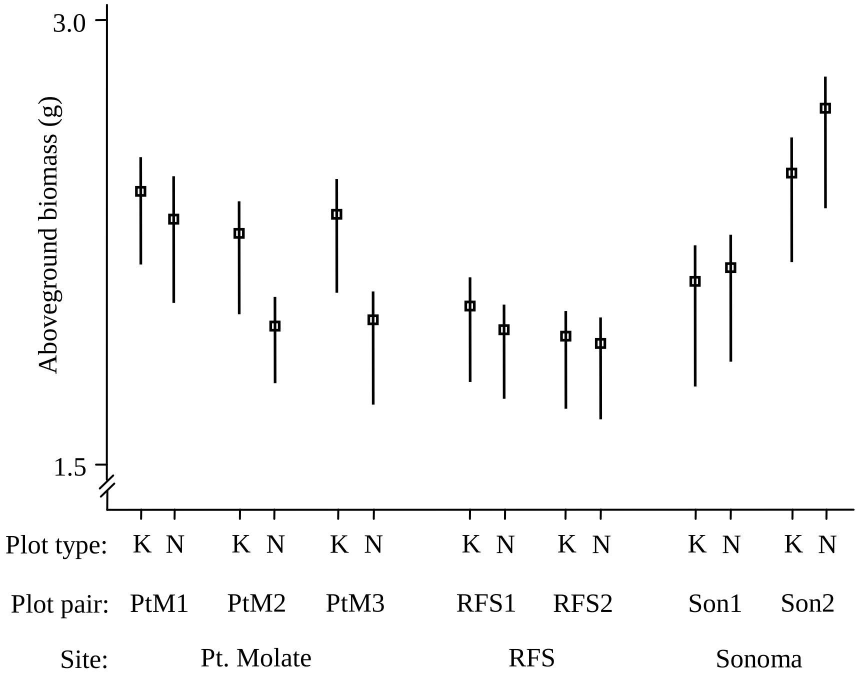

Figure 21.
Aboveground Biomass at Harvest in the Common Garden

Squares are arithmetic means; lines are 95% confidence intervals back-calculated from ln(*aboveground biomass* + 0.711). K = thick plot; N = thin plot. $N = 785$.

---

[25] Formula adapted from Stanton (1985).

Table 37.
ANCOVA of Belowground Biomass in the Common Garden (Subsample of Plants)

$N = 186$
$R^2 = 0.1917$
Adjusted $R^2 = 0.1552$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	1.849	8	0.231	5.25	<0.0001
Block	0.036	1	0.036	0.81	0.3702
Absolute cover	0.575	1	0.575	13.05	0.0004
Culm count in field	0.685	1	0.685	15.56	0.0001
Planted seed weight	0.478	1	0.478	10.85	0.0012
Emergence time	0.649	1	0.649	14.73	0.0002
Block × seed weight	0.135	1	0.135	3.07	0.0815
Block × emergence time	0.228	1	0.228	5.18	0.0241
Absolute cover × emergence time	0.683	1	0.683	15.51	0.0001
Residual	7.794	177	0.044		
Total	9.642	185	0.052		

Data transformation: ln(*belowground biomass* + 0.533)

Plants receiving more water had greater aboveground RGR (Table 40). Plants in the first block had the greatest growth rate, and those in the third block the least, possibly reflecting increasing temperatures and lesser overall water received by the plants in the later blocks. Sonoma plants grew about five percent faster than plants from the other sites. The multivariate ANCOVA indicated small but significant differences among plot pairs within site in aboveground RGR. These differences are significant in one comparison between plot pairs at Pt. Molate ($p < 0.05$) and marginally significant for Sonoma ($p < 0.10$). Plants from Pt. Molate plots with high culm count grew slightly faster than other plants, resulting in a site × culm count interaction; culm count is not a significant influence on aboveground relative growth rate in univariate analysis.

Table 38.
ANCOVA of Total Biomass of Common-Garden Plants (Subsample of Plants)

$N = 186$
$R^2 = 0.3149$
Adjusted $R^2 = 0.2998$

	Sum of squares	*df*	Mean square	*F*	*p*
Model	1.971	4	0.493	20.80	<0.0001
Block	0.126	1	0.126	5.34	0.0220
Watering	1.330	1	1.330	56.13	<0.0001
Planted seed weight	0.132	1	0.132	5.59	0.0192
Emergence time	0.156	1	0.156	6.60	0.0110
Residual	4.288	181	0.024		
Total	6.260	185	0.034		

Data transformation: ln(*total biomass* + 1.542)

Weight of planted seeds strongly influenced aboveground RGR. While larger initial seed mass and rapid emergence were associated with greater aboveground biomass, *lesser* initial seed weight and *slower* emergence were associated with greater aboveground RGR, that is, plants that started out smaller and later to some extent caught up with the others (Table 41). An inverse relationship between growth rate and seed weight or seedling size has been found in several intraspecific studies (Gross & Smith 1991; Houssard & Escarré 1990; Meyer & Carlson 2001; Roach 1986).

Belowground relative growth rate. Belowground RGR was calculated for plants in the first two blocks from plot pairs PtM1, RFS2, and Son1 as

$$\ln\left(\frac{\textit{belowground biomass}}{\textit{planted seed weight}}\right)\Big/\textit{growing days}$$

where the term "growing days" indicates the time between seedling emergence and harvest. Plants in the first block had slightly greater belowground RGR compared to the other blocks; block was not significant in univariate ANOVA. Common-garden belowground RGR correlated

Table 39.
ANCOVA of Percent Green Foliage of Common-Garden Plants at Harvest

$N = 751$
$R^2 = 0.4259$
Adjusted $R^2 = 0.4045$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	497.579	27	18.429	19.87	<0.0001
Block	0.480	2	0.240	0.26	0.7720
Watering	69.144	1	69.144	74.55	<0.0001
Site	7.641	2	3.821	4.12	0.0166
Plot pair	21.759	4	5.440	5.86	0.0001
Culm count in field	3.351	1	3.351	3.61	0.0578
Simpson's index	4.809	1	4.809	5.18	0.0231
Emergence time	9.082	1	9.082	9.79	0.0018
Aboveground biomass in common garden	5.154	1	5.154	5.56	0.0187
Water × site	10.644	2	5.322	5.74	0.0034
Water × aboveground biomass	10.271	1	10.271	11.07	0.0009
Plot pair × aboveground biomass	16.308	6	2.718	2.93	0.0079
Simpson's index × aboveground biomass	2.896	1	2.896	3.12	0.0777
Block × water × aboveground biomass	12.474	4	3.118	3.36	0.0097
Residual	670.613	723	0.928		
Total	1168.192	750	1.558		

Data transformation:

$$\frac{[(\ln[x/(1-x)]) + 3]^{1.17} - 1}{1.17}$$

where x= 0.01 × *percent green foliage at harvest*.

Table 40.
ANCOVA of Aboveground Relative Growth Rate in the Common Garden

N = 781
$R^2 = 0.5495$
Adjusted $R^2 = 0.5413$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	50.426	14	3.602	66.75	<0.0001
Block	1.599	2	0.800	14.82	<0.0001
Water	16.144	1	16.144	299.15	<0.0001
Site	3.398	2	1.699	31.48	<0.0001
Plot pair	1.306	4	0.327	6.05	0.0001
Culm count in field	0.261	1	0.261	4.83	0.0282
Planted seed weight	14.983	1	14.983	277.64	<0.0001
Emergence time	2.643	1	2.643	48.98	<0.0001
Site × culm count in field	0.755	2	0.378	7.00	0.0010
Residual	41.337	766	0.054		
Total	91.763	780	0.118		

positively with culm count and absolute cover in the field (Table 42). If the ANCOVA is cast with site in place of absolute cover, the result is nearly the same with $R^2 = 0.4610$. Belowground RGR correlated negatively with planted seed weight. For slow-emerging Sonoma and RFS plants, belowground RGR correlated positively with days to emergence, but in plants from plots with lower absolute cover (i.e., the plots in PtM1), belowground RGR decreased with greater time to seedling emergence. For fast-emerging plants, the influence of absolute cover in the field on common-garden belowground RGR was limited.

Root: shoot ratio. The root: shoot ratio of common-garden plants (from the first two temporal blocks, plot pairs PtM1, RFS2, and Son1) averaged 0.56. Well-watered plants had an average root: shoot ratio about 40 percent less than that of dry-treatment plants (Table 43). Among plot pairs, RFS2 plants had the greatest root: shoot ratio overall ($p < 0.01$). While the root: shoot ratio of well-watered plants varied little among the three plot pairs, the ratio varied substantially among these plot pairs for dry-treatment plants, and was greatest for RFS2 plants (Table 44). Root: shoot ratio correlated positively with culm count in the field. Although the

Table 41.
Aboveground Biomass and Proportional Growth by Planted Seed Weight Group

Planted seed weight	*n*	Mean aboveground biomass (g)	Mean $\frac{\text{(aboveground biomass)}}{\text{(planted seed weight)}}$
< 4.7 mg	407	2.16	543.8
≥ 4.7 mg	378	2.26	408.0

Table 42.
ANCOVA of Belowground Relative Growth Rate in the Common Garden (Subset of Plants)

$N = 186$
$R^2 = 0.4613$
Adjusted $R^2 = 0.4402$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	10.266	7	1.467	21.78	<0.0001
Block	0.628	1	0.628	9.33	0.0026
Absolute cover in field	0.986	1	0.986	14.65	0.0002
Culm count in field	1.171	1	1.171	17.39	<0.0001
Planted seed weight	2.006	1	2.006	29.79	<0.0001
Emergence time	0.502	1	0.502	7.46	0.0070
Block × emergence time	0.448	1	0.448	6.66	0.0107
Absolute cover × emergence time	1.108	1	1.108	16.45	0.0001
Residual	11.987	178	0.067	0.00	<0.0001
Total	22.253	185	0.120	0.00	<0.0001

Table 43.
ANCOVA of Root: Shoot Ratio of Common Garden Plants (Subset of Plants)

N = 186
R^2 = 0.4034
Adjusted R^2 = 0.3693

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	6.920	10	0.692	11.83	<0.0001
Block	0.181	1	0.181	3.10	0.0801
Watering	2.480	1	2.480	42.41	<0.0001
Site	0.744	2	0.372	6.36	0.0022
Culm count in field	0.846	1	0.846	14.47	0.0002
Planted seed weight	0.228	1	0.228	3.91	0.0496
Emergence time	0.222	1	0.222	3.80	0.0530
Block × emergence time	0.232	1	0.232	3.97	0.0478
Water × site	0.437	2	0.219	3.74	0.0257
Residual	10.233	175	0.058		
Total	17.154	185	0.093		

Data transformation $[(\textit{root biomass/aboveground biomass})^{0.4293} - 1] / 0.4293$

ANCOVA does not indicate the existence of interactions between culm count and other factors, the correlation between culm count and root: shoot ratio was strongest for RFS plants and for dry-treatment plants. Slow-emerging plants, particularly in the second block, developed relatively high root-shoot ratios. In univariate tests, block is not significant and emergence time is. Planted seed weight correlated positively with root: shoot ratio in the multivariate ANCOVA but was not a significant factor in univariate regression. The ANCOVA can be cast with absolute cover replacing site with a reduction in R^2 to 0.3607 (Table 44).

The ANCOVA can also be cast to include whether or not plants set seed as an explanatory variable, in which case R^2 is 0.4294, with little effect on the other variables. Reproductive RFS and Sonoma plants averaged mean root: shoot ratio nearly 30% lower than that of

Table 44.
Absolute Cover in Field and Root: Shoot Ratio by Plot Pair and Watering Treatment

Plot pair	Absolute cover (%)	Root: shoot ratio by watering treatment Dry treatment	 Wet treatment
PtM1 (*n* = 56)	38.6	0.57 (0.51–0.61)	0.46 (0.37–0.51)
RFS2 (*n* = 71)	90.9	0.82 (0.74–0.87)	0.52 (0.42–0.57)
Son1 (*n* = 61)	88.5	0.62 (0.54–0.67)	0.46 (0.36–0.51)

Root: shoot ratios are arithmetic means; 95% confidence limits (in parentheses) are back-transformed from confidence limits of

$$[(\textit{root biomass/aboveground biomass})^{0.4293} - 1] / 0.4293.$$

nonreproductive plants ($p < 0.002$). (All subsampled Pt. Molate plants set seed.) Among reproductive plants, root biomass correlated negatively with the ratio of culms to tillers ($R^2 = 0.0996$; $p = 0.0001$) and the number of florets on median culms ($R^2 = 0.1639$; $p < 0.0001$.)

Reproduction by Seed

Measures of reproduction by seed in the common garden included percentage of plants that reproduced, time to initial reproduction, number of culms per plant and seeds per culm, and weight of seeds. In *Stipa pulchra*, the panicle gradually extends upward within the enclosing terminal leaf until the upper florets begin to emerge. The awns are the first part of these florets to become visible. Sexual reproduction is defined here as production of one or more culms mature enough to have visible awns.

Which plants reproduced. Out of 785 plants, 655 set seed. Plants in the heavily-watered group were a fraction of a percent less likely to reproduce than plants receiving less water (Table 45); while significant in the multivariate logistic regression, this difference was not significant in a chi-squared test addressing the effect of watering alone. Among sites, 89.5 percent of Pt. Molate plants, 80.2 percent of RFS plants, and 78.4 percent plants from Sonoma set seed (Table 46). The difference between Pt. Molate and each other site is significant ($p < 0.05$). All plants originating from plot pair PtM1 set seed, as did all plants from the thin plots in plot pairs RFS1 and Son2. All differences between plot pairs within site were at least marginally significant in simple chi-squared testing. The likelihood of reproduction correlated negatively with culm count in the field, although this difference was small for Pt. Molate plants (Figure 22).

Table 45.
Logistic Regression of Reproduction by Seed in the Common Garden

$N = 690$
Log likelihood = -226.60
Likelihood Ratio Chi-Squared (8) = 214.57 ($p < 0.0001$)
Pseudo-$R^2 = 0.3213$

Source	Odds Ratio	Standard Error	z	*p*
Watering	0.337	0.094	-3.880	<0.001
Pt. Molate (vs. other sites)	0.397	0.198	-1.852	0.064
Sonoma (vs. other sites)	2.058	1.139	1.304	0.192
PtM2 (vs. PtM1 & PtM3)	0.124	0.057	-4.526	<0.001
Son1 (vs. Son1)	0.012	0.010	-5.199	<0.001
Culm count in the field	0.057	0.020	-8.013	<0.001
Aboveground biomass in common garden	43.983	25.012	6.654	<0.001
Sonoma × culm count	3.612	1.850	2.507	0.012

All plants from plot pair PtM1 set seed in the common garden; this plot pair is omitted from the logistic regression. Culm count in the field is transformed as

$$3.85 + \ln\left[\frac{\mathit{culm\ count}/150}{1 - (\mathit{culm\ count}/150)}\right]$$

Aboveground biomass of common garden plants transformed as ln(*biomass* + 0.7110).

For all plot pairs except PtM1, plants from the plot with lower culm density were more likely to set seed. Plants with greater aboveground biomass at harvest were more likely to reproduce. Plants grown from seeds collected in 2001 were about 11 percent more likely to reproduce than plants from seeds gathered in 2000; this was significant in a chi-squared test but not in the multivariate logistic regression, presumably due to nonsignificant interactions involving other factors.

Time to reproduction. Awns first became visible on common-garden plants in the ninth week, and over 90 percent of reproductive plants began setting seed by 15 weeks (Figure 23). Pt. Molate plants initiated reproduction first, followed about one week later by Sonoma and RFS

Table 46.
Percentage of Plants Setting Seed in the Common Garden by Site and Plot Pair

Site	*n*	Percent reproduction	Plot pair	*n*	Percent reproduction
Pt. Molate	315	89.5	PtM1	95	100.0
			PtM2	106	77.4
			PtM3	114	92.1
RFS	106	80.2	RFS1	124	91.9
			RFS2	124	68.5
Sonoma	114	78.4	Son1	102	57.8
			Son2	102	95.8

plants respectively (difference between Pt. Molate and each other site: $p < 0.005$). Inspection of the data indicates that differences between Pt. Molate plot pairs in time to initial reproduction are greater than differences between sites, however, and site is not significant in simple nested ANOVA comparing differences among sites to differences among plot pairs within sites.

The number of weeks to first reproduction correlated positively with field culm count in the multivariate ANCOVA, and in univariate regressions within site for RFS and Sonoma plants (for RFS and Sonoma $p < 0.05$; Figure 23; Table 47). For Pt. Molate plants these variables were negatively correlated for one plot pair and positively for another ($p < 0.005$ for the Pt. Molate plot pairs). Weeks to first reproduction correlated positively with Simpson's index in the multivariate ANCOVA and in univariate regression (i.e., across sites), but in single-site regressions the correlation is negative for Pt. Molate and Sonoma, and null for RFS.

Block was not a significant factor in the multivariate ANCOVA, but interacted significantly with other factors. Plants in the first block initiated seed production more slowly than plants in the other blocks, likely because of cooler temperatures; this effect was stronger for Sonoma and RFS plants than for Pt. Molate plants. For all three blocks, plants starting from larger seeds began reproduction more quickly than other plants; this effect was weakest for the first block and strongest for the last. Plants that emerged slowly as seedlings initiated seed production relatively late. This correlation was larger in plants from plots with low culm counts; conversely, the slower initiation of reproduction for plants from plots with high culm counts was more marked in plants that had emerged quickly as seedlings. Plants receiving more water began seed production a fraction of a day later than plants receiving less; this was not significant in univariate analysis.

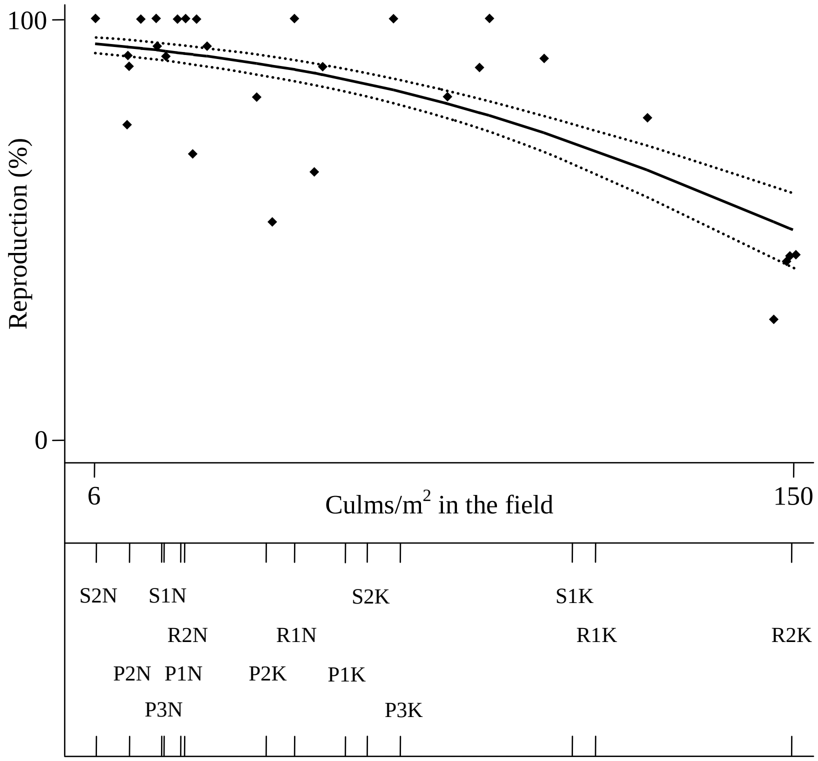

Figure 22.
Percent Reproduction by Seed in the Common Garden versus Culm Count in the Field

Upper part of figure: diamonds indicate mean percent reproduction grouped by plot × year. Graphed lines show likelihood of reproduction (logistic regression predicted probability and 95% confidence interval of the prediction). Bottom of figure: culms/m^2 in the field by plot, two-year average. Tick marks in lower graph line up with plot designations (e.g., S2N). Plot designations are grouped into lines by site for clarity. *N* = 785.

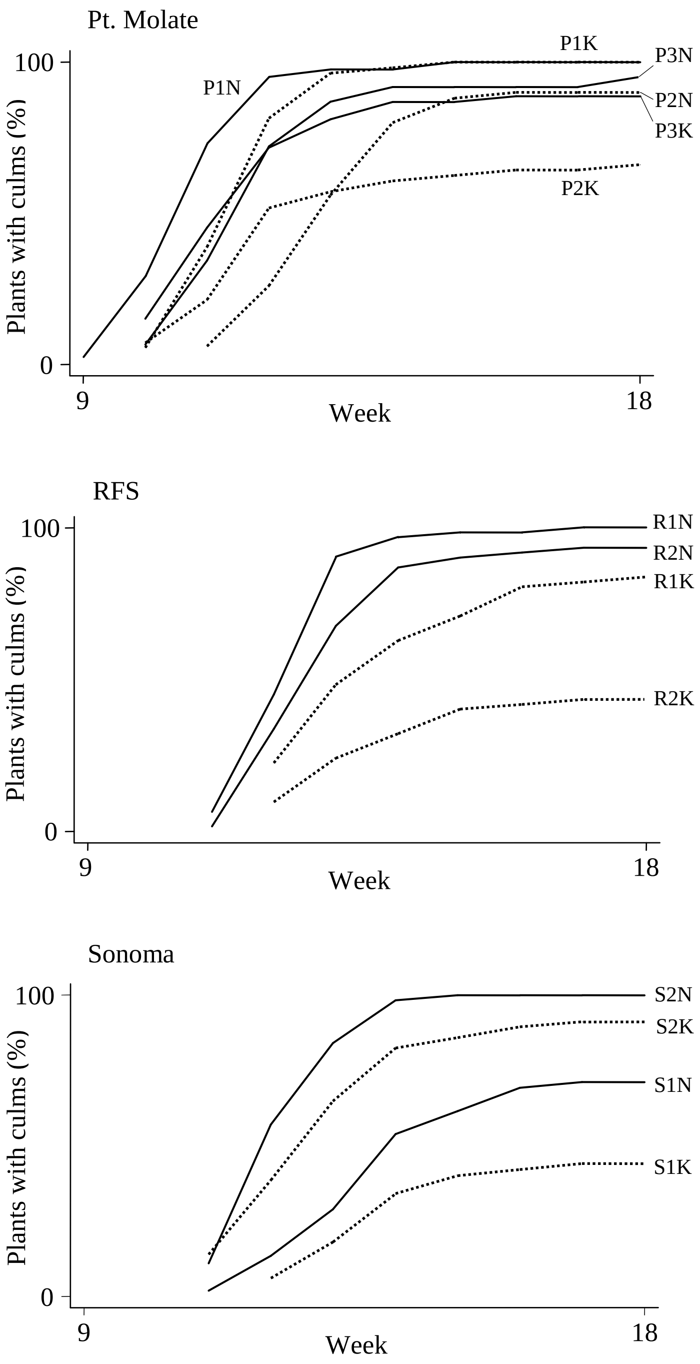

Figure 23.
Percentage of Common Garden Plants Bearing Culms by Number of Weeks Since Initial Watering

Graphed lines represent averages of individual plots. Dotted lines = thick plots, solid lines = thin plots.

Table 47.
ANCOVA of Weeks to First Seed Set

$N = 655$
$R^2 = 0.3973$
Adjusted $R^2 = 0.3783$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	6.631×10^{-2}	20	3.316×10^{-3}	20.89	<0.0001
Block	3.674×10^{-4}	2	1.837×10^{-4}	1.16	0.3149
Watering	5.756×10^{-4}	1	5.756×10^{-4}	3.63	0.0573
Site	8.970×10^{-3}	2	4.485×10^{-3}	28.26	<0.0001
Plot pair	1.347×10^{-2}	4	3.367×10^{-3}	21.22	<0.0001
Culm count in field	2.000×10^{-3}	1	2.000×10^{-3}	12.60	0.0004
Simpson's index	1.764×10^{-3}	1	1.764×10^{-3}	11.11	0.0009
Planted seed weight	7.517×10^{-4}	1	7.517×10^{-4}	4.74	0.0299
Emergence time	2.748×10^{-3}	1	2.748×10^{-3}	17.32	<0.0001
Block × site	1.994×10^{-3}	4	4.984×10^{-4}	3.14	0.0142
Block × seed weight	1.075×10^{-3}	2	5.377×10^{-4}	3.39	0.0344
Culm count × emergence time	7.630×10^{-4}	1	7.630×10^{-4}	4.81	0.0287
Residual	1.006×10^{-1}	634	1.587×10^{-4}		
Total	1.669×10^{-1}	654	2.552×10^{-4}		

Data transformation: $(weeks^{-0.7621} - 1)/-0.7621$.

Culms per common-garden plant. Reproductive plants each produced an average of 4.5 culms. Factors having the largest effects on culms per reproductive plant included aboveground biomass at harvest and weeks to initial reproduction—plants that grew larger and started setting seed sooner produced more culms (Table 48). Plants receiving more water produced about 23 percent more culms than those receiving less. Block 3 reproductive plants

Table 48.
ANCOVA of Culms per Reproductive Plant in the Common Garden

$N = 655$
$R^2 = 0.6908$
Adjusted $R^2 = 0.6795$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	577.930	23	25.127	61.29	<0.0001
Block	13.346	2	6.673	16.28	<0.0001
Watering	1.228	1	1.228	3.00	0.0840
Site	9.820	2	4.910	11.98	<0.0001
Plot pair	11.406	4	2.852	6.96	<0.0001
Absolute cover in field	2.460	1	2.460	6.00	0.0146
Culm count in field	1.557	1	1.557	3.80	0.0518
Planted seed weight	3.884	1	3.884	9.47	0.0022
Emergence time	6.269	1	6.269	15.29	0.0001
Aboveground biomass in common garden	137.403	1	137.403	335.15	<0.0001
Week to first seed set	70.157	1	70.157	171.12	<0.0001
Block × aboveground biomass	7.871	2	3.936	9.60	0.0001
Water × site	7.588	2	3.794	9.25	0.0001
Water × weeks	2.557	1	2.557	6.24	0.0128
Absolute cover × seed weight	1.724	1	1.724	4.21	0.0407
Culm count × weeks	2.883	1	2.883	7.03	0.0082
Water × culm count × weeks	1.766	1	1.766	4.31	0.0384
Residual	258.697	631	0.410		
Total	836.626	654	1.279		

Data transformation: $(\textit{culms per reproductive common-garden plant}^{0.5118} - 1) / 0.5118$

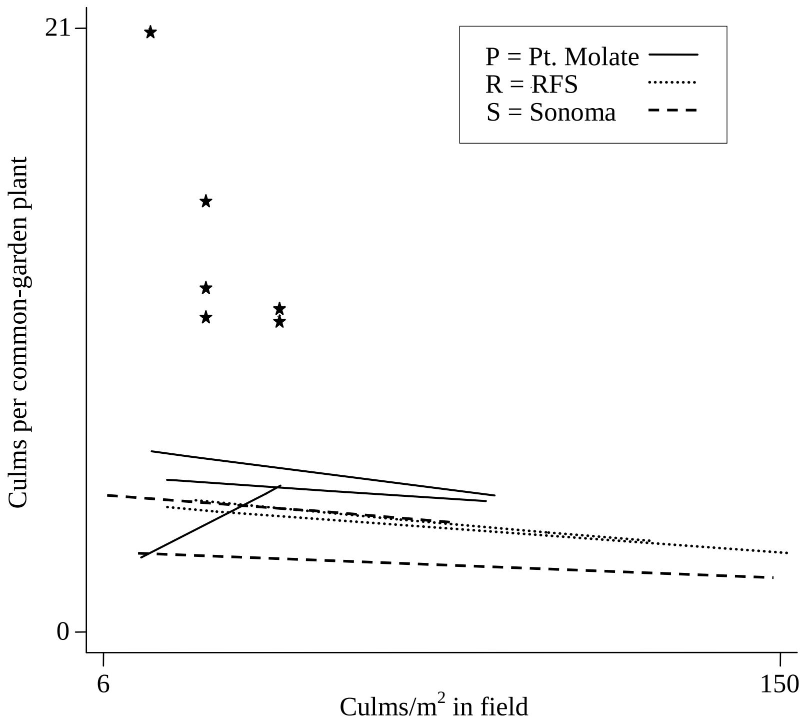

Figure 24.
Culms per Reproductive Plant in the Common Garden at Harvest and Culms/m^2 on Field Plots

Each regression line includes all data for its respective plot pair. Stars are included to illustrate outlying points, four of which came from the plot P1N (three from seed collected from the same maternal plant), and two from plot P3N. The outlying data is included in the regression lines, without which the graphed lines for these two plot pairs would be less steep but still significant. The graphed line trending upward to the right represents plot pair PtM2.

had relatively few culms at harvest, possibly due to high temperatures in June and early July and the resulting reduction in reproduction by seed; the increase in culm production with greater biomass was more pronounced in block 3 than in the other blocks.

Reproductive Pt. Molate plants produced about 25 percent more culms each than did reproductive RFS or Sonoma plants, and Pt. Molate plants responded more strongly to greater watering than did other plants. Differences in average culm production in reproductive plants were greater between plot pairs at Pt. Molate and at Sonoma than they were between sites

(Figure 24), and site is not significant in simple nested ANOVA. The number of culms in reproductive common-garden plants correlated negatively with absolute cover in the field; this correlation was more strongly negative for plants grown from larger seeds. For all but one plot pair (at Pt. Molate), plants from the thin plot produced more culms. The negative correlation between culm count in the field and culms on common-garden plants was more pronounced in plants that initiated reproduction relatively early. Plants grown from larger seeds or that emerged quickly produced relatively few culms; neither the weight of the planted seed nor emergence time is significant in univariate regression.

Florets per median culm. The median culms of reproductive common-garden plants bore an average of 23 florets each. Plants receiving more water produced about 15 percent more florets per median culm (Table 49), and plants in the second block had about nine percent more florets per median culm than plants in the first block ($p < 0.005$). Aboveground biomass at harvest had the largest effect in the multivariate ANCOVA, with larger plants producing more florets per median culm, particularly among dry-treatment plants. Among sites, Sonoma plants produced the most florets per median culm, and RFS the fewest (all between-site differences $p < 0.01$; Table 50). Florets per culm in the common garden and culm count in the field correlated negatively in dry-treatment plants and were uncorrelated in plants receiving more water. Florets per culm correlated positively with culm count in the field for Pt. Molate plants. Common-garden RFS plants with more culms also had more florets per culm; this correlation was weakly negative for Pt. Molate and Sonoma plants. Sonoma plants responded slightly more to extra water, but the site × watering interaction is not significant in simpler models. Although plot pair is not significant as a main effect in the multivariate ANCOVA nor in simple models that include site, there were nonsignificant differences between plot pairs within site in block 1 (Pt. Molate plot pairs) and block 3 (Sonoma plot pairs). Florets per median common-garden culm increased with later dates of seed collection in the field. Florets per median culm correlated negatively with weeks to first reproduction in multivariate analysis, but in univariate analysis the effect of weeks to reproduction was not significant.

Ripeness of individual offspring seeds. Seeds were collected from 512 of the 655 plants that reproduced. As seeds ripened in the common garden, they dropped from the plants. Ensuring that collected seeds came from specific plants meant that seeds could only be collected if they had not yet been shed. As a result, about 51 percent of the collected seeds were not completely ripe. To control for this artifact, seed color classification was used as a proxy for seed ripeness in statistical analyses of seed weight. In addition, seeds harvested from 18 harvested plants were included in weight analysis in cases where few or no seeds had been collected from these plants while still growing, typically from plants that produced very few culms; pre- or post-harvest class was included as an explanatory variable in the ANCOVA.

Collected seeds varied in color from grayish tan (i.e., ripe) to light green. Ripe seeds weighed 5.3 mg on average and unripe seeds 4.6 mg. The proportion of collected seeds that appeared ripe declined as the experiment moved from one block to the next, particularly for RFS plants (Table 51). Seeds from plants that received less water appeared greener than seeds from

Table 49.
ANCOVA of Florets per Median Culm in Common-Garden Plants

$N = 637$
$R^2 = 0.4958$
Adjusted $R^2 = 0.4691$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	17.861	32	0.558	18.56	<0.0001
Block	0.281	2	0.141	4.68	0.0096
Watering	0.125	1	0.125	4.16	0.0417
Site	0.799	2	0.400	13.29	<0.0001
Plot pair	0.088	4	0.022	0.73	0.5697
Seed collection date	0.131	1	0.131	4.35	0.0374
Culm count in field	0.004	1	0.004	0.12	0.7239
Aboveground biomass in common garden	4.107	1	4.107	136.56	<0.0001
Weeks to first reproduction in common garden	0.302	1	0.302	10.04	0.0016
Culms per common-garden plant	0.870	1	0.870	28.93	<0.0001
Block × plot pair	1.177	12	0.098	3.26	0.0001
Water × site	0.256	2	0.128	4.26	0.0145
Water × culm count in field	0.205	1	0.205	6.83	0.0092
Site × culms in common garden	0.950	2	0.475	15.80	<0.0001
Water × aboveground biomass in common garden	0.257	1	0.257	8.54	0.0036
Residual	18.165	604	0.030		
Total	36.025	636	0.057		

Data transformation: ln[(*floret count on median culm*) + 3.696]

Table 50.
Florets per Median Culm on Common Garden Plants by Site and Plot Pair

Site	*n*	Florets per culm	Plot pair	*n*	Florets per culm
Pt. Molate	279	22.0 (20.8–22.1)	PtM1	94	22.0 (20.6–22.6)
			PtM2	81	21.9 (19.9–22.5)
			PtM3	104	22.0 (20.4–22.6)
RFS	190	20.3 (19.1–20.5)	RFS1	110	20.0 (18.7–20.5)
			RFS2	80	20.7 (18.9–21.3)
Sonoma	168	27.9 (26.2–28.2)	Son1	55	29.2 (26.4–30.4)
			Son2	113	27.2 (25.6–27.8)

Means are arithmetic; 95% confidence intervals are back-calculated from confidence limits for ln[(*floret count on median culm*) + 3.696]

plants that had received more, again particularly for RFS plants. Pt. Molate seeds appeared relatively ripe compared to RFS and Sonoma seeds; however, differences between Sonoma plot pairs are greater than differences between sites. Seeds collected from plants that had relatively many culms generally appeared riper.

Unit weight of common-garden offspring seeds. Individual seeds harvested from common-garden plants had an average weight of 4.9 mg. Seeds harvested from plants receiving more water were heavier than seeds from dry-treatment plants (Table 52). In well-watered plants, the average unit weight of seeds harvested in the common garden increased from one block to the next despite the greater apparent ripeness of seeds in the earlier blocks. Pt. Molate and Sonoma plants produced heavier seeds than RFS plants, and significant differences existed in two of three comparisons between plot pairs within site for Pt. Molate ($p < 0.05$). Culm count

Table 51.
Logistic Regression: Color Classification of Seeds Collected from Common-Garden Plants

$N = 512$
Log likelihood = -234.220
Likelihood Ratio Chi-Squared (9) = 241.15 ($p < 0.0001$)
Pseudo-$R^2 = 0.3398$

Source	Odds Ratio	Standard Error	*z*	*p*
Block 1 (vs. blocks 1 & 2)	0.624	0.176	-1.674	0.094
Watering	0.229	0.066	-5.102	<0.001
RFS (vs. the other sites)	41.052	29.829	5.112	<0.001
Sonoma (vs. the other sites)	32.154	13.293	8.395	<0.001
Son1 (vs. Son2)	0.039	0.021	-6.005	<0.001
Culms per common-garden plant	0.721	0.085	-2.781	0.005
Seed harvest*	14.759	13.205	3.009	0.003
Block 1 × RFS	0.190	0.125	-2.53	0.011
Watering × RFS	0.129	0.096	-2.746	0.006

Culms per common-garden plant transformed as

$$[(\textit{culms per common-garden plant})^{0.5126} - 1]/0.5126$$

* I.e., seeds collected from live versus harvested plants.

in the field correlated positively with unit offspring seed weight in the multivariate ANCOVA, and for six of seven plot pairs, plants from the thick plot produced heavier seeds. Culm count, however, was not a significant factor affecting common-garden seed weight in univariate regression. Unit offspring seed weight increased with greater planted seed weight, faster seedling emergence, and greater aboveground biomass. Although the weight of seeds harvested from live versus cut plants did not differ significantly in univariate ANOVA, the multivariate ANCOVA classes seeds collected from live plants as lighter than those harvested from cut plants because seeds from live plants were riper-looking relative to their weight.

Table 52.
ANCOVA of Unit Weight of Seeds Collected from Common Garden Plants

N = 512 plants
$R^2 = 0.6501$
Adjusted $R^2 = 0.6328$

Source	Sum of Squares	*df*	Mean Square	*F*	*p*
Model	287.368	24	11.974	37.69	<0.0001
Block	10.783	2	5.392	16.97	<0.0001
Watering	2.576	1	2.576	8.11	0.0046
Site	40.311	2	20.155	63.45	<0.0001
Plot pair	14.171	4	3.543	11.15	<0.0001
Culm count in field	1.926	1	1.926	6.06	0.0142
Planted seed weight	4.838	1	4.838	15.23	0.0001
Emergence time	7.216	1	7.216	22.72	<0.0001
Culms on common-garden plants	6.598	1	6.598	20.77	<0.0001
Aboveground biomass in common garden	17.559	1	17.559	55.28	<0.0001
Seed harvest	2.766	1	2.766	8.71	0.0033
Seed color	6.965	1	6.965	21.93	<0.0001
Block × water	5.919	2	2.959	9.32	0.0001
Site × seed color	3.417	2	1.709	5.38	0.0049
Seed harvest × seed color	1.166	1	1.166	3.67	0.0560
Water × site × seed color	3.324	3	1.108	3.49	0.0157
Residual	154.702	487	0.318		
Total	442.070	511	0.865		

Ratio of flowering to vegetative tillers in sexually reproductive plants. After a tiller produces seeds, it senesces. Tillers that have not flowered can continue to grow and may generate additional tillers. Common-garden plants producing more total tillers generally also produced more flowering tillers. The number of flowering tillers correlated somewhat negatively with the number of vegetative tillers, however, implying a partial tradeoff between sexual reproduction and further growth (Table 53).

Reproductive plants receiving more water had a higher ratio of reproductive to vegetative tillers (Table 54). The effect of greater watering in reproductive plants was an increase in the number of culms they produced; the number of vegetative tillers did not much change with watering treatment. Site is not significant as a main effect, and differences between plot pairs at Pt. Molate and Sonoma were as large as differences between sites (Figure 25). Pt. Molate plants responded more strongly than RFS or Sonoma plants to additional water (Table 55). A greater proportional allocation to flowering tillers in the common garden correlated negatively with culm count in the field for all plot pairs except two at Pt. Molate. Plants in the third block had a lower ratio of culms to tillers than those in the second block ($p < 0.01$). Plants that had emerged

Table 53.
Plants That Set Seed Finished with Fewer Vegetative Tillers

		Mean tillers per plant by tiller type	
Site	Tiller type	Plants without seeds	Plants producing seeds
Pt. Molate	Vegetative	31.7	29.8
	Reproductive	—	5.1
	Total	31.7	34.9
	n	33	282
RFS	Vegetative	39.1	37.8
	Reproductive	—	4.0
	Total	39.1	41.8
	n	49	199
Sonoma	Vegetative	32.9	30.2
	Reproductive	—	4.0
	Total	32.9	34.3
	n	48	174

Table 54.
ANCOVA of Ratio of Flowering to Vegetative Tillers in Flowering Plants

$N = 655$
$R^2 = 0.6442$
Adjusted $R^2 = 0.6318$

Source	Sum of squares	*df*	Mean square	*F*	*p*
Model	98.375	27	3.644	43.15	<0.0001
Block	4.581	2	2.291	27.13	<0.0001
Watering	0.277	1	0.277	3.29	0.0704
Site	0.101	2	0.051	0.60	0.5490
Plot pair	2.623	4	0.656	7.77	<0.0001
Culm count in field	0.239	1	0.239	2.83	0.0930
Emergence time	1.585	1	1.585	18.76	<0.0001
Weeks to first seed set	29.404	1	29.404	348.22	<0.0001
Aboveground biomass in common garden	11.400	1	11.400	135.00	<0.0001
Block × site	0.694	4	0.174	2.06	0.0852
Block × aboveground biomass	2.967	2	1.483	17.57	<0.0001
Water × site	2.719	2	1.359	16.10	<0.0001
Plot pair × culm count	1.175	6	0.196	2.32	0.0318
Residual	52.944	627	0.084		
Total	151.320	654	0.231		

Data transformation:

$$\ln\left(\frac{flowering\ tillers}{vegetative\ tillers} + 0.0434\right)$$

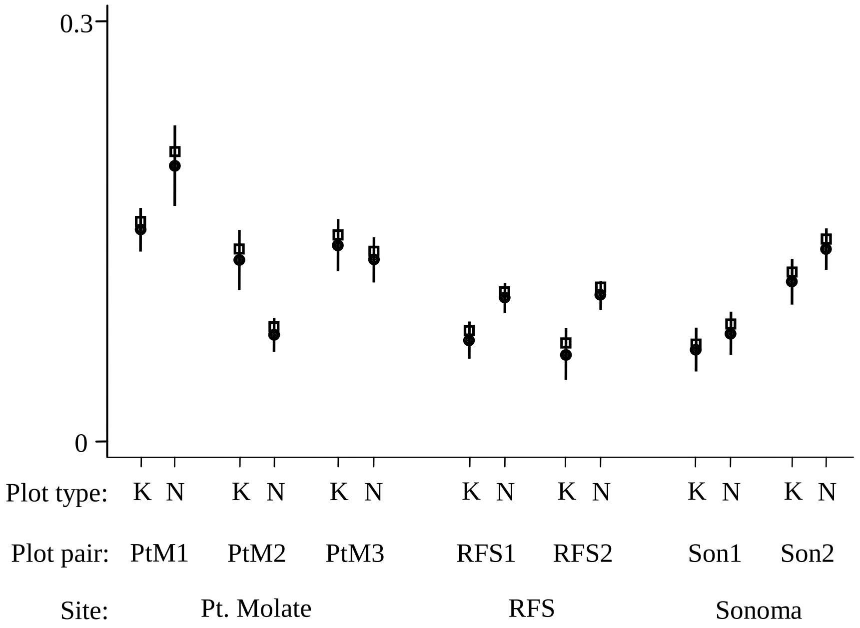

Figure 25.
Ratio of Culms to Vegetative Tillers in Reproductive Plants in the Common Garden

Filled circles and lines are means and 95% confidence intervals back-calculated from $(\mathit{culms/tillers})^{0.468}$ - 1)/0.468. Open squares are arithmetic means. K = thick plot; N = thin plot. N = 655.

quickly as seedlings allocated slightly more to flowering tillers. The ratio of flowering to vegetative tillers correlated strongly and negatively with weeks to first seed set, and correlated positively with aboveground biomass, particularly in the third block.

Total seed mass and seed mass: biomass allocation ratio. The total weight of seeds produced by individual common-garden plants was not directly measured and cannot be treated statistically with precision; however, some trends can be discussed. The total weight of seeds per plant may be estimated as

average individual seed weight × *florets per median culm* × *culms per plant*.

Table 55.
Mean Ratio of Flowering to Vegetative Tillers by Site and Watering Treatment in Reproductive Plants

	Watering treatment			
	Dry		Wet	
Site	*n*	Ratio	*n*	Ratio
Pt. Molate	153	0.15	129	0.23
RFS	100	0.11	99	0.12
Sonoma	96	0.14	78	0.15

Table 56.
Coefficients of Variation of Culms per Reproductive Plant, Seeds per Median Culm, and Weight of Individual Seeds

Variable	*N*	Mean	Standard deviation	CV
Culms per reproductive plant	655	4.485	—	—
ln(*culms per plant*)	655	1.345	0.604	0.664
Seeds per median culm	637	23.046	6.488	0.282
Weight of individual seeds	512	4.946	0.934	0.189

The variable culms per reproductive plant is approximately log-normal, and the CV of log-normal data is calculated as $(\exp[(sd_{ln})^2] - 1)^{0.5}$ where sd_{ln} is the standard deviation of the natural-log transformed data. The variables seeds per median culm and individual seed weight are approximately normally distributed.

Of these three variables, the number of culms per reproductive plant has the largest coefficient of variation (and presumably contributes the most variability to total seed mass), followed respectively by seeds per culm and weight of individual seeds (Table 56).

The allocation by a parent plant to seeds can be described in terms of

total weight of seeds/aboveground biomass.

The average total weight of seeds as estimated above was 581 mg per reproductive plant, and the seed mass: aboveground biomass ratio in reproductive plants averaged 0.24. Plants having large aboveground biomass were more likely to set seed, produced more culms, more florets per culm, and heavier individual seeds, thus probably produced more seed mass per plant overall. In contrast, belowground biomass was uncorrelated with likelihood of reproduction, culms per plant, seeds per median culm, or weight of individual seeds. Plants receiving more water appear to have allocated proportionally more to seed production than to biomass.

Reproductive Pt. Molate plants produced the largest number of culms, Sonoma plants the largest number of florets per median culm, and RFS plants the least massive individual seeds. As a result, among plants from the three sites, those from RFS appear to have had both the lowest total seed mass per plant and the smallest ratio of seed mass to aboveground biomass. Inspection of the data implies that variation in total seed mass per plant between plot pairs at Pt. Molate and at Sonoma was probably substantial. Culm count in the field and Simpson's index appeared to have little effect on total seed mass per reproductive plant or proportional allocation to seeds; thus the major effect on reproductive allocation by field culm count and Simpson's index is on likelihood of seed set.

Effect Size of Explanatory Variables

The foregoing parts of this chapter focused on response variables. The remainder summarizes these results in terms of explanatory variables. Because a large sample size can lend statistical significance to small effects, the following pages also address effect sizes in common-garden results (Tables 57–62). Effect size in multivariate ANCOVA or regression is estimated here as eta squared (η^2), calculated as SS_{effect}/SS_{total}. Some of the explanatory variables incorporated in this study are collinear or causally related; univariate and multivariate analyses are compared here to shed light on these relationships. Temporal block, watering treatment, site, and plot pair in general had substantially larger effect sizes than most of the other explanatory variables.

Temporal blocks. Dividing the common-garden study into temporal blocks was aimed only at easing experimental logistics, but it affected nearly every response variable. Plants in the first block experienced cooler, somewhat moister growing conditions than plants in the subsequent blocks. Block 1 plants emerged relatively slowly, began setting seed relatively slowly, and had more green foliage at harvest than those in the later blocks. Plants in the third block, which experienced the warmest, driest conditions; initially grew rapidly; by the end of the experiment, however, they had lesser overall growth rates and produced fewer culms and heavier individual seeds. Temporal blocking more strongly influenced initial than later measurements of tiller number and plant height, potentially implying that blocking most strongly affected early growth.

Watering treatment. Watering treatment significantly influenced the great majority of response variables. Plants receiving more water had more rapid emergence, wider leaves, a larger percentage of green foliage at harvest, greater basal area, greater aboveground biomass, and a higher relative growth rate. At seven weeks they were taller and had more tillers than dry-treatment plants, though these differences became proportionally smaller over later

Table 57.

Effect Size Estimates R^2 and η^2 for Common-Garden Main-Effects Response Variables: Days to Emergence, Basal Area, Leaf Width, and Percent Green Foliage at Harvest

	Response variables							
	Days to emergence*		Leaf width*†		Basal area at harvest*		Green foliage at harvest*	
Explanatory variables	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2
Block	0.3857	0.1009	*ns*	*0.0056*	0.0819	0.0208	0.0157	*ns*
Watering treatment	0.0062	0.0070	0.0290	0.0397	0.2021	0.1917	0.2601	0.0592
Site	0.0191	0.0124	0.3881	0.1497	0.0379	*ns*	0.0305	0.0065
Plot pair	0.0393	0.0210	0.3935	*ns*	0.0940	0.0638	0.0645	0.0186
Seed-collection year	*0.0036*	0.0052	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Seed-collection date	0.0145	*ns*	0.0396	*ns*	0.0066	*ns*	*0.0037*	*ns*
Absolute cover in field	0.0207	*ns*	*ns*	*ns*	0.0609	0.0031	0.0084	*ns*
Culm count in field	*ns*	0.0063	0.0166	0.0138	0.0610	0.0297	*ns*	*0.0029*
Simpson's index	0.0410	*0.0016*	*ns*	*ns*	*0.0044*	*ns*	*ns*	0.0041
Planted seed weight	0.0314	0.0108	*0.0076*	0.0103	*ns*	0.0042	0.0087	*ns*
Days to emergence	na	na	0.0089	*ns*	0.0938	0.0226	0.0157	0.0078

R^2 calculated via univariate regression or ANOVA for each explanatory variable; eta squared (η^2) calculated as $SS_{\text{effect}}/SS_{\text{total}}$ from the multivariate ANCOVA. Numbers in italics are marginally significant ($0.05 < p \leq 0.10$); numbers in regular type are significant to $p \leq 0.05$.

* Site not significant and plot pair significant in simple nested ANOVA. ** Site significant and plot pair not significant in simple nested ANOVA. † Subsample of plants.

Table 58.
Effect Size Estimates R^2 and η^2 for Common-Garden Main-Effects Response Variables: Height and Tiller Counts Across Measurement Periods

	Response variables			
	Plant height		Tiller counts	
Explanatory variables	R^2	η^2	R^2	η^2
Block	0.0695	0.0641	0.1535	0.0622
Watering treatment	0.0102	*ns*	*0.0025*	0.0020
Measurement period	*ns*	0.0054	*ns*	0.0109
Site	0.1034	0.0039	0.0503	0.0020
Plot pair	0.1719	0.0169	0.0638	0.0121
Seed-collection year	0.0038	*ns*	*ns*	*ns*
Seed-collection date	0.0029	*ns*	*ns*	*ns*
Absolute cover in field	0.0732	*ns*	0.0160	0.0008
Culm count in field	0.0573	0.0019	0.0204	0.0019
Simpson's index	0.0175	*ns*	0.0063	*ns*
Field culm height	0.0289	*ns*	na	na
Planted seed weight	0.0630	0.0113	*ns*	*ns*
Days to emergence	0.1404	0.0265	0.1467	0.0314

R^2 values derived from univariate cluster regressions; number in italics marginally significant ($0.05 < p \leq 0.10$); all others $p \leq 0.05$. Eta squared (η^2) calculated as $SS_{\text{effect}}/SS_{\text{total}}$ from ANCOVAs that are similar but not identical to the cluster regressions in Tables 27 and 32; please refer to those tables for statistical significance.

Table 59.
Effect Size Estimates R^2 and η^2 for Common-Garden Main-Effects Response Variables: Height in Single Measurement Periods

	Response variables									
	First height measurement*		Second height measurement*		Third height measurement*		Foliage height at harvest*		Culm height at harvest*	
Explanatory variables	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2
Block	0.2363	0.0389	0.1281	0.0476	0.0271	0.0205	0.0190	0.0158	0.0348	0.0404
Watering treatment	0.0304	0.0229	0.0194	0.0250	0.0719	0.0214	0.0218	0.0231	0.1391	0.1324
Site	0.1504	0.0031	0.1305	0.0393	0.0800	0.0059	0.0849	0.0466	0.1447	0.0814
Plot pair	0.1664	0.0374	0.2603	0.0938	0.2257	0.0147	0.2438	0.0280	0.2002	0.0479
Seed-collection year	*0.0038*	*ns*	*0.0041*	*ns*	*0.0035*	*ns*	0.0056	*ns*	*ns*	*ns*
Seed-collection date	0.0168	*ns*	*0.0048*	*ns*	*ns*	*ns*	0.0105	*ns*	*0.0058*	*ns*
Absolute cover in field	0.0855	*ns*	0.1051	*ns*	0.0380	*ns*	0.0133	*ns*	0.0131	*ns*
Culm count in field	*ns*	0.0091	0.1000	0.0252	0.1256	0.0027	0.0976	*ns*	0.0167	*ns*
Simpson's index	0.0318	0.0080	0.0159	*ns*	0.0086	*ns*	*ns*	*ns*	*ns*	*ns*
Planted seed weight	0.1254	0.0386	0.0642	0.0081	0.0213	0.0019	0.0133	*ns*	0.0190	0.0052
Days to emergence	0.4166	0.1049	0.1402	0.0146	0.0113	0.0058	0.0134	0.0029	0.0127	0.0120

R^2 calculated via univariate regression or ANOVA for each explanatory variable; eta squared (η^2) calculated as $SS_{\text{effect}}/SS_{\text{total}}$ from the multivariate ANCOVA. Numbers in italics are marginally significant ($0.05 < p \leq 0.10$); numbers in regular type are significant to $p \leq 0.05$.
* Site not significant and plot pair significant in simple nested ANOVA.

Table 60.
Effect Size Estimates R^2 and η^2 for Common-Garden Main-Effects Response Variables: Tiller Counts in Single Measurement Periods

	Response variables					
	First tiller count*		Second tiller count*		Third tiller count**	
Explanatory variables	R^2	η^2	R^2	η^2	R^2	η^2
Block	0.4168	0.0938	0.3973	0.2260	0.0119	0.0255
Watering treatment	0.0234	0.0132	0.0028	0.0062	*ns*	*ns*
Site	*ns*	0.0040	0.0592	0.0152	0.1499	0.0343
Plot pair	0.0185	0.0107	0.0719	0.0128	0.1673	0.0180
Seed-collection year	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Seed-collection date	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Absolute cover in field	*ns*	0.0023	0.0305	*ns*	0.0431	*ns*
Culm count in field	0.0069	*ns*	0.0173	*ns*	0.0473	*ns*
Simpson's index	*ns*	*ns*	0.0121	*ns*	0.0191	0.0063
Planted seed weight	0.0356	0.0136	*ns*	*ns*	0.0072	*ns*
Days to emergence	0.5005	0.1397	0.1707	0.0144	*ns*	0.0168

R^2 calculated via univariate regression or ANOVA for each explanatory variable; eta squared (η^2) calculated as $SS_{\text{effect}}/SS_{\text{total}}$ from the multivariate ANCOVA. Data are transformed as for cluster regression. Numbers are significant to $p \leq 0.05$.
* Site not significant and plot pair significant in simple nested ANOVA. **Both site and plot pair at least marginally significant in simple nested ANOVA.

Table 61.
Effect Size Estimates R^2 and η^2 for Common-Garden Main-Effects Response Variables: Biomass and Relative Growth Rate

	Response variables											
	Aboveground biomass*		Belowground biomass*†		Total biomass*†		Root: shoot ratio*†		Aboveground RGR**		Belowground RGR*†	
Explanatory variables	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2
Block	0.0116	0.0222	*ns*	*ns*	*ns*	0.0201	*ns*	*0.0106*	0.0930	0.0174	*ns*	0.0282
Watering treatment	0.2636	0.2533	*ns*	*ns*	0.2501	0.2125	0.2064	0.1446	0.1729	0.1759	*ns*	*ns*
Site	0.0446	0.0526	*ns*	*ns*	*ns*	*ns*	0.0985	0.0434	0.0433	0.0370	0.0917	*ns*
Plot pair	0.0790	0.0169	na	na	na	na	na	na	0.0612	0.0142	na	na
Seed- collection year	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Seed-collection date	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	0.0089	*ns*	*0.0170*	*ns*
Absolute cover in field	*0.0035*	*ns*	*ns*	0.0596	*ns*	*ns*	0.0674	*ns*	0.0113	*ns*	0.0851	0.0443
Culm count in field	0.0070	*0.0024*	0.0453	0.0710	*ns*	*ns*	0.1172	0.0493	*ns*	0.0028	0.0891	0.0526
Simpson's index	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	0.0685	*ns*	0.0108	*ns*	0.0337	*ns*
Planted seed weight	0.0116	0.0044	0.0223	0.0496	0.0272	0.0211	*ns*	0.0133	0.2262	0.1633	0.1956	0.0901
Days to emergence	0.0232	0.0163	*ns*	0.0673	0.0498	0.0249	0.0297	*0.0129*	0.1048	0.0288	*ns*	0.0226

R^2 calculated via univariate regression or ANOVA; eta squared (η^2) calculated as $SS_{\text{effect}}/SS_{\text{total}}$ from the multivariate ANCOVA. Numbers in italics are marginally significant ($0.05 < p \leq 0.10$); numbers in regular type are significant to $p \leq 0.05$.
* Site not significant and plot pair significant in simple nested ANOVA. **Both site and plot pair at least marginally significant in simple nested ANOVA. † Subsample of plants.

Table 62.
Effect Size Estimates R^2 and η^2 for Common-Garden Main-Effects Response Variables: Reproduction by Seed

	Response variables									
	Weeks to reproduction*		Culms per reproductive plant*		Ratio of culms to vegetative tillers*		Seeds per median culm*		Individual seed weight**	
Explanatory variables	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2	R^2	η^2
Block	0.0741	*ns*	0.0115	0.0160	0.0147	0.0303	0.0171	0.0078	*ns*	0.0244
Watering treatment	*ns*	*0.0034*	0.0310	*0.0015*	0.0216	*0.0018*	0.0622	0.0035	0.0994	0.0058
Site	0.1790	0.0537	0.0489	0.0117	0.0994	*ns*	0.2034	0.0222	0.2680	0.0912
Plot pair	0.2684	0.0807	0.1552	0.0136	0.2224	0.0173	0.2073	*ns*	0.3039	0.0321
Seed-collection year	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	0.0094	*ns*	*ns*	*ns*
Seed collection date	0.0370	*ns*	0.0251	*ns*	0.0219	*ns*	0.0724	0.0036	*ns*	*ns*
Absolute cover in field	0.1737	*ns*	0.0645	0.0029	0.1136	*ns*	0.0071	*ns*	0.1182	*ns*
Culm count in field	0.0361	0.0120	0.0356	*0.0019*	0.0615	*0.0016*	*ns*	*ns*	*ns*	0.0044
Simpson's index	*0.0055*	0.0106	*ns*	*ns*	*ns*	*ns*	*0.0056*	*ns*	0.0096	*ns*
Planted seed weight	0.0540	0.0045	*ns*	0.0046	0.0161	*ns*	*0.0046*	*ns*	0.0795	0.0109
Days to emergence	0.1154	0.0165	*ns*	0.0075	*0.0045*	0.0105	0.0177	*ns*	0.0116	0.0163
Aboveground biomass in common garden	*ns*	*ns*	0.1921	0.1642	0.1301	0.0753	0.2313	0.1140	0.1986	0.0397
Weeks to reproduction	na	na	0.3619	0.0839	*0.3867*	0.1943	*ns*	0.0084	0.0446	*ns*

Plants that did not set seed are omitted from this table. R^2 calculated via univariate regression or ANOVA; eta squared (η^2) calculated as $SS_{\text{effect}}/SS_{\text{total}}$ from the multivariate ANCOVA. Numbers in italics are marginally significant ($0.05 < p \leq 0.10$); numbers in regular type are significant to $p \leq 0.05$.

* Site not significant and plot pair significant in simple nested ANOVA. **Both site and plot pair at least marginally significant in simple nested ANOVA.

measurements. Plants receiving more water were slower and slightly less likely to set seed. In other measures of sexual reproduction, however, they exceeded dry-treatment plants: they had more culms per plant and a larger ratio of culms to vegetative tillers, more seeds per median culm, and riper-looking individual seeds. Seeds produced by well-watered plants were individually heavier than seeds from dry-treatment plants, particularly in the third temporal block. Plants receiving more water, however, did not differ from dry-treatment plants in root biomass and had lower root: shoot ratios.

Site versus plot pair (and plot). Seed-source site was a significant factor in most of the statistical analyses in this study. Pt. Molate plants emerged and began setting seed relatively fast. They were more likely to reproduce sexually, allocated a larger share of tillers to reproduction, and had lesser basal area at harvest than RFS or Sonoma plants. Pt. Molate plants differed from RFS and Sonoma plants in their response to temporal blocking; emergence of Pt. Molate seedlings was more accelerated in the warmer conditions experienced by block 3, and initial reproduction of these plants was delayed less in the cooler conditions experienced by plants in blocks 1 and 2. Unlike plants from the other sites, Pt. Molate plants did not increase tillering in response to extra water. Well-watered Pt. Molate plants, however, increased allocation of extant tillers to reproduction by about 35 percent, versus 15 percent and eight percent respectively for RFS and Sonoma plants.

Plants grown from RFS seeds emerged more slowly, produced narrower leaves and more tillers, and allocated less to sexual reproduction than did plants from the other sites. RFS plants were relatively short but had the largest basal area and belowground biomass among plants from the three sites, and increased their root: shoot ratio more in response to dry treatment. Leaves of RFS plants became wider from one temporal block to the next. The negative correlation between culm count in the field and likelihood of reproduction in the common garden was greatest for RFS plants, as was the positive correlation between culm count in the field and root: shoot ratio.

Sonoma plants had the fewest tillers and the widest leaves. In contrast to RFS plants, Sonoma plants had increasingly narrow leaves from one block to the next. Although they had lesser belowground biomass and a lower root: shoot ratio, they had a larger proportion of green foliage at harvest.

Plants from the three sites, however, seem less sharply differentiated when within-site variation is taken into account. In the majority of multivariate tests, the variance explained by site (η^2) is less than the variance explained by plot pair. As discussed in Chapter 6, thick and thin plots were broadly matched in pairs in terms of slope, aspect, and background vegetation in order to prevent, for example, comparing thin plots dominated by *Bromus* to thick plots otherwise full of *Avena*. An unanticipated result of this approach was that for many common-garden response variables, paired plots indeed appear to have performed as pairs. This raises the question of whether within-site variation equals or exceeds between-site variation for the plants examined in this study. Because plots (and therefore pairs) were not randomly selected, nested ANOVA cannot be used here with analytical rigor. Nested ANOVA considered as a descriptive method coupled with nonstatistical examination of results, however, may suggest relationships that might be formally examined with a different sampling protocol.

For the majority of cases where both site and plot pair were significant factors in multivariate tests, simple nested ANOVA broadly suggests that plot pair overshadowed site. The differences between plot pairs within site exceeded those between sites, in terms of raw numbers, for the second and third height measurements, foliage height at harvest, likelihood of reproduction, and ratio of culms to vegetative tillers in reproductive plants. For aboveground biomass and percent green tissue at harvest, the differences in raw numbers between sites were similar in size to differences between plot pairs within site. For the first height measurement and for culm height at harvest, the differences between sites in raw numbers were larger than those between plot pairs within site. Where simple nested ANOVA indicated significance both for site and for plot pairs within site, raw-number differences between sites were greater than those between plot pairs; cases included the final tiller count, aboveground RGR, and the average weight of individual seeds.

For several variables, however, it appears that the locus of variation could be more accurately placed at the level of plots within pairs; that is, in raw averaged numbers the differences between plots within pairs roughly equaled or exceeded differences between plot pairs within sites. These variables include days to emergence, first and second tiller counts, basal area, weeks to reproduction, and number of culms per reproductive plant. In addition, root: shoot ratio and belowground RGR was larger for plants from the thick plot in each of the pairs tested.

While not analytically rigorous, taken together the results described above imply that variations within site at the level of plot pairs are potentially on a scale similar to that of variations between sites. Dissimilarities between plants from different plot pairs within sites (and similarities within pairs) may indicate that the loose matching of these plots based on background vegetation in fact reflected ecological similarities between patches. The variation among plots within sites and pairs, which often exceeded differences among sites and among plot pairs within sites, implies pervasive small-scale variation in *S. pulchra.*

Site versus absolute cover across sites. Differing absolute cover was an important part of differences among sites. In both univariate and multivariate tests, absolute cover as an explanatory variable readily substituted for site, in most cases with reduced R^2 or η^2. Absolute cover was at least marginally significant in six out of 25 multivariate tests, potentially implying a role for absolute cover beyond collinearity with site.[26] Assuming a 10 percent chance of committing a Type I error if α is set at 0.10, and if the 25 multivariate tests could be considered independent of one another, a result of six out of 25 significant tests would itself be a significant result. In univariate regression within site, however, for three of these six response variables absolute cover was significant within only one site; for two response variables absolute cover was not significant within any site, and for one variable the slope differed in sign between sites.

Site, but not absolute cover, was a significant variable in multivariate testing for 17 of the remaining response variables. For eight of these, Pt. Molate plants and RFS plants are most dissimilar in terms of average results; that is, for these eight response variables the differences between sites parallel the variation among sites in absolute cover. For example, weeks to

---

[26] These 25 variables are likelihood of root rot and likelihood of reproduction, plus the response variables in Tables 57 and 59–62. Absolute cover is significant in univariate tests with 21 of these response variables.

reproduction follows the same pattern as absolute cover: PtM < Son < RFS. Absolute cover was thus arguably implicated in another eight tests, for a total of 14 of 25 response variables.

There remain nine response variables for which differences among the sites did not parallel absolute cover.[27] For six of these nine variables (such as aboveground biomass at harvest and florets per culm), plants from Sonoma and RFS (the sites with highest absolute cover) are most dissimilar in terms of average results; for the final three, plants from Pt. Molate and Sonoma are the least similar. These nine results may be due to factors reflecting site proximity, such as climate, soil, or metapopulation dynamics.

Absolute cover within site. Among the 17 response variables for which absolute cover was significant in univariate but not multivariate testing, absolute cover was significant within site in five univariate tests for Pt. Molate plants alone, in five univariate tests for RFS and Pt. Molate plants, and in one for Pt. Molate and Sonoma plants. Where absolute cover was significant within two sites, the correlation of absolute cover with the response variable differed in sign between sites. Weeks to reproduction, for example, correlated positively with absolute cover for Pt. Molate plants and negatively for RFS plants, though in both cases the correlation was very small. The effects of absolute cover and culm count in the field in general were positively correlated for Pt. Molate plants.

Field culm count. Culm count in the field was at least marginally significant as a main effect in 16 of the 23 multivariate statistical tests and 16 of the univariate tests summarized in Tables 57 and 59–62. Culm count was also the factor with the largest effect (i.e., odds ratio) in likelihood of reproduction, and correlated significantly with likelihood of root rot. Plants originating in plots with higher culm counts developed wider leaves when considered within site, lower stature (particularly in later measurements), larger basal area, lesser likelihood of seed set, fewer culms, greater root biomass, and higher root: shoot ratios. In most tests the effect size of field culm count was small; however, its effect was larger in measurements of sexual reproduction versus allocation to growth. Absolute cover and culm count were correlated at Pt. Molate. In simple regressions addressing Pt. Molate plants alone, absolute cover correlated more strongly than culm count for basal area, likelihood of seed set, ratio of reproductive to vegetative tillers, and weeks to first reproduction.

Simpson's index. Simpson's index was at least marginally significant in five of 25 multivariate statistical tests summarized in Tables 57 and 59–62, a result that itself would be marginally significant ($p < 0.10$) if the tests could be considered as independent of one another. The index, however, was not significant in likelihood of root rot or sexual reproduction, which combined with the other tests pushes the total outside of marginal significance. Simpson's index was at least marginally significant in 13 of the 23 univariate tests, reflecting the index's correlation with culm count, absolute cover, and site. Most effect sizes associated with Simpson's index were very small; plants from plots with higher Simpson's index emerged more slowly, and developed somewhat higher root: shoot ratios than other plants.

Emergence time. Time to seedling emergence was a significant factor affecting most response variables. Quickly emerging plants had greater above- and belowground biomass and basal area at harvest; they grew taller, had more tillers and wider leaves, and began setting seed

---

[27] For eight of these nine response variables, absolute cover is at least marginally significant in univariate testing.

sooner than slow-emerging plants. The effect of emergence time on plant height and tiller count, as measured by R^2 and η^2, appears to have been greater during the early growth of the plants, in that early tiller counts and height measurements were more strongly affected by emergence time, and slow-emerging plants had greater above- and belowground relative growth rates. The slower growth of plants in the first block appears tied at least in part to slower seedling emergence.

Seed weight. Planted seed weight affected nearly as many response variables as did emergence time. Plants grown from heavier seeds emerged faster, had wider leaves, greater above- and belowground biomass, and greater basal area. They began reproducing sooner, had more culms per plant, more seeds per median culm, and heavier individual offspring seeds. Seed weight may have exerted a diminishing effect on overall growth over time, in that the effect size of seed weight on plant height and tiller count, as measured by R^2 and η^2, diminished from one measurement period to the next. While plants grown from large seeds had substantially more tillers at seven weeks, by harvest they had somewhat fewer tillers than did plants from smaller seeds. Plants grown from larger seeds had lower above- and belowground relative growth rates.

Year and date. Seed collection year was at least marginally significant in only one multivariate test summarized in Tables 57 and 59–62. As previously noted, seeds collected from a few plots in 2000 were of lower quality than seeds collected in 2001 from the field. Year was significant in six of 23 univariate tests, likely because of the effect of this quality difference on seed weight and emergence time. Seed collection date was a significant factor in only one multivariate test, less than might be expected by chance; the significance of date in 14 of the 23 univariate tests stems from the correlation of date with site.

Summary

The plants in the common garden were strongly affected by growing conditions experimentally imposed by temporal blocking and watering treatment. Initial seed weight and time to emergence were important influences, particularly on early growth. Results stemming from the location where seeds were collected point to inherited variation in plant characteristics. While the site where seeds were collected was clearly an important factor in growth and reproduction, the plot, plot pair, or both appear to have been similarly important. The density of culms, which was the starting point for this study, was generally of smaller effect than growing conditions, site, or plot pair, but nevertheless had notable effects particularly on reproduction and potential perenniation. Results entailing absolute cover *per se* (arguably) and Simpson's index (more arguably) imply that these measures may also reflect ecologically localized plant variation that might be better captured with a study design keyed to these measurements. The following chapter discusses the implications of these results, particularly as they apply to characteristics of plants based on small-scale variation, and the implications for ecological restoration and other endeavors where capturing variability among plants is of critical importance.

Chapter 9. Discussion

This study emerged from the observation that seed collection for environmental restoration encounters issues of cost and convenience that might result in unconscious, unintended genetic selection during harvesting of seeds from wild populations. The field and common garden studies described in the previous chapters focused primarily on patch density, which would affect seed-collection efficiency, and secondarily on potential correlations between background vegetation and inherited variation in *Stipa pulchra*. The first part of this chapter provides expanded interpretation of these results.

- Within-site variation among plants may indicate differential competitive versus colonizing abilities.
- Other within-site variations may reflect patch-level differentiation keyed to background vegetation.
- Comparison of field and common-garden results speaks to physical versus ecological distance.
- Responses to blocking and watering treatments point to plastic responses to climate variation.

The next part of this chapter describes potential limitations of this study, and discusses transgenerational effects in experimentation. Finally, this discussion suggests broader implications for the fields of ecology and ecological restoration, and concerns about appropriate application of ecological restoration.

Differences Among Subpopulations

The results of the common-garden study provide evidence that within populations of *S. pulchra*, patch characteristics may correlate with inherited differences among plants. While the focus of the research project was intraspecific density of *S. pulchra*, the results suggest that absolute cover, background vegetation, and possibly species diversity may also correlate with inherited variation. Variation among *S. pulchra* plants from different subpopulations within sites appears to be smaller yet comparable to variation among plants from different populations.

Absolute cover and *S. pulchra* culm density: competition. For RFS and Sonoma common-garden plants, several characteristics that affect life history correlated with culm count in the field. Plants grown from seeds collected on thick plots at these sites had larger basal areas at harvest, less likelihood of setting seed, lower ratios of culms to vegetative tillers, and later seed set. For most plot pairs, reproductive plants from the thick plot had wider leaves and produced heavier seeds. In sum, Sonoma and RFS plants from plots with high culm counts allocated somewhat more to long-term growth and less to near-term sexual reproduction than their counterparts from plots with less *S. pulchra*. Basal area also correlated positively with absolute cover for Sonoma plants.

The effect of intra- versus interspecific competition (i.e., of *S. pulchra* culm count versus absolute cover) differed for Pt. Molate plants compared to RFS and Sonoma plants. Overall absolute cover was relatively high at RFS and Sonoma, respectively averaging 94 and 86% at these sites, versus 49% at Pt. Molate. In addition, absolute cover at Pt. Molate correlated with *S.*

pulchra density in the field. For Pt. Molate plants, absolute cover on seed-source field plots correlated in the common garden with basal area, likelihood of setting seed, time to first seed set, and the ratio of culms to vegetative tillers. The first three of these response variables also correlated with field-plot culm frequency, but the absolute-cover relationship was stronger.

Lower *S. pulchra* density in thin patches at RFS and Sonoma, and lower *S. pulchra* density plus lower absolute cover in thin patches at Pt. Molate, suggests that plants in these plots experienced less intra- and interspecific competition than their thick-plot counterparts. The characteristics of common-garden plants originating in these patches may reflect a colonizing lifestyle expressed as higher likelihood of sexual reproduction, shorter time to first seed set, and larger ratios of culms to vegetative tillers. Earlier and greater allocation to sexual reproduction, and less to growth and perenniation, would improve fitness in disturbed, open habitats where adult mortality is relatively high, competition is less intense, and seedlings have greater chances of establishing **(**Grime 1977 and 1988; MacArthur & Wilson 1967). When grown in the common garden, plants originating from plots with potentially higher levels of inter- and intraspecific competition (i.e., plots with greater density of *S. pulchra* or greater absolute cover) allocated less to sexual reproduction, and somewhat more to perenniation in the form of greater basal area and higher root: shoot ratios. Limiting immediate sexual reproduction in favor of long-term growth would contribute to survival in relatively stable, closed habitats where seedlings have limited potential for establishment and the ability to occupy space, compete for light and water, and survive from year to year is critical to fitness (Dietz et al. 1998; E. Garnier 1992; Grime 1977 and 1988; Gross & Smith 1991; Hautekèete et al. 2002; Keddy et al. 2002; Lankau & Strauss 2011). The pattern found here may reflect the interrelated tradeoffs of growth versus reproduction and competition versus colonization. It is important to note that this study did not entail measurements of competition, colonization, or longevity, nor of environmental factors that would affect competitive conditions in the field, such as soil fertility or moisture availability. Proof would require direct study of competitive ability, such as replacement-series experiments (Jolliffe 2000).

***Resource and meristem tradeoffs in growth versus reproduction*.** Plants face tradeoffs in allocating growth within and among roots, shoots, and reproductive structures (Bloom 1986; E. Garnier 1991). These tradeoffs include differential allocation of limited resources among plant tissues, and differential allocation of meristems among functions such as vegetative growth and sexual reproduction. Resource limitation is associated with negative correlations between immediate fecundity versus growth, survival, and long-term fecundity (Ronsheim & Bever 2000; Sugiyama & Bazzaz 1997 and 1998; van Kleunen et al. 2002; Watson 1984). Within a given overall allocation to seeds, a plant can produce many small seeds or fewer larger ones, balancing greater seed production against better provisioning of individual seeds (C. Smith & Fretwell 1974).

Resource trade-offs. In the pot study, plants receiving more water grew relatively larger than their drier counterparts. While well-watered plants overall were no more likely to set seed, those that did had larger ratios of reproductive to vegetative tillers, more seeds per median culm, and heavier individual seeds. Well-watered seed-producing plants did not finish with more vegetative tillers than their drier counterparts; the absence of additional vegetative growth in these plants implies that the extra resources (water) mostly contributed to seed production. The positive intercorrelation of vegetative growth measures (e.g., aboveground biomass and basal area) with reproductive allocation (e.g., ratios of culms to vegetative tillers, seeds per median culm, and weight of individual seeds) among plants in both watering regimes suggests that aboveground resource allocation was balanced between overall growth and sexual reproduction.

Root: shoot ratios. Plants subsampled for root biomass showed significant reductions in root: shoot ratio if they set seed. Among plants that set seed, root: shoot ratio correlated negatively with both the ratio of culms to tillers and the number of seeds per median culm. Taken together, these results imply a reduction in long-term growth potential in plants that set seed.

Meristem trade-offs. Plants can face meristem tradeoffs a result of their modular structure. Early commitment of meristems to sexual reproduction can ultimately limit the final size and reproductive output of a plant. Conversely, continuing immediate-term vegetative growth may limit sexual reproduction in the short run while potentially increasing resource capture and the number of meristems available for subsequent sexual reproduction (Geber 1990; Huber & During 2000; Pan & Price 2002). Plants generally maintain a pool of quiescent meristems, and under natural conditions probably experience resource limitation more frequently than meristem limitation (Geber 1990).

In the present study, plants that set seed had somewhat fewer vegetative tillers at harvest than did non-reproductive plants. Huber and During (2000) modeled meristem allocation and found that total fecundity correlated negatively with meristem allocation to flowering if their modeled plants allocated more than 30 percent of meristems to flowering. Twelve of the total 655 reproductive plants in this study allocated over 30 percent of total tillers to seed production, yet the remaining 643 reproducing plants still averaged fewer vegetative tillers than did nonreproducing plants. Of these twelve plants, ten were from Pt. Molate, and nine were from thin plots.

Growth versus reproduction in clonal plants. Variation in *S. pulchra* plants in how they balance short-term seed production against long-term growth raises questions about the role of sexual versus asexual reproduction in this species. Sexual reproduction can be biologically costly and risky **(**Silvertown & Lovett-Doust 1993), yet provides a means to repair DNA, combine beneficial mutations, purge deleterious alleles, respond to environmental changes, and generate density- and frequency-dependent advantages mediated by competitors, pathogens, and predators where differing from one's neighbors is advantageous (Antonovics & Ellstrand 1984; Ellstrand & Antonovics 1985; Kelley 1984 and 1989; Nürnberger & Gabriel 1999; W. Rice 2002; West et al. 1999). Clonality, in contrast, allows for dedication of resources and meristems to indefinite extension of the genetic individual. The advantages of clonal growth, such as persistence in habitats unfavorable for sexual reproduction, ability to spread the risk of death among ramets, and availability of alternative means of reproduction, however, come at the cost of potential effects on sexual reproduction. Clonal growth can trade off against reproduction by seed (Cheplick 1995). The larger a clonal organism becomes, moreover, the greater the chances its flowers will receive pollen from within the clump versus from other conspecifics (Vallejo-Marín et al. 2010), particularly in plants with a phalanx growth form, such as *S. pulchra*.

In *S. pulchra,* high levels self-pollination by homozygous parents (Larson et al. 2001) obviates many of the adaptive advantages of sexual reproduction. *S. pulchra*, as a clonal plant with a phalanx growth habit, cannot readily disperse as vegetative propagules and may even interfere with its own growth more than that of its neighbors (Schmid & Harper 1985). Production of seeds provides an effective means of dispersal (Stöcklin & Winkler 2004). Where sexual and asexual reproduction differ little in genetic terms, selection would favor sexual reproduction or clonal expansion depending on whether the likelihood of genotype survival is increased more by seed generation or ramet production. High production of seeds can help ensure genotype survival in a frequently disturbed habitat, particularly if vegetative dispersal distances are small compared to the typical size of disturbed patches, as would commonly be the case in phalanx species (Winkler & Fischer 1999).

Competition versus colonization. The allocation tradeoff between growth and fecundity contributes to a tradeoff between competitive ability versus ability to disperse and colonize unoccupied sites. A large literature focuses on interspecific competition-colonization models, varying in assumptions about the importance of factors such as a strict competitive hierarchy or environmental heterogeneity for maintaining coexistence, and the extent to which stochastic factors also affect biodiversity (e.g., Aremasekare 2003; Calcagno et al. 2006; J. Clark et al. 2007; Pacala & Rees 1998; Yu & Wilson 2001). Tilman (1994) models the stable coexistence of two species, a poor competitor with a high rate of colonizing empty patches, versus another that is more competitive but less fecund. The strong colonizer, as modeled, can coexist with the strong competitor as long as sufficient empty patches continue to become available. Even if it lacks a high colonization rate, moreover, a weak competitor can coexist with a strong competitor if it has greater longevity than the strong competitor and the habitat is at least 50 percent unoccupied. Tilman's competition-colonization tradeoff model broadly accords with aspects of MacArthur and Wilson's (1967) concept of r- and K-selection and Grime's (1977 and 1988) ruderal versus competitive plant-strategy categories, in that the probability of seedling establishment versus adult survival determines the theoretical fitness benefit of contrasting allocation strategies.

Intra- versus interspecific competition and colonization. The great majority of empirical studies of competition-colonization tradeoffs deal with interspecific comparisons (Lankau & Strauss 2011). In *S. pulchra*, competitive ability would entail allocating substantially to resource capture (for example, allocating to roots in habitats with limiting soil resources), and colonizing ability would entail greater seed production. Plants grown from seeds collected at Pt. Molate, the site with the lowest and most varied absolute cover, produced seeds earlier than plants from the other sites, were more fecund, and increased root: shoot ratio less in response to water limitation, potentially reflecting overall greater allocation to colonization. Within Pt. Molate plants, the greater allocation to growth versus seed production in plants from plots that had both high culm counts and high levels of absolute cover may reflect more competitive conditions.

At RFS and Sonoma, absolute cover and culm count were weakly and negatively correlated, and the differential allocation patterns (to long-term growth versus reproduction) correlated with culm count rather than with absolute cover. The pattern in these plants may reflect a competition-colonization tradeoff at the intraspecific level. The earlier reproduction and greater seed production of thin-plot plants from these sites implies greater colonization rates.

If the results of the common garden study can be taken as suggesting that differential competitive versus colonizing ability correlates with absolute cover and S. *pulchra* density, further conjectures may follow. Traits conferring greater intraspecific competitive ability may trade off against traits favored under interspecific competition. Contrasting distributions of *S. pulchra* and resulting selection may create feedbacks that strengthen the distribution pattern.

Few studies have directly tested whether there are evolutionary tradeoffs between inter- and intraspecific competitive ability, particularly in the complex context of field communities (Lankau & Strauss 2011). In a pot study, T.E. Miller (1995) grew three generations of *Brassica rapa* in two environments: intraspecific competition and interspecific competition with *Raphanus sativus*. In each competitive environment, plants producing the most flowers were outcrossed to provide seeds for the next treatment generation, and a random set were outcrossed to produce seeds for control plants. After one generation without competition, plants from the intraspecific-selection line grew faster and increased flower production by more than 50% over that of the control line and by more than 19% over the interspecific-selection line. Linhart (1988) found that inter- versus intraspecific competitive ability in *Veronica peregrina*, a self-pollinating California vernal-pool endemic, depended on where seeds were collected from within an undisturbed population: plants grown from seeds collected from largely monospecific central subpopulations were better adapted to growing in intraspecific neighborhoods, whereas plants grown from seeds collected at the patch periphery, where *Veronica* plants were surrounded by grasses, were better adapted to living among with grasses. In a comparison *Veronica* population that was disturbed by yearly plowing, these differences were greatly attenuated. R. Shaw et al. (1995) found evidence that some genotypes of *Nemophila menziesii* (baby blue eyes) that have high fitness at high intraspecific densities do poorly at high densities of the interspecific competitor *Bromus diandrus. Brassica nigra* (black mustard) plants encounter conflicting selection pressures on investment in sinigrin, a toxic secondary compound, depending on whether the plants experience greater levels of intra- versus intraspecific competition. Lankau (2008) grew black mustard with heterospecific neighbors, and found the plants undergo selection favoring higher sinigrin content, while those grown with conspecific neighbors experience selection that favored lesser sinigrin investment. Similar patterns were observed in naturally occurring patches of black mustard that varied in percent composition of conspecifics and heterospecifics. Lankau (2012 & 2013) found a similar pattern with the invasive herb *Alliaria petiolata* (garlic mustard), mediated by the toxic effect of sinigrin on the soil microbial community. Where they co-occur with *Alliaria*, populations of the native herb *Pilea pumila* develop tolerance of the conditions generated by *Alliaria* at the cost of reduced fitness where *Alliaria* is absent.

How did thick versus thin patches get that way? Results of the present study raise the question of how density variations came to occur in the study populations, if not simply by means of stochastic processes. In California, higher levels of disturbance have been associated with greater cover of annual grasses and lower species richness (Robinson et al. 1995). Stromberg and Griffin (1996) suggested a positive feedback loop between gopher disturbance and the density of annual grasses, which was confirmed for some circumstances by Seabloom et al. (2003). The present study found no difference in rodent disturbance of thick versus thin field-plots; however, differences in relative cover of perennial grasses would correlate with past rather than immediate disturbance. The amount of rodent disturbance noted in this study is a great deal less than described, for example, by Stromberg and Griffin (1996) for annual grasslands. Pt. Molate had the greatest relative cover of native perennial grasses, the most evidence of digging activity, and produced common-garden plants with the highest fecundity levels. There is no evidence of substantial disturbance by other causes, such as tilling, at any of the sites for several decades.

An alternative explanation of density variation is that *S. pulchra* may itself create thick versus thin distributions. Theory and experimental observations indicate that abundant species are generally more competitive than their less-abundant neighbors (Gurevitch 1986; Harpole & Tilman 2006; Howard & Goldberg 2001; Tilman 2004). If more-competitive species are more abundant on a local basis, then perhaps more-competitive genotypes within a population would also be more abundant on a microsite basis, and may produce denser patches than less-competitive conspecifics. In this case, stochastic factors may have scattered *S. pulchra* genotypes over a given site, and those with greater competitive ability may have ultimately generated thick patches.

Plot pairs within sites: background vegetation and differentiation. At the outset of field work, the thin and thick plots within each pair were very roughly matched in terms of plot characteristics other than *S. pulchra* density. Using paired plots was intended to prevent confounding of *S. pulchra* culm density with other plot characteristics, such as species composition. Consistent variations in common-garden plants correlated with plot pairs within sites were therefore not anticipated. In the common garden, plot pair as an explanatory variable was nevertheless at least marginally significant as a main effect in ANCOVAs addressing emergence time, basal area, tiller counts, height and number of culms, aboveground biomass and growth rate, proportion of green tissue at harvest, likelihood of sexual reproduction, weight of individual offspring seeds, and the ratio of culms to vegetative tillers in reproductive plants. That is, plot pairs differed from one another.

Variation in the common garden among plants grown from seeds originating in different plot pairs, and similarity within pairs, may imply inherited variation among *S. pulchra* that in turn reflects interspecific neighbors in source plots. Species identity of neighbors can correlate with the abiotic conditions that plants experience. An individual *S. pulchra* plant and its heterospecific neighbors, moreover, form important parts of each other's environment. Neighbor identity, even neighbor genotype, can influence differential allocation to secondary compounds and among tissues (Barton & Bowers 2006; Chen et al. 2012; Fridley et al. 2007). California grassland species differ in their effects on microsite ecosystem properties such as litter quantity and quality, soil temperature and moisture, and soil biota (Bastow et al. 2008, Eviner 2004, Hawkes et al. 2005), with effects that can persist longer than the plants that produce them (Grman & Suding 2010). Hull and Muller (1977) cite indications of complex interactions between *S. pulchra* and different species of introduced grasses.

Because *S. pulchra* is perennial and most other species in the field plots were annual, it is possible that species composition of plot pairs reflected abiotic conditions, or that differences among *S. pulchra* genotypes affected conditions for other species, excluding some or facilitating others. The extent to which plots within pairs paralleled one another in the common garden is nevertheless surprising, given the coarse matching of plot pairs in the field. Spatial autocorrelation, either genetic or environmental, may have been a factor at Sonoma, where thick and thin members of each plot pair were a few meters apart from one another and the pairs more widely spaced. Similarities within plot pairs for RFS and Pt. Molate plants were unlikely to have stemmed from proximity of plots within pairs. The sample of plot pairs within sites is too small to draw any conclusions about how variation among specific neighbor species may reflect mechanisms that underlie differences among *S. pulchra* plants. The potential existence of genetic variation correlated with background vegetation nevertheless implies that comprehensive sampling of genetic variation would require collecting germplasm from across the full range of vegetative environments associated with a target plant population.

Plots. As described in Chapter 8, much of the variation among plants in the common garden appeared to lie at the plot level. Variation existing beyond differences attributable to site, plot type, or plot pair may reflect genetic similarities among plants within plots as much as differences among plants from different plots. The extensive homozygosity found in *S. pulchra* (Larson et al. 2001) implies that offspring would be nearly identical genetically to their parents and siblings. Seeds fall within a meter of the parent plant (Stromberg & Griffin 1996, citing unpublished data), increasing potential for mating among close relatives and genetic autocorrelation within a patch. Over the life of a genetic individual, moreover, a single *S. pulchra* clump may break up into pieces so that multiple clumps in a patch might originate from a single seed. As a result, common-garden plants in this study may have been very closely related to nominal non-siblings originating in the same plot.

Patch variation and seed collection for restoration. The pattern of variation found in the common-garden study implies appreciable levels of subpopulation differentiation in this species. Microhabitat correlates of genetic differentiation may underlie systematic variation such as that indicated by this study among plants from plots varying in absolute cover, *S. pulchra* density, or background vegetation. Variation in soil fertility, disturbance history, and other selective factors reflected in this pattern might be unapparent to seed collectors. Even if inherited variation among plots followed no pattern, however, the extent of differences among plots indicates that capturing the full range of genetic variation within a population of *S. pulchra* via seed collection would require sampling broadly across the patches comprising a population. This result contrasts with Larson et al. (2001), who found limited genetic variation within *S. pulchra* populations.

Differences Among Populations

Significant differences existed among sites in both the field and the common garden. Percent cover, aboveground biomass, culm count, and culm height were greater on the field plots at RFS and Sonoma than at Pt. Molate, but there was no significant difference among sites in overall absolute cover of *S. pulchra*. Simpson's index varied among sites only in interaction with year. In the common garden, however, plants from different sites diverged on many measured characteristics, including morphology, growth, and reproduction.

Variation among plants originating at different sites is wholly expected, given the differing soil and climate regimes at the three sites.[28] There were few positive correlations among sites, however, between field- and common-garden results. Common-garden Pt. Molate plants began reproduction earlier than plants from other sites, likely reflecting the shorter growing season of the parental site. Pt. Molate plots had the smallest number of culms per m^2 *S. pulchra* cover area in the field, yet in the pot study Pt. Molate plants produced the most culms. Conversely, RFS had the highest level of absolute cover, implying high levels of competition, and in the common garden, RFS plants had the lowest culms: tillers ratios. In the field, however, RFS plants had the largest number of culms relative to *S. pulchra* cover area. Culm height varied significantly by site in both field and common garden, but Pt. Molate plants had relatively tall culms in the common garden, versus shorter ones in the field. The lesser height and fecundity of Pt. Molate plants in the field versus the common garden may reflect the drier, rockier soil at that site compared to RFS and Sonoma.

The pattern of differences among these study sites sheds light on the practice in restoration of using physical distance between populations as a proxy for genetic distance. Pt. Molate and RFS lie within 12 km of each other in the same USDA ecological section and subregion, while Sonoma, about 70 km from the other sites, is in a different ecological section and subregion (Miles & Goudey 1997). If genetic differentiation among populations is correlated with distance, Pt. Molate and RFS plants should be relatively alike. Perusal of the graphs in Chapter 8 reveals, however, that relatively few significant differences were recorded in the common garden between Pt. Molate and Sonoma plants and substantially more between Pt. Molate and RFS plants. This echoes the finding by Knapp and Rice (1996) that proximity between populations may not always indicate quantitative-genetic similarity. While distant sites may experience isolation by distance (IBD), nearby populations may be isolated from one another by environmental differences. Sexton et al. (2014) performed a meta-analysis of empirical studies examining the relative prevalence of IBD versus isolation by environment (IBE), and found that IBE is only slightly less prevalent than IBD alone; combined IBD and IBE was the commonest pattern. Grey et al. (2014) characterized neutral genetic diversity and structure in *Andropogon gerardii* from 11 prairies across a precipitation gradient between Kansas and Illinois, and concluded that IBE explained their results better than IBD. In the present study, phenotypic differences between Pt. Molate and RFS common-garden plants may reflect the substantial differences in soil and slope at the two sites, resulting in a longer annual period of moisture availability at RFS.

---

[28] The differences in growing season among the three sites meant that sampling was sequential (Pt. Molate followed a month later by RFS, then Sonoma another month later). As a result, site as a factor could be confounded with variations in flowering phenology rather than true variations in growing conditions. Seed collection for all sites occurred about two months later in the second field season, however, and site interacted statistically with date and year less than might be expected by chance.

Treatment Effects and Interactions

The common-garden study applied two treatments, differential watering regime and temporal blocking. Variations in growth and allocation among plants in different treatments may indicate phenotypic plasticity. Interactions between seed sources and watering treatment or block could reflect inherited variation in plasticity of measured traits (Stearns 1989). In this study, watering and blocking treatments interacted most often with site. To the extent that the treatments may have corresponded, from the plants' perspective, to climate variation, these interactions may represent adaptive plasticity.

Watering treatment and site. Higher levels of watering in the common garden significantly affected most measurements and resulted in bigger, more fecund plants. Watering treatment interacted at the $\alpha = 0.10$ level with site in nearly a third of statistical tests, more than would be expected by chance alone. In response to more water, for example, Sonoma plants developed relatively taller culms and foliage than plants from the other sites. Pt. Molate plants given extra water had slightly fewer tillers and greater ratios of culms to tillers than dry-treatment plants. In a climate characterized by limited availability of water and by variation in annual precipitation, plastic response to water may be adaptive. The frequency of significant interactions between watering treatment and the other seed-source factors (plot pair, culm count, absolute cover, and Simpson's index) did not exceed chance. Plants in the common garden veered between root rot and desiccation, and more finely-tuned watering treatments may have elicited more evidence of among- and within-population variations in plasticity.

Temporal blocks. The common-garden experiment was divided into temporal blocks in order to make the experiment manageable, with no presumptive systematic effects. Instead, block was a significant factor in most measurements, from emergence through growth and reproduction, probably because of higher temperatures experienced by the second and especially the third block compared to the first. Planting block, moreover, interacted with site at the $\alpha = 0.10$ level in over a quarter of statistical tests, more than would be expected by chance.

Several block × site interactions involved reproduction. Pt. Molate plants varied among blocks more than plants from the other sites in terms of the culms: tillers ratio. Conversely, Pt. Molate plants showed the least variation in time to reproduction, and Sonoma plants the greatest variation, in response to temporal blocking. This result may reflect the shorter growing season at Pt. Molate, where more-plastic allocation to sexual reproduction may be coupled with an earlier, narrower reproductive window. Other interactions involved morphology. For example, leaves of Sonoma plants became narrower, and those of RFS plants wider, as the experiment moved from one block to the next. The effects of block seem to have echoed those of watering treatment (drier conditions paralleling hotter ones). Pt. Molate plants, for example shifted reproductive allocation similarly in response to both treatment factors. The frequency of interactions between block and the other seed-source factors (plot pair, culm count, absolute cover, and Simpson's index) did not exceed chance.

Study Limitations

Some aspects of this study may limit its applicability to natural systems. Growth and phenology of plants grown singly in pots may differ substantially from growth of plants in natural soil under competitive conditions (Martin & Harding 1982; Mehrhoff & Turkington 1990; R. Shaw & Platenkamp 1993; R. Shaw et al. 1995). Mortality in *S. pulchra* and many other plant species is disproportionately high during emergence and establishment (Bartolome & Gemmill 1981; Larson et al. 2001), and self-thinning can impose differential selective effects that would not occur in pot studies (Lankau & Strauss 2011). Experiments measuring short-term growth can yield only limited information on long-term growth, competition, survival, and reproduction (Aarssen & Keogh 2002; Bennington et al. 2012; Gordon & Rice 1998). Finally, use of seed collected in the field for common-garden research potentially compounds genetic differences with transgenerational effects.

Transgenerational effects. Parental environmental effects are nongenetic phenotypic effects on plants stemming from the parental (commonly maternal) environment (Galloway 2001; Roach & Wulff 1987; Weiner et al. 1997; Weis et al. 1987). These effects are commonly defined as the influence of the environment experienced by the parental plant on the phenotype of its offspring, via factors such as seed provisioning, seed architecture, seed-coat thickness, and germination timing (Donahue 2009; Wolf & Wade 2009). Under this definition, maternal effects do not result directly from maternal nuclear and cytoplasmic DNA, but from maternal phenotype, which in turn is influenced by genetic and environmental sources of variation, including genotype-by-environment interactions.

Perhaps the most commonly cited parental effect is variation in seed weight, which can reflect seed provisioning and seed-coat thickness, and has been correlated with drought, temperature extremes, defoliation, and other factors in the maternal environment; seed position on the inflorescence; number of ovules pollinated; and timing within the flowering season (Donahue 2009; Hendrix & Trapp 1992; Roach & Wulff 1987; Vaughton & Ramsey 1998; Weiner et al. 1997; Wolfe 1995). Seed weight can vary by a factor of five to 10 within a single maternal plant (Sultan 1996; Vaughton & Ramsey 1998). While large seeds generally have higher germination rates, emerge faster, and are more likely to establish, seed weight effects often diminish or disappear within weeks under experimental conditions (Houssard & Escarré 1990; Paz & Martínez-Ramos 2003; Roach 1986; Roach & Wulff 1987; Weiner et al. 1997; Weis et al. 1987). Under competitive field conditions, however, the initial size differences stemming from varying seed weights may translate into disproportionate fitness differences in adults (Roach & Wulff 1987; Stanton 1985; Stratton 1989). Seed weight reflects quantitative but not necessarily qualitative provisioning; the nitrogen content of the seed, for example, may correlate with nitrogen available to the maternal plant, even if seed weight is unaffected (Violle et al. 2009).

Most research on maternal effects focuses on domesticated species. Wild species often show less variation than cultivated species in effects of maternal environment on seed characteristics. Wild plants may reduce number and seed-weight variation rather than mean weight of seeds in the face of resource limitation (Roach & Wulff 1987; Sultan 1996; Violle et al. 2009; Weiner et al. 1997). The present study repeats this pattern, in that well-watered plants produced 23 percent more culms, and 15 percent more florets per median culm than plants in the dry group; ripe seeds harvested from well-watered plants, however, were individually only about 12 percent heavier than seeds taken from dry-treatment plants.

Maternal seed provisioning is only one form of transgenerational effect. Epigenetic effects can modify genetic expression through mechanisms such as DNA methylation, chromatin structural changes, or small, non-coding RNA molecules (Bossdorf et al. 2008). These epigenetic changes may be inherited from either parent and can pass through multiple generations (Bischoff & Müller-Schärer 2010). Transgenerational environmental effects not mediated by maternal provisioning may be adaptive if they improve the offspring's ability to thrive under conditions that in effect are predicted by the parent's experience. Examples of such effects include induction of resistance traits against herbivores (Bischoff & Müller-Schärer 2010; Holeski et al. 2012) and ability to maintain fitness despite stressfully warm growing conditions (Whittle et al. 2009). Medrano et al. (2014) found that epigenetic polymorphism was greater than genetic polymorphism in the perennial herb *Helleborus foetidus* sampled at ten sites in Spain, and suggest that epigenetic variation may provide an important measure of functional diversity in a species with modest genetic diversity.

Environmentally and genetically based relationships between species within a patch can be difficult to untangle. Aarssen and Turkington (1985) found evidence of "precisely-defined" biotic specialization in genotype pairs of *Trifolium repens* and *Lolium perenne* growing together in a British Columbia pasture, and suggested that *Trifolium* clonal foraging allowed it to "choose" suitable *Lolium* neighbors. Evans and Turkington (1988), working in the same pasture or a similar one, found that a significant proportion of morphological variation among *Trifolium* genets was accounted for by the species of grass the *Trifolium* was growing with in the field; this variation, however, disappeared over time when the plants were grown in standard soil in a greenhouse, implying that the variation was an environmental carry-over. Turkington (1989), working in a pasture with much larger patches dominated by single grass species, concluded in this case that variation among *Trifolium* clones correlating with neighboring grass species was genetically based. Chanway et al. (1989) and Turkington (1989) concluded that the genetically based relationship between *Trifolium* and neighboring grasses is mediated by soil microorganisms associated with, and perhaps regulated by, the grass species or genotype. This relationship would be lost in the standard soil used in the greenhouse, thus disguising the role of genetics.

Methods of managing transgenerational effects in experimentation are imperfect. A common method is growing out wild-collected seeds for a generation in a common environment and using F_1 progeny for experimentation. Several generations, however, would be needed to eliminate epigenetic effects. Drift, selection, and inadvertent cross-pollination can occur in a common environment, moreover, potentially shifting the genetic characteristics of the sample within even a single generation. The present study illustrates this problem, in that some sibships, particularly from Sonoma, produced no offspring seeds in the common garden. Producing seeds in a common environment might also result in new epigenetic effects and varying genotype-by-environment interactions stemming from different maternal genotypes.

Another method for addressing transgenerational effects is using seed weight or juvenile plant size as a covariate, or planting same-size juvenile plants at the beginning of an experiment. Latzel (2015) notes that using seed weight as a covariate would help account for quantitative provisioning, and that measuring growth during early stages would account for seed quality.

Size-based methods, however, would not address some forms of epigenetic variation, and seed weight may also reflect genotype of the seed (Houssard & Escarré 1990). Finally, Roach & Wulff (1987) suggest collecting and storing seeds over several years to control for year-to-year environmental variation.

The challenge of managing transgenerational effects appears correlated with a tendency to ignore them. Latzel (2015) examined all journal articles published during 2011–2013 that studied local adaptation by conducting reciprocal transplants, a total of 44 articles.[29] Of these, 21 studies neither incorporated measures in their study design to deal with transgenerational effects nor discussed these effects in their findings. Eleven studies grew out seeds for a generation in a common environment and used F_1 seeds for experimentation, or grew ramets of clonal plants in a common environment for two or more months. Five used seed weight or seedling size as a covariate, and one compared plants at different life stages based on the assumption that maternal effects would be most apparent in early life stages.

The present study uses seeds collected in the wild, and incorporates seed weight, collection date, year, and emergence time in statistical analyses as partial proxies for parental environmental effects. As discussed in Chapter 8, seed weight affected emergence time, overall growth, and reproduction, but the effect of seed size appeared to diminish over time. The weight of offspring seeds correlated with the weight of seeds planted in the common garden. Seeds collected in 2001 were about 3 percent heavier, and emerged about 4 percent slower, than those collected in 2000; nevertheless, collection year and date were significant in fewer multivariate analyses than might be expected by chance alone.

Among studies examining parental effects, an article by Bergum et al. (2012) is particularly relevant to the present study. They propagated two offspring generations of *Sporobolus airoides* from maternal plants originally transplanted to a greenhouse from areas invaded by *Acroptilon repens* and from adjacent non-invaded areas in three rangeland sites. Offspring derived from both invaded and non-invaded subpopulations changed phenotypically from one generation to the next, with the offspring of plants collected from the invaded areas showing greater differences between generations. Despite these changes, offspring derived from the two subpopulation types remained significantly different from one another.

Broader Implications of This Study

The field and common garden studies described here found correlations between *S. pulchra* density variation and subpopulation differentiation. The results may also imply inherited variation reflecting other dissimilarities among patches, including cover and composition of other species. The remainder of this chapter focuses on some implications stemming from these results, including

- speculations regarding *S. pulchra* under post-European selection regimes,
- speculations regarding unintended effects of density differences in ecological studies, and
- implications for environmental restoration.

---

[29] The query was conducted on the Web of Knowledge on December 1, 2013 and used the search rule "local adaptation* AND plant* AND transplant* AND Year Published=(2011–2013)."

Post-European selection in *Stipa pulchra.* The present study provides evidence that *S. pulchra* varies in characteristics potentially associated with competitive ability, and that this variation correlates with indications of competitive environment (absolute cover and *S. pulchra* patch density). If greater patch density in *S. pulchra* results from more effective competition with introduced species, *S. pulchra* and potentially other native species may be capable of adapting to compete more effectively with exotic annuals. A growing body of research indicates that at least some native species undergo inherited phenotypic and genotypic shifts in response to invaders, which in some cases appears to enhance the ability of native species to compete with introduced species (Bergum et al. 2012; Deck et al. 2013; Lankau 2012 and 2013; Mealor et al. 2004; Oduor 2013; Rowe & Leger 2011).

S. pulchra is a long-lived species, and plants now growing in the field may be few generations removed from initial European colonization. These plants nevertheless need to survive and reproduce in what has become a substantially novel selective environment. The introduction of both cattle and invasive annual grasses following European colonization meant a radical shift in disturbance and competition regimes. High levels of cattle grazing such as those of the 19th century may have selected for more fecund *S. pulchra* genotypes such as this study found in sparse patches. Subsequent reduction in grazing and increasing competition with annual grasses may have shifted selection in favor of the more competitive-seeming genotypes present in dense patches. Differentiation in allocation can be induced in a few generations of vigorous selection for competitive traits (Agrawal et al. 2013; T.E. Miller 1995; van Kleunen et al. 2002).

Unintended effects of density differences on ecological research. The present study raises the speculation that intrapopulation differences, such as those found here in *S. pulchra*, may influence research results in unintended and unrecognized ways. Many studies of natural populations employ seeds collected from the wild, whether these seeds are used directly or propagated for later experimentation. Resulting journal articles often make no statement indicating whether seeds were collected at random, even though they are meant to represent entire wild populations (Violle et al. 2012). Where articles state that seeds were collected at random, they rarely describe the randomization procedure. If researchers collect seeds from dense patches, or otherwise unconsciously favor one type of patch over another, they may skew seed sampling in terms of inherited characteristics. The intrinsically time-consuming and counter-intuitive nature of collecting plant material from sparse patches or from areas heavily vegetated with thistles or poison oak, characteristics potentially correlated with subpopulation differentiation, were very apparent during field work for this study; indeed, simply finding enough seeds on thin plots was sometimes problematic. In the common garden, some sibships produced no seeds, implying that laboratory propagation might additionally skew representation of genotypes.

Seed collection and propagation for research may thus impose unintended selective effects with regard to unobvious subpopulation differentiation, potentially affecting experimental results. Such artifacts may explain some differences among studies. For example, K. Rice and Knapp (2008) point to evidence that *S. pulchra* is an outcrossing species, whereas Larson et al. (2001) found no heterozygotes among the *S. pulchra* plants they analyzed. Larson et al. (2001)

obtained their wild-collected seed from sites having a spatial scale of one hectare or less, and do not indicate that the seeds were collected at random. Both small population size and the potential for seed to have come from within dense patches may have reduced the likelihood of encountering heterozygotes.

Practical implications for restoration. The initial question prompting this study was whether cost control in seed collection could skew the inherited characteristics of a restored population; the answer is yes. In the case of *S. pulchra,* conspecific density, which is an important factor affecting seed collection cost and convenience, correlates with inherited variation in life-history traits. In addition, differences found among plot pairs within sites, and in plants from Pt. Molate plots varying in absolute cover, suggest that the identity and density of background species may also correlate with inherited traits in *S. pulchra*. Taken together, these subpopulation differences are both substantial and consistent.

These results imply that a restored population founded using germplasm collected from a restricted subset of patch types could have lower genetic variance and skewed genetic means compared to the source population. This finding may well be applicable to other species characterized by subpopulation differentiation. For such species, comprehensive representation of genetic variation within populations, which is a goal of seed collection for restoration, would clearly require thorough sampling of differentiated subpopulations. It is unrealistic, however, to expect that many seeds would be collected from thin patches, or from patches representing the full range of background vegetation on a site, unless this is explicitly required of seed collectors. Collecting sufficient seed from thin plots for the present study proved challenging and time-consuming; attempting to harvest seeds in quantity where they are least available may seem nonsensical in a budget-limited context. In response to a talk about the present study, a Bay Area restoration consultant said its results would trouble commercial seed collectors, who already face many challenges in collecting locally-adapted seeds (D. Amme 2004 *pers. comm.*).

The choice of harvesting seeds only from dense patches, or from both dense and sparse areas, may depend on restoration goals. If the characteristics of common-garden plants grown from seeds collected on thick patches translate to greater competitiveness in the field, planting seeds collected from dense patches alone may produce a restored population that is more competitive with introduced annuals. Collecting seeds for restoration specifically from stands of native plants that have persisted despite invasion is an approach advocated by some authors (Ferrero-Serrano et al. 2011; Sebade et al. 2012). The value of restoring with unusually competitive genotypes is debatable, however, if these genotypes tend to exclude other species (Cronn et al. 2003; Gustafson et al. 2004a). In the present study, moreover, plants from thick plots displayed relatively low seed production in the common garden, implying that limiting planting to seeds from dense patches could exacerbate seed limitation, which has been identified as problematic for native species in California and elsewhere (A.J. Brandt & Seabloom 2012; C. Clark et al. 2007; Seabloom et al. 2003; Tilman 1997 and 2004).

The added cost of collecting seeds from sparse as well as dense patches might be alleviated by collecting a smaller but more diverse seed pool for agronomic increase. If the present study serves as a model, however, agronomic increase would rapidly shift proportions of collected genotypes to the more fecund genotypes found in less-competitive patches. Sibships within plots, moreover, varied substantially in common-garden seed production, as illustrated by Figure 24; some sibships produced large numbers of seeds while others produced none. Shifts in gene frequencies could be reduced by harvesting equal numbers of seeds from each reproductive plant in seed-increase fields, at considerable loss of the advantages of agronomic increase.

Another option would be collecting and planting a wider range of genotypes at the cost of planting fewer species. The long-term effect of making this short-term trade-off could depend in part on how species richness and within-species genotypic richness interact. As discussed in Chapter 2, species diversity and genetic diversity are often correlated (Vellend et al. 2014; Vellend & Geber 2005; Violle et al. 2012), although the causality of the relationship can be difficult to determine. Restorationists sometimes plant a limited range of species, expecting (or hoping) that additional desired species will establish at a site on their own. If greater intraspecific genetic variation would create more competition for available niche breadth, as niche theory suggests, then planting a wider range of genotypes within species may result in exclusion of would-be arrivals, be they natives or undesirable invaders (Crutsinger, Souza & Sanders 2008). If genetic variation supports species richness, then planting a wider range of genotypes within species may help support establishment of new arrivals (Vellend 2006).

Problems in Restoration Beyond Germplasm

Results of this study provide evidence that complete sampling of genetic diversity in natural populations may be intrinsically difficult and costly, simply because some of that diversity is associated with circumstances that would hinder seed collection. Garnering appropriate and adequately diverse germplasm is only one of many challenges in effective ecosystem restoration. A substantial body of research indicates that restoration projects often fail to meet ecosystem goals, such as primary productivity, nutrient accumulation, and species and functional-group diversity (Garcia et al. 2015; Hilderbrand et al. 2005; Mack & Micacchion 2006; Polley et al. 2005; Suding 2011; Zedler & Callaway 1999). In a study combining a survey and a literature meta-analysis, Godefroid et al. (2011) found that reintroduced plants often have low survival, flowering and fruiting rates, respectively averaging 52%, 19% and 16%. They noted also that survival rates reported in the literature are over twice as high as rates reported by survey participants, underscoring concerns that publication bias may encourage unwarranted expectations of restoration success. Some ecological processes, such as soil development, mycorrhizal associations, and hydrologic regimes, may take decades or more to restore (Curran et al. 2014; Hilderbrand et al. 2005). Restorations that might superficially appear successful can have unintended negative outcomes, such as failing to support or even imperiling the survival of desirable species (Longcore 2003; Severns 2011). Monitoring periods are typically short, five years or less, meaning that delayed but correctable problems in restoration may go unnoticed, increasing the likelihood of failure (BenDor 2009; Maron et al. 2012). For many restoration projects, no monitoring or assessment is recorded, omitting "even the most rudimentary information on project actions and outcomes" (Bernhardt et al. 2005).

This pattern of limited success is confirmed in Suding's 2011 extensive review of restoration studies and meta-analyses. While some restoration projects are successful, a discouragingly large proportion of them result in partial or failed recovery, and in divergence of seemingly-parallel restorations toward differing ecological endpoints. Successful restorations can take decades, even centuries, to progress toward reference conditions (Curran et al. 2014). Suding (2011) noted that incomplete recovery can persist indefinitely because of constraints that do not self-correct over time, such as isolation and invasive species. Other factors cited as impeding restoration success include strong abiotic-biotic feedbacks, historical legacies, introduction of desirable species that inadvertently exclude colonizing natives, and inappropriate genetic structure of introduced populations. Restoration meta-analyses by Rey Benayas et al. (2009) and Moreno-Mateos et al. (2012) reached similar conclusions.

Limited restoration success would be discouraging enough if restoration attempts were limited to addressing past disturbances and if the potential for failure was seen as sufficient reason to avoid future ecosystem damage. As described in Chapter 4, however, compensatory mitigation policies mean that habitats lost to development are nominally replaced (offset) through creation or restoration of habitats elsewhere. Restoration is being called upon to deliver replacement habitat in order that intact habitat may be destroyed, exchanging "certain losses for uncertain gains" (Maron et al. 2012). The unfortunate result is often net loss of biodiversity (Curran et al. 2014; Moreno-Mateos et al. 2012).

This cost to biodiversity and ecosystem function results from both the restoration failures discussed above, and the time lag that exists even for successful projects between habitat lost and habitat gained. Aggregated over many mitigation efforts, this time lag represents a substantial net loss of habitat function (BenDor 2009). Moilanen et al. (2009) liken this result to "making a zero interest rate (biodiversity) loan to someone who is known to be unreliable and might pay back decades later."

As Suding (2011) points out, if some restorations succeed, then restoration is possible at least in some situations. Restoration failures are frequently ascribed to social factors, including inadequate goal-setting, planning, implementation, and management (Bernhardt et al. 2005; Godefroid et al. 2011; Mack & Micacchion 2006; Suding 2011; Tischew et al. 2010) These social factors, in turn, largely boil down willingness to commit sufficient economic resources to restoration in order to improve outcomes. The results of this study indicate that cost control could directly affect genetic variation of seeds collected from the wild, which in turn is only one of many facets of what successful restoration might require.

Even if economic and institutional constraints could be overcome, the intertwined complexity of natural systems that lend them much of their beauty and fascination may hinder efforts at restoration. As Hilderbrand et al. (2005) note, ecological restoration strives to recreate complex systems using simplified guiding principles that can reduce its success. The intricate relationships that bind a bunch of organisms into an ecosystem can take far more time to develop than impatient humans want to invest. Restorationists, moreover, cannot prevent new insults, such as invasive species or climate change, from threatening restored ecosystems. Restoring an ecosystem to predisturbance conditions may often be impossible; in particular, California prairies as they existed before European colonization are probably forever lost.

The prospect of expensive, labor-intensive projects that may never meet original objectives raises question regarding the goals of restoration. In the face of climate change, invasive species, land-use change, and other anthropogenic impacts, some have recently come to suggest considering some altered ecosystems as "novel ecosystems" that warrant being protected as such (Hobbs et al. 2009). A few restoration experts suggest lowering the standards for restoration, asking, for example, whether we want genetic conservation at all costs, or expedient, affordable restoration (Cronn et al. 2003). Others suggest a hierarchy of goals from restoration with local genotypes through "restoration" using non-native species (Jones 2003), an approach that many restorationists would find objectionable.

This study has explored one example of how cost management might impinge on restoration results. Using ecological restoration to mitigate damage from economic activity pits effective restoration against profits. A better alternative would be preventing damage to ecosystems when possible, rather than permitting losses and hoping for successful ecological compensation. Restorationists should vigorously reiterate the scientific, technical, and economic impediments to restoration, to supplant the optimistic vision of recreating nature with a more realistic perspective of the limited but still valuable benefits of restoration. A.D. Bradshaw described restoration as the "acid test" of ecological knowledge (Bradshaw 1996). It may also be a test of our willingness to face the limits of our ability to manipulate nature.

Literature Cited

30 Code of Federal Regulations. Revegetation: Standards for success. 30 CFR §816.116. Accessed at https://www.ecfr.gov on 3/20/2018.

36 Code of Federal Regulations, Part 228. Accessed at https://www.ecfr.gov on 3/20/2018.

Aarssen, Lonnie W. 2000. Why are most selfers annuals? A new hypothesis for the fitness benefits of selfing. *Oikos* 89(3): 606-612. doi: 10.1034/j.1600-0706.2000.890321.x

Aarssen, Lonnie W., and Teri Keogh. 2002. Conundrums of competitive ability in plants: what to measure? *Oikos* 96(3): 531–542. doi:10.1034/j.1600-0706.2002.960314.x

Aarssen, Lonnie W., and Roy Turkington. 1985. Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *The Journal of Ecology* 77: 605–614. doi: 10.2307/2260497

Adams, Rachel I., and Mark Vellend. 2011. Species diversity of grasses promotes genotypic diversity of clover populations in simulated communities. *Oikos* 120: 1584–1594. doi: 10.1111/j.1600-0706.2011.19107.x

Agrawal, Anurag A., Marc T.J. Johnson, Amy P. Hastings, and John L. Maron. 2013. A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedback to seed predator populations. *The American Naturalist* 181(S1): S35–S45. doi: 10.1086/666727

Agrecol Native Nursery. Undated. Shop for native seeds (webpage). Retrieved 1/2/2016 from http://www.agrecol.com/NativeSeed.

Aguilar, Ramiro, Mauricio Quesada, Lorena Ashworth, Yvonne Herrerias-Diego, and Jorge Lobo. 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. *Molecular Ecology* 17(24): 5177–5188. doi: 10.1111/j.1365-294X.2008.03971.x

Ailstock, Steve, and Deborah Shafer. 2006. Protocol for large-scale collection, processing, and storage of seeds of two mesohaline submerged aquatic plant species (Report No. ERDC/TN-SAV-06-3). United States Army Engineer Research and Development Center, Engineer Research and Development Center, Vicksburg, MS. Accessed at http://erdc.summon.serialssolutions.com on 3/3/2018.

Alden, J. 1991. *Provisional Tree Seed Zones and Transfer Guidelines for Alaska.* US Department of Agriculture Forest Service Pacific Northwest Research Station. Portland, Oregon. PNW-GTR-270. Accessed at https://www.fs.fed.us/pnw/pubs/pnw_gtr270.pdf on 3/20/2018.

Anderson, Jill T., John H. Willis, and Thomas Mitchell-Olds. 2011. Evolutionary genetics of plant adaptation. *Trends in Genetics* 27(7): 258–266. doi: 10.1016/j.tig.2011.04.001

Anderson, M. Kat. 2007. Indigenous uses, management, and restoration of oaks of the far western United States (technical note). Unites States. Department of Agriculture Natural Resources Conservation Service, Washington D.C. Accessed at https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1042292.pdf on 3/3/2018.

Antonovics, Janis, and Norman C. Ellstrand. 1984. Experimental studies of the evolutionary significance of sexual reproduction. I. A test of the frequency-dependent selection hypothesis. *Evolution* 38: 103–115. doi: 10.2307/2408550

ArcGIS. Undated. Sonoma County Soils 1972 map. Accessed at www.arcgis.com on 5/5/2014.

Archibald, Colleen, Steve Feigner, and Johann Visser. 2000. Seed and seedling production of blue wild-rye (*Elymus glaucus*). *Native Plants Journal* 1(1): 32–34. Accessed at http://npj.uwpress.org/content/15/3/257.full.pdf on 3/8/2018.

Amarasekare, Priyanga. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6(12): 1109–1122. doi: 10.1046/j.1461-0248.2003.00530.x

Baer, S.G., D.J. Kitchen, J.M. Blair, and C.W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. *Ecological Applications* 12(6): 1688–1701. doi: 10.2307/3099932

Bailey, Joseph K., Jennifer A. Schweitzer, Francisco Úbeda, Julia Koricheva, Carri J. LeRoy, Michael D. Madritch, Brian J. Rehill, Randy K. Bangert, Dylan G. Fischer, Gerard J. Allan, and Thomas G. Whitham. 2009. From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364(1523): 1607–1616. doi: 10.1098/rstb.2008.0336

Bailey, Pamela, and Chester O. Martin. 2007. *Regional Availability of Plants for Prairie Restoration* (ERDC TN-EMRRP-SI-31). US Army Corps of Engineers Engineer Research and Development Center Library, Vicksburg, VA. Retrieved from acwc.sdp.sirsi.net on 10/15/2015.

Bailey, Robert. G. 1976. *Ecoregions of the United States 1:7,500,000* (map). United States Department of Agriculture Forest Service, Intermountain Region, Ogden, Utah.

Bakker, Jan P. and Frank Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution* 14(2): 63–68. doi: 10.1016/S0169-5347(98)01544-4

Barbour, Robert C., Julianne M. O'Reilly-Wapstra, David W. De Little, Gregory J. Jordan, Dorothy A. Steane, Jonathon R. Humphreys, Joseph K. Bailey, Thomas G. Whitham, and Bradley M. Potts. 2009. A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* 90(7): 1762-1772. doi: 10.1890/08-0951.1

Bartolome, James W. 1979. Germination and seedling establishment in California annual grassland. *The Journal of Ecology* 67(1): 273–281. doi: 10.2307/2259350

Bartolome, James W., Jeffrey S. Fehmi, Randall D. Jackson, and Barbara Allen-Diaz. 2004. Response of a native perennial grass stand to disturbance in California's coast range grassland. *Restoration Ecology* 12(2): 279–289. doi: 10.1111/j.1061-2971.2004.00355.x

Bartolome, James W. and Barbara Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madroño* 28: 172–184. Accessed at http://www.jstor.org/stable/41424320 on 5/10/2017.

Bartolome, James W., Steven E. Klukkert, and W. James Barry. 2013. Opal phytoliths as evidence for displacement of native Californian grassland. *Madroño* 60(4): 342–347. doi:10.3120/0024-9637-60.4.342

Bartolome, James W., Michael C. Stroud, and Harold F. Heady. 1980. Influence of natural mulch on forage production on differing California annual range sites. *Journal of Range Management* 33: 4–8. doi: 10.2307/3898219

Barton, Kasey E., and M. Deane Bowers. 2006. Neighbor species differentially alter resistance phenotypes in *Plantago*. *Oecologia* 150: 442–452. doi: 10.1007/s00442-006-0531-z

Basey, Adrienne C., Jeremie B. Fant, and Andrea T. Kramer. 2015. Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal* 16(1): 37–53. doi: 10.3368/npj.16.1.37

Bastow, Justin L., Evan L. Preisser, and Donald R. Strong. 2008. *Holcus lanatus* invasion slows decomposition through its interaction with a macroinvertebrate detritivore, *Porcellio scaber*. *Biological Invasions* 10: 191–199. doi: 10.1007/s10530-007-9122-0

Baughman, Owen W., 2014. Will Local or Commercial Native Plants Succeed Where Exotic Invaders Fail? Cheatgrass Die-offs as an Opportunity for Restoration in the Great Basin, USA (master's thesis). University of Nevada, Reno. Retrieved from http://gradworks.proquest.com/1559677.pdf on 6/25/2015

Beckman, Joseph S., and Jeffry B. Mitton. 1984. Peroxidase allozyme differentiation among successional stands of ponderosa pine. *American Midland Naturalist* 112(1): 43–49. http://www.jstor.org/stable/2425455

Begon, Michael, John L. Harper, and Colin R. Townsend. 1990. *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Cambridge, MA.

BenDor, Todd. 2009. A dynamic analysis of the wetland mitigation process and its effects on no net loss policy. *Landscape and Urban Planning* 89(1–2): 17–27. doi:10.1016/j.landurbplan.2008.09.003

BenDor, Todd, T. William Lester, Avery Livengood, Adam Davis, and Logan Yonavjak. 2015. Estimating the size and impact of the ecological restoration economy. *PLoS ONE* 10 (6): e0128339. doi: 10.1371/journal.pone.0128339

Bennington, Cynthia C., Ned Fetcher, Milan C. Vavrek, Gaius R. Shaver, Kelli J. Cummings, and James B. McGraw. 2012. Home site advantage in two long-lived arctic plant species: results from two 30-year reciprocal transplant studies. *The Journal of Ecology* 100(4): 841–851. doi: 10.1111/j.1365-2745.2012.01984.x

Bergum, Karin E., Ann L. Hild, and Brian A. Mealor. 2012. Phenotypes of two generations of *Sporobolus airoides* seedlings derived from *Acroptilon repens*-invaded and non-invaded grass populations. *Restoration Ecology* 20(2): 227–233. doi: 10.1111/j.1526-100X.2010.00754.x

Bernhardt, Emily S., Margaret A. Palmer, J.D. Allan, G. Alexander, Katie Barnas, Shane Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S.Katz, G.M.Kondolf, P. S. Lake, R. Lave, J.L.Meyer, T.K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing US river restoration efforts. *Science* 308(5722): 636–637. doi: 10.1126/science.1109769

Bischoff, Armin, and Heinz Müller-Schärer. 2010. Testing population differentiation in plant species—how important are environmental maternal effects. *Oikos* 1193: 445–454. doi: 10.1111/j.1600-0706.2009.17776.x

Bischoff, Armin, Thomas Steinger, and Heinz Müller-Schärer. 2010. The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. *Restoration Ecology* 18(3): 338–348. doi: 10.1111/j.1526-100X.2008.00454.x

(BLM) United States Department of the Interior Bureau of Land Management. 1999. *The Great Basin Restoration Initiative: Out of Ashes, An Opportunity.* Bureau of Land Management National Office of Fire and Aviation, Boise, Idaho.

(BLM) United States Department of the Interior Bureau of Land Management. 2008. *Integrated Vegetation Management Handbook.* BLM Handbook H-1740-2. U.S. Department of the Interior, Washington, DC. Retrieved from https://www.blm.gov/wo/st/en/info/regulations/Instruction_Memos_and_Bulletins/blm_handbooks.html on 6/12/2015.

(BLM) United States Department of the Interior Bureau of Land Management. 2009. *Native Plant Materials Development Program Progress Report for 2001-2007*. Retrieved from http://www.blm.gov on 10/9/2015.

(BLM) United States Department of the Interior Bureau of Land Management. 2011. Colorado Plateau Native Plant Program Operational Plan (*Draft*). Retrieved from http://www.blm.gov/style/medialib/blm/ut/natural_resources/Colorado_Plateau/meeting.Par.79150.File.dat/2011-03-01%20DRAFT%20Operational%20Plan.pdf on 12/12/2015.

(BLM) United States Department of the Interior Bureau of Land Management. 2014a. *Abandoned Mine Lands*. http://www.blm.gov/wo/st/en/prog/more/Abandoned_Mine_Lands.html accessed 4/5/2015.

(BLM) United States Department of the Interior Bureau of Land Management. 2014b. Federal Native Plant Conservation Memorandum of Understanding. Retrieved from http://www.blm.gov on 1/20/2016.

(BLM) United States Department of the Interior Bureau of Land Management. 2014c. *National Seed Strategy for Rehabilitation and Restoration 2015-2012*. Accessed at https://nativeseed.info on 4/27/2018.

(BLM) United States Department of the Interior Bureau of Land Management. 2014d. Plant Conservation Alliance (webpage). Retrieved from http://www.blm.gov on 12/15/2015.

(BLM) United States Department of the Interior Bureau of Land Management. 2014e. Seeds of Success. Retrieved from http://www.blm.gov/wo/st/en/prog/more/fish__wildlife_and/plants/seeds_of_success.html on 11/23/2015.

(BLM) United States Department of the Interior Bureau of Land Management. 2015a. *Native Plant Materials Development Program*. Retrieved from http://www.blm.gov on 1/15/2016.

(BLM) United States Department of the Interior Bureau of Land Management. 2015b. *Technical Protocol for the Collection, Study, and Conservation of Seeds from Native Plant Species for Seeds of Success*. Retrieved from http://www.blm.gov/style/medialib/blm/wo/Planning_and_Renewable_Resources/fish__wildlife_and/plants/sos0.Par.67406.File.dat/protocol.pdf on 2/12/2016.

(BLM) United States Department of the Interior Bureau of Land Management. 2015c. A threatening legacy. Retrieved from http://www.abandonedmines.gov on 5/12/2015.

(BLM) United States Department of the Interior Bureau of Land Management. Undated a. Native Plant Materials Development Program. Retrieved from http://www.blm.gov/wo/st/en/prog/more/fish__wildlife_and/plants/1.html on 5/18/2015.

(BLM) United States Department of the Interior Bureau of Land Management. Undated b. Native plant species program: Policy on native species plant materials. Accessed at http://www.or.blm.gov:80/efoia/fy98/IBs/b98317a.htm on 2/29/2000.

(BLM) United States Department of the Interior Bureau of Land Management. Undated c. Native species program guidelines. Accessed at http://www.or.blm.gov:80/efoia/fy98/IBs/b98317a.htm on 2/29/2000.

Bloom, Arnold J. 1986. Plant economics. *Trends in Ecology & Evolution* 1(4): 98–100. doi: 10.1016/0169-5347(86)90033-9

Bockelmann, A.C., T.B.H. Reusch, R. Bijlsma, and J.P. Bakker. 2003. Habitat differentiation vs. isolation-by-distance: the genetic population structure of Elymus athericus in European salt marshes. *Molecular Ecology* 12(2): 505–515. doi: 10.1046/j.1365-294X.2003.01706.x

Booth, Rosemary E., and J. Philip Grime. 2003. Effects of genetic impoverishment on plant community diversity. *The Journal of Ecology* 915: 721–730. doi: 10.1046/j.1365-2745.2003.00804.x

Booy, G.R., J.J. Hendriks, M.J.M. Smulders, J.M. Van Groenendael, and B. Vosman. 2000. Genetic diversity and the survival of populations. *Plant Biology* 2: 379–395. doi: 10.1055/s-2000-5958

Borders, Brianna. 2009. Central Valley Project Improvement Act Land Retirement Demonstration Project — A Synthesis of Native Plant Seed Production Efforts in the San Joaquin Valley, California. California State University (Stanislaus) Endangered Species Program, Fresno, CA. Retrieved from http://esrp.csustan.edu/publications/reports/lrdp/esrp_2009_npspsynthesis_e.pdf on 12/14/2015.

Bossdorf, Oliver, Christina L. Richards, and Massimo Pigliucci. 2008. Epigenetics for ecologists. *Ecology Letters* 11(2): 106–115. doi: 10.1111/j.1461-0248.2007.01130.x

Bower, Andrew D., J. Bradley St. Clair, and Vicky Erickson. 2014. Generalized provisional seed zones for native plants. *Ecological Applications* 24(5): 913-919. doi: 10.1890/13-0285.1

Bowles, M. L., J. L. McBride, and T. J. Bell. 2015. Long-term processes affecting restoration and viability of the federal threatened Mead's milkweed (*Asclepias meadii*). *Ecosphere* 6(1): 1–22. doi: 10.1890/ES14-00240.1

Bracmort, Kelsi. 2013. *Wildfire management: Federal funding and related statistics* (Congressional Research Service report #RL 43077). Accessed at https://fas.org/sgp/crs/misc/R43077.pdf on 3/9/2018.

Bradshaw, Anthony D. 1996. Underlying principles of restoration. *Canadian Journal of Fisheries and Aquatic Sciences* 53(S1): 3–9. doi: 10.1139/f95-265

Bragg, John. Dec. 11, 2000. Feds on lookout now for sagebrucsh *[sic]* thieves. *Herald and News*, Klamath Falls, Oregon. Retrieved from http://www.heraldandnews.com/feds-on-lookout-now-for-sagebrucsh-thieves/article_e5612c26-f123-5044-aca2-3e7199939ae2.html on 5/2/2017.

Brandt, Adam R., G.A. Heath, E.A. Kort, F. O'Sullivan, G. Pétron, S.M. Jordaan, P. Tans, J. Wilcox, A.M. Gopstein, D. Arent, S. Wofsy, N.J. Brown, R. Bradley, G.D. Stucky, D. Eardley, and R. Harriss. 2014a. Methane leaks from North American natural gas systems. *Science* 343(6172): 733-735. doi: 10.1126/science.1247045

Brandt, Adam R., G.A. Heath, E.A. Kort, F. O'Sullivan, G. Pétron, S.M. Jordaan, P. Tans, J. Wilcox, A.M. Gopstein, D. Arent, S. Wofsy, N.J. Brown, R. Bradley, G.D. Stucky, D. Eardley, and R. Harriss. 2014b. Supplementary materials for "Methane leaks from North American natural gas systems." Retrieved from www.sciencemag.org/content/343/6172/733/suppl/DC1 on 4/7/2016.

Brandt, Angela J. and Eric W. Seabloom. 2012. Seed and establishment limitation contribute to long-term native forb declines in California grasslands. *Ecology* 936: 1451–1462. doi: 10.1890/11-0579.1

Breed, Martin F., Michael G. Stead, Kym M. Ottewell, Michael G. Gardner, and Andrew J. Lowe. 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* 14(1): 1–10. doi: 10.1007/s10592-012-0425-z

Broadhurst, Linda M., Andrew Lowe, David J. Coates, Saul A. Cunningham, Maurice McDonald, Peter A. Vesk, and Colin Yates. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1(4): 587–597. doi: 10.1111/j.1752-4571.2008.00045.x

Brooker, Rob W., Fernando T. Maestre, Ragan M. Callaway, Christopher L. Lortie, Lohengrin A. Cavieres, Georges Kunstler, Pierre Liancourt, Katja Tielbörger, Justin M.J. Travis, Fabien Anthelme, Cristina Armas, Lluis Coll, Emmanuel Corcket, Sylvain Delzon, Estelle Forey, Zaal Kikvidze, Johan Olofsson, Francisco Pugnaire, Constanza L. Quiroz, Patrick Saccone, Katja Schiffers, Merav Seifan, Blaize Touzard, and Richard Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. *The Journal of Ecology*, 96(1): 18–34. doi: 10.1111/j.1365-2745.2007.01295.x

Brown, A.H.D., C.L. Brubaker, and J.P. Grace. 1997. Regeneration of germplasm samples: wild versus cultivated plant species. *Crop Science* 37(1): 7–13. doi:10.2135/cropsci1997.0011183x003700010002x

Brown, Cynthia S., and Robert L. Bugg. 2001. Effects of established perennial grasses on introduction of native forbs in California. *Restoration Ecology* 9(1): 38–48. doi:10.1046/j.1526-100x.2001.009001038.x

Bugg, Robert L., Cynthia S. Brown, and John H. Anderson. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. *Restoration Ecology* 5(3): 214–225. doi: 10.1046/j.1526-100x.1997.09726.x

Byrne, Margaret, Lynley Stone, and Melissa A. Millar. 2011. Assessing genetic risk in revegetation. *Journal of Applied Ecology* 48(6): 1365–1373. doi: 10.1111/j.1365-2664.2011.02045.x

(CA-AMLU) California Department of Conservation Abandoned Mine Lands Unit. 2000. *Abandoned Mines Land Report.* Retrieved from http://www.conservation.ca.gov/dmr/abandoned_mine_lands/AML_Report/Pages/index.aspx on 5/12/2015.

Calcagno, Vincent, Nicolas Mouquet, Philippe Jarne, and P. David. 2006. Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecology Letters* 9(8): 897–907. doi: 10.1111/j.1461-0248.2006.00930.x

California Department of Fish and Game. 2005. Hillshade map. Accessed at http://www.cdfg.ca.gov on 5/5/2005.

Callaway, John C., Gary Sullivan, and Joy B. Zedler. 2003. Species-rich plantings increase biomass and nitrogen accumulation in a wetland restoration experiment. *Ecological Applications* 13(6): 1626–1639. doi: 10.1890/02-5144

Carlsen, Tina M., John W. Menke, and Bruce M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology* 8(1): 18-29. doi: 10.1046/j.1526-100x.2000.80004.x

Carter, Andrew J., and Ernest R Robinson. 1993. Genetic structure of a population of the clonal grass *Setaria incrassata*. *Biological Journal of the Linnean Society,* 48: 55-62. doi: 10.1111/j.1095-8312.1993.tb00876.x

(CDC) United States Centers for Disease Control and Prevention, Office of Mine Safety and Health Research. 2015. Mining facts - 2013. Retrieved from http://www.cdc.gov/niosh/mining/statistics/allmining.html on 1/28/2016.

(CDF-FRAP) California Department of Forestry and Fire Protection Fire and Resource Assessment Program. 2003. *The Changing California: Forest and Range 2003 Assessment.* State of California, The Resources Agency, Sacramento.

Chanway, C.P., F.B. Holl, and R. Turkington. 1989. Effect of *Rhizobium leguminosarum* biovar *trifolii* genotype on specificity between *Trifolium repens* and *Lolium perenne*. *The Journal of Ecology* 77: 1150–1160. doi: 10.2307/2260829

Chapela, Ignacio H., Laurie J. Osher, Thomas R. Horton, and Matthew R. Henn. 2001. Ectomycorrhizal fungi introduced with exotic pine plantations induce soil carbon depletion. *Soil Biology and Biochemistry* 33(12–13): 1733–1740. doi: 10.1016/s0038-0717(01)00098-0.

Chen, Bin J.W., Heinjo J. During, and Niels P.R. Anten. 2012. Detect thy neighbor: identity recognition at the root level in plants. *Plant Science* 195: 157–167. doi: 10.1016/j.plantsci.2012.07.006

Cheplick, Gregory P. 1995. Life history trade-offs in *Amphibromus scabrivalvis* (Poaceae): allocation to clonal growth, storage, and cleistogamous reproduction. *American Journal of Botany* 82(3): 621-629. doi: 10.2307/2445420

Christensen, Jon. 2000. A deadly dance on the steppes of Nevada. *New York Times*, February 1, 2000. Accessed at http://www.nytimes.com on 5/10/2017.

Chu, Cheng-Jin, Fernando T. Maestre, Sa Xiao, Jacob Weiner, You-Shi Wang, Zheng Hu Duan, and Gang Wang. 2008. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. *Ecology Letter*s 11(11): 1189–1197. doi: 10.1111/j.1461-0248.2008.01228.x

Cione, Nancy K., Pamela E. Padgett, and Edith B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration Ecology* 10(2) 376-384. doi: 10.1046/j.1526-100x.2002.02038.x

Clare, Shari, Naomi Krogman, Lee Foote, and Nathan Lemphers. 2011. Where is the avoidance in the implementation of wetland law and policy? *Wetlands Ecology and Management* 192: 165–182. doi: 10.1007/s11273-011-9209-3

Clark. C.J., J.R. Poulsen , D.J. Levey , and C.W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist* 170(1): 128–142. doi: 10.1086/518565

Clark, James S. 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327: 1129–1132. doi: 10.1126/science.1183506

Clark, James S., Mike Dietze, Sukhendu Chakraborty, Pankaj K. Agarwal, Inés Ibáñez, Shannon LaDeauand, and Mike Wolosin. 2007. Resolving the biodiversity paradox. *Ecology Letters* 10(8): 647–662. doi: 10.1111/j.1461-0248.2007.01041.x

Clements, Frederick E. 1934. The relict method in dynamic ecology. *The Journal of Ecology* 22(1): 39–68. Available at http://www.jstor.org/stable/2256095

Clewell, Andre, and John P. Rieger. 1997. What practitioners need from restoration ecologists. *Restoration Ecology* 5(4): 350–354. doi: 10.1046/j.1526-100X.1997.00548.x

(CNPS) California Native Plant Society. 2001. *CNPS guidelines for landscaping to protect native vegetation from genetic degradation.* CNPS. Sacramento, California. Retrieved from www.cnps.org on 6/22/2015.

(CNPS) California Native Plant Society. 1995. *Statement of policy – seeding after wildfire.* CNPS. Sacramento, California. Retrieved from www.cnps.org on 6/22/2015.

Coates, David J., Matthew R. Williams, and Sally Madden. 2013. Temporal and spatial mating-system variation in fragmented populations of *Banksia cuneata*, a rare bird-pollinated long-lived plant. *Australian Journal of Botany* 61: 235–242. doi: 10.1071/BT12244

Cole, Christopher T., 2003. Genetic variation in rare and common plants. *Annual Review of Ecology, Evolution, and Systematics* 34(1): 213–237. doi: 10.1146/annurev.ecolsys.34.030102.151717

Conover, W.J. 1980. *Practical Nonparametric Statistics*. John Wiley and Sons, New York. P. 337.

Corbin, Jeffrey D., and Carla M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85(5): 1273–1283. doi: 10.1890/02-0744

Corbin, Jeffrey D., and Carla M. D’Antonio. 2010. Not novel, just better: competition between native and non-native plants in California grasslands that share species traits. *Plant Ecology* 209(1): 71–81. doi:10.1007/s11258-010-9722-0

Corbin, Jeffrey D., Carla M. D’Antonio, and Susan J. Bainbridge. 2004. Tipping the balance in the restoration of native plants: experimental approaches to changing the exotic: native ratio in California grassland. pp 154–179 in Gordon, Malcolm S., and Soraya M. Bartol (eds.), *Experimental Approaches to Conservation Biology.* University of California Press, Berkeley, California.

Cox, C.M., W.W. Bockus, R.D. Holt, L. Fang, and K.A. Garrett. 2013. Spatial connectedness of plant species: potential links for apparent competition via plant diseases. *Plant Pathology* 62(6): 1195–1204. doi:10.1111/ppa.12045

Crawford, Kerri M., and Jennifer A. Rudgers. 2012. Plant species diversity and genetic diversity within a dominant species interactively affect plant community biomass. *The Journal of Ecology* 100(6): 1512–1521. doi: 10.1111/j.1365-2745.2012.02016.x

Crawford, Kerri M., and Jennifer A. Rudgers. 2013. Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* 94(5): 1025–1035. doi: 10.1890/12-1468.1

Crawford, K.M., and K.D. Whitney. 2010. Population genetic diversity influences colonization success. *Molecular Ecology* 19(6): 1253–1263. doi: 10.1111/j.1365-294X.2010.04550.x

Cronn, R., M. Cruzan, L. Hanson, T. Kaye, A. Liston, B. Roy, and B. Wilson, with K. Kuykendall, moderator. 2003. Genetics panel discussion. In Kaye, T.N., M. Gisler, and R. Fiegener (eds.), *Proceedings of a Conference on Native Plant Restoration and Management on Public Lands in the Pacific Northwest: Rare Plants, Invasive Species and Ecosystem Management.* Co-sponsors: US Department of the Interior Bureau of Land Management, Institute for Applied Ecology, US Department of Agriculture Forest Service, and Native Plant Society of Oregon.

Crossa, J., C.M. Hernandez, P. Bretting, S.A. Eberhart, and S. Taba. 1993. Statistical genetic considerations for maintaining germ plasm collections. *Theoretical and Applied Genetics* 86(6): 673–678. doi:10.1007/BF00222655

Crossa, José, and Roland Vencovsky. 2011. Basic sampling strategies: Theory and practice. Guarino, l., V. Ramanatha Rao, and R. Reid, (eds.), *Collecting plant genetic diversity: Technical guidelines – 2011 update.* https://cropgenebank.sgrp.cgiar.org/images/file/procedures/collecting2011/Chapter5-2011.pdf, accessed 3/4/2018.

Crutsinger, Gregory M., W. Nicholas Reynolds, Aimée T. Classen, and Nathan J. Sanders. 2008. Disparate effects of plant genotypic diversity on foliage and litter arthropod communities. *Oecologia*, 158(1): 65–75. doi: 158: 65. doi:10.1007/s00442-008-1130-y

Crutsinger, Gregory M., Lara Souza, and Nathan J. Sanders. 2008. Intraspecific diversity and dominant genotypes resist plant invasions. *Ecology Letters* 11(1): 16–23. doi: 10.1111/j.1461-0248.2007.01118.x

Curran, Michael, Stefanie Hellweg, and Jan Beck. 2014. Is there any empirical support for biodiversity offset policy? *Ecological Applications* 24(4): 617–632. doi: 10.1890/13-0243.1

David Amme Associates. 1993. *Richmond Research Center Master Plan Environmental Impact Report: Existing Conditions of Grassland Resources.* Prepared by David Amme Associates for Brady and Associates, Berkeley, California.

Deblauwe, Vincent, Pierre Couteron, Olivier Lejeune, Jan Bogaert, and Nicolas Barbier. 2011. Environmental modulation of self-organized periodic vegetation patterns in Sudan. *Ecography* 34(6): 990–1001. doi: 10.1111/j.1600-0587.2010.06694.x

DeBolt, Ann, and Carol S. Spurrier. 2002. Seeds of Success and the Millenium Seed Bank Project. In Hild, Ann L., Nancy L. Shaw, Susan E. Meyer, D. Terrance Booth, and E. Durant McArthur (compilers), *Seed and Soil Dynamics in Shrubland Ecosystems: Proceedings (RMRS-P-31).* United States Department of Agriculture Forest Service Rocky Mountain Research Station. Laramie, Wyoming, August 12–16, 2002. Retrieved from https://www.fs.fed.us/rm/pubs/rmrs_p031.pdf on 5/9/2017.

Deck, Anna, Adrianna Muir, and Sharon Strauss. 2013. Transgenerational soil-mediated differences between plants experienced or naïve to a grass invasion. *Ecology and Evolution* 3(11): 3663–3671. doi: 10.1002/ece3.716

Delaney, John T., and Eric J. Baack. 2012. Intraspecific chromosome number variation and prairie restoration – A case study in Northeast Iowa, USA. *Restoration Ecology* 20(5): 576–583. doi: 10.1111/j.1526-100X.2011.00825.x

Dennis, Ann. 1989. Effects of defoliation on three native perennial grasses in the California Annual Grassland (dissertation). University of California, Berkeley.

Dickie, Gloria. 2015. BLM launches a native seeds strategy for damaged landscapes. *High Country News* August 1, 2015. Retrieved from http://www.hcn.org/articles/blm-aims-to-restore-the-wests-post-fire-landscape on 10/30/2015.

Dietz, Hansjörg, Thomas Steinlein, and Isolde Ullmann. 1998. The role of growth form and correlated traits in competitive ranking of six perennial ruderal plant species grown in unbalanced mixtures. *Acta Oecologica* 19(1): 25–36. doi: 10.1016/s1146-609x(98)80005-2

Dixon, Kingsley W. 2009. Pollination and restoration. *Science* 325: 571–573. doi: 10.1126/science.1176295

(DOD) United States Department of Defense. 2013. Natural resources conservation compliance program (brochure). Retrieved from http://www.dodnaturalresources.net on 10/15/2015.

(DOI) United States Department of the Interior. 2012. *The Department of the Interior's Economic Contributions Fiscal Year 2011*. Retrieved from https://www.doi.gov/sites/doi.gov/files/migrated/ppa/upload/DOI-Econ-Report-6-21-2011.pdf on 11/20/2016.

(DOI) United States Department of the Interior. 2013. *Economic Report: FY 2012*. Retrieved from http://www.doi.gov on 6/10/2015.

(DOI and USDA) United States Department of the Interior and United States Department of Agriculture. 2007. *Surface Operating Standards and Guidelines for Oil and Gas Exploration and Development* (BLM/WO/ST-06/021+3071/REV 07). Bureau of Land Management. Denver, Colorado. Accessed at https://www.blm.gov/sites/blm.gov/files/Chapter%206%20-%20Reclamation%20and%20Abandonment.pdf on 3/18/2018.

(DOI-OPA) Department of the Interior Office of Policy Analysis. 2012. *Wildland Fire Management Program Benefit - Cost Analysis: A Review of Relevant Literature*. Retrieved from https://www.doi.gov/sites/doi.gov/files/migrated/ppa/upload/Wildland_fire_literature_review_060812FINAL.pdf on 1/12/2016.

Donohue, Kathleen. 2009. Completing the cycle: maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B: Biological Sciences* 3641530: 1059–1074. doi: 10.1098/rstb.2008.0291

Dorner, Jeanette. 2002. An introduction to using native plants in restoration projects. Prepared for Plant Conservation Alliance, Bureau of Land Management, United States Department of Interior and Unites States Environmental Protection Agency. Accessed at https://www.fs.fed.us/wildflowers/Native_Plant_Materials/documents/intronatplant.pdf on 3/8/2018.

Drummond, Emily B.M., and Mark Vellend. 2012. Genotypic diversity effects on the performance of *Taraxacum officinale* populations increase with time and environmental favorability. *PLoS ONE* 7(2): e30314. doi: 10.1371/journal.pone.0030314

Dudley, Susan A., Guillermo P. Murphy, and Amanda L. File. 2013. Kin recognition and competition in plants. *Functional Ecology* 27(4): 898–906. doi: 10.1111/1365-2435.12121

Dumroese, R. Kasten, Tara Luna, and D. Thomas (eds.). 2009. *Nursery manual for native plants: A guide for tribal nurseries. Volume 1: Nursery management*. Agriculture Handbook 730. United States Department of Agriculture Forest Service, Washington, D.C. Retrieved from https://www.fs.fed.us/rm/pubs_other/wo_AgricHandbook730.pdf on 1/22/2016.

Dunwiddie, Peter, and Eric Delvin. 2006. Inadvertent selection in the propagation of native plants: a cautionary note. *Native Plants Journal* 7(2): 121–124. doi: 10.2979/NPJ.2006.7.2.121

Dyer, Andrew R. 2002. Burning and grazing management in a California grassland: effect on bunchgrass seed viability. *Restoration Ecology* 10(1): 107–111. doi: 10.1046/j.1526-100X.2002.10111.x

Dyer, Andrew R., A. Fenech, and Kevin J. Rice. 2000. Accelerated seedling emergence in interspecific competitive neighbourhoods. *Ecology Letters* 3(6): 523–529. doi: 10.1111/j.1461-0248.2000.00187.x

Dyer, Andrew R., Eric E. Knapp, and Kevin J. Rice. 2016. Unintentional selection and genetic changes in native perennial grass populations during commercial seed production. *Ecological Restoration* 34(1): 39–48. doi: 10.3368/er.34.1.39

Dyer, Andrew R., and Kevin J. Rice. 1997-. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* 7(2): 484–492. doi: 10.1890/1051-0761(1997)007[0484:IADCTR]2.0.CO;2

Dyer, Andrew R., and Kevin J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80(8): 2697–2710. doi: 10.1890/0012-9658(1999)080[2697:EOCORA]2.0.CO;2

Dyer, Dave. 2001. Propagation protocol for production of propagules (seeds, cuttings, poles, etc.): *Elymus glaucus* seeds. USDA NRCS - Lockeford Plant Materials Center Lockeford, California. United States Department of Agriculture Forest Service National Center for Reforestation, Nurseries, and Genetic Resources. Retrieved from http://NativePlantNetwork.org on 4/30/2017.

Earth Source & Heartland Restoration Services. 2013. Available species (webpage). Retrieved from http://www.earthsourceinc.net on 12/20/2015.

ECOMAP. 2007. Delineation, peer review, and refinement of subregions of the conterminous United States. Gen. Tech. Report WO-76A. US Department of Agriculture Forest Service, Washington, D.C. Retrieved from http://www.fs.fed.us/research/publications/misc/73329-wo-gtr-76a-keys2007.pdf on 12/22/2015.

Edmands, Suzanne. 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Molecular Ecology* 16(3): 463–475. doi: 10.1111/j.1365-294X.2006.03148.x

Ehlers, Bodil K., Christian F. Damgaard, and Fabien Laroche. 2016. Intraspecific genetic variation and species coexistence in plant communities. *Biological Letters* 12(1): 20150853. doi: 10.1098/rsbl.2015.0853

Ellstrand, Norman C., and Janis. Antonovics. 1985. Experimental studies of the evolutionary significance of sexual reproduction. II. A test of the density-dependence hypothesis. *Evolution* 39(3): 657–666. doi: 10.2307/2408660

Ellstrand, Norman C., and Mikeal L. Roose. 1987. Patterns of genetic diversity in clonal plant species. *American Journal of Botany* 74(1): 123-131. doi: 10.2307/2444338

Ennos, R.A. 1985. The significance of genetic variation for root growth within a natural population of white clover (*Trifolium repens*). *The Journal of Ecology* 73: 615–624. doi: 10.2307/2260498

ENSCONET. 2009. *ENSCONET Seed Collecting Manual for Wild Species*. Royal Botanic Gardens, Kew, U.K., and Universidad Politécnica de Madrid, Spain (eds.),. European Native Seed Conservation Network. Retrieved from https://www.luomus.fi/sites/default/files/files/collecting_protocol_english.pdf on 3/12/2016.

(EPA) United States Environmental Protection Agency. 2010. Federal Facility Cleanup Dialogue - Department of the Interior and Department of Agriculture Sites: October 21, 2010 Meeting Summary. Retrieved from http://www.epa.gov/sites/production/files/documents/ffcd_doi-usda_meeting_summary_report.pdf on 2/5/2016.

(EPA) UnitedStates Environmental Protection Agency. 2016. Ecoregion maps and GIS resources. Retrieved from http://archive.epa.gov/wed/ecoregions/web/html/ecoregions-2.html on 1/20/2016.

(EPA) United States Environmental Protection Agency. Undated. Section 404 of the Clean Water Act (website). Accessed at https://www.epa.gov/cwa-404 on 4/3/2018.

Epp, Gary A., and Lonnie W. Aarssen. 1989. Predicting vegetation patterns from attributes of plant growth in grassland species. *Canadian Journal of Botany* 67(10): 2953–2959. doi: 10.1139/b89-378

Erickson, David L., and Charles B. Fenster. 2006. Intraspecific hybridization and the recovery of fitness in the native legume *Chamaecrista fasciculata. Evolutio*n 60(2): 225–233. doi: 10.1554/05-020.1

Espeland, Erin K., Nancy C. Emery, Kristin L. Mercer, Scott A. Woolbright, Karin M. Kettenring, Paul Gepts, and Julie R. Etterson. 2016. Evolution of plant materials for ecological restoration: insights from the applied and basic literature. *Journal of Applied Ecology* 54(1): 102–115. doi: 10.1111/1365-2664.12739

Etterson, Julie R., Rachel H. Toczydlowski, Katharine J. Winkler, Jessica A. Kirschbaum, and Tim S. McAulay. 2015. *Solidago altissima* differs with respect to ploidy frequency and clinal variation across the prairie-forest biome border in Minnesota. *American Journal of Botany* 103(1): 22–32. doi: 10.3732/ajb.1500146

Evans, R.C., and R. Turkington. 1988. Maintenance of morphological variation in a biotically patchy environment. *New Phytologist* 109(3): 369–376. doi:10.1111/j.1469-8137.1988.tb04207.x

Evett, Rand R., and James W. Bartolome. 2013. Phytolith evidence for the extent and nature of prehistoric Californian grasslands. *The Holocene, 23*(11): 1644-1649. doi: 10.1177/0959683613499056

Eviner, Valerie T. 2004. Plant traits that influence ecosystem processes vary independently among species. *Ecology* 85(8): 2215–2229. doi: 10.1890/03-0405

Fajardo, Alex, and Eliot J.B. McIntire. 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *The Journal of Ecology* 99: 642–650. doi: 10.1111/j.1365-2745.2010.01771.x

Fajardo, Alex, Cristian Torres-Díaz, and Irène Till-Bottraud. 2016. Disturbance and density-dependent processes (competition and facilitation) influence the fine-scale genetic structure of a tree species' population. *Annals of Botany* 117(1): 67–77. doi: 10.1093/aob/mcv148

Falk, Donald A. 2006. Process-centred restoration in a fire-adapted ponderosa pine forest. *Journal for Nature Conservation* 14(3–4): 140–151. doi: 10.1016/j.jnc.2006.04.005

Fehmi, Jeffrey S. and James W. Bartolome. 2001. A grid-based method for sampling and analysing spatially ambiguous plants. *Vegetation Science* 12(4): 467–472. doi: 10.2307/3236998

Fehmi, Jeffrey S., Michele Hammond, and James W. Bartolome. 2008. Research note: alignment of elongated *Nassella pulchra* plants with hill-slope contours. *Arid Land Research and Management* 22(3): 212–215. doi: 10.1080/15324980802183038

Fenster, Charles B., and Laura F. Galloway. 2000. Population differentiation in an annual legume: genetic architecture. *Evolution* 54(4) 1157–1172. doi: 10.1554/0014-3820(2000)054[1157:PDIAAL]2.0.CO;2

Ferdinandez, Yasas S.N., Bruce E. Coulman, and Yong-Bi Fu. 2005. Detecting genetic changes over two generations of seed increase in an awned slender wheatgrass population using AFLP markers. *Crop Science* 45(3): 1064–1068. doi:10.2135/cropsci2004.0332

Ferrero-Serrano, Ángel, Ann L. Hild, and Brian A. Mealor. 2011. Can invasive species enhance competitive ability and restoration potential in native grass populations? *Restoration Ecology* 19(4): 545–551. doi: 10.1111/j.1526-100X.2009.00611.x

Fitzsimmons, J. 2002. Corvallis company is cleaning up. *Western Montana InBusiness.* Fall 2002. Retrieved from http://missoulian.com/business/montana-inbusiness on 3/12/2003.

Flessner, Theresa R., and Joan D.C. Trindle. 2007. Propagation protocol for production of *Bromus carinatus* Hook. & Arn seeds (Seed). USDA NRCS - Corvallis Plant Materials Center, Corvallis, Oregon. In: Native Plant Network. Retrieved 4/15/2016 from http://NativePlantNetwork.org.

Florabank. Undated a. Florabank Guideline 5: Seed collection from woody plants for local revegetation. Retrieved from https://www.florabank.org.au/default.asp?V_DOC_ID=755 on 2/17/2016.

Florabank. Undated b. Florabank Guideline 6: Native seed collection methods. Retrieved from https://www.florabank.org.au/default.asp?V_DOC_ID=755 on 2/17/2016.

Florabank. Undated c. Florabank Guideline 9: Using native grass seed in revegetation. Retrieved from https://www.florabank.org.au/default.asp?V_DOC_ID=755 on 2/17/2016.

Forests and Rangelands (website). 2015. Retrieved from https://www.forestsandrangelands.gov/leadership/index.shtml on 1/4/2016.

Forsman, Anders, and Lina Wennersten. 2015. Inter-individual variation promotes ecological success of populations and species: evidence from experimental and comparative studies. *Ecography* 39(7): 630–648. doi: 10.1111/ecog.01357

Frankham, Richard. 2005. Genetics and extinction. *Biological Conservation* 126(2): 131–140. doi: 0.1016/j.biocon.2005.05.002

Frankham, Richard, Jonathan D. Ballou, Mark D.B. Eldridge, Robert C. Lacy, Katherine Ralls, Michele R. Dudash, and Charles B. Fenster. 2011. Predicting the probability of outbreeding depression. *Conservation Biology* 25(3): 465–475. doi: 10.1111/j.1523-1739.2011.01662.x

Frankham, Richard, Corey J.A. Bradshaw, and Barry W. Brook. 2014. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation* 170: 56–63. doi: 10.1016/j.biocon.2013.12.036

Fridley, Jason D., J. Philip Grime, and Mark Bilton. 2007. Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *The Journal of Ecology* 95(5): 908–915. doi: 10.1111/j.1365-2745.2007.01256.x

(FWS) United States Department of the Interior Fish and Wildlife Service. 1994. *Report to Congress: Recovery Programs: Threatened and Endangered Species 1994*. US Department of Interior, Washington. Retrieved from https://www.fws.gov on 1/20/2016.

(FWS) United States Fish and Wildlife Service Division of Realty. 2014. *U.S. Fish and Wildlife Service Annual Report of Lands As of September 30, 2014.* U.S. Department of Interior Fish and Wildlife Service, Washington D.C. Retrieved from https://www.fws.gov/refuges/land/PDF/2014_AnnualReport.pdf on 4/7/2016

(FWS) Unites States Department of the Interior Fish and Wildlife Service. Undated. Legislative history of the Sikes Act. Retrieved from http://www.fws.gov on 9/10/2015.

Galloway, Laura F. 2001. Parental environmental effects on life history in the herbaceous plant *Campanula americana*. *Ecology* 82(10): 2781–2789. doi:10.2307/2679960.

(GAO) United States Government Accountability Office. 2011. Hardrock mining: BLM needs to revise its systems for assessing the adequacy of financial assurances. Retrieved from http://www.gao.gov/assets/590/586874.pdf on 1/28/2016.

(GAO) United States Government Accountability Office. 2012. *Uranium Mining: Opportunities Exist to Improve Oversight of Financial Assurances* (GAO-12-544). Retrieved from http://www.gao.gov/assets/600/590929.pdf on 4/8/2017.

Garcia, Letícia Couto, Marcus Vinicius Cianciaruso, Danilo Bandini Ribeiro, Flavio Antonio Maës dos Santos, and Ricardo Ribeiro Rodrigues. 2015. Flower functional trait responses to restoration time. *Applied Vegetation Science* 183: 402–412. doi: 10.1111/avsc.12163

Garnier, Eric. 1991. Resource capture, biomass allocation and growth in herbaceous plants. *Trends in Ecology & Evolution* 6(4): 126–131. doi:10.1016/0169-5347(91)90091-b

Garnier, E. 1992. Growth analysis of congeneric annual and perennial species. *The Journal of Ecology* 80: 665–675. doi 10.2307/2260858

Garnier, Lisa M., Jacques Durand, and Isabelle Dajoz. 2002. Limited seed dispersal and microspatial population structure of an agamospermous grass of West African savannahs, *Hyparrhenia diplandra* (Poaceae). *American Journal of Botany* 89(1): 1785–1791. doi: 10.3732/ajb.89.11.1785

Gaudet, Connie L., and Paul A. Keddy. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* 334(6179): 242–243. doi:10.1038/334242a0

Geber, Monica A. 1990. The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* 44(4): 799–819. doi: 10.2307/2409547

Gehring, Janet L., and Yan B. Linhart. 1992. Population structure and genetic differentiation in native and introduced populations of *Deschampsia caespitosa* (Poaceae) in the Colorado alpine. *American Journal of Botany* 79(12): 1337–1343. doi: 10.2307/2445131

Genung, Mark A., Joseph K. Bailey, and Jennifer A. Schweitzer. 2012. Welcome to the neighbourhood: interspecific genotype by genotype interactions in *Solidago* influence above- and belowground biomass and associated communities. *Ecology Letters* 15(1): 65–73. doi: 10.1111/j.1461-0248.2011.01710.x

Ghazoul, Jaboury. 2005. Pollen and seed dispersal among dispersed plants. *Biological Reviews* 80(3): 413–443. doi: 10.1017/S1464793105006731

Gibbs, James P., Cruz Marquez, and Eleanor J. Sterling. 2008. The role of endangered species reintroduction in ecosystem restoration: tortoise–cactus interactions on Española Island, Galápagos. *Restoration Ecology* 16(1): 88–93. doi: 10.1111/j.1526-100X.2007.00265.x

Gibbs, James P., Lawrence B. Smart, Andrew E. Newhouse, and Donald J. Leopold. 2012. A molecular and fitness evaluation of commercially available versus locally collected blue lupine *Lupinus perennis* L. seeds for use in ecosystem restoration efforts. *Restoration Ecology* 20(4): 456–461. doi: 10.1111/j.1526-100x.2011.00809.x

Gibson, David J., Andrew J. Allstadt, Sara G. Baer, and Matt Geisler. 2012. Effects of foundation species genotypic diversity on subordinate species richness in an assembling community. *Oikos* 121(4): 496–507. doi: 10.1111/j.1600-0706.2011.19447.x

Gibson, David J., Sara G. Baer, Ryan P. Klopf, Lewis K. Reed, Ben R. Wodika, and Jason E. Willand. 2013. Limited effects of dominant species population source on community composition during community assembly. *Journal of Vegetation Science* 24(3): 429–440. doi: 10.1111/j.1654-1103.2012.01475.x

Giles, Barbara E., Elisabeth Lundqvist, and Jérôme Goudet. 1998. Restricted gene flow and subpopulation differentiation in *Silene dioica. Heredit*y 80(6): 715–723. doi: 10.1046/j.1365-2540.1998.00348.x

Godefroid, Sandrine, Carole Piazza, Graziano Rossi, Stéphane Buord, Albert-Dieter Stevens, Ruth Aguraiuja, Carly Cowell, Carl W. Weekley, Gerd Vogg, José M. Iriondo, Isabel Johnson, Bob Dixon, Doria Gordon, Sylvie Magnanon, Bertille Valentin, Kristina Bjureke, Rupert Koopman, Magdalena Vicens, Myriam Virevaire, and Thierry Vanderborght. 2011. How successful are plant species reintroductions? *Biological Conservation* 144: 672–682. doi:10.1016/j.biocon.2010.10.003

Goodwin, Jay. 1994. RE: Native Seed Collection *(reply to Lippett et al. 1994)*. *Restoration Ecology* 2(4): 218–218. doi:10.1111/j.1526-100x.1994.tb00053.x

Gordon, Doria R., and Kevin J. Rice. 1998. Patterns of differentiation in wiregrass (*Aristida beyrichiana*): implications for restoration efforts. *Restoration Ecology* 6(2): 166–174. doi:10.1046/j.1526-100x.1998.00627.x

Govindaraju, D.R. 1990. Gene flow, spatial patterns and seed-collection zones. *Forest Ecology and Managemen*t 35(3–4): 291–302. doi: 10.1016/0378-1127(90)90010-9

Grey, Miranda M., Paul St. Amand, Nora M. Bello, Matthew B. Galliart, Mary Knapp, Karen A. Garrett, Theodore J. Morgan, Sarah G. Baer, Brian R. Maricle, Eduard D. Akhunov, and Loretta C. Johnson. 2014. Ecotypes of an ecologically dominant prairie grass *Andropogon gerardii* exhibit genetic divergence across the U.S. Midwest grasslands' environmental gradient. *Molecular Ecology* 23: 6011–6028. doi: 10.1111/mec.12993.

Grime, J. Philip. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111(982): 1169–1194. doi: 10.1086/283244.

Grime J. Philip. 1988. The C-S-R model of primary plant strategies — origins, implications and tests. In: Gottlieb, Leslie. D., and Subodh K. Jain. *Plant Evolutionary Biology*. Springer, Dordrecht. doi: 10.1007/978-94-009-1207-6_14

Grime, J. Philip. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *The Journal of Ecology* 86(6): 902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Grman, Emily, and Katharine N. Suding. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology* 18(5): 664–670. doi: 10.1111/j.1526-100X.2008.00497.x

Gross, Katherine L., and Alison D. Smith. 1991. Seed mass and emergence time effects on performance of *Panicum dichotomoflorum* Michx. across environments. *Oecologia* 87(2) 270–278. doi: 10.1007/bf00325266

Gulmon, S.L. 1979. Competition and coexistence: three annual grass species. *American Midland Naturalist* 101(2): 403-416. doi: 10.2307/2424606

Guo, Qinfeng. 2007. The diversity–biomass–productivity relationships in grassland management and restoration. *Basic and Applied Ecology* 8(3): 199–208. doi: 10.1016/j.baae.2006.02.005

Gurevitch, Jessica. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology* 67(1): 46–57. doi: 10.2307/1938502

Gustafson, D.J., D.J. Gibson, and D.L. Nickrent. 2004a. Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology* 18: 451–457. doi: 10.1111/j.0269-8463.2004.00850.x

Gustafson, D.J., D.J. Gibson, and D.L. Nickrent. 2004b. Conservation genetics of two co-dominant grass species in an endangered grassland ecosystem. *Journal of Applied Ecology* 41: 389–397. doi: 10.1111/j.0021-8901.2004.00904.x

Gustafson, Danny J., Charles Major, Dewitt Jones, John Synovec, Sara G. Baer, and David J. Gibson. 2014. Genetic sorting of subordinate species in grassland modulated by intraspecific variation in dominant species. *PLoS ONE* 9(3): e91511. doi: 10.1371/journal.pone.0091511

Halpern, Benjamin S., Brian R. Silliman, Julian D. Olden, John P. Bruno, and Mark D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. *Frontiers in Ecology and the Environment* 5(3): 153–160. doi: 10.1890/1540-9295(2007)5[153:IPIIAR]2.0.CO;2

Hamilton, Jason G. 1997. Changing perceptions of pre-European grasslands in California. *Madroño* 44 (4): 311–33. http://www.jstor.org/stable/41425222

Hamilton, Jason G., Claus Holzapfel, and Bruce E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121: 518–526. doi: 10.1007/s004420050958

Hamilton, Matthew B. 1994. Ex situ conservation of wild plant species: time to reassess the genetic implications of seed banks. *Conservation Biology* 8(1): 39–49. doi: 10.1046/j.1523-1739.1994.08010039.x

Hancock, Nola, and Rachael Gallagher. 2014. How ready are we to move species threatened from climate change? Insights into the assisted colonization debate from Australia. *Austral Ecology* 39(7): 830–838. doi: 10.1111/aec.12151

Hancock, Nola, and Lesley Hughes. 2012. How far is it to your local? A survey on local provenance use in New South Wales. *Ecological Management & Restoration* 13(3): 259–266. doi: 10.1111/j.1442-8903.2012.00660.x

Handel, Steven N. 1985. The intrusion of clonal growth patterns on plant breeding systems. *The American Naturalist* 125(3): 367–384. doi: 10.1086/284348

Handel, Steven N., George R. Robinson, and Andrew J. Beattie. 1994. Biodiversity resources for restoration ecology. *Restoration Ecology* 2(4): 230–241. doi: 10.1111/j.1526-100X.1994.tb00055.x

Hargrove, William W., and Forrest M. Hoffman. 2004. Potential of multivariate quantitative methods for delineation and visualization of ecoregions. *Environmental Management* 34(1): S39-S60. doi: 10.1007/s00267-003-1084-0

Harpole, W. Stanley, and David Tilman. 2006. Non-neutral patterns of species abundance in grassland communities. *Ecology Letters* 9(1): 15–23. doi: 10.1111/j.1461-0248.2005.00836.x

Harris, James A., Richard J. Hobbs, Eric Higgs, and James Aronson. 2006. Ecological restoration and global climate change. *Restoration Ecology* 14(2): 170–176. doi: 10.1111/j.1526-100X.2006.00136.x

Hartl, Daniel L., and Andrew G. Clark. 1997. *Principles of Population Genetics.* Sinauer Associates, Sunderland, Massachusetts.

Hastey, E. 1996. *Policy on the Use of Native Plant Materials in California: Instruction Memorandum No. CA-97-34*. US Department of the Interior Bureau of Land Management, California State Office, Sacramento, California.

Hatch, Daphne, James.W. Bartolome, and Deborah S. Hillyard. 1991. Testing a management strategy for restoration of California's native grasslands. Pp.343–349 in *Yosemite Centennial symposium proceedings: natural areas and Yosemite, prospects for the future, a global issues symposium joining the 17th annual Natural Areas Conference with the Yosemite Centennial Celebration.* National Park Service, Davis, CA.

Hautekèete, Nina-Coralie, Yves Piquot, and Henk van Dijk. 2002. Life span in *Beta vulgaris* ssp. *maritima*: the effects of age at first reproduction and disturbance. *The Journal of Ecology* 90: 508–516. doi: 10.1046/j.1365-2745.2002.00688

Hawkes, Christine V., Jayne Belnap, Carla D'Antonio, and Mary K. Firestone. 2005. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and Soil* 281(1–2): 369–380. doi: 10.1007/s11104-005-4826-3

Heady, Harold F. 1956. Evaluation and measurement of the California annual type. *Journal of Range Management* 9(1): 25–27. doi: 10.2307/3894646

Heady, Harold F. 1977. Valley grassland. Pp. 491–514 in Barbour, M.G., and J. Major (eds.) *Terrestrial Vegetation of California*. Wiley lnterscience, New York.

Heady, H.F., J.W. Bartolome, M.D. Pitt, and M.C. Stroud. 1992. California prairie. Pp. 313–335 in Coupland, R.T. (ed.) *Natural Grasslands: Introduction and Western Hemisphere, Vol. 8A, Ecosystems of the World*. Elsevier Scientific Publishing Company, New York, New York.

Helenurm, K., and L.S. Parsons. 1997. Genetic variation and the reintroduction of *Cordylanthus maritimus* ssp. *maritimus* to Sweetwater Marsh, California. *Restoration Ecology* 5(3): 236–244. doi: 10.1046/j.1526-100x.1997.09728.x

Hendrix, Stephen D., and E. Joseph Trapp. 1992. Population demography of *Pastinaca sativa* (Apiaceae): effects of seed mass on emergence, survival, and recruitment. *American Journal of Botany* 79(4): 365–375. doi: 10.2307/2445148.

Herget, Mollie E., Kristina M. Hufford, Daniel L. Mummey, and Lauren N. Shreading. 2015. Consequences of seed origin and biological invasion for early establishment in restoration of a North American grass species. *PLoS ONE* 10(3): p.e0119889. doi: 10.1371/journal.pone.0119889

Herget, Mollie E., Kristina M. Hufford, Daniel L. Mummey, Brian A. Mealor, and Lauren N. Shreading. 2015. Effects of competition with *Bromus tectorum* on early establishment of *Poa secunda* accessions: can seed source impact restoration success? *Restoration Ecology* 23(3): 277–283. doi: 10.1111/rec.12177

Heritage Seedlings & Liners, Inc. 2015. Seed prices, native Willamette Valley species (webpage). Accessed at http://www.heritageseedlings.com on 12/2/2015.

Heywood, J.S. 1991. Spatial analysis of genetic variation in plant populations. *Annual Review of Ecology and Systematics* 22(1): 335–355. doi:10.1146/annurev.ecolsys.22.1.335

Hild, Ann L.. 2004. Effectiveness of selected native plants as competitors with non-indigenous and invasive knapweed and thistle species (CS-1389) (fact sheet). United States Department of Defense Strategic Environmental Research and Development Program, Arlington, Virginia. http://www.serdp.org/research

Hilderbrand, Robert, Adam Watts, and April Randle. 2005. The myths of restoration ecology. *Ecology and Society* 10(1): article 19. doi: 10.5751/ES-01277-100119

HilleRisLambers, Janneke, Stephanie G. Yelenik, Benjamin P. Colman, and Jonathan M. Levine. 2010. California annual grass invaders: the drivers or passengers of change? *The Journal of Ecology* 98(5): 1147–1156. doi: 10.1111/j.1365-2745.2010.01706.x

Hobbs, R.J, and D.A. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4(2): 93–110. doi: 10.1111/j.1526-100x.1996.tb00112.x

Hobbs, Richard J., Eric Higgs, and James A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24(11): 599–605. doi: 10.1016/j.tree.2009.05.012

Holeski, Liza M., Georg Jander, and Anurag A. Agrawal. 2012. Transgenerational defense induction and epigenetic inheritance in plants. *Trends in Ecology & Evolution* 27(11): 618–626. doi: 10.1016/j.tree.2012.07.011

Holl, Karen D., and Richard B. Howarth. 2000. Paying for restoration. *Restoration Ecology* 8(3): 260–267. doi: 10.1046/j.1526-100x.2000.80037.x

Holmes, T.H. and K.J. Rice. 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Annals of Botany (London)* 78(2): 233-243. doi: 10.1006/anbo.1996.0117

Holmstrom, Rebecca M., Julie R. Etterson, and David J. Schimpf. 2010. Dune restoration introduces genetically distinct American beachgrass, *Ammophila breviligulata*, into a threatened local population. *Restoration Ecology* 18(s2): 426–437. doi: 10.1111/j.1526-100X.2009.00593.x

Honnay, Olivier, and Hans Jacquemyn. 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology* 21(3): 823–831. 10.1111/j.1523-1739.2006.00646.x

Hopkinson, Peter, and Lynn Huntsinger. 2005. Are East Bay hills grasslands a historical artifact? Phytolith evidence and a potential candidate for the true East Bay vegetation type. *Grasslands* 15(1): 7–9.

Houseal, Greg. 2009. Seed collecting from tallgrass prairies. Prairie Restoration Series #1.Tallgrass Prairie Center, University of Northern Iowa, Cedar Falls. Accessed at https://www.tallgrassprairiecenter.org/publications on 2/4/2016.

Houssard, C., and J. Escarré. 1990. Effects of seed weight on growth and competitive ability of *Rumex acetosella* from two successional old-fields. *Oecologia* 86: 236–242. doi: 10.1007/bf00317536

Howard, Timothy G, and Deborah E. Goldberg. 2001. Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* 82(4): 979–990. doi: 10.1890/0012-9658(2001)082[0979:CRHFGG]2.0.CO;2

Huber, Heidrun, and Heinjo J. During. 2000. No long-term costs of meristem allocation to flowering in stoloniferous *Trifolium* species. *Evolutionary Ecology* 14(8): 731–748. doi:10.1023/a:1011643904616

Hufford, Kristina M., and Susan J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology & Evolution* 18(3): 147–155. doi: 10.1016/S0169-5347(03)00002-8

Hufford, Kristina M., and Susan J. Mazer. 2012. Local adaptation and the effects of grazing on the performance of *Stipa pulchra*: implications for seed sourcing in restoration. *Restoration Ecology* 20(6): 688–695. doi: 10.1111/j.1526-100X.2011.00843.x

Hughes, A. Randall, Brian D. Inouye, Marc TJ Johnson, Nora Underwood, and Mark Vellend. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11(6): 609–623. doi: 10.1111/j.1461-0248.2008.01179.x

Hughes, A. Randall, and John J. Stachowicz. 2011. Seagrass genotypic diversity increases disturbance response via complementarity and dominance. *The Journal of Ecology*, 99(2): 445–453. doi: 10.1111/j.1365-2745.2010.01767.x

Hull, James C., and Cornelius H. Muller. 1977. The potential for dominance by *Stipa pulchra* in a California grassland. *American Midland Naturalist* 97: 146–195. doi: 10.2307/2424692

Humphrey, L. David, and Eugene W. Schupp. 2002. Seedling survival from locally and commercially obtained seeds on two semiarid sites. *Restoration Ecology* 10(1): 88-95. doi: 10.1046/j.1526-100x.2002.10109.x

Huntsinger, Lynn, Mitchel P. McClaran, Ann Dennis, and James W. Bartolome. 1996. Defoliation response and growth of *Nassella pulchra* (A. Hitchc.) Barkworth from serpentine and non-serpentine populations. *Madroño* 43(1): 46–57. Retrieved from http://www.jstor.org/stable/41425116 on 5/9/2017.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52(4): 577-586. doi: 10.2307/1934145

Ishizuka, Wataru, and Susumu Goto. 2012. Modeling intraspecific adaptation of *Abies sachalinensis* to local altitude and responses to global warming, based on a 36-year reciprocal transplant experiment. *Evolutionary Applications* 5(3): 229–244. doi: 10.1111/j.1752-4571.2011.00216.x

Jackson, Louise E. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* 12: 349-361. doi: 10.2307/2844866

Jepson Flora Project (eds.). 2017. Jepson eFlora. Accessed at http://ucjeps.berkeley.edu/eflora on on 4/7/2017.

Ji, Baoming, Stephen P. Bentivenga, and Brenda B. Casper. 2010. Evidence for ecological matching of whole AM fungal communities to the local plant-soil environment. *Ecology* 91(10): 3037–3046. doi: 10.1890/09-1451.1

Johansen-Morris, A.D., and Robert G. Latta. 2006. Fitness consequences of hybridization between ecotypes of *Avena barbata*: hybrid breakdown, hybrid vigor, and transgressive segregation. *Evolution* 60(8): 1585–1595. doi: 10.1554/05-680.1

Johnson, Randy, Frank C. Sorensen, J. Bradley St. Clair, and Richard C. Cronn. 2004. Pacific Northwest forest tree seed zones: a template for native plants? *Native Plants Journal* 5(2): 131–140. doi:10.1353/npj.2005.0009

Johnson, Randy, Larry Stritch, Peggy Olwell, Scott Lambert, Matthew E. Horning, and Richard Cronn. 2010. What are the best seed sources for ecosystem restoration on BLM and USFS lands? *Native Plants Journal* 11(2): 117-131. doi: 10.2979/NPJ.2010.11.2.117

Jolliffe, Peter A. 2000. The replacement series. *The Journal of Ecology* 883: 371–385. doi: 10.1046/j.1365-2745.2000.00470.x

Jones, T.A. 2003. The restoration gene-pool concept: beyond the native versus non-native debate. *Restoration Ecology* 11(3): 281-290. doi: 10.1046/j.1526-100x.2003.00064.x

Jones, Thomas A. 2013. When local isn't best. *Evolutionary Applications* 6(7): 1109–1118. doi: 10.1111/eva.12090

Jones, Thomas A., and Douglas A. Johnson. 1998. Integrating genetic concepts into planning rangeland seedings. *Journal of Range Management* 51(6): 594–606. doi:10.2307/4003599

Jones, Thomas A., and Joseph G. Robins. 2011. Appropriate use of genetic manipulation for the development of restoration plant materials. Pp. 249–264 in Lüttge, Ulrich E., Wolfram Beyschlag, Burkhard Büdel, and Dennis Francis (eds.), *Progress in Botany* 72. Springer Berlin Heidelberg, Germany. doi: 10.1007/978-3-642-13145-5

Jump, Alistair S., and Josep Penuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* 8(9): 1010–1020. doi: 10.1111/j.1461-0248.2005.00796.x

Kaiser, Betsy, Karen Prudhomme, Bill Lydie, Scott Riley, and Vicky Erickson. 2003. Developing and implementing a forest-wide native seed program: ten years of experience on the Umatilla National Forest in the Blue Mountains of eastern Oregon and Washington. In Kaye, T.N., M. Gisler, and R. Fiegener (eds.), *Proceedings of a Conference on Native Plant Restoration and Management on Public Lands in the Pacific Northwest: Rare Plants, Invasive Species and Ecosystem Management.* Co-sponsors: US Department of the Interior Bureau of Land Management, Institute for Applied Ecology, US Department of Agriculture Forest Service, and Native Plant Society of Oregon. Retrieved from http://appliedeco.org/wp-content/uploads/NativePlantProceedings03.pdf on 4/29/2017.

Kang, Mary, Cynthia M. Kanno, Matthew C. Reid, Xin Zhang, Denise L. Mauzerall, Michael A. Celia, Yuheng Chen, and Tullis C. Onstott. 2014. Direct measurements of methane emissions from abandoned oil and gas wells in Pennsylvania. *Proceedings of the National Academy of Sciences* 111(51): 18173-18177. doi: 10.1073/pnas.1408315111

Karban, Richard, and Kaori Shiojiri. 2010. Identity recognition and plant behavior. *Plant Signaling & Behavior* 5(7): 854–855. doi: 10.4161/psb.5.7.11828

Kardol, Paul, and David A. Wardle. 2010. How understanding aboveground–belowground linkages can assist restoration ecology. *Trends in Ecology & Evolution* 25(11), 670–679. doi: 10.1016/j.tree.2010.09.001

Keddy, P., K. Nielsen, E. Weiher, and R. Lawson, 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* 13: 5–16. doi: 10.1111/j.1654-1103.2002.tb02018.x

Kéfi, Sonia, Milena Holmgren, and Marten Scheffer. 2016. When can positive interactions cause alternative stable states in ecosystems? *Functional Ecology* 30(1): 88–97. doi: 10.1111/1365-2435.12601

Keller, M., J. Kollmann, and P.J. Edwards. 2000. Genetic introgression from distant provenances reduces fitness in local weed populations. *Journal of Applied Ecology* 37(4): 647–659. doi: 10.1046/j.1365-2664.2000.00517.x

Kelley, Steven E. 1984. Viral pathogens and the advantage of sex in *Anthoxanthum odoratum*. *Philosophical Transactions of the Royal Society, London* B 346:295–302. doi: 10.1098/rstb.1994.0146

Kelley, Steven E. 1989. Experimental studies of the evolutionary significance of sexual reproduction. V. A field test of the sib-competition lottery hypothesis. *Evolution* 43(5) 1054–1065. doi: 10.1111%2Fj.1558-5646.1989.tb02550.x

Kelley. Steven E., and Keith Clay. 1987. Interspecific competitive interactions and the maintenance of genotypic variation within two perennial grasses. *Evolution* 41(1): 92–103. doi: 10.2307/2408975

Kettenring, Karin M., and Susan M. Galatowitsch. 2011. Seed rain of restored and natural prairie wetlands. *Wetlands* 31(2): 283–294. doi: 10.1007/s13157-011-0159-6

Kettenring, Karin M., Kristin L. Mercer, Carrie Reinhardt Adams, and Jes Hines. 2014. Editor's Choice: Application of genetic diversity–ecosystem function research to ecological restoration. *Journal of Applied Ecology* 51(2): 339–348. doi: 10.1111/1365-2664.12202

Kigathi, Rose N., Wolfgang W. Weisser, Daniel Veit, Jonathan Gershenzon, and Sybille B. Unsicker. 2013. Plants suppress their emission of volatiles when growing with conspecifics. *Journal of Chemical Ecology* 39(4): 537–545. doi: 10.1007/s10886-013-0275-2

Kitzmiller, J.H. 1990. Managing genetic diversity in a tree improvement program. *Forest Ecology and Management* 35: 131-149. doi: 10.1016/0378-1127(90)90237-6

Klopf, Ryan P., and Sara G. Baer. 2011. Root dynamics of cultivar and non-cultivar population sources of two dominant grasses during initial establishment of tallgrass prairie. *Restoration Ecology* 19(1): 112–117. doi: 10.1111/j.1526-100X.2009.00539.x

Knapp, Eric E., and Kevin J. Rice. 1994. Starting from seed: genetic issues in using native grasses for restoration. *Restoration and Management Notes* 12(1): 40–45. doi: 10.3368/er.12.1.40

Knapp, Eric E., and Kevin J. Rice. 1996. Genetic structure and gene flow in *Elymus glaucus* (blue wildrye): implications for native grassland restoration. *Restoration Ecology* 4(1): 1–10. doi: 10.1111/j.1526-100X.1996.tb00101.x

Knapp, Eric E., and Kevin J. Rice. 1997. Ecotypes of native species: how local is local in restoration plantings? In Kelly, Mike, Ellie Wagner, and Peter Warner (eds.), *Proceedings: California Exotic Pest Plant Council Symposium Volume 3: 1997*. California Exotic Pest Plant Council, Berkeley, California.

Knapp, Eric E., and Kevin J. Rice. 1998. Comparisons of isozymes and quantitative traits for evaluating patterns of variation in purple needlegrass (*Nassella pulchra*). *Conservation Biology* 12(5): 1031–1041. doi: 10.1046/j.1523-1739.1998.97123.x

Kölliker, R., F.J. Stadelmann, B. Reidy, and J. Nöeberger. 1998. Fertilization and defoliation frequency affect genetic diversity of *Festuca pratensis* Huds. in permanent grasslands. *Molecular Ecology* 7: 1557–1567. doi: 10.1046/j.1365-294x.1998.00486.x

Kosco, Barbara H., and James W. Bartolome. 1981. Forest grazing: past and future. *Journal of Range Management* 34(3): 248. doi:10.2307/3898057

Kramer, Andrea T., and Kayri Havens. 2009. Plant conservation genetics in a changing world. *Trends in Plant Science* 14(11): 599–607. doi: 10.1016/j.tplants.2009.08.005

Krauss, Siegfried L., Bob Dixon, and Kingsley W. Dixon. 2002. Rapid genetic decline in a translocated population of the endangered plant *Grevillea scapigera*. *Conservation Biology* 16(4): 986–994. doi: 10.1046/j.1523-1739.2002.01105.x

Krauss, Siegfried L., and Tian Hua He. 2006. Rapid genetic identification of local provenance seed collection zones for ecological restoration and biodiversity conservation. *Journal for Nature Conservation* 14(3): 190–199. doi: 10.1016/j.jnc.2006.05.002

Krauss, Siegfried L., Elizabeth A. Sinclair, John D. Bussell, and Richard J. Hobbs. 2013. An ecological genetic delineation of local seed-source provenance for ecological restoration. *Ecology and Evolution* 3(7): 2138–2149. doi: 10.1002/ece3.595

Lambert, Allison M., Sara G. Baer, and David J. Gibson. 2011. Intraspecific variation in ecophysiology of three dominant prairie grasses used in restoration: cultivar versus non-cultivar population sources. *Restoration Ecology* 19(101): 43–52. doi: 10.1111/j.1526-100X.2010.00673.x

Lambert, Scott. 1997. Natural Resources Conservation Service (NRCS) native plants for the Pacific Northwest. *National Proceedings: Forest and Conservation Nursery Associations—1997*: 68–76. Retrieved from https://www.fs.fed.us/pnw/pubs/pnw_gtr419.pdf#page=79 on 4/24/2017.

Lankau, Richard. 2008. A chemical trait creates a genetic trade-off between intra- and interspecific competitive ability. *Ecology* 89(5): 1181–1187. doi: 10.1890/07-1541.1

Lankau, Richard. 2012. Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proceedings of the National Academy of Sciences* 10928:11240–11245. doi: 10.1073/pnas.1201343109

Lankau, Richard. 2013. Species invasion alters local adaptation to soil communities in a native plant. *Ecology* 941: 32–40. doi: 10.1890/12-0675.1

Lankau, Richard A., and Sharon Y. Strauss. 2011. Newly rare or newly common: evolutionary feedbacks through changes in population density and relative species abundance, and their management implications. *Evolutionary Applications* 4: 338–353. doi: 10.1111/j.1752-4571.2010.00173.x

Lara-Romero, Carlos, Raúl García-Camacho, Adrián Escudero, and Jose M. Iriondo. 2014. Genetic variation in flowering phenology and reproductive performance in a Mediterranean high-mountain specialist, *Armeria caespitosa* (Plumbaginaceae). *Botanical Journal of the Linnean Society* 176(3): 384–395. doi: 10.1111/boj.12208

Larios, Loralee, Rebecca J. Aicher, and Katharine N. Suding. 2013. Effect of propagule pressure on recovery of a California grassland after an extreme disturbance. *Journal of Vegetation Science* 24(6): 1043–1052. doi: 10.1111/jvs.12039

Larson, S.R., E. Cartier, C.L. McCracken, and D. Dyer. 2001. Mode of reproduction and amplified fragment length polymorphism variation in purple needlegrass (*Nassella pulchra*): utilization of natural germplasm sources. *Molecular Ecology* 10: 1165–1177. doi: 10.1046/j.1365-294X.2001.01267.x

Latzel, Vít. 2015. Pitfalls in ecological research–transgenerational effects. *Folia Geobotanica* 501: 75–85. doi: 10.1007/s12224-015-9208-x

Laverack, G., S. Matthews, A.A. Powell, and M.K. Hosseini. 2006. Scottish wildflower seeds: production and use. *Botanical Journal of Scotland* 58(1): 49–58. doi: 10.1080/03746600608685106

Lawrence, Beth A., and Thomas N. Kaye. 2011. Reintroduction of *Castilleja levisecta*: effects of ecological similarity, source population genetics, and habitat quality. *Restoration Ecology* 19(2): 166–176. doi: 10.1111/j.1526-100X.2009.00549.x

Leicht-Young, Stacey, Andrew M. Latimer, and John A. Silander. 2011. Lianas escape self-thinning: experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 163–172. doi: 10.1016/j.ppees.2011.04.002

Leimu, Roosa, and Markus Fischer. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3(12): e4010. doi:10.1371/journal.pone.0004010

Lepik, Anu, Maria Abakumova, Kristjan Zobel, and Marina Semchenko. 2012. Kin recognition is density-dependent and uncommon among temperate grassland plants. *Functional Ecology* 26(5): 1214–1220. doi: 10.1111/j.1365-2435.2012.02037.x

Lesica, Peter, and Fred W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? *Restoration Ecology* 7(1): 42–50. doi: 10.1046/j.1526-100X.1999.07105.x

Levin, Donald A., and Harold W. Kerster. 1971. Neighborhood structure in plants under diverse reproductive methods. *The American Naturalist* 105: 345–354. doi: 10.1086/282729

Li, Y.C., T. Fahima, J.H. Peng, M.S. Röder, V.M. Kirzhner, A. Beiles, A.B. Korol, and E. Nevo. 2000. Edaphic microsatellite DNA divergence in wild emmer wheat, *Triticum dicoccoides,* at a microsite: Tabigha, Israel. *Theoretical and Applied Genetics* 101(7): 1029–1038. doi: 10.1007/s001220051577

Li, Yuan-Yuan, Xiao-Yong Chen, Xin Zhang, Tian-Yi Wu, Hui-Ping Lu, and Yue-Wei Cai. 2005. Genetic differences between wild and artificial populations of *Metasequoia glyptostroboides*: implications for species recovery. *Conservation Biology* 19(1): 224–231

Li, Yuan-Yuan, Eric Po Keung Tsang, Min-Yan Cui, and Xiao-Yong Chen. 2012. Too early to call it success: an evaluation of the natural regeneration of the endangered *Metasequoia glyptostroboides*. *Biological Conservation* 150(1): 1–4. doi:10.1016/j.biocon.2012.02.020.

Linhart, Yan B. 1988. Intrapopulation differentiation in annual plants. III. The contrasting effects of intra- and interspecific competition. *Evolution* 42(5): 1047–1064. doi: 10.2307/2408920

Linhart, Yan B. 1991. Disease, parasitism, and herbivory: multidimensional challenges in plant evolution. *Trends in Ecology & Evolution* 6(12): 392–396. doi: 10.1016/0169-5347(91)90160-Y

Linhart, Yan B. 1995. Restoration, revegetation, and the importance of genetic and evolutionary perspectives. In Roundy, Bruce A., E. Durant McArthur, Jennifer S. Haley, and David K. Mann (compilers), *Proceedings of the Wildland Shrub and Arid Land Restoration Symposium*. US Forest Service. Gen. Tech Rep. INT-GTR-315. Ogden, UT.

Linhart, Yan B., and Michael C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27(1): 237–277. doi: 10.1146/annurev.ecolsys.27.1.237

Lippitt, Laurie, Matthew W. Fidelibus, and David A. Bainbridge. 1994. Native seed collection, processing, and storage for revegetation projects in the western United States. *Restoration Ecology* 2(2): 120–131. doi: 10.1111/j.1526-100X.1994.tb00049.x

Liston, Aaron. 2003. Restoration with native lupines: the role of taxonomy and population genetics. In Kaye, T.N., M. Gisler, and R. Fiegener (eds.), *Proceedings of a Conference on Native Plant Restoration and Management on Public Lands in the Pacific Northwest: Rare Plants, Invasive Species and Ecosystem Management.* Co-sponsors: US Department of the Interior Bureau of Land Management, Institute for Applied Ecology, US Department of Agriculture Forest Service, and Native Plant Society of Oregon. Retrieved from http://appliedeco.org/wp-content/uploads/NativePlantProceedings03.pdf on 4/29/2017.

Lively, Curtis M. 2010. The effect of host genetic diversity on disease spread. *The American Naturalist* 175(6): E149-E152. doi: 0.1086/652430

Lloyd, Michael W., Robert K. Burnett Jr., Katharina A.M. Engelhardt, and Maile C. Neel. 2012. Does genetic diversity of restored sites differ from natural sites? A comparison of *Vallisneria americana* (Hydrocharitaceae) populations within the Chesapeake Bay. *Conservation Genetics* 13(3): 753–765. doi:10.1007/s10592-012-0324-3

Longcore, Travis. 2003. Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, U.S.A). *Restoration Ecology* 11(4): 397–409. doi: 10.1046/j.1526-100X.2003.rec0221.x

Longcore, Travis, Rudi Mattoni, Gordon Pratt, and Catherine Rich. 1997. On the perils of ecological restoration: lessons from the El Segundo blue butterfly. J.E. Keeley (coordinator), *2nd Interface Between Ecology and Land Development in California.* Occidental College, CA. Retrieved from http://www.urbanwildlands.org/Resources/perils.pdf on 4/30/2016.

Loveless, Marilyn D., and James L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics* 15(1): 65–95. doi: 10.1146/annurev.es.15.110184.000433

Lovett-Doust, Leslie. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramets in contrasting habitats. *The Journal of Ecology* 69(3): 743–755. doi: 10.2307/2259633

Lowe, J.L. 1994. *Use of Native and NonnativePlants on National Forests and Grasslands* (memorandum to Directors and Forest Service Supervisors in Pacific Northwest Region). US Forest Service Region 6, Portland, Oregon. http://www.fs.fed.us/r6/nr-botany/revegpolicy.htm, accessed June 28, 2005.

MacArthur, Robert H., and Edward O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.

MacCleery, Doug. 2008. Re-Inventing the United States Forest Service: Evolution from custodial management, to production forestry, to ecosystem management. In Durst, Patrick, Chris Brown, Jeremy Broadhead, Regan Suzuki, Robin Leslie and Akiko Inoguchi (eds), *Re-inventing Forestry Agencies: Experiences of Institutional Restructuring in Asia and the Pacific.* Food and Agriculture Organization of the United Nations Regional Office for Asia and the Pacific. Bangkok. Retrieved from http://www.fao.org/docrep/010/ai412e/AI412E06.htm on 1/12/2016.

MacDonald, S. Ellen, and Victor J. Lieffers. 1991. Population variation, outcrossing, and colonization of disturbed areas by *Calamagrostis canadensis*: evidence from allozyme analysis. *American Journal of Botany* 78(8): 1123-1129. doi: 10.2307/2444900

Mack, John J., and Mick Micacchion. 2006. *An ecological assessment of Ohio mitigation banks: vegetation, amphibians, hydrology and soils.* Ohio EPA Technical Report WET/2006-1. Ohio Environmental Protection Agency, Division of Surface Water, Wetland Ecology Group, Columbus, Ohio. Accessed at http://www.epa.state.oh.us/Portals/35/wetlands/Bank_Report_Ohio_Final.pdf on 3/16/2018.

Madsen, Becca, Nathaniel Carroll, Daniel Kandy, and Genevieve Bennett. 2011. *2011 Update: State of Biodiversity Markets*. Forest Trends, Washington. Accessed at http://www.forest-trends.org/documents/files/doc_2848.pdf on 1/22/2018.

Maestre, Fernando T., Ragan M. Callaway, Fernando Valladares, and Christopher J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *The Journal of Ecology* 97: 199–205. doi: 10.1111/j.1365-2745.2008.01476.x

Mahieu, Stéphanie, Souhir Soussou, Jean-Claude Cleyet-Marel, Brigitte Brunel, Lucette Mauré, Claude Lefèbvre, and José Escarré. 2013. Local adaptation of metallicolous and non-metallicolous *Anthyllis vulneraria* populations: their utilization in soil restoration. *Restoration Ecology* 21(5): 551–559. doi: 10.1111/j.1526-100X.2012.00927.x

Majerus, Mark. 2000. Restoration with native indigenous plants in Yellowstone and Glacier National Parks. Pp. 207–215 in *Proceedings of the 2000 Billings Land Reclamation Symposium: Striving for Restoration, Fostering Technology and Policy for Reestablishing Ecological Function*. Retrieved from https://www.osmre.gov/resources/library/proceedings.shtm on 5/10/2017.

Maron, Martine, Richard J. Hobbs, Atte Moilanen, Jeffrey W. Matthews, Kimberly Christie, Toby A. Gardner, David A. Keith, David B. Lindenmayer, and Clive A. McAlpine. 2012. Faustian bargains? Restoration realities in the context of biodiversity offset policies. *Biological Conservation* 155: 141–148. doi: 10.1016/j.biocon.2012.06.003

Martin, Mary M., and James Harding. 1982. Estimates of fitness in *Erodium* populations with intra- and interspecific competition. *Evolution* 36(6): 1290–1298. doi:10.2307/2408161

Maschinski, Joyce, Samuel J. Wright, Suzanne Koptur, and Elena C. Pinto-Torres. 2013. When is local the best paradigm? Breeding history influences conservation reintroduction survival and population trajectories in times of extreme climate events. *Biological Conservation* 159: 277–284. doi: 10.1016/j.biocon.2012.10.022

McArthur, E. Durrant, and Robin J. Tausch. 1995. Genetic aspects of the biodiversity of rangeland plants. *Natural Resources and Environmental Issues 4,* article 3. Available at: https://digitalcommons.usu.edu/nrei/vol4/iss1/3

McCann, Erin. 2014. Restoration genetics and propagule collection in the Golden Gate National Recreation Area. Golden Gate National Parks Conservancy, San Francisco, CA. Accessed 3/6/2018 at http://www.sfnps.org/download_product/4569/0

McIntyre, S., S. Lavorel, J. Landsberg, and T.D.A. Forbes. 1999. Disturbance response in vegetation: towards a global perspective on functional traits. *Journal of Vegetation Science* 10: 621-630. doi: 10.2307/3237077

McKay, John K., Caroline E. Christian, Susan Harrison, and Kevin J. Rice. 2005. "How local is local?"– A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13(3): 432–440. doi: 10.1111/j.1526-100X.2005.00058.x

McKenney, Bruce A., and Joseph M. Kiesecker. 2010. Policy development for biodiversity offsets: a review of offset frameworks. *Environmental Management* 45: 165–176. doi: 10.1007/s00267-009-9396-3

McLachlan, Jason S., Jessica J. Hellmann, and Mark W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21(2): 297–302. doi: 10.1111/j.1523-1739.2007.00676.x

McLeod, Kylie. A., M. Scascitelli, and Mark Vellend. 2012. Detecting small-scale genotype–environment interactions in apomictic dandelion (*Taraxacum officinale*) populations. *Journal of Evolutionary Biology* 25(8): 1667–1675. doi: 10.1111/j.1420-9101.2012.02549.x

McNaughton S.J. 1968. Structure and function in California grasslands. *Ecology* 49(5): 962–972. doi: 10.2307/1936547

Mead, Roger. 1988. *The Design of Experiments: Statistical Principles for Practical Applications.* New York, Cambridge University Press.

Mealor, Brian A., Ann L. Hild, and Nancy L. Shaw. 2004. Native plant community composition and genetic diversity associated with long-term weed invasions. *Western North American Naturalist* 64(4): 503–513. Available at http://www.jstor.org/stable/41717407.

Medrano, Mónica, Carlos M. Herrera, and Pilar Bazaga. 2014. Epigenetic variation predicts regional and local intraspecific functional diversity in a perennial herb. *Molecular Ecology* 23(20): 4926–4938. doi: 10.1111/mec.12911

Mehrhoff, Loyal A., and Roy Turkington. 1990. Microevolution and site-specific outcomes of competition among pasture plants. *The Journal of Ecology* 78: 745–756. doi: 10.2307/2260896

Meissen, Justin C., Susan M. Galatowitsch, and Meredith W. Cornett. 2015. Risks of overharvesting seed from native tallgrass prairies. *Restoration Ecology* 23(6): 882–891. doi: 10.1111/rec.12295

Meyer, S.E., and S.L. Carlson. 2001. Achene mass variation in *Ericameria nauseosus* (Asteraceae) in relation to dispersal ability and seedling fitness. *Functional Ecology* 15(2): 274–281. doi:10.1046/j.1365-2435.2001.00520.x

Mijangos, Jose Luis, Carlo Pacioni, Peter B.S. Spencer, Michael D. Craig. 2015. Contribution of genetics to ecological restoration. *Molecular Ecology* 24(1): 22–37. doi:10.1111/mec.12995

Miles, Scott R., and Charles B. Goudey (eds.). 1997. *Ecological Subregions of California: Sections and Subsections Description (R5-EM-TP-005-NET).* US Forest Service Pacific Southwest Region, San Francisco, California.

Millar, Melissa A., Margaret Byrne, Ian K. Nuberg, and Margaret Sedgley. 2012. High levels of genetic contamination in remnant populations of *Acacia saligna* from a genetically divergent planted stand. *Restoration Ecology* 20(2): 260–267. doi: 10.1111/j.1526-100X.2010.00758.x

Miller, John. 2007 (August 9). Alien invader clings to socks, stokes fires. *Casper Star Tribune*. Retrieved from www.trib.com on 5/20/2016.

Miller, Stephanie A., Amy Bartow, Melanie Gisler, Kimiora Ward, Amy S. Young, and Thomas N. Kaye. 2011. Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. *Restoration Ecology* 19(201) 268-276. doi: 10.1111/j.1526-100X.2010.00702.x

Miller, T.E. 1995. Evolution of *Brassica rapa* L. (Cruciferae) populations in intra- and interspecific competition. *Evolution* 49(6): 1125–1133. doi:10.1111/j.1558-5646.1995.tb04439.x

Miller, V.C. 1972. *Soil Survey of Sonoma County, California*. US Department of Agriculture Forest Service and Soil Conservation Service in cooperation with the University of California Agricultural Experiment Station. US Government Printing Office, Washington, D.C.

Moilanen, Atte, Astrid J.A. Van Teeffelen, Yakov Ben-Haim, and Simon Ferrier. 2009. How much compensation is enough? A framework for incorporating uncertainty and time discounting when calculating offset ratios for impacted habitat. *Restoration Ecology* 17(4): 470–478. doi: 10.1111/j.1526-100X.2008.00382.x

Molinari, Nicole A. and Carla M. D'Antonio. 2014. Structural, compositional and trait differences between native- and non-native-dominated grassland patches. *Functional Ecology* 28(3): 745–754. doi: 10.1111/1365-2435.12206

Monson, R.K., S.D. Smith, J.L. Gehring, W.D. Bowman, and S.R. Szarek. 1992. Physiological differentiation within an *Encelia farinosa* population along a short topographic gradient in the Sonoran desert. *Functional Ecology* 6: 751–759. doi: 10.2307/2389973

Montalvo, Arlee M., and Norman C. Ellstrand. 2000. Transplantation of the subshrub *Lotus scoparius*: Testing the home-site advantage hypothesis. *Conservation Biology* 14(4): 1034–1045. doi: 10.1046/j.1523-1739.2000.99250.x

Montalvo, Arlee M., Susan L. Williams, Kevin J. Rice, Stephen L. Buchmann, Coleen Cory, Steven N. Handel, Gary P. Nabhan, Richard Primack, and Robert H. Robichaux. 1997. Restoration biology: a population biology perspective. *Restoration Ecology* 5(4): 277–290. doi: 10.1046/j.1526-100X.1997.00542.x

Moreno-Mateos, David, Mary E. Power, Francisco A. Comín, and Roxana Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. *PLoS Biology* 101: e1001247. doi:10.1371/journal.pbio.1001247

Morris, Lesley R., and Rebecca J. Rowe. 2014. Historical land use and altered habitats in the Great Basin. *Journal of Mammalogy*, 95(6):1144–1156. doi: 10.1644/13-MAMM-S-169

Mortlock, Warren. 2000. Local seed for revegetation. *Ecological Management & Restoration* 1(2): 93–101. doi: 10.1046/j.1442-8903.2000.00029.x

Muhn, James, and Hanson R. Stuart, H.R. 1988. Opportunity and challenge: The story of BLM. US Department of the Interior Bureau of Land Management, Washington, D.C. Retrieved from http://www.blm.gov/wo/st/en/info/history/features/opportunity_and_challenge.html on 1/15/2016.

Müller, Martina S., Scott R. McWilliams, David Podlesak, Jack R. Donaldson, Helen M. Bothwell, and Richard L. Lindroth. 2006. Tri-trophic effects of plant defenses: chickadees consume caterpillars based on host leaf chemistry. *Oikos* 114(3): 507–517. doi: 10.1111/j.2006.0030-1299.14668.x

Münzbergová, Zuzana, Hana Skálová, and Věra Hadincová. 2009. Genetic diversity affects productivity in early but not late stages of stand development. *Basic and Applied Ecology* 10(5): 411–419. doi: 10.1016/j.baae.2008.10.005

Mustoe, Mark. 2014. Statement before the United States House of Representatives Committee on Appropriations, Subcommittee on Interior, Environment, and Related Agencies Regarding Efficient Native Seed Use by the Bureau of Land Management, April 10, 2014. United States House of Representatives Document Repository, Washington, D.C. Retrieved from http://docs.house.gov on 1/2/2016.

Mutegi, Evans, Amy L. Stottlemyer, Allison A. Snow, and Patricia M. Sweeney. 2014. Genetic structure of remnant populations and cultivars of switchgrass (*Panicum virgatum*) in the context of prairie conservation and restoration. *Restoration Ecology* 22(2): 223–231. doi: 10.1111/rec.12070

Navarrete-Tindall, Nadia and Becky Erickson. 2003. Developing techniques to produce native warm and cool season grasses and forbs in Missouri. *Combined Proceedings, International Plant Propagators' Society* 62: 429–434. IPPC, Seattle, Washington.

Nevill, P. G., S. Tomlinson, C.P. Elliott, E.K. Espeland, K.W. Dixon, and D.J. Merritt. 2016. Seed production areas for the global restoration challenge. *Ecology and Evolution*, 6: 7490–7497. doi:10.1002/ece3.2455

(NOAA) United States Dpepartment of Commerce National Oceanic and Atmospheric Administration National Climatic Data Center. 2014. Climate data for zip code 94720. Accessed at https://www.ncdc.noaa.gov/cdo-web/datasets on 12/12/2014.

(NRCS) United States Department of Agriculture Natural Resources Conservation Service Plant Materials Program. 2007. Plant Releases and Conservation *(brochure)*. Retrieved from https://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/plantmaterials/pmc/areamap/?cid=nrcs143_022368 on 3/18/2016.

(NRCS) Unites States Department of Agriculture Natural Resources Conservation Service 2015. *Outcomes in Conservation: Sage Grouse Initiative*. Retrieved from http://www.sagegrouseinitiative.com on 1/29/2016.

(NRCS) United States Department of Agriculture Natural Resources Conservation Service. Undated a. Conservation plants (website). Accessed at http://www.nrcs.usda.gov/wps/portal/nrcs/main/plantmaterials/technical/cp on 3/19/2016.

(NCRS) United States Department of Agriculture Natural Resources Conservation Service. Undated b. *Plant Materials Project Summary Report*s from the Natural Resources Conservation Service to the National Park Service FY 2013. Retrived from http://www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/copmspu12575.pdf on 3/20/2016.

(NRCS) Unites States Department of Agriculture Natural Resources Conservation Service. Undated c. *Restoring America's Wetlands: A Private Lands Conservation Success Story.* Retrieved from http://www.nrcs.usda.gov on 1/28/2016.

(NRCS) Unites States Department of Agriculture Natural Resources Conservation Service. Undated d. *Working Lands for Wildlife*. Retrieved from http://www.nrcs.usda.gov on 1/28/2016.

Nürnberger, B., and W. Gabriel. 1999. Continued hope for a general explanation of sex. *Journal of Evolutionary Biology* 12(6): 1040–1042. doi: 10.1046/j.1420-9101.1999.00132.x

O'Brien, Eleanor K., and Siegfried L. Krauss. 2010. Testing the home-site advantage in forest trees on disturbed and undisturbed sites. *Restoration Ecology* 18(3): 359-372. doi: 10.1111/j.1526–100X.2008.00453.x

O'Brien, Eleanor K., Richard A. Mazanec, and Siegfried L. Krauss. 2007. Provenance variation of ecologically important traits of forest trees: implications for restoration. *Journal of Applied Ecology* 44(3): 583–593. doi: 10.1111/j.1365-2664.2007.01313.x

Ocean Song Farm and Wilderness Center. 2003. Ocean Song Farm and Wilderness Center (brochure). Accessed at http://oceansong.org on 9/12/2014.

Oduor, Ayub M.O. 2013. Evolutionary responses of native plant species to invasive plants: a review. *New Phytologist* 200(4): 986–992. doi:10.1111/nph.12429

Ohsowski, Brian M., John N. Klironomos, Kari E. Dunfield, and Miranda M. Hart. 2012. The potential of soil amendments for restoring severely disturbed grasslands. *Applied Soil Ecology* 60: 77–83. doi: 10.1016/j.apsoil.2012.02.006

Oldfield, Sara, and Peggy Olwell. 2015. The right seed in the right place at the right time. *BioScience* 65(10): 955–956. doi: 10.1093/biosci/biv127

Olwell, Peggy. 2002. National need for seed. *Greener Roadsides* Winter 2002. U.S. Department of Transportation Federal Highway Administration, Washington D.C.

Olwell, Peggy. 2012. Native Plant Materials Development Program: Twelve years and growing (PowerPoint presentation). Accessed at https://www.fs.fed.us/rmrs on 2/12/2017.

Omernik, James M. 1987. Ecoregions of the Conterminous United States (map). *Annals of the Association of American Geographers* 77(1): map supplement. doi: 10.1111/j.1467-8306.1987.tb00149.x

(OSMRE) United States Department of the Interior Office of Surface Mining Reclamation and Enforcement. 2002. *FY 2002 Annual Performance Plan—FY 2000 Annual Performance Report*. Retrieved from http://www.osmre.gov/resources/budget/docs/PerfPlan02.pdf. on 10/12/2015.

(OSMRE) United States Department of the Interior Office of Surface Mining Reclamation and Enforcement. 2016. Budget justifications and performance information: fiscal year 2016. Retrieved from https://www.doi.gov/sites/doi.gov/files/migrated/budget/appropriations/2016/upload/FY2016_OSMRE_Greenbook.pdf on 1/5/2016.

Owuor, Edward D., Tzion Fahima, Alex Beharav, Abraham Korol, and Eviatar Nevo. 1999. RAPD divergence caused by microsite edaphic selection in wild barley. *Genetica* 105: 177–192. doi: 10.1023/A:1003781711908

Pacala, Stephen W., and Mark Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist* 152(5): 729–737. doi: 10.1086/286203

Pacific Northwest Natives. 2005. Guidelines for establishing natives from seed (fact sheet). Pacific Northwest Natives. Retrieved from http://pnn.dtsonline.us/Plantingguidelines.pdf on 10/20/05.

Palazzo, A. 2004. Identify resilient characteristics and develop wear resistant plant cultivars for use on military training lands (CS-1103) (fact sheet). United States Department of Defense Strategic Environmental Research and Development Program, Arlington, Virginia. http://www.serdp.org/research.

Pan, Jean P., and Jason S. Price. 2002. Fitness and evolution in clonal plants: the impact of clonal growth. *Evolutionary Ecology* 15: 583–600. doi: 10.1023/a:1016065705539

Parker, Sophie S., Eric W. Seabloom, and Joshua P. Schimel. 2012. Grassland community composition drives small-scale spatial patterns in soil properties and processes. *Geoderma* 170: 269–279. doi: 10.1016/j.geoderma.2011.11.018

Pawnee Butte Seeds. 2013. AM 120 mycorrihizal inoculum. Retrieved from http://www.pawneebuttesseed.com/am-120-mycorrihizal-inoculum on 6/3/2016.

Paz, Horacio, and Miguel Martínez-Ramos. 2003. Seed mass and seedling performance within eight species of *Psychotria* (Rubiaceae). *Ecology* 84(2): 439–450. doi: 10.1890/0012-9658(2003)084[0439:smaspw]2.0.co;2

(PCA) Plant Conservation Alliance Federal Committee. 2015. *National Seed Strategy for Rehabilitation and Restoration 2015-2020.* Retrieved from www.blm.gov/seedstrategy on 12/15/2015.

Pélabon, Christophe, Matthew L. Carlson, Thomas F. Hansen, and W. Scott Armbruster. 2005. Effects of crossing distance on offspring fitness and developmental stability in *Dalechampia scandens* (Euphorbiaceae). *American Journal of Botany* 92(5): 842–851. doi:10.3732/ajb.92.5.842

Pelini, Shannon L., Jason D.K. Dzurisin, Kirsten M. Prior, Caroline M. Williams, Travis D. Marsico, Brent J. Sinclair, and Jessica J. Hellmann. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences* 106(27): 11160–11165. doi: 10.1073/pnas.0900284106

Pendleton, Rosemary L., Stanley G. Kitchen, Joann Mudge, and E. Durant McArthur. 2008. Origin of the flax cultivar "Appar"and its position within the *Linum perenne* complex. *International Journal of Plant Science*s 169(3): 445–453. doi: 10.1086/526464

Peppin, Donna L., Peter Z. Fulé, Carolyn Hull Sieg, Jan L. Beyers, and Molly E. Hunter. 2010. Post-wildfire seeding in forests of the west: trends, costs, effectiveness, and use of native seed. Final report to the Joint Fire Sciences Program (JSFP), JFSP, National Interagency Fire Center, Boise, ID, USA. Project ID 08-2-1-11. Retrieved from http://nau.edu/uploadedFiles/Centers-Institutes/ERI/_Forms/Research/JFSP-final-report-PostFireSeedingReview.pdf on 1/22/2016.

Pickup, Melinda, David L. Field, David M. Rowell, and A. G. Young. 2013. Source population characteristics affect heterosis following genetic rescue of fragmented plant populations. *Proceedings of the Royal Society of London B: Biological Science*s, 280(1750), p.20122058–20122058. doi: 10.1098/rspb.2012.2058

Poelman, Erik H., Jeffrey A. Harvey, Joop J.A. van Loon, Louise E.M. Vet, and Marcel Dicke. 2013. Variation in herbivore-induced plant volatiles corresponds with spatial heterogeneity in the level of parasitoid competition and parasitoid exposure to hyperparasitism. *Functional Ecology* 27(5): 1107–1116. doi: 10.1111/1365-2435.12114

Polley, H. Wayne, Justin D. Derner, and Brian J. Wilsey. Patterns of plant species diversity in remnant and restored tallgrass prairies. *Restoration Ecology* 13(3): 480–487. doi:10.1111/j.1526-100x.2005.00060.x

Powell, Elizabeth. 1994. Recovery plan for the Mauna Kea silversword (*Argyroxiphium sandwicense* ssp. *sandwicense*). US Fish and Wildlife Service, Region 1. Retrieved from http://www.fws.gov/ecos/ajax/docs/recovery_plan/930930a.pdf on 5/27/2106.

Prati, Daniel, and Bernhard Schmid. 2000. Genetic differentiation of life-history traits within populations of the clonal plant *Ranunculus reptans*. *Oikos* 90(3): 442–456. doi: 10.1034/j.1600-0706.2000.900303.x

Prentice, Honor C., and Wolfgang Cramer. 1990. The plant community as a niche bioassay: environmental correlates of local variation in *Gypsophila fastigata. The Journal of Ecology* 78: 313–325. doi: 10.2307/2261114

Prettyman, Brett. 2012. DWR begins reseeding early using four times the usual seed. *The Salt Lake Tribune*, October 5, 2012. Retrieved from www.sltrib.com on 5/20/2016.

Procaccini, Gabriele, and Luigi Piazzi. 2001. Genetic polymorphism and transplantation success in the Mediterranean seagrass *Posidonia oceanica*. *Restoration Ecology* 9(3): 332–338. doi: 10.1046/j.1526-100x.2001.009003332.x

Proffitt, C. Edward, Rebecca L. Chiasson, Alaina B. Owens, Keith R. Edwards, and Steven E. Travis. 2005. *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. *The Journal of Ecology* 93: 404–416. doi: 10.1111/j.0022-0477.2005.00983.x

Pywell, Richard F., James M. Bullock, David B. Roy, Liz Warman, Kevin J. Walker, and Peter Rothery. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* 40(1): 65–77. doi: 10.1046/j.1365-2664.2003.00762.x

Recon Native Plants, Inc. 2013. Our unique restoration quality protocol. Retrieved from http://www.reconnativeplants.com/habres.html on 6/3/2016.

Reusch, Thorsten B.H., Anneli Ehlers, August Hámmerli, and Boris Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences* 102(8): 2826–2831. doi:10.1073/pnas.0500008102.

Rey Benayas, José M., Adrian C. Newton, Anita Diaz, and James M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325(5944): 1121–1124. doi: 10.1126/science.1172460

Reynolds, Laura K., Karen J. McGlathery, and Michelle Waycott. 2012. Genetic diversity enhances restoration success by augmenting ecosystem services. *PLoS ONE* 7(6): e38397. doi: 10.1371/journal.pone.0038397

Ricciardi, Anthony, and Daniel Simberloff. 2009. Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution* 24(5): 248–253. doi: 10.1016/j.tree.2008.12.006

Rice, Kevin J. 1995. What is native? Pp. 28–30 in *Proceedings of the Symposium on Sustaining Rangeland Ecosystems.* Oregon State University Press, Corvallis, OR.

Rice, K.J., D.R. Gordon, J.L. Hardison, and J.M. Welker. 1993. Phenotypic variation in seedlings of a "keystone" tree species (*Quercus douglasii*): the interactive effects of acorn source and competitive environment. *Oecologia* 96:537-547. doi:10.1007/bf00320511

Rice, Kevin J., and Eric E. Knapp. 2008. Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. *Restoration Ecology* 16(1): 12–23. doi: 10.1111/j.1526-100X.2007.00257.x

Rice, William R. 2002. Experimental tests of the adaptive significance of sexual recombination. *Nature Reviews Genetics* 3(4): 241–251. doi: 10.1038/nrg760.

Richards, Rebecca T., Jeanne C. Chambers, and Christopher Ross. 1998. Use of native plants on federal lands: policy and practice. *Journal of Range Management* 51(6): 625–632. doi: 10.2307/4003603

Rietkerk, Max, Stefan C. Dekker, Peter C. de Ruiter, and Johan van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305(5692): 1926–1929. doi: 10.1126/science.1101867

Rietkerk, Max, and Johan van de Koppel. 2008. Regular pattern formation in real ecosystems. *Trends in Ecology & Evolution* 23(3): 169–175. doi: 10.1016/j.tree.2007.10.013

Ritchie, Euan G., and Christopher N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12(9): 982–99. doi: 10.1111/j.1461-0248.2009.01347.x

Roach, Deborah Ann. 1986. Life history variation in *Geranium carolinianum*. 1. Covariation between characters at different stages of the life cycle. *The American Naturalist* 128(1): 47–57. doi: 10.1086/284538.

Roach, Deborah A., and Renata D. Wulff. 1987. Maternal effects in plants. *Annual Review of Ecology and Systematics* 18(1): 209–235. doi: 10.1146/annurev.es.18.110187.001233

Robichaud, Peter R., Hakjun Rhee, and Sarah A. Lewis. 2014. A synthesis of post-fire Burned Area Reports from 1972 to 2009 for western US Forest Service lands: trends in wildfire characteristics and post-fire stabilisation treatments and expenditures. *International Journal of Wildland Fire* 23(7): 929–944. doi: 10.1071/WF13192

Robinson, George R., James F. Quinn, and Maureen L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76(3): 786–794. doi: 10.2307/1939344

Rogers, Deborah L. 2004. Genetic erosion no longer just an agricultural issue. *Native Plants Journal* 5(2): 112–122. doi: 10.2979/NPJ.2004.5.2.112

Ronsheim, Margaret L., and James D. Bever. 2000. Genetic variation and evolutionary trade-offs for sexual and asexual reproduction in *Allium vineale* (Liliaceae). *American Journal of Botany* 87(12): 1769–1777. doi: 10.2307/2656827

Rowe, Courtney L.J., and Elizabeth A. Leger. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* big squirreltail in response to cheatgrass invasion. *Evolutionary Applications* 43: 485–498. doi: 10.1111/j.1752-4571.2010.00162.x

Sackville-Hamilton, N. Ruaraidh. 2001. Is local provenance important in habitat creation? A reply. *The Journal of Ecology* 38(6): 1374–1376. doi: 10.1046/j.0021-8901.2001.00670.x

Salazar, Ken. 2009. Addressing the impacts of climate change on America's land, water, and other natural and cultural resources. U.S. Department of the Interior, Washington, D.C. Accessed at https://www.doi.gov/sites/doi.gov/files/migrated/whatwedo/climate/cop15/upload/SecOrder3289.pdf on 1/16/2016.

Schierenbeck, Kristina A., and Norman C. Ellstrand. 2009. Hybridization and the evolution of invasiveness in plants and other organisms. *Biological Invasions* 11(5): 1093–1105. doi: 10.1007/s10530-008-9388-x

Schmid, Bernhard, and John L. Harper. 1985. Clonal growth in grassland perennials: I. Density and pattern-dependent competition between plants with different growth forms. *The Journal of Ecology* 73(3): 793–808. doi: 10.2307/2260147

Schmitt, Thomas. 2007. Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology* 4(1): 1–13. doi: 10.1186/1742-9994-4-11

Schoen, Daniel J., and A.H.D. Brown. 1991. Intraspecific variation in population gene frequency and effective population size correlates with the mating system in plants. *Proceedings of the National Academy of Sciences, USA* 88: 4494–4497. doi: 10.1073/pnas.88.10.4494

Schröder, Roland, Martha D. Graf, Johanna Jochum, Gesa Rode, Janika Schemmel, and Insa Thimm. 2013. Testing the effects of a regionalized seed production on the germination behavior of wild plant species. *Ecological Restoration* 31(3): 295–301. doi: 10.3368/er.31.3.295

Schröder, Roland, and Rüdiger Prasse. 2013a. Cultivation and hybridization alter the germination behavior of native plants used in revegetation and restoration. *Restoration Ecology* 21(6): 793–800. doi: 10.1111/rec.12018

Schröder, Roland, and Rüdiger Prasse. 2013b. Do cultivated varieties of native plants have the ability to outperform their wild relatives? *PLoS ONE* 8(8): e71066. doi: 10.1371/journal.pone.0071066

Schwartz, Mark W., Jason D. Hoeksema, Catherine A. Gehring, Nancy C. Johnson, John N. Klironomos, Lynette K. Abbott, and Anne Pringle. 2006. The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecology Letters* 9(5): 501–515. doi: 10.1111/j.1461-0248.2006.00910.x

Scianna, Joseph D. 2003. Nursery cost-estimating at the NRCS Bridger Plant Materials Center. In: Riley L.E., R.K. Dumroese, and T.D. Landis (technical coordinators), *National Proceedings: Forest and Conservation Nursery Associations—2002.* Ogden, UT: USDA Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-28: 133–13. Retrieved from https://www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/mtpmcsy5004.pdf on 1/21/2016

Seabloom, Eric W., W. Stanley Harpole, and David Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences* 100(23): 13384–13389. doi: 10.1073/pnas.1835728100

Sebade, Brian M., Ann L. Hild, and Brian A. Mealor. 2012. Native grasses collected from invasions demonstrate invasion resistance. *Ecological Restoration* 303: 209–217. doi: 10.3368/er.30.3.209

Seliskar, Denise M., John L. Gallagher, David M. Burdick, and Laurie A. Mutz. 2002. The regulation of ecosystem functions by ecotypic variation in the dominant plant: a *Spartina alternifolia* salt-marsh case study. *The Journal of Ecology* 90(1): 1–11. doi: 10.1046/j.0022-0477.2001.00632.x

Semchenko, Marina, Maria Abakumova, Anu Lepik, and Kristjan Zobel. 2013. Plants are least suppressed by their frequent neighbours: the relationship between competitive ability and spatial aggregation patterns. *The Journal of Ecology* 101(5): 1313–1321. doi: 10.1111/1365-2745.12127

(SER) Society for Ecological Restoration Science & Policy Working Group. 2004. *SER International Primer on Ecological Restoration* (Version 2, October, 2004). Society for Ecological Restoration. Washington, D.C.

Severns, Paul M. 2011. Habitat restoration facilitates an ecological trap for a locally rare, wetland-restricted butterfly. *Insect Conservation and Diversity* 4(3): 184–191. doi: 10.1111/j.1752-4598.2010.00120.x

Severns, Paul M., and Aaron Liston. 2008. Intraspecific chromosome number variation: a neglected threat to the conservation of rare plants. *Conservation Biology* 22(6): 1641–1647. doi: 10.1111/j.1523-1739.2008.01058.x

Sexton, Jason P., Sandra B. Hangartner, and Ary A. Hoffmann. 2014. Genetic isolation by environment or distance: Which pattern of gene flow is most common? *Evolution* 68(1): 1–15. doi: 10.1111/evo.12258

Sgro, Carla M., Andrew J. Lowe, and Ary A. Hoffmann. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications* 4(2): 326–337. doi: 10.1111/j.1752-4571.2010.00157.x

Shaw, Pete. 2014. Life and limb risked for the rarest of seeds. *The Northland Age* October 23, 2014, Kaitaia, Northland, New Zealand. Retrieved from http://www.nzherald.co.nz/northland--age/news/article.cfm?c_id=1503402&objectid=11347023 on 5/27/2016.

Shaw, Ruth G., and Gerrit A.J. Platenkamp. 1993. Quantitative genetics of response to competitors in *Nemophila menziesii*: a greenhouse study. *Evolution* 47(3): 801–812. doi: 10.2307/2410185

Shaw, R.G., G.A.J. Platenkamp, F.H. Shaw, and R.H. Podolsky. 1995. Quantitative genetics of response to competitors in *Nemophila menzieseii*-a field experiment. *Genetics* 139(1): 397–406.

Sheffer, Efrat, Jost Hardenberg, Hezi Yizhaq, Moshe Shachak, and Ehud Meron. 2013. Emerged or imposed: a theory on the role of physical templates and self-organisation for vegetation patchiness. *Ecology Letters* 16(2): 127–139. do: 10.1111/ele.12027

Sheley, Roger L., and Jeremy J. James. 2014. Simultaneous intraspecific facilitation and interspecific competition between native and annual grasses. *Journal of Arid Environments* 104: 80–87. doi: 10.1016/j.jaridenv.2014.01.019

Silvertown, Jonathan W., and Jonathan Lovett Doust. 1993. *Introduction to Plant Population Biology* (third edition) Blackwell Scientific Publications, Oxford.

Simms, Ellen L. 1990. Examining selection on the multivariate phenotype: plant resistance to herbivores. *Evolution* 44(5): 1177–1188. doi: 10.2307/2409281

Smith, Christopher C., and Stephen D. Fretwell. 1974. The optimal balance between size and number of offspring. *The American Naturalist* 108(962): 499–506. doi: 10.1086/282929

Smith, Sierra L., Anna A. Sher, and Thomas A. Grant. Genetic diversity in restoration materials and the impacts of seed collection in Colorado's restoration plant production industry. 2007. *Restoration Ecology* 15(3): 369–374. doi: 10.1111/j.1526–100x.2007.00231.x

Smith, Thomas, and Ann L. Hild. 2011. Effectiveness of selected native plants as competitors with non-indigenous and invasive knapweed and thistle species (ERDC/CERL TR-11-28). US Army Engineer Research and Development Center and Construction Engineering Research Laboratory. Accessed at http://www.dtic.mil/dtic/tr/fulltext/u2/a553671.pdf on 12/12/2016.

Soleri, Daniela, and Steven E. Smith. 1995. Morphological and phenological comparisons of two Hopi maize varieties conserved in situ and ex situ. *Economic Botany* 49(1): 56–77. doi: 10.1007/bf02862278

Solomeshch, A.I., and M.G. Barbour. 2004. Could California grasslands all have been derived from bunchgrass? *(presentation abstract)*. Ecology and Management of California Grasslands Conference, April 2004, University of California, Berkeley.

St. Clair, Brad J., and Randy Johnson. 2004. Structure of genetic variation and implications for the management of seed and planting stock. Pp. 64–71 in Riley, Lee E., R. Kasten Dumroese, Thomas D. Landis (technical coordinators), *National Proceedings: Forest and Conservation Nursery Associations—2003.* June 9–12, 2003, Coeur d'Alene, ID; and July 14–17, 2003, Springfield, IL. Proc. RMRS-P-33. Fort Collins, CO: US Department of Agriculture Forest Service Rocky Mountain Research Station. Retrieved from https://www.fs.fed.us/rm/pubs/rmrs_p033/rmrs_p033_064_071.pdf on 5/10/2017.

Stahl, Peter D., Lachlan J. Ingram, Abbey F. Wick, and Sadikshya Rana. 2006. Relating mineland reclamation to ecosystem restoration. R.I. Barnhisel (ed.), *Billings Land Reclamation Symposium*, June 4–8, 2006, Billings MT. Published jointly by Billings Land Reclamations Symposium and American Society of Mining and Reclamation, Lexington, KY.

Stanton, Maureen L. 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum*): the establishment of a fitness hierarchy. *Oecologia* 67(4): 524–531. doi: 10.1007/bf00790024

Stark, Mike. 2009. Men admit stealing seed pods from Utah nat'l park. KSL Broadcasting, December 16, 2009, Salt Lake City. Retrieved from KSL.com 10/10/2015.

StataCorp. 1999. *Stata Statistical Software: Release 6.0*. Stata Corporation, College Station, Texas.

Stearns, Steven C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3(3): 259-268. doi: 10.2307/2389364

Stebbins, G. Ledyard. 1957. Self fertilization and population variability in the higher plants. *The American Naturalist* 151(861): 337–354. doi: 10.1086/281999

Stevenson, Mark J., Lena K. Ward, and Richard F. Pywell. 1997. Re-creating semi-natural communities: vacuum harvesting and hand collection of seed on calcareous grassland. *Restoration Ecology* 5(1): 66–76. doi: 10.1046/j.1526-100X.1997.09707.x

Stöcklin, Jürg, and Eckart Winkler. Optimum reproduction and dispersal strategies of a clonal plant in a metapopulation: a simulation study with *Hieracium pilosella*. 2004. *Evolutionary Ecology* 18(5–6): 563–584. doi: 10.1007/s10682-004-5144-6

Strategic Marketing Services. 2002. *Summary Report: Iowa Prairie Seed Market Study*. Prepared for The Nature Conservancy of Iowa. University of Northern Iowa, College of Business Administration. Cedar Falls, Iowa.

Stratton, Donald A. 1994. Genotype-by-environment interactions for fitness of *Erigeron annuus* show fine-scale selective heterogeneity. *Evolution* 48(5): 1607–1618. doi: 10.2307/2410251

Strauss, Sharon Y. 2014. Ecological and evolutionary responses in complex communities: implications for invasions and eco-evolutionary feedbacks. *Oikos* 123: 257–266**.** doi: 10.1111/j.1600-0706.2013.01093.x

Streever, W., and E. Perkins. 2000. Importing plant stock for wetland restoration and creation: Maintaining genetic diversity and integrity. *WRAP Technical Notes Collection (ERDC TN-WRAP-00-03)*. US Army Engineer Research and Development Center. Vicksburg, MS.

Stromberg, Mark R. and James R. Griffin. 1996. Long-term patterns in coastal California grasslands in response to cultivation, gophers, and grazing. *Ecological Applications* 6(4): 1189–1211. doi: 10.2307/2269601

Suding, Katharine N. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics* 42(1): 465–87. doi: 10.1146/annurev-ecolsys-102710-145115

Sugiyama, S., and F.A. Bazzaz. 1997. Plasticity of seed output in response to soil nutrients and density in *Abutilon theophrasti* : implications for maintenance of genetic variation. *Oecologia* 112(1): 35–41. doi: 10.1007/s004420050280

Sugiyama, S., and F.A. Bazzaz. 1998. Size dependence of reproductive allocation: the influence of resource availability, competition and genetic identity. *Functional Ecology* 12(2): 280–288. doi: 10.1046/j.1365-2435.1998.00187.x

Sultan, S. E. 1996. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. *Ecology* 77(6): 1791–1807. doi: 10.2307/2265784.

Tallmon, David A., Gordon Luikart, and Robin S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution* 19(9): 489–496. doi: 10.1016/j.tree.2004.07.003

Taylor, Douglas R., and Lonnie W. Aarssen. 1990. Complex competitive relationships among genotypes of three perennial grasses: implications for species coexistence. *American Naturalist* 136(3): 305–327. doi: 10.1086/285100

Thomas, Chris D., Jane K. Hill, Barbara J. Anderson, Sallie Bailey, Colin M. Beale, Richard B. Bradbury, Caroline R. Bulman, Humphrey Q.P. Crick, Felix Eigenbrod, Hannah M. Griffiths, William E. Kunin, Tom H. Oliver, Clive A. Walmsley, Kevin Watts, Nicholas T. Worsfold, and Tim Yardley. 2011. A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution* 2(2): 125–142. doi: 10.1111/j.2041-210X.2010.00065.x

Tilman, David. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75(1): 2–16. doi: 10.2307/1939377

Tilman, David. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78(1): 81–92. doi: 10.1890/0012-96581997078[0081:CIRLAG]2.0.CO;2

Tilman, David. 2004. Niche tradeoffs, neutrality, and community: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* 101(30): 10854–10861. doi: 10.1073/pnas.0403458101

Tilman, David, David Wedin, and Johannes Knops. 1996. Productivity and sustainability influences by biodiversity in grassland ecosystems. *Nature* 379(6567): 718-720. doi: 10.1038/379718a0

Tischew, Sabine, Annett Baasch, Mareike K. Conrad, and Anita Kirmer. 2010. Evaluating restoration success of frequently implemented compensation measures: results and demands for control procedures. *Restoration Ecology* 18(4): 467–480. doi: 10.1111/j.1526-100X.2008.00462.x

Todesco, Marco, Mariana A. Pascual, Gregory L. Owens, Katherine L. Ostevik, Brook T. Moyers, Sariel Hübner, Sylvia M. Heredia, Min A. Hahn, Celine Caseys, Dan G. Bock and Loren H. Rieseberg, 2016. Hybridization and extinction. *Evolutionary Applications* 9(7): 892–908. doi: 10.1111/eva.12367

Turkington, R. 1989. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. V. The coevolution of competitors. *The Journal of Ecology* 77(3): 717–733. doi: 10.2307/2260981

UCLA Statistical Consulting Group. 2011. Accessed at https://stats.idre.ucla.edu on 3/15/2011.

(USACE) United States Army Corps of Engineers. 2002. Regulatory Guidance Letter (No. 02-2) December 24, 2002. Army Corps of Engineers, Washington, DC. Accessed at https://www.epa.gov/cwa-404/2002-mitigation-regulatory-guidance-letter-rgl-02-2 on 5/12/2018.

(USACE) United States Army Corps of Engineers. 2005. Enhancing military training lands with selective breeding of high-quality plants for arid lands (fact sheet). Army Corps of Engineers Cold Regions Research and Engineering Laboratory Environmental Sciences Branch. Hanover, New Hampshire.

(USDA) United States Department of Agriculture Office of Communications. 2015. USDA begins 49th enrollment period for the Conservation Reserve Program (News Release No. 0332.15). Retrieved from http://www.usda.gov on 1/28/2016.

(USFS) United States Department of Agriculture Forest Service, Eastern Region. 2004. Native plant framework. USDA Forest Service Eastern Region - R9. Milwaukee, Wisconsin.

(USFS) United States Department of Agriculture Forest Service. 2006. *Ecosystem Restoration: A Framework for Restoring and Maintaining the National Forests and Grasslands.* Retrieved from http://www.fs.fed.us/restoration/documents/RestFramework_final_010606.pdf on 1/20/2015.

(USFS) United States Department of Agriculture Forest Service. 2008. *Forest Service Manual* Chapter 2070 – Vegetation Ecology. USDA USFS, Washington D.C

(USFS) United States Department of Agriculture Forest Service. 2013. Ecological Restoration Policy: A Notice by the Forest Service. 2013. 78 *Federal Register* 56202 (Sept. 9, 2013). Retrieved from https://federalregister.gov/a/2013-22149 on 1/10/2016.

(USFS) United States Department of Agriculture Forest Service. 2104. *Fiscal Year 2015 Budget Overview.* USDA Forest Service, Washington, D.C. Retrieved from http://www.fs.fed.us on 10/15/2015.

(USFS) Unites States Department of Agriculture Forest Service. 2015a. *Forest Service Manual* Chapter 2020. USDA Forest Service, Washington, D.C. Accessed at https://www.fs.fed.us/im/directives/dughtml/fsm.html on 3/18/2018.

(USFS) United States Department of Agriculture Forest Service. 2015b. *Forest Service Manua*l Chapter 2520 - Watershed Protection and Management, Accessed at https://www.fs.fed.us/cgi-bin/Directives/get_dirs/fsm?2500 on 4/9/2018.

(USFS) United States Department of Agriculture Forest Service. 2016. Ecosystem Restoration Policy: Notice of Final Directive. 81 *Federal Register* 24785, April 27, 2016.

(USGS) United States Geological Survey. 2016. Bailey's Ecoregions of the Conterminous United States. Retrieved from https://www.sciencebase.gov/catalog/item/imap/54244abde4b037b608f9e23d on 1/20/2016.

Vallejo-Marín, Mario, Marcel E. Dorken, and Spencer C.H. Barrett. 2010. The ecological and evolutionary consequences of clonality for plant mating. *Annual Review of Ecology, Evolution, and Systematics* 41(1): 193–213. doi: 10.1146/annurev.ecolsys.110308.120258

Van de Koppel, Johan, Joanna C. Gascoigne, Guy Theraulaz, Max Rietkerk, Wolf M. Mooij, and Peter M.J. Herman. 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. *Science* 322(5902): 739-742. doi: 10.1126/science.1163952

van Kleunen, Mark, Markus Fischer, and Bernhard Schmid. 2002. Experimental life-history evolution: selection on the allocation to sexual reproduction and its plasticity in a clonal plant. *Evolution* 56(11): 2168–2177. doi: 10.1111/j.0014-3820.2002.tb00141.x

Vandegehuchte, Martijn L., Eduardo de la Peña, Peter Breyne, and Dries Bonte. 2012. Non-local genotypes of a resident grass species reduce invertebrate species richness. *Insect Conservation and Diversity* 5(6):453–60. doi: 10.1111/j.1752-4598.2011.00181.x

Vander Mijnsbrugge, Kristine, Armin Bischoff, and Barbara Smith. 2010. A question of origin: where and how to collect seed for ecological restoration. *Basic and Applied Ecology* 11(4): 300–311. doi: 10.1016/j.baae.2009.09.002

Vaughton, Glenda, and Mike Ramsey. 1998. Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). *The Journal of Ecology* 86(4): 563–573. doi: 10.1046/j.1365-2745.1998.00279.x

Vekemans, Xavier, and Olivier J. Hardy. 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology* 13(4): 921–935. doi: 10.1046/j.1365-294X.2004.02076.x

Vellend, Mark. 2006. The consequences of genetic diversity in competitive communities. *Ecology* 87(2): 304–311. doi: 10.1890/05-0173

Vellend, Mark, and Monica A. Geber. 2005. Connections between species diversity and genetic diversity. *Ecology Letters* 8(7): 767–781. doi: 10.1111/j.1461-0248.2005.00775.x

Vellend, Mark, Geneviève Lajoie, Audrey Bourret, Cesc Múrria, Steven W. Kembel, and Dany Garant. 2014. Drawing ecological inferences from coincident patterns of population-and community-level biodiversity. *Molecular Ecology* 23(12): 2890–2901. doi: 10.1111/mec.12756

Verhoeven, Koen J.F, Mirka Macel, Lorne M. Wolfe, and Arjen Biere. 2011. Population admixture, biological invasions and the balance between local adaptation and inbreeding depression. *Proceedings of the Royal Society of London B: Biological Sciences* 278(1702): 2–8. doi: 10.1098/rspb.2010.1272

Vincent, Carol Hardy, Laura A. Hanson, and Jerome P. Bjelopera. 2014. *Federal Land Ownership: Overview and Data*. Report No. R42346, Congressional Research Service, Washington, D.C, Retrieved from https://fas.org on 2/3/2016.

Violle, Cyrille, Helena Castro, Jean Richarte, and Marie-Laure Navas. 2009. Intraspecific seed trait variations and competition: passive or adaptive response? *Functional Ecology* 233: 612–620. doi: 10.1111/j.1365-2435.2009.01539.x

Violle, Cyrille, Brian J. Enquist, Brian J. McGill, Lin Jiang, Cécile H. Albert, Catherine Hulshof, Vincent Jung, and Julie Messier. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27(4): 244–252. doi: 10.1016/j.tree.2011.11.014

Vogelsang, Keith M., and James D. Bever. 2009. Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. *Ecology* 90(2): 399–407. doi: 10.1890/07-2144.1.

Waser, Nikolas M., and Mary V. Price. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* 43(5): 1097–1109. doi: 10.2307/2409589

Waser, Nikolas M., Mary V. Price, and Ruth G. Shaw. 2000. Outbreeding depression varies among cohorts of *Ipomopsis aggregata* planted in nature. *Evolution* 54(2): 485–491. doi: 10.1554/0014-3820(2000)054[0485:ODVACO]2.0.CO;2

Watson, Maxine A. 1984. Developmental constraints: effect on population growth and patterns of resource allocation in a clonal plant. *The American Naturalist* 123(3) 441–426. doi: 10.1086/284212

Weeks Andrew R., Carla M. Sgro, Andrew G. Young, Richard Frankham, Nicki J. Mitchell, Kim A. Miller, Margaret Byrne, David J. Coates, Mark D. B. Eldridge, Paul Sunnucks, Martin F. Breed, Elizabeth A. James, and Ary A. Hoffmann. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications* 4(6): 709–725. doi: 10.1111/j.1752-4571.2011.00192.x

Weerman, E.J., J. Van Belzen, M. Rietkerk, S. Temmerman, S. Kéfi, P.M.J. Herman, and J. Van de Koppel. 2012. Changes in diatom patch-size distribution and degradation in a spatially self-organized intertidal mudflat ecosystem. *Ecology* 93(3): 608–618. doi: 10.1890/11-0625.1

Weiher, Evan, Adrie van der Werf, Ken Thompson, Michael Roderick, Eric Garnier, and Ove Eriksson. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10(5): 609-620. doi: 10.2307/3237076

Weinbaum, Barbara S., Michael F. Allen, and Edith B. Allen. 1996. Survival of arbuscular mycorrhizal fungi following reciprocal transplanting across the Great Basin, USA. *Ecological Applications*: 6(4): 1365–1372. doi: 10.2307/2269614

Weiner, J., S. Martinez, H. Müller-Schärer, P. Stoll, and B. Schmid. 1997. How important are environmental maternal effects in plants? A study with *Centaurea maculosa*. *The Journal of Ecology* 85(2): 133–142. doi: 10.2307/2960645.

Weis, Arthur E., Heidi G. Hollenbach, and Warren G. Abrahamson. 1987. Genetic and maternal effects on seedling characters of *Solidago altissima* (Compositae). *American Journal of Botany* 74(10): 1476–1486. doi: 10.2307/2444042

Welch, L.E. 1977. *Soil Survey of Contra Costa County, California*. US Department of Agriculture Soil Conservation Service in cooperation with the University of California Agricultural Experiment Station. U.S. Government Printing Office, Washington, D.C.

West, S.A., C.M. Lively, and A.F. Read. 1999. A pluralist approach to sex and recombination. *Journal of Evolutionary Biology* 12(6): 1003–1012. doi: 10.1046/j.1420–9101.1999.00119.x

Western Regional Climate Center. Accessed at http://www.wrcc.dri.edu on 3/2/2015.

Whalley, R.D.B., Ian H. Chivers, and Cathy M. Waters. 2013. Revegetation with Australian native grasses–a reassessment of the importance of using local provenances. *The Rangeland Journal* 35(2): 155–166. doi: 10.1071/RJ12078

White, Abbey, Andrea Kramer, and Jeremie Fant. 2017. Restoring species diversity: uncovering gaps in the United States native seed market. Paper presented at the National Native Seed Conference, 13–16 February 2017, Washington D.C. Retrieved from www.nativeseed.info/presentation/NativeSeed2017-White-GapsUSNativeSeedMarket.pdf on 5/2/2017.

White, Keith L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation, California. *Ecology* 48(6): 949–955. doi: 10.2307/1934539

Whitham, Thomas G., Joseph K. Bailey, Jennifer A. Schweitzer, Stephen M. Shuster, Randy K. Bangert, Carri J. LeRoy, Eric V. Lonsdorf, Gery J. Allan, Stephen P. DiFazio, Brad M. Potts, Dylan G. Fischer, Catherine A. Gehring, Richard L. Lindroth, Jane C. Marks, Stephen C. Hart, Gina M. Wimp, and Stuart C. Wooley. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* 7(7): 510–523. doi: 10.1038/nrg1877

Whitham, Thomas G., William P. Young, Gregory D. Martinsen, Catherine A. Gehring, Jennifer A. Schweitzer, Stephen M. Shuster, Gina M. Wimp, Dylan G. Fischer, Joseph K. Bailey, Richard L. Lindroth, Scott Woolbright, and Cheryl R. Kuske. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84(3): 559–573. doi: 10.1890/0012-9658(2003)084[0559:CAEGAC]2.0.CO;2

Whitlock, Raj. Relationships between adaptive and neutral genetic diversity and ecological structure and functioning: a meta-analysis. 2014. *The Journal of Ecology* 102(4): 857–872. doi: 10.1111/1365-2745.12240

Whittle, C.A., S.P. Otto, Mark Owen Johnston, and J.E. Krochko. 2009. Adaptive epigenetic memory of ancestral temperature regime in *Arabidopsis thaliana. Botany* 87(6): 650–657. doi: 10.1139/B09-030

Williams, Charles F. 1994. Genetic consequences of seed dispersal in three sympatric forest herbs. II. Microspatial genetic structure within populations. *Evolution* 48(6): 1959–1972. doi: 10.2307/2410520

Williams, Gerald W. 2005. *The USDA Forest Service— The First Century.* United States Department of Agriculture Forest Service, Washington, DC. Retrieved from http://www.foresthistory.org/ASPNET/Publications/first_century/ on 12/20/2015.

Williams, Susan L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11(5): 1472–1488. doi: 10.1890/1051-0761(2001)011[1472:RGDIET]2.0.CO;2

Williams, Susan. L., and Christopher A. Davis. 1996. Population genetic analyses of transplanted eelgrass (*Zostera marina*) beds reveal reduced genetic diversity in Southern California. *Restoration Ecology* 4(2): 163–180. doi:10.1111/j.1526-100X.1996.tb00117.x

Winkler, E., and M. Fischer. 1999. Two fitness measures for clonal plants and the importance of spatial aspects. *Plant Ecology* 141(1–2): 191–199. doi: 10.1023/a:1009843619713

Winslow, Susan R. 2002a. Propagation protocol for production of Propagules (seeds, cuttings, poles, etc.): *Elymus glaucus* seeds. USDA NRCS - Bridger Plant Materials Center Bridger, Montana. Accessed at http://NativePlantNetwork.org on 3/11/2018. US Department of Agriculture Forest Service, National Center for Reforestation, Nurseries, and Genetic Resources.[30]

Winslow, Susan R. 2002b. Propagation protocol for production of Propagules (seeds, cuttings, poles, etc.): *Elymus glaucus* seeds. USDA NRCS - Bridger Plant Materials Center Bridger, Montana. Accessed at http://NativePlantNetwork.org on 3/11/2018. US Department of Agriculture Forest Service, National Center for Reforestation, Nurseries, and Genetic Resources.[30]

Wise, Carla A., Tom A. Ranker, and Yan B. Linhart. 2002. Modeling problems in conservation genetics with *Brassica rapa*: genetic variation and fitness in plants under mild, stable conditions. *Conservation Biology* 16(6): 1542–1554. doi: 10.1046/j.1523-1739.2002.00309.x

Wolf, Jason B., and Michael J. Wade. 2009. What are maternal effects and what are they not? *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364(1520): 1107-1115. doi: 10.1098/rstb.2008.0238

Wolfe, Lorne M. 1995. The genetics and ecology of seed size variation in a biennial plant, *Hydrophyllum appendiculatum* (Hydrophyllaceae). *Oecologia* 101(3): 343–352. doi: 10.1007/bf00328821.

Wright, Sewall. 1943. Isolation by distance. *Genetics* 28(2): 114–138. Accessed at http://www.genetics.org/content/genetics/28/2/114.full.pdf on 3/17/2018.

---

[30] There are two differing propagation protocols with identical citation information; figures provided in the text of this dissertation reflect both protocols.

(WWETAC) United States Department of the Interior Forest Service Western Wildland Environmental Threat Assessment Center. Undated. Retrieved from http://www.fs.fed.us/wwetac/threat_map/SeedZones_Intro.html on 1/21/2016.

Young, Stanford A., Barry Schrumpf, and Eugene Amberson. 2003. *The AOSCA Native Plant Connection.* Association of Official Seed Certifying Agencies, Meridian, Idaho. Retrieved from http://aosca.org on 2/2/2016.

Yu, Douglas W., and Howard B. Wilson. 2001. The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *The American Naturalist* 158(1): 49–63. doi: 10.1086/320865

Zedler, Joy B., and John C. Callaway. 1999. Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology* 7(1): 69–73. doi: 10.1046/j.1526-100X.1999.07108.x