J. Range Manage.
45:159-164, March 1992

Seedbed ecology of winterfat: Imbibition temperature affects post-germination growth

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Abstract

Seed imbibition is a critical first step in the awakening of an embryo plant. To determine if imbibitional conditions influenced post-germination growth, seeds of 3 winterfat *(Eurotia lanata)* ecotypes were imbibed at 5 temperatures from 0 to 20° C, and at 5 oxygen concentrations from 0 to 40%. After a 4-day imbibition period the seeds were either dried and weighed or they were cultured in the dark at 20° C. Seedling axial length was measured 5 times between 5 and 14 days post-germination to assure that maximum growth was measured. The study was repeated 3 times for each ecotype. Oxygen concentration had little effect except at 0%. As imbibition temperature increased both post-imbibition dried seed weight and seedling axil length decreased. This indicates the probability for successful germination, establishment, and survival of winterfat decreases when seeds are imbibed at 15–20° C as compared to 5° C. Therefore winterfat should be sown during those parts of the year when diaspores will imbibe at cool temperatures. Winterfat should be imbibed and held at 5° C for 4 days, then germinated at 15° C when testing germination.

Key Words: ecotype, seed physiology, seed weight

Winterfat [*Eurotia*[1] *lanata* (Pursh) Moq.; *Ceratoides lanata* (Pursh) J. T. Howell]; has been recognized since 1895 as a desirable forage plant worthy of cultivation (US Forest Service 1948). Range managers, ranchers, and researchers have worked to re-establish natural stands lost or depleted by over-grazing, fire, or mining (Nelson 1899, Plummer et al. 1968, Wasser 1982, Pellant and Reichert 1984). Seedling mortality is a major reason for stand failure from direct seeded plants. For example, Luke and Monsen (1984) report sowing over 1,000 diaspores for every 3 winterfat plants surviving the first year.

Earlier researchers reported that winterfat germination was improved by a month of cold-moist pretreatment of seeds (Hilton 1941) or diaspores (Strickler 1956). Similar improvement was obtained by soaking diaspores for 2 days at 2° C (Booth and Schuman 1983). Detteroi et al. (1984) measured germination of 2 species of winterfat over 55 temperature combinations ranging from 0/0 to 40/40° C. They reported optimum germination at temperatures of 0 to 5° C alternating with 15 to 20° C. Allen et al. (1987) recommended incubating winterfat diaspores at a constant 15° C for 14 days without light for laboratory germination. For fresh seedlots, they recommended prechilling at 5° C for 14 days. Gastro (1969) observed that winterfat germinates best in the field during early spring when low temperature, high moisture conditions prevail at the soil surface. High surface moisture can produce anaerobic conditions for seeds.

Appreciation is extended to L.W. Griffith for his technical assistance, to Dr. G.V. Richardson for statistical assistance, to Dr. R.A. Abernathy for the Hatch diaspores, to Dr. J.A. Young for the Mill City diaspores.

Manuscript accepted 25 May 1991.

[1]Proposals for conservation of this long-used generic name have been invited (Brummitt 1978).

Although several researchers have tested for optimum temperatures conditions for germination, they have not related imbibitional conditions to post-germination seedling vigor. I determined the effect of oxygen concentration and temperature during imbibition on post-imbibition dried seed weight and on post-germination growth.

Materials and Methods

Plant Materials

Only clean winterfat seeds in good condition with bracts and pericarp removed were used. This was so that bracts and pericarp would not interfere with measurements of seed weight. Both diaspores and threshed seeds were stored at 5° C (Springfield 1974). Seeds were taken from storage, divided into groups of 20 and the groups weighed to 0.01 mg using an electronic analytical balance. Seeds were then dried at 30° C for 24 hours in a forced-air oven, reweighed, held in a closed chamber above water (humidity chamber) at 0–2° C for 24 hours and weighed again.

Drying seeds at 30° C for 24 hours removed free moisture, giving a stable reference weight without damaging the embryo. Holding the dried seeds in the humidity chamber raised seed moisture content to 13–23% above the dried weight, reducing the chance of imbibitional injury (Vertucci and Leopold 1984, Vertucci 1989).

Seeds of 1 cultivar, 'Hatch', and 2 ecotypes, Cheyenne and Mill City, were used to represent widely spaced origins. Hatch originated from a native stand near the town of Hatch, Utah (Stevens and Monsen 1988). Our diaspores were harvested in 1987 from an experimental seed orchard at Torrington, Wyo. The elevation at Torrington is 1,249 m; the average annual precipitation is 32.6 cm. The average 20-seed bag weight was 50.1 ± 5.1 mg ($\bar{x}$ ± SD) and 2.5% of this weight was lost by drying.

Diaspores of the Cheyenne ecotype were collected from native stands on the High Plains Grasslands Research Station near Cheyenne, Wyo., in 1986. The station elevation is 1,909 m and annual precipitation is 36.5 cm. The average 20-seed bag weight was 49.9 ± 4.9 mg with 3.8% lost by drying.

Mill City diaspores were collected in 1987 along Interstate Highway 80 at Mill City, Nev., 63 km south of Winnemucca. Elevation at Winnemucca is 1,316 m and average annual precipitation is 19.7 cm. The average 20-seed bag weight was 38.9 ± 8.1 mg with 1.3% lost by drying.

Treatments

Seeds were rolled in 3 by 5-cm sheets of embossed dental towel (paper) with 1 seed group per roll. Rolls were placed in 8-ml test tubes with 2 rolls per tube. One ml of distilled, degassed water was added to each test tube and tubes were placed in 1-liter glass jars. Jars were flushed with nitrogen for 1 minute, then sealed with a lid containing a rubber septum. Nitrogen was withdrawn from the jar and oxygen added to obtain atmospheres of 0, 10, 20, 30, and 40% oxygen. The 30 and 40% treatments were included to learn if seed

weight loss would be accelerated by supra-natural oxygen levels. Initial mixtures were checked using a gas chromatograph. The seeds were imbibed for 4 days at 0, 5, 10, 15, or 20° C. After 4 days 1 roll of each pair was randomly selected to be weighed, dried at 30° C for 24 hours, and reweighed. These weights were subtracted from the preimbibed dried weight to determine the weight lost by seed groups during imbibition. Seeds of the remaining roll were mounted on Cobb-Jones germination plates (Jones and Cobb 1963) and incubated for 14 days in the dark at 20° C. Seeds were incubated in the dark to avoid any chance of photosynthesis confounding the effects of imbibitional conditions on seedling growth. Axial length of seedlings was measured at 5, 7, 10, 12, and 14 days using a digitizing tablet with a personal computer (Griffith and Booth 1990). Axial length was measured at these 5 intervals to assure that seedlings of all treatments were measured when they reached their maximum length and before they began to atrophy.

An exception to the treatment methods described above was that the paper rolls for the Cheyenne ecotype were of 15.5- by 20.5-cm germination paper and were placed directly into liter jars containing 50 ml of distilled, degassed water. Ethanol analysis (described below) was not conducted for this ecotype.

Post-imbibition Seed Moisture

The concentration of water in the seeds after imbibition was calculated as the difference between the post-imbibed seed weight and the post-imbibed dried seed weight, divided by the post-imbibed dried seed weight to give grams of water per gram of post-imbibed dried seed weight.

Ethanol Analysis

One μl of the liquid remaining in the test tube after imbibition was analyzed for ethanol using gas chromatography. A flame ionization detector was used with a 183- by 0.21-cm Porapak N column. Column temperature was 150° C; injector and detector temperatures were 190° C. Helium was the carrier gas. Ethanol was measured to evaluate early glycolysis and to correlate possible affects of anerobic imbibition with subsequent axial length.

Experimental Design and Statistical Analysis

The sequence for implementing the temperature by oxygen-concentration treatments was random within blocked time periods (randomized complete block). Three replications were used. Oxygen concentration was a subplot of temperature. The different ecotypes were treated as separate experiments.

Data on seed-weight loss, post-imbibition seed moisture, and ethanol produced during imbibition were tested by analysis of variance. The effects on seedling length of imbibition temperature, oxygen concentration, and age of seedling were analyzed by multiple regression using stepwise variable selection to determine the best regression model. Finally, simple linear regression was used to compare the relationship between seedling length and pre-imbibed dried seed weight with the relationship between seedling length and post-imbibed dried seed weight. This comparison was made across all ecotypes and treatments.

Results and Discussion

Seed-weight loss during imbibition was not affected by oxygen concentration (Table 1). The observed significance levels (OSL) for oxygen treatments (all ecotypes) were >0.30. In 2 of the 3 ecotypes seedling axil length was significantly reduced when seeds were imbibed without oxygen (Table 2). Ethanol production was inversely related to oxygen concentration (Table 2) and, when oxygen was absent, was directly related to temperature. Averaged across ecotypes at 0% oxygen, ethanol was 132 pl/μl at 0° C and ranged up to a maximum of 660 pl/μl at 15° C. At 10% oxygen ethanol production was not significantly ($P<0.05$) higher than at 20%. The relatively large amount of ethanol produced at 0% oxygen and the lack of differences in seed weight loss among oxygen treatments indicate there was no end-product inhibition of glycolysis.

Table 1. Mean loss of dried seed weight for 20-seed groups during 4 days imbibition of winterfat seeds at 5 different oxygen concentrations (averaged across temperature treatments).

Imbibition oxygen concentration	Ecotype		
	Hatch	Cheyenne	Mill City
(%)	(mg)		
0	9.3	9.8	4.0
10	7.2	9.5	3.8
20	9.7	8.7	3.6
30	8.4	9.3	3.8
40	8.7	8.4	3.9
OSL[1]	0.31	0.83	0.65

[1]Observed significance level.

Ethanol is formed under anaerobic respiration from the conversion of pyruvate. The net reaction of glucose to ethanol yields 2 units each of ethanol, CO_2, ATP, and water from a unit of glucose (Stryer 1981) and thus supplies some energy for metabolism. Anaerobiosis often occurs when imbibed seed coats form a continuous wet layer around the embryo. Anerobic conditions and ethanol production are not necessarily detrimental to germination if they do not persist (Côme and Tissaoui 1973). However, ethanol will disturb membrane function and with sufficient concentration, will inhibit germination (Taylorson and Hendricks 1979). Ethanol may have been a factor reducing axil elongation from seeds imbibed without oxygen (Table 2).

Table 2. Mean concentration of ethanol in solution after 4 days imbibition of winterfat seeds at 5 concentrations of oxygen, and the mean axial length of the corresponding seedlings averaged over 5 imbibition temperatures and 5 measuring dates. After imbibition all seeds were held at 20° C for 14 days.

Imbibitional oxygen concentration	Ecotype					
	Hatch		Cheyenne		Mill City	
	ETOH	Length	ETOH	Length	ETOH	Length[1]
(%)	(pl/μl)	(mm)	(pl/μl)	(mm)	(pl/μl)	(mm)
0	287	29	—	26	314	36
10	31	27	—	42	34	38
20	20	34	—	44	16	42
30	6	34	—	45	2	43
40	3	33	—	45	4	42
$LSD_{.05}$	106	NS	—	8	117	6

[1]Stepwise regression indicates significant interaction of seedling age with oxygen concentration for this ecotype (Table 5).

The concentration of water in imbibed seeds increased progressively with temperature and with oxygen concentration for all 3 ecotypes. For the Cheyenne ecotype, main effects interacted significantly (OSL<0.001) so that seeds at the highest temperature and highest oxygen concentration had the greatest concentration of water (Table 3). The interaction for the Mill City ecotype was weaker (OSL = 0.047), with moisture concentrations at treatment extremes being more comparable to those at intermediate levels and with more variability (data not shown). Main effects were significant for Hatch, bud did not interact (OSL for: temperature<0.001, oxygen concentration = 0.046, interaction = 0.307). Progressive increases in temperature and oxygen concentration will, to a point, promote respiration. Increases in moisture concentration appear related to greater water uptake, probably the result of temperature and respiration increases.

Table 3. Concentration of water in Cheyenne winterfat seeds imbibed for 4days at various levels of oxygen and temperature. The observed significance level for the temperature × oxygen interaction was <0.001.

Imbibitional temperature	Imbibitional oxygen concentration (%)				
	0	10	20	30	40
(° C)	---- mg H_2O/mg post-imbibed dried seed weight ----				
0	1.7	1.8	1.7	1.9	1.8
5	1.9	2.1	2.4	2.5	2.6
10	1.9	2.5	3.2	3.4	3.8
15	2.0	3.8	4.7	5.2	5.8
20	2.5	5.7	6.9	7.1	7.5

Progressively higher imbibition temperatures increased seed weight loss and decreased axil length of all ecotypes (Table 4). The OSL for the temperature effect was <0.001 for all 3 ecotypes. Seed weight loss was expected to increase as temperature increased because seed metabolism is temperature dependant. However if the weight loss was connected to growth, average axil length should have increased as weight loss increased. That axil length decreased as imbibition temperature and seed weight loss increased implies that the lost seed material was not used for seedling growth.

Table 4. Mean loss of dried seed weight from 20-seed groups during 4 days imbibition of winterfat seeds at 5 different temperatures, and mean axial length of corresponding seedlings averaged over 5 measuring dates. Seed weight loss and seedling axil length are averaged across imbibitional oxygen concentration. After imbibition all seeds were held in the air at 20° C for 14 days.

Imbibition temperature	Ecotype					
	Hatch		Cheyenne		Mill City	
	Wt. Loss	Length	Wt. Loss	Length	Wt. Loss	Length
(° C)	(mg)	(mm)	(mg)	(mm)	(mg)	(mm)
0	6.9	36	6.0	51	2.7	41
5	7.6	43	6.0	48	3.4	47
10	9.1	33	6.0	45	3.5	48
15	9.9	28	9.0	34	4.0	37
20	12.0	14	18.7	24	4.5	27
$LSD_{.05}$	1.5	4	3.5	8	0.6	6

The regression equations for axil length show that in every case imbibition temperature-squared was the most important variable (OSLs<0.001, Table 5), accounting for more than 3 times the variation in axil length than was accounted for by any other variable. The temperature-squared fit is evidence that imbibition temperature had a progressively greater influence on seedling length at higher temperatures than at low. In 2 of the 3 ecotypes, seed-weight loss was a less important independent variable than imbibition temperature, and much less important than temperature-squared (Table 6).

Table 6. Independent Variables in order of entry, partial r^2s, and observed significance levels (OSL) from stepwise multiple regression procedure for winterfat seedling axial length (dependent variable) when imbibitional seed-weight loss (IWL) was included in the model. Data are presented for 3 ecotypes.

Ecotype	Independant variables	Partial r^2	OSL
Hatch	$(Temp.)^2$	0.423	<0.001
	Temp.	0.022	<0.001
	$\%0_2$	0.021	<0.001
	Temp. × IWL	0.005	0.071
	IWL	0.012	0.004
	$\%0_2$ × IWL	0.004	0.094
	Temp. × $\%0_2$	0.003	0.128
Cheyenne	Temp. × IWL	0.458	<0.001
	$\%0_2$	0.122	<0.001
	$(\%0_2)^2$	0.081	<0.001
	$(IWL)^2$	0.029	<0.001
	IWL	0.005	0.014
	Temp.	0.003	0.053
Mill City	$(Temp.)^2$	0.383	<0.001
	Temp.	0.104	<0.001
	$\%0_2$ × age	0.054	<0.001
	$(IWL)^2$	0.004	0.067
	IWL	0.021	<0.001
	Temp. × %0	0.003	0.094

The stepwise models show seedling age (i.e., the 5 different days on which axil length was measured) was not an important factor in predicting the effect of imbibition temperature on seedling axial length for any ecotype (Table 5). Seedling age did interact with oxygen concentration in the case of the Mill City ecotype (Table 5).

Cold-moist seed treatments and late fall or winter sowing allow seeds to imbibe moisture at cold (2–5° C) temperatures. This enhances vigor (Hilton 1941, Strickler 1956, Booth and Schuman 1983). Similar observations have been made for *Grayia* (Smith 1974, Shaw and Haferkamp 1990) and *Kochia prostrata* (Hafer-

Table 5. Summary statistics for stepwise multiple regression procedure for 3 winterfat ecotypes showing the relationship between the dependent variable, seedling axial length, with the most important independent variables.

Ecotype	Independent variables and intercepts	Last step coefficient values	Step	Partial R^2	Model R^2	OSL
Hatch	$(Temp.)^2$	-0.113	1	0.4234	0.4234	<0.001
	Temp.	1.066	2	0.0219	0.4453	<0.001
	$\%0_2$	0.146	3	0.0206	0.4659	<0.001
	Intercept	34.577				
Cheyenne	$(Temp.)^2$	0.073	1	0.4313	0.4313	<0.001
	$\%0_2$	1.255	2	0.1431	0.5744	<0.001
	$(\%0_2)^2$	-0.024	3	0.0711	0.6455	<0.001
	Temp. × $\%0_2$	0.008	4	0.0035	0.6491	0.054
	Intercept	38.762				
Mill City	$(Temp.)^2$	-0.125	1	0.3832	0.3832	<0.001
	Temp.	1.731	2	0.1040	0.4872	<0.001
	$\%0_2$ × age	0.016	3	0.0543	0.5415	<0.001
	Intercept	38.533				

kamp et al. 1990). Prolonged cold-moist conditions will remove embryo dormancy from many seeds. However, embryo dormancy is not a characteristic of *Eurotia, Grayia, Kochia,* or other seeds with similar morphology (Atwater 1980). Therefore the greater axil length of seedlings from seed imbibed at cold temperatures appears more likely to be related to greater post-imbibition dried seed weight than to other effects of cold imbibition, such as a release of embryo dormancy.

A further analysis of the data was conducted to clarify the importance of post-imbibition seed weight to axil elongation. The relationship between the pre-imbibed dried seed weight of all ecotypes and treatments and the maximum axil length of the corresponding seedlings was tested by simple linear regression. Then the analysis was repeated for the post-imbibed dried seed weights and the 2 analyses were compared. The OSL for pre-imbibed seed weights with axil length was 0.95 (Fig. 1-A), indicating no detectable linear relationship. The OSL for post-imbibed dried seed weights was <0.001 (Fig. 1-B), indicating post-imbibed dried weights were of significant value in explaining the variability in seedling axil length. Seed weight is a well-recognized predictor of seedling vigor for a variety of endospermic (and perispermic) seeds. This has been established by comparing seedling growth from seeds grouped by seed weight and imbibed and germinated at common temperatures (Carleton and Cooper 1972, Evers 1982, Choe et al. 1988). Similarly, Springfield (1973) established that large winterfat seeds (3.3 × 2.0 mm) germinate better than small (2.4 × 1.4 mm). Therefore a positive relationship between pre-imbibed seed weight and axil length should have been evident in the data unless imbibition temperature had significantly altered the seed weight/seedling growth relationship. Conversely, using post-imbibed seed weight is not likely to have given a significant regression line if seed weight loss was random or if undefined cold temperature effects had a dominant influence on seedling growth. The significant regression line of Figure 1-B, and the relative values of the 2 data sets are additional evidence that seed weight losses were influenced by imbibition temperature, and that post-imbibition nutrition (i.e., dried seed weight) was a dominant factor in axil elongation for seeds in all treatments, ecotypes, and over the total population of pre-imbibed seed weights.

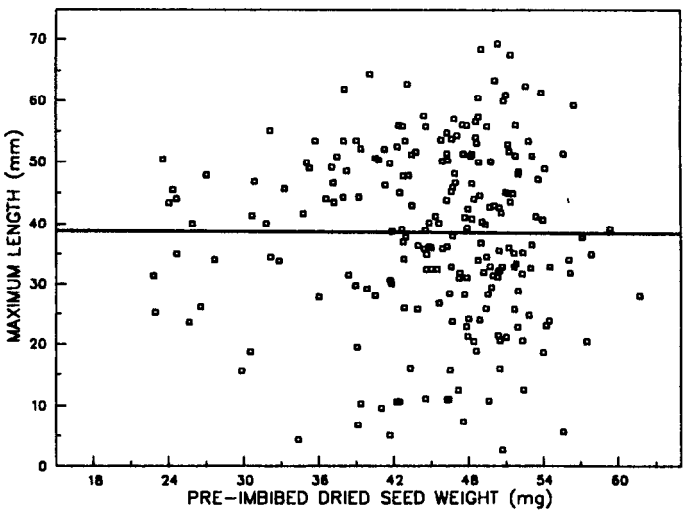

Fig. 1-A. Scatter plot and regression line showing the relationship between winterfat pre-imbibed dried seed weight and maximum length attained by seedlings grown for 14 days in the dark after being imbibed at 5 different temperatures (averaged across 5 oxygen levels). N = 225, Correlation = 0.004, r^2<0.001, S E of Est. = 14.34, Intercept = 38.86, Slope = -7.97, Observed Significance Level = 0.95.

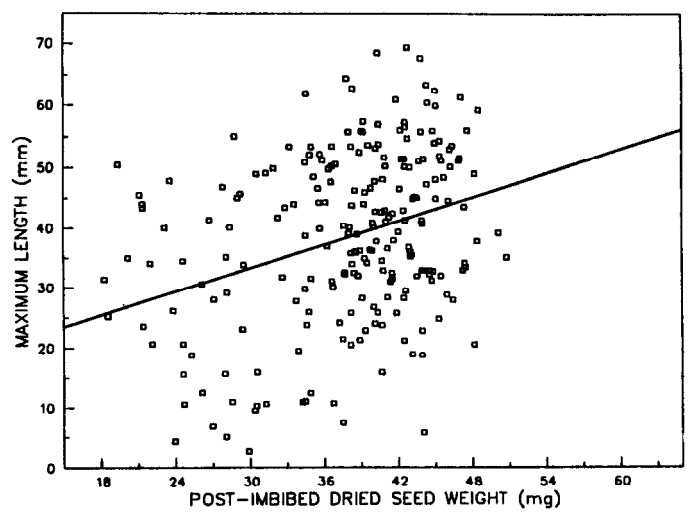

Fig. 1-B. Scatter plot and regression line showing the relationship between winterfat post-imbibed dried seed weight and maximum length attained by seedlings grown for 14 days in the dark after being imbibed at 5 different temperatures (averaged across 5 oxygen levels). N = 225, Correlation = 0.33, r^2=0.11, S E of Est. = 13.56, Intercept = 13.59, Slope = 656.8, Observed Significance Level <0.001.

Why did Imbibition Temperature Affect Post-imbibition Seed Weight?

Seed imbibition is largely a physical process driven by the matric potential of the seed's hydrophilic colloids (Bewley and Black 1978, Mayer and Poljakoff-Mayber 1982). Uptake is initially rapid, with primary, secondary, and then multiple layers of water molecules enveloping structural as well as soluble cellular constituents. Reactivation of cell walls and of the cytosol appears to be among the first events of seed imbibition (Ching 1972). Initial water uptake is accompanied by leakage of sugars, organic acids, amino acids, and electrolytes (Bewley and Black 1978). Rapid imbibition can cause epidermal cracks in soybean *(Glycine max)* testa epidermis allowing leakage sufficient to reduce seedling survival (Duke et al. 1986). Imbibitional damage to soybean seeds is most likely to occur when rapid imbibition occurs with the initial seed moisture content below 8% (Vertucci and Leopold 1984). The moisture level in winterfat seeds used in this test was above 8%; however, it is possible that despite the precautions taken to raise seed moisture content (see methods), rapid imbibition damaged seed membranes resulting in large solute leakage. Since the rate of imbibition can be expected to increase as the temperature increases (Vertucci and Leopold 1983), imbibitional damage and solute leakage might increase with temperature. Perhaps this resulted in the observed temperature related differences in post-imbibed seed weights.

An alternate possibility is that early, inefficient respiration, exacerbated by warm temperatures, catabolized food reserves. Below 8% moisture the water in the seed is strongly bound and there is no measurable respiration (Vertucci and Leopold 1984). This is consistent with the lack of activity for most enzymes at such dry conditions. Eight to 25% moisture is termed a region of restricted metabolism, and between 25 and 32% is a wetting range at which respiration begins to expand rapidly. The dormant seed harbors most of the enzymes needed in early respiration, and most of these appear easily reactivated by hydration (Ching 1972). Evidence of the operation of glycolysis (located in the cytosol) during early imbibition comes from the work of Wilson and Harris (1966) and Wilson (1970), who reported phosphorylation of hexose phosphate in seeds containing 16.2% water. At 23% water, NAD, UDP-hexose, ATP and inositol hexa- and tetra-esters were phosphorylated. At 29.8% water, seed enzymes phosphorylated AMP

and other inositol esters and many unknowns. The early phosphorylation of hexose indicates the glycolysis of pre-existing hexose and sucrose. So, glycolysis begins before seeds are fully hydrated.

Winterfat seed morphology (Booth 1988) seems to allow relatively rapid seed hydration. However, general evidence of respiration dysfunction in some imbibing seeds (Wilson and Bonner 1971, Nawa and Ashai 1973, Puntarulo et al. 1987) indicates that some aspects of seed awakening may require time, regardless of the fact that cell walls and cytoplasm may be fully functional, or that the reactions of glycolysis have begun. Winterfat seeds imbibed at 0 to 5° C retained a greater seed weight and had greater post-germination, seed-supported growth than did seeds imbibed at 15 to 20° C. A possible explanation is that cold temperatures suppressed inefficient respiration during imbibition. After 4 days of imbibition, at any temperature, respiration functioned more efficiently; but cold-imbibed seeds had retained more stored food. Therefore they were capable of greater seed-supported growth.

A third possibility is that both phenomena are contributors to the observed effects of imbibitional temperature. Differentiating among these possibilities will require further investigation into the physiology of winterfat seed imbibition.

Conclusions and Recommendations

Seed imbibition is a critical process for winter fat seed. The conditions surrounding this process affect germination and growth. Oxygen concentration has little effect on the efficient use of stored food or (except at very low levels) on seedling vigor, but temperature does affect the efficient use of stored food and exponentially affects seedling vigor.

The results of this study enlarge upon previous findings that cold imbibition improves winter germination. Winterfat germination should be tested by imbibing diaspores at 5° C for 4 days followed by incubation at 15° C. Winterfat should be sown in the field in late fall, winter, or early spring to give the greatest probability of cold imbibition. An alternative sowing scheme is to imbibe diaspores at 5° C for 4 days before sowing them with a gel carrier onto a wet seedbed (Booth 1987). This method should be used only if there is a reasonable expectation that the soil surface will remain wet through the period of seedling establishment.

The peripheral-linear morphology of the winterfat seed embryo is shared by other members of Chenopodiacae (i.e., *Atriplex, Beta, Kochia, Grayia, Spinacia* and others) and by related families like Amaranthaceae, Caryophyllaceae, and Portulacaeae (Martin 1946). It is probable that cold imbibition will benefit other species with perhipheral-linear embryo morphology that show cold tolerance similar to that of winterfat.

Literature Cited

Allen, P.S., S.E. Meyer, and T.D. Davis. 1987. Determining seed quality of winterfat [*Ceratoides lanata* (Pursh) J.T. Howell]. J. of Seed Tech. 11:7–14.

Atwater, B.R. 1980. Germination, dormancy and morphology of the seeds of herbaceous ornamental plants. Seed Sci. & Technol. 8:523–573.

Bewley, J.D., and M. Black. 1978. Physiology and biochemistry of seeds, Vol. I. Springer-Verlag, N.Y.

Booth, D.T. 1987. Contributions to the reproductive autecology of winterfat [*Eurotia lanata* (Pursh) Moq.] with notes on direct seedling methods. Ph.D. Diss., Univ. Wyoming, Laramie. Diss. Abstr. 48:1568-B.

Booth, D.T. 1988. Winterfat diaspore morphology. J. Range Manage. 41:351–353.

Booth, D.T., and G.E. Schuman. 1983. Seedbed ecology of winterfat: fruits versus threshed seeds. J. Range Manage. 36:387–390.

Brummitt, R.K. (secretary). 1978. Proposal 413. 2232. *Eurotia* Adanson (1763) Chenopodiaceae) vs. *Axyris* Linnaeuus (1753). Taxon 27:288.

Carleton, A.E., and C.S. Cooper. 1972. Seed size effects upon seedling vigor of three forage legumes. Crop Sci. 12:183–186.

Ching, Te May. 1972. Metabolism of germinating seeds, p. 103–205. *In:* T.T. Kosloushi (ed.), Seed biology. Academic Press. N.Y.

Choe, H.S., C. Chu, G. Koch, J. Gorham, and H.A. Mooney. 1988. Seed weight and seed resources in relation to plant growth rate. Oecologia 76:158–159.

Côme, D., and T. Tissaoui. 1973. Interrelated effects of imbibition, temperature and oxygen on seed germination, p. 157–168. *In:* W. Heydecker (ed.), Seed ecology. Penn. State Univ. Press. Univ. Park.

Dettori, M.L., J.F. Balliette, J.A. Young, and R.A. Evans. 1984. Temperature profiles for germination of two species of winterfat. J. Range Manage. 37:218–222.

Duke, S.H., G. Kakefuda, C.A. Henson, N.L. Loeffler, and N.M. Van Hulle. 1986. Role of the testa epidermis in the leakage of intracellular substances from imbibing soybean seeds and its implications for seedling survival. Physiol. Plantarum 68:625–631.

Evers, G.W. 1982. Seedling growth and nodulation of arrowleaf, crimson, and subterranean clovers. Agron. J. 74:629–632.

Gasto, J.M. 1969. Comparative autecological studies of *Eurotia lanata* and *Atriplex conferifolia.* Ph.D. Diss., Utah State Univ., Logan.

Griffith, L.W., and D.T. Booth. 1990. Method for monitoring early seedling growth. *In:* Abstr. 43rd Annu. Meeting. Soc. Range Manage. Abstract #210.

Haferkamp, M.R., D.C. Ganskopp, K.L. Marietta, B.W. Knapp. 1990. Environmental influences on germination of utricles and seedling establishment of 'Immigrant' forage kochia. J. Range Manage. 43:518–522.

Hilton, J.W. 1941. Effects of certain micro-ecological factors on the germinability and early development of *Eurotia lanata.* Northwest Sci. 15:86–92.

Jones, L.G., and R.D. Cobb. 1963. A technique for increasing the speed of laboratory germination a testing. Proc. Assoc. Offic. Seed Analysts. 53:144–160.

Luke, F., and S.B. Monsen. 1984. Methods and costs for establishing shrubs on mined lands in southwestern Wyoming, p. 286–291. *In:* (Arthur R. Tiedeman et al. compilers), Proc. Symp. on the Biology of Atriplex and Related Chenopods General Tech. Rep. INT-172. Intermountain Forest and Range Exp. Sta. Ogden, Utah.

Martin, A.C. 1946. The comparative internal morphology of seeds. Amer. Midland Natur. 36:513–660.

Mayer, A.M., and A. Poljakoff-Mayber. 1982. The germination of seeds. 3rd Ed. Pergamon Press, N.Y.

Nawa, Y., and T. Asahi. 1973. Biochemical studies on development of mitochondria in pea cotyledons during the early stages of germination. Plant Physiol. 51:833–838.

Nelson, A. 1899. Some native forage plants for alkali soils. Univ. Wyoming Exp. Sta. Bull. 42.

Pellant, M., and L. Reichert. 1984. Management and rehabilitation of a burned winterfat community in southwestern Idaho, p. 281–285. *In:* (Arthur R. Tiedemann et al. compilers), Proc. Symp. on the Biology of Atriplex and Related Chenopods. Gen. Tech. Rep. INT-172. Intermountain Forest and Range Exp. Sta. Ogden, Utah.

Plummer, A. Perry, D.R. Christensen, and S.B. Monsen. 1968. Restoring big game range in Utah. Utah Div. Fish and Game Publ. 68-3.

Puntarulo, Susana, Martha T. Beconi, Rodolfo A. Sanchez, and Alberto Boveris. 1987. Oxidative activities in soybean embryonic axes during germination. Plant Sci. 57:33–39.

Shaw, N.L., and M.R. Haferkamp. 1990. Field establishment of spiny hopsage, p. 193–199. *In:* (E.E. McArthur et al. compilers), Proc. Symp. on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management. Gen. Tech. Rep. INT-276. Intermountain Forest and Range Exp. Sta. Ogden, Utah.

Smith, J.G. 1974. *Grayia* Hook. & Arn Hopsage. p. 434–436. *In:* (C.S. Schopmeyer, Tech. Coord.) Seeds of woody plants in the United States. Agr. Handb. 450 USDA, Forest Serv.., Gov. Print. Off., Washington, D.C.

Springfield, H.W. 1973. Large seeds of winterfat germinate better. J. Range Manage. 26:2.

Springfield, H.W. 1974. Winterfat seeds viable after 8 years refrigerated storage. J. Range Manage. 27:78.

Stevens, R., and S.B. Monsen. 1988. 'Hatch' Winterfat: a quality shrub for ranges and wildlands. Rangelands 10:104–105.

Strickler, G.S.S. 1956. Factors affecting the growth of whitesage *Eurotia lanata* (Pursh.) Moq. M.S. Thesis, Univ. Nevada, Reno.

Stryer, L. 1981. Biochemistry (2nd Ed.) W.H. Freeman and Company. San Francisco.

Taylorson, R.B. and S.B. Hendricks. 1979. Overcoming dormancy in seeds with ethanol and other anesthetics. Planta 145:507–510.

U.S. Forest Service. 1948. Woody plant seed manual. USDA Misc. Pub. 654.

Vertucci, C.W. 1989. The effects of low water content on physiological activities of seeds. Physiol. Plant. 77:172–176.

Vertucci, C.W., and A.C. Leopold. 1983. Dynamics of imbibition by soybean embryos. Plants Physiol. 72:190–193.

Vertucci, C.W., and A.C. Leopold. 1984. Bound water and its relation to respiration and imbibitional damage. Plant Physiol. 75:114–117.

Wasser, C.H. 1982. Ecology and culture of selected species useful in revegetating disturbed in lands in the West. Western Energy and Land Use Team. U.S. Fish and Wildl. Serv., Washington, D.C.

Wilson, A.M. 1970. Incorporation of ^{32}P in seeds at low water potentials: evaluation of microbiological contamination. Plant Physiol. 45:524.

Wilson, A.M., and G.A. Harris. 1966. Hexose-, inositol-, and nucleoside phosphate esters in germinating seeds of crested wheatgrass. Plant Physiol. 41:14–16.

Wilson, S.B., and Walter D. Bonner. 1971. Studies of electron transport in dry and imbibed peanut embryos. Plant Physiol. 48:340–344.