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Seed weight variation of wyoming sagebrush in Northern Nevada

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ABSTRACT: Seed size is a crucial plant trait that may potentially affect not only immediate seedling success but also the subsequent generation. We examined variation in seed weight of Wyoming sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young), an excellent candidate species for rangeland restoration. The working hypothesis was that a major fraction of spatial and temporal variability in seed size (weight) of Wyoming sagebrush could be explained by variations in mean monthly temperatures and precipitation. Seed collection was conducted at Battle Mountain and Eden Valley sites in northern Nevada, USA, during November of 2002 and 2003. Frequency distributions of seed weight varied from leptokurtic to platykurtic, and from symmetry to skewness to the right for both sites and years. Mean seed weight varied by a factor of 1.4 between locations and years. Mean seed weight was greater ($P<0.05$) in 2003 than in 2002 at both sites. This can partially be attributed to 55% greater precipitation in 2003 than 2002, since mean monthly temperatures were similar ($P>0.05$) in all study situations. Simple linear regression showed that monthly precipitation (March to November) explained 85% of the total variation in mean seed weight ($P=0.079$). Since the relationship between mean monthly temperature (June-November) and mean seed weight was not significant ($r^2=0.00$, $P=0.431$), this emphasizes the importance of precipitation as an important determinant of mean seed weight. Our results suggest that the precipitation regime to which the mother plant is exposed can have a significant effect on sizes of seeds produced. Hence, seasonal changes in water availability would tend to alter size distributions of produced offspring.

Introduction

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young) has a wide ecological amplitude (Beetle and Johnson, 1982) in the western United States. It helps prevent erosion, provides wildlife habitat and forage, and improves rangeland aesthetics (Vale, 1974). Knowledge about the ecophysiology of Wyoming sagebrush will contribute to a more efficient use of this species in degraded rangeland restoration activities of the Intermountain West Region of North America. Western rangelands cannot be restored without native plant materials.

Seed size is a crucial plant trait, associated with the ability of species to disperse and establish, seed water relations and carrying attributes of the adult plant such us growth form and plant height (Leishman *et al*., 2000). Moreover, carry-over effects have been described for some species: plants originating from smaller seeds produce smaller seeds than those originating from larger seeds (Ahmed and Zuberi, 1973). Seed size may potentially affect not only immediate seedling success but also the subsequent generation (Wulff, 1986b). The effect is usually inversely proportional to seed number per unit biomass, across species in a given community (Henery and Westoby, 2001). Giles (1995) proposed that

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it is not a particular seed size that characterizes a genotype but a particular distribution of size.

Considerable variation in seed size has been reported across shrub populations within a species, and even within populations (Vaughton and Ramsey, 1998). Since most species exhibit continuous variation in seed size (Manasse and Stanton, 1991), it has been suggested that the within-plant seed size variation may have evolved as a strategy in a spatially or temporally unpredictable environment where a single intermediate seed size has low fitness (Silvertown, 1984).

Maier *et al*. (2001) concluded that climatic conditions supporting widespread pulses of big sagebrush [*Artemisia tridentata* Nutt.; a regionally dominant shrub species over large areas of the Intermountain West (McArthur *et al*., 1979)] establishment on native sites should be examined in greater depth. They reported strong evidence that precipitation variables significantly affect high levels of seedling recruitment on native, undisturbed big sagebrush sites throughout Wyoming. Additionally, successful recruitment of big sagebrush is partially dependent on seed viability (McDonough and Harniss, 1974). Determination of specific precipitation and temperature conditions favorable for greater seed sizes in big sagebrush are then of primary importance. Greater seed sizes often contribute to better sagebrush seedling establishment (Geritz, 1995). Infrequent patterns of sagebrush seedling establishment have been attributed, at least in part, to periods of unfavourable weather (Lommasson, 1949), but little supporting evidence has been available.

It is likely that temporal and spatial patterns of seed size variation in plant species, with subsequent consequences in seedling establishment, would reflect climatic fluctuation (Wulff, 1986a). Thus, we hypothesized that a major fraction of the temporal variability in seed weight variation could be explained by variations in the regional climate. Analysis of such frequency patterns will permit the identification of particular climatic elements that influence, for example, reproductive success. These climatic elements should be related to particular physiological or ecological processes within the population. The analysis will serve, for example, to test existing hypotheses about the causes of recruitment variability in this species.

Our goal was to examine the current unexplored within-species variation in seed weight in Wyoming sagebrush. This shrub was chosen because it is an excellent candidate species for rangeland restoration. The working hypothesis was that a major fraction of spatial and temporal variability in seed weight variation could be explained by variations in mean monthly temperatures and precipitation. The specific objective was to determine seed weight distribution, and effects of monthly precipitation and mean monthly temperature on mean seed weight in populations of Wyoming sagebrush.

Materials and Methods

Study Area

Seed collection was conducted at two sites during 2002 and 2003: Izzenhood Ranch Site and Eden Valley Site. Mature Wyoming sagebrush stands were sampled near Battle Mountain, Lander County, Nevada (116°58' N, 40°57' W), and Winnemucca, Humboldt County, Nevada (117°23' N, 41°12' W). The first site was in the BLM Elko District, approximately 40 km north/northwest of the town of Battle Mountain, Nevada (NV). The second site was in the BLM Winnemucca District, between the Hot Springs Range and Osgood Mountains, approximately 38 km north/northwest of the town of Golconda, NV.

At Izzenhood Ranch, the study area consisted of approximately 23 ha of Bureau of Land Management (BLM) land with 0-2% slope. Elevation was between 1350-1740 m. Enko-Shabliss-Orvada was the predominant soil series association (very fine sandy loam and fine sandy loam). Vegetation composition included Wyoming big sagebrush, Thurber needlegrass (*Stipa thurberiana* Piper) and Indian ricegrass (*Achanatherum hymenoides* [Roem. and Schult.]) (USDA-NRCS, 1992); cheatgrass (*Bromus tectorum* L.) and tumblemustard (*Sisymbrium altissimum* L.) dominated this site. Mean annual precipitation is 203-254 mm (USDA-NRCS, PRISM Climate Mapping Project, 1998). At Eden Valley site, the research area consisted of approximately 42 ha of BLM land on a 0-8% east-facing hillslope. Elevation was between 1500-1740 m. Hunnton-Zevadez-Enko was the predominant soil series association (very fine sandy loam and fine sandy loam). The vegetation composition for the site included: Wyoming big sagebrush, Sandberg bluegrass (*Poa secunda* Presl.), and Bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) (USDA-NRCS, 1992). As in the first site, cheatgrass and tumblemustard were dominant. Average annual precipitation is between 254 and 305 mm (USDA-NRCS, PRISM Climate Mapping Project, 1998).

Within each site and year, seed collection stands were selected for similar size of Wyoming big sagebrush plants, similar cover and topography, and absence of excessive grazing or other disturbances. Sites were also selected to minimize supplemental moisture or subsurface runoff due to microsite influences to reduce variations in demography between sites (Bonham *et al*., 1991). Climatic data, as monthly values of temperature (June-November) and precipitation (March-November) for the periods 2002 and 2003 were obtained from National Weather Service climate stations located in Battle Mountain and Paradise Valley, the closest to the sampled sites. Temperature or precipitation values were taken beginning in June or March, respectively, because flowerstalks or initiation of leaf growth were reported for this species during these months in Nevada (Everett *et al*., 1980). November was used as the endpoint because seed collections were initiated. Although climatic conditions at individual sites undoubtedly differ from those at the weather stations, the direction and magnitude of major climatic variations should be similar throughout the area.

Field and laboratory methods

Seeds were sampled from a minimum of 100 randomly selected, similar-size sagebrush plants at each location and year. At the first site, sampling was conducted along a transect of at least 10 km because of the patchy distribution of sagebrush. In Eden Valley, sampling was conducted along a 5 km-transect.

Fruits were air-dried and stored at 4°C until use (Welch *et al*., 1996). Seeds (achenes) were then hand picked using a magnifier glass, and stored in paper bags at 4 °C until tested. Seed size was measured as dry weight. The seed-weight distribution of each population was described by its mean, skewness and kurtosis (Sokal and Rohlf, 1981). The relationship between mean seed weight at each site and year versus cumulative precipitation (March to November) or mean monthly temperature (June to November) was studied using simple linear regression.

Statistical analysis

The experiment was organized in a completely randomized block design arranged in a 2 x 2 factorial. Treatments included 2 sites and 2 years. Seed weight differences between years and sites were tested using two-way ANOVA and a Fisher's (protected) least significant difference test was utilized for mean separation when F tests indicated that a variable was significant ($P<0.05$). Data were tested for normality and homoscedasticity of variance following Neter and Wasserman (1974). Monthly precipitation (March to November) and mean

TABLE 1.

Total precipitation (March-November), mean monthly temperatures (June-November) and seed weight variation (n=880-976) between years and *Artemisia tridentata* ssp. *wyomingensis* sites. Each value is the mean ± SEM for temperature and seed weight.

Year		Precipitation (March-November)	Temperature (June-November)	Seed weight
		---------(mm)---------	------(°C)------	---(mg seed^{-1})---
2002				
	Eden Valley	95.50	14.8 ± 3.0^{a}[1]	$0.248 \pm 0.002^{a,a}$[2]
	Battle Mountain	113.28	15.9 ± 3.5^{a}	$0.298 \pm 0.003^{b,b}$
2003				
	Eden Valley	140.72	15.9 ± 3.4^{a}	$0.302 \pm 0.003^{b,b}$
	Battle Mountain	183.39	15.4 ± 5.1^{a}	$0.337 \pm 0.003^{c,c}$

[1] Different letters indicate significant differences at $P<0.05$.

[2] Different letters to the left of the comma indicate significant differences ($P<0.05$) between years within each site; different letters to the right of the comma indicate significant differences ($P<0.05$) between sites within each year.

monthly temperatures (June to November) were used as independent variables in simple linear regression analysis and mean seed weight was employed as the dependent variable. The relationship between mean seed weight for each site (dependent variable) and seed number per unit seed biomass was also analyzed using regression analysis.

Results and Discussion

Seeds from both locations in 2002 and 2003 showed different seed weight frequency distributions (Fig. 1). The 2002 sample (n=880) from Eden Valley had a mean seed weight of 0.248 ± 0.002 mg seed^{-1} (mean ± 1 SEM), was significantly leptokurtic with a pronounced peak (kurtosis=1.80 ± 0.1651; $P<0.01$), and was skewed to the right (skew=0.77 ± 0.0826; $P<0.01$). A leptokurtic curve has more items near the mean and at the tails, with fewer items in the intermediate regions relative to a normal distribution with the same mean and variance (Sokal and Rohlf, 1981). Positive kurtosis indicates that there were more seeds near the mean than expected for a normal distribution. Skewness to the right indicated that there were more seeds that weighed less than the mean than would be expected for normal distribution. Seeds in the larger sample (n=938) at Eden Valley in 2003 averaged 0.302 ± 0.003 mg seed^{-1}. The frequency distribution was symmetric (-0.1 ± 0.08; $P>0.05$) and significantly platykurtic (-0.56 ± 0.16; $P<0.01$). A platykurtic curve has fewer items at the mean and at the tails than the normal curve but has more items in intermediate regions. The 2002 population in Battle Mountain had a mean seed weight of 0.298 ± 0.003 mg seed^{-1} (n=976), was significantly platykurtic (kurtosis= -0.38 ± 0.1568; $P<0.05$), and was skewed to the right (skew=0.29 ± 0.0784; $P<0.01$). Finally, the 2003 sample in Battle Moutain had a mean seed weight of 0.337 ± 0.003 mg seed^{-1} (n=912). Its frequency distribution was symmetric (0.06 ± 0.0811; $P>0.05$) and significantly platykurtic (kurtosis= -0.46 ± 0.1622; $P<0.01$). The great range of seed weights within each population seed crop can be interpreted as an adaptive characteristic, generating a more homogeneous seed rain than would otherwise be the case with a narrower range of seed weights.

The seed weight coefficient of variation for the 4 populations were 26.31% for Eden Valley, 2002; 28.68% for Eden Valley 2003; 28.52% for Battle Mountain, 2002, and 31.75% for Battle Mountain, 2003. This was comparable to the average coefficient of variation (28%)

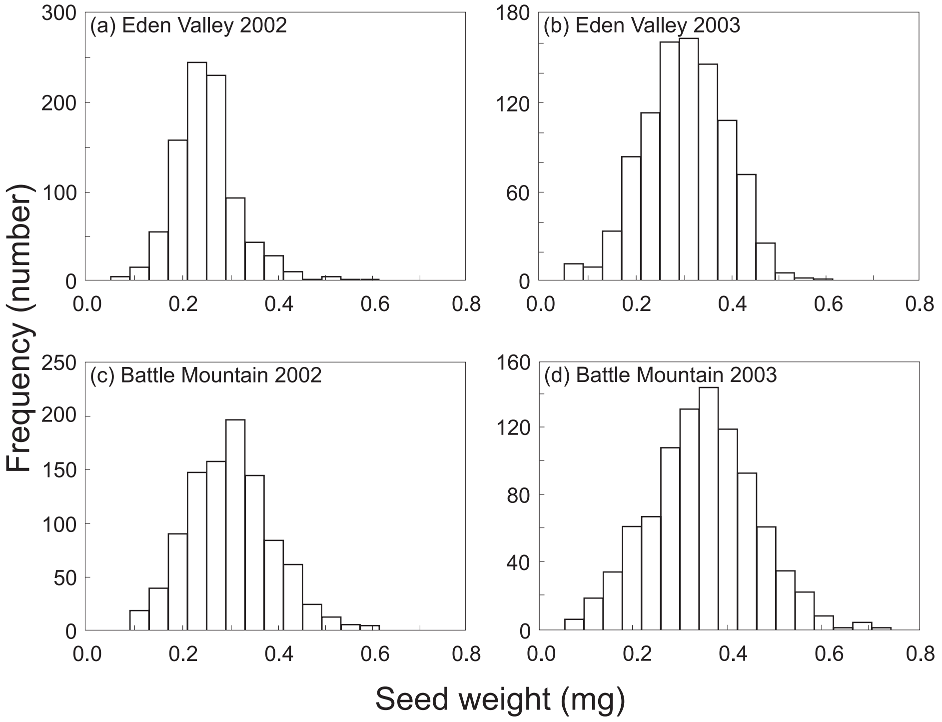

FIGURE 1. Frequency distribution of seed weight of *Artemisia tridentata* spp. *wyomingensis* from population samples in (a) Eden Valley, 2002 (n=880), (b) Eden Valley, 2003 (n=938), (c) Battle Mountain, 2002 (n=976) and (d) Battle Mountain, 2003 (n=912) in northern Nevada. Note the change of scale on the Y axis for each of the 4 populations.

documented in a review of data for 39 species (Michaels *et al*., 1988). Variation in seed size may be the result of a myriad of factors (Wulff, 1986a). For example, Winn (1991) suggested that plants may not have the capability of producing a completely uniform seed weight, simply as a result of variations in resource availability (i.e., soil moisture) during seed development. The range of size variation among seeds is expected to increase if individual seeds compete for resources during development (Rees, 1996). It is very unlikely that a plant, even if one seed weight was always superior, could produce exact copies of this particular seed weight. If allocation of resources to developing seeds proceeds as long as there are resources to allocate, and the possibility to adjust the number of developing seed is limited, the result will be a variation in seed weight. Therefore, the simple theoretical expectation of a single optimal offspring size (Smith and Fretwell, 1974) may have to be replaced with explanations for the maintenance of variation *per se*. Considerable variation in seed weight has been reported within shrub populations (Vaughton and Ramsey, 1998).

Seed weight was greater ($P<0.05$) in 2003 than in 2002 at both sites (Table 1). It was also greater in Battle Mountain than in Eden Valley in both years (Table 1). The greatest percentage of seeds was between >0.20-0.25 mg seed^{-1} in Eden Valley in 2002 (33.5%), >0.25-0.35 mg seed^{-1} in Eden Valley in 2003 (43.4%), >0.25-0.35 mg seed^{-1} in Battle Mountain in 2002 (43.9%), and >0.3—0.4 mg seed^{-1} in Battle Mountain in 2003 (36.4%). However, there were a greater number of seed size ranges in Battle Mountain in 2003 than at any other site in both years (Fig. 1). These findings may be partially explained because the amount of precipitation (March-November) was > 23% greater in Battle Mountain during 2003 than at any other site in 2002 and 2003 (Table 1). Geritz (1995) reported that the range of seed sizes increases as the total amount of resources available to plants increases. Other studies of seed size variation and factors influencing seed size have also reported results obtained from 2 years and two sites (Wulff, 1986a; Vaughton and Ramsey, 1998).

Giles (1995) reported that a seed, regardless of its initial size, is capable of regenerating the same mean size. Johannsen's data (1903) also showed that the same variation is regenerated. This suggests that it is not a particular seed size that is inherited but a distribution of sizes, and that the mean alone, is insufficient to describe the seed size of a genotype. Position effects within the inflorescence are, at least in part, agents creating these size distributions and they ensure that seed size variation is produced every generation. This is why the expected reduction in seed size variance is not observed in spite of strong selection on seed size under natural conditions. A common observation is that characteristics related to fitness are positively correlated with seed size, such that larger seeds have the higher fitness (Geritz, 1995). This observations has been used as an assumption in several theoretical models (McGinley *et al*., 1987) that predict a reduction of seed size variance, due to strong selection towards seeds of a similar and larger size, should be observed. This should occur as frequencies of genotypes producing seeds of favoured sizes increase at the expense of genotypes producing seeds of other sizes, if variation in seed size, and consequently variation in fitness is genetically determined. Unfortunately, these expectations are not borne out; high levels of variation in seed size are continuosly produced in natural populations. That is why one of the central questions in seed size evolution studies is despite the striking differences in fitnesses of plants growing from seeds of different sizes, why the predicted reduction in seed size variance is not observed. One explanation is that the variation in the seed size produced by a plant genotype may be highly environmental. For example, we found that monthly precipitation (March-November) explained 85% of the total variation in mean seed weight (Fig. 2). However, the relationship between mean monthly temperature (June-November) and mean seed

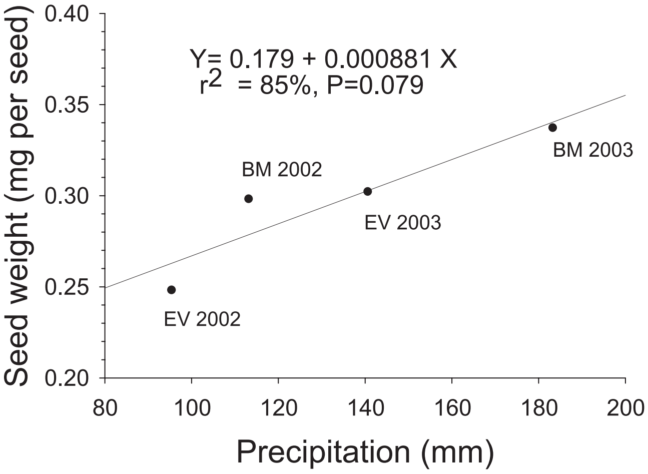

FIGURE 2. Relationship between precipitation and seed weight in *Artemisia tridentata* spp. *wyomingensis* in northern Nevada. Each symbol is the mean of n=880 [Eden Valley (EV) 2002], n=938 (EV 2003), n=976 [Battle Mountain (BM) 2002] and n=912 (BM 2003).

weight was not significant (r^2=0.00, P=0.431), since mean monthly temperature during that period was similar (P>0.05) in both sites and years. Wulff (1986a) reported that exposure of *Desmodium paniculatum* L. parent plants to higher temperatures during growth and seed development significantly reduced the mean seed weights. Our results emphasize the importance of amount and periodicity of precipitation as a major determinant of seed size. Wulff (1986a) also found that a reduced water supply significantly reduced seed weight in *Desmodium paniculatum* L. with respect to the controls. Assuming that seed size is limited either directly or indirectly by the availability of resources or current photosynthesis, it is not surprising that seed size should be reduced in conditions of reduced water availability, since it affects photosynthetic rates (Boyer, 1976). Infrequent patterns of sagebrush seedling establishment have been attributed, at least in part, to periods of unfavourable weather (Lommasson, 1949), although Maier *et al*. (2001) reported that recruitment is different from germination. There are models that predict variance in seed size should decrease in natural populations due to strong selection towards seeds of a similar and larger size. However, the fact that seeds of different sizes germinate, grow and reproduce at different rates in the same environment (Stanton, 1984; Wulff, 1986 b,c; Andersson, 1996) suggests that seed size variation could be advantageous in varying environments.

Mean seed weight was correlated to seed number per unit biomass. The greater the mean seed weight (MSW) on each site, the lower the seed number per unit seed biomass (SN/UB) (MSW=0.575 – 0.0816 SN/UB; r^2=0.99; P=0.004). This result was similar to that reported by Henery and Westoby (2001) on various shrub species in Australia.

Conclusions

Our results suggest that the precipitation regime to which the mother plant is exposed can have a significant effect on the sizes of seeds produced.

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