

Nondestructive Age Estimation of Mountain Big Sagebrush (*Artemisia tridentata* ssp. *vaseyana*) Using Morphological Characteristics[☆]

Melissa L. Landeen^{a,c}, Stanley G. Kitchen^b, Loreen Allphin^c, Steven L. Petersen^{c,*}

^a Utah Division of Wildlife Resources, Great Basin Research Center, Ephraim, UT 84627, USA

^b US Department of Agriculture Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT 84606, USA

^c Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84604, USA

ARTICLE INFO

Article history:

Received 29 April 2018

Received in revised form 20 November 2018

Accepted 19 December 2018

Key Words:

dendrochronology

plant growth rate

stem diameter

woody plant age estimation

ABSTRACT

Current methods for determining plant age of shrub species require destructive sampling and annual growth ring analysis on the primary stem. Although individual plant ages can frequently be determined in this manner, the method is time consuming and of limited value for plants that have lost stem wood from stem splitting and rot. Nondestructive methods for estimating big sagebrush (*Artemisia tridentata* Nutt.) plant age would be useful in assessing stand age structure and population dynamics at variable spatial scales. The purpose of this study was to test a suite of traits for potential use in estimating mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle) age. We evaluated traits including plant height, crown area, subcanopy litter depth, percent crown mortality, bark furrow depth, bark fiber length, circumference and diameter of plant basal stem, and circumference of secondary and tertiary branches. We measured and harvested basal cross-sections from 163 plants of varying sizes from five locations in central and south-central Utah. Plant age was determined from annual growth rings. Linear regression analyses revealed that stem diameter ($r^2 = 0.507$, $P < 0.0001$) was the most highly correlated variable with plant age across all sites, followed by stem circumference ($r^2 = 0.474$, $P < 0.0001$), secondary branch circumference ($r^2 = 0.360$, $P < 0.0001$), tertiary branch circumference ($r^2 = 0.405$, $P < 0.0001$), and bark fiber length ($r^2 = 0.373$, $P < 0.0001$). Results support previous findings that stem girth has value for estimating mountain big sagebrush plant age and that this trait is a better indicator of age than any other tested traits. Although the relationship between stem diameter and plant age was significant, substantial stem size variability associated with plants of the same approximate age indicates that the method is most appropriate when precise age estimates are not required. This technique was developed specifically for mountain big sagebrush, but it is expected that it can be adapted for other sagebrush taxa.

© 2019 The Society for Range Management. Published by Elsevier Inc. All rights reserved.

Introduction

Plant community dynamics are largely a product of the inherent life-history attributes of component species interacting with the stressors and disturbance patterns of the abiotic environment (Grime, 1977, 1979). Dominant species tend to monopolize resource capture and retention (Whittaker, 1965). Stable plant communities perpetuate existing patterns of dominance over time (Kitchen et al., 2015). Hence, a knowledge of population age structure dynamics with and without disturbance can be vital for predicting long-term stability of dominant species in general, as well as for identifying conditions that could

potentially be destabilizing (Perryman and Olson, 2000; Wambolt and Hoffman, 2001; Miller et al., 2008).

Individual plant ages for woody plants are often estimated through examination of annual growth rings in the primary stem (Ferguson, 1964). Dendrochronological aging was first used with trees (Stokes and Smiley, 1968); however, the general approach has also been successfully applied to a number of shrub species (Roughton, 1972; Schweingruber and Poschod, 2005; Kitchen et al., 2015; Myers-Smith et al., 2015). Although highly accurate for individual plants, scaling the method up is generally impractical for stand level assessments of multiaged shrub communities because adequate sampling and analysis are too time intensive and destructive in nature. Alternative methods that can be quickly and reliably employed in a nondestructive manner are needed.

Age estimates based on easily observed morphological traits have received limited testing. A study in southern Australia used canopy height and diameter as a surrogate for age of acacia trees (Crisp and Lange, 1976). In colder environments, bark on some woody tree species increases in thickness over time and is a rough indicator of tree age

[☆] This study was funded by the US Dept of Agriculture Forest Service, Rocky Mountain Research Station, Utah Division of Wildlife Resources, Great Basin Research Center and Brigham Young University.

* Correspondence: Steven Petersen, Professor, Dept of Plant and Wildlife Sciences, Brigham Young University, Provo, UT, USA. Tel.: +1 801 422 4885 (Work), +1 541 609 0131 (Cell).

E-mail address: Steven_Petersen@byu.edu (S.L. Petersen).

(Molina et al., 2016). Similarly, certain lichen on bark in some desert shrub communities may indicate plant or stand maturity (Rosentreter, 1990). The trait most commonly used to estimate age of woody plants is stem girth (diameter or circumference), which, as might be expected, correlates strongly with plant age (Brotherson et al., 1983, 1984; Perryman and Olson, 2000). Although many of these characteristics have proven to be useful for estimating the age of trees, most age assessment methods have not been adequately tested on shrubs or shrub communities.

Big sagebrush (*Artemisia tridentata* Nutt.) has been described as “the most common and widespread shrub of western North America” (McArthur and Stevens, 2004). Although the full extent of sagebrush ecosystems before Euro-American settlement (c. 1850) remains uncertain (Kitchen and McArthur, 2007), they are now believed to occupy < 60% of their historic ranges (Chambers et al., 2017). Many have become fragmented and degraded due to invasive annual grasses, tree encroachment, grazing, changes in fire return intervals, and other factors (Knick et al., 2011; Miller et al., 2011). Little is known about the relationship between sagebrush population age structure and the processes that lead to ecosystem degradation. Management decisions for sagebrush communities are frequently based on stand conditions such as plant density, percent cover, or herbaceous species composition. A greater understanding of the relationship between sagebrush population demographics and

community resilience could provide new opportunities for improved management. For example, knowledge about postfire establishment and maturation rates could be used to estimate minimum intervals needed for full stand recovery (Nelson et al., 2014; Hourihan et al., 2018). A thorough investigation of that relationship and identification of opportunities for its application are dependent on development of efficient and reliable methods for characterization of big sagebrush population age structures under larger-scale spatial scenarios.

In this study, we evaluated the utility of easily measured morphological characteristics for estimating the age of individual plants of one subspecies of big sagebrush, mountain big sagebrush (*A. tridentata* ssp. *vaseyana* [Rydb.] Beetle; MBS). Our objective was to develop a method for rapid estimation of plant age using regression analysis. We hypothesized that plant age would correlate with one or more physical characteristics of sagebrush and that these characteristics could be used to efficiently and accurately estimate plant age.

Methods

We measured morphological characteristics and determined age for 163 MBS individuals from five sagebrush-steppe communities in central and south-central Utah with similar elevation and climate (Fig. 1; Table 1). All sites had experienced fire within 15–26 yr before



Figure 1. Map of Utah depicting the location of each big sagebrush sample study site.

Table 1

Coordinate locations, elevation, mean annual precipitation (PRISM, 2011), yr since most recent fire, and number of mountain big sagebrush samples collected (*n*) from each study site.

Site name	Latitude (north)	Longitude (west)	Elevation (m)	Mean annual precipitation	Time since fire (yr)	<i>n</i>
Sunrise	39.8492	–112.0968	2 108	470	17	44
Milford	38.3697	–112.8443	2 127	472	15	30
Big Twist	38.1873	–112.5089	2 312	478	24	30
Choke Cherry	38.1382	–112.4204	2 571	522	26	30
Coyote	38.3678	–112.9592	1 995	366	21	29

sampling, and shrub populations were in various stages of recovery. For each study site, 15 points were randomly located within each of two subunits (Milford, Big Twist, Choke Cherry, and Coyote sites) or three subunits (Sunrise site) defined by contrasting topographies. Proximal to each study point, we sampled three plants of varying sizes in a conscious effort to capture the full range of plant sizes represented on each site. 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 orientations before cross-sections were cut for aging.

For each study plant we measured a suite of morphological characteristics based on our expectation that metrics would vary proportional to plant age and on probable ease and repeatability of data collection (Fig. 2; Table 2). Measured traits included maximum plant height (excluding inflorescences), crown diameter (maximum and perpendicular to maximum), crown diameter (maximum and perpendicular to maximum), litter depth beneath the crown (averaged from three locations from a randomly selected plant quarter), litter depth at the base of the stem, and percent crown mortality (ocular estimation). We estimated crown area as the area of a circle with a radius equal to one-half of the mean of the two crown diameter measurements. After measurements were taken, plants were harvested (cut below the root collar), labeled, and placed in large bags in an attempt to minimize excessive breakage during transport. Additional characteristics measured post harvest included depth of most prominent bark furrow on

the primary stem (side of stem selected randomly), length of a detached representative bark fiber (side selected randomly), diameter of the primary stem between root collar and first branch (maximum and minimum using calipers), and maximum primary stem circumference (using string). We also determined an average circumference for three secondary and three tertiary branches proximal to their point of attachment.

A 3- to 5-cm-long cross-section of the primary stem was prepared from each plant for growth ring analysis. Limbs and roots were removed using hand clippers, and cuts were made perpendicular to the growth axis immediately above and below the root collar using a band saw. Top and bottom cuts were surfaced with a belt sander and progressively finer sand paper (60–220 grit) until annual growth rings were clearly visible using a stereo-microscope. Plant age was determined by counting annual growth rings on top and bottom cut surfaces and independently verified by at least two individuals (Stokes and Smiley, 1968). Samples that could not be aged due to center rot ($n = 2$) were excluded from further analysis. We calculated an estimate of plant growth rate by dividing the mean primary stem diameter by plant age (cm yr^{-1}) for each study plant.

Statistical Analysis

We tested the data for normality and then transformed it using square root transformations. Due to multicollinearity, we were unable

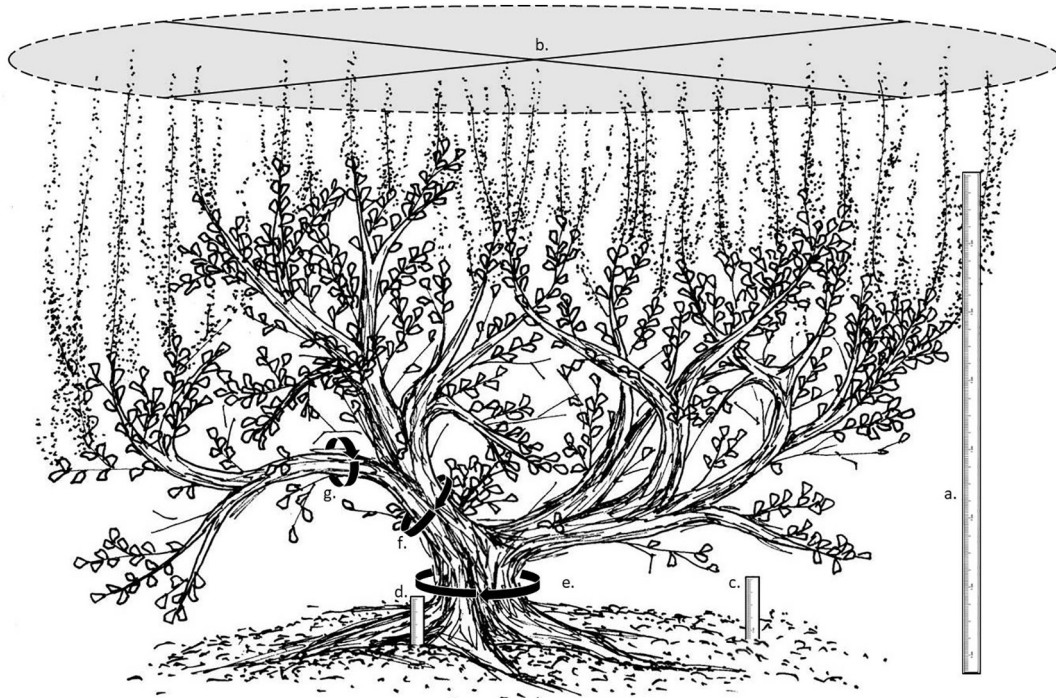


Figure 2. For each plant the following characteristics were measured: a) maximum plant height excluding inflorescences, b) crown area (maximum diameter and perpendicular to maximum), c) litter depth beneath the crown, d) litter depth at the base of the stem, e) diameter and circumference of primary basal stem, f) average circumference of three secondary branches, and g) average circumference of three tertiary branches.

Table 2

Mean vegetative data and mean shrub age generated from 5 study locations (sites) of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) in Utah. Standard errors are given in parentheses below each mean. Means followed by the same letter (in a column) do not differ significantly at $P \leq 0.05$, using a one-way analysis of variance and Tukey pairwise comparisons where data were normally distributed and nonparametric, Kruskal-Wallis test using Dwass-Steel-Critchlow-Fligner pairwise comparisons, where data were non-normally distributed. Stem diameter growth rate was calculated as primary stem diameter growth (cm) per year. All statistical analyses were generated in *Systat 13.1*.

Site	Plant height (cm)	Crown area (cm ²)	Mean stem diameter (cm)	Mean stem circum. (cm)	Mean 2° stem circum. (cm)	Mean 3° stem circum. (cm)	Prop. crown mortal.	Litter depth (cm)	Litter depth below crown (cm)	Bark furrow depth (mm)	Bark fiber length (mm)	Stem diam. growth rate (cm/yr)	Plant age (yr)
Sunrise	67.36 a (4.77)	10 070.82 a (1 568.43)	5.34 a (0.54)	19.40 a (2.00)	1.53 a (0.14)	0.86 a (0.08)	0.161 a (0.017)	2.34 ab (0.23)	1.40 a (0.10)	4.10 a (0.52)	12.43 a (1.38)	0.36 a (0.02)	14.5 a (1.03)
Big Twist	52.56 b (4.07)	5 835.41 b (991.67)	4.70 a (0.43)	16.00 a (1.38)	1.61 a (0.13)	0.95 a (0.09)	0.153 a (0.022)	2.29 ab (0.23)	0.89 b (0.09)	2.53 b (0.37)	11.19 a (1.40)	0.35 a (0.02)	13.0 a (0.72)
Milford	53.72 b (3.64)	5 448.26 b (904.12)	4.33 a (0.43)	14.80 a (1.41)	1.30 a (0.11)	0.78 a (0.08)	0.187 a (0.022)	2.77 a (0.19)	1.82 c (0.15)	2.97 ab (0.33)	11.36 a (1.43)	0.33 a (0.02)	12.5 a (0.68)
Choke Cherry	57.14 b (6.07)	6 697.75 b (1 267.39)	5.00 a (0.50)	17.17 a (1.66)	1.76 a (0.18)	0.99 a (0.12)	0.149 a (0.022)	1.55 ab (0.25)	1.55 ab (0.25)	2.03 b (0.31)	13.31 a (1.54)	0.40 a (0.05)	14.2 a (1.34)
Coyote	54.73 b (4.24)	7 566.60 b (1 324.18)	4.88 a (0.50)	17.48 a (1.69)	1.38 a (0.12)	0.74 a (0.07)	0.168 a (0.021)	2.62 a (0.43)	1.21 b (0.16)	2.53 b (0.36)	10.23 a (1.31)	0.37 a (0.03)	12.2 a (0.82)
Range/Mean	2.78	5.13	3.18	2.98	2.74	3.35	3.06	3.86	2.41	4.80	3.12	4.44	2.24
Mean													13.2

to perform multiple regression analysis. We tested for significant differences among all populations for vegetative traits using *Systat 13.1*, one-way analysis of variance, and Tukey pairwise comparisons, where data were normally distributed. For data that were non-normally distributed, we implemented a nonparametric Kruskal-Wallis test with Dwass-Steel-Critchlow-Fligner pairwise comparisons (*Systat Software Inc., 2009*).

We ran linear regressions between all vegetative characteristics and plant age for each site individually and all sites combined using the least squares method. Significance of correlative relationships was also assessed between growth rate (cm/yr) and mean annual precipitation (obtained from PRISM [2011] climate data), as well as between growth rate and time since fire (yr) using least squares linear regression. We performed all regressions using *Systat 13.1*.

Results

Across all sites, plant ages ranged from 2 to 32 yr, with a mean of 13.2 yr (Table 2). Mean values for plant age did not vary significantly among the sites at $P \leq 0.05$. Ages for 7% ($n = 12$) of the plants indicated establishment occurred during the same years that sites burned. This is highly unlikely because sagebrush seedlings typically emerge in early spring from the prior yr's seed. Instead, results suggest the possibility of minor aging errors most likely associated with improper classification of innermost growth rings and pith or failure to identify false rings. Establishment for an additional 14% ($n = 23$) of the study plants occurred 1 – 15 yr before the sites burned. Because big sagebrush plants of all sizes are easily killed by fire, the presence of plants that predate fire events suggests that fire effects at our sites were not uniform on the landscape and likely included unburned islands.

Mean values for primary stem diameter, stem circumference (primary, secondary, tertiary), proportion crown mortality, bark fiber length, and growth rate did not vary significantly among the five study sites ($P > 0.05$; Table 2). Plant height, crown area, and bark furrow depth were significantly higher for plants at the Sunrise site relative to the other sites ($P \leq 0.05$). We hypothesized that plant characteristics which express a wide range of variability (relative to the means) would be more sensitive to detection for age-related variability. Across all sites, the range-to-mean ratio varied from 5.13 for crown area to 2.41 litter depth below crown. Other variables with high range-to-mean ratios were bark furrow depth, growth rate, litter depth, tertiary stem circumference, primary stem diameter, and bark fiber length (see Table 2).

Regression analysis revealed that all morphologic characteristics were to some degree significantly correlated with MBS plant age ($P < 0.0001$), although the strength of the relationships varied. Across all sites, the strength of r^2 values between vegetative characteristics and age ranged from $r^2 = 0.116$ ($P < 0.0001$) for litter depth beneath the crown to $r^2 = 0.507$ ($P < 0.0001$) for mean diameter of the primary stem (Table 3). Age-trait relationships were consistently strongest for mean diameter of primary stems ($r^2 = 0.507$; Fig. 3a); circumference of primary, secondary ($r^2 = 0.360$; Fig. 3b), and tertiary ($r^2 = 0.405$; Fig. 3c) stems; and bark fiber length ($R^2 = 0.373$; Fig. 3d). Intermediate predictive values were associated with calculated crown area ($r^2 = 0.374$), plant height ($r^2 = 0.326$; Fig. 3f), bark furrow depth ($r^2 = 0.297$), and proportion crown mortality ($r^2 = 0.224$). Site-to-site variability in r^2 values was greatest for these traits of intermediate predictive capability (see Table 3). Among sites, age-trait relationships were consistently strongest for Sunrise and Coyote and weakest for Chokecherry sites (see Table 3). Contrary to our expectations, characteristics with wide range-to-mean ratios were no better for predicting plant age than those with narrower ratios.

Individual plant growth rates (primary stem diameter/age) ranged from 0.06 to 0.85 cm/yr (excluding one outlier of 1.67 cm/yr from the Chokecherry site). Mean growth rate did not vary significantly among sites ($P > 0.05$)—a result not surprising in light of the lack of among-

Table 3

Regression statistics (r^2 and P values) and standardized regression coefficients (β) between 11 vegetative characteristics and shrub age generated from 5 study locations (sites) of mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana*, in Utah. Significant linear relationships were assessed using least squares regression lines. These P values are given next to each r^2 value. All statistical analyses were generated in Systat 13.1.

Trait vs. age	Plant height (cm)			Crown area (cm ²)			Mean stem diam. (cm)			Mean stem circum. (cm)			Mean 2° stem circum. (cm)			Mean 3° stem circum. (cm)		
Site	r^2	P	β	r^2	P	β	r^2	P	β	r^2	P	β	r^2	P	β	r^2	P	β
Sunrise	0.570	0.000	0.755	0.614	0.000	0.784	0.674	0.000	0.821	0.631	0.000	0.794	0.587	0.000	0.766	0.641	0.000	0.801
Big Twist	0.253	0.005	0.503	0.213	0.010	0.462	0.536	0.000	0.732	0.464	0.000	0.681	0.457	0.000	0.761	0.413	0.000	0.643
Milford	0.367	0.000	0.606	0.429	0.000	0.655	0.535	0.000	0.731	0.474	0.000	0.689	0.631	0.000	0.794	0.417	0.000	0.646
Choke Cherry	0.078	0.136	0.279	0.084	0.120	0.290	0.236	0.005	0.485	0.046	0.253	0.468	0.349	0.059	0.215	0.148	0.036	0.385
Coyote	0.445	0.004	0.667	0.488	0.000	0.699	0.642	0.000	0.801	0.619	0.000	0.787	0.665	0.000	0.816	0.698	0.000	0.836
All sites	0.326	0.000	0.571	0.374	0.000	0.611	0.507	0.000	0.712	0.474	0.000	0.689	0.360	0.000	0.434	0.405	0.000	0.636

Trait vs. age	Prop. crown mortality			Litter depth (cm)			Litter depth below crown (cm)			Bark furrow depth (mm)			Bark fiber length (mm)		
Site	r^2	P	β	r^2	P	β	r^2	P	β	r^2	P	β	r^2	P	β
Sunrise	0.565	0.000	0.752	0.238	0.001	0.488	0.270	0.006	0.520	0.539	0.000	0.734	0.606	0.000	0.778
Big Twist	0.072	0.153	0.268	0.069	0.179	0.252	0.188	0.000	0.433	0.168	0.025	0.410	0.152	0.033	0.389
Milford	0.063	0.182	0.251	0.126	0.055	0.355	0.147	0.036	0.384	0.315	0.001	0.561	0.396	0.000	0.630
Chokecherry	0.154	0.032	0.393	0.266	0.004	0.515	0.215	0.010	0.464	0.082	0.125	0.287	0.362	0.002	0.601
Coyote	0.394	0.000	0.628	0.309	0.002	0.556	0.167	0.028	0.409	0.475	0.000	0.689	0.268	0.004	0.518
All sites	0.224	0.000	0.474	0.152	0.000	0.390	0.116	0.000	0.532	0.297	0.000	0.545	0.373	0.000	0.611

site differences in primary stem diameter and plant age (see Table 2) – and suggesting considerable within-site variation. Growth rate also did not vary with mean annual precipitation ($r^2 = 0.02$; $P = 0.791$). Across sites, growth rate did not vary significantly with plant age ($P = 0.330$) but did vary substantially (~threefold to fourfold) among plants of the same or similar age (Fig. 4).

Discussion

With appropriate calibration, mean stem diameter can be used as a metric for estimating the age of woody plants. Studied example species include salt cedar (*Tamarisk ramosissima* Ledeb.), 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), and Gambel oak (*Quercus gambelii* Nutt.; Brotherson et al., 1983, 1984). Similarly, Perryman and Olson (2000) found a strong correlation between plant age and stem diameter for Wyoming (*A. tridentata* ssp. *wyomingensis*), basin (*A. tridentata* ssp. *tridentata*), and MBS subspecies. Our results are in general agreement.

Although the relationship between stem diameter and age was relatively strong, the utility of this variable in estimating plant age is limited. A primary cause for this limitation is the considerable plasticity in growth rate we observed manifest as relatively high variability in plant age for plants with similar stem diameter (see Fig. 4) and in stem diameter for similar-aged plants (Fig. 3a). This growth rate plasticity also limits the utility of other variables related to plant size (i.e., stem circumference, plant height, crown area) as proxies for plant age.

Growth rate for big sagebrush varies by subspecies and is impacted by environmental factors, such as weather, disease, and competition (McArthur and Welch, 1982; Meyer, 1994). Variability in precipitation is typically responsible for variation in annual ring growth in semiarid environments (Ferguson and Humphrey, 1959), with recent work identifying hydrologic year precipitation and growing season temperatures as being the most influential factors for big sagebrush (Apodaca et al., 2017). Plants that have greater access to soil moisture in the spring generally grow faster than those with more limited soil moisture recharge. Heavy herbivory also causes stunted vegetative growth and reduced seed production, especially in areas of heavy winter use by wildlife (Wagstaff and Welch, 1991). In addition, interspecific and intraspecific competition for limited resources affects seedling establishment and growth in natural sagebrush communities (Brabec et al., 2015; Ott et al., 2017).

Although measures of stem diameter (primary, secondary, and tertiary) correlated most strongly with plant age, other measured variables are more easily assessed and were sufficiently strong to suggest potential utility. For example, plant height and crown area are among the easiest and quickest variables to estimate at the stand scale. Plant densities for distinct height or crown-area groupings could be easily converted to densities for age-class groupings, which could then be used to provide useful characterizations of stand age structure with little investment of time and resources. Unfortunately, the relationship between these traits and plant age was less consistent across sites (see Table 3), suggesting that investment in site-situational pretrials and calibration could reduce efficiencies associated with these alternative metrics.

Defensible extrapolation of our results may be limited because they were derived from relatively young plants sampled at sites where recent disturbance had reset succession. In contrast, it is probable that results will differ for plants sampled from sagebrush communities in areas long undisturbed. Subsequently, we predict that growth rates would differ in a largely closed plant community compared with that of an early seral postfire environment.

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

Although we sampled a variety of plant sizes, extremely small (and presumed young individuals) and plants older than 32 yr old were not included. Only two plants had a stem diameter < 1 cm, with the smallest having a stem diameter of 0.6 cm and being aged to 2 yr. While results showed that stem diameter and other variables were correlated with age for moderately and large-sized plants of modest age, further research is required to determine the utility of this method when applied to small plants and plants older than 35 yr.

Management Implications

Rapid and accurate assessment of sagebrush plant age could have many useful applications in rangeland ecology and management. These techniques can be employed to more accurately assess variability

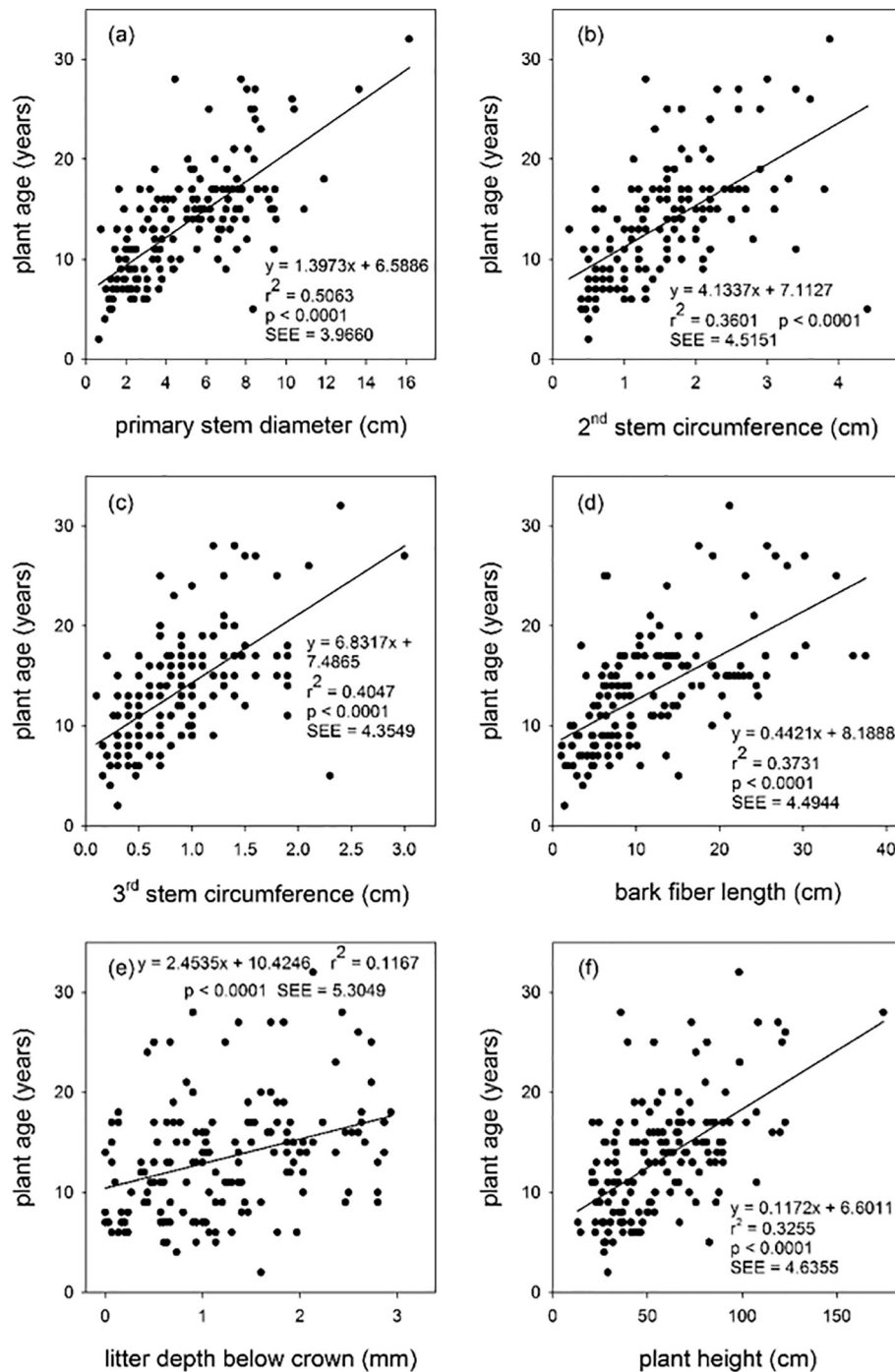


Figure 3. Scatter plots that show plant age as a function for (a) primary stem diameter, (b) secondary stem circumference, (c) tertiary stem circumference, (d) bark fiber length, (e) litter depth below the crown, and (f) plant height for mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*) plants on five Utah sites combined. Slope, intercept, r^2 , and standard error of estimate were derived from regression analysis.

in stand age structure for MBS and other sagebrush taxa. In addition, this knowledge will lead to a better understanding of the relationship between stand age structure and the ecological resilience of sagebrush ecosystems. For example, predicting age can be used to assess regional shifts in sagebrush structure, determine impacts related to fragmentation, and quantify the influence of annual grass invasion and anthropogenic development (Brown et al., 2005; Davies et al., 2011). This knowledge will also further our understanding of postdisturbance recovery (i.e., wildfire, rangeland improvements), emphasizing fecundity and stand development and maturation rates (Baker, 2010; Bates et al., 2011). These topics are becoming increasingly important due to the

threats posed by land use conversion, development, invasive grasses, and encroaching woodlands (Miller et al., 2008, 2011).

Characterizing sagebrush structure and age class can provide a more reliable assessment of landscape patchiness and the influence of habitat suitability for sagebrush obligate (i.e., greater sage-grouse, pygmy rabbits, sage sparrow, sage thrasher) and facultative (i.e., Rocky Mountain elk, mule deer, pronghorn) wildlife species (Pierce et al., 2011; Baruch-Mordo et al., 2013). The loss of suitable sagebrush habitat was considered the primary factor in the extirpation of greater sage-grouse populations (Aldridge et al., 2008). Predicting age structure can provide a valuable management tool for determining sagebrush condition or recovery for

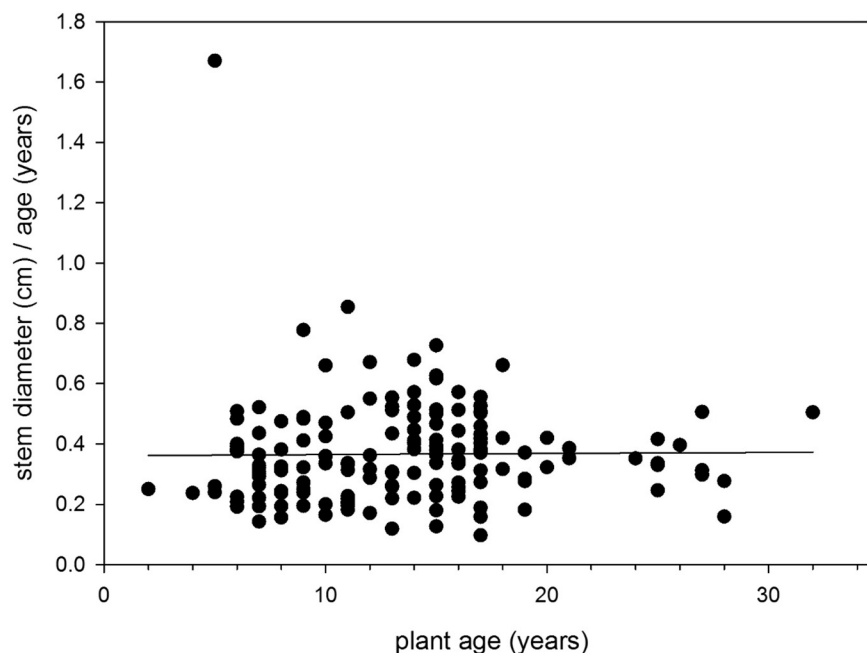


Figure 4. Scatter plot showing relationship between plant age and annual stem diameter growth rate of mountain big sagebrush.

sage-grouse and other sagebrush dependent wildlife (Austin and Urness, 1983). A more robust understanding of the range of applications and associated limitations of our approach will emerge as the methods explored in this study are broadly applied and subjected to further refinement.

Acknowledgments

Thanks to Stephanie Carlson, Brian Reeves, and Kevin Costa for field and laboratory assistance. We also thank Dr. Randy Larsen for statistical consultation and three anonymous reviewers for thoughtful feedback on earlier versions of the manuscript. We appreciate the financial support provided by the United States Forest Service, RMRS Shrub Science Laboratory (09-JV-11221632-285), Utah Division of Wildlife Resources (Federal Aid Project R-82-R) and Brigham Young University. We also appreciate the use of facilities at Brigham Young University and the Geospatial Habitat Analysis Lab.

References

- Aldridge, C.L., Nielsen, S.E., Beyer, H.L., Boyce, M.S., Connelly, J.W., Knick, S.T., Schroeder, M.A., 2008. Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14, 983–994.
- Apodaca, L.F., Devitt, D.A., Fernstermaker, L.F., 2017. Assessing growth response to climate in a Great Basin big sagebrush (*Artemisia tridentata*) plant community. *Dendrochronologia* 45, 52–61.
- Austin, D.D., Urness, P.J., 1983. Overwinter forage selection by mule deer on seeded big sagebrush-grass range. *Journal of Wildlife Management* 47, 1203–1207.
- Baker, W.L., 2010. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34, 177–185.
- Baruch-Mordo, S., Evans, J.E., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biological Conservation* 167, 233–241.
- Bates, J.D., Davies, K.W., Sharp, R.N., 2011. Shrub-steppe early succession following juniper cutting and prescribed fire. *Environmental Management* 47, 468–481.
- Brabec, M.M., Germino, M.J., Shinneman, D.J., Pilliod, D.S., McIlroy, S.K., Aride, R.S., 2015. Challenges of establishing big sagebrush (*Artemisia tridentata*) in rangeland restoration: effects of herbicide, mowing, whole-community seeding, and sagebrush seed sources. *Rangeland Ecology & Management* 68, 432–435.
- Brotherson, J.D., Carman, J.G., Szyska, L.A., 1984. Stem-diameter age relationships of *Tamarix ramosissima* in central Utah. *Journal of Range Management* 37, 362–364.
- Brotherson, J.D., Rushforth, S.R., Evenson, W.E., Johansen, J.R., Morden, C., 1983. Population dynamics and age relationships of 8 tree species in Navajo National Monument, Arizona. *Journal of Range Management* 36, 250–256.
- Brown, D.G., Johnson, K.M., Loveland, T.R., Theobald, D.M., 2005. Rural land-use trends in the conterminous United States, 1500–2000. *Ecological Applications* 15, 1851–1863.
- Chambers, J.C., Maestas, J.D., Pyke, D.A., Boyd, C.S., Pellant, M., Wuenschel, A., 2017. Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and greater sage-grouse. *Rangeland Ecology & Management* 70, 149–164.
- Crisp, M.D., Lange, R.T., 1976. Age structure, distribution and survival under grazing of the arid-zone shrub *Acacia burkittii*. *Oikos* 27, 86–92.
- Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144, 2573–2584.
- Ferguson, C.W., 1964. Annual rings in big sagebrush. *Papers of the Laboratory of Tree-Ring Research*. No. 1. University of Arizona Press, Tucson, AZ, USA 95 p.
- Ferguson, C.W., Humphrey, R., 1959. Growth rings of sagebrush reveal rainfall records. *Progressive Agriculture in Arizona* 11, 1959–1960.
- Frischknecht, N.C., Baker, M.F., 1972. Voles can improve sagebrush rangelands. *Journal of Range Management* 25, 466–468.
- Gates, D.H., 1964. Sagebrush infested by leaf defoliating moth. *Journal of Range Management* 17, 209–210.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169–1194.
- Grime, J.P., 1979. Primary strategies in plants. *Journal of Scotland* 43, 151–160.
- Hourihan, E., Schultz, B.W., Perryman, B.L., 2018. Climatic influences on establishment pulses of four *Artemisia* species in Nevada. *Rangeland Ecology & Management* 71, 77–86.
- Kitchen, S.G., McArthur, E.D., 2007. Big and black sagebrush landscapes. Hood, S. M. and Miller, M. [comps.]. *Fire ecology and management of the major ecosystems of southern Utah*. General Technical Report. RMRS-GTR-202. US Department of Agriculture, Forest Service, Fort Collins, CO, USA, pp. 73–95.
- Kitchen, S.K., Meyer, S.E., Carlson, S.C., 2015. Mechanisms for maintenance of dominance in a nonclonal desert shrub. *Ecosphere* 6, 252.
- Knick, S.T., Hanser, S.E., Miller, R.F., Pyke, M.J., Wisdom, M.J., Finn, S.P., Rinkes, T.E., Henny, C.J., 2011. Ecological influence and pathways of land use in sagebrush. In: Knick, S.T., Connelly, J.W. (Eds.), *Greater sage grouse—ecology and conservation of a landscape species and its habitats*. *Studies in Avian Biology* 38. University of California Press, Berkeley, CA, USA, pp. 203–251.
- McArthur, E.D., Blauer, A.C., Sanderson, S.C., 1988. Mule deer-induced mortality of mountain big sagebrush. *Journal of Range Management* 41, 114–117.
- McArthur, E.D., Stevens, R., 2004. Composite shrubs. Mosen, S. B., Stevens, R., Shaw, N. L. [comps.]. *Restoring western ranges and wildlands*. General Technical Report. RMRS-GTR-136-vol 2. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA, pp. 493–537.
- McArthur, E.D., Welch, B.L., 1982. Growth rate differences among big sagebrush (*Artemisia tridentata*) accessions and subspecies. *Journal of Range Management* 35, 396–401.
- Meyer, S.E., 1994. Germination and establishment ecology of big sagebrush: implications for community restoration. Mosen, S. B., and Kitchen, S. G. [comp.]. *Proceedings of Symposium on the Ecology, Management, and Restoration of Intermountain Annual Rangelands*; 18–21 May 1992, Boise, ID, USA. General Technical Report INT-GTR-313. US Department of Agriculture, Forest Service, Ogden, UT, USA, pp. 244–251.
- Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L., 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), *Greater sage grouse—ecology and conservation of a landscape species and its habitats*. *Studies in avian biology* 38. University of California Press, Berkeley, CA, USA, pp. 145–185.
- Miller, R.F., Tausch, R.J., McArthur, E.D., Johnson, D.D., Sanderson, S.C., 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the

- Intermountain West. Research Paper RMRS-RP-69. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA 15 p.
- Molina, J.G.A., Hadad, M.A., Dominguez, D.P., Roig, F.A., 2016. Tree age and bark thickness as traits linked to frost ring probability on *Araucaria araucana* trees in northern Patagonia. *Dendrochronologia* 37, 116–125.
- Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S., Trant, A.J., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M.A., Wheeler, J.A., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Wilmking, M., 2015. Methods for measuring arctic and alpine shrub growth: a review. *Earth-Science Reviews* 140, 1–13.
- Nelson, Z.J., Weisberg, P.J., Kitchen, S.G., 2014. Influence of climate and environment on post-fire recovery of mountain big sagebrush. *International Journal of Wildland Fire* 23, 131–142.
- Ott, J.E., Cox, R.D., Shaw, N.L., 2017. Comparison of postfire seeding practices for Wyoming big sagebrush. *Rangeland Ecology & Management* 70, 625–632.
- Perryman, B.L., Olson, R.A., 2000. Age-stem diameter relationships of big sagebrush and their management implications. *Journal of Range Management* 53, 342–346.
- Pierce, J.E., Larsen, R.T., Flinders, J.T., Whiting, J.C., 2011. Fragmentation of sagebrush communities: does an increase in habitat edge impact pygmy rabbits? *Animal Conservation* 14, 314–321.
- PRISM Climate Group, 2011. PRISM Climate Group. PRISM Climate Group, Oregon State University, Corvallis, OR, USA.
- Rosentreter, R., 1990. Indicator value of lichen cover on desert shrubs. In: McArthur, D.E., Romney, E.M., Smith, S.D., Tueller, P.T. (Eds.), *Proceedings-Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management*. GTR-INT-276, Intermountain Research Station, USDA Forest Service, Ogden, UT, USA, pp. 282–289.
- Roughton, R.D., 1972. Shrub age structures on a mule deer winter range in Colorado. *Ecology* 53, 615–625.
- Schweingruber, F.H., Poschod, P., 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *Forest Snow and Landscape Research* 79, 195–415.
- Stokes, M.A., Smiley, T.L., 1968. *Introduction to tree-ring dating*. University of Chicago Press, Chicago, IL, USA (73 pages).
- Systat 13. [computer program], 2009. Systat Software Inc. Crane Software International, Chicago, IL, USA.
- Wagstaff, F.L., Welch, B.L., 1991. Seedstalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. *Journal of Range Management* 44, 72–74.
- Wambolt, C.L., Hoffman, T.L., 2001. Mountain big sagebrush age distribution on the northern Yellowstone winter range. McArthur, E. D., and Fairbanks, D. J. [comps.]. *Shrubland Ecosystem Genetics and Biodiversity*. USDA, Forest Service, Rocky Mountain Research Station, RMRS-P-21, Ogden, UT, USA, pp. 330–335.
- Whittaker, R.H., 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. *Science* 147, 250–260.