

Mountain Big Sagebrush (*Artemisia tridentata* ssp *vaseyana*)

Seed Production

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ABSTRACT

Mountain Big Sagebrush (*Artemisia tridentata* ssp *vaseyana*) Seed Production

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Big sagebrush (*Artemisia tridentata* Nutt.) is the most widespread and common shrub in the sagebrush biome of western North America. Of the three most common subspecies of big sagebrush (*Artemisia tridentata*), mountain big sagebrush (ssp. *vaseyana*; MBS) is the most resilient to disturbance, but still requires favorable climactic conditions and a viable post-fire seedbank for successful unassisted recovery. This study was designed to assess MBS seed production throughout post-fire recovery. We performed 2 pilot studies to develop methods for estimating seed production and plant age. The results of the pilot studies and a space-for-time substitution strategy were used to measure seed production on 13 sites ranging from 10-33 years post-fire. We hypothesized that seed rain (mean seeds produced/ m²) would peak before stand density had maximized due to decreasing individual plant fecundity (mean seeds produced/ plant) in high density stands. We measured population density and individual plant fecundity for three size classes of MBS and used forward stepwise regression analysis to identify environmental factors influencing seed production over time. Density for small (basal stem diameter <1 cm) and medium-sized (basal stem diameter =1-3 cm) plants was consistently low and was not affected by time since fire (TSF), while large-sized (basal stem diameter > 3 cm) plant density increased steadily with TSF ($p=0.0002$). Plant fecundity decreased with TSF for all three size classes (p range = 0.019 – 0.0506), with large plants dominating reproductive output. Small and medium-sized plant fecundity was negatively correlated with winter precipitation (p range = 0.0106-0.0174), while large plant fecundity was positively correlated with winter precipitation ($p<0.0001$) and negatively correlated with elevation ($p=0.0001$). Despite losses in plant fecundity over time for all size classes, steady recruitment in population density resulted in increased seed rain ($p=0.0039$), suggesting that increases in stand density compensated for losses in individual plant fecundity. Results partially support our hypothesis that the time required for MBS seed rain to be maximized was not tightly bound to indicators of stand maturation. Understanding the factors that influence post-fire seed production can help land managers better manage for successful recovery by providing them with tools for evaluating seed production capabilities of MBS communities.

Keywords: age estimation, fire, plant fecundity, plant density, seed rain, shrub cover

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Introduction

Historically, the sagebrush biome was the most widespread non-forest vegetation type in temperate North America, covering 62 million hectares (McArthur and Plummer, 1978; Barbour and Billings, 1988). Today, this biome is considered one of the most at-risk ecosystems in the United States (Davies et al., 2011; Wisdom et al., 2005). It was reported (2002 survey) that sagebrush ecosystems occupy only 43 million hectares of their original range, a loss of more than 30% (Comer et al., 2002; Wisdom et al., 2003). While this decline in spatial distribution is troubling, perhaps of greater concern is the decline in sagebrush habitat quality. Lower quality results from fragmentation and ecological degradation caused by land conversion (e.g. agriculture, urbanization, energy development, etc.), overgrazing, invasive species, displacement by conifer tree encroachment, annual grass invasion, and altered fire regimes, all of which are difficult and costly to restore (Davies et al., 2011; Miller et al., 2011; Schroeder et al., 2004; Knick, et al., 2003). These influences can alter natural ecological processes that can further degrade rangeland resources availability (West and Young, 2000; Connelly et al., 2004; Monson and Shaw, 2000; Billings 1994; Miller and Rose, 1999; Miller et al., 2000). Consequently, sagebrush communities have become the focus of significant conservation efforts pointing to a need for improved land management practices (Davies, et al. 2011; Connelly et al., 2004, Davis et al., 2015).

The most widespread and dominant shrub in the sagebrush biome is big sagebrush (*Artemisia tridentata* Nutt.). This species grows on plains, valleys, foothills, and mountain slopes between 490-3,400 m elevation (McArthur and Stevens, 2004). Mountain big sagebrush (*A. tridentata* Nutt. ssp *vaseyana* (Rydb.) Beetle; MBS) is a subspecies of big sagebrush that is found throughout the Intermountain West and is an important component of the shrub-steppe

ecoregion. Compared to two other common big sagebrush subspecies, Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle and Young) and basin big sagebrush (*A. tridentata* ssp. *tridentata*), mountain big sagebrush occurs at relatively high elevations (2100-3200m) in semi-arid regions where soil and climate conditions are cooler and wetter (mean annual precipitation 300-700 mm; Beetle and Young, 1965; Meyer, 1994; Connelly et al., 2004; Cleary et al., 2010).

Mountain big sagebrush occurs in association with numerous tree species including quaking aspen (*Populus tremuloides* Michx.), true (*Pinus edulis* Engelm.), and single-needle (*P. monophylla* Torr. & Frém) pinyon pines, Utah (*Juniperus osteosperma* (Torr.) Little) and Rocky Mountain (*Juniperus scopulorum* Sarg.) junipers, ponderosa (*Pinus ponderosa* Lawson & C. Lawson) and limber (*Pinus flexilis* James) pines, white (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) and subalpine (*Abies lasiocarpa* (Hook.) Nutt.) firs, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco; Tueller et al. 1979). At lower elevations mountain big sagebrush may also dominate large treeless landscapes and co-exist with shrub species such as Gambel oak (*Quercus gambelii* Nutt.), snowberry (*Symphoricarpos oreophilus* A. Gray), common juniper (*Juniperus communis* L.), currants (*Ribes* L. spp.), Oregon grape (*Mahonia repens* (Lindl.) G. Don), mountain mahogany (*Cercocarpus* Kunth spp.), serviceberry (*Amerlanchier* Medik. spp.), antelope bitterbrush (*Purshia tridentata* Curran), rabbitbrush (*Chrysothamnus* Nutt. spp.), and green ephedra (*Ephedra viridis* Peebles; Kitchen and McArthur, 2007). The understory of mountain big sagebrush communities is composed of numerous species of perennial forbs and grasses. Many forbs and a host of insect species associated with this ecosystem make up a substantial portion of the diet for juvenile greater sage-grouse (*Centrocercus urophasianus* Bonaparte) while sagebrush plants provide food, cover and nesting locations for both young and adult birds (Barnett and

Crawford, 1994; Welch et al. 1991). MBS is also considered an important habitat and food source for mule deer throughout the Intermountain West (Welch and McArthur, 1986).

Fire is the most common natural disturbance that occurs in MBS dominated communities (Write and Bailey, 1982). There has been much research done on historical fire return intervals for MBS communities, using varying methods and producing varying results. Estimates of fire free intervals range from 12-25 years (Miller and Rose, 1999) to 40-80 years (Houston, 1973; Arno and Gruell, 1983; Heyerdahl et al., 2006; Kitchen and McArthur, 2007) or even 130-200 years (Baker et al, 2006). Most studies suggest that sufficient recovery requires at least 20-35 years under favorable conditions, or longer when climatic conditions do not allow for rapid recovery (Kitchen and McArthur, 2007). However, pre-settlement fire regimes have been altered and are continuing to change as a result of introduced exotic plant species, woody species encroachment (i.e. pinyon-juniper woodlands), and human-related activities (i.e. livestock grazing, human-caused fires, fire suppression, etc.) (Bukowski and Baker, 2013; Connelly et al., 2004, Miller and Rose, 1999; Billings, 1994).

An adult MBS plant may produce more than 350,000 seeds per year under ideal conditions (Goodwin, 1956); however, seed production may vary from year to year depending on resource availability, disease, excessive browsing, and competition (Young et al., 1989; Wagstaff and Welch, 1991; Meyer, 1994). Seed ripens in mid-September at higher elevations, but may not ripen until November at lower elevations (Bleak and Miller, 1955). Big sagebrush seeds are relatively short-lived. The majority of the seed does not generally persist longer than one growing season (Wijayratne and Pyke 2012; Ziegenhagen and Miller, 2009; Young and Evans, 1989). Therefore, seedbank persistence requires annual replenishment.

Based on life history models developed by Grime's (1974), mountain big sagebrush is classified as a "competitive" species, adapted to low stress and low disturbance environments (Bonham et al. 1991). These adaptations include faster growth rates, moderate annual seed production, and high energy investment in vegetative growth (McArthur and Welch, 1982; Meyer, 1994). MBS seedlings exhibit slower root growth rates and moderate tissue growth rates compared to other big sagebrush subspecies (Booth et al., 1990; Welch and Jacobson, 1988). At higher elevations where plants are less limited by water, competition for space and light become key factors for survival.

The purpose of this study was to examine temporal trends in post-fire seed production of mountain big sagebrush. Two pilot studies were conducted in order to develop methods for estimating floret production (Chapter 1) and plant age (Chapter 2). The results from the first pilot allowed us to develop estimates of fecundity (seeds produced per individual) for MBS plants on each site. The results of the second pilot were used to designate plant size class groupings and helped ensure that we were sampling plants across a range of ages, and also allowed us to examine changes in fecundity over time. We used a space-for-time substitution to examine differences in seed production among 13 recovering mountain big sagebrush communities varying in time since fire (Chapter 3). We identified factors impacting plant density, fecundity and total seed rain.

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Chapter 1

Estimating seed production of mountain big sagebrush (*Artemisia tridentata* spp *vaseyana*) in sagebrush dominated communities

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Abstract

Seed production of mountain big sagebrush (*Artemisia. tridentata* Nutt. ssp *vaseyana* (Rydb.) Beetle; MBS) is an important component of site recovery following disturbance. It may also be a useful indicator of ecological resiliency, site condition, and stability. The purpose of this study was to develop and test a method for rapidly and accurately predicting potential seed production using non-destructive field-based measurements. We collected a total of 750 MBS inflorescences from five different sites in central and southcentral Utah. Along with obtaining a count of seeds (florets) per inflorescence, we measured a suite of other variables of the inflorescence, including inflorescence length, inflorescence length from first branch, diameter, weight, and number of branches, to determine correlation significance. We used regression analysis to test for associations between all variables and total seed production. We evaluated each characteristic based on its ability to predict seed production (r^2 value) and its efficiency and practicality for field use. Stem weight was identified as the most useful characteristic for predicting seed production ($p < 0.0001$, $r^2 = 0.92$), although all other variables tested were also significantly correlated to seed production, but to a lesser degree. We used a regression equation based on inflorescence weight to predict inflorescence seed production. Because of the inherent variability among and within sagebrush communities, a regression equation may need to be developed on a case by case basis before this method could be applied to a broader geographical area. However, the ability to quickly and accurately estimate seed production using the methods proposed in this

manuscript could be a valuable tool for land managers and an important tool for tracking sagebrush recovery.

Keywords: mountain big sagebrush, seed production, fire

Introduction

Sagebrush seed production and subsequent sagebrush establishment is an important mechanism for long-term stability and ecological resiliency of mountain big sagebrush communities in relation to disturbance (Young et al., 1989, Chambers et al., 2014). Mature mountain big sagebrush (*A. tridentata* Nutt. ssp *vaseyana* (Rydb.) Beetle; MBS) plants can produce more than 350,000 seeds per square meter under ideal conditions (Goodwin 1956). Seed production varies from year to year in response to general site conditions, within stand competition and periodic pulses of disturbance by insect defoliators, disease, and excessive browsing by ungulates (Carpenter and West 1988; Meyer 1994; Rodriguez and Welch, 1989; Wagstaff and Welch, 1991; Welch, 1997; Welch and Nelson, 1995; Young et al., 1989).

MBS cannot sprout from roots or crown and relies entirely on seed for regeneration following a fire (Young and Evans, 1975). The soil seed bank in sagebrush communities is short-lived, with most seed germinating by late spring of the following year (Young at Evans, 1989; Stevens et al., 1981). There is some evidence that a small fraction of the seed may remain viable for up to 5 years (Bakker et al., 1996; Thompson et al., 2003; Wijayratne and Pyke, 2012); however, the majority of the seed bank must be replenished annually (Meyer, 1994; Young and Evans, 1989; Ziegenhagen and Miller, 2009). Because annual seed production is highly variable, but also a useful indicator of site condition, it would be beneficial to further investigate

sagebrush community dynamics and disturbance recovery in relation to seed production potential.

The purpose of this study was to develop a method for rapid and accurate prediction of MBS potential seed production using non-destructive field-based measurements. Our objective was to identify inflorescence characteristics that are highly correlated with inflorescence seed production, and use these correlations to develop a method for estimating seed production. This method could be a valuable tool for measuring and predicting post-disturbance ecological response within sagebrush communities. The ability to efficiently assess sagebrush seed production will expand our knowledge of ecological succession, leading to more informed management decisions and new methods for assessing ecological resilience.

Methods

Study Site Description and Plot Selection

Five MBS dominated sites were selected for this study, four located in south-central Utah and one in central Utah (Table 1.1, Fig. 1.1). Preference was given to sites with low to moderate livestock use and the presence of a well-developed native perennial understory where seed production would be representative of a typical healthy MBS community. There was little to no tree encroachment observed at any site.

Sample Collection

We collected samples in fall 2009 when fruits (achenes) were partially developed but before full maturation and dispersal had occurred (September 4- October 15; Bleak and Miller, 1955). Sample collection was timed to occur in advance of seed maturation and indeterminate seed shatter. We selected and harvested inflorescences from 5-20 plants at each site, representing

a wide range of inflorescence lengths. Inflorescences were picked by hand or clipped with pruning shears at the intersection between the reproductive and vegetative tissues. This was repeated until the desired number of inflorescences had been collected, approximately 350 from the central Utah site and 100 from each of the south-central Utah sites. The weight of each individual inflorescence was measured to the nearest gram in the field using a digital hanging scale, or in the laboratory soon after sample collection using a digital balance scale. Samples were placed in zip-lock style bags on ice during transport and stored in the lab at $\sim 2-4^{\circ}\text{C}$ until processed.

Lab Analysis

In addition to inflorescence weight, we also measured inflorescence length (using a standard ruler), the maximum diameter of each inflorescence stem (using digital calipers), the length from the point of the first branch to the end of the inflorescence (using a standard ruler), and the total number of branches. A branch was defined as being at least 2 cm long. The number of florets or achenes (hereafter referred to as seeds) per inflorescence was counted using dissecting forceps and recorded for each stem. Pedicels were counted if the seeds had become dislodged. Germination rates were not considered or measured, and therefore only potential seed production could be estimated. A total of 750 individual samples were measured, removing any samples that had been damaged during transport to the lab (i.e. broken stems, broken or missing branches, broken or missing tips, etc.).

Statistical Analysis

To test the relationship between each stem characteristic and the number of seeds produced per inflorescence, we conducted model selection in program R (R Development Core Team, 2011). We performed a square-root transformation to normalize the data and decrease the

variance for statistical testing. We tested for multicollinearity when comparing variables to prevent combining multiple correlated independent variables into a single model. This limited the number of possible models that we could create. Five models were developed to compare the strength of each individual characteristic as an indicator of seed production. Five additional models were created to include “site” as a variable, making it possible to test for effects of multiple sampling locations (Table 1-2). We assessed the r^2 values of the ten models to compare model fitness. We accepted p-values <0.05 as significant.

Results

All explanatory variables included in this study demonstrated a significant ($p<0.001$) correlative relationship with the response variable (Table 1.2). The strongest relationship was observed between total seed production and inflorescence weight ($r^2=0.92$, Fig. 1.2a), followed by stem diameter ($r^2=0.76$, Fig. 1.2b) and stem length to 1st branch ($r^2=0.75$, Fig 1.2c). Total stem length ($r^2=0.69$) and number of branches ($r^2=0.54$) were the least correlated with seed production, likely due to the non-linear nature of the relationships (Fig. 1.2d and 1.2e). While samples collected from different sites often differed from one another, the strength of the relationship between the independent variables and seed production remained highly significant ($p<0.001$) regardless of site (Table 1.2).

Discussion

Methods for estimating seed production based on vegetative characteristics have been developed for several other plant species. Laubhan and Fredrickson (1992) developed a method for estimating seed production of 11 moist-soil plants in the Mississippi Alluvial Valley using vegetative characteristics such as inflorescence number, length, base diameter, and plant height.

A similar method for predicting seed production based on seed mass was developed for estimating annual seed production of certain tree species (Green and Johnson, 1994). In each case the method used linear regression based on a vegetative characteristic that was easily and rapidly quantifiable. We used a similar approach.

Our data illustrate that the best characteristic for estimating MBS seed production was inflorescence weight. While other characteristics may be measured more rapidly, inflorescence weight appears to yield the most accurate estimates of seed production and is still more practical than harvesting and counting individual seeds. The linear relationship between inflorescence weight and seed production allows for prediction of seed production based on stem weight using a simple linear regression equation.

In addition to accuracy, we also considered how rapidly each characteristic could be measured. Although no data were taken, we observed that some characteristics - such as inflorescence weight - require inflorescences to be harvested, which is both destructive and time consuming. Other characteristics, such as inflorescence length or diameter, could be measured using a ruler or calipers without harvesting the inflorescence. We also observed that counting the number of branches per inflorescence was most time consuming and often subjective depending on how we defined a branch.

We selected inflorescence weight for estimating MBS seed production because we found that inflorescence weight provided the most accurate means for predicting seed number. It is clear that many inflorescence characteristics are related to seed production, and while a rough estimate of seed production could likely be derived using several different characteristics, weight was the most accurate as well as the best candidate for regression analysis due to the linear relationship between inflorescence weight and seed production.

Management Implications

The ability to estimate MBS seed production can be a useful tool for land managers to assess recovery potential, predict seed bank establishment, and understand succession patterns following disturbance. Additionally, seed production potential can be used as an indicator of resource availability, in particular since sagebrush allocates resources to both root and shoot growth before allocating resources to reproduction (Miller et al., 1986). It could also easily be incorporated into methods for monitoring and restoring wildlife habitat, in particular for greater sage-grouse.

The results of this study can be used to estimate MBS seed production over time, and to identify the peak of seed bank development. Most fires in the sagebrush-steppe occur in the late summer or early fall, before the current year's seeds have dispersed. The post fire sagebrush seed bank is, therefore, composed almost entirely of previous season's seeds, which typically only remain in the soil for short time before germinating, but have been known to germinate up to 2 years after the fire (Ziegenhagen and Miller, 2009). The soil seed bank may contain viable seeds from multiple seasons which may germinate under favorable conditions, although the majority of the seed germinates within the first season after entering the soil (Wijayratne and Pyke, 2012).

While useful and practical, this method may be limited by temporal and spatial inter-stand variation. Thus, an initial regression model must be established before the method can be applied to a larger geographic area. Once this has been done, this method could serve as a useful tool for estimating seed production within a MBS community.

While this method was developed specifically for MBS, it is likely that similar methods could easily be developed for Wyoming big sagebrush and basin big sagebrush. However, seed

production varies greatly among the three subspecies which experience different growing conditions and different seed production strategies (McArthur and Welch, 1982).

Acknowledgments

Many thanks to Stephanie Carlson, Brian Reeves, Kevin Costa and the skilled technicians from the USFS Shrub Science Lab and Brigham Young University for the time and effort put forth to collect this data. We would also like to thank Dr. Randy Larsen for statistical assistance.

Tables

Table 1.1 Pilot 1 Site Information

All sites had an annual precipitation of 400-500 mm, although in 2009 the precipitation was 230-550 mm. Temperature and Precipitation data were calculated from PRISM data (PRISM Climate Group, 2011). All coordinates were recorded in NAD27.

Site Name	Easting	Northing	Elevation (m)	Temperature (max/min)	Slope
Sunrise	405456	4413071	1,972	84/14 F	30-60%
Milford	338694	4248667	2,103	80/13 F	10-25%
Coyote Rocky	367683	4226065	2,284	78/9 F	3-20%
Big Twist	367778	4226476	2,255	76/9 F	3-20%
Coyote Pond	325857	4209253	1,892	86/15 F	2-15%

Table 1.2 Results of Model Selection

K indicates the number of variables (both explanatory and response) included in the model. AIC is Akaike Information Criterion, which is used to evaluate and compare models against one another. All models were significant with $p < 0.001$. Adjusted r^2 accounts for the number of predictors in the model and increases only if the new term improves predictability.

	Model	K	AIC	adj r^2	r^2	p-value
M1	number of seeds ~ stem diameter + site	3	4407.402	0.7681	0.7697	< 0.001
M2	number of seeds ~ stem diameter	2	4407.402	0.7638	0.7642	< 0.001
M3	number of seeds ~ length + site	3	4612.45	0.6952	0.6973	< 0.001
M4	number of seeds ~ length	2	4626.21	0.6879	0.6884	< 0.001
M5	number of seeds ~ length to first branch + site	3	4453.567	0.7534	0.7551	< 0.001
M6	number of seeds ~ length to first branch	2	4465.798	0.748	0.7484	< 0.001
M7	number of seeds ~ number of branches + site	3	4811.269	0.6027	0.6054	< 0.001
M8	number of seeds ~ number of branches	2	4911.35	0.5436	0.5442	< 0.001
M9	number of seeds ~ weight + site	3	3619.888	0.9189	0.9194	< 0.001
M10	number of seeds ~ weight	2	3635.791	0.9167	0.9168	< 0.001

Figures

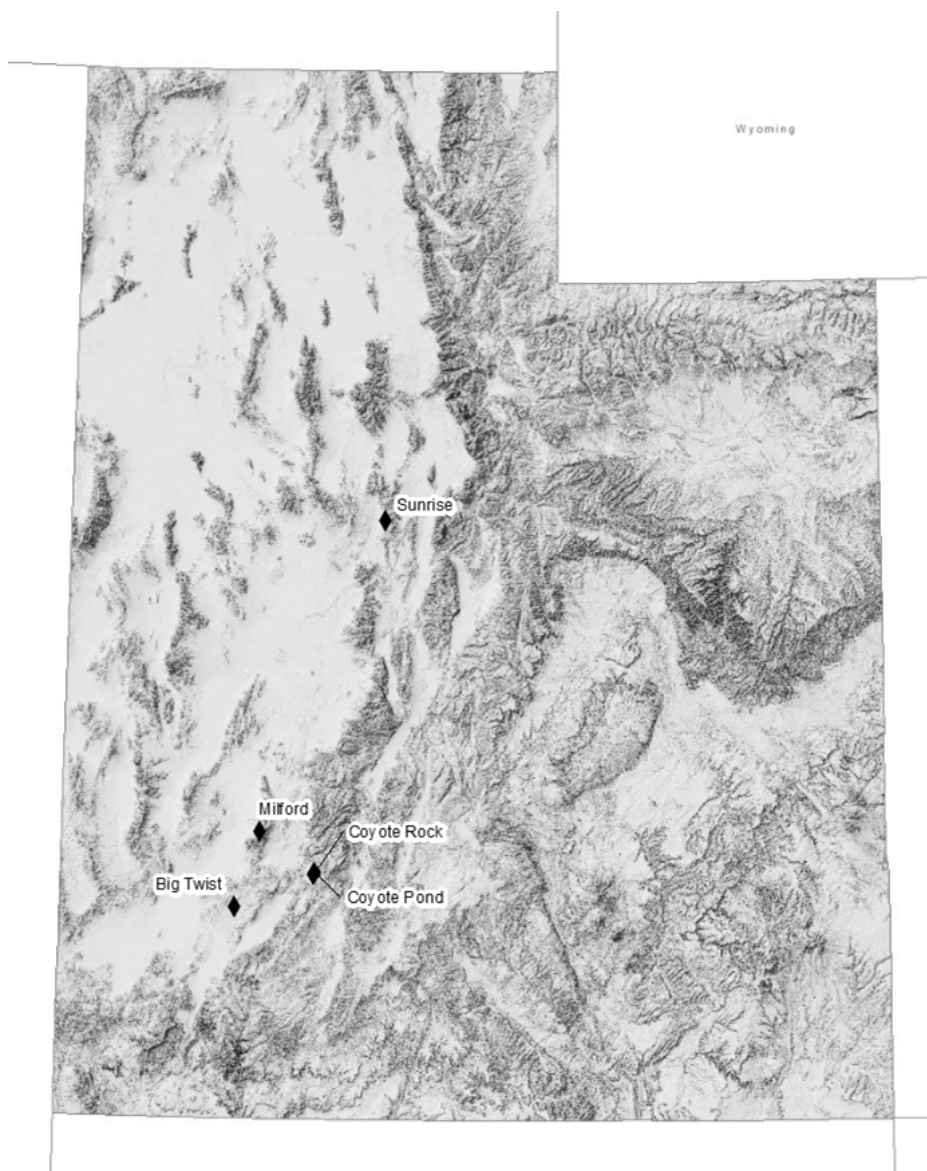


Figure 1.1 Map of Locations Sampled

Samples were taken from five locations across central and south-central Utah. Sunrise Mountain was located at 405456 E 4413071 N; Milford was located at 338694 E 4248667 N; Coyote Rocky was located at 367683 E 4226065 N; Big Twist was located at 367778 E 4226476 N; Coyote Pond was located at 325857 E 4209253 N. All coordinates were recorded in NAD27.

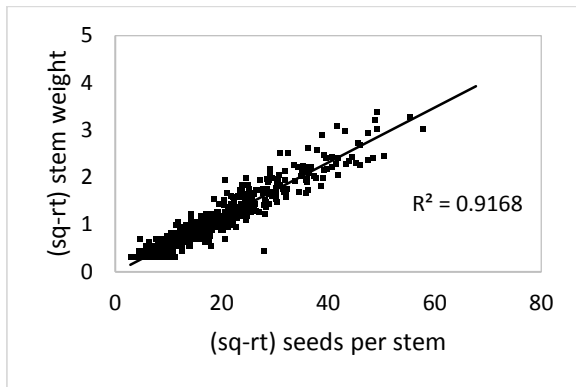


Figure 1.2a – Inflorescence weight

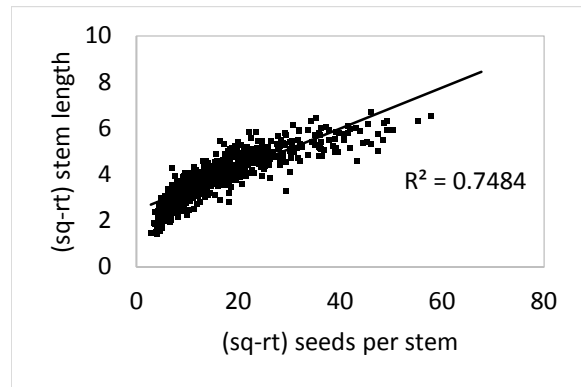


Figure 1.2d – Inflorescence stem length from the 1st branch to the tip of the rachis.

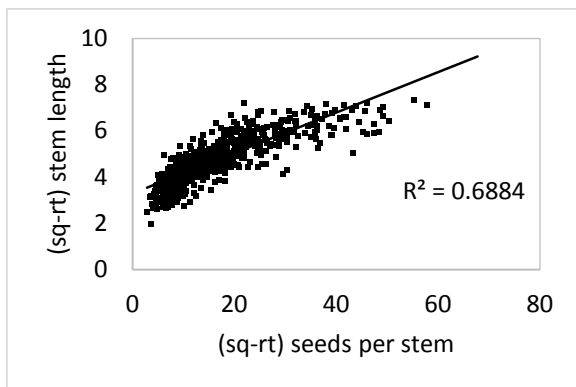


Figure 1.2b – Inflorescence stem length from the base of the stem to the tip of the rachis.

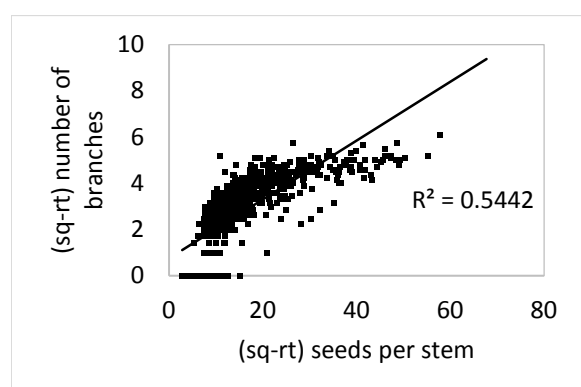


Figure 1.2e – Number of branches per inflorescence

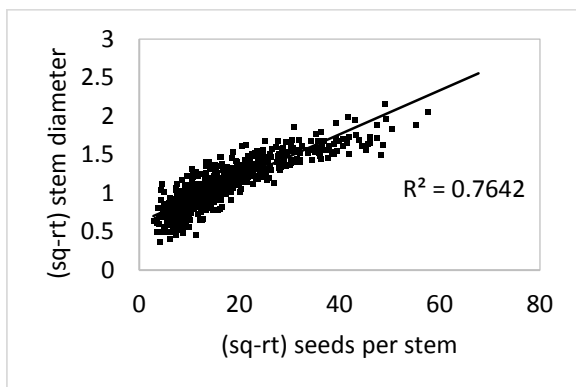


Figure 1.2c – Inflorescence stem diameter

Figure 1.2a-e Pilot 1 scatter plots

Scatter plots showing the relationships between each independent variable and the number of seeds produced by each inflorescence (or stem). All data in these figures were transformed using a square-root transformation to normalize the variance.

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Chapter 2

Non-destructive age estimation of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) using morphological characteristics

Melissa L. Landeen, Steven L. Petersen, Stanley G. Kitchen, Loreen Allphin

Abstract

Current methods for determining plant age require cutting the plant and counting annual growth rings in the primary stem. Non-destructive methods for accurately estimating mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle; MBS) plant age would be useful in developing quick and inexpensive estimates of age structure and community dynamics at stand to population scales. Although individual plant age can be accurately determined by counting annual growth rings on a cross section of the stem, this method is both destructive and time consuming. The purpose of this study was to develop a method for estimating age for individual, MBS plants based on easily measured morphological characteristics. A total of 155 plants of varying sizes were selected, measured, and then harvested from five locations in central and south-central Utah. Measurements included plant height, crown area, sub-canopy litter depth, percent crown mortality, depth of bark furrows, length of bark fibers, and circumference and diameter (minimum and maximum) of the plant basal stem. Plants were excavated and a horizontal cross-section was removed from near the root collar of each to determine plant age. Age was determined by counting annual growth rings after cut surfaces were sanded to reveal cell and ring structure. Model selection in program R identified the variables that were most highly correlated with age. The strength of the relationship was determined using a least square linear regression. Analysis suggest that maximum stem diameter ($r^2=0.505$) and minimum stem diameter ($r^2=0.524$) were the most highly correlated to plant age, regardless of site. While

several other characteristics were also significantly correlated to age, stem diameter was the most accurate and among the fastest and easiest to measure. Since maximum and minimum stem diameter are nearly equal in accuracy and efficiency, we determined that average stem diameter is the most practical measurement for a rapid assessment. These results support previous findings that stem diameter can be used to estimate plant age and also confirm that no other morphological characteristic was a better indicator of plant age. While useful, this method has limitations. A regression equation using sampled plants may need to be developed before application to each community of interest. This method was developed specifically for MBS, but it is likely that a similar method could be applied to other big sagebrush subspecies, although further testing is required. This technique can be used by land managers to quickly assess the relative age of individual plants, which can then be used to estimate stand age and stand age structure.

Keywords: *Artemisia tridentata* ssp *vaseyana*, age estimation, stem diameter, fire

Introduction

A knowledge of sagebrush (*Artemisia tridentata* Nutt.) stand age and population age structure can be useful for understanding sagebrush community structure, stability and ecological function (Perryman and Olson, 2000). Many management decisions for sagebrush communities are based on stand conditions (plant density, cover, community composition, etc.) and could benefit from the added understanding of stand age structure and demographics. While stand age is commonly estimated as the length of time that has passed since the most recent disturbance (i.e. fire; Write and Baily 1982), individual plants can be aged more precisely by examining the annual growth rings in primary stems (Ferguson, 1964). However, the process of determining age based on annual growth rings is both time consuming and destructive. It is also impractical

when determining the age structure of a large community, which would require harvesting and aging a large portion of the stand.

In this study we evaluated easily-measured morphological characteristics that might be used to nondestructively estimate the age of mountain big sagebrush (*A. tridentata* Nutt. ssp *vaseyana* (Rydb.) Beetle; MBS) plants growing in sagebrush dominated communities. Our objective was to develop a method for rapid estimation of plant age using regression analysis. We hypothesized that plant age was correlated with one or more physical characteristics of sagebrush and that these characteristics could be used to accurately estimate plant age. A method for rapidly determining plant age would further our understanding of disturbance response and recovery in MBS communities and allow land managers access to new tools for making ecological based management decisions.

Methods

In 2010 we assessed morphological characteristics and determined age for 155 MBS plants from five communities in central and south-central Utah (Fig. 2.1). All sites were MBS-dominated communities with similar elevation, annual precipitation, and climate (Table 2.1). For each site, at least 10 points were randomly located (15 locations at Sunrise Mountain site). We selected three individuals of varying sizes near each study point. Priority was given to plants that had a relatively intact basal stem (minimal stem splitting) so that an accurate age estimate could be obtained from annual growth rings. If split stems were unavoidable, we bound the stems with wire to hold them in their original positions before cross-sections were cut for aging.

For each plant we measured a suite of morphological characteristics, including: maximum plant height (excluding inflorescences), crown area (maximum crown diameter x

crown diameter perpendicular to the maximum diameter), litter depth beneath the crown (averaged depth measurements taken at three random locations beneath the crown), litter depth at the base of the stem, and percent crown mortality (based on ocular estimation). After measurements were taken, plants were harvested, labeled and placed in large garbage bags to prevent breakage prior to transport. In the lab, additional measurements were taken including average depth of bark furrows (selected a random location on the plant using coin-flipping system and then measured the depth of the most prominent furrow), average length of bark fibers, (several strips of bark were randomly selected using a coin-flipping system, peeled off the stem, and measured), average circumference (obtained by wrapping a string around the stem between the root collar and the base of the first branch) and minimum and maximum diameter of the primary stem (measured at the widest and narrowest points on the primary stem between the root collar and the base of the first branch), and average diameter of the secondary and tertiary branches (based on measurements of three randomly selected secondary branches and three randomly selected tertiary branches respectively).

A cross-section was cut at or just above the root collar for each plant. Each cross-section sample was sanded with a belt sander and progressively finer grit until annual growth rings were clearly visible using a stereo-microscope. Plant age was determined by counting annual growth rings and independently verified by at least two individuals (Stokes and Smiley, 1968; Moss, 1940; Diettert, 1938).

Statistical Analysis

Data were tested for normality and transformed using square root transformations as needed. Using program R we tested for multicollinearity to identify any correlated variables and then built models within the limits of the results. We used model selection to identify the

variables that best explain the variation in age. A best model was identified and a least squares regression performed in SYSTAT 13 (Systat 13, 2009) confirmed results.

Results

Multicollinearity prevented us from combining multiple variables in a single model; however, all morphological characteristics showed some degree of correlation with MBS plant age, though the strength of correlation varied. Ages ranged from 2 to 32 years, with mean and modal ages of 13 and 17 years, respectively. Correlations ranged from $r^2=0.11$ ($p<0.0001$) for litter depth beneath the canopy to $r^2 = 0.52$ ($p<0.0001$) and $r^2=0.51$ ($p<0.0001$) for minimum and maximum stem diameter (Table 2.2). We evaluated both maximum and minimum stem diameter as potential proxies for plant age; however, since the two measurements are equal in their correlative relationship with age, we determined that it was more practical to average the two measurements and assess “average stem diameter” as a potential basis for our method ($r^2=0.52$; Fig. 2.2).

Several other variables emerged as being highly correlated with age. Stem circumference, which is highly correlated with stem diameter, was also related to age (basal ($r^2=0.426$, $p<0.0001$), secondary ($r^2=0.383$, $p<0.0001$) and tertiary ($r^2=0.423$, $p<0.0001$), as well as bark fiber length ($r^2=0.401$, $p<0.0001$). However, depth of litter at the base of the stem ($r^2=0.14$, $p<0.0001$) and below the canopy ($r^2= 0.105$, $p<0.0001$) and crown mortality ($r^2=0.190$, $p<0.0001$) were only loosely correlated with age.

Although stem diameter was the variable best correlated with plant age, growth rate (and thus stem diameter) was highly variable, limiting its predictive ability (Table 2.3, Fig. 2.3). If we separate the data into 1 cm increments of stem diameter size as has been done in Table 2.3, we

see that the mean age is often equal to or greater than the range of ages represented by the cohort. The error bars displayed on Figure 2.3 represent the maximum and minimum ages within each 1 cm increment, suggesting limitations to the usefulness of stem diameter as a predictor of absolute plant age.

Discussion

The results of this study suggest that stem diameter was the most reliable indicator for estimating MBS age. This is consistent with the findings of Perryman and Olson (2000), who also found a strong correlation between plant age and stem diameter on big sagebrush in Wyoming. While stem diameter has often been used as an indicator of age in woody species, Perryman and Olson (2000) were the first to test stem diameter as a method for estimating sagebrush plant age for Wyoming big sagebrush, basin big sagebrush, and mountain big sagebrush. Brotherson et al. (1984) used stem diameter as a method for estimating age for salt cedar (*Tamarisk ramosissima* Ledeb.) in central Utah. In another study Brotherson et al. (1983) used stem diameter to estimate ages for eight species of trees on the Navajo National Monument in Arizona including box elder (*Acer negundo* L.), Utah juniper (*Juniperus osteosperma* ssp. *utahensis* [Torr.] Little), pinyon pine (*Pinus edulis* Englem.), Fremont cottonwood (*Populus fremontii* S. Wats.), quaking aspen (*Populus tremuloides* Michx.), Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), Gambel oak (*Quercus gambelii* Nutt.) and salt cedar. Our findings confirm that no other morphological characteristic is a better predictor of age in than stem diameter in MBS.

It is interesting to note that percent crown mortality was not highly correlated with plant age. While it is possible that our method of measuring crown mortality by ocular estimation led to sampling error, it is more likely that some crown mortality is induced by factors unrelated to

plant age. Crown mortality is often associated with mule deer (*Odocoileus hemionus* Rafinesque) browsing, especially in winter (McArthur et al., 1988). Insect defoliation and vole infestations have also been responsible for sagebrush defoliation and mortality (Gates, 1964; Frischknecht and Baker 1972).

Correlation between stem diameter and age is relatively strong, but its predictive ability is limited. As expected, results show that mean stem diameter increases with age, but there is high variability in the rate of increase and a wide range of ages associated with each stem measurement (Fig. 2.3). A regression equation using sampled plants may need to be developed before application to plant communities across a broad geographic area.

Although we sampled a variety of plant sizes, extremely small individuals were underrepresented. Only 2 plants had a stem diameter <1 cm, with the smallest having a stem diameter of 0.6 cm and being aged to 2 years. While results showed that stem diameter is correlated with age for moderate and large sized plants, further research is required to determine the accuracy of this method when applied to very small plants.

Management Implications

The ability to quickly and accurately assess sagebrush age could have many ecological and management implications. This knowledge will better allow land managers to more accurately assess stands of sagebrush, as well as make management decisions based on age in addition to cover, density or size. It will also further our understanding of ecological recovery as it relates to stand age and production, a subject that has become increasingly important due to the threat posed by invasive grasses and encroaching woodlands.

Acknowledgments

Many thanks to Stephanie Carlson, Brian Reeves, Kevin Costa, and the skilled technicians from the USFS Shrub Science Lab and Brigham Young University for the time and effort put forth to collect this data. We would also like to thank Dr. Randy Larsen for statistical assistance.

Tables

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Site	Easting	Northing	Elevation (m)	Temp. (max/min)	Most Recent Fire
Sunrise Mountain	338694	4248667	2,050-2,166	84/14 F	1992
Milford	338694	4248667	2,112-2,142	80/13 F	1994
Big Twist	367778	4226476	2,280-2,344	76/9 F	1985
Choke Cherry	375524	4222099	2,551-2,590	78/14 F	1983
Coyote Pond	325857	4209253	1,987-2,003	86/15 F	1988

Table 2.2 Results

Each variable was regressed against plant age. While all variables showed significance, levels of correlation varied.

Variables	r²	p-value
Height	0.319	< 0.0001
Crown Area	0.330	< 0.0001
Litter Depth (canopy)	0.105	< 0.0001
Litter Depth (stem)	0.141	< 0.0001
% Crown Mortality	0.190	< 0.0001
Depth of Bark Furrows	0.300	< 0.0001
Length of Bark Fibers	0.401	< 0.0001
Basal Stem Circumference	0.426	< 0.0001
Maximum Basal Stem Diameter	0.505	< 0.0001
Minimum Basal Stem Diameter	0.524	< 0.0001
Secondary Stem Circumference	0.383	< 0.0001
Tertiary Stem Circumference	0.423	< 0.0001

Table 2.3 Age variability for each cm increase in stem diameter

K represents the sample size for each stem diameter range.

Basal stem diameter	K	Min. Age	Max Age.
0 – 0.9 cm	2	2	4
1 – 1.9 cm	19	5	17
2 – 2.9 cm	29	6	17
3 – 3.9 cm	23	6	19
4 – 4.9 cm	11	9	28
5 – 5.9 cm	16	11	19
6 – 6.9 cm	14	10	25
7 – 7.9 cm	14	9	28
8 – 8.9 cm	14	5	27
9 – 9.9 cm	6	11	17
10 + cm	6	15	32

Figures

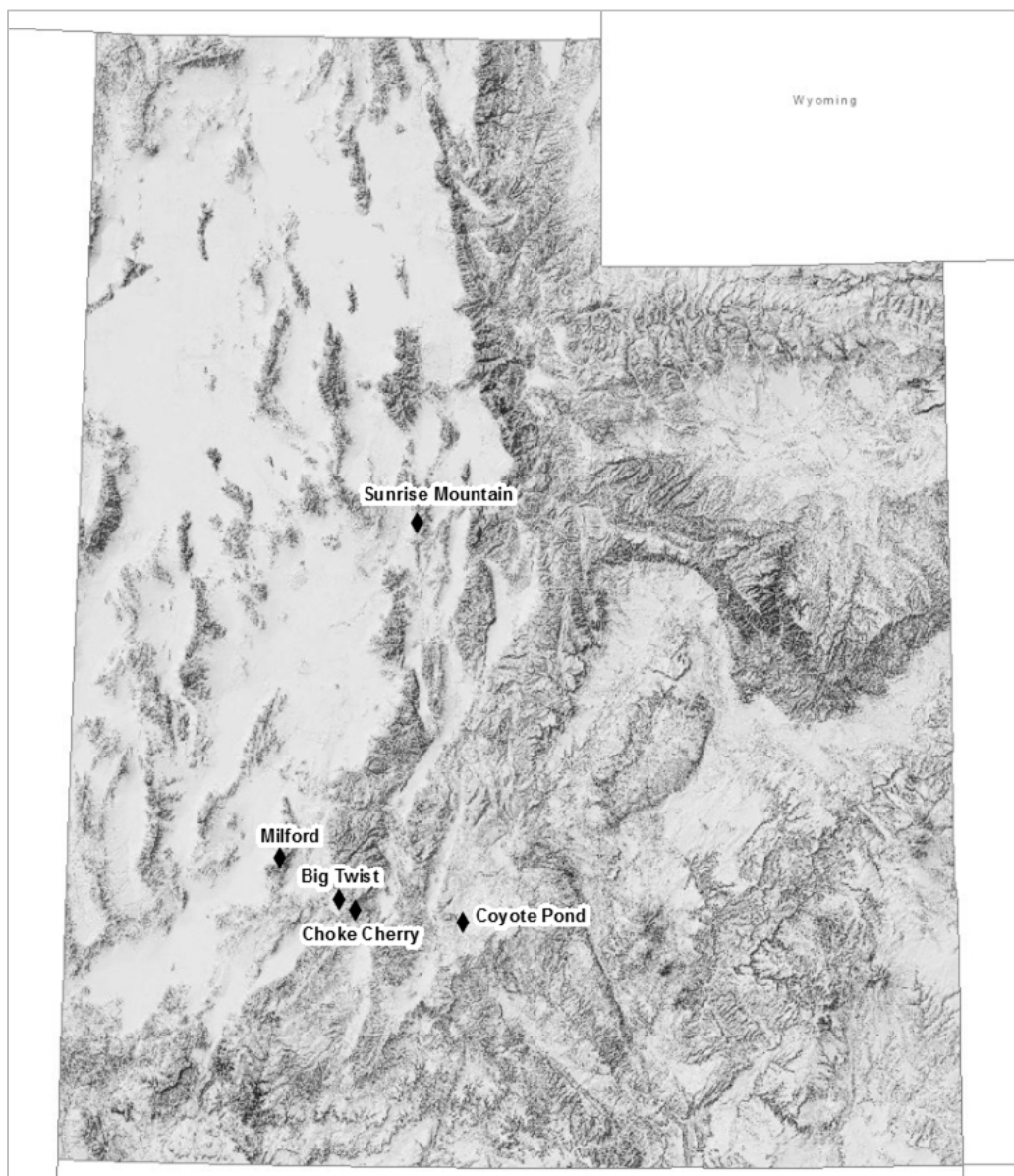


Figure 2.1 Map of Locations Sampled

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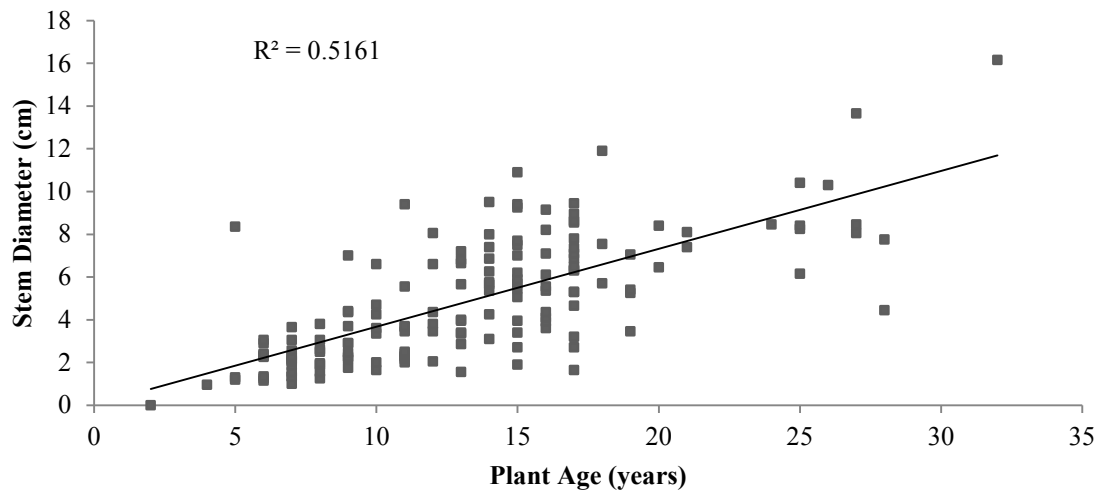


Figure 2.2 Correlation between average stem diameter and plant age
Age ranged from 2 to 32 years for 154 samples ranging in size from 0.6 to 16.15 cm.

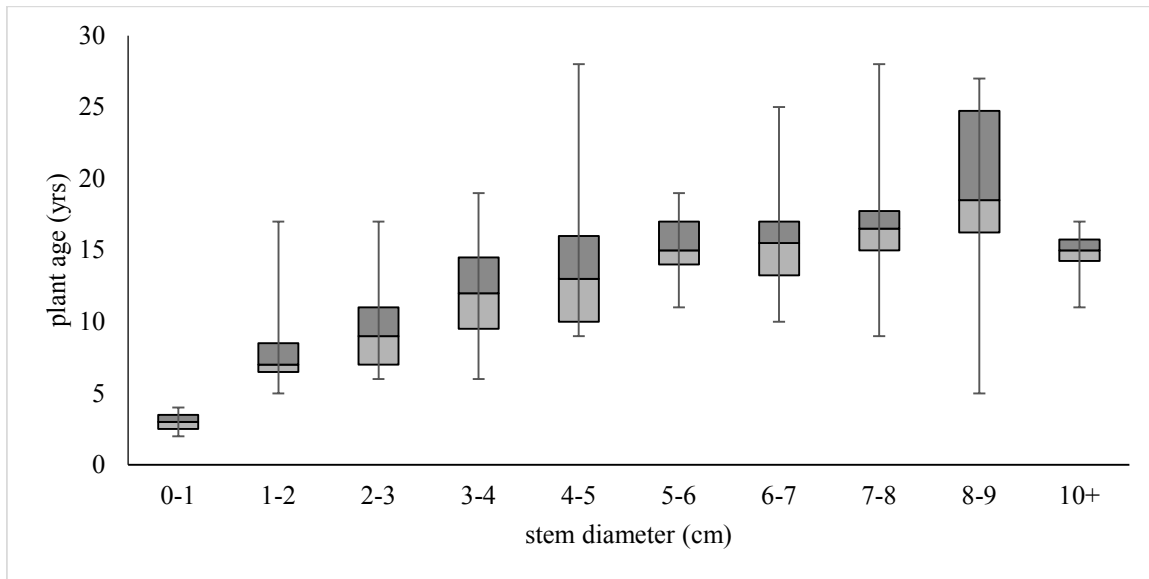


Figure 2.3 Boxplots showing approximate plant age associated with each 1 cm increase in stem diameter

Boxes show upper and lower quartiles and horizontal lines in boxes show medians, with vertical lines showing minimum and maximum values.

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Chapter 3

Post-fire seed production of mountain big sagebrush

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Abstract

Fire is the dominant disturbance in big sagebrush ecosystems. Of the three subspecies of big sagebrush (*Artemisia tridentata*), mountain big sagebrush (ssp. *Vaseyana*; MBS) is the most resilient to disturbance, but still requires favorable climactic conditions and a viable post-fire seedbank for rapid recovery. We used data from 13 central Utah burn sites and a space-for-time substitution strategy to identify trends in seed production during post-fire recovery. We hypothesized that seed rain (mean seeds produced/m²) would peak before stands reached maximum density due to lower individual plant fecundity caused by intraspecific competition in high density stands. Using estimates of population density and individual plant fecundity, we estimated potential seed rain for three size classes of MBS and used forward stepwise regression analysis to identify significant factors influencing seed production over time. Density for small (basal stem diameter < 1 cm) and medium-sized (basal stem diameter = 1-3 cm) plants was consistently low and was not affected by time since fire (TSF), while large plant (basal stem diameter > 3 cm) density steadily increased ($p=0.0002$), suggesting continual recruitment over time. Plant fecundity decreased with TSF for all three size classes (p range = 0.019 – 0.0506), with large plants dominating reproductive output. Small and medium-sized plant fecundity was negatively correlated with winter precipitation (p range = 0.0106-0.0174), while large plant fecundity was positively correlated with winter precipitation ($p<0.0001$) and negatively correlated with elevation ($p=0.0001$). Although plant fecundity for all size classes decreased with TSF, increases in population densities resulted in increased seed rain over time ($p=0.0039$).

suggesting that losses in individual plant fecundity were more than compensated by higher densities of seed-producing plants. Seed rain increased with MBS cover ($r^2=0.4841$) and appears to level off between 20 and 30 years TSF even though MBS cover and stand structural characteristics may not have fully stabilized. Results partially support our hypothesis that the time required to reach MBS seed rain maximum was not tightly bound to indicators of stand maturation. Understanding the factors that influence post-fire seed production can help land managers better manage for successful recovery.

Keywords: *Artemisia tridentata* ssp *vaseyana*, seed production, post-fire recovery, plant fecundity, plant density, seed rain

Introduction

The most widespread and common shrub in the sagebrush biome is big sagebrush (*Artemisia tridentata* Nutt.). Mountain big sagebrush (*A. tridentata* Nutt. ssp *vaseyana* (Rydb.) Beetle; MBS) is a subspecies of big sagebrush that is found throughout the Intermountain West and is an important component of the shrub-steppe ecoregion. Compared to two other common big sagebrush subspecies, Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle and Young) and basin big sagebrush (*A. tridentata* ssp. *tridentata*), MBS occurs at relatively high elevations (2100-3200m) in semi-arid regions where soil and climate conditions are cooler and wetter (mean annual precipitation 300-700mm; Beetle and Young, 1965; Meyer, 1994; Connelly et al., 2004; Cleary et al., 2010).

Fire is the most important natural disturbance that occurs in MBS dominated communities (Write and Bailey, 1982). Many changes to the sagebrush biome may be attributed to altered fire regimes. When fire free intervals are too short for sagebrush recovery, sagebrush is

displaced by herbaceous species (Chambers et al., 2007). When fire-free intervals are too long, trees may encroach and displace the sagebrush community (Miller and Rose, 1999; Miller et al., 2013). Although fire is the most common natural disturbance in sagebrush-dominated ecosystems, sagebrush is poorly adapted to fire (Kitchen and McArthur, 2007). Sagebrush does not sprout from roots or crown after fire and must regenerate from seed. Recovery from fire is primarily dependent on residual, short-lived seed deposited annually in the soil. In addition, fires generally occur before seeds mature and have a chance to enter the seed bank (Meyer, 1994; Ziegenhagen and Miller, 2009; Young and Evans, 1989). Plants outside the burn perimeter or on unburned islands may contribute some seed to post-fire recovery; however, seed dispersal over distance is slow as most seeds remain within 1 m of the parent plant (Meyer, 1994). Therefore, unassisted, rapid recovery requires a source viable seed in the soil following fire.

An adult MBS plant may produce more than 350,000 seeds per year under ideal conditions (Goodwin, 1956); however, seed production varies from year to year depending on resource availability, disease, browsing pressure, and competition (Young et al., 1989; Wagstaff and Welch, 1991; Meyer, 1994). Seed ripens in mid-September at higher elevations, but may not ripen until November at lower elevation (Bleak and Miller, 1955).

Most studies suggest that post-fire recovery for MBS requires at least 20-35 years under favorable conditions, or longer when climatic conditions do not allow for rapid recovery (Kitchen and McArthur, 2007; Nelson et al., 2014). However, pre-settlement fire regimes have been altered and are continuing to change as a result of introduced exotic plant species, woody species encroachment (i.e. pinyon-juniper woodlands), and human-related activities (i.e. livestock grazing, human-caused fires, fire suppression, etc.) (Bukowski and Baker, 2013; Connelly et al., 2004; Miller and Rose, 1999; Billings, 1994).

The purpose of this study is to characterize MBS seed production in relation to time since fire (TSF) for both individual sagebrush plants and the entire MBS community. We explore factors that we hypothesize will explain variability in the recovery rate for post-fire seed production. These include:

Density – MBS plant density varies within populations by size class. We hypothesize that continual recruitment and plant growth will result in an exponential increase of large, mature plants, while small and medium-sized plant densities will gradually decrease due to the constraints of competition. The rate of increase in large plant density will gradually decrease as the population approaches maximum density.

Fecundity – Individual plant fecundity is a measure of potential propagule production for a given time period and is directly correlated with plant size. We hypothesize that while controlling for plant size, fecundity and plant density will be inversely related due to intra-specific completion.

Seed Production per unit of area (seed rain) – Due to higher expected fecundity for individual plants at low to moderate densities, we hypothesize that post-fire seed rain will peak before MBS communities reach maximum density or cover.

Methods

Site Selection

We applied a space-for-time substitution strategy to investigate effects of time since fire (TSF) on MBS reproductive output. Thirteen sites were selected in central and south-central Utah and east-central Nevada (Fig. 3.1), representing fires occurring between 1978 and 2001

(Table 3.1). Study sites were dominated by MBS, although sites with other sagebrush taxa present were not excluded. We selected sites that had little or no impact from seeded species (not seeded after fire or seeding largely failed) and that were apparently not adversely affected by excessive livestock grazing. Sites were found at similar elevations, but differed in aspect, slope, size of burned area, and time since the most recent fire. Sites also likely differ in pre-fire cover, pre-fire understory composition and fire intensity, although we were unable to consistently obtain this information for all sites. We ensured that all sampling took place within the burned area and that all plots were placed at least 8 meters away from the detectable edge of the burned area to avoid sampling pre-fire vegetation. Sampling took place between August and October in 2010 and 2011; months in which seed development and maturation occurs.

Pre-sampling

Two pilot studies were conducted in order to develop methods for estimating floret production and plant age (Chapter 1 and Chapter 2). The results from the first pilot showed a strong correlation between the weight of an inflorescence and the number of seeds produced (Chapter 1). We used this relationship to develop estimates of fecundity for MBS plants on each site. The second pilot revealed that, of all morphological characteristics tested, basal stem diameter is the most reliable indicator of plant age (Chapter 2). This information was used to designate plant size class groupings and helped ensure that we were sampling plants across a range of ages, and also allowed us to examine changes in fecundity over time.

Density

MBS density for each site was determined using a combination of the center point-quarter and nearest neighbor methods (Cottam and Curtis, 1956). Data were collected at 8-m intervals along a 100-m transect. We stratified sampling by plant size in order to obtain a representative estimate of density. Individual plants were classified as small (basal stem diameter < 1 cm), medium (basal stem diameter = 1-3 cm) or large (basal stem diameter > 3 cm). At each of 12, regularly-spaced (8-m spacing) points (plot centers) along the transect, a 1-m bar was placed perpendicular to the transect line creating four 90-degree quadrants from plot center. We measured the distance from the plot center to the nearest MBS plant of each size class in each of the four quadrants. We then measured the distance from that plant to its nearest same-sized neighbor. If no suitable plant of a given size class could be found within 8 meters of the plot center, we noted the absence and recorded the distance from the plot center as >8 meters. This rule also applied to the nearest neighbor measurement.

Plant density was calculated using Diggle's (1975) estimator, which combines the center-point-quarter method and the nearest neighbor method. Densities were calculated separately by size class (small, medium and large) and treated as separate populations throughout analysis due to their inherent differences in seed production.

Cover

Canopy cover was measured using the line intercept method (Eberhardt, 1978) using the same 100-m transect as previously described. Shrub canopy was measured by species and recorded to the nearest centimeter. Gaps in the canopy ≤ 5 cm were read as continuous canopy cover.

Ground cover was measured using a 1.0 x 0.5 meter Daubenmire frame made of PVC pipe (Daubenmire, 1959) placed along the transect at 10 meter intervals.. We estimated the percentage of frame area occupied by each cover class, or ground cover type. Cover classes included: annual grass, perennial grass, annual forb, perennial forb, shrub, litter, rock (≥ 2.5 cm diameter), cryptobiotic (mosses and lichens), and bare ground.

Fecundity

We define fecundity as a measure of annual floret production per MBS plant. This proxy relationship works because one, single-seeded achene can be produced from each floret. Fecundity estimates were based on florets rather than viable seed count because the indeterminate nature of seed maturation and short time gap from seed maturity to dispersal made it impractical to recover mature seeds without substantial losses. We measured fecundity for each study site by harvesting floret-bearing inflorescences from sagebrush plants proximal to 12 study points (same as used for plant density) along a 100-m transect. In order to ensure an accurate representation of the entire population, we stratified sampling by MBS plant size (and presumed age groups) based on stem diameter. Only mature plants with the potential of producing seed were included in this study. Seedlings that were less than 20 cm tall were considered immature and were not sampled. Inflorescences were harvested from small, medium, and large MBS individual size classes for each plot for a total of up to 36 samples per site. We harvested all of the current year's inflorescences, except in cases of extremely large and highly productive plants in which case a percentage (approximately 50%, 30% or 25%) of the total inflorescences were harvested. The percentage was recorded along with the number of stems collected so that an estimate of total florets (hereafter called seeds) produced by each plant could be calculated. Inflorescences were clipped at the attachment point to vegetative branches and enclosed in zip-

lock style plastic bags and placed in a cooler until they could be transported to the lab, where they were stored at 2° C until processed.

Inflorescences of a broad range of sizes (lengths) from each site were weighed to the nearest 0.01 grams using a digital balance accurate to 0.0001 g. Seeds (florets) were counted on a subset of samples (six to seven plants of varying sizes per site) – using dissecting forceps as needed. Regression equations were derived from floret number and inflorescence weights that allowed us to estimate floret production for all study plants based on inflorescence weight.

Seed Rain

Seed Rain is the amount of seed dispersed per unit area, or the potential amount of seed available for augmentation of the seed bank. We estimated potential seed rain for each site based on estimates of fecundity and density of each plant size class. Seed rain was calculated separately for each size class and then totaled for each site. Plots that did not contain any plants of a given size class and plants that did not produce seed were given a value of zero to avoid inflating seed production estimates.

Other Variables

Data for a suite of additional variables were collected from each site. Slope (expressed as a percent) and aspect were measured on location. Elevation was obtained from Digital Elevation Models. Estimates of average annual precipitation, April-June precipitation (Spring), October-March precipitation (Winter), and October-June precipitation (Spring – Winter) of the year prior to sampling (were obtained from PRISM data for each site (PRISM climate group, 2011).

At 10 points along the 100-m transect a soil probe was inserted into the soil as deeply as possible. The depth of penetration was recorded to the nearest centimeter and the 10 samples

were averaged for each site. This measurement reflected the stoniness of the soil and served as a proxy for soil volume available for root growth.

These data, along with data obtained about ground cover composition, were used in our statistical models as explanatory variables for variation in density, fecundity and seed rain.

Statistical Analysis

We performed a forward stepwise regression to identify significant variables effecting seed production. Independent variables included fire type (wild vs. prescribed), percent slope, elevation, mean annual precipitation, April-June precipitation (spring precipitation), October-March precipitation (winter precipitation), October-July precipitation (winter and spring precipitation), perennial grass cover, annual forb cover, perennial forb cover, percent litter, percent rock, percent cryptogams, soil depth and TSF. Density and fecundity were tested separately and by plant size class. We also tested seed rain, looking for any variables, other than density and fecundity, which could explain the variation among the sites. Fecundity and seed rain data were transformed using a natural log transformation. Independent variables were tested for significance ($p < 0.1$) and sequentially added to the model one at a time until no significant variables were returned. TSB was withheld from the selection process and then added to the model last to test for an effect of time on the dependent variable. TSF was modeled quadratically because we expected to see a leveling-off effect over time. However, we also modeled TSF linearly and accepted this model if the quadratic model was insignificant.

Results

Density

The most influential term in the small plant density model was percent slope ($p=0.0043$). Density of small plants was inversely related to slope, indicating plant density was greater on sites with less slope. The next term included in the model was perennial grass ($p=0.0047$). Small plant density was higher on sites with a higher percentage of perennial grass. After adjusting for the other variables in the model, TSF was not significant, indicating no significant difference in density of small plants related to TSF (Fig. 3.2a).

None of the independent variables, including TSF, were significant in explaining variation in medium plant density (Fig. 3.2b).

TSF was the only significant term in explaining variation in large MBS plant density ($p=0.0002$). Density of large MBS plants increased with TSF ($r^2=0.72$; Fig. 3.2c).

Fecundity

The first term added to the regression model for small plant fecundity was April – June precipitation ($p=0.0174$), which represents spring precipitation. This explained the greatest amount of variation in fecundity of small plants, however the sign of the relationship was unexpectedly negative (sites with higher spring precipitation exhibited lower individual fecundity than sites with lower spring precipitation). Other significant variables were percent rock cover ($p=0.0038$) and winter (October – March) precipitation ($p=0.0112$). Similar to the pattern observed for spring precipitation, the correlation for winter precipitation was also negative. After adjusting for all other variables in the model, TSF was negatively correlated with

small plant seed fecundity ($p=0.0190$), the relationship showing a slight downward trend (Fig. 3.3a, $r^2=0.12$).

The first term to be added to the medium-sized plant regression model was for October-July precipitation ($p=0.0174$). This negative relationship of plant fecundity to precipitation immediately preceding seed development, although unexpected, was consistent with the precipitation responses observed for small plants. After adjusting for the other terms in the model, medium plant fecundity was negatively correlated with time since fire ($p=0.0506$, $r^2=0.16$, Fig. 3.3b).

Soil depth (a proxy for soil root volume) was the first significant term affecting large plant fecundity ($p=0.0894$). This term is only significant if we accept p-value of $p<0.1$ as significant, which we feel is justified given our small sample size. Soil depth was negatively related to large plant fecundity (fecundity increased with decreasing soil volume). Previous winter (October – March) precipitation was positively correlated with large plant fecundity ($p<0.0001$). Elevation ($p=0.0001$) was negatively correlated with large plant fecundity, indicating that large plants were more fecund at lower elevation sites than at higher elevation sites. TSF was significant ($p=0.0279$) with large plant fecundity decreasing over time after fire ($r^2=0.06$, Fig. 3.3c).

Seed Rain

The majority of seed produced came from the large plants for most sites where large plants were present. Seven terms were significant in explaining variation in seed rain (Table 3.2). These include: soil depth, percent rock, winter precipitation, percent slope, percent annual grass,

and percent bare ground. TSF was also significant ($p=0.0039$) with a negative quadratic relationship to seed rain ($r^2=0.25$, Fig. 3.4).

Cover

A simple regression showed a positive relationship between MBS cover and TSF. The correlation fit a quadratic trend ($r^2=0.39$) with a leveling out effect taking place with time (Fig. 3.5). We also saw a strong positive correlation between MBS cover and seed rain ($r^2=0.5$, Fig. 3.6).

Discussion

Smaller plants grew most abundantly on sites with less slope and higher perennial grass cover (Sheep Trail, Uinta River A and Uinta River B). A gentler slope allowed for better retention of resources and provided more favorable growing conditions, which would be ideal for smaller plants with shorter roots. These favorable conditions may be expected to account for the abundant perennial understory as well. However, small and medium-sized MBS density did not increase over time. The consistent presence of small and medium-sized plants at all sites, regardless of TSF, suggests that continual recruitment and plant growth over time contributed to the increasing density of large plant populations.

Since large plant density is driven by TSF, we expected that plant density would eventually stabilize. However, our data suggests that 33 years was insufficient time to reach a stable equilibrium. These results are in agreement with previous studies done on MBS recovery that suggested 35+ years were required for post-fire stand recovery (Harniss and Murray, 1973; Humphrey, 1984; Wambolt et al., 1999; Wambolt et al., 2001; Kitchen and McArthur 2007; Nelson et al., 2014).

Low seed output by small and medium-sized plants correlated with high levels of precipitation in the growing season. This was the opposite of what we would expect (Young et al., 1989). There were many possible explanations for this perplexing response. It is possible that small plants on sites receiving high levels of winter and spring precipitation were young and reproductively immature and incapable of producing as much seed as small but older plants on drier sites. Consistently high levels of precipitation could have allowed seedlings to grow at an accelerated rate, attaining size but not maturity. However, it is important to note that all sites sampled in 2011 received more precipitation than those sampled in 2010 and that small plants on all of the sites sampled in 2011 (with one exception) were less fecund than sites sampled in 2010. It was likely that the difference in seed production by small plants was an effect of other environmental and climactic factors associated with that year, which were unaccounted for in this study, rather than a direct response to precipitation alone.

Large MBS plants at lower elevation sites had a higher fecundity than those at higher elevation sites. This may be due to the restricted length of growing season at higher elevation, which would limit the amount of time and resources plants can dedicate toward reproduction (Billings and Bliss, 1959). On many of the high elevation sites (Sheep Trail, Granite, and Dry Fork) there were fewer large shrubs, and the average height of large shrubs was shorter than those on low elevation sites. The majority of the vegetation was comprised of small-medium shrubs and grasses, rather than the dense, large shrub dominated communities found at lower elevation sites. It is likely that MBS growth and reproduction at higher elevations is limited by resource availability and growing season.

A steady increase in seed rain over time suggested that losses in individual plant fecundity were more than compensated by higher densities of large plants. We observed that the

fecundity and seed rain of small and medium-sized plants decreased over time, likely due to intraspecific competition with larger MBS plants. However, small and medium-sized plants contributed very little seed to the total seed rain. Therefore total seed rain was unaffected by changes in small and medium-sized plant seed production. The quadratic trend of large plant and total seed rain over time (Figs. 3.4c,d), which parallels large MBS seed rain over time (Fig. 3.4c), suggests that seed rain may be leveling off between 20 and 30 years after a fire. To the extent that this is the case, these results support our hypothesis that seed production would be maximized before stands reached maximum density.

While seed rain was calculated as a product of plant density and fecundity, it was also influenced by a number of other variables (Table 3.2). Soil depth (a proxy for soil rockiness), percent rock, winter precipitation, percent slope, and bare ground all affected the amount of seed produced by the community. These variables suggested that seed production was influenced by soil moisture availability. This was consistent with other studies showing that post-fire MBS recovery was related to moisture availability (Young et al., 1989; Nelson et al., 2014).

The use of space-for-time substitution was effective in allowing us to collect more data in a shorter period of time, but also places constraints on the conclusions we can draw from our results. Despite our efforts to select sites that were similar in climate, all sites experienced slight variations in temperature, precipitation and numerous other biotic and abiotic factors. Differences in conditions immediately preceding and following fire may have a lasting impact on recovery processes (Nelson et al., 2014). However, we have identified apparent patterns in MBS density, fecundity and seed production despite variation due to differences in location.

Management Implications

While previous studies have examined factors affecting recovery immediately following fire (Ziegenhagen, 2003; West and Hassan, 1985; Nelson et al., 2013), required recovery time (Baker, 2006; Miller and Rose, 1999), and pre-settlement mean fire return intervals (Lesica et al., 2007; Kitchen and McArthur, 2007; Miller and Rose, 1999), there is a lack of knowledge concerning minimum fire return intervals. An understanding of soil seed bank dynamics (Meyer, 1994; Ziegenhagen and Miller, 2009; Young and Evans, 1989) seed production recovery rates, and the factors that influence this process may assist land managers in making better informed decisions regarding sagebrush fire recovery and restoration.

MBS communities are known for being relatively resilient to disturbance compared to many other sagebrush communities due to the greater resource availability and favorable growing conditions associated with the cool, moist environment (Chambers et al., 2014; Davies et al., 2012). Climactic stability produces a relatively consistent annual reproductive output which more consistently allows for soil seed bank replenishment (McArthur and Welch, 1982; Young et al., 1982). Understanding factors that affect seed production may help explain how MBS communities are able to recover more rapidly than other sagebrush communities following a fire.

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Tables

Table 3.1 Site Information

Coordinates and information about mountain big sagebrush (MBS) sampling locations. All coordinates are recorded in NAD83, Zone 12 (with the exception of Granite which is Zone 11). Elevation was retrieved from Digital Elevation Maps. Precipitation was taken from PRISM data (PRISM climate groups, 2011). Slope was recorded at the sampling location. An * by the year of most recent fire indicates a prescribed burn.

Site Name	Easting	Northing	Elevation (m)	Slope (%)	Shrub Cover (%)	Relative MBS Cover	Mean Annual Precip. (mm)	Yr. of Most Recent Fire
Granite	741055	4304474	2515	42	14.47	35.04	487	2001
Sheep Trail 1	626945	4506153	2569	19	19.84	83.86	593	1998*
Sheep Trail 2	626945	4506153	2553	40	23.29	2.96	593	1998*
Willow Creek	272126	4243677	2426	12	32.81	96.37	485	1999
Milford	338801	4248708	2154	5	43.27	100.00	433	1994
Dry Fork	604103	4497249	2544	36	23.76	60.31	540	1994
Sunrise Mountain 1	405508	4413272	1968	25	39.66	89.74	471	1992
Sunrise Mountain 2	405508	4413272	2048	29	34.41	93.72	500	1992
Coyote Pond 1	328833	4214613	1976	16	14.04	94.52	366	1988
Coyote Pond 2	328833	4214613	1980	19	26.88	65.48	366	1988
Big Twist	367745	4227045	2256	25	49.00	99.82	488	1985*
Uinta River B (85)	574900	4494199	2249	11	59.24	94.36	499	1985*
Birch Creek East (83)	379900	4225748	2385	16	~16.8	unkn	409	1983*
Yellowstone River	555616	4487907	2367	12	38.56	95.15	494	1979*
East Birch Creek (78)	379771	4225854	2493	27	~38	unkn	471	1978*
Uinta River A (78)	574664	4494393	2256	11	55.66	97.09	505	1978*

Table 3.2 Results

Results of forward stepwise regression for logarithm of total seed rain. All variables are modeled linearly, except for time since fire (TSF), which is modeled quadratically (time since fire x time since fire). Soil depth is a proxy for soil root volume and was obtained by inserting a 1-m probe into the soil as far as possible. Percent rock, and percent bare ground were measured using ocular estimation of cover classes in a 0.5 meter Daubenmire frame. Precipitation data came from PRISM climate data (2011). TSF was modeled quadratically.

Independent Variable	F-value	t-value	p-value
Soil Depth	386.54	-8.88	0.0001
% Rock	148.08	-5.06	0.0023
Oct-Mar Precipitation	141.84	9.43	<0.0001
% Slope	62.87	-3.82	0.0088
% Bare Ground	22.83	5.58	0.0014
Time Since Fire (quad)	20.75	-4.56	0.0039

Figures

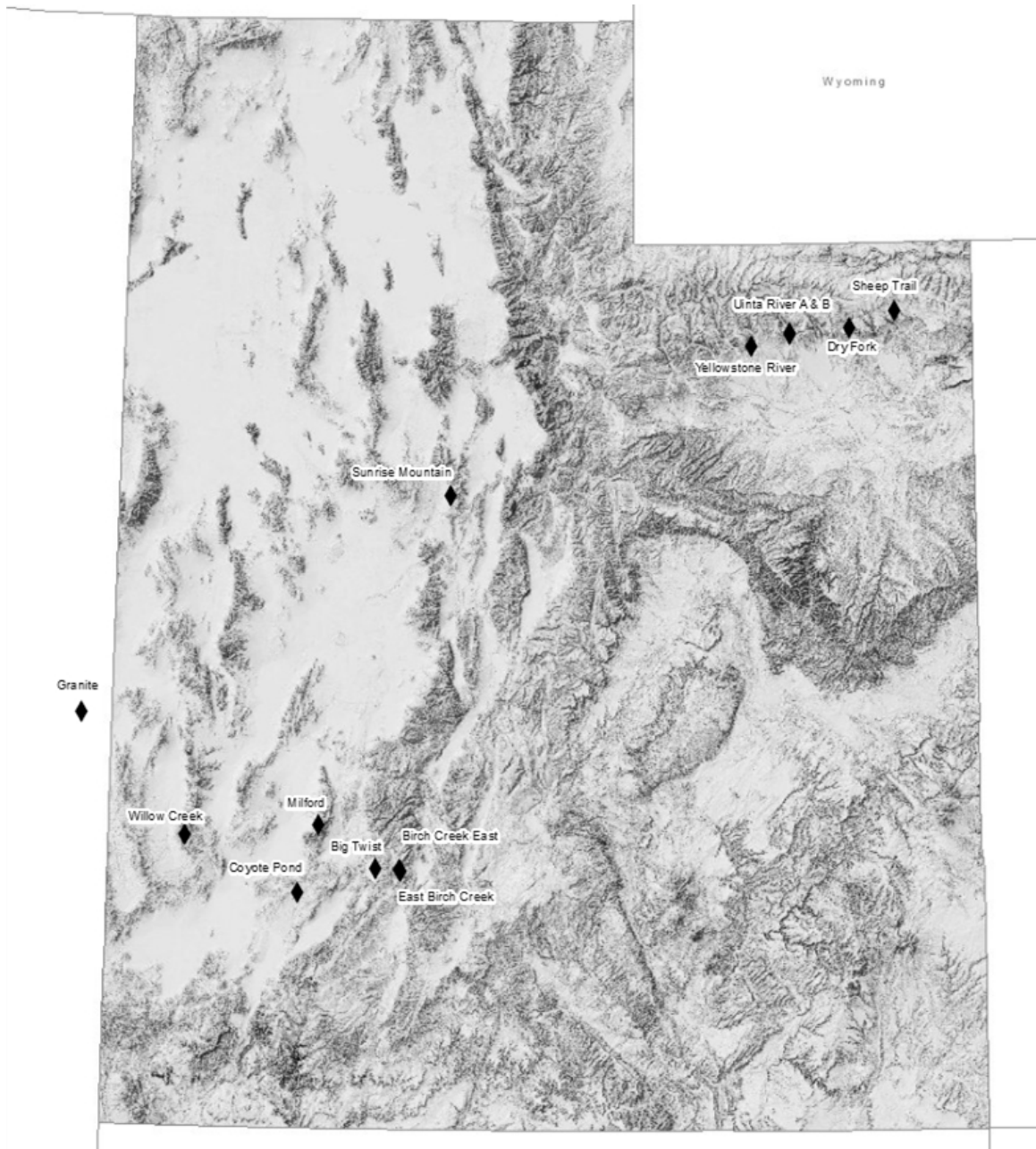


Figure 3.1 Map of locations sampled

Samples were taken from 12 locations across central and south-central Utah and 1 location in eastern Nevada. See Table 3.1 for location coordinates.

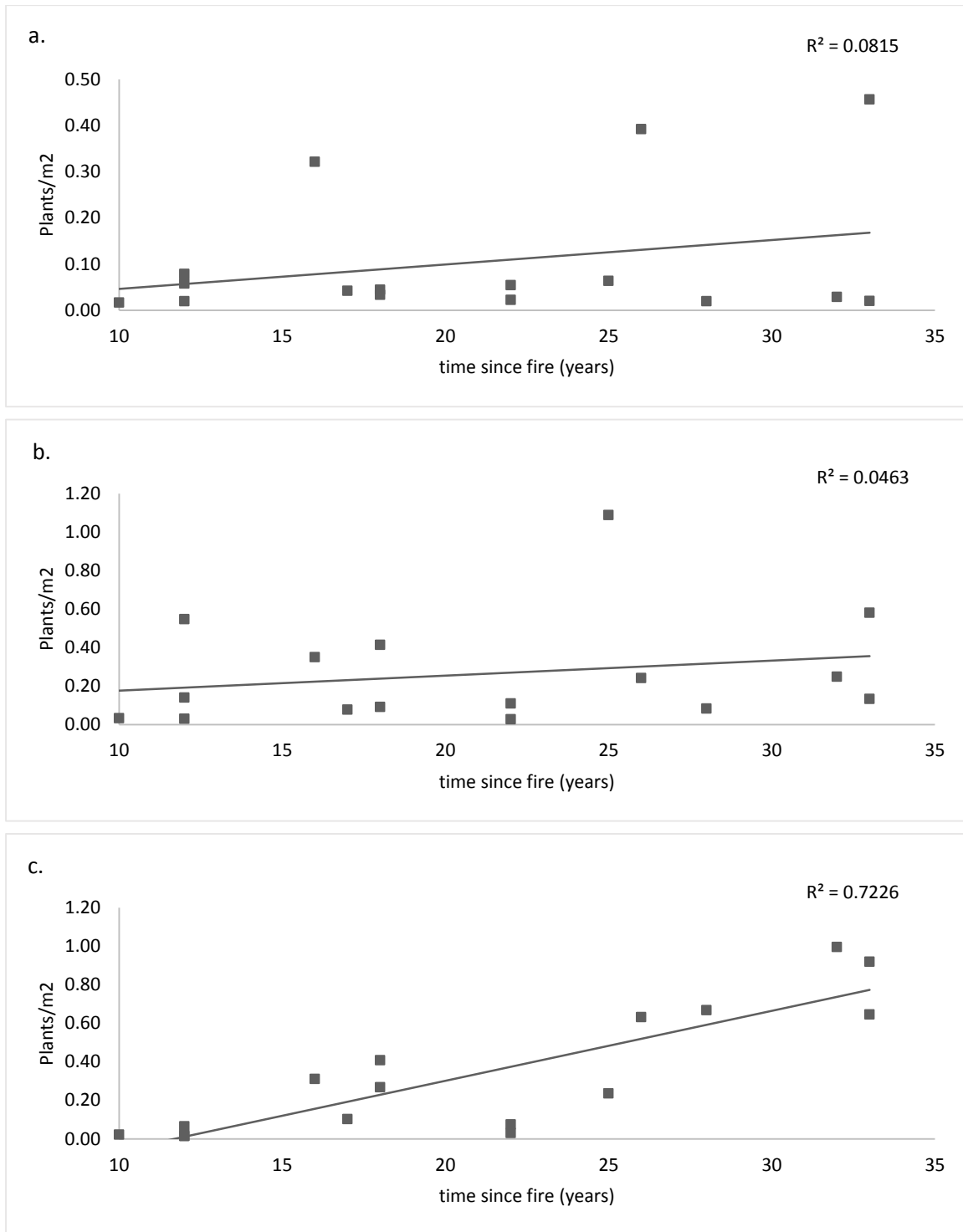


Figure 3.2 Plant density over time (by size class)

Mountain big sagebrush (MBS) plant density for small (a), medium (b), and large (c) size classes as affected by time since fire (TSF).

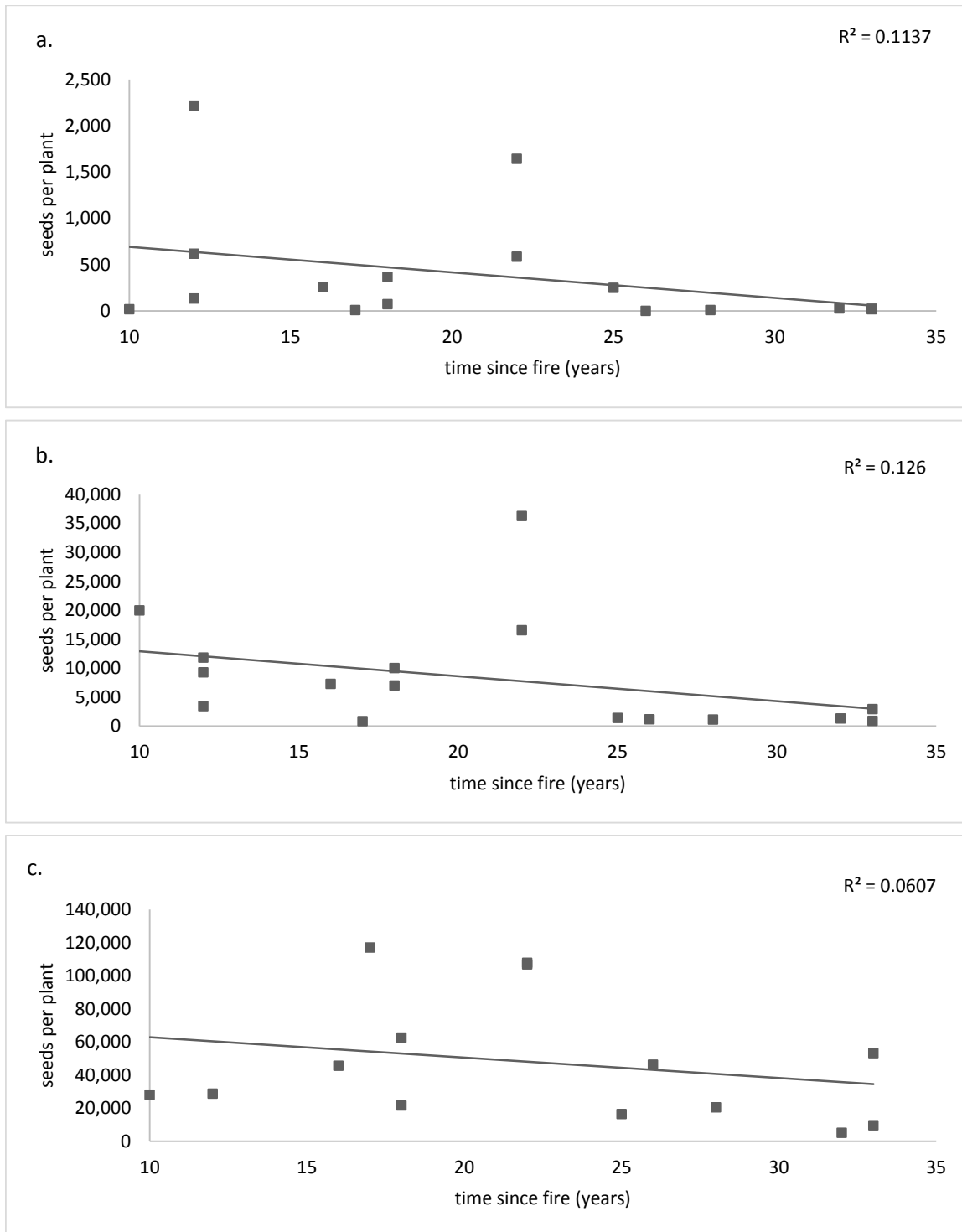


Figure 3.3 Plant fecundity over time (by size class)

Mountain big sagebrush (MBS) fecundity expressed as mean seeds per plant for small (a), medium (b) and large (c) plant size classes in response to time since fire (TSF).

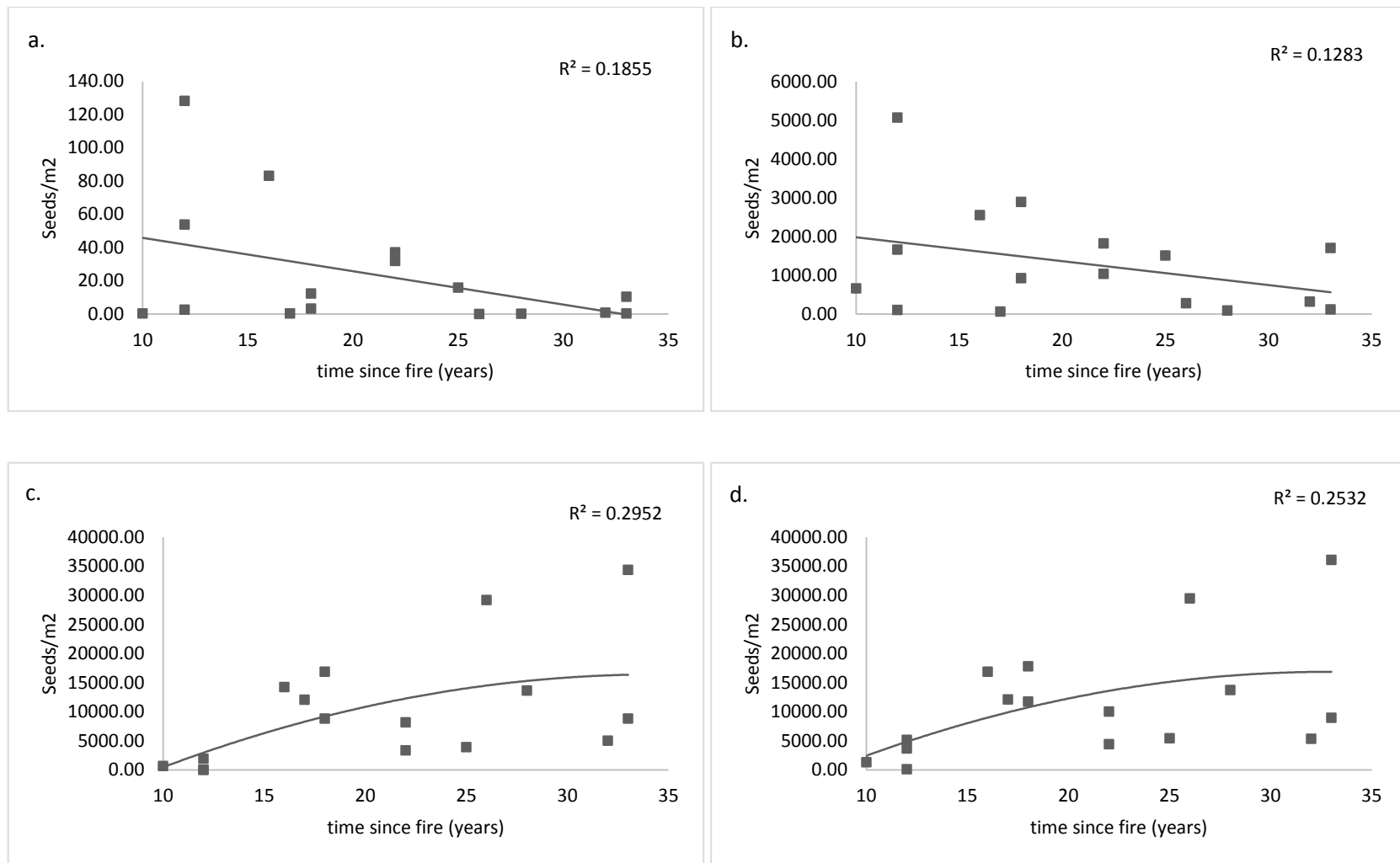


Figure 3.4 Seed rain over time (by size class)

Mountain big sagebrush (MBS) seed rain expressed as seeds per square-meter for small (a), medium (b), large (c), and combined (d) size classes in response to time since fire.

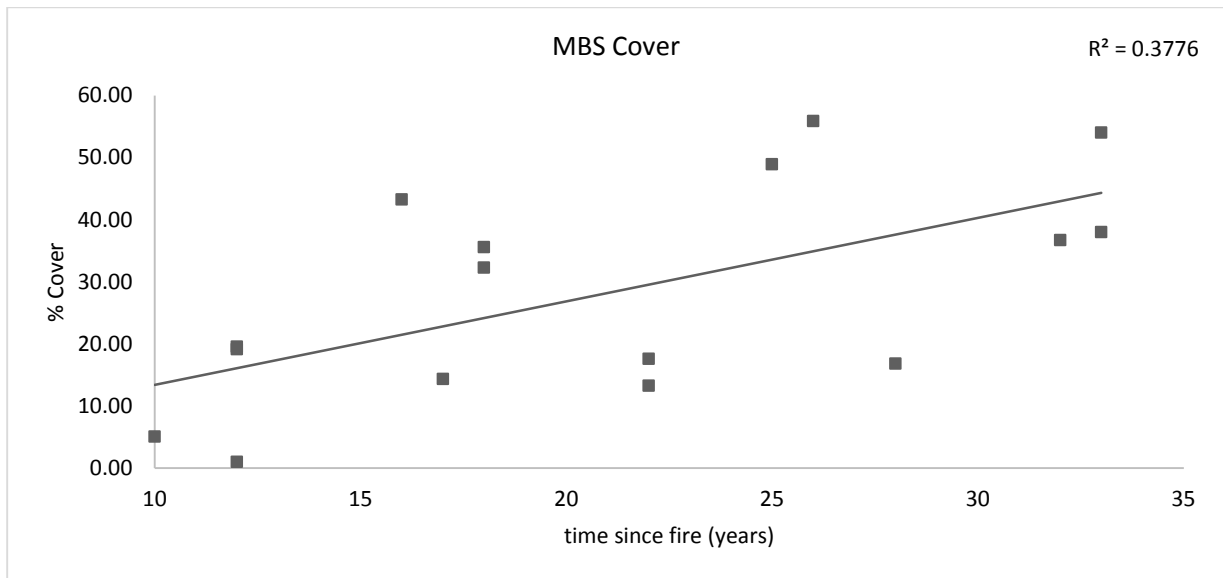


Figure 3.5 Percent cover over time
Percent cover in response to time since fire (TSF).

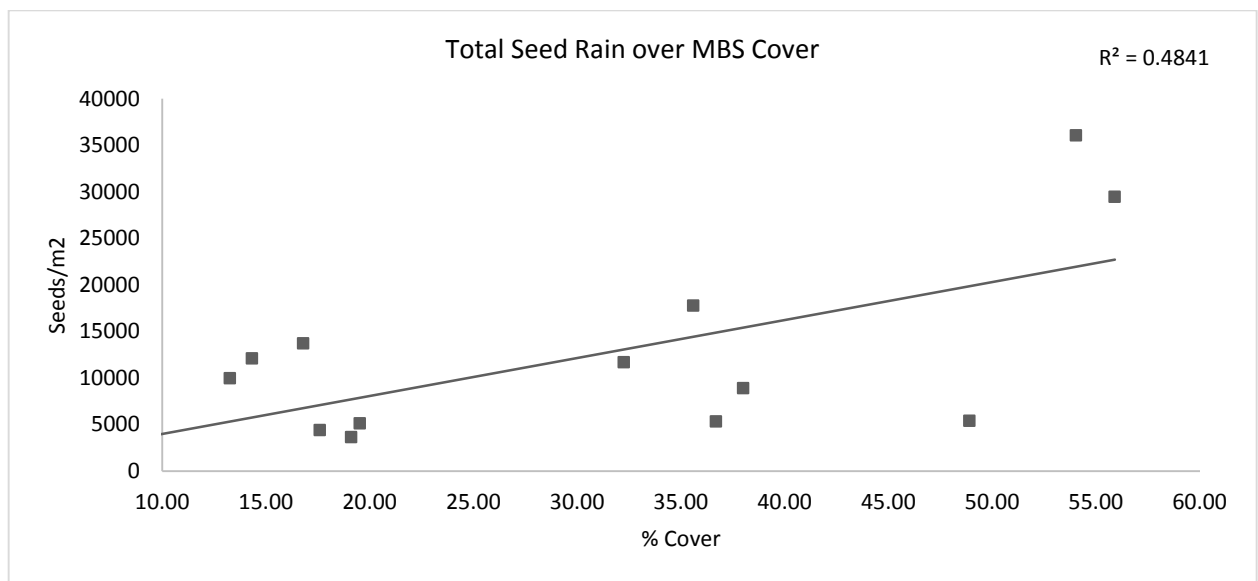


Figure 3.6 Total seed rain over MBS cover
Total mountain big sagebrush (MBS) seed rain per site in relation to cover for all sites.

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Appendix

Data compiled from 13 sites included in Chapter 3 study.

		Site Information							Precipitation			
Site Name	Region	Year Burned	Time Since Burn	Year Sampled	Type of Fire	% Slope	Aspect	Elevation (m)	Mean Annual Precip (mm)	Apr-Jun Precip	Oct-Mar Precip	Oct-Jul Precip
Granite	SE Great Basin	2001	10	2011	Wild	42	96	2515	487.17	200.56	428.90	663.83
Willow Creek	SE Great Basin	1999	12	2011	Wild	12	214	2426	484.91	146.57	376.45	561.66
Sheep Trail 1	Uinta Mtn	1998	12	2010	Rx	19	225	2569	592.90	164.67	233.27	444.33
Sheep Trail 2	Uinta Mtn	1998	12	2010	Rx	40	83	2553	592.90	164.67	233.27	444.33
Milford	SE Great Basin	1994	16	2010	Wild	5	278	2154	432.89	109.45	260.48	404.46
Dry Fork	Uinta Mtn	1994	17	2011	Wild	36	190	2544	540.13	212.54	394.67	715.50
Sunrise Mountain 1	Wasatch Mtns	1992	18	2010	Wild	25	270	1968	470.80	146.63	163.34	321.94
Sunrise Mountain 2	Wasatch Mtns	1992	18	2010	Wild	29	111	2048	499.29	151.39	176.83	340.70
Coyote Pond 1	Tushar Mtn	1988	22	2010	Wild	16	48	1976	366.48	94.25	241.37	358.74
Coyote Pond 2	Tushar Mtn	1988	22	2010	Wild	19	232	1980	366.48	94.36	242.67	360.30
Big Twist	Tushar Mtn	1985	25	2010	Rx	25	164	2256	488.07	138.39	296.75	474.58
Uinta River B (85)	Uinta Mtn	1985	26	2011	Rx	11	185	2249	498.86	186.36	387.26	663.24
Birch Creek East (83)	Tushar Mtn	1983	28	2011	Rx	16	240	2385	408.83	168.65	410.82	633.89
Yellowstone River	Uinta Mtn	1979	32	2011	Rx	12	89	2367	493.81	156.53	381.46	616.39
East Birch Creek (78)	Tushar Mtn	1978	33	2011	Rx	27	181	2493	471.05	184.35	445.68	686.24
Uinta River A (78)	Uinta Mtn	1978	33	2011	Rx	11	225	2256	504.88	191.16	391.85	674.56

Site Name	Ground Cover Class Percentages										
	An. Grass	Per. Grass	An. Forb	Per. Forb	Shrub	Litter	Rock	Crypt	Bare Ground	Soil Depth	% Cover
Granite	1.72	5.64	0.83	7.69	25.90	16.71	12.78	0.17	28.56	33.40	71.44
Willow Creek	1.70	0.20	0.30	0.00	15.08	8.89	58.44	0.05	15.33	17.50	84.67
Sheep Trail 1	0.20	8.64	1.02	4.65	12.63	19.74	5.52	0.00	47.57	29.90	52.43
Sheep Trail 2	0.00	13.76	0.10	3.71	16.46	58.91	0.20	0.00	6.86	50.80	93.14
Milford	2.15	5.25	0.40	0.90	21.11	12.16	0.00	0.00	58.03	27.10	41.97
Dry Fork	0.05	9.97	0.63	5.96	13.24	19.83	17.30	0.21	32.81	25.65	67.19
Sunrise Mountain 1	0.30	5.11	0.25	0.00	12.64	18.76	10.77	0.61	51.57	13.00	48.43
Sunrise Mountain 2	0.49	4.85	0.59	0.38	12.18	17.63	5.01	0.11	58.76	17.30	41.24
Coyote Pond 1	2.43	3.81	0.28	0.22	1.99	6.79	20.43	0.00	64.05	16.40	35.95
Coyote Pond 2	10.40	3.08	4.04	0.51	7.27	16.31	17.98	0.00	40.40	17.10	59.60
Big Twist	1.57	1.89	0.94	8.33	6.92	43.40	33.65	0.47	2.83	11.67	97.17
Uinta River B (85)	0.00	11.07	0.25	10.12	42.88	11.73	0.05	0.30	23.60	26.50	76.40
Birch Creek East (83)	1.30	5.92	2.84	15.74	16.80	21.30	23.20	2.25	10.65	23.6	89.35
Yellowstone River	0.21	0.99	1.62	4.13	29.52	27.80	4.23	0.26	31.24	35.60	68.76
East Birch Creek (78)	0.62	0.21	0.31	4.35	38.00	16.02	20.17	0.41	19.91	24.65	80.09
Uinta River A (78)	0.00	10.03	0.47	10.50	45.80	15.73	0.69	0.16	16.62	18.10	83.38

Site Name	Average Shrub Height				Center Point Quarter				Line Intercept		
	Small	Medium	Large	All	Shrubs per m2	Density (Small)	Density (Medium)	Density (Large)	Shrub Cover	MBS Cover	Relative MBS Cover
Granite	24.14	34.39	46.05	37.23	0.07	0.02	0.03	0.02	14.47	5.07	35.04
Willow Creek	22.37	29.80	40.74	31.00	0.26	0.06	0.14	0.07	19.84	19.12	96.37
Sheep Trail 1	25.39	44.44	0.00	35.33	0.64	0.08	0.55	0.02	23.29	19.53	83.86
Sheep Trail 2	27.95	45.61	0.00	39.15	0.07	0.02	0.03	0.02	32.81	0.97	2.96
Milford	22.13	48.67	71.69	39.15	0.98	0.32	0.35	0.31	43.27	43.27	100.00
Dry Fork	22.19	30.20	62.78	39.81	0.22	0.04	0.08	0.10	23.76	14.33	60.31
Sunrise Mountain 1	29.59	52.25	81.06	57.39	0.39	0.03	0.09	0.27	39.66	35.59	89.74
Sunrise Mountain 2	28.51	56.88	70.58	52.83	0.87	0.04	0.41	0.41	34.41	32.25	93.72
Coyote Pond 1	25.08	43.91	84.84	52.12	0.24	0.05	0.11	0.08	14.04	13.27	94.52
Coyote Pond 2	24.60	51.03	84.41	56.67	0.08	0.02	0.03	0.03	26.88	17.60	65.48
Big Twist	23.23	40.52	67.33	44.43	1.39	0.06	1.09	0.24	49.00	48.91	99.82
Uinta River B (85)	17.69	40.56	72.33	43.53	1.27	0.39	0.24	0.63	59.24	55.90	94.36
Birch Creek East (83)	23.88	34.66	67.94	47.63	0.77	0.02	0.08	0.67	*16.8	*16.8	unkn
Yellowstone River	22.13	36.60	56.85	40.58	1.27	0.03	0.25	1.00	38.56	36.69	95.15
East Birch Creek (78)	23.87	30.44	59.35	40.58	1.07	0.02	0.13	0.92	*38	*38	unkn
Uinta River A (78)	20.02	33.81	67.50	40.44	1.68	0.46	0.58	0.65	55.66	54.04	97.09

* Lost or missing data. Filled with estimation from ground cover class data.

Site Name	Seed Production			
	Fecundity (Small)	Fecundity (Medium)	Fecundity (Large)	Total Seed Rain
Granite	17	19,956	28,016	1289.55
Willow Creek	2,214	11,835	28,714	3658.07
Sheep Trail 1	618	9,261	0	5119.65
Sheep Trail 2	135	3,437	0	109.018
Milford	259	7,297	45,561	16836
Dry Fork	8	841	117,079	12091.9
Sunrise Mountain 1	369	10,013	62,636	17770.5
Sunrise Mountain 2	74	6,984	21,518	11698.6
Coyote Pond 1	586	16,536	107,732	9981.87
Coyote Pond 2	1,643	36,265	106,785	4413.48
Big Twist	250	1,385	16,454	5412.97
Uinta River B (85)	0	1,149	46,146	29474.1
Birch Creek East (83)	10	1,110	20,389	13718.1
Yellowstone River	27	1,299	5,033	5337.82
East Birch Creek (78)	17	907	9,554	8913.71
Uinta River A (78)	23	2,935	53,151	36070