



10-31-2000

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Recommended Citation

Jorgensen, Eric E. and Chesser, Kelly L. (2000) "Interspecific differences in grass seed imbibition," *Western North American Naturalist*. Vol. 60 : No. 4 , Article 10.
Available at: <https://scholarsarchive.byu.edu/wnan/vol60/iss4/10>

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INTERSPECIFIC DIFFERENCES IN GRASS SEED IMBIBITION

Eric E. Jorgensen¹ and Kelly L. Chesser²

ABSTRACT.—Seeds from 12 grass species were studied relative to mode of wetting and time of exposure to water to document interspecific differences in imbibition characteristics. Imbibition causes seeds to become wet, and wet seeds are more detectable to consumers than dry seeds. Thus, germination potential and ability to remain undetected by consumers may represent an important trade-off. Seeds wetted for 0–192 h in vials imbibed water at rates equivalent to seeds wetted by contact with wet paper towels pressing against their seed coat, except for seeds of *Avena sativa*, which weighed more after wetting in 2-mL vials with free water (0.471 g vs. 0.432 g). Seeds from different species imbibed water at different rates. These data show that interspecific variation in imbibition for seeds is high and support an expectation that imbibition potential can interact with detectability to consumers in an evolutionary trade-off.

Key words: consumers, depredation, detectability, grass seed, imbibition, olfaction, volatile compounds.

Seeds are an important resource in ecosystems of the Intermountain western United States, serving as plant reproductive units and food resources for consumers. Rodents are adept at locating seeds in soil by olfaction (Howard and Cole 1967, Howard et al. 1968, Lockard and Lockard 1971, Reichman 1981, Vander Wall 1998). In their dual role as reproductive units and food sources, seeds are potentially excellent subjects for studying evolutionary trade-offs and interactions between biota.

The distribution of seeds in the environment is spatially and temporally variable (Nelson and Chew 1977, Reichman 1984, Jorgensen 1996). Therefore, the ability of seeds to survive and germinate is dependent upon spatial and temporal foraging characteristics of consumers (Price and Reichman 1987), particularly in arid lands. However, detectability and subsequent survivorship of seeds is more than a function of their distribution and the foraging characteristics of consumers. Vander Wall (1995, 1998) observed that rodents more easily found wet-seed caches than dry-seed caches, locating 449 of 450 wet-seed caches but only 60 of 450 dry-seed caches. Seeds release volatile compounds (Fielding and Goldsworthy 1982, Zhang et al. 1993) that are apparently detectable to rodents (Simon and Raja Harun 1972). Therefore, it may be expected that plant species with hydrophobic

seeds would be able to avoid detection by consumers, thereby increasing their survivorship. However, even hydrophobic seeds need to imbibe water to germinate.

Germination depends, in part, on exposure to water in the substrate. Imbibition (the adsorption of water by nonliving or senescent materials and subsequent swelling caused by adhesion of the water to internal surfaces of materials) is the initial step in germination (Bradford 1995). Vertucci and Leopold (1984) found that soybean (*Glycine max*) seeds fully dried from initial water contents of <24% were severely damaged, whereas soybean seeds fully dried from initial water contents of >24% were only slightly affected. Thus, seeds that imbibe water slowly, or to a low level of seed moisture, may be damaged and display reduced germination ability compared with seeds that imbibe water quickly or to saturation. Therefore, it may be expected that seeds would either easily imbibe water and thereby be detectable to consumers, or strongly resist imbibition and thereby suffer possible tissue damage and reduced ability to germinate.

Seeds must imbibe water to germinate, but imbibition may also make seeds detectable to consumers and susceptible to depredation. There may be a trade-off between imbibition characteristics and the ability to remain hidden from consumers. Hart et al. (1959) and Christian and Lederle (1984) demonstrated

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that seeds from different species contain different amounts of water at the same relative humidity. Additionally, we hypothesize that seeds will exhibit interspecific variation in their relative ability to imbibe or resist water. In part, such a response may be based upon competition between seed adaptations to germinate and adaptations to resist detection by consumers. A 1st step toward investigating this question is documentation of seed imbibition response under different wetting conditions, particularly comparing how repeatable laboratory methods (seeds wetted en mass in 2-mL vials) may compare to conditions that better approximate those experienced by seeds in soil (seeds wetted by paper towels pressing against their seed coat). Finally, we measured the imbibition characteristics of seeds from 12 grass species from the Intermountain western United States relative to time of exposure to water in an effort to detect and measure interspecific differences.

METHODS

We investigated imbibition characteristics of seeds from 12 species of grass common to the Intermountain western United States (states where seeds were actually collected are identified in Table 1) relative to mode of wetting and imbibition rate during June and July 1997. Seeds were supplied by Granite Seed Company, Lehi, Utah, and were dried appropriately for storage. Experiments were con-

ducted on seed samples weighed to the nearest 0.001 g with a digital balance, with each sample comprising 10 individual seeds. Wetting experiments were conducted using water purified by reverse osmosis. All analyses were conducted with SPSS for Windows (Norusis 1993), and multiple comparisons were conducted with the LSD test.

To investigate imbibition in an ecologically relevant way (i.e., seeds wetted by moist soil pressing against their seed coat), we mimicked the soil environment by wrapping seeds in paper towels and placing them in the bottom of tubs with sufficient free water to ensure saturation; seeds in tubs were pressed against the paper towel with sponges placed under a 2nd tub that was partially filled with water. We compared mass between 10 dry-seed samples, 10 samples wetted in 2-mL vials, and 10 samples wrapped in paper towels. Wetting was conducted overnight for times ranging between 16 and 20 h. Wetted samples were pat-dried with paper towels to remove free water immediately before weighing. One-way analysis of variance was used to compare dry, vial-wetted, and paper-towel-wetted seed mass. The assumption of normality was assessed using the Shapiro-Wilk test, and heteroscedasticity was assessed using Levene's test.

To measure the effect of time of exposure, we used only samples in vials. Percent mass gain was compared for 5 samples each, from the same 12 grass species used in the 1st experiment, wetted for times ranging from 0 (weighed

TABLE 1. Mean mass (g) of 10 samples of 10 seeds each from 12 grass species from the western United States (State) under 3 conditions of exposure to water (unwetted [Dry], wetted in a vial [Vial], wetted in contact with wet paper towels [Towel] for 16–20 h), and probability of equality (P). Values accompanied by the same superscript in the same row are not different.

Species	State	Exposure			$s_{\bar{x}}$	P
		Dry	Vial	Towel		
<i>Achnatherum hymenoides</i>	CO	0.048 ^b	0.059 ^a	0.058 ^a	0.001	0.000
<i>Agropyron dasystachyum</i>	WA	0.039 ^b	0.056 ^a	0.051 ^a	0.002	0.000
<i>Andropogon gerardii</i>	TX	0.019 ^b	0.038 ^a	0.038 ^a	0.002	0.000
<i>Agropyron intermedium</i>	WA	0.063 ^b	0.110 ^a	0.109 ^a	0.005	0.000
<i>Agropyron spicatum</i>	WA	0.053 ^b	0.087 ^a	0.085 ^a	0.003	0.000
<i>Avena sativa</i>	UT	0.308 ^c	0.471 ^a	0.432 ^b	0.014	0.000
<i>Bromus biebersteinii</i>	WA	0.069 ^b	0.092 ^a	0.091 ^a	0.001	0.000
<i>Hordeum brachyantherum</i>	CA	0.068 ^b	0.129 ^a	0.129 ^a	0.006	0.000
<i>Hordeum vulgare</i>	UT	0.386 ^b	0.568 ^a	0.570 ^a	0.017	0.000
<i>Secale cereale</i>	SD	0.240 ^b	0.354 ^a	0.347 ^a	0.011	0.000
<i>Stipa neomexicana</i>	AZ	0.187 ^b	0.221 ^a	0.218 ^a	0.003	0.000
<i>Triticum arvense</i>	UT	0.496 ^b	0.708 ^a	0.727 ^a	0.020	0.000

immediately after wetting) to 192 h (8 d). Seeds were pat-dried to remove free water immediately before weighing. The effects of species and wetting time were analyzed with a 2-way factorial analysis of variance. Data were square-root transformed to near normality (Johnson and Wichern 1992), and the homoscedasticity assumption was assessed using Levene's test.

RESULTS

For all species, exposure to water for 16–20 h resulted in seeds that weighed more than dry seeds (Table 1). However, only for *Avena sativa* did mass differ between vial-wetted and paper-towel-wetted seeds (0.471 g vs. 0.432 g; *F*-test, $P < 0.00$; LSD test, $P = 0.019$; Table 1). *Agropyron dasystachyum* (*F*-test, $P < 0.000$; LSD test, $P = 0.070$) and *Triticum arvense* (*F*-test, $P < 0.000$; LSD test, $P = 0.096$) vial-wetted and towel-wetted seeds were marginally different (Table 1).

Species imbibed water at different rates ($P < 0.000$; Figs. 1, 2, 3) when wetted for times ranging between 1 and 192 h (1, 2, 3, 4, 5, 6, 7, 8, 9, 24, 48, 72, 96, 120, 144, 168, 192 h; $P < 0.000$). Imbibition varied widely between species, resulting in maximum mass gains ranging from 23% for *Stipa neomexicana* to 305% for *Agropyron dasystachyum* after 8 d.

DISCUSSION

We began this study by documenting that seeds wetted in vials imbibed water at rates equivalent to seeds wetted by contact with wet paper towels. The inclusion of dry seeds in this experiment increases the statistical power of the analysis, thereby increasing the chance of detecting a difference between vial-wetted and paper-towel-wetted seeds. Even with this bias, we detected no tendency for seeds to increase in mass to a greater extent when wetted pressing against paper towels. A difference was observed only for *Avena sativa*, and its seeds were actually wetted more efficiently in vials (Table 1). We regard this experiment as an important piece of methodological documentation. Therefore, by showing that vial-wetted seeds achieved equivalent mass compared to paper-towel-wetted seeds, we offer a measure of confidence that the succeeding experiments are good models of naturally occurring phenomena.

Seeds displayed wide interspecific variation in their ability to imbibe water (Figs. 1, 2, 3). We believe this is attributable to structural adaptations that regulate imbibition (Boesewinkel and Bouman 1995). Immediately upon wetting, seeds gain some mass. Observations ranged from 1.7% mass gain for *Achnatherum hymenoides* to 24.8% mass gain for *Andropogon gerardii*. This immediate mass gain is probably caused by adhesion to the surface of the seeds. The point of this is that not all mass gain is due to imbibition. Some mass gain is simply due to water adhering to the seed surface, and the amount apparently varies by species. Mass gain attributable to adhesion was subtracted from our samples prior to analysis.

Andropogon gerardii mass increased immediately (due to adhesion) but then plateaued through 9 h of imbibition (Fig. 1). *Stipa neomexicana* (Fig. 2) imbibed the least amount of water, followed by *Achnatherum hymenoides* (Fig. 1) and the 4 grain species (Fig. 3). Finally, the 4 grain species appeared to display substantially less sample-to-sample variation in their imbibition characteristics than the other species (Figs. 1, 2, 3).

At the beginning of this experiment, we hypothesized that seeds from various plant species would display interspecific differences in imbibition characteristics because of a trade-off between ability to remain undetected by consumers (Vander Wall 1995; i.e., remain dry) and ability to germinate, driven in part by a need to imbibe water. These data provide ample support for this hypothesis.

Somewhat unexpectedly, there was wide sample-to-sample variation in percent mass gain for some species. For instance, after 8 d of exposure *Agropyron dasystachyum* displayed mass gains ranging between 115% and 305% (Fig. 1). Similar variation is clearly evident for other species (Figs. 1, 2). However, it is also apparent that sample-to-sample variation for the 4 grain species (Fig. 3) appears to be less than for the other species. It is possible that this sample-to-sample variation may be caused by genotypic or phenotypic differences between individual seeds (McGinley et al. 1987, Roach and Wulff 1987). Also, seed mass is highly variable within some species (Kranntz 1997), and this may affect imbibition. The relative lack of variation observed for grain species may be attributable to a lack of genotypic or phenotypic variation caused by selective breeding. If

Small Seeds

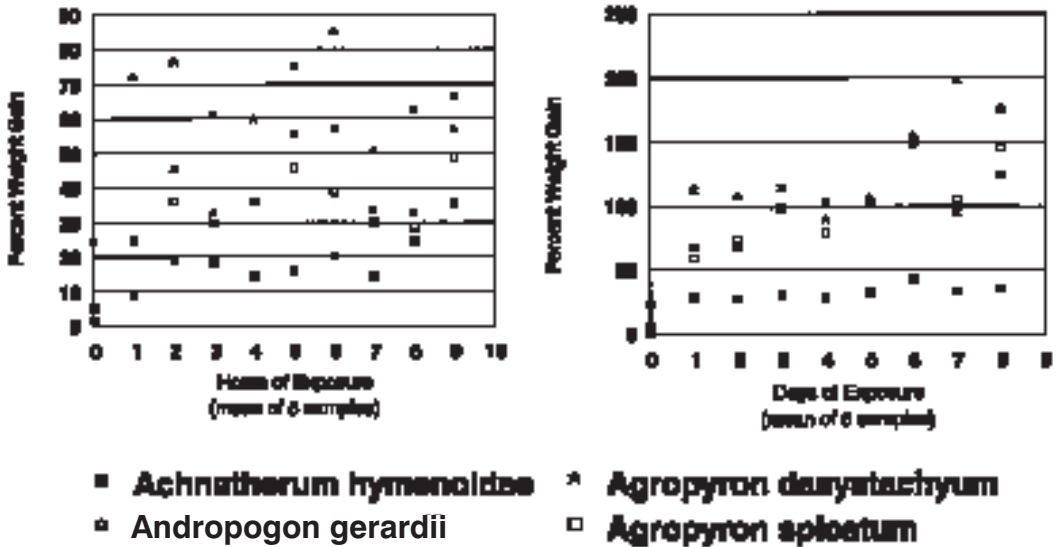


Fig. 1. Percent mass gain as a function of hours of exposure (left) and days (right) to water for seeds from 4 grass species with small-sized seeds. Data points from the hours of exposure experiment are mean mass gain from 5 samples of 10 seeds each; data points from the days of exposure experiment are mass gain of individual 10-seed samples. Note different ordinate scales.

Medium Seeds

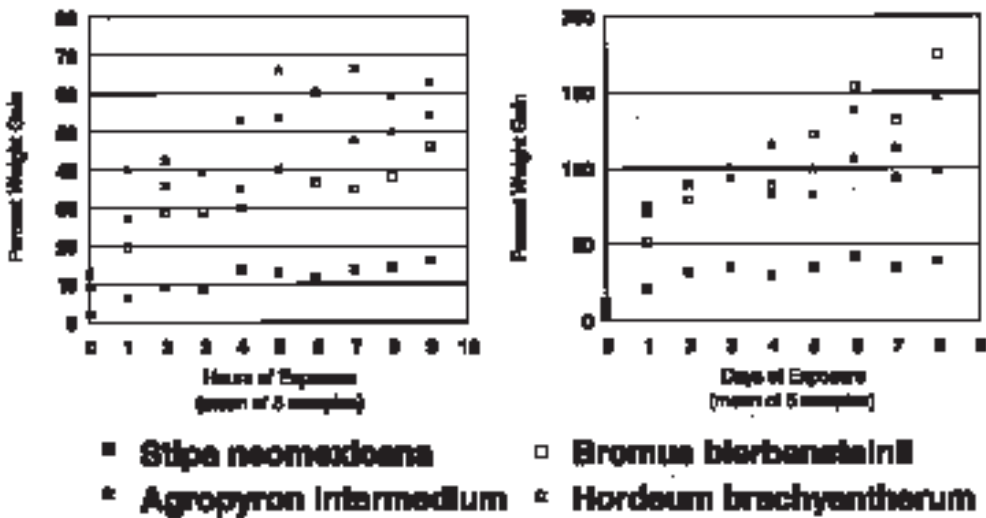


Fig. 2. Percent mass gain as a function of time of exposure to water for seeds from 4 grass species with medium-sized seeds. Data point descriptions are as in Figure 1. Note different ordinate scales.

Grain Crop - Large Seeds

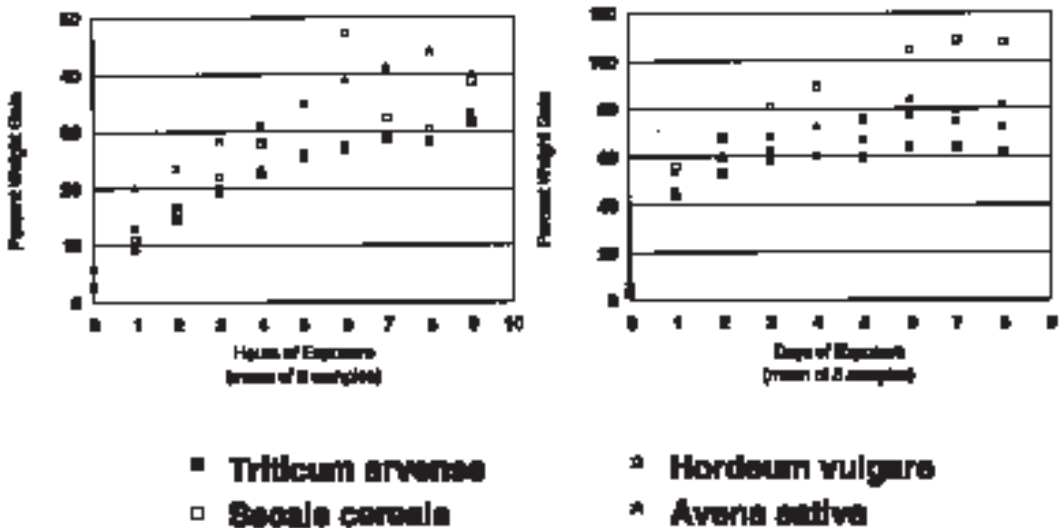


Fig. 3. Percent mass gain as a function of time of exposure to water for seeds from 4 grain crops (grasses) with large-sized seeds. Data point descriptions are as in Figure 1. Note different ordinate scales.

the observed differences are attributable to genotypic or phenotypic differences, then these data suggest that individual seeds are important, and their survival is very much under the influence of natural selection.

Because small mammals are important consumers of seeds (Chew and Chew 1970, Sohlt 1973, Price and Joyner 1997), the interaction between them and seed resources is an important concern in ecology, particularly in arid lands. The dual role of seeds as plant reproductive units and food for primary consumers justifies the interest. It is clear that seeds are unevenly distributed in the ecosystem (Reichman 1984, Jorgensen 1996). This may influence small mammal foraging (Reichman 1981, Price and Reichman 1987) and may influence microhabitat use (e.g., Price 1978). However, Vander Wall's (1995, 1998) results illustrate that seeds interact with the ability of rodents to find them in the soil. Our results demonstrate that imbibition of seeds varies between species. These differences could result from our hypothesized trade-off between the ability to remain undetected to consumers and the ability to germinate. Other factors, such as dispersal ability (Donohue 1997, Lord et al. 1997), may

also be involved by interacting with imbibition characteristics to affect seed survival.

ACKNOWLEDGMENTS

The views expressed in this manuscript are those of the authors and do not necessarily reflect the views and policies of the U.S. Environmental Protection Agency (EPA). We acknowledge the assistance of the McNair Scholars Program, East Central University, Ada, Oklahoma. M.M. Huckleberry, P.D. Sutton, M.A. Huckleberry, M.D. Cole, D.L. Hutchins, and J.R. Williams provided guidance and logistic support. Reviews by T.J. Canfield and B. Pievitz improved the manuscript.

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Received 11 March 1999
Accepted 28 October 1999