

AN ABSTRACT OF THE DISSERTATION OF

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Title: Seed and Seedling Ecology of *Artemisia tridentata* in a Restoration Context

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The semi-arid sagebrush steppe ecosystem is one of the largest biomes in North America. The steppe provides critical habitat and forage for wildlife and is economically important to recreation and livestock industries. However, the ecosystem is threatened primarily due to several negative effects associated with expansion of the exotic annual grass *Bromus tectorum* (cheatgrass). Because of these changes rehabilitation of the habitat is extremely difficult and energy intensive. Restoration of one of the foundation species, *Artemisia tridentata* (big sagebrush), is a function of seed availability, seed germination, seedling establishment and mature plant survival. Many studies have addressed various aspects of *A. tridentata* seed germination and mature plant ecophysiology, but gaps in our knowledge include seed bank dynamics and biotic interactions that may hinder seedling survival.

The prevalence of large fires in *B. tectorum*-invaded habitat limits availability of dispersed seeds in the interior of burned areas, leaving pre-existing viable seeds in the soil seed bank as the primary natural seed source. I investigated seed longevity of two *A. tridentata* subspecies over a 2-year period by retrieving seed bags that were placed at varying depths and sampling soil and litter fractions of the existing seed

bank across six locations in the Great Basin. *Artemisia tridentata* ssp. *wyomingensis* and *A. t.* ssp. *vaseyana* exhibited patterns of a steadily decreasing abundance of viable seeds on the surface and beneath litter, with 100% loss of surface seed viability in 24 months. However, 29-36% (*A. t.* ssp. *wyomingensis*) and 30-40% (*A. t.* ssp. *vaseyana*) of buried seeds remained viable throughout the duration of the experiment. Abundance of naturally occurring seeds varied considerably among locations and between years across the Great Basin for both subspecies. Loss of viable seeds from the existing seed bank between post-dispersal and pre-dispersal the following season was higher in magnitude for *A. t.* ssp. *wyomingensis* soil fractions compared to litter fractions, and higher overall than for *A. t.* ssp. *vaseyana*.

Access to resources is critical during early spring when resources are plentiful, and this access affects the probability of survival through the summer drought period. *Artemisia tridentata* resource acquisition may be adversely affected during this time via root interaction mechanisms that are not mediated through resources (interference competition). I examined whether and how root interactions affected growth of *A. t.* ssp. *wyomingensis* by forcing its roots to interact with roots of conspecifics, *B. tectorum*, *Elymus wawawaiensis* (Snake River wheatgrass), and *Agropyron xhybrid* (cultivar 'Hycrest'). Activated carbon was used to counteract any potentially negative effects of root exudates. *Artemisia tridentata* above- and belowground biomass was not affected when grown with *E. wawawaiensis* or *A. xhybrid* compared to control seedlings, but root growth rate and branching density decreased when grown with *B. tectorum* (root growth: $p < 0.01$; branching density: $p = 0.07$). These effects did not occur in potting media amended with activated carbon but may have been the result of unintentional fertilization. Roots of *A. tridentata* seedlings changed direction or stopped growing altogether more often when grown into roots of conspecific seedlings than when contacting roots of other species ($p = 0.08$). The odds of this occurring decreased when seedlings were grown in activated carbon-amended potting medium. These results suggest that *A. tridentata* may have a chemical signaling mechanism to avoid roots of conspecifics.

I also assessed whether root and shoot competition (resource-mediated or exploitative competition) of the three grass species affected *A. t. ssp. wyomingensis* seedling growth and survival, and whether root and shoot competition interacted to affect growth. Size-asymmetric competition takes place when a resource is preempted by a larger individual over a smaller individual, and the larger individual receives a disproportionately larger share of the resource for its relative size. Following wildfires, *B. tectorum* cover can increase significantly more than that of other species, potentially promoting asymmetric aboveground competition between it and *A. tridentata* seedlings. Root and shoot competition from *B. tectorum* lowered *A. tridentata* biomass dramatically compared to that of control seedlings, with shoot competition alone decreasing growth by over 80%. Only full competition from *E. wawawaiensis* tended to decrease *A. tridentata* growth compared to control seedlings, while *A. xhybrid* had no significant effect at all seedling growth. *Bromus tectorum* had an average of 92% cover and may explain why shoot competition from this species had such a substantial effect, whereas cover of *E. wawawaiensis* and *A. xhybrid* was 71% and 43%, respectively. Root and shoot competition did not interact for any of the grasses, indicating that there was no mechanism for positive or negative feedbacks between one form of competition and the other. Competition from shoots is likely not severe enough for asymmetric light competition to occur.

The first study provides land managers with a bet-hedging application while the others offer insight into why the seedling life history stage, already vulnerable, has become more so with *B. tectorum* invasion. Reseeding techniques promoting burial of some *A. tridentata* seeds in the soil seed bank may increase restoration success by hedging against the potential for failure of establishment in the initial year of seeding. Selective thinning or removal of potential competitors may be required to benefit resource status of *A. tridentata* seedlings before the summer drought period commences. This is especially important in areas that are dominated by *B. tectorum* as competition from the annual reduces *A. tridentata* root growth substantially and may impact its ability to take up soil resources.

Seed and Seedling Ecology of *Artemisia tridentata* in a Restoration Context

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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**SEED AND SEEDLING ECOLOGY OF *ARTEMISIA TRIDENTATA* IN A
RESTORATION CONTEXT**

CHAPTER 1

General Introduction

The semi-arid sagebrush steppe ecosystem of western North America provides habitat and forage for wildlife, prevents erosion, and is economically important to both recreation and livestock industries (Sands et al. 1999, Knick et al. 2003, Maher 2007, Evans and Rollins 2008, Miller et al. 2011). Historically, over 60 million ha were dominated by shrub-steppe communities (Miller and Eddleman 2001, Knick et al. 2003). However, land-use changes such as livestock grazing, agriculture, mineral extraction, energy development and urban expansion, as well as climate change and exotic species invasion, makes the sagebrush steppe one of the most endangered ecosystems in the United States (Noss et al. 1995, West 2000, McArthur and Goodrich 2004).

Artemisia tridentata Nutt. (big sagebrush) is the foundation shrub and namesake of the sagebrush steppe ecosystem. Pioneers in the 19th century described the ecosystem as visually dominated by shrubs (Vale 1975) where one finds “below, and on all sides, the omni-present sage” (Bailey 1869). The ecosystem is dominated more or less equally by sagebrush and perennial caespitose grasses under semi-arid conditions characterized by cold and wet winters (West 1983). Common bunchgrasses include *Poa secunda* J. Presl (Sandberg bluegrass), *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail), *Festuca idahoensis* Elmer (Idaho fescue), and *Achnatherum thurberianum* (Piper) Barkworth (Thurber’s needlegrass). Approximately 20 woody *Artemisia* taxa are present in North America, three of which comprise the main subspecies of *A. tridentata* (McArthur 2000). The three are *A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush), *A. tridentata* Nutt. ssp. *tridentata* (basin big sagebrush), and *A. tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) with annual precipitation levels for each subspecies in the Intermountain area ranging from 20–30 cm, 32–36 cm, and above 30 cm, respectively (Goodrich et al. 1999).

Artemisia tridentata is a relatively long-lived shrub, often living 70–100 yr or more (McArthur and Stevens 2004), flowering in late summer to early autumn with 1-

seeded achenes ripening in autumn (Meyer 2008). An individual can produce hundreds of thousands of seeds a year (Goodwin 1956) though many factors such as insects (McArthur and Stevens 2004), pathogen attack (Welch and Nelson 1995), heavy browsing (Wagstaff and Welch 1991), and intraspecific competition and rainfall (Young et al. 1989) can restrict seed production in the wild. The species utilizes a ruderal-like strategy as its primary means of seedling recruitment in that seedlings likely recruit into vegetation gaps created by disturbances or wildfires. The species is highly dependent on the amount and timing of precipitation for germination and seedling establishment, which results in pulse recruitment into the population (Maier et al. 2001, Perryman et al. 2001).

Within the last century, considerable changes to ecosystem properties have occurred, primarily due to livestock grazing and invasion by the exotic annual grass *Bromus tectorum* L. (cheatgrass). Livestock selectively graze on bunchgrasses, causing a shift towards a shrub-dominated system which then may be invaded by *B. tectorum*. *Bromus tectorum* was introduced to western North America around 1890 and by the late 1920s had essentially reached its present distribution (Mack 1981). Currently, *B. tectorum* dominates 20,000 km² or 7% of the Great Basin (Bradley and Mustard 2005) and 50% of the range has a moderate to high probability of its dominance in the herbaceous understory (Suring et al. 2005). The exotic grass germinates anytime from autumn to spring, given adequate moisture. Plants that germinate in fall and winter are larger and more productive (Stewart and Hull 1949, Mack and Pyke 1984), which allows *B. tectorum* to exploit soil resources or ‘cheat’ before native grasses begin actively growing (Melgoza et al. 1990). *Bromus tectorum* produces highly flammable litter (Link et al. 2006) that accumulates on the soil surface and provides a continuous source of fuel (Brooks and Pyke 2001, Ziska et al. 2005), promoting wildfires that are more frequent and widespread than fires in native communities (Whisenant 1990, Johnson et al. 1999). This creates a positive feedback in which invasion is followed by an altered fire regime and replacement of native vegetation by near monocultures of *B. tectorum* (D'Antonio and Vitousek 1992).

Additionally, *B. tectorum* invasion has changed nutrient cycling (Evans et al. 2001, Norton et al. 2004), hydrologic function (Ryel et al. 2010), and carbon source/sink dynamics (Prater et al. 2006) in sagebrush steppe communities resulting in substantial ecological and economic losses (Vitousek et al. 1996).

Fire is a natural disturbance in sagebrush ecosystems, and historically the majority of fires in this ecosystem were probably patchy and locally less frequent than under the current regime because surface fuels were relatively limited and discontinuous (Bond and van Wilgen 1996). Fire return intervals in the Intermountain West were generally on the order of decades (Whisenant 1990, Miller and Rose 1999, Miller and Tausch 2001, Miller et al. 2011) prior to *B. tectorum* invasion. Presently, fires fueled by monotypic *B. tectorum* stands can burn tens of thousands of hectares of sagebrush steppe habitat annually and can return every few years (Whisenant 1990, Johnson et al. 1999). A direct result of more frequent, devastatingly large fires is that management agencies have had to actively attempt to restore the sagebrush steppe ecosystem by reseeding or revegetating an area because propagules of desirable native species, such as *A. tridentata*, are poorly represented or absent (Pyke 2011).

Reestablishment of *A. tridentata* is a function of seed availability, seed germination, seedling establishment and mature plant survival. Many studies have addressed aspects of *A. tridentata* seed production and germination (Young and Evans 1989, Young et al. 1989, Meyer et al. 1990, Meyer and Monsen 1992), and adult plants have been used as a model arid lands species in ecophysiological studies for decades (Richards and Caldwell 1987, Caldwell and Richards 1989, Bilbrough and Caldwell 1997, Leffler et al. 2004, Leffler and Caldwell 2005). Gaps in our knowledge of *A. tridentata* reestablishment include seed bank dynamics and biotic interactions that may hinder seedling survival. The studies presented here attempt to address these gaps by examining *A. tridentata* seed persistence in soil seed banks, investigating whether and how interspecific interactions influence seedling root development, and studying whether and how root and shoot competition with commonly found Great Basin grasses affect *A. tridentata* seedling growth.

Changes in historical fire patterns may affect establishment of big sagebrush seedlings because most *A. tridentata* subspecies reproduce solely by seed (Daubenmire 1975, Meyer 2008). Regeneration of *A. tridentata* is generally not limited by seed production or germination (Daubenmire 1975, Harniss and McDonough 1976, Meyer and Monsen 1992); it largely depends on local seed availability and seedling survival. Fires in areas dominated by *B. tectorum* are more frequent and often less complex (i.e., more homogenous) than fires historically, and this phenomenon may interfere with local availability of seeds. Because seeds are dispersed over short distances (Goodwin 1956, Johnson and Payne 1968, Daubenmire 1975), the historic patchiness of fire both spatially and temporally was probably important for successful re-colonization of burned areas by dispersed seeds of *A. tridentata* individuals on the burn perimeter or in unburned areas. The current prevalence of large uniform fires in *B. tectorum*-invaded habitat limits availability of dispersed seeds in the interior of burned areas, leaving viable seeds in soil as the primary natural source for re-establishment. In Chapter 2, I investigated whether *A. tridentata* seeds are able to survive for more than one year in a soil seed bank. The ability to do so could provide a hedge against unfavorable germination or establishment conditions (Gutterman 1994, Holmgren et al. 2006) and also a refuge from lethal temperatures created by passing fires. Knowledge of seed longevity is a critical element in decision processes regarding restoration (Brooks and Pyke 2001, Pyke et al. 2010).

Once seeds are germinated, *A. tridentata* seedling requirements for water are immediate because they lack stored reserves in their minute seeds (Jones 1991) and must begin photosynthesizing. Biotic root interactions may have a negative effect on resource acquisition by seedlings, particularly in resource poor ecosystems. Root interactions are much more complex than previously thought (Callaway 2002, Schenk 2006) and root growth can be inhibited by both resource-mediated and nonresource-mediated (e.g., allelopathy) competition from neighbor species. In Chapter 3, I examined whether and how *A. t. ssp. wyomingensis* root growth and overall

performance were affected by interactions with roots of *B. tectorum*, *Elymus wawawaiensis* (Snake River wheatgrass), and *Agropyron xhybrid* ('Hycrest' cultivar).

Invasion by *B. tectorum* into the sagebrush steppe is successful, in part, because it germinates in fall and winter when native species are largely dormant (Stewart and Hull 1949, Mack and Pyke 1983) and can preempt resources when they become available in spring. Resource competition occurs simultaneously aboveground (e.g., light) and belowground (e.g., water, nutrients) and the two forms of competition can interact to either intensify or assuage effects of the other (Cahill 2002, Song et al. 2006). *Bromus tectorum* cover can increase significantly more than does that of other species after fires (West and Hassan 1985, Jessop and Anderson 2007, Shinneman and Baker 2009), and individuals may compete with *A. tridentata* seedlings more intensively aboveground than native perennial grasses. Shoot competition from *B. tectorum* may act asymmetrically on *A. tridentata* growth and interact with root competition to compound the effects of total competition over time. In Chapter 4, I explored whether and how root and shoot competition from of *B. tectorum*, *E. wawawaiensis*, and *A. xhybrid* affected *A. t. ssp. wyomingensis*. I also asked whether the combined effects of root and shoot competition magnified total competition or if one form alleviated the effects of the other.

Establishment of *A. tridentata* is one of the most difficult hurdles land managers have to overcome to achieve a fully functioning sagebrush steppe ecosystem. These studies provide information about seed source and biotic interactions at the vulnerable seedling stage that may help restoration efforts. Restoring native ecosystems and controlling exotic species invasions is a costly endeavor (Pimentel et al. 2005); therefore, it is in our best interests to be as fully informed as possible about the biotic and abiotic factors that constrain establishment of one of the foundation species.

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CHAPTER 2

Burial increases seed longevity of two *Artemisia tridentata* (Asteraceae) subspecies

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Abstract

Seed longevity and persistence in soil seed banks may be especially important for population persistence in ecosystems where opportunities for seedling establishment and disturbance are unpredictable. Fire regime, an important driver of population dynamics in sagebrush steppe ecosystems, has been altered by exotic annual grass invasion. Soil seed banks may play an active role in post-fire recovery of the foundation shrub *Artemisia tridentata*, yet conditions under which seeds persist are largely unknown.

We investigated seed longevity of two *A. tridentata* subspecies *in situ* by retrieving seed bags that were placed at varying depths over a 2-year period. We also sampled naturally dispersed seeds in litter and soil immediately after seed dispersal and before flowering in subsequent seasons to estimate seed persistence.

After 24 months, seeds buried at least 3 cm below the soil surface retained 30-40% viability whereas viability of seeds on the surface and under litter declined to 0 and < 11%, respectively. The density of naturally dispersed seeds in the seed bank was highly heterogeneous both spatially and temporally, and attrition significantly varied by region.

Our study suggests that *A. tridentata* has the ability to form a viable soil seed bank that persists longer than has been commonly assumed, and that burial is necessary for seed longevity. Use of seeding techniques that promote burial of some seeds to aid in formation of a soil seed bank may increase restoration potential.

Keywords: *Artemisia tridentata*; nondeep physiological dormancy; restoration; soil seed bank; seed longevity; seed persistence; seed burial

Introduction

Seed longevity and persistence in soil seed banks can compensate for effects of unfavorable environmental conditions on seedling germination over the long-term (Guterman 1994, Holmgren et al. 2006) and increase odds that viable seeds are available when conditions are optimal for recruitment. Seed banks may be especially important for population persistence in ecosystems where opportunities for seedling establishment and disturbance are unpredictable (Baskin and Baskin 2001, Fenner and Thompson 2005). Primary seed dormancy, the dormancy state of a freshly mature seed (Crocker 1916, Baskin and Baskin 2001), was widely assumed to be the only mechanism for a persistent seed bank, but recent studies have shown that there is little correlation between seed dormancy and seed bank persistence (Thompson et al. 2003, Honda 2008). If suitable conditions are not present to cue germination when primary dormancy is broken, secondary dormancy may be induced (Bouwmeester and Karssen 1992, Vleeshouwers et al. 1995, Baskin and Baskin 2001), wherein seeds must experience proper cues for breaking dormancy again before they can respond to a germination cue. Viable seeds can persist in soil seed banks as a result of many interacting factors including dormancy state, germination cues or lack thereof, seed size, predation, and burial (Thompson et al. 1993, Hulme 1998, Hulme and Borelli 1999, Ooi et al. 2007, Honda 2008).

Artemisia tridentata Nutt. (big sagebrush) is an ecologically and economically important foundation shrub (Sands et al. 1999, Knick et al. 2003, Maher 2007, Evans and Rollins 2008, Miller et al. 2011) of one of the largest biomes in North America. Seeds of *A. tridentata* display characteristics of nondeep physiological dormancy (Baskin and Baskin 2001) that can be broken by relatively short periods of cold stratification (Meyer and Monsen 1991, 1992), and also can require light to varying degrees for germination (Meyer et al. 1990). It has been assumed that seeds will either germinate or perish within a growing a season and that seed banks are transient not persistent (Thompson and Grime 1979). There is some evidence to suggest *A.*

tridentata can form seed banks but reports of its significance and magnitude disagree. On one hand, very little viable seed has been found in soil samples less than a year after natural seed dispersal (Hassan and West 1986, Young and Evans 1989) or broadcast-seeding (Chambers 2000). On the other hand, repeated establishment of seedling cohorts for years following a one-time seed application (Schuman et al. 1998) and a large fire (Ziegenhagen and Miller 2009) suggest the possibility of seed bank persistence for multiple years.

Historically, the sagebrush steppe ecosystem comprised over 63 million hectares of the Great Basin (Miller and Eddleman 2001, Knick et al. 2003). The ecosystem is threatened (Noss et al. 1995, West 2000), due largely to several negative ecosystem effects (D'Antonio and Vitousek 1992, Norton et al. 2004, Norton et al. 2007) associated with *Bromus tectorum* (cheatgrass) dominance of approximately 20 million hectares (Bradley and Mustard 2005). Prior to *B. tectorum* invasion, fires were more complex (Bond and van Wilgen 1996) and had return intervals on the order of decades to centuries (Whisenant 1990, Miller and Rose 1999, Miller and Tausch 2001). *Bromus tectorum* invasion has reduced fire return intervals to less than a decade, lengthened fire seasons and promoted more extensive burns (Whisenant 1990, Johnson et al. 1999, Brooks and Pyke 2001, Miller et al. 2011). The drastic change in the fire regime has brought about an alternative stable state (Westoby et al. 1989), making restoration of native vegetation and their community dynamics extremely difficult.

Expansion of invasive annual grasses has altered historic fire regimes to the point where a viable soil seed bank may play a larger role in population persistence of *A. tridentata*. In ecosystems where fire is a regular occurrence, plants species that are killed by fire depend on regeneration from seed after fires (Lavorel and Garnier 2002, Pyke et al. 2010). Seeds may come from soil seed banks or from adult plants that persist after spatially complex fires (Ooi et al. 2006). Obligate-seeders are adapted to fire intervals that exceed their juvenile periods (Lamont et al. 1991), else subsequent fires would eliminate post-fire seedling cohorts before they were able to contribute to

the population as reproducing adults. An increase in fire frequency or decrease in fire complexity may make obligate-seeders vulnerable to local extinction as seed banks deplete over time and no adult plants remain to re-populate areas (Bradstock et al. 1998, Pausas 2001). Local regeneration of *A. tridentata* is limited by seed availability rather than seed production or germination (Daubenmire 1975, Harniss and McDonough 1976, Meyer and Monsen 1992). As an obligate-seeder (Meyer 2008), spatial and temporal patchiness of fires are important attributes for successful re-colonization of burned areas by locally dispersed *A. tridentata* seeds. The prevalence of large fires in *B. tectorum*-invaded habitat limits availability of seeds dispersed into the interior of burned areas, leaving seeds in soil seed banks as the primary natural source for re-establishment immediately following fires.

Mechanisms by which *A. tridentata* seeds may persist in a soil seed bank are not well understood, but a possibility for formation of a seed bank may be seed burial. To our knowledge, there have been no direct field experiments or observations to confirm that only buried *A. tridentata* seeds persist in soil seed banks and no verification whether seeds can remain viable in the field beyond one year. Our main objectives were to determine whether *A. tridentata* seeds can form a soil seed bank and, if so, whether seeds persist for longer than one year. We asked three questions to achieve our objectives:

1. *Can seeds remain viable in soil for more than one year?*
2. *Does seed longevity depend on a seed's depth in the seed bank?*
3. *Does seed longevity change with environmental conditions?*

Materials and Methods

Study areas

Artemisia tridentata is composed of three main subspecies: *A. tridentata* subsp. *tridentata* Nutt. (basin big sagebrush), *A. tridentata* subsp. *wyomingensis* Beetle and Young (Wyoming big sagebrush), and *A. tridentata* subsp. *vaseyana*

(Rydb.) Beetle (mountain big sagebrush). We focused our investigation of seed longevity on two subspecies, *A. tridentata* subsp. *wyomingensis* (hereafter *A. t.* subsp. *wyomingensis*) and *A. tridentata* subsp. *vaseyana* (hereafter *A. t.* subsp. *vaseyana*), by using both a seed retrieval experiment and seed bank sampling of field sites throughout the Great Basin for two years.

In August 2006, we selected six study locations in Oregon, Idaho, Utah and Nevada (Table 2.1). Locations are representative of sagebrush communities and were chosen to capture variability across the Great Basin, with more mesic areas to the north and more arid to the south (West 1983). At each location, we established one study site in an *A. t.* subsp. *wyomingensis* community, found in low- to mid-elevations in valleys and foothills on shallow soils, and one in an *A. t.* subsp. *vaseyana* community which typically occurs in higher elevations on cooler, wetter sites with deeper soils (Mahalovich and McArthur 2004). The two communities ranged from 10–27 km apart at each location. Sites were chosen based on visual estimation of co-dominance by *A. tridentata* and native caespitose grasses, and low cover of *B. tectorum*. Prominent grasses included *Poa secunda* J. Presl (Sandberg bluegrass), *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), and *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail).

Each study site encompassed an area measuring 35 m x 40 m and was established at least 20 m from the nearest road. Data on elevation, slope, aspect, and latitude/longitude were recorded; slope, aspect, and latitude were used in calculating potential direct incident radiation (PDIR) (McCune 2007). Long-term average annual precipitation estimates for each site were obtained with the PRISM Data Explorer (Parameter-elevation Regressions on Independent Slopes Model, PRISM Climate Group, Oregon State University, <http://www.prismclimate.org> [accessed 31 Oct 2009]).

Seed burial experiment

We evaluated seed longevity of each subspecies separately as this was not a reciprocal experiment. We placed seeds of a subspecies in their community and assessed their viability in a randomized complete block design with a two-way factorial treatment structure. Factors were seed depth with three levels (buried 3 cm below soil surface, at the soil surface beneath 2 cm of sagebrush leaf litter, and above soil and litter) and collection time with four levels (late spring after normal germination during the first season – April 2007; autumn around the time of seed dispersal and one year after placement – November 2007; after germination during the second field season – April 2008; and autumn at seed dispersal at the end of 2 years – November 2008). Each treatment combination was replicated 8 times for a total of 96 experimental units in each plot.

To keep the experiment manageable, we purchased source-identified seeds of both subspecies that had been collected by a certified commercial supplier (Granite Seed Co., Lehi, Utah) in autumn 2005. Although this did not allow comparisons of genetic differences among populations, it allowed for comparisons among sites because all seeds of a subspecies came from a single population. Seeds were actually 1-seeded achenes (hereafter referred to as seeds), approximately 1-2 mm long and enclosed in a papery pericarp. Seed collections of this species often include plant material such as small twigs, leaves and chaff in addition to seeds. Seeds lots were cleaned (separation of seed and non-seed material) using a series of sieves and blowers. The pericarp can be removed during the seed cleaning process (Booth et al. 1997) but this has minor effects on seed germinability (Bai et al. 1999). Because *A. tridentata* seeds are small, we used seed bags to ensure that seeds could be retrieved. Seed bags were 5 x 5 cm and constructed from fine mesh (<0.5 mm aperture), white polyester. We took measurements of light in- and outside bags on a bright, sunny day with a quantum sensor (Apogee Instruments, Inc., Logan, Utah) and determined that the mesh allowed 85% ambient light penetration. We placed 100 seeds of a single subspecies in each bag using an automated seed-counter (± 0.52 seeds *A. t.* subsp.

wyomingensis and ± 0.90 seeds *A. t.* subsp. *vaseyana*) after cleaning seed lots to about 95% seed by weight. A set of eight replicates was randomly selected during seed bag construction as a pre-treatment control to determine initial viability of seeds placed in the experiment. Fresh seeds and seed bags were stored at 4°C at all times for the few months before they were deployed in the field.

In late November 2006, we located 96 *A. tridentata* shrubs (three depths x four collection times x eight replicates) with a minimum canopy size of 0.25 m² in each plot. Each bag was randomly assigned to one of twelve treatment combinations and placed beneath a shrub 10 cm towards the main trunk from the outer canopy edge and directly beneath an inflorescence. After seed bags were retrieved from the field, they were stored at 4°C for up to one month until seeds could be examined and placed into categories: (1) germination *in situ* – having evidence of either green cotyledons or a white radicle protruding from the seed (achene), (2) intact and possibly viable, and (3) not intact and/or obviously decomposing. Viability of intact seeds was tested by a tetrazolium (TZ) test using standard Association of Official Seed Analysts techniques and conducted by the Utah Department of Agriculture (State Seed Laboratory, Salt Lake City, Utah).

Seed bank sampling

We sampled the seed bank to determine whether seeds persisted from one season to the next. We took 48 soil cores under big sagebrush shrubs (one core per shrub) within each of the 12 study plots. Samples were approximately 5 cm in diameter and 3 cm deep. We sampled twice during the growing season for two seasons (2006–07 and 2007–08), once immediately after seed dispersal (November) and again 9 mo later (August) before the next season's flower production. Soil cores were divided into litter and soil fractions. Litter fractions were mixed with ~300 g of sterile sand to increase water-holding ability of samples. Water was then added to both fractions, bringing them to field capacity, and cold-stratified in a dark cooler for 3–4 months at 4 °C. Because we quantified seed bank density by counting emerging

seedlings, it was important to break primary dormancy in these seeds. Additionally, storing seeds in a cooler prevented them from decaying between collecting and growing out samples. After stratification, samples were spread in small trays and placed in an unheated greenhouse in Corvallis, Oregon during spring (February–April 2007 and 2008) and monitored for big sagebrush seedling emergence. Day temperatures ranged from 20.8–41.3 °C and night temperatures ranged from -2.2–5.4 °C. Samples received ambient light and were kept continuously moist until emergence of new seedlings stopped. We then mixed the soil to bring any potential ungerminated seeds to the surface and continued to water samples until emergence of new seedlings stopped once again. Germinated seeds were counted and discarded every few days.

Bag effect experiment

To account for potential effects of seed bags on seed viability or germinability, we reproduced field burial treatments with and without seed bags in an experiment conducted in a greenhouse. Topsoil and litter from an area adjacent to each field plot were collected in June, 2008, and bulked separately by subspecies. We sieved soil to remove large debris and rocks and homogenize across sites, then mixed it with sterile sand in a 1:1 ratio to use as potting media. All seeds (seed bags containing 100 seed each and sets of 100 free seeds) were subjected to a 21-day, cold stratification (4 °C) in darkness before being placed in treatment pots. We were primarily interested in whether seed bags prevented germination and subsequently bias results towards an overestimation of persistent seeds; therefore, we followed the minimum requirements to break dormancy in this species as defined by an International Seed Testing Association accredited laboratory (Sabry Elias, Oregon State University Seed Laboratory, personal communication). Seed bags and free seeds were placed in 5 x 5-cm pots, either 3 cm below the soil surface, on the soil surface under litter, or above 2 cm of litter. Control pots were filled with soil and topped with litter but contained no added seeds to control for seeds naturally present in field-collected soil. Treatments were replicated 6 times and pots placed in an unheated greenhouse in Corvallis,

Oregon and monitored for germination. Day temperatures ranged from 24.0–44.1°C and night temperatures from 4.6–13.9°C. Newly germinated seeds were counted and discarded. After 1 mo, we extracted seeds from the soil medium of control and bagless treatment pots using a modification of the method by Malone (1967). Soil was first passed through sieves (2 mm, 1 mm, 425 µm opening) to obtain the seed-containing soil fraction. The fraction was mixed with a high-density 1 M sugar solution and centrifuged for 10 min at 2600 rpm. Seeds were manually sorted from the small amount of organic matter that floated to the top of the supernatant. Intact seeds from all treatments were sent to the Utah Department of Agriculture (State Seed Laboratory, Salt Lake City, Utah) to test for viability.

Statistical analysis

Data were analyzed separately by subspecies using SAS 9.13 statistical software (SAS Institute Inc., Cary, NC). Seed bag burial data was modeled using logistic regression with site, seed depth and collection time as fixed effects. Viability of surface seeds dropped rapidly to zero across almost all sites after 6 mo for both subspecies; therefore, we analyzed only buried and litter treatments to better accommodate assumptions of a logistic regression (Andy Olstad, Oregon State University Statistical Consulting Laboratory, personal communication). We modeled seed bank data (number of germinable seeds) and bag effect data (number of viable seeds) with Poisson regression. Seed bank data was analyzed separately by year and fraction (litter or soil), due to sparseness of data for the second year of sampling and because litter and soil fractions per sample were not spatially independent of one another. Site and collection time were used as fixed effects. Analysis of bag effect data was performed similarly with bag and seed depth as fixed effects. The control treatment of bag effect data was not included in the analysis since no naturally occurring seeds were found in soil of either subspecies. Bonferroni adjustments for posthoc multiple comparisons were applied where appropriate for all analyses.

Results

Bag effect experiment

We found a higher proportion of viable seeds in bags compared to free in soil for surface treatments (*A. t. subsp. wyomingensis*: $P < 0.001$; *A. t. subsp. vaseyana*: $P = 0.08$; Fig. 2.1). Bags did not have an effect on viability of buried seeds.

Seed burial experiment

Seeds had an initial average viability of 91.6% (± 1.4 standard error) for *A. t. subsp. wyomingensis* and 81.1% (± 2.6 standard error) for *A. t. subsp. vaseyana*. No germination *in situ* occurred during the first spring and subsequent sampling revealed slightly more germination within burial treatments for both subspecies (Table 2.2). Seed viability at all depths dropped rapidly within the first 6 mo for both subspecies (Fig. 2.2 and 2.3). The rate at which *A. t. subsp. wyomingensis* seeds lost viability depended on depth of seeds in the seed bank ($F_{1,301} = 22.59$, $P < 0.001$) and varied marginally among sites ($F_{5,301} = 2.04$, $P = 0.07$). For *A. t. subsp. vaseyana* the change in seed viability over time depended on both seed depth and site ($F_{5,282} = 2.69$, $P < 0.02$). Viability of seeds on the surface and under litter continued to decrease for the duration of the study but 29-36% and 30-40% (95% confidence interval) of buried *A. t. subsp. wyomingensis* and *A. t. subsp. vaseyana* seeds, respectively, remained viable over the 24 mo period. We observed a drop in viability at 12 months across most regions (Fig. 2.2 and 2.3) and believe this to be an artifact of TZ testing. Tests may be conducted by different technicians at different time points and the test can be subjective. However, TZ tests conducted within a time point was likely performed by the same technician.

Seed bank sampling

Number of viable seeds in the seed bank was highly variable among and within sites (Fig. 2.4) for the first year of sampling. The change in seed density over time depended on site for *A. t. subsp. wyomingensis* (litter: $F_{5,564} = 2.16$, $P = 0.06$; soil: $F_{5,564} = 12.20$, $P < 0.001$) and varied across sites for *A. t. subsp. vaseyana* (litter: $F_{5,564}$

= 28.71, $P < 0.001$; soil: $F_{5,564} = 63.26$, $P < 0.001$). There was more seed bank attrition in *A. t.* subsp. *wyomingensis* soil samples than litter samples, and more attrition overall compared to *A. t.* subsp. *vaseyana*. Sampling in the second season revealed a considerably smaller seed bank than was observed in the first season. In November 2007 we found no viable seeds for *A. t.* subsp. *wyomingensis* in litter or soil samples and only three out of 576 samples, from three different sites (western Idaho - MHWY, eastern Idaho - LLWY, and eastern Nevada - HUWY), yielded any viable seeds in August 2008. Litter samples from only one *A. t.* subsp. *vaseyana* site (eastern Oregon - JUVA) had viable seeds in November 2007; however, in August 2008 just before seed dispersal, we found an average of 11-53 viable seeds/m² for *A. t.* subsp. *vaseyana* in litter and soil samples from three regions (eastern Idaho - LLVA, northern Utah - SAVA, and eastern Nevada - HUVA).

Discussion

Ours is the first study to experimentally document that *A. tridentata* can form a seed bank and that seed longevity is greatly enhanced by burial of seeds in the soil. This is in contrast to previous assertions that *A. tridentata* seeds do not stay viable for more than a season (Hassan and West 1986, Young and Evans 1989, Chambers 2000). The proportion of viable buried seeds was fairly constant for both subspecies throughout the 2-year study period. Seeds on the surface and under litter steadily decreased in viability over time but varied by site as to how quickly this happened. We also observed low densities of viable seeds in litter and soil fractions of both subspecies 9 mo after *in situ* seed dispersal, persisting longer than previous studies had indicated.

Seed bank persistence is affected by many things, both biotic and abiotic environmental factors and traits inherent to the seed itself. Burial of seeds can ameliorate environmental effects and increase longevity of seeds that might otherwise be lost to death or germination (Hulme and Borelli 1999, Facelli et al. 2005). For example, diurnal temperature fluctuations become increasingly dampened by soil

depth (Pierson and Wight 1991). This can increase seed longevity since temperature is one of the factors that impacts the rate at which seeds age (Walters 1998). Crist and Friese (1993) determined that decomposition and attack by fungi were responsible for the greatest decrease in seed viability among shrub-steppe species during winter, with the greatest decrease occurring in *A. tridentata*. We determined that more than 75% of all surface and litter samples showed signs of fungal infection whereas less than 50% of buried seeds were infected. We found a higher proportion of moldy seeds in *A. t.* subsp. *vaseyana* samples than *A. t.* subsp. *wyomingensis* samples after winter, and seed bank sampling consistently yielded more viable seeds of *A. t.* subsp. *vaseyana* in the soil fraction than in the litter fraction. Seeds collected from cold winter sites are nearly 100% light-requiring for germination, perhaps as an adaption to prevent seeds from germinating under snow (Meyer et al. 1990). Seeds of both subspecies used in our experiment were collected from areas with cold winters; therefore most of these seeds likely needed a light cue for germination. Because we did not test for germinability of intact seeds we cannot say for certain whether they were dormant or merely lacking a germination cue. Buried seeds of the two subspecies in our study experienced two winter seasons where soil temperatures 3 cm below the surface can range from 0 to 10 °C even in autumn (Evans and Young 1972). This may have been cold enough to break primary dormancy (Meyer et al. 1990, Meyer and Monsen 1991).

Seed bags used in our study likely affected the microenvironment of seeds. These bags reduced ambient light by about 15% and may have inhibited seed germination, and thus increased the proportion of viable seeds in surface and litter treatments. However, buried seeds were unaffected by this design artifact and may represent the potential maximum viability of seeds buried beneath the soil surface. There is also the possibility that these mesh bags maintained a higher level of moisture and potentially increased the risk of fungal infection through unnaturally high seed densities (Van Mourik et al. 2005) which would result in a conservative estimate of seed persistence. Alternatively, seed bags could inhibit macroinvertebrates in the soil and litter from preying on or damaging seeds, resulting in overestimation of seed

persistence. Though we did not add soil to seed bags when they were deployed, we did observe that buried bags contained soil that was of uniform particle size upon retrieval. This may have provided a similar microenvironment and thus veiled potential heterogeneity in seed persistence within and across regions. Much like safe sites for seed germination, the microenvironment likely plays a role in the patchiness of a persistent soil seed bank.

Estimates of germinable seeds in the seed bank for the 2006–07 growing season varied among and within both subspecies, and there was high interannual variation in our two years of sampling the seed bank. Many factors may impact *A. tridentata* seed production including browsing (Wagstaff and Welch 1991), disease (Welch and Nelson 1995), and dry years (Young et al. 1989). Abortion of seeds and fruits is a strategy that plants may adopt to compensate for resource limitation (Pyke 1989). This may explain why there were lower densities of seeds in the seed bank during the second year as compared to the first year. Precipitation during the 2006-07 growing season was roughly 73% and 76% (*A. t.* subsp. *wyomingensis* and *A. t.* subsp. *vaseyana*) of the long term average for those sites (1971-2000 Normals, climate data from PRISM Climate Group, Oregon State University), and may have affected seed production in the second year of the study. We found much higher seed densities in autumn 2006, which had been influenced by annual precipitation that was slightly higher than long term averages. Differences in biotic and abiotic characteristics between sites likely account for differences in seed bank density and attrition. For example, both litter and soil fractions of *A. t.* subsp. *wyomingensis* in western Idaho (MHWY) lost a significant number of viable seeds between sampling periods during the first season. Among *A. t.* subsp. *wyomingensis* communities, this site has the highest average annual precipitation and could have resulted in a higher incidence of fungal infection. However, because seed longevity is affected by many interacting factors it is difficult to identify specific characteristics of our study sites that may have influenced seed bank attrition.

We determined density of viable seeds in the seed bank by germinating *A. tridentata* seeds from soil and litter cores instead of extracting seeds physically because the latter method was very labor intensive given our large number of samples. However, the germination method may underestimate seed persistence because dormant seeds or seeds that do not receive a germination cue will remain undetected in samples (Thompson et al. 2003). Furthermore, less than 25% of samples at all sites yielded germinable seeds despite taking samples directly beneath the inflorescence of an *A. tridentata* shrub. Young and Evans (1989) determined that the dispersal pattern of *A. tridentata* seeds in their study area was skewed to the east due to prevailing winds from the west. We did not take dispersal direction into account when taking seed bank samples. Buried seeds can be extremely patchy and the number of samples needed for density estimation increases as patchiness increases (Fenner and Thompson 2005). Our *A. t.* subsp. *wyomingensis* estimates were an order of magnitude higher than estimates by Hassan and West (1986) though they took pains to extract all seeds from their samples prior to testing for viability. Our estimates were an order of magnitude lower than estimates by Young and Evans (1989) who determined seed persistence in the same manner we did. No viable seeds were found in the soil by 6 mo after dispersal by either study. Future studies of the seed bank in this species may warrant sampling using a more stratified random approach in addition to increasing the number of samples taken. Density estimates of viable seeds presented here and in previous studies using similar sampling techniques may not give an accurate picture of seed bank persistence in this species because of the high clumping observed within and across regions in our study.

Naturally occurring soil disturbances could enhance seed bank persistence by incorporating a portion of seeds into the soil and potentially bringing seeds to the surface in subsequent years. Disturbances such as frost-heaving or burrowing by subterranean mammals could displace seeds from the surface to beneath the soil surface. Livestock grazing during or immediately after seed dispersal in the late-autumn or early-winter may also enhance seed burial through hoof action turning or

depressing soils (Winkel et al. 1991) and has been shown to increase *A. t.* subsp. *wyomingensis* seedling emergence under certain conditions (Eckert et al. 1986, Winkel and Roundy 1991), potentially by turning up previously buried seeds. Young et al. (1990) found that texture of soil surfaces can change from autumn to spring through a winnowing action of wind. They suggest that *A. tridentata* seeds are affected by wind in the same manner as sand-sized particles of granitic soils and may become buried. The same processes that promote burial of *A. tridentata* seeds may operate to bring seeds to the surface.

Restoration efforts of sagebrush steppe often involve aerial seeding, which would leave many seeds on the surface and can result in poor shrub establishment (Dalzell 2004). After seeds were broadcast onto the surface of a mulch layer, seedling emergence of *A. tridentata* through four post-seeding growing seasons (Booth 2002) indicates that some portion of the seeds may have worked into the soil over time. Providing a soil surface disturbance or mulch that aids in seed burial may increase restoration success. Restoration methods that ensure seed contact with soil such as pressing seeds into the soil surface (Pyke 1994), creating microdepressions in the soil (Haferkamp et al. 1987), and harrowing or raking (Turner et al. 2006) can greatly increase seedling establishment. An unintended consequence of some of these methods may be burial of a small percentage of seed, which had long been thought to be undesirable. Our results suggest that there may be a middle ground between surface exposure and deep burial that maximizes restoration potential. We argue that techniques to help *A. tridentata* seeds remain viable in the soil as a hedge against unfavorable germination or establishment conditions may be one of the keys to long-term restoration success, and additionally may also spare seeds from incineration during wildfires (Lattera et al. 2006). Mixing high densities of *A. tridentata* seeds into seed drills for intentional burial, combined with broadcasting seeds onto the surface, may provide a seed source for several years and, in the long-term, be more economically feasible than reseeding annually. However, if the mechanism for a

persistent buried seed bank is lack of a light cue, then this tactic may work only with cold-adapted populations that are particularly dependent on light cues for germination.

In conclusion, our results indicate that dynamics of seed viability over time are similar in these two subspecies of *A. tridentata* and depend on depth of seeds in the seed bank. After the initial loss of seeds, most probably due to germination of physiologically non-dormant fraction, both subspecies exhibited patterns of a steadily decreasing abundance of viable seeds on the surface and beneath litter. However, 30-40% of buried seeds remained viable across all sites for at least 24 mo. Our study suggests that reseeded techniques that promote burial of some seeds in the soil seed bank may increase restoration success.

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Table 2.1 Location and environmental characteristics of study sites.

<i>Artemisia tridentata</i> subsp. and plot location	Plot code	UTM			Precip ¹ (cm)	Aspect (°)	Elevation (m)	Slope (%)	PDIR ²	ARTR cover ³ (%)
		Zone	Easting	Northing						
<i>wyomingensis</i>										
E. Oregon	JUWY	11	415270	4843486	27.5	83	1072	11.9	0.77	17
W. Idaho	MHWY	11	592788	4801890	37.5	175	1096	4.6	0.84	25
E. Idaho	LLWY	12	273518	4789807	30.2	62	1451	2.3	0.79	13
N. Utah	SAWY	12	319756	4651825	30.5	269	1651	2.9	0.82	21
W. Utah	TOWY	12	374946	4451101	32.5	102	1903	3.4	0.84	32
E. Nevada	HUWY	11	735855	4329506	33.2	351	2034	5.7	0.78	34
<i>vaseyana</i>										
E. Oregon	JUVA	11	406674	4870576	32.2	150	1277	9.7	0.86	18
W. Idaho	MHVA	11	602396	4799358	50.5	108	1317	2.9	0.80	16
E. Idaho	LLVA	12	286703	4813701	40.6	77	1806	2.9	0.79	67
N. Utah	SAVA	12	307686	4647142	45.2	51	1919	4.6	0.79	33
W. Utah	TOVA	12	366248	4441482	42.9	352	1916	11.9	0.70	19
E. Nevada	HUVA	11	727196	4324108	40.2	231	2274	6.3	0.87	31

¹Long-term annual precipitation averages (PRISM Normals 1971-2000 800m Normals, Parameter-elevation Regressions on Independent Slopes Model, PRISM Climate Group, Oregon State University, <http://www.prismclimate.org> [accessed 31 Oct 2009])

²Potential direct incident radiation ($\text{MJ}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) (McCune 2007)

³*Artemisia tridentata* cover

Table 2.2 Mean proportion of seed germination in situ ($\% \pm 1$ standard error) by subspecies and seed depth.

<i>Artemisia</i> <i>tridentata</i> subsp. and seed depth	Collection ($\% \pm 1$ SE)			
	Spring 2007	Autumn 2007	Spring 2008	Autumn 2008
<i>wyomingensis</i>				
Burial	0 (0)	2.24 (0.75)	0.95 (0.47)	0.89 (0.37)
Litter	0 (0)	2.08 (0.75)	0.08 (0.06)	0 (0)
Surface	0 (0)	0.11 (0.05)	0 (0)	0 (0)
<i>vaseyana</i>				
Burial	0 (0)	0.63 (0.18)	0.19 (0.08)	0.26 (0.14)
Litter	0 (0)	0.09 (0.06)	0.09 (0.07)	0 (0)
Surface	0 (0)	0.03 (0.03)	0 (0)	0 (0)

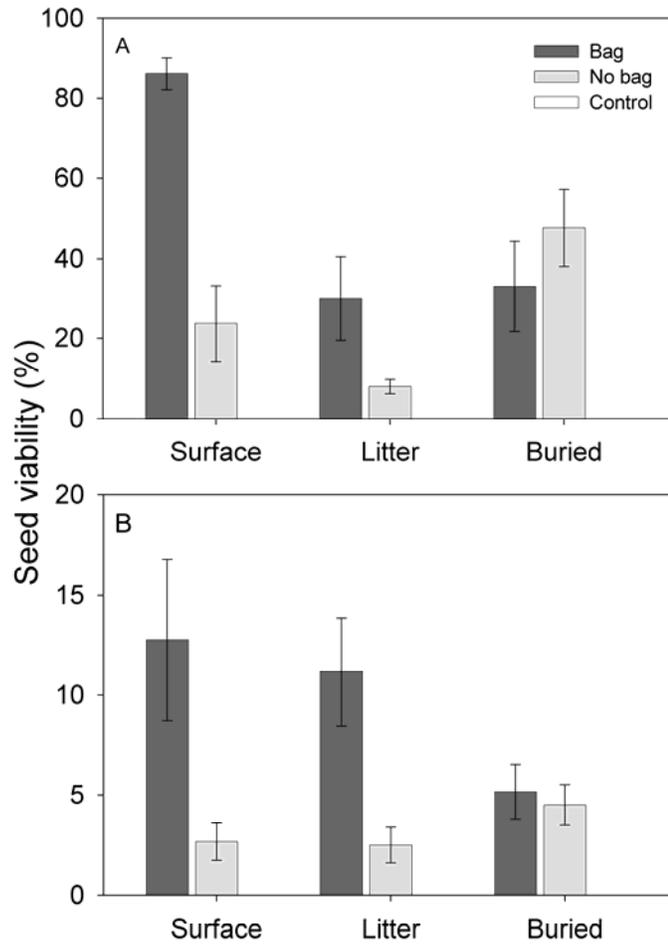


Figure 2.1 Effect of mesh bags on mean seed viability of (A) *Artemisia tridentata* subsp. *wyomingensis* and (B) *A. t.* subsp. *vaseyana*. Note different scales on Y-axes. Bars represent ± 1 standard error.

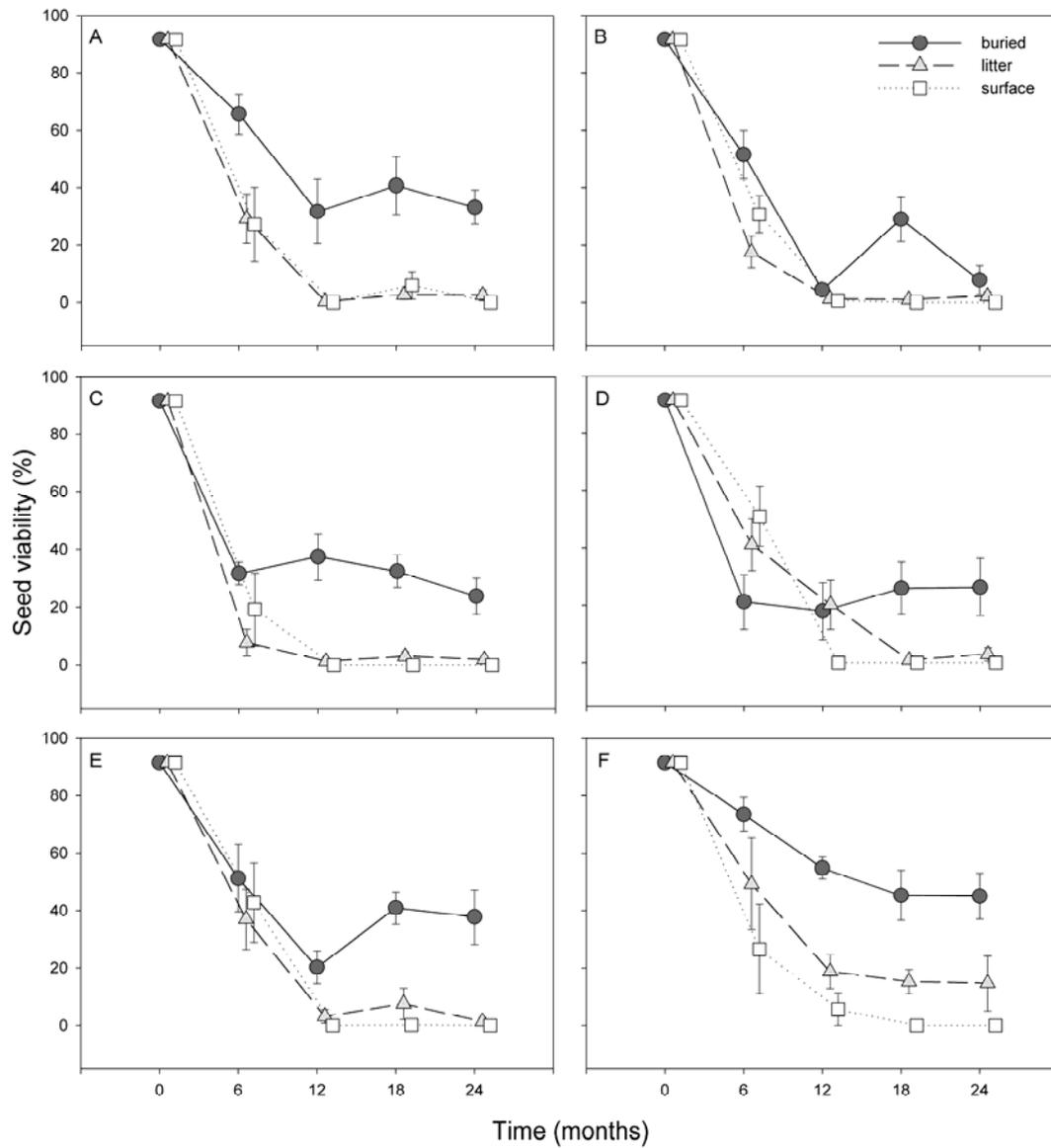


Figure 2.2 Mean seed viability of *Artemisia tridentata* subsp. *wyomingensis* over a period of 24 months in (A) eastern Oregon, (B) western Idaho, (C) eastern Idaho, (D) northern Utah, (E) western Utah, and (F) eastern Nevada. Bars represent ± 1 standard error.

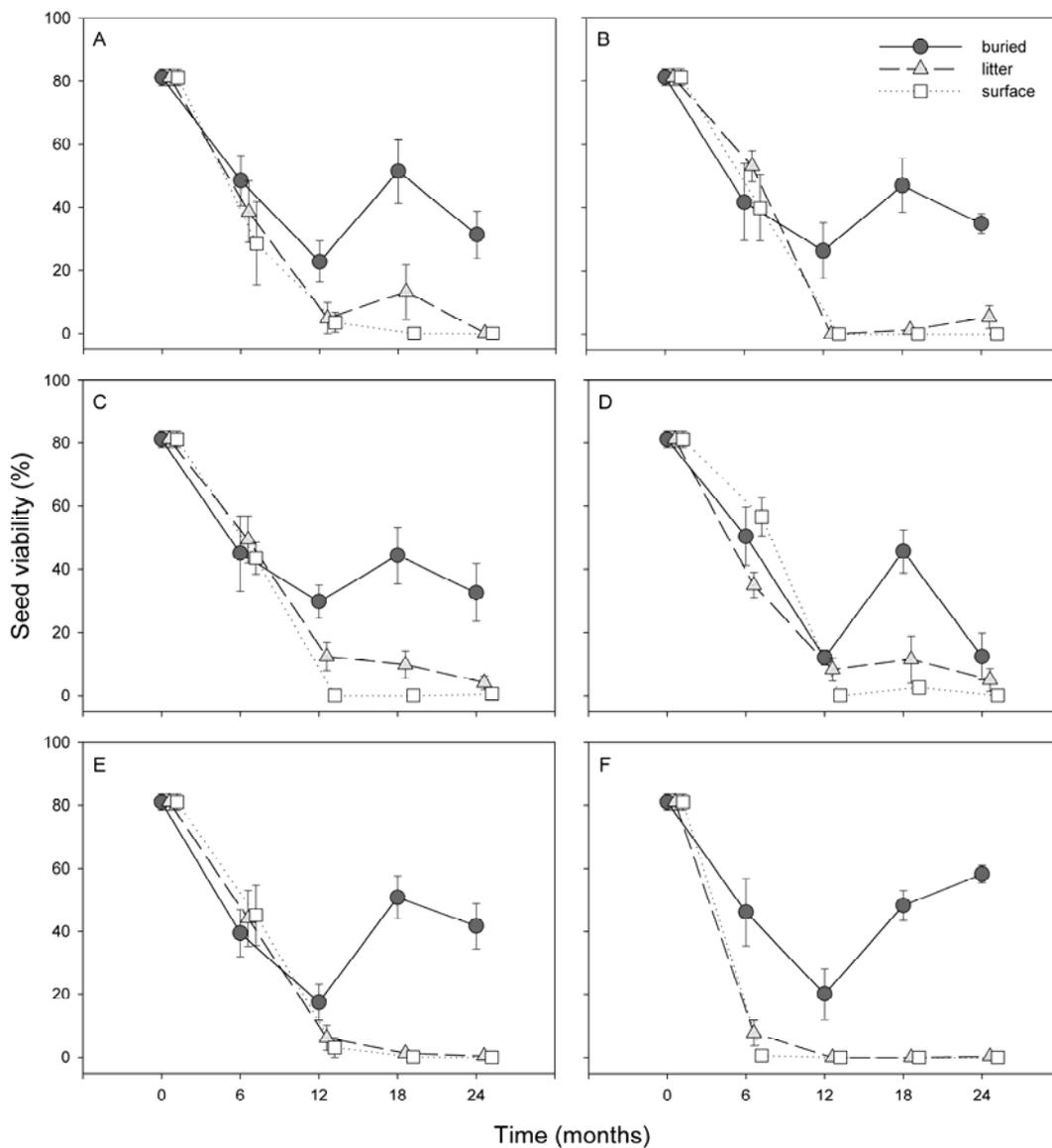


Figure 2.3 Mean seed viability of *Artemisia tridentata* subsp. *vaseyana* over a period of 24 months in (A) eastern Oregon, (B) western Idaho, (C) eastern Idaho, (D) northern Utah, (E) western Utah, and (F) eastern Nevada. Bars represent ± 1 standard error.

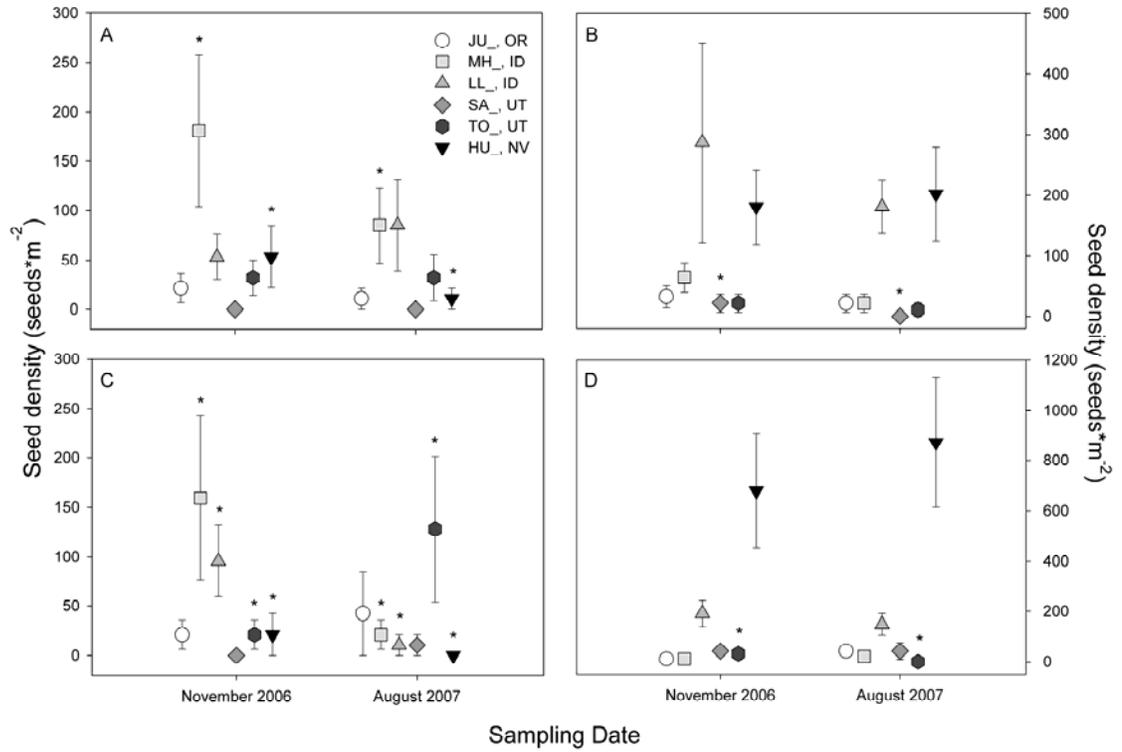


Figure 2.4 Mean seed density for (A,C) *Artemisia tridentata* subsp. *wyomingensis* and (B,D) *A. t.* subsp. *vaseyana* sites in (A,B) litter and (C,D) soil fractions. Note different scales on Y-axes. Bars represent ± 1 standard error.

CHAPTER 3

Effects of intra- and interspecific root interactions on *Artemisia tridentata* growth

Upekala C. Wijayratne and David A. Pyke

Abstract

Extensive and frequent fires in sagebrush steppe habitat often require active reseeding of native and nonnative perennial grasses along with *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush). Desirable and undesirable grasses may inhibit establishment of *A. t.* ssp. *wyomingensis* by inhibiting access to resources. We investigated whether root interactions interfere with *A. t.* ssp. *wyomingensis* growth and if so, whether those interactions are mediated through root exudates.

We grew focal *A. tridentata* ssp. *wyomingensis* seedlings with one of four neighbor species (*A. t.* ssp. *wyomingensis*, *Bromus tectorum* L. (cheatgrass), *Elymus wawawaiensis* J. Carlson & Barkworth (Snake River wheatgrass), and *Agropyron xhybrid* auct. ('Hycrest')) and alone as a control. Finely ground activated carbon (AC) was used to detect root interactions that may be chemically mediated. We measured focal seedling root elongation and biomass of control, focal and neighbor seedlings.

Focal seedling root growth rate and branching density was lower when grown with *B. tectorum* compared to control *A. t.* ssp. *wyomingensis* seedlings (growth rate: $p < 0.01$; branching density: $p = 0.07$). Focal seedlings grown with *A. t.* ssp. *wyomingensis*, *E. wawawaiensis*, or *A. xhybrid* neighbors did not differ from control seedlings. Root growth behavior of *A. t.* ssp. *wyomingensis* altered marginally when grown into roots of conspecific seedlings more often than when contacting roots of other species ($p = 0.08$), and occurred 4–5 times more without AC than with AC.

Growth of *A. t.* ssp. *wyomingensis* decreased considerably when grown with *B. tectorum* in comparison to other species despite there being plentiful resources. We found no evidence of chemically-mediated root interactions between *A. t.* ssp. *wyomingensis* and the grasses; however, there was some evidence to indicate that *A. t.* ssp. *wyomingensis* potentially uses a chemically-mediated mechanism to distinguish between roots of conspecifics and other species.

Keywords: *Elymus wawawaiensis*; *Agropyron xhybrid*; *Bromus tectorum*; root interactions; activated carbon; root exudates; interference competition

Introduction

Belowground plant interactions have traditionally been viewed as primarily resource-mediated (e.g., water, nutrients). However, increasing evidence suggests more complex interactions (Callaway 2002, Schenk 2006) including root growth responses to mechanisms that inhibit root access to resources (interference competition) (Schenk 2006). Root responses are much more sophisticated than originally believed and include a number of unique behaviors. For example, root systems can detect and avoid root systems of conspecifics, identify root systems of another individual, and even recognize near-kin versus far-kin (Mahall and Callaway 1991, 1992, Huber-Sannwald et al. 1996, Mahall and Callaway 1996, Falik et al. 2003, Semchenko et al. 2007b). Studies have also shown that roots can avoid physical objects (Falik et al. 2005, Semchenko et al. 2008) and root growth behaviors such as growing away from (avoidance) or towards (contest) root systems of other individuals may be species-specific (Semchenko et al. 2010). Though these root growth behaviors are not mediated by resources, they can still negatively affect resource acquisition by plants. Root density and distribution, key factors in resource acquisition, can be reduced or otherwise changed by the presence of neighbor root systems.

Root exudates are thought to play a key role in root growth behaviors. Roots continuously produce and secrete compounds into the rhizosphere (~ 0-2 mm from root surface) where they are involved in belowground interactions between roots, insects, and microbes (Bertin et al. 2003, Bais et al. 2006). The functions of most root exudates have not been determined, but some have been isolated as agents of allelopathic interactions and implicated in the success of some biological invasions (Bais et al. 2003, Weir et al. 2003).

The semi-arid sagebrush (*Artemisia tridentata* Nutt.) steppe ecosystem is one of the largest biomes in North America and is ecologically and economically

important (Sands et al. 1999, Knick et al. 2003, Maher 2007, Evans and Rollins 2008, Miller et al. 2011). The foundation shrub, *A. tridentata*, can facilitate the herbaceous plant community through provision of resource islands (Ryel et al. 1996, Halvorson et al. 1997), nurse plants (Huber-Sannwald and Pyke 2005), water via hydraulic lift (Caldwell and Richards 1989), and herbivore resistance (Karban et al. 2004, Karban 2007). In addition, it enhances native species diversity and abundance (Prevey et al. 2010) which indirectly increases biotic resistance to invasion by (Levine 2000, Naeem et al. 2000). Currently, over half of its original extent has been modified through land-use changes, altered fire regimes and conversion to near monocultures of *Bromus tectorum* L. (Whisenant 1990, D'Antonio and Vitousek 1992, Johnson et al. 1999, West 2000, Knick et al. 2003, Bradley and Mustard 2005, Miller et al. 2011). Restoration of *A. tridentata* is difficult and expensive (Hemstrom et al. 2002), but is nevertheless critical for overall ecosystem resilience and sustainability. Management agencies often seed large burned areas with mixtures of native and nonnative species to increase propagule pressure and provide immediate erosion control (Hilty et al. 2003). This sets the stage for interactions between *A. tridentata* seedlings and seedlings of other commonly seeded species. The importance of restoring *A. tridentata* indicates that we need improved understanding of the biotic interactions that constrain *A. tridentata* seedling establishment.

Resource acquisition is especially crucial in resource-poor ecosystems such as the semi-arid sagebrush steppe where resource status of juveniles at the beginning of summer determines whether they will survive the dry season (Donovan and Ehleringer 1994). Newly germinated seedlings of *A. tridentata* have low seed reserves to draw upon (Jones 1991) and seedlings must access water and nutrients soon after germination in order to establish a root system that ensures survival during summer drought periods. Interference from roots of conspecifics or other species may hinder root growth enough to inhibit a seedling's ability to survive. For example, *A. tridentata* seedling survival has been shown to increase significantly when neighbor roots were excluded (Reichenberger and Pyke 1990). We examined the effect of root

interactions, both resource-mediated and potentially inhibitory, on *A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (hereafter *A. tridentata*) seedlings in the context of restoration. The objectives of this study were to investigate whether root interactions interfere with *A. tridentata* growth and if so, whether those interactions are mediated, at least in part, through root exudates.

Methods

Study species

We selected three grasses to assess whether and how root interactions affect *A. tridentata* growth: *B. tectorum* (exotic annual), *Elymus wawawaiensis* J. Carlson & Barkworth (native perennial), and *Agropyron xhybrid* auct. (nonnative perennial). We obtained *A. tridentata* seeds from Bureau of Land Management personnel, collected from populations in Beaver County, Utah. *Bromus tectorum* seeds were collected from populations in Lake County, Oregon. We used seed of commercially available cultivars ‘Hycrest’ and ‘Secar’ (Granite Seed Co., Lehi, UT). ‘Hycrest’ is a hybrid cross of *A. desertorum* (Fisch. ex Link) Schult. and *A. cristatum* [L.] Gaertn. and is commonly used in rangeland restoration. The cultivar tends to be larger and more robust than either parental species with superior root development in comparison to other wheatgrass hybrids (Asay et al. 1985). ‘Secar’ is now recognized as a cultivar of *E. wawawaiensis*, but was originally released as a cultivar of *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* and continues to be seeded as a surrogate for that species throughout rangelands (Jones 2008, Ogle et al. 2010).

Root growth experiments

We studied effects of root interactions on *A. tridentata* seedling root growth and morphology using root observation planters in a greenhouse. Roots grew against a clear acrylic viewing wall that angled downward at 45° from the vertical, and was covered with a removable black cover. To determine whether root interactions were mediated at least in part by chemical signaling, we used powdered activated carbon

(Gro-Safe, Norit Americas Inc.) to counteract the effects of root exudates (Mahall and Callaway 1992, Ridenour and Callaway 2001, Semchenko et al. 2007a). Activated carbon binds to large organic compounds (i.e., root exudates) with minor impacts on nutrient dynamics because of its weak affinity to inorganic nutrients (Cheremisinoff and Morresi 1978, Inderjit and Callaway 2003).

We grew the focal species (*A. tridentata*) in competition with one of four neighbor species (*A. tridentata*, *E. wawawaiensis*, *A. xhybrid*, *B. tectorum*) crossed with potting medium (presence or absence of activated carbon) in a completely randomized design. Forty root observation planters (20cm x 20cm and 56cm, Fig. 3.1) were filled with pasteurized river sand only and forty filled with pasteurized sand mixed with activated carbon (1 L sand:20mL activated carbon). In March 2009, we planted five seeds of *A. tridentata* and five seeds of a neighbor species (10 replicate planters for each neighbor species x potting medium treatment) into each planter. After one week of germination and establishment, seedlings were thinned to one focal *A. tridentata* and one neighbor seedling. Twenty additional planters, half with the activated carbon:sand mixture and half with plain sand, were seeded in the same manner and thinned to a single *A. tridentata* seedling to assess potential direct effects of activated carbon on plant growth. Sand was kept continuously moist and fertilized with one-tenth strength Hoagland's solution once a week. The study took place in a greenhouse in Corvallis, OR under ambient light and was monitored for three months. Maximum temperatures ranged from 17.9–40.5 °C and minimum temperatures ranged from 7.9–14.4°C.

Very few focal *A. tridentata* roots made visible direct contact with roots of neighbor species in the first experiment so we constructed root observation chambers that forced contact (*sensu* Mahall and Callaway 1991) for a second experiment. The experimental plan was identical to the first experiment, with four neighbor treatments fully crossed with two potting medium treatments in a completely randomized design. Paired chambers (15cm x 15cm x 2cm each) were constructed, with one for focal *A. tridentata* seedlings and the other for neighbor seedlings (Fig. 3.2A). Twenty pairs of

chambers were filled with washed silica sand (Sakrete Natural Play Sand, Bonsal American Inc., Charlotte, N.C.) and twenty filled with a 1 L sand:20mL activated carbon mixture. In April 2010, we planted five *A. tridentata* seeds in one chamber and five neighbor species seeds in the other, and thinned to one seedling each after one week of establishment (10 replicate paired chambers for each neighbor species x potting medium treatment). Sand was kept continuously moist and fertilized with one-tenth strength Hoagland's solution applied weekly. After a period of growth, the bottoms of the chambers containing focal *A. tridentata* seedlings were connected to the sides of the paired chambers containing neighbor species (Fig. 3.2B). This forced roots of focal *A. tridentata* seedlings to grow perpendicularly into roots of neighbor species. The experiment took place in a heated greenhouse under ambient light in Corvallis, OR and was monitored for three months. Maximum temperatures ranged from 20.6–41.7 °C and minimum temperatures ranged from 8.0–16.7 °C.

Once roots of *A. tridentata* seedlings started appearing on the viewing window, we measured elongation every two days by tracing roots onto acetate paper. We used ArcGIS to calculate root length of scanned root tracings. Root segments were coded by root order (primary or lateral), Julian day, and whether or not the segment visibly contacted or crossed roots of neighbor species.

Biomass experiment

To investigate the apparent influence of root interactions on *A. tridentata* growth, we also grew seedlings in pots (~ 3.8 L) in the same completely randomized experimental design (4 neighbor species x 2 potting medium x 10 replicates) as the second root growth experiment, under similar conditions. Seeds were first germinated in plastic dish, and in April 2010 similar sized seedlings (cotyledon-stage for *A. tridentata* and 1-leaf stage for grasses) were planted equidistantly from each other and the edge of the pot. In June 2010, seedlings were harvested over a two week period with their root systems intact by washing away soil over a screen (1 mm x 1 mm aperture). We looked for floating root fragments in the wash water from a subset of

samples to confirm that very little root mass was getting through the screen (losses averaged $0.002 \text{ g} \pm 0.004$ dry weight). Root systems of the two seedlings per pot were separated from each other by submerging both seedlings in a shallow basin of water and gently teasing the roots apart. *Artemisia tridentata* roots appeared brown in color in contrast to the white roots of the perennial grasses and the yellow roots of *B. tectorum*. A small portion of root fragments could not be identified and were discarded. Seedlings were dried at 65° C for 48 hours and weighed. It was difficult to separate roots in treatments where two *A. tridentata* seedlings (one focal and one neighbor) were grown together because of the method used to extract roots from soil; therefore, shoot and root biomass were combined and the average calculated as the response for each seedling.

Activated carbon can have a fertilizing effect on focal species growth and compromise the ability to detect whether effects of competition by neighbors is driven by root exudates (Lau et al. 2008). Therefore, we analyzed focal *A. tridentata* seedlings to determine if N concentration differed across treatments. Analysis was performed by the Stable Isotope Research Unit, Dept. of Crop and Soil Science, Oregon State University. Samples were finely ground, packaged in tin capsules, and combusted using a SerCon GSL prep unit. Combustion gases were analyzed using a PDZ-Europa 20-20 continuous flow isotope ratio mass spectrometer (SerCon Ltd., Crewe, Cheshire, England).

Statistical analysis

All statistical analyses were carried out with SAS 9.13 statistical software (SAS Institute Inc., Cary, NC). Responses were log-transformed if necessary to meet assumptions of a normal distribution and homogenous variance. We used the Tukey-Kramer test for multiple post-hoc comparisons of root growth rate and biomass between treatments.

Few focal *A. tridentata* roots came into visible contact with neighbor roots and most seedlings had one primary root with short laterals in the large root chamber

experiment (Fig. 3.3); therefore, we used average daily root growth rate (sum of all root lengths per individual divided by number of growing days) as a response, rather than evaluating growth rates of individual roots. Branching density was calculated as the number of branch nodes divided by total root length. We used a general linear model (PROC MIXED) to test for effects of potting medium and neighbor species on focal *A. tridentata* root growth rate and branching density.

For the paired root chamber experiment, individual root growth rates of the focal *A. tridentata* seedling were converted to mm/hr and standardized by aligning their days of visible contact with a neighbor root. We used a general linear model (PROC MIXED) with repeated measures to analyze root growth rate relative to that contact, with neighbor identity and potting medium as main effects and contact day as a covariate. Several focal *A. tridentata* roots within a chamber usually came into contact with neighbor roots. Some were disrupted in their downward progress, apparently by the presence of a neighbor root. These roots either appeared to stop growing, or turned $\sim 90^\circ$ and grew alongside the neighbor roots that they contacted for a period of time. A few of these turned $\sim 90^\circ$ again and continued their downward progress, usually because they encountered the wall of the root chamber. Roots that appeared to stop growing could, in fact, have been turning away from the viewing window. We used a generalized linear model (PROC GENMOD) to analyze the proportion of focal *A. tridentata* roots within a chamber whose growth was modified in such ways.

We analyzed the effect of neighbor species and potting medium on shoot and root biomass, and root/shoot biomass ratios of focal *A. tridentata* seedlings using a general mixed model with harvest date as a covariate. A general linear model (PROC MIXED) was also used to analyze tissue nitrogen concentration as a function of neighbor species, potting medium, and tissue type (root or shoot).

Results

Root growth experiments

Because of the potential for activated carbon to directly affect growth rates, we focused primarily on comparing growth rates of control seedlings to growth rates of seedlings grown with neighbors within a potting medium treatment. Focal seedlings grown with *B. tectorum* in unaltered potting medium (i.e., without activated carbon) experienced a significant decrease in root growth rate compared to controls ($t_{69} = -4.13, p < 0.01$). This effect did not occur in the presence of activated carbon ($t_{69} = -0.29, p = 1.00$). In contrast, *Artemisia tridentata* root growth rates when grown with conspecifics, *E. wawawaiensis*, or *A. xhybrid* were not significantly different from growth rate of control seedlings, either with or without activated carbon (Fig. 3.4). Most focal *A. tridentata* seedlings in the large root chambers only had one primary root with a few, small lateral roots. A few had primary roots that stopped growing while a nearby lateral continued to elongate vertically. Branching density followed the same general trend as overall root growth rate. Compared to control seedlings, *A. tridentata* had reduced branching density when grown with *B. tectorum* ($t_{69} = -3.12, p = 0.07$) in potting medium without activated carbon and this effect disappeared in the presence of activated carbon ($t_{69} = -1.31, p = 0.95$). Branching density did not differ from control seedlings when grown with conspecifics, *E. wawawaiensis*, or *A. xhybrid* regardless of potting medium.

The pattern of *A. tridentata* root growth rate over time in the second root growth experiment significantly differed across neighbor species ($F_{24,1075} = 1.73, p = 0.02$; Fig. 5) and marginally differed between soil media ($F_{8,1052} = 1.79, p = 0.08$). Root elongation rates of focal *A. tridentata* seedlings when grown with *E. wawawaiensis* were slightly higher in activated carbon treatments than in unaltered potting media ($t_{60} = 1.96, p = 0.05$), and the effect tended to become more pronounced as focal roots approached roots of neighbor seedlings (Fig. 5). The odds of *A. tridentata* roots stopping their growth or changing direction of elongation were higher

when *A. tridentata* roots were grown into roots of conspecific seedlings than when contacting roots of other species (Table 3.1). These odds were 4- to 5-fold higher in unaltered potting media than in potting media with activated carbon ($X^2 = 3.03$, $p = 0.08$).

Biomass experiment

Activated carbon marginally increased shoot biomass ($t_{71} = 3.04$, $p = 0.09$) and significantly increased root biomass ($t_{71} = 3.66$, $p = 0.02$) of control *A. tridentata* seedlings (Fig. 3.6). *Artemisia tridentata* seedlings grown with *B. tectorum* had significantly lower shoot biomass and marginally lower root biomass compared to control seedlings (shoots $t_{71} = -4.15$, $p < 0.01$; roots $t_{71} = -3.13$, $p = 0.07$). Root biomass of focal *A. tridentata* seedlings was about twice the mass of shoots in all treatments. The effect of activated carbon on neighbor biomass depended on species identity (shoot $F_{3,54} = 4.48$, $p < 0.01$; root $F_{3,54} = 3.16$, $p = 0.03$; Fig. 3.7). Unlike other neighbor species, *B. tectorum* responded to the activated carbon treatment by increasing allocation to roots ($t_{54} = 3.60$, $p = 0.01$). All individuals of *B. tectorum* had fine, highly branched roots that had proliferated up to and around the inside wall of the pots and surrounded roots of *A. tridentata* (Fig. 3.8). *Bromus tectorum* seedlings also had 2–3 times more shoot biomass than the other grasses (BRTE - ELWA: $t = 8.31$, $p < 0.01$; BRTE - AGHY: $t = 7.80$, $p < 0.01$).

Activated carbon had no effect on tissue nitrogen concentration of control *A. tridentata* seedlings for shoots (no carbon: 1.3–1.9%, carbon: 1.5–2.2%; 95% confidence interval) or roots (no carbon: 0.8–1.1%, carbon: 0.8–1.2%; 95% confidence interval), nor did it have an effect when focal seedlings were grown with bunchgrasses. However, focal *A. tridentata* seedlings grown with *B. tectorum* in activated carbon had significantly lower root nitrogen concentration (0.4–0.7%; 95% confidence interval) in comparison to those without activated carbon (0.6–0.9%; 95% confidence interval).

Discussion

Growth dynamics

Average root growth rate varied little across neighbor treatments. Even when forced to contact roots of neighbors in the paired root chamber experiment, *A. tridentata* roots generally grew at similar rates across neighbor treatments. However, compared to control seedlings, *A. tridentata* focal seedlings had the greatest decrease in both root and shoot biomass when grown with *B. tectorum* but showed no decrease when grown with the perennial grasses or conspecifics. Control *A. tridentata* seedlings in the biomass experiment had access to twice the volume of soil and nutrients, yet did not differ in mass from their counterparts growing in a shared resource environment with perennial grasses or conspecifics. This is in contrast to focal seedlings growing with *B. tectorum* neighbors where biomass was generally lower than that of control seedlings.

Bromus tectorum seedlings differed from the perennial grasses in root morphology and development, shoot mass, and also germinated and initiated growth earlier than *A. tridentata* focal seedlings (*personal observation*). These differences may explain the relative competitive effect of the grasses on *A. tridentata* growth. This is consistent with other studies showing that *B. tectorum* exhibits early growth, root elongation and initiation of adventitious roots compared to *E. wawawaiensis* or *A. xhybrid* (Aguirre and Johnson 1991, Johnson and Aguirre 1991). Though all seedlings were planted on the same day, early germination and growth would enable *B. tectorum* to preempt resources from *A. tridentata*. Additionally, the high density of *B. tectorum* roots in the same volume of soil could create overlapping resource depletion zones and potentially reduce growth of *A. tridentata* (Casper and Jackson 1997). Furthermore, the mass of fine roots surrounding roots of focal *A. tridentata* seedlings may have been physically restricting. Potential soil substrate fragmentation and volume reduction resulting from dense *B. tectorum* roots may have decreased *A. tridentata* root growth

independent of nutrient availability (McConnaughay and Bazzaz 1991, 1992, Hess and de Kroon 2007).

Bromus tectorum seedlings had over 2–3 times more shoot mass than the perennial grasses, and potential competition for light by *B. tectorum* may have also contributed to the decrease in *A. tridentata* growth. Competition for light is generally thought to be size-asymmetric and takes place when a resource is preempted by a larger individual over a smaller individual, and the larger individual gets a disproportionate share of the resource for its relative size (Weiner 1986, 1990). Shading can compromise a plant's ability to take up nutrients. For example, phosphorous uptake increased in unshaded *A. desertorum* in response to enriched microsites but did not in shaded plants (Jackson and Caldwell 1992). *Artemisia tridentata* focal seedlings may have experienced more shoot competition from *B. tectorum* than from conspecifics or perennial grasses.

Root behaviors

Comparable biomass in *A. tridentata* seedlings, grown alone and with conspecifics was a surprising result. Avoidance, or segregation, of individual roots is a common phenomenon, particularly in arid and semi-arid environments (Schenk et al. 1999), and may have allowed *A. tridentata* roots to proliferate uniformly in the soil to forage more efficiently. This may be a chemically mediated response at the level of individual roots, as shown for *A. tridentata* ssp. *vaseyana* (Rydb.) Beetle whose roots segregated from roots of *P. spicata* more than they did from *A. desertorum* (Caldwell et al. 1991a, 1996). A post-hoc analysis of the proportion of lateral roots growing towards and away from conspecific neighbor roots in the large root box experiment supports this idea. A slightly higher proportion of laterals grew towards neighbors in activated carbon-amended potting medium than in the unaltered potting medium ($F_{1,9} = 2.76$, $p = 0.09$; $N = 6$ activated carbon, $N = 5$ no activated carbon). Reduced growth of roots as they approach other roots or physical objects may be caused by sensitivity

of roots to their own exudates accumulating in the vicinity of obstacles (Falik et al. 2005) and may serve as a possible mechanism for segregation of individual roots.

A closer look at the hourly growth rates of individual *A. tridentata* roots in the paired root chamber experiment revealed that, in activated carbon treatments, growth rates of individual *A. tridentata* roots increased slightly when contacting a conspecific root or approaching an *E. wawawaiensis* root but remained the same when contacting *B. tectorum* and *A. xhybrid* roots. In a similar experiment, Krannitz and Caldwell (1995) observed a slight slowing of *A. tridentata* ssp. *vaseyana* (mountain big sagebrush) root growth after contacting conspecific roots as well as one instance of slowing when sister roots were contacted. We observed that speed of root growth was comparable across neighbor treatments, but direction of growth was not. Only *A. tridentata* roots contacting conspecific roots had high odds of changing direction or stopping, an effect that was ameliorated with the addition of activated carbon. If this species-specific response was due solely to some physical difference between *A. tridentata* roots and grass roots, or if activated carbon was merely having a beneficial resource effect on *A. tridentata* root growth, then we would not have seen evidence of a behavioral change (i.e., roots growing straight instead of turning off course) when activated carbon was added. Taken together, these arguments suggest that *A. tridentata* roots may have a chemical signaling mechanism to avoid roots of conspecifics. In an inland sand dune system in Germany, researchers demonstrated that under intraspecific competition plants tended to segregate their root systems, while under interspecific competition plants tended to aggregate their roots towards their neighbors (Bartelheimer et al. 2006).

Methodological considerations

Activated carbon positively affected growth of *A. tridentata* individuals in the absence of competitors; therefore, our ability to distinguish whether the effect of competition by neighbors is resource-mediated or driven by root exudates is compromised. While it did not have a direct effect on average root growth rate, both

root and shoot biomass of control seedlings were higher when grown in activated carbon-amended potting medium. Activated carbon can have a fertilizing effect by increasing water retention (Ridenour and Callaway 2001), increasing nutrient availability (Lau et al. 2008, Weisshuhn and Prati 2009), changing pH of the substrate (Kabouw et al. 2010), or by affecting soil microbial communities (Kulmatiski 2011), all of which can affect resource availability.

Mature *Artemisia* shrubs have shown rapid root proliferation in response to nutrient additions (Jackson and Caldwell 1989), which could enable them to swiftly take up a potentially ephemeral resource. Generally, plants from infertile habitats respond to an increase in nutrients with an increase in tissue nutrient concentration rather than an increase in growth (Chapin 1980), which is what one might expect if activated carbon increased nutrients in the potting medium. Activated carbon can increase the availability of nutrients such as nitrate, potassium, and phosphate in potting media (Lau et al. 2008, Weisshuhn and Prati 2009). In the present study, *A. tridentata* control seedlings responded to activated carbon with increased growth rather than an increase in nitrogen concentration of roots or shoots. It is possible that, despite being from a nutrient-poor system, *A. tridentata* seedlings started and grown in a controlled greenhouse respond like a fast-growing species from a fertile habitat. Lau et al. (2008) suggests that total tissue nitrogen (i.e., nitrogen concentration x biomass) is a better estimate of nutrient availability in potting media when plants are started from seed. Using this metric, we can infer that activated carbon increased nutrient availability in potting media as *A. tridentata* control seedlings had significantly higher total tissue nitrogen in activated carbon-amended soils compared to seedlings in unaltered soils.

We observed that biomass of *B. tectorum* did not significantly increase in activated carbon treatments. This is in contrast to a study by Lau et al. (2008) who reported increased biomass even in the absence of competition. They also found that total nitrogen and phosphorous content of *B. tectorum* grown in activated carbon was greater than that of individuals grown without activated carbon, implying that

activated carbon increased the availability of those two nutrients. Resource competition with *B. tectorum* may, in fact, have been strengthened because the annual may have competed for soil nutrients more effectively than *A. tridentata* (Casper and Jackson 1997, Blank 2010, Mangla et al. 2011).

The use of activated carbon to detect chemically-mediated versus resource-mediated effects of competition assumes that the magnitude of resource competition between two individuals remains constant across potting media treatments (Lau et al. 2008). For example, in unaltered potting medium focal *A. tridentata* had a 75% reduction in shoot biomass when grown with *B. tectorum*, compared to control seedlings. However, in activated carbon-amended potting medium, focal *A. tridentata* seedlings grown with *B. tectorum* experienced over 90% reduction in shoot biomass compared to control seedlings (Fig. 3.6A). The effects of *B. tectorum* were heightened in the presence of activated carbon rather than reduced as one would expect if the competitor were allelopathic and activated carbon successfully adsorbed allelopathic root exudates. Though there may be confounding effects of activated carbon on focal *A. tridentata* biomass in the present study, our observations of the behavior (i.e., avoidance or slowed growth when approaching neighbor roots) of individual roots in the paired root observation experiment should be influenced by such effects.

Management implications

We found no evidence to indicate that seeding *E. wawawaiensis* and *A. xhybrid* with *A. tridentata* would be detrimental to the shrub's establishment given abundant resources. Root growth rate and overall biomass of *A. tridentata* seedlings grown with the perennial grasses was similar to control seedlings grown alone. However, water and nutrients were plentiful by design to isolate chemically-mediated interference, and may not be indicative of typical field conditions in which competition could be predominately resource-mediated. It would be prudent to conduct similar root interference experiments under field conditions. *Artemisia tridentata* seedlings grown with *B. tectorum* had lower root growth rates, root

branching density and biomass compared to control seedlings. Seeding *A. tridentata* into areas with a substantial *B. tectorum* seed bank or where *B. tectorum* was not cleared will likely fail regardless of the availability of resources. Competition with *B. tectorum* may reduce resource status of *A. tridentata* to the point where seedlings have a diminished ability to acquire resources during the summer drought.

Root avoidance in *A. tridentata* warrants further attention, particularly with regard to determining at what level of relatedness the behavior operates. Mahall and Callaway (1996) showed that contact inhibition of *Ambrosia dumosa* Payne (burrobush) roots occurred only between plants within the same population; when roots of plants from different geographic origins contacted each other root growth rate remained unchanged. They speculated that contact inhibition could reduce belowground competition between closely related shrubs. If similar population-specific behavior was discovered in *A. tridentata*, using plant materials from different populations to rehabilitate an area may actually enhance competitive interactions between individuals and undermine seedling establishment efforts.

Increases in the spatial aggregation of herbaceous perennial vegetation and the size and connectivity of aboveground gaps between vegetation are associated with a loss in ecosystem resilience and a potential increase in ecosystem invasibility (Reisner 2010). Reducing the size and connectivity of belowground gaps may also be critical to maintaining ecosystem resistance to invasion. Large belowground gaps may be correlated with an increased risk of colonization by *B. tectorum*. Our study showed that individual *A. tridentata* roots potentially utilize chemical signaling to avoid roots of conspecifics. The consequence of this behavior in intact habitats is that the belowground neighborhood can be more fully occupied by *A. tridentata* roots, rather than individual roots aggregating and leaving gaps in the rhizosphere to be exploited by exotic species. While occupation by native species over exotics is preferred regardless of species identity, the degree to which native species can suppress *B. tectorum* growth and reproduction is species specific. Root competition with established *A. tridentata* shrubs suppressed *Bromus tectorum* seed production and thus

the subsequent generation of plants more than did root competition with bunchgrasses (Reichenberger and Pyke 1990), illustrating one aspect of the importance of shrub restoration.

In summary, *A. tridentata* growth and overall growth rate decreased considerably when grown with *B. tectorum* in comparison to other species, suggesting that traits associated with an annual life history (e.g., rapid growth, high uptake kinetics) are important to competitive ability. We found some evidence that root interactions between species may be chemically mediated. *Artemisia tridentata* roots appear to be able to distinguish between conspecifics and other species. More studies of this specific phenomenon, both field and greenhouse based, will be required to support this speculation.

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Table 3.1 Odds (95% confidence interval) of an individual *Artemisia tridentata* ssp. *wyomingensis* root stopping growth or changing direction when coming into contact with a neighbor root. Experiment is *A. t.* ssp. *wyomingensis* seedlings grown with four neighbor species (ARTR = *A. t.* ssp. *wyomingensis*, BRTE = *Bromus tectorum*, ELWA = *Elymus wawawaiensis*, AGHY = *Agropyron xhybrid*) and in the presence or absence of activated carbon. The difference between carbon treatments within a test species was tested using a Bonferroni correction for multiple comparisons. Odds of an *A. t.* ssp. *wyomingensis* root stopping growth or changing direction was marginally higher in unaltered soil than in soil amended with activated carbon ($X^2 = 3.03$, $p = 0.08$).

Neighbor species	Odds of stopping growth or changing direction (95% CI)	
	<i>No activated carbon</i>	<i>Activated carbon</i>
ARTR	1.2 - 26.1	0.3 - 5.6
BRTE	0.2 - 2.6	0.2 - 2.5
ELWA	0.1 - 1.2	0.1 - 1.7
AGHY	0.0 - 1.1	0.1 - 1.4



Figure 3.1 Large root observation planters in a greenhouse in Corvallis, OR. *Artemisia tridentata* ssp. *wyomingensis* seedlings were grown with one of four neighbor species (*A. t.* ssp. *wyomingensis*, *Elymus wawawaiensis*, *Agropyron xhybrid*, *Bromus tectorum*) or alone, fully crossed with potting medium (presence or absence of activated carbon) in a completely randomized design.

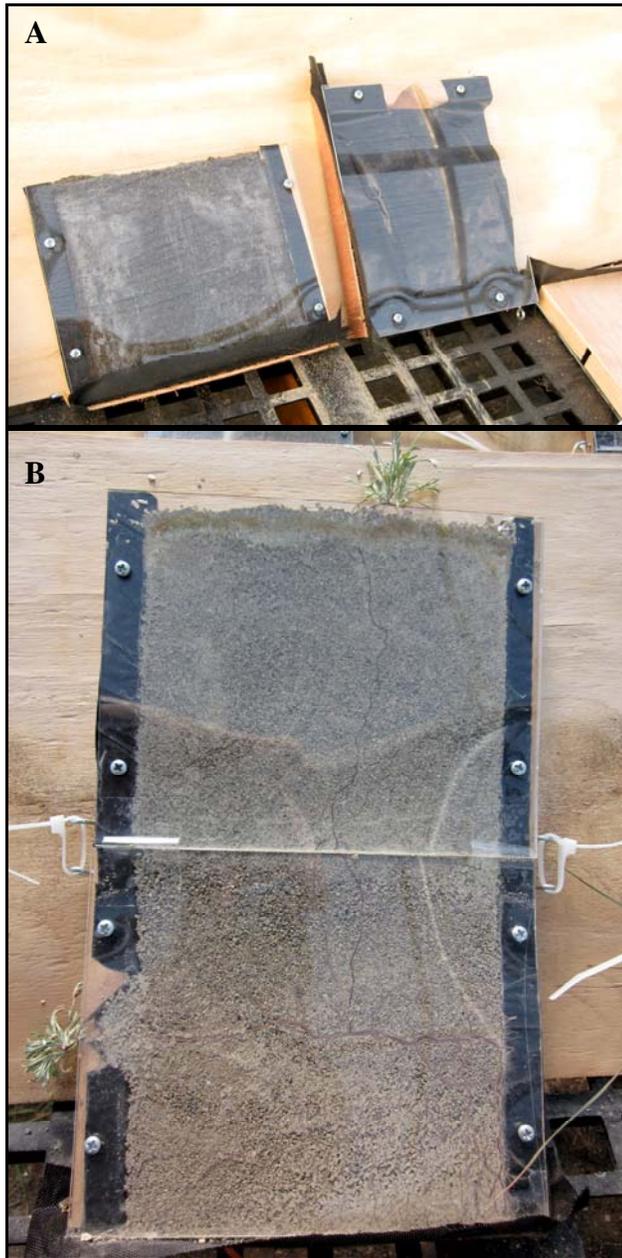


Figure 3.2 Paired root observation planters. *Artemisia tridentata* ssp. *wyomingensis* roots were grown into four neighbor species (*A. t.* ssp. *wyomingensis*, *Elymus wawawaiensis*, *Agropyron xhybrid*, *Bromus tectorum*) and crossed with potting medium (presence or absence of activated carbon) in a completely randomized design. Focal *A. tridentata* were planted in the left chamber and neighbors planted in the right chamber (A). After a period of growth, chambers with focal seedlings were connected to chambers with neighbor species (B).

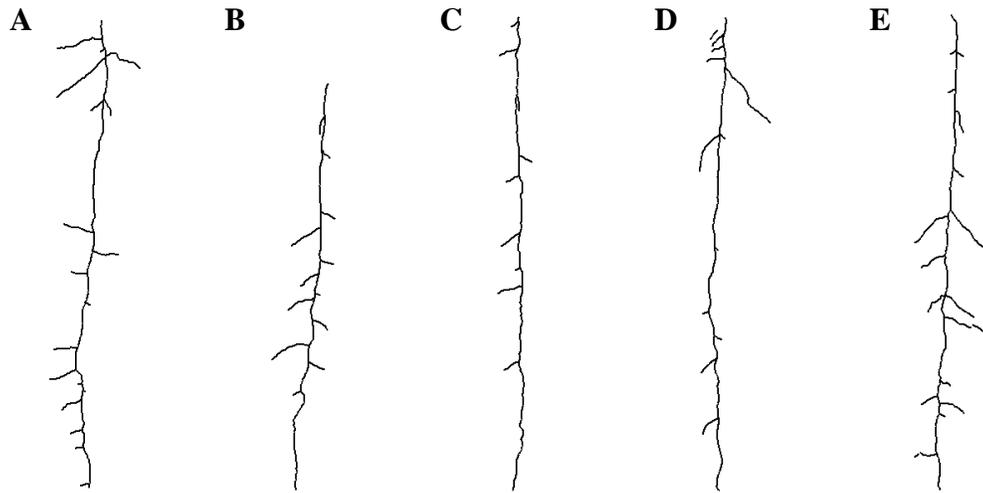


Figure 3.3 Examples of *Artemisia tridentata* ssp. *wyomingensis* focal root growth in first 30 cm of soil in large root observation planters. Focal plants are from treatments without activated carbon and grown alone (A), with *A. t.* ssp. *wyomingensis* (B), with *Bromus tectorum* (C), with *Elymus wawawaiensis* (D), and with *Agropyron xhybrid* (E).

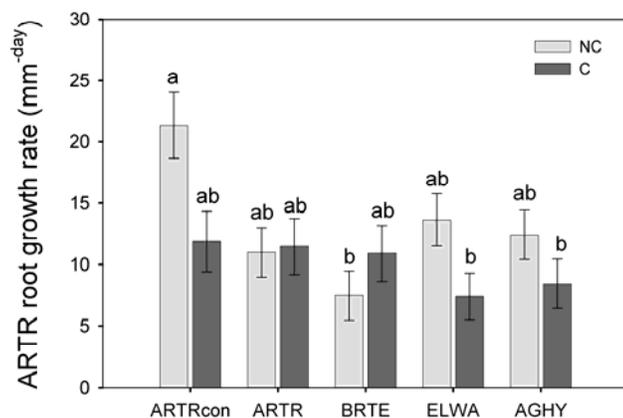


Figure 3.4 Average daily root growth rate (\pm SE) of *Artemisia tridentata* ssp. *wyomingensis* seedlings. Seedlings are grown alone or with four different test species (ARTRcon = *A. t.* ssp. *wyomingensis* control, ARTR = *A. t.* ssp. *wyomingensis*, BRTE = *Bromus tectorum*, ELWA = *Elymus wawawaiensis*, AGHY = *Agropyron xhybrid*) and in the presence (dark gray bars - C) or absence (light gray bars - NC) of activated carbon. Means sharing letters are not significantly different from each other (Tukey-Kramer test).

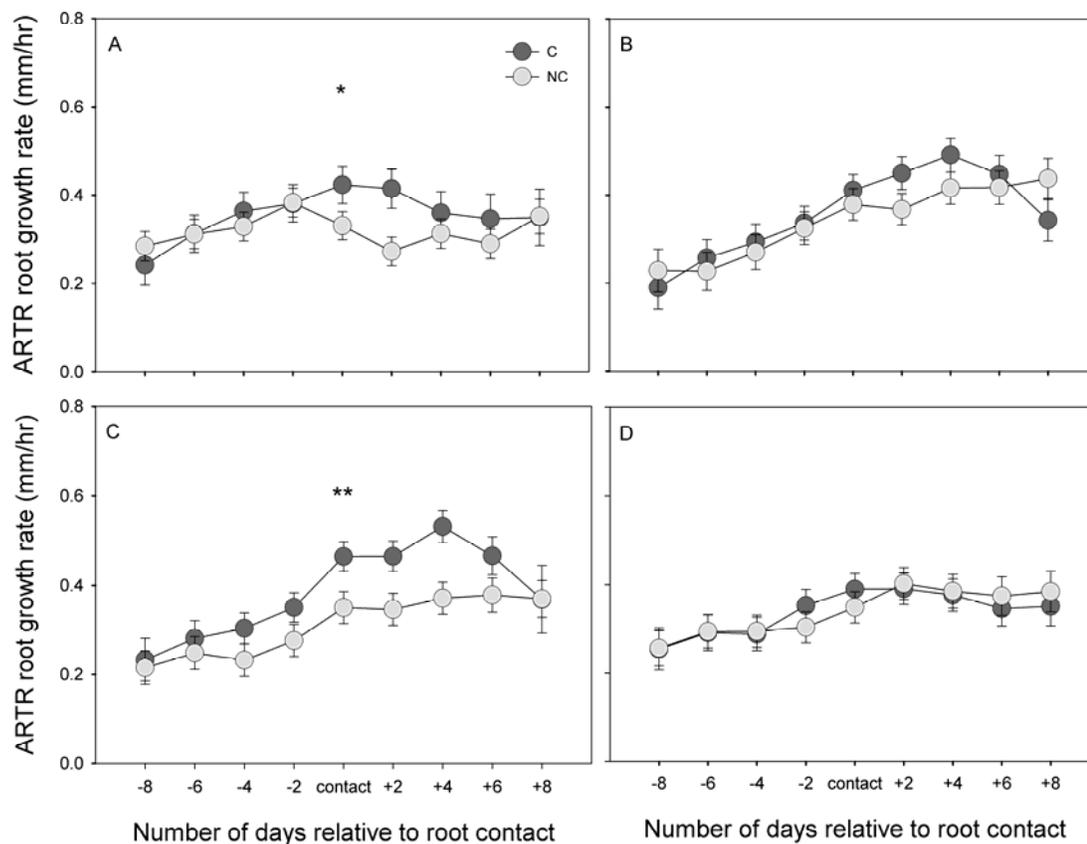


Figure 3.5 Hourly root growth rate (\pm SE) of *Artemisia tridentata* ssp. *wyomingensis* seedlings relative to contact with a neighbor root. Seedlings were grown with four different neighbor species: *A. t.* ssp. *wyomingensis* (A), *Bromus tectorum* (B), *Elymus wawawaiensis* (C), and *Agropyron xhybrid* (D), and in the presence (dark gray circles - C) or absence (light gray circles - NC) of activated carbon. The difference in growth rates between potting media on the day of contact was tested using a Bonferroni correction for multiple comparisons (* $p < 0.10$, ** $p < 0.05$).

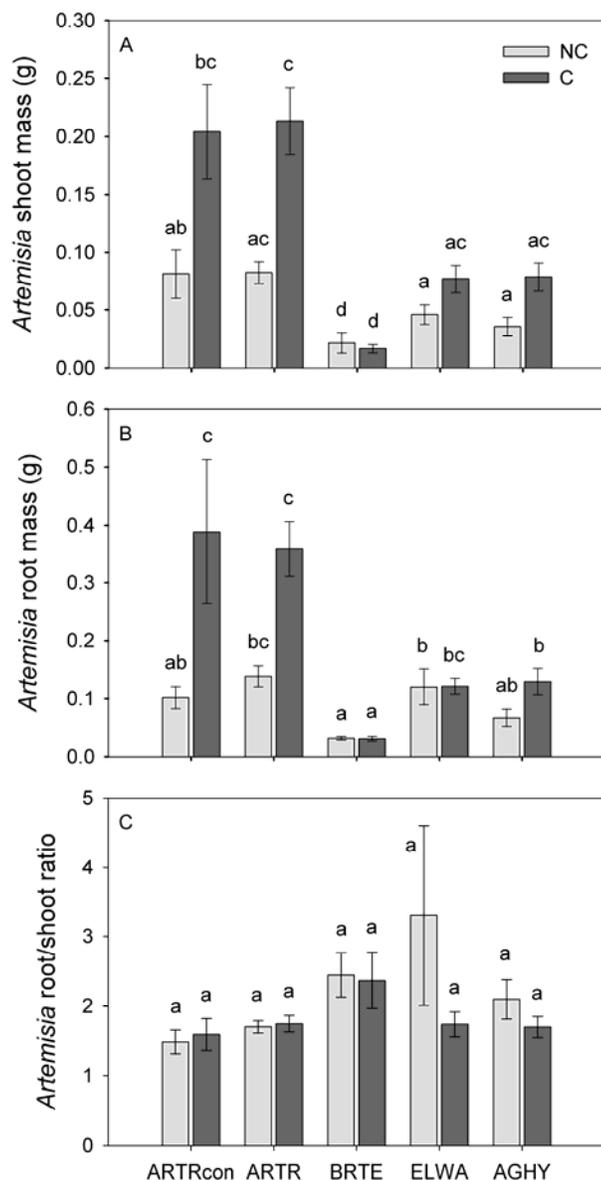


Figure 3.6 Shoot (A) and root (B) biomass, and root/shoot ratio (C) of *Artemisia tridentata* ssp. *wyomingensis* focal seedlings. Seedlings are grown alone or with four different neighbor species (ARTRcon = *A. t. ssp. wyomingensis* control, ARTR = *A. t. ssp. wyomingensis*, BRTE = *Bromus tectorum*, ELWA = *Elymus wawawaiensis*, AGHY = *Agropyron x hybrid*) and in the presence (dark gray bars - C) or absence (light gray bars - NC) of activated carbon. Means sharing letters are not significantly different from each other (Tukey-Kramer test). Error bars represent ± 1 standard error.

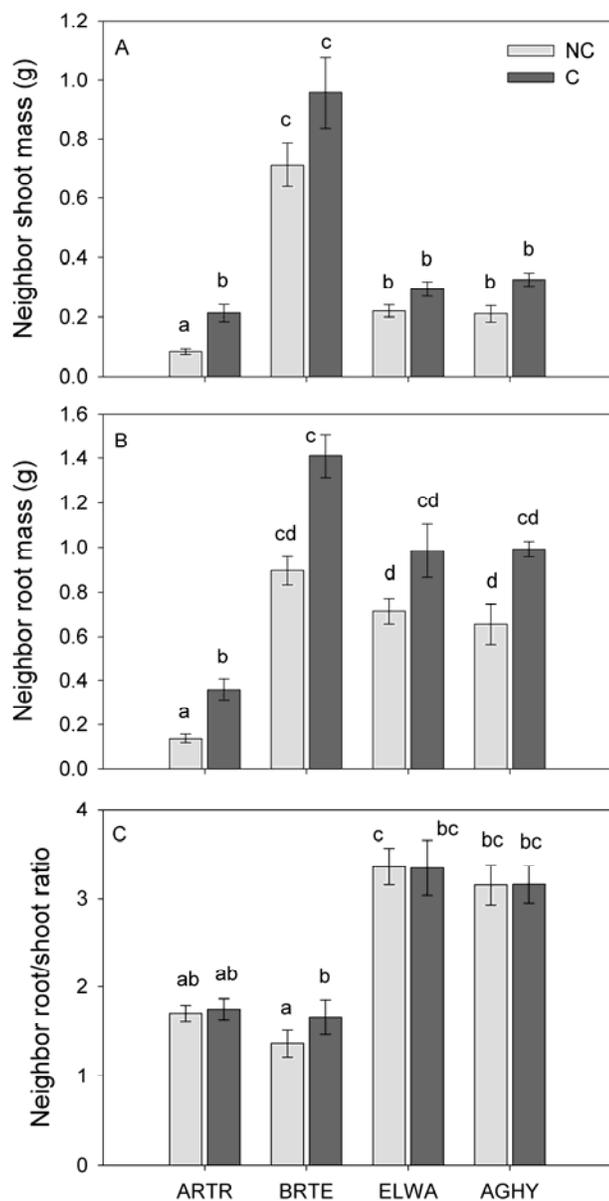


Figure 3.7 Shoot (A) and root (B) biomass, and root/shoot ratio of neighbors. Neighbors are (C) of *Artemisia tridentata* ssp. *wyomingensis* (ARTR), *Bromus tectorum* (BRTE), *Elymus wawawaiensis* (ELWA), and *Agropyron xhybrid* (AGHY) neighbors grown with focal *A. tridentata* seedlings, and in the presence (dark gray bars - C) or absence (light gray bars - NC) of activated carbon. Means sharing letters are not significantly different from each other (Tukey-Kramer test). Error bars represent ± 1 standard error.



Figure 3.8 *Bromus tectorum* roots surrounding *Artemisia tridentata* ssp. *wyomingensis* roots.

CHAPTER 4

Responses of *Artemisia tridentata* seedlings to above- and belowground competition

Upekala C. Wijayratne and David A. Pyke

Introduction

Competition for limited resources can play a key role in determining growth, survival, and reproduction of individual plants (Fowler 1986, Reichenberger and Pyke 1990, Humphrey and Schupp 2004). Resource competition may occur simultaneously aboveground (e.g., light) and belowground (e.g., water, nutrients), and can interact to either intensify or counteract effects of the other (Cahill 2002, Song et al. 2006). Root and shoot competition can only interact if there is a mechanism for positive or negative feedback between the two forms. For example, shading from neighbors may reduce a plant's ability to take up nutrients (Jackson and Caldwell 1992) which may reduce aboveground growth and compound effects of shading. In contrast, when competition takes place primarily belowground (Cahill 1999), the two forms of competition typically do not interact because root competition is often proportional to the size of individuals competing (Weiner et al. 1997, Cahill and Casper 2000). Size-asymmetric competition takes place when a resource is preempted by a larger individual over a smaller individual, and the larger individual receives a disproportionately larger share of the resource for its relative size (Weiner 1990). The classic example of asymmetric competition is competition for light, where larger individuals compete more effectively than smaller individuals and compound effects of asymmetric competition over time (Weiner 1986). Competition for belowground resources can also be size-asymmetric if resources are heterogeneous in time and space (Schwinning and Weiner 1998, Rajaniemi 2003), if individuals have different uptake kinetics (Raynaud and Leadley 2005), or if individuals have a 'head start' (i.e., early phenology) (Rajaniemi 2003).

The relative importance of above- and belowground competition and their interactions may be species-specific, influenced by life history stage, and dependent on resource availability. In arid systems, where competition is primarily belowground (Casper and Jackson 1997), mature *Artemisia tridentata* Nutt. (hereafter *Artemisia*) plants compete successfully with grasses (Caldwell et al. 1985, Reichenberger and

Pyke 1990, Caldwell et al. 1991a, Caldwell et al. 1991b). However, when the size hierarchy is reversed at the *Artemisia* seedling stage, aboveground competition may influence successful seedling establishment. Invasion of the semi-arid sagebrush steppe ecosystem by *Bromus tectorum* L. (hereafter *Bromus*) is successful, in part, because the exotic annual grass germinates in the fall and winter when most native species are dormant (Stewart and Hull 1949, Mack and Pyke 1983). Rapid growth and uptake kinetics (Link et al. 1995, Monaco et al. 2003) enables *Bromus* to preempt resources when they become available. Within a few years after wildfires, *Bromus* cover increases significantly more than that of other species, especially in wet years (West and Hassan 1985, Jessop and Anderson 2007, Shinneman and Baker 2009) and the species is able to exploit water and suppress growth of native species (Melgoza et al. 1990). Furthermore, *Bromus* can form dense near-monocultures that may contribute to a more intense aboveground competitive environment than that experienced with native vegetation. This suite of traits may promote asymmetric competition between *Bromus* and *Artemisia* seedlings.

The sagebrush steppe is one of the largest biomes in North America and is ecologically and economically important (Sands et al. 1999, Knick et al. 2003, Maher 2007, Evans and Rollins 2008, Miller et al. 2011), but over the last century more than half of its original extent has been modified through various land-use changes, altered fire regimes and ensuing conversion to *Bromus* dominance (Whisenant 1990, D'Antonio and Vitousek 1992, Johnson et al. 1999, West 2000, Knick et al. 2003, Bradley and Mustard 2005, Miller et al. 2011). Restoration of one of the foundation species, *Artemisia tridentata*, is important for overall ecosystem resilience and sustainability. The species facilitates the herbaceous plant community (Caldwell and Richards 1989, Ryel et al. 1996, Halvorson et al. 1997, Karban et al. 2004, Huber-Sannwald and Pyke 2005), enhancing both native species diversity and biotic resistance to invasion (Levine 2000, Naeem et al. 2000, Prevey et al. 2010). Post-fire restoration of *Artemisia* can be difficult (Dalzell 2004, Lysne and Pellant 2004), and made even more so by the prevalence of *Bromus*. Mixtures of native and nonnative

species are often seeded by management agencies onto degraded sites to increase propagules pressure of desired species, inhibit establishment of exotic species, and provide immediate erosion control (Hilty et al. 2003, Mazzola et al. 2010). Consequently, understanding competitive interactions between *Artemisia* seedlings, *Bromus*, and other herbaceous vegetation is important to enhance success of restoration efforts.

The objectives of this study were to investigate whether and how root and shoot competition from three common Great Basin grasses affected *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (hereafter *Artemisia*) seedling growth, and whether root and shoot competition interacted or operated additively. *Agropyron ×hybrid* auct. (hereafter *Agropyron*), *Elymus wawawaiensis* J. Carlson & Barkworth (hereafter *Elymus*), and *Bromus tectorum* (hereafter *Bromus*) are examples of grasses that *Artemisia* seedlings may interact with during post-fire establishment: nonnative perennial bunchgrass, native perennial bunchgrass, and nonnative annual grass, respectively. Because of the rapid growth and potential preemption of resources by *Bromus*, we hypothesized that root and shoot competition would interact positively to amplify competitive intensity and decrease *Artemisia* plant growth. We also hypothesized that the two forms of competition from the perennial grasses would act additively on *Artemisia* growth because competition would primarily be from roots.

Methods

Study species

We obtained *Artemisia* seeds that were collected in Beaver County, Utah by Bureau of Land Management personnel, and *Bromus* seeds were collected from populations in Lake County, Oregon. For the perennial grasses, we used commercially available cultivars (Granite Seed Co., Lehi, UT). *Agropyron xhybrid* is the hybrid cultivar ‘Hycrest’, a cross between *Agropyron desertorum* (Fisch. ex Link) Schult. and *Agropyron cristatum* [L.] Gaertn. *Elymus wawawaiensis* was originally released as the ‘Secar’ cultivar of *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* and

continues to be seeded as a surrogate for that species throughout rangelands (Jones 2008, Ogle et al. 2010).

Experimental design

We placed 24 fiber nursery pots (22” diameter x 16” height [approx. 56 x 41 cm], Western Pulp Products, Corvallis, OR) in a completely randomized split-plot design (Fig. 4.1), with neighbor species as the whole-plot factor and fully crossed root and shoot competition treatments as split-plot factors. Neighbor treatments consisted of one of the three grass species described above and competition treatments included all neighbors (AN), root neighbors (RN), shoot neighbors (SN), and no neighbors (NN). Neighbor treatments were randomly assigned to pots and competition treatments were randomly assigned to each quadrant within a pot. There were eight replicates of each whole-plot factor (neighbor treatment) and 24 replicates of each split-plot factor (competition treatment).

We excluded roots for SN and NN treatments using vinyl tubes (2 x 3-inch downspouts [approx. 5 x 8 cm], Home Depot, Inc.) that were cut to approximately 35 cm in length. Shoots were excluded for RN and NN treatments with wire poultry netting surrounding focal *A. tridentata* seedlings, and maintained by pulling grass shoots out of the netting every few days. We filled pots with a mixture of two parts pasteurized loamy sand (Oregon State University greenhouses) and one part washed silica sand (Sakrete Natural Play Sand, Bonsal American Inc., Charlotte, N.C.). Root exclusion tubes were installed at the time when pots were filled with soil to minimize differences in bulk density of soil in- and outside tubes.

The experiment was conducted in a greenhouse in Corvallis, OR under ambient light. Temperatures ranged from 18.4–39.7°C during the day and 8.9–15.4°C at night over the course of the study. In early March 2011 each pot was planted with a neighbor grass species following the spatial arrangement shown in Fig. 4.1 (stars). Pots were watered daily for approximately 1 wk to allow grasses to germinate and establish, then watering decreased to once a week. In mid-March 2011 we sowed

several *Artemisia* seeds in the designated areas of each quadrant (Fig. 4.1, squares). Pots were watered daily for approximately 3 wk, until *Artemisia* germinants started to emerge. After 10 d, we thinned *Artemisia* seedlings to two replicates per quadrant and installed shoot exclusion treatments. At that time, seedlings were given one-tenth strength Hoagland's solution once and then watered once a week for the remainder of the experiment. After approximately 7 wk (51 d) of growth with all experimental treatments implemented, aboveground biomass of target plants was harvested, dried at 65°C for 48 h, and weighed. Cover of neighbor species at the whole-plot level was also recorded at this time.

Competitive response metrics

Root, shoot and total competition intensity were calculated as competitive responses (Cahill 1999, 2002) using the following equations:

$$\text{Belowground competitive response (BCR)} = \ln(\text{RN}/\text{NN})$$

$$\text{Aboveground competitive response (ACR)} = \ln(\text{SN}/\text{NN})$$

$$\text{Total competitive response}_{\text{observed}} (\text{TCR}_{\text{obs}}) = \ln(\text{AN}/\text{NN})$$

NN is focal plant biomass (always *A. tridentata*) when grown without neighbors (root exclusion tube and poultry fencing), RN is focal plant biomass when grown with root neighbors only (poultry fencing), SN is focal plant biomass when grown with shoot neighbors only (root exclusion tube), and AN is focal plant biomass when grown with shoot and root neighbors (no tube or fencing). The competitive response metrics are similar to the response ratio (Goldberg et al. 1999) where positive values indicate facilitation and negative values indicate competition, and is an index of a plant's response to competition. If root and shoot competition are additive, then predicted total competitive response is simply the sum of aboveground competitive response and belowground competitive response:

$$\text{Total competitive response}_{\text{predicted}} (\text{TCR}_{\text{pred}}) = \text{BCR} + \text{ACR}$$

Since BCR and ACR are calculated in a logarithmic scale, summing BCR and ACR is the equivalent of multiplying the proportional plant growth resulting from each competitive form in the back-transformed scale (Cahill 1999). If root and shoot competition do not interact, then TCR_{pred} would equal TCR_{obs} . If $\text{TCR}_{\text{obs}} < \text{TCR}_{\text{pred}}$, then plant growth is less than predicted and would indicate a positive interaction. $\text{TCR}_{\text{obs}} > \text{TCR}_{\text{pred}}$ would indicate a negative interaction.

Statistical analysis

Establishment of *Artemisia* focal plants was poor and did not occur in some split plots so we used PROC MIXED (SAS 9.2, SAS Institute Inc., Cary, N.C.) for analysis because it can appropriately handle unbalanced data. We examined effects of neighbor species and competition treatment on *Artemisia* biomass with a 2-way analysis of variance, using germination date of focal seedlings as a covariate (Littell et al. 2006). Biomass was natural log-transformed to meet assumptions of normally distributed data and a Bonferroni correction was used for multiple comparisons.

Competitive response metrics were calculated at the whole plot (neighbor species) level so only replicates with established *Artemisia* seedlings in the AN, SN, and RN split-plot treatments could be used. We further constrained this by using whole plots in which seedlings had germinated within 1-2 days of each other because variation in germination date may confound effects of competition treatments on focal plant biomass and bias response metrics. Additionally, poor establishment left some whole plots with no focal seedling in the NN split-plot treatment. Rather than discard records for lack of data in the NN treatment (that otherwise met the first two criteria), we averaged NN focal plant biomass within each neighbor species treatment and used that value to calculate ACR, BCR, TCR_{obs} , and TCR_{pred} for each whole plot. These constraints left a small number of replicates for each neighbor species (*Agropyron*, $N = 6$; *Bromus*, $N = 5$; *Elymus*, $N = 4$).

Because of the small sample sizes, we used a bootstrapping procedure to test whether there was a significant difference between TCR_{obs} and TCR_{pred} ($TCR_{obs} - TCR_{pred}$) within each neighbor species treatment (*sensu* Cahill 2002, Ramsey and Schafer 2002). We first calculated the actual difference between TCR_{obs} and TCR_{pred} . Then values of TCR_{obs} and TCR_{pred} were randomly assigned among true and predicted categories and the resulting mean difference calculated. Randomization was repeated 10,000 times with each resulting mean difference recorded (Resampling Stats Add-In, MS Excel 2003). Significance was determined as the proportion of randomized differences greater than or equal to (upper tail), or less than or equal to (lower tail) the actual mean difference between TCR_{obs} and TCR_{pred} for *Agropyron* and *Elymus*. A one-tailed test was performed for *Bromus* because we hypothesized that root and shoot competition would interact to magnify total competitive effects on *Artemisia* plant growth. If fewer than 5% of the randomized mean differences were found to be as extreme as the actual mean difference, then we could conclude that TCR_{obs} and TCR_{pred} were significantly different.

Results

Agropyron cover was lower and patchier than that of either *Bromus* or *Elymus* (Fig. 4.2). *Artemisia* focal plant biomass was significantly affected by neighbor identity and competition treatment independently (Table 4.1, Fig. 4.3). On average, plants grown in competition with *Bromus* had lower biomass than when grown with other species (*Bromus* - *Agropyron*: $t_{11.6} = -4.85$, $p < 0.001$; *Bromus* - *Elymus*: $t_{13.2} = -2.70$, $p = 0.02$). Both forms of competition with *Bromus* tended to decrease *Artemisia* biomass compared to biomass of seedlings grown with root and shoot exclusion treatments (root: $t_{70} = -1.84$, $p = 0.07$; shoot: $t_{68} = -1.88$), but full competition significantly decreased biomass (full: $t_{71.1} = -3.61$, $p < 0.001$). Only full competition with *Elymus* marginally decreased *Artemisia* biomass compared to control seedlings (*Elymus*: $t_{65.1} = -1.81$, $p = 0.07$) and *Agropyron* competition had no effect on *Artemisia* biomass at all.

There was no significant difference between TCR_{obs} and TCR_{pred} of *Artemisia* seedlings grown with any of the grasses (Table 4.2, Fig. 4.4). This indicates that root and shoot competition, when present, acted additively to affect *Artemisia* seedling growth.

Discussion

Competitive effects of these grasses on *Artemisia* growth were consistent with previous studies (Chapter 3) with *Bromus* having the most detrimental effect overall on *Artemisia* biomass. Total competitive intensity was highest with *Bromus* neighbors, where simultaneous root and shoot competition decreased *Artemisia* biomass by over 95%, relative to its biomass when grown without neighbors. Shoot competition alone decreased *Artemisia* growth by over 80%. This is in contrast to shoot competition with *Elymus*, which tended to decrease *Artemisia* biomass by approximately 50%. *Agropyron* shoot cover was low and heterogeneous in the present study, so we did not expect shoot competition to be a strong factor in affecting biomass of *Artemisia* seedlings growing with *Agropyron*.

Competition from *Bromus* is well documented to have negative effects on plant growth (Harris 1967, Melgoza et al. 1990, Melgoza and Nowak 1991, Humphrey and Schupp 2004, Vasquez et al. 2008) but to our knowledge this study is the only one that has isolated competitive effects of *Bromus* shoots from those of its roots. With the exception of *Agropyron*, stand structure was similar across neighbor treatments; therefore, any differences in shoot competition between neighbor treatments can be attributed to inherent differences in shoot traits of the different species. In a greenhouse study, *Bromus* seedlings had higher leaf area and specific leaf area than *A. desertorum* (one of the parent species to the *Agropyron* cultivar used in this study) (Svejcar 1990). High leaf area suggests that *Bromus* has the potential to cast more shade than *Agropyron* and may hold true for *Elymus* also. Variation in light quality is determined almost entirely by the structure of the canopy and the filtering effect of grasses can be described by a combination of cover, height and biomass (Skalova et al.

1999). Decreased germination and subsequent survival of *Artemisia californica* Less. in the presence of annual grasses (predominantly of the genera *Bromus* and *Avena*) was thought to be a result, at least in part, of reduced light at the soil surface due to the grass canopy and thatch (Eliason and Allen 1997). Surprisingly, even control *Artemisia* seedlings, grown with *Bromus* neighbors but excluded from both root and shoot competition, tended to have lower biomass than when grown with other neighbor species in similar competition scenarios. It is possible that some shading occurred from *Bromus* plants outside the shoot exclusion zone when the sun was at a low angle.

Root and shoot competition from any of the neighbor species did not interact, implying that competition between *A. tridentata* and grasses is size-symmetric. Plasticity in growth form or allocation of biomass may also reduce size-asymmetric competition (Schwinning and Weiner 1998). For example, grass-induced root competition increased woody plant seedling allocation to roots at the expense of leaves and vice versa with grass-induced shoot competition (Bloor et al. 2008). Another mechanism that can reduce size-asymmetric competition is contact avoidance, which has been demonstrated at the level of individual roots for some species of the sagebrush steppe (Krannitz and Caldwell 1995, Caldwell et al. 1996). However, we found no evidence that *Artemisia* seedlings change biomass allocation or avoid root contact when grown with these grasses (Chapter 3), and conclude that *Artemisia* and these grasses competed for resources in proportion to their size.

The caveat to this study is that it was conducted in a controlled environment with homogenous soil resources and low grass seedling densities (approx. 96 m⁻²) compared to field settings (Mack and Pyke 1983, Pyke 1990, Halvorson et al. 1994). Soil resources can be patchy in arid systems; therefore, root competition between *Artemisia* and these grasses may be more asymmetric than demonstrated here because larger plants can reach and preempt nutrient-rich patches from smaller individuals (Rajaniemi 2003). In a field experiment examining root interactions of *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, *Agropyron desertorum*, and *Pseudoroegneria*

spicata, nutrient patches between large grass plants and small shrubs had a greater ratio of grass to shrub roots than patches between small grass plants and large shrubs (Caldwell et al. 1996). This effect was not found in control patches devoid of nutrient enrichment, suggesting that larger grass plants were able to forage and take up a disproportionately larger share of the nutrients. Inorganic nitrogen can increase immediately after fire (Rau et al. 2007) and spatial heterogeneity of soil resources can be retained and may actually become more pronounced (Stubbs and Pyke 2005, Davies et al. 2009). Consequently, opportunities for asymmetric belowground competition still exist following fires.

In order for competition for water to be asymmetric, there must be a mechanism by which one plant obtains a disproportionate share of the resource. *Bromus* can germinate and begin growing during autumn or winter, giving it a ‘head start’ compared to native perennials which are typically dormant during winter or seedlings which germinate in early spring. *Bromus* competes strongly for water and can deplete soil moisture rapidly, reducing water status of other species (Melgoza et al. 1990). Water status of *Artemisia* seedlings has been linked to their ability to survive summer drought periods; smaller plants typically develop more water stress (Donovan and Ehleringer 1991, Donovan and Ehleringer 1994). *Artemisia* recruitment into monodominant *Bromus* stands in Utah was virtually nonexistent in comparison to recruitment into native perennial stands (Booth et al. 2003). They concluded that this was due, at least in part, to seedlings encountering moisture stress earlier in the season in *Bromus* stands. The early phenology of *Bromus*, combined with the ability to rapidly deplete soil moisture, essentially brings about summer drought conditions earlier.

In summary, root and shoot competition from the test grasses did not interact to affect *Artemisia* growth. *Bromus* competition suppressed growth the most, and both root and shoot competition independently had the ability to decrease *Artemisia* biomass by over 90%. Though asymmetric competition from any of the grasses was not evident, the proportional share of resources that establishing *Artemisia* seedlings

receive may be insufficient to maintain growth and allow survival. For example, dominance of perennial grasses can slow recovery of *Artemisia* in experimental removal plots (Boyd and Svejcar 2011). Moreover, even if *Artemisia* seedlings survive active competition during early spring when resources are plentiful, resource status of surviving seedlings may be too low to survive the stressful conditions of summer. Successful establishment of *Artemisia* in a restoration context may require selective thinning of desirable perennial grasses as well as removal of exotic annual grasses.

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Table 4.1 Effect of neighbor species identity (BRTE, AGHY, ELWA) and competition treatment (AN, RN, SN, NN) on *Artemisia tridentata* ssp. *wyomingensis* biomass.

Factor	df	<i>F</i>	<i>P</i>
Neighbor species	2, 12.6	11.86	< 0.01
Competition treatment	3, 67.2	5.32	< 0.01
Species X competition trt	6, 67.1	0.58	0.75
Germination date	1, 73.7	9.15	< 0.01

Notes: Experimental design was a completely randomized split-plot, with neighbor species as the whole-plot factor and competition treatment as the split-plot factor. An analysis of variance was conducted with neighbor species (BRTE = *Bromus tectorum*, AGHY = *Agropyron xhybrid*, ELWA = *Elymus wawawaiensis*) and competition treatment (AN = all neighbors, RN = root neighbors, SN = shoot neighbors, NN = no neighbors) as fixed effects and germination date as a covariate.

Table 4.2 Results of the bootstrapping procedure to test whether root and shoot competition act additively on *Artemisia tridentata* ssp. *wyomingensis* growth. $TCR_{obs} < TCR_{pred}$ indicates root and shoot competition interact to amplify effects of each form. $TCR_{obs} > TCR_{pred}$ indicates that one form of competition reduces the severity of the other form. Proportions indicate significance at $\alpha = 0.05$ in a 2-tailed test for *Agropyron xhybrid* and *Elymus wawawaiensis* neighbors, and a 1-tailed test for *Bromus tectorum*.

Species	Difference between TCR_{obs} and TCR_{pred}	Proportion of randomized mean differences more extreme than actual mean difference
<i>Agropyron xhybrid</i>	1.55	0.23
<i>Bromus tectorum</i>	-0.11	0.50
<i>Elymus wawawaiensis</i>	2.12	0.14

Notes: We first calculated the actual difference between actual total competitive response (TCR_{obs}) and predicted total competitive response (TCR_{pred}). Then the values of TCR_{obs} and TCR_{pred} were randomly assigned among the true and predicted categories and the resulting mean difference calculated. Randomization was repeated 10,000 times with each resulting mean difference recorded. Significance was determined as the proportion of randomized differences greater than (upper tail) or less than (lower tail) the actual mean difference between TCR_{obs} and TCR_{pred} . A one-tailed test was performed for *B. tectorum* because we hypothesized that root and shoot competition would interact to magnify total competitive effects on *A. t. ssp. wyomingensis* plant growth.

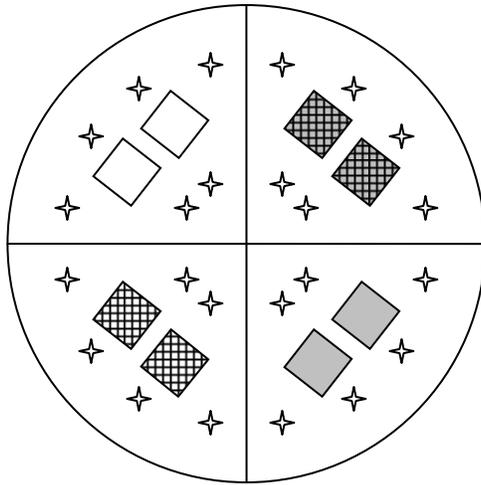


Figure 4.1 Schematic of planting arrangement and example split-plot treatments within a whole plot (defined by neighbor species). Squares represent location of *Artemisia tridentata* ssp. *wyomingensis* focal seedlings within a split plot. Stars represent location of neighbor seedlings. Competition treatments are root and shoot competition (open), root competition only (cross hatch), shoot competition only (shading), and no competition (cross hatch + shading).

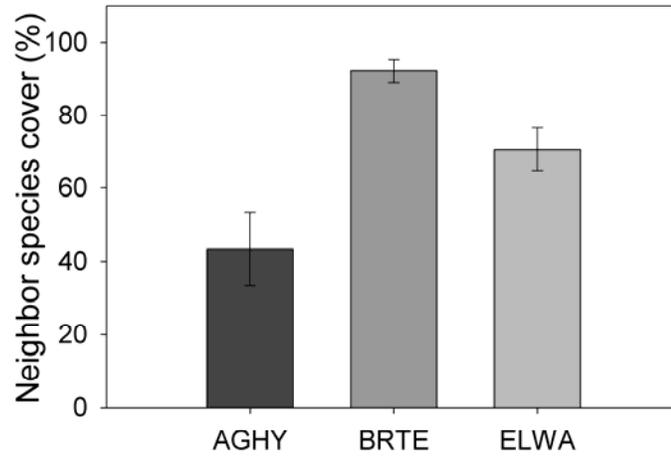


Figure 4.2 Mean percent cover (\pm SE) of neighbor species in whole plots. $N = 6$ for *Agropyron xhybrid* (AGHY), $N = 7$ for *Bromus tectorum* (BRTE), and $N = 8$ for *Elymus wawawaiensis* (ELWA).

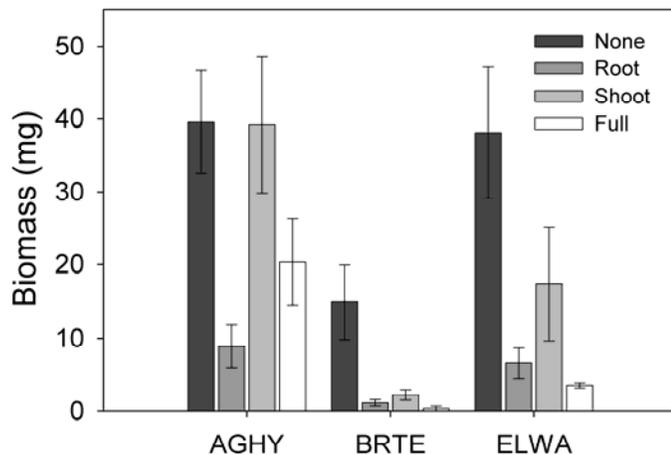


Figure 4.3 Mean *Artemisia tridentata* ssp. *wyomingensis* dry biomass (\pm SE) grown with *Agropyron xhybrid* (AGHY), *Bromus tectorum* (BRTE), and *Elymus wawawaiensis* (ELWA). Shading indicates competition treatment: none, root only, shoot only, and full (both root and shoot).

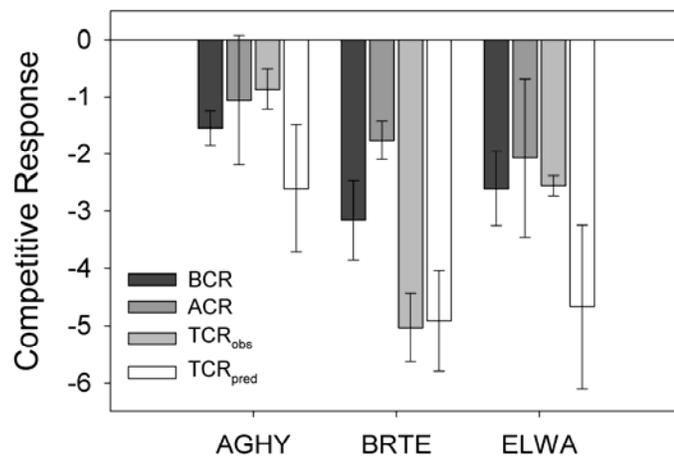


Figure 4.4 Mean competitive response (\pm SE) of *Artemisia tridentata* ssp. *wyomingensis* grown with *Agropyron x hybrid* (AGHY), *Bromus tectorum* (BRTE), and *Elymus wawawaiensis* (ELWA). Shading indicates response to competition treatment: belowground (BCR), aboveground (ACR), total as directly measured (TCR_{obs}), and total as predicted by summing BCR and ACR (TCR_{pred}).

CHAPTER 5

General Conclusions

One of the major obstacles to overcome in restoring sagebrush steppe ecosystem is establishment of one of the foundation species, *Artemisia tridentata*. The species plays a critical role for wildlife species and also provides many positive benefits to the herbaceous community, thus increasing overall biotic resistance and resilience to invasion. The ecosystem has undergone a vast transformation over the last century and, unfortunately, continues to degrade through land-use changes, exotic species invasions and altered ecological processes. As a result of crossing an ecological threshold, degraded areas require active restoration costing huge amounts of effort and money to achieve successfully. A thorough understanding of *A. tridentata* establishment ecology would be beneficial to this endeavor. To that end, I sought to contribute to the body of knowledge regarding *A. tridentata* restoration with studies on short-term seed longevity after dispersal and on interference responses of seedling roots and growth. The major objectives were to determine 1) if *A. tridentata* can form a seed bank and under what conditions it does so, 2) whether *A. tridentata* seedling growth is affected by root interactions, chemically mediated or not, with common Great Basin grasses or conspecifics, and 3) how root and shoot competition from common Great Basin grasses affect *A. tridentata* seedling growth.

Results from Chapter 2 suggest seeding techniques that allow burial of some seeds in the soil may increase restoration success by enhancing the ability of the species to maintain a seed pool and hedging against the potential for failure of establishment in the initial year of seeding. Preliminary results from monitoring rehabilitation projects indicate that successful establishment from aerial seeding depends on precipitation in the following year (Wirth and Pyke, *unpublished data*), but this relationship does not hold true for drill seedings. Since precipitation is already somewhat unpredictable and may become more so with climate change, seeding methods that promote formation of a seed bank may be in order. Soil seed banks can compensate for unpredictable and unfavorable environmental conditions over the long-term (Guterman 1994, Holmgren et al. 2006) and increase odds that viable seeds are available when conditions are optimal for recruitment. Restoration methods that

ensure seed contact with soil such as pressing seeds into the soil surface, creating microdepressions in the soil, drilling, and harrowing or raking can greatly increase seedling establishment (Haferkamp et al. 1987, Pyke 1994, Turner et al. 2006). A consequence of these methods may be shallow burial of some seeds which could potentially become a seed source for future years (Booth 2002). An added benefit to burial may occur if seeds survive subsequent wildfires and contribute to shrub re-establishment (Lattera et al. 2006, Ziegenhagen and Miller 2009). Millions of dollars are spent seeding areas after fires (Knutson et al. 2009); therefore, intentional burial of some *A. tridentata* seeds may yield better results both ecologically and economically than do surface-seeding methods.

The role of competition and its importance in determining vegetation dynamics in resource-poor environments has been debated for decades (Grime 1973, 1979, Tilman 1982, Welden and Slauson 1986, Tilman and Cowan 1989, Goldberg and Novoplansky 1997). Harsh abiotic conditions may be the ultimate overriding factor determining seedling establishment in the sagebrush steppe; however, plant competition may reduce *A. tridentata* seedling performance during periods of benign abiotic conditions (i.e. early spring) to the point of negatively influencing survival during stress periods. Competition may not kill seedlings immediately but it may decrease the ability of seedlings to withstand summer drought. For example, I demonstrated that competition from *B. tectorum* reduced lateral branching of *A. tridentata* roots (Chapter 3). If this occurs, seedlings may be less able to effectively capture shallow soil moisture during the growing season, an important resource for juvenile *A. tridentata* (Donovan and Ehleringer 1994). This is consistent with studies that have found that *A. tridentata* seedling establishment is negatively affected by high densities of *B. tectorum* (Mazzola et al. 2010). This effect likely results from competition for water (Booth et al. 2003). These results suggest that selective thinning or removal of potential competitors may be required to benefit resource status of seedlings before the summer drought period commences. This is especially important in areas with a substantial *B. tectorum* seed bank, where pre-seeding treatment with

herbicides may not be enough to curtail all *B. tectorum* competition. Perennial grass competition was not as detrimental as competition with *B. tectorum*; however, root competition with perennial grasses did decrease *A. tridentata* growth to some extent. A recent study showed that *A. tridentata* increased in abundance over a 10-year period in plots where perennial grasses had been removed, suggesting that *A. tridentata* seedling establishment may have benefited from reduced competition (Boyd and Svejcar 2011).

An unintended consequence of the experimental design in Chapter 3 was the fertilizing effect of activated carbon on plant growth. Activated carbon can affect soil nutrients in numerous ways (Lau et al. 2008). In a promising study by Kulmatiski and Beard (2006), activated carbon amendments to soil (1% by mass) decreased ground cover of *B. tectorum* in experimentally seeded plots and increased native perennial grass cover after six years. In my study, activated carbon (2% by volume) did not change aboveground biomass of *B. tectorum* plants but did significantly increase root biomass, potentially increasing competitive ability of *B. tectorum*. Activated carbon also increased root biomass of *A. tridentata* seedlings which may be beneficial for surviving the summer drought. While these experimental conditions were vastly different from each other, it is clear that more research regarding use of activated carbon as a restoration tool is needed. Managing microbial communities through soil amendments is a relatively new restoration application but there is still little known about how activated carbon affects soil microbial communities and consequently alters plant communities (but see Kulmatiski 2011).

Future Directions

Management of the sagebrush steppe has changed radically since the early part of the 20th century. Historically, *A. tridentata* was actively eradicated to increase herbaceous production on rangelands (Suring et al. 2005), but with several studies underscoring the importance of the shrub to overall ecosystem function the emphasis has shifted to its restoration. The most critical stage in restoring *A. tridentata* is

seedling establishment. At what point do seedlings become “established”? What factors increase the probability of this happening?

Studies suggest that recruitment of *A. tridentata* occurs in pulses coinciding with favorable climatic conditions (Cawker 1980, Maier et al. 2001, Perryman et al. 2001). Historic recruitment of *A. t. ssp. wyomingensis* and *A. t. ssp. vaseyana* was correlated with above-average winter precipitation and below-average early spring precipitation, respectively, occurring after the first growing season (Maier et al. 2001). But what climatic conditions are required to get seedlings of these subspecies to survive through the first growing season and into the second? Soils are typically saturated with winter or early spring precipitation and shallow soil layers can be recharged with summer precipitation (Caldwell 1985). Mortality of juvenile *A. t. ssp. tridentata* in the summer, however, is correlated with water stress (Donovan and Ehleringer 1991) and 2-year old juvenile plants were found to take up more summer precipitation than adult plants, presumably because they were more reliant on shallow roots (Donovan and Ehleringer 1994). Under climate change scenarios, an overall warming trend from 1 to 4°C is predicted and availability of water is expected to increase in the form of rain and earlier snowmelt during winter, while summers become drier and hotter (Chambers et al. 2008, Hughson et al. 2011). The implication of this forecast is that establishing seedlings will become nearly solely reliant on winter precipitation as there will be little summer precipitation. Is there a tradeoff between allocating more resources toward extension of the taproot versus branching in the shallow soil layers? Do precipitation patterns during root development influence root morphology? Elucidating traits and characteristics of successfully established seedlings may provide a basis for choosing certain morphotypes for use in restoration projects.

Naturally recruiting *A. tridentata* is likely highest in vegetation gaps where there is some release from soil resource competition. Many restoration plans call for seeding with mixtures of native and nonnative perennial grasses in addition to *A. tridentata*. Because the early seedling stage is so vulnerable, this may not be the best

method for optimal shrub recruitment. The goal of many of these restoration efforts is to prevent erosion and quickly get vegetation established that will effectively exclude annual grass invasion, with shrub establishment as an afterthought. Under these circumstances, it may be useful to know which perennial grasses or combination of grasses can accomplish stabilization of the area and may be most beneficial (or least constraining) to *A. tridentata* seedling establishment. For example, Booth et al. (2003) found no natural *A. t. ssp. wyomingensis* recruitment in monotypic *B. tectorum* stands but did find seedlings in mixed-grass stands where *Elymus elymoides* was displacing the exotic grass (Booth et al. 2003). The authors concluded that shrub seedlings recruiting into *B. tectorum* stands would have encountered earlier water stress than when establishing in *A. tridentata* or *E. elymoides* stands, and that displacement of *B. tectorum* by *E. elymoides* may have returned the soil moisture environment to pre-invasion conditions. More research of this type would be helpful in identifying appropriate seeding mixes for optimal shrub recruitment.

It is clear that restoration of *A. tridentata* hinges upon many different factors. Complex, interacting ecological processes have been at work for thousands of years determining a single seedling's chance of establishment; this strategy had been extremely successful at the population level as evidenced by the journals of pioneers. The difference today is that key ecosystem processes have been altered from historic conditions, and the rate of that change over the last century has outpaced the ability of *A. tridentata* to adapt. Restoration in the face of climate change will prove to be even more challenging. How will the predicted warming and precipitation scenarios affect *A. tridentata* seedling establishment? While higher winter precipitation appears to be good for *A. tridentata* recruitment, more precipitation may increase productivity of, and potentially competition from, other species as well. Because we cannot control the climate, successful restoration of this species will require simultaneously minimizing constraints that decrease the probability of establishment (e.g., removal of competition) and maximizing or manipulating processes that increase establishment probability (e.g., overcoming propagule limitation) (Suding et al. 2004). Practices that

are bet-hedging, such as promoting seed bank formation, will be especially useful in an increasingly unpredictable environment.

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Appendix

Appendix A. Species list (non-comprehensive) by site.

Species	JUWY	JUVA	MHWY	MHVA	LLWY	LLVA	SAWY	SAVA	TOWY	TOVA	HUWY	HUVA
Trees/Shrubs/Sub-shrubs												
<i>Abies lasiocarpa</i>								X				
<i>Amelanchier alnifolia</i>								X		X		X
<i>Artemisia nova</i>										X		
<i>Artemisia tridentata</i>	X	X	X	X	X	X	X	X	X	X	X	X
<i>Artemisia tripartita</i>					X							
<i>Atriplex spinosa</i>									X			
<i>Chamaebatiara millefolium</i>						X						
<i>Chrysothamnus viscidiflorus</i>		X										
<i>Ericameria nauseosa</i>	X		X	X	X	X	X	X	X		X	X
<i>Juniperus occidentalis</i>	X	X					X			X		
<i>Mahonia repens</i>								X				
<i>Pinus monophylla</i>								X				
<i>Purshia tridentata</i>		X				X				X		X
<i>Rosa sp.</i>						X						
<i>Sarcobatus vermiculatus</i>											X	
<i>Sphaeralcea sp.</i>									X			
<i>Symphoricarpos oreophilus</i>						X		X				
Grasses												
<i>Achnatherum hymenoides</i>									X		X	
<i>Achnatherum thurberianum</i>	X		X	X					X			
<i>Agropyron cristatum</i>						X						
<i>Bromus arvensis</i>		X										

Notes: X = presence

Appendix A. (continued)

Species	JUWY	JUVA	MHWY	MHVA	LLWY	LLVA	SAWY	SAVA	TOWY	TOVA	HUWY	HUVA
Grasses (continued)												
<i>Bromus tectorum</i>	X	X	X	X	X		X		X	X	X	X
<i>Elymus elymoides</i>	X	X	X	X	X				X		X	X
<i>Koeleria macrantha</i>										X		X
<i>Leymus cinereus</i>			X			X					X	
<i>Melica spectabilis</i>								X				
<i>Pascopyrum smithii</i>		X										
<i>Poa bulbosa</i>		X										
<i>Poa fendleriana</i>						X		X				
<i>Poa nemoralis</i> ssp. <i>interior</i>								X				
<i>Poa secunda</i>	X	X	X	X	X		X	X	X	X	X	X
<i>Pseudoroegneria spicata</i>	X	X		X		X	X	X		X		X
<i>Taeniatherum caput-medusae</i>		X										
<i>Vulpia microstachys</i>	X		X	X								
<i>Vulpia octoflora</i>	X											
Forbs												
<i>Achillea millefolium</i>						X						
<i>Agoseris</i> sp.			X	X	X	X				X		
<i>Allium acuminatum</i>	X	X	X			X	X	X		X		X
<i>Alyssum desertorum</i>					X				X			
<i>Amsinckia</i> sp.	X	X		X								
<i>Antennaria</i> sp.	X	X	X	X	X					X		
<i>Arenaria</i> sp.	X									X		

Notes: X = presence

Appendix A. (continued)

Species	JUWY	JUVA	MHWY	MHVA	LLWY	LLVA	SAWY	SAVA	TOWY	TOVA	HUWY	HUVA
Forbs (continued)												
<i>Astragalus filipes</i>	X		X				X					
<i>Astragalus purshii</i>	X	X		X				X	X	X		X
<i>Astragalus sp.</i>							X			X		X
<i>Balsamorhiza sagittata</i>			X			X		X		X		
<i>Blepharipappus scaber</i>	X	X										
<i>Calachortus sp.</i>		X			X							X
<i>Castilleja angustifolia</i>							X	X		X		
<i>Ceratocephalus testiculatus</i>	X	X			X		X	X	X			X
<i>Chaenactis sp.</i>				X	X							
<i>Cirsium sp.</i>		X	X									
<i>Collomia sp.</i>	X	X										
<i>Collinsia parvifolia</i>		X				X	X	X				X
<i>Comandra umbellata</i>								X		X		
<i>Crepis sp.</i>	X	X		X			X			X		X
<i>Cryptantha sp.</i>				X	X				X			X
<i>Cymopterus longipes</i>								X				
<i>Delphinium nuttallianum</i>				X				X	X			
<i>Draba sp.</i>	X											
<i>Epilobium sp.</i>	X	X										
<i>Erigeron sp.</i>	X				X			X				
<i>Eriogonum sp.</i>		X					X			X		X
<i>Erysimum sp.</i>	X								X	X		

Notes: X = presence

Appendix A. (continued)

Species	JUWY	JUVA	MHWY	MHVA	LLWY	LLVA	SAWY	SAVA	TOWY	TOVA	HUWY	HUVA
Forbs (continued)												
<i>Fritillaria atropurpurea</i>						X						
<i>Fritillaria pudica</i>			X			X						
<i>Gayophytum ramosissimum</i>					X							
<i>Hollisteum umbellatum</i>	X			X	X							
<i>Lepidium campestre</i>			X	X	X							
<i>Lepidium perfoliatum</i>	X								X			
<i>Lewisia sp.</i>	X											
<i>Linum sp.</i>										X		
<i>Lithospermum ruderale</i>						X						
<i>Lomatium sp.</i>	X	X		X		X	X	X		X		X
<i>Lupinus sp.</i>				X		X		X				
<i>Mentzelia sp.</i>	X								X			
<i>Mertensia longiflora</i>						X						
<i>Myosotis sp.</i>												X
<i>Nothocalais troximoides</i>							X				X	X
<i>Oenothera caespitose</i>									X			
<i>Opuntia sp.</i>								X	X		X	
<i>Penstemon sp.</i>											X	
<i>Phlox longifolia</i>	X	X	X	X		X	X	X	X	X	X	X
<i>Phlox multiflora</i>							X					
<i>Tragopogon sp.</i>		X		X								
<i>Viola sp.</i>						X						
<i>Zigadenus sp.</i>		X					X					X

Notes: X = presence

