Rangeland Ecology & Management 70 (2017) 633–637

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

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

Melissa L. Landeen [a], Loreen Allphin [a], Stanley G. Kitchen [b], Steven L. Petersen [a,*]

[a] *Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84602, USA*
[b] *USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT 84602, USA*

ARTICLE INFO

Article history:
Received 22 December 2016
Received in revised form 19 April 2017
Accepted 8 May 2017

Key Words:
rapid assessment
reproductive potential
sagebrush steppe

ABSTRACT

Seed production is an essential component of postdisturbance recovery for mountain big sagebrush (*Artemisia tridentata* Nutt. ssp *vaseyana* [Rydb] Beetle; MBS). We tested a method for rapid estimation of MBS seed production using measurements of inflorescence morphology. We measured total stem length, stem length from first branchlet to stem tip, stem diameter, fresh weight, and number of stem branchlets for 750 inflorescences collected from five central and southern Utah sites. Florets per inflorescence were counted to provide an estimate of seed production potential. We used regression analysis to assess associations between morphological traits and potential seed production and evaluated the efficiency and scalability of each measure for field application. Site means for morphological measures varied ~2 to 11-fold while mean number of florets per inflorescence varied ~ 8-fold. Inflorescence weight was the best predictor of seed production potential ($P < 0.0001$, $r^2 = 0.897$), although correlations for all tested variables were highly significant. Among-site differences in regression equations for this relationship were not significant ($P = 0.226$), suggesting that a single conversion factor may have broad application. However, validation will require additional testing across a broader range of sites and field conditions. Scalable methods for efficient estimation of sagebrush seed production potential, such as those evaluated in this study, could be useful for managers charged with assessing variability in sagebrush community stability.

Introduction

Historically, the sagebrush biome was the most widespread nonforest vegetation type in temperate North America, covering perhaps 62 million ha (McArthur and Plummer 1978). Compared with historic conditions, current sagebrush ecosystems are reduced in extent, fragmented, degraded, and face multiple threats (Welch 2005), including altered fire regimes (USDI 2015). Present and projected habitat reductions for sagebrush-dependent species, such as greater sage-grouse (*Centrocercus urophasianus* Bonaparte) and pygmy rabbits (*Brachylagus idahoensis* Merriam), have become a priority concern for land managers in the western United States and have provided the impetus for changes in land management practices (Davies et al. 2011; USDI 2015). Management practices that maintain or improve ecological resilience to disturbance are deemed crucial to preserve sagebrush ecosystems and associated species (Chambers et al. 2014).

The most widespread and common sagebrush is big sagebrush (*Artemisia tridentata* Nutt.; McArthur and Stevens 2004) with three prominent subspecies. Compared with Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle and Young) and basin big sagebrush (*A. tridentata* ssp. *tridentata* Nutt.), mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle; MBS) occurs at relatively high elevations (1 000 – 3 200 m) in semiarid regions where soil and climate conditions are relatively cool and wet (Beetle and Young 1965; Winward 1980). Mountain big sagebrush-dominated communities are generally more resilient than those occupied by the other subspecies (Chambers et al., 2014).

Big sagebrush does not root or crown sprout but relies entirely on seed for regeneration. The soil seed bank in sagebrush communities is short-lived, with most seeds germinating within 1 yr of dispersal (Ziegenhagen and Miller 2009). Therefore, recovery following disturbance is dependent on regular replenishment of the seed bank. A better understanding of seed production variability and how that variability regulates seed bank dynamics is needed.

This study was funded by the US Dept of Agriculture Forest Service, Rocky Mountain Research Station, and Brigham Young University.

[*] Correspondence: Steven L. Petersen, Dept of Plant and Wildlife Sciences, 4105 LSB, Brigham Young University, Provo, UT 84602, USA.
E-mail address: steven_petersen@byu.edu (S.L. Petersen).

http://dx.doi.org/10.1016/j.rama.2017.05.002
1550-7424/

Seed production in MBS varies among and within sites and across years (Young et al. 1989; Schlaepfer et al. 2014). Factors that affect reproductive growth and output include soil moisture availability (Booth et al. 2003), disease (Welch and Nelson 1995; Takahashi and Huntly 2010), ungulate (Wagstaff and Welch 1991) and insect herbivory (Takahashi and Huntly 2010), plant age, intraspecific and interspecific competition and genetics (Welch 2005 and references therein). Seeds are small (4 000–6 000 per g; Meyer et al., 1988) but may be produced and dispersed in relatively high densities under favorable conditions (Welch 2005).

Methods that can be used to efficiently estimate MBS seed production potential should be useful for predicting postdisturbance recovery and variability in stand resilience through time. However, obtaining accurate production estimates by field-harvesting seeds from representative plants is time-consuming and difficult due to the indeterminate ripening/dispersal nature of the species. Protocols for estimating seed production based on morphological characteristics have been developed for several plant species. For example, Laubhan and Fredrickson (1992) developed a method for estimating seed production of 11 moist-soil plants in the Mississippi Alluvial Valley using characteristics such as inflorescence number, length, base diameter, and plant height. Greene and Johson (1994) developed a similar method for predicting seed production in trees. In these examples, simple linear regressions were used to assess the relationships between easily measured and rapidly quantifiable morphological characteristics and seed production. Young et al. (1989) suggested that individual plant characteristics could also be used to explain most of the variation in seed production for big sagebrush.

Our objective was to test the utility of various, easily measured morphological traits for estimating MBS seed production potential. We compare the reliability of each trait across multiple sites and consider the practicality of scaling up protocols for making quick, stand-level assessments.

Methods

Study Site Description and Plot Selection

Five MBS-dominated sites were selected in central and south-central Utah (Table 1). Sites were selected 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 intact sagebrush community. Sites had soils ranging from loam or clay-loam in texture.

Sample Collection

We collected sample inflorescences in the fall (September 4–October 15, 2009) when fruits (achenes) were partially developed but before full maturation and dispersal had occurred. Samples were collected from 5 − 20 plants at each site. Although the ages of plants were not known, samples were collected from mature plants of various sizes. Study plants were selected to include a full range of inflorescence sizes/lengths available at each site. We cut ~350 inflorescences at Sunrise and ~100 inflorescences at each of the other four sites. Inflorescences were removed from plants at the point of attachment. We weighed individual inflorescences (to nearest gram) in the field using a hanging scale or in the laboratory soon after collection using a digital balance. We opted for wet weight over dry weight because it may be obtained quickly and easily in the field, allowing for more rapid assessment. Samples were placed in zip-lock style bags on ice during transport and stored at ~2 − 4°C until fully processed. Samples damaged during transport were excluded from the study.

Table 1
Coordinate location, elevation, annual precipitation (30-yr average obtained from PRISM) and average precipitation of sampling yr (2009; obtained from PRISM) of each of 5 study locations in Utah, United States, of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities sampled reproductively in this study.

Site name	Latitude (north)	Longitude (west)	Elevation (m)	Precipitation (mm)	Precipitation 2009 (mm)
Sunrise	39.8627	−112.1039	1972	470	394
Big Twist	38.1784	−112.5109	2255	488	413
Milford	38.3696	−112.8440	2140	431	351
Rocky Flat	38.1710	−112. 5149	2284	463	413
Coyote Pond	38.0147	−112.9901	1892	345	247

Laboratory Analyses

We measured additional morphological traits in the laboratory, including total inflorescence stem length and stem length from first inflorescence branchlet (minimum length = 2 cm) to stem tip, basal diameter of inflorescence stem, and number of branchlets on each inflorescence. We counted florets or achenes (hereafter referred to as florets) per inflorescence as a measure of potential seed production. If florets had become dislodged, we counted bare pedicels. Seed viability was not considered, as seeds were not universally mature and our interest was in determining an estimate of the potential fecundity, not actual values. We measured a total of 750 samples from all sites.

Statistical Analyses

Means and standard errors for each of the variables measured were calculated using *Systat 13.1* (Systat Software Inc. 2009). We compared means across all populations sampled for statistically significant differences using one-way analysis of variance and Tukey pair-wise comparisons using *Systat 13.1* (Table 2; Systat Software Inc. 2009). Where necessary, we performed a square-root transformation to normalize the data and decrease the variance for statistical testing.

To test the relationship between each stem characteristic and the number of florets produced per inflorescence, we conducted regression analyses in *Systat 13.1* (SYSTAT 2009). We ran separate regressions for each stem characteristic against the number of florets. These regressions were run for each population and for all populations combined. We analyzed confidence bands around regression lines to assess statistical significant of site-level differences in regression results. For all statistical analyses, we used a P value of ≤ 0.05 for significance.

Results

The five sites sampled in this study varied significantly among all morphological traits measured (see Table 2). Proportional differences between maximum and minimum site means ranged from 10.8 for inflorescence weight to 2.2 for length of stem. The range in site averages for each variable include 1) inflorescence weight: 0.172–1.852 g, 2) stem diameter: 0.568–1.639 cm, 3) length of stem: 13.44–28.34 cm, 4) length of stem from first branchlet to stem tip: 8.73–19.36 cm, 5) length of longest branchlet: 2.89–7.59 cm, and 6) number of branchlets: 3–14. Mean number of florets varied from 64–531 per inflorescence (see Table 2). Across all variables, the Coyote Pond population exhibited the smallest values and the Sunrise population exhibited the highest values ($P \leq 0.05$; see Table 2).

All explanatory variables included in this study demonstrated a significant ($P \leq 0.0001$) positive regression relationship with the response variable, total number of florets. The strongest relationship was observed for inflorescence weight ($r^2 = 0.897$, $P = 0.000$; Fig. 1, a) based on the equation $y = 273.52x$. A strong positive relationship was also observed between the number of florets and the length of the longest branchlet ($r^2 = 0.713$, $P = 0.000$; see Fig. 1, b), noted with the equation $y = 95.632x – 182.32$. There were no differences in seed production potential among sites ($P = 0.793$).

Table 2
Mean reproductive and vegetative data generated from 5 study locations (sites) of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), in Utah, United States. Standard errors are given in parentheses below each mean. Means followed by the same letter (in a column) do not differ significantly at $P \le 0.05$.

Site	Weight (kg)	Stem diameter (cm)	Stem length (cm)	Stem length from first branchlet to stem tip (cm)	Length of longest branchlet (cm)	No. of stem branchlets	Total number florets per inflorescence
Sunrise	1.852 a (0.107)	1.639 a (0.039)	28.34 a (0.503)	19.36 a (0.435)	7.59 a (0.256)	14.3 a (0.389)	531.2 a (30.12)
Big Twist	0.447 bc (0.050)	0.898 b (0.042)	18.60 b (0.832)	12.65 b (0.728)	4.95 b (0.427)	6.19 b (0.695)	161.1 bc (20.72)
Milford	0.898 b (0.123)	1.047 bc (0.058)	18.26 b (0.633)	13.38 b (0.565)	4.46 b (0.332)	6.35 b (0.650)	229.9 b (23.65)
Rocky Flat	0.820 b (0.052)	1.223 c (0.047)	23.87 c (0.640)	16.62 c (0.486)	5.46 b (0.234)	12.08 c (0.540)	285.7 b (18.58)
Coyote Pond	0.172 c (0.009)	0.568 d (0.021)	13.44 d (0.339)	8.73 d (0.258)	2.89 c (0.114)	3.57 d (0.435)	64.4 c (2.45)

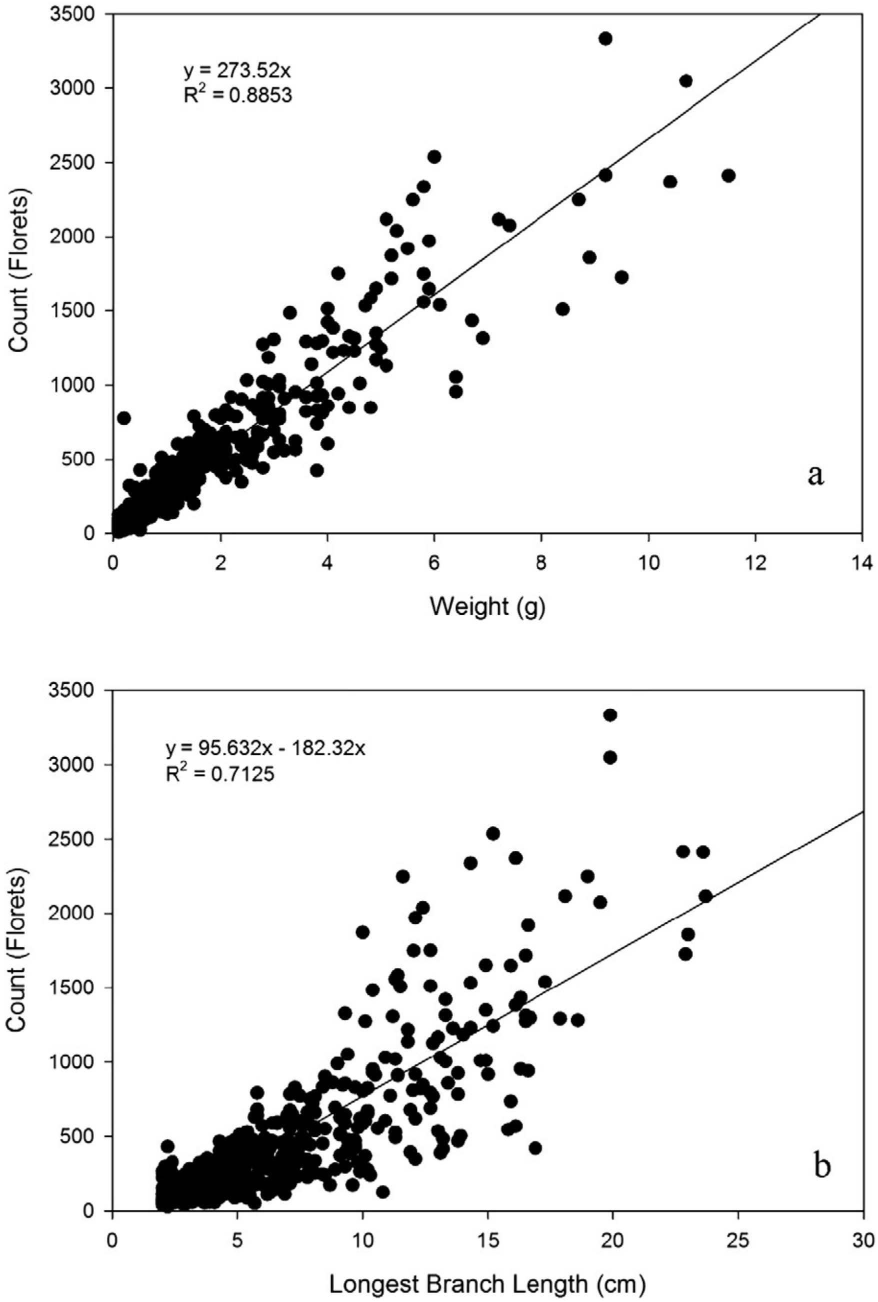

Figure 1. Relationship between the number of florets and inflorescence weight (a) and total inflorescence length (b) across five study locations of mountain big sagebrush (*Artemisia tridentata* ssp *vaseyana*) in Utah, USA.

Both stem diameter ($r^2 = 0.714$, $P = 0.000$) and stem length from first branchlet to stem tip ($r^2 = 0.650$, $P = 0.000$) were positively correlated with number of florets using linear regression. Total stem length ($r^2 = 0.577$, $P = 0.000$) and number of branchlets ($r^2 = 0.516$, $P = 0.000$) were the least correlated with total number of florets of the measurements taken. While morphological measures for samples collected from different sites often differed from one another (see Table 2), the strength of the relationship between the independent variables and total number of florets remained strong ($P < 0.0001$) regardless of site. For example, using linear regression, the most strongly correlated variable, inflorescence weight, was related to total number of florets at each site (Rocky Flat: $r^2 = 0.923$, $P = 0.000$; Milford: $r^2 = 0.888$, $P = 0.000$; Big Twist: $r^2 = 0.812$, $P = 0.000$; Coyote Pond: $r^2 = 0.702$, $P = 0.000$; Sunrise: $r^2 = 0.884$; $P = 0.004$). Among-site differences in the slope and intercept of the regression line were not significant ($P = 0.226$), suggesting stability in the relationship.

Discussion

Several factors are known to influence seed production in plants including plant density (Allison 1990); pollination success (Willson and Burley 1983; Charlesworth 1989); seed predation (Zimmerman 1980; Ehrlen 1992); resource limitation in the form of water and/or essential elements (Stephenson 1981; Charlesworth 1989; Ehrlen 1992; Booth et al. 2003); and genetic factors (Wiens et al. 1987; Allphin et al. 2002; Allphin et al. 2007). Plant seed production has been shown to vary among individuals (Allphin et al. 2002; Yasaka et al. 2008); among sites (Lubbers 1986; Allphin et al. 2007); and across years (Booth et al. 2003; Allphin et al. 2007; Yasaka et al. 2008). We documented an eight-fold range in floret number per inflorescence, suggesting a potential for high site-to-site variability in MBS seed production potential. Actual variability among these sites would also depend upon the number of inflorescences per plant, plant density, and viable seed set; variables not measured in this study. Although untested here, year-to-year variability is also expected to be high (Young et al. 1989; Schlaepfer et al. 2014).

Inflorescence weight was the best trait for estimating MBS seed production potential using a simple linear equation. The stability of the equation across sites with clear differences in measured morphological traits and reproductive output suggests that a generalized equation could have broad application; however, a more robust analysis using a more diverse range of sites, years, and environmental conditions is needed.

In addition to accuracy, we also considered measurement efficiency and how easily the method could be scaled up to stand level assessments. Of the measures we tested, it is our judgment that estimation of total inflorescence stem length has the most potential for quick and efficient cross-scale (inflorescence, plant, and stand) application when combined with plant density estimates. This measure is easily calibrated, can be completed on site without destructive sampling, and is relatively insensitive to the timing of assessment once stem elongation is complete. Unfortunately, the strength of the correlation for this trait was considerably lower than that calculated for inflorescence weight. However, tradeoffs of increased efficiency may more than offset minor losses in accuracy in field application.

While this method was developed specifically for mountain big sagebrush, adaptation of these methods for other sagebrush taxa should be explored. Adaptation should include development and testing of separate regression equations for each taxa as seed production varies greatly among and within sagebrush types.

Management Implications

The ability to estimate sagebrush seed production potential can be a useful tool for both land managers and researchers to assess recovery potential, predict seed bank establishment and maintenance, and understand succession patterns following disturbance. Additionally, seed production potential can be used as an indicator of resource availability. Estimates of reproductive output might also be incorporated into monitoring protocols for high-priority management areas (e.g., greater sage-grouse Priority Areas for Conservation).

Most fires in the sagebrush-steppe occur in the late summer or early fall, before the current year's seed crop has matured and dispersed. The postfire sagebrush seed bank is, therefore, composed almost entirely of residual seeds from the previous year's production, which typically only remain viable in the soil for a short time before germinating but have been known to survive ungerminated for up to 2 yr after fire (Ziegenhagen and Miller 2009). Seed production potential estimation based upon easily measured variables (e.g., inflorescence weight or length) may be useful for identifying stand-level peaks in seed bank input potential and thus for estimating minimum fire-free episodes needed for sagebrush postfire recovery. This information may also be useful when determining seeding rate following tree removal or other sagebrush improvement treatments in sagebrush steppe communities. However, we recognize that the total amount of seed produced is only one preemergent variable that determines reproductive success of sagebrush from seed (Ziegenhagen and Miller 2009; Schlaepfer et al. 2014).

Acknowledgments

Thanks to S. Carlson, B. Reeves, and K. Costa for field and laboratory assistance. We also thank Randy Larsen for statistical consultation and two anonymous reviewers for thoughtful feedback on earlier versions of the manuscript.

Literature Cited

Allison, T.D., 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. Ecology 71, 516–522.

Allphin, L., Hunt, L.A., Anderson, V.J., 2007. Genetic diversity and low reproductive success in isolated populations of Utah juniper, *Juniperus osteosperma (Cupressaceae)*. Western North American Naturalist 67, 323–337.

Allphin, L., Wiens, D., Harper, K.T., 2002. The relative effects of resources and genetics on reproductive success in the rare Kachina daisy *Erigeron kachinensis (Asteraceae)*. International Journal of Plant Sciences 163, 599–612.

Beetle, A.A., Young, A., 1965. A third subspecies in the *Artemisia tridentata* complex. Rhodora 67, 405–406.

Booth, D.T., Bai, Y., Roos, E.E., 2003. Wyoming big sagebrush seed production from mined and unmined rangelands. Journal of Range Management 56, 542–546.

Chambers, J.C., Miller, R.F., Board, D.I., Pyke, D.A., Roundy, B.A., Grace, J.B., Schupp, E.W., Tausch, R.J., 2014. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology & Management 67, 440–454.

Charlesworth, D., 1989. Evolution and low fertility in plants: pollen limitation, resource allocation, and genetic load. Trends in Ecology and Evolution 4, 289–292.

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.

Ehrlen, J., 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. Ecology 73, 1820–1831.

Greene, D.F., Johnson, E.A., 1994. Estimating the mean annual seed production of trees. Ecology 75, 642–647.

Laubhan, M.K., Fredrickson, L.H., 1992. Estimating seed production of common plants in seasonally flooded wetlands. Journal of Wildlife Management 56, 329–337.

Lubbers, A.E., 1986. Spatial variation in seed production among and within sites and within individuals of *Thalictrum thalictroides (Ranunculaceae)*. Canadian Journal of Botany 64, 658–667.

McArthur, E.D., Plummer, P.A., 1978. Biogeography and management of native western shrubs: a case study, section *Tridentatae* of *Artemisia*. Great Basin Naturalist Memoirs 2, 229–243.

McArthur, E.D., Stevens, R., 2004. Composite shrubs. In: Monsen, S.B., Stevens, R., Shaw, N.S. (Eds.), Restoring western ranges and wildlands. General Technical Report RMRS-GTR-136-vol-2. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA, pp. 493–537.

Meyer, S.E., Kitchen, S.G., Wilson, R.G., Stevens, R., 1988. Proposal for addition of *Artemisia tridentata*–big sagebrush to the rules. Association of Official Seed Analysts Newsletter 62, 17–18.

Schlaepfer, D., Lauenroth, W.K., Bradford, J.B., 2014. Natural regeneration processes in big sagebrush *(Artemisia tridentata)*. Rangeland Ecology & Management 67, 344–357.

Stephenson, A.G., 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review Ecology Systematics 12, 253–279.

SYSTAT [computer program]. Systat Software, San Jose, CA, USA.

Takahashi, M., Huntly, N., 2010. Herbivorous insects reduce growth and reproduction of big sagebrush *(Artemisia tridentata)*. Arthropod-Plant Interactions 4, 257–266.

US Department of Interior [USDI], 2015. Secretarial order number 3336, rangeland fire prevention, management and restoration.Available at:. http://www.forestsandrangelands.gov/rangeland/documents/SecretarialOrder3336.pdf Accessed 13 June, 2016.

Wagstaff, F.J., Welch, B.L., 1991. Seed-stalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. Journal of Range Management 44, 72–74.

Welch, B.L., 2005. Big sagebrush: a sea fragmented into lakes, ponds, and puddles. General Technical Report RMRS-GTR-144. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA 210 pp.

Welch, B.L., Nelson, D.L., 1995. Black stem rust reduces big sagebrush seed production. Journal of Range Management 48, 398–401.

Wiens, D., Calvin, C.L., Wilson, C.A., Davern, C.I., Frank, D., Seavey, S.R., 1987. Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia 71, 501–509.

Willson, M., Burley, N., 1983. Mate choice in plants: tactics, mechanisms and consequences. Princeton University Press, Princeton, NJ, USA.

Winward, Alma H., 1980. Taxonomy and ecology of sagebrush in Oregon. Station Bulletin 642. Oregon State University, Agricultural Experiment Station, Corvallis, OR, USA 15 pp.

Yasaka, M., Takiya, M., Watanabe, I., Oono, Y., Mizui, N., 2008. Variation in seed production among years and among individuals in 11 broadleaf tree species in northern Japan. Journal of Forest Research 13, 83–88.

Young, J.A., Evan, R.A., Palmquist, D.E., 1989. Big sagebrush *(Artemisia tridentata)* seed production. Weed Science 37, 47–53.

Ziegenhagen, L.L., Miller, R.F., 2009. Postfire recovery of two shrubs in the interiors of large burns in the Intermountain West, USA. Western North American Naturalist 69, 195–205.

Zimmerman, M., 1980. Reproduction in Polemonium: pre-dispersal seed predation. Ecology 61, 502–506.