Seedbed ecology of winterfat: cations in diaspore bracts and their effect on germination and early plant growth

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Abstract

The concentrations of Ca^{++}, Mg^{++}, K^{+}, and Na^{+} in seeds and bracts of winterfat [*Eurotia lanata* (Pursh) Moq.] diaspores were studied using atomic absorption spectrophotometry. The concentration of Ca^{++} in the bracts was about 9 times that of seed concentrations. Bract and seed concentrations for the other cations were more equal. All cation concentrations were highly variable. Analyses of seed for cation concentrations before and after diaspore imbibition, and after seed imbibition in prepared cation solutions, revealed significant imbibitional increases in seed-cation concentrations. Increases in seed Ca^{++} or Na^{+} improved moisture absorption and germination by the seed, and hypocotyl elongation in the seedling. It is concluded that diaspore bracts are a source of nutrients for the winterfat seed and that these inorganic nutrients are a positive factor in plant establishment.

Key Words: calcium, magnesium, potassium, sodium, seed imbibition, diaspore functions, *Eurotia*

Winterfat [*Eurotia lanata*[1] (Pursh) Moq.; *Ceratoides lanata* (Pursh) J.T. Howell] is a low, Chenopod shrub of western North America. Its diaspore is 2 united, subtending bracts enclosing a pubescent-covered utricle (Booth 1988). White hairs, 2 to 8 mm long, cover the bracts. The seed has a thin testa and a well-developed embryo. The diaspore disarticulates below the bracts, and bracts and utricle function as a unit in dispersal (Hilton 1941) and in seedling establishment (Booth 1982, Booth and Schuman 1983).

Seedlings from diaspores establish and survive better than those from threshed seed. This is partly due to the anchoring function of bract hairs (Strickler 1956, Booth and Schuman 1983); however, diaspore seedlings also have greater hypocotyl elongation than that of seedlings from threshed seed (Booth and Schuman 1983). The transfer of growth substances from bracts into embryos, during imbibition, was identified as a possible reason for this growth difference. Booth (1985) presented evidence that transferred substances are, at least partially, cationic. Therefore it was postulated that cations in diaspore bracts move into the embryo during imbibition and enhance germination and growth.

Three questions were posed as a test of this postulation. First, is there a concentration gradient to indicate potential cation movement from bracts to seed? Second, are there significant increases of seed cations after diaspore imbibition? Third, is germination or seedling elongation improved if cations move into seeds during imbibition?

Materials and Methods

Experimental

Four experiments were used to address the 3 questions. In Experiment 1, the concentration of Ca^{++}, Mg^{++}, K^{+}, and Na^{+} in bracts and in seeds was measured for 9 different diaspore collections from Wyoming, Colorado, and Utah.

A test for cation movement from bracts to seed during imbibition was made in Experiment 2. Six 5-g samples were randomly selected from a thoroughly mixed collection of diaspores. Three of the samples were individually threshed and bracts and seeds analyzed separately for cations. The remaining 3 samples were each soaked in 100 ml of deionized water at 0 ± 2° C for 2 days (Booth and Schuman 1983), the seeds and bracts were then separated by hand, and the bracts and seeds separately analyzed for cations.

Experiment 3 was a test for cation movement into seeds from prepared solutions, and for growth effects due to the cations. Twelve test solutions, described in Table 1, were prepared using chloride and sulfate salts (equal proportions w/w). Sulfate salts were used to reduce the possibility of Cl^{-} toxicity (Clarke and West 1971). The only difficultly soluble salt was CaSO$_4$. About half of the CaSO$_4$ calcium in 500 ug/g and saturated solutions (Table 1) was thought to have been in solution as ion pairs (Masterton and Slowinski 1978, page 437). Treatments are referred to by symbols listed in Table 1.

Table 1. Description of the 12 test solutions used in Experiment 3.

Symbol	Test cation	Measured concentration[1] test cations (ug/g)	Electrical[2] conductivity (dS/m)	Estimated osmotic potential (M Pa)
CA50	Ca^{++}	46	0.26	0.01
CA500		456	2.08	0.08
Ca-saturated		2914	12.51	0.45
MG50	Mg^{++}	50	0.44	0.02
MG500		488	3.28	0.12
MG5000		5461	23.50	0.85
K50	K^{+}	49	0.18	0.01
K500		491	1.71	0.06
K5000		4943	14.45	0.53
NA50	Na^{+}	49	0.27	0.01
NA500		494	2.39	0.09
NA5000		5445	21.67	0.79

[1] Solution concentration measured using a Varian model 1250 Atomic Absorption Spectrophotometer.
[2] Value represents the mean of 3 separate subsamples using a Y.S.I. Model 32 conductivity meter.
[3] Osmotic potential estimated according to U.S. Salinity Laboratory Staff (1954).

Subsamples (2 g) of threshed winterfat seed were soaked in 25 ml of solution for 2 days at 0 ± 2° C. Imbibed seed were drained for 30 min on Whatman 40 filter paper[2], and the filtrate and seed saved for analyses. Treatments were replicated 3 times in a randomized complete block design, with blocks being different times. After imbibition, 200 seeds from each 2-g subsample were mounted on Cobb-Jones germination plates (Jones and Cobb 1963) and incubated for 10 days at 15° C with 12 hour of light at 160 uE/s/m^2. The remaining seed was dried and analyzed for cations.

Experiment 4 compared germination, seedling growth, and seed-

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

[2] Mention of trade names is for information only and does not imply an endorsement by the USDA.

Table 2. Cation concentrations of bracts and seeds in nine collections of winterfat diaspores.

Source	Year	Samples	Ca^{++}		Mg^{++}		K^{+}		Na^{++}	
			Bracts	Seeds	Bracts	Seeds	Bracts	Seeds	Bracts	Seeds
			(ug/g)							
Cheyenne, WY	1981	2	10550**	1210	1700	2130	7930	11550	630*	390
Cheyenne, WY	1983	5	8500**	940	1950	2060	13870**	12580	530	540
Cheyenne, WY	1984	5	7950**	1080	1770	2200	9060	12070	580	360
Pine Bluffs, WY	1980	2	10430**	1200	1210	1960	10410	12200	540**	290
Sterling, CO	1981	5	10790**	1220	1470	2300	6720	12340	530**	370
Sterling, CO	1983	5	10800**	1400	1320	2120	10400	14300	680**	460
Sanpete County, UT	1980	4	9650**	1070	3750**	2050	13900	14370	390	340
Canyonlands, Natl. Park, UT	1980	4	4430**	810	1980	2150	12130	11530	760**	420
Manti, UT	1980	5	12800**	840	4220*	1900	10870	11510	570**	480
Total samples		37								
Overall Mean			9580	1070	2180	2100	10630	12570	590	420
95% Confidence limits (±)			4840	420	2200	300	5060	2570	420	250

*,**indicates a bract concentration that is significantly larger than the paired seed concentration at 0.10 and 0.05 levels respectively.

ling dry weight from: (1) diaspores soaked in deionized water, (2) seed soaked in deionized water, and (3) seed soaked in the best treatment from Experiment 3. Seed samples, (0.7 g) and diaspore samples (2 g) were soaked in 25 and 50 ml of water or solution, respectively. Cultural methods and experimental design were the same as in Experiment 3.

Plant Material

Winterfat diaspores collected from 1980 to 1984 were stored under refrigeration (Springfield 1974) until used in 1985. Threshed seed was obtained by air threshing (Booth and Griffith 1984). A Manti, Utah, collection, obtained from the Utah Division of Wildlife Resources, was used in experiments 2, 3, and 4.

Cation Analysis

To prevent cation contamination of samples, surgical gloves, rinsed in deionized water, were used in each of the procedures where individual seeds or diaspores were handled. Samples were dried at 60° C for 24 hours, ground, weighed, then ashed at 550° C for 6 hours (Jackson 1958). The ash was dissolved in 6 *N*, HCl, evaporated to near-dryness, rinsed into 25-ml volumetric flasks and brought to volume with deionized water. Calcium, Mg^{++}, K^{+}, and Na^{+} were determined on the ash digest and on the filtrate by atomic absorption spectrophotometry.

Other Data Collection

Seedling hypocotyl lengths were measured by hand after the 10-day incubation. The hypocotyl was defined as that part of the seedling below the cotyledons. Estimates of the amount of solution imbibed per gram of seed, and of the average moisture content per seedling, were determined by weight (to 0.1 mg) of the total seed sample and of the seedlings. Imbibed seed weights were measured after seeds had drained on filter paper for 30 min.

Data Analysis

In Experiment 1, one-tailed, paired *t*-tests were used to compare bract and seed cation concentrations for each collection. Confidence intervals (95%) were calculated for the concentration range of cations across all collections. Cation concentrations in bracts and in seeds were compared, in Experiment 2, for each cation by a one-way analysis of variance (AOV). For Experiment 3, a sequential sums of squares AOV was used to compare the effect of treatment solutions on: (1) Ca^{++}, Mg^{++}, K^{+}, and Na^{+} concentrations in the seed, (2) weight of solution imbibed per gram of seed, (3) percent germination, (4) percent moisture in the seedling, (5) seedling dry weight, (6) hypocotyl length, and (7) standard deviations of hypocotyl lengths. A similar analysis was used to compare the treatments in Experiment 4. Mean separations used the least significant differences (L.S.D.) protected at 95% level of probability unless otherwise noted.

Results

Experiment 1

Bract Ca^{++} concentrations were consistently higher than seed Ca^{++}, averaging 9 times that of the seed concentration (Table 2). Concentrations of bract Mg^{++} were usually less than seed Mg^{++}; however, 2 Utah collections (Manti and Sanpete County) had bract concentrations about twice that of seed concentrations. Potassium was slightly higher in seeds than bracts (2 exceptions) and sodium was usually higher in bracts. There was considerable variability in cation concentrations, both within and between collections, but the data are evidence of a concentration gradient of Ca^{++}, usually of Na^{+}, and sometimes of Mg^{++} or K^{+} from diaspore bracts to the seed.

Experiment 2

Seed from imbibed diaspores had significantly ($P \leq 0.05$) more Ca^{++} and Mg^{++} than nonimbibed seed (Table 3). Bracts had less of each cation after soaking, but only K^{+} decreased significantly at $P \leq 0.05$.

Table 3. Pre- and post-imbibition cation concentrations in winterfat bracts and seeds[1].

	Ca^{++}		Mg^{++}		K^{+}		Na^{+}	
	Bracts	Seeds	Bracts	Seeds	Bracts	Seeds	Bracts	Seeds
	(ug/g)							
Pre-imbibition	13667	992	4604	1717	13187	11005	493	240
Post-imbibition	13593	1627	4269	2129	6295	11465	173	134
Change	–74	+635**[2]	–334*	+412**	–6892**	+460	–315	–106*

[1] Values are mean of 3 replications.

[2] Testing the null hypothesis that post-imbibition concentrations are not different from pre-imbibition concentrations. *, ** = significant at 0.10 and 0.05 levels respectively.

Experiment 3

Seed cation concentration was significantly increased by treatment with a solution containing that cation and by increasing cation concentrations (Table 4); except that seeds treated with 500 ug/g K^+ solution did not exhibit higher K^+ than seeds treated with the solution containing 50 ug/g K^+.

Table 4. Measured concentrations of test cations in winterfat seeds after imbibing test solution.

Test solution symbol[1]	Concentration in seeds	L.S.D. 0.05
	(ug/g)	
CA50	2700	
CA500	5400	
CA-saturated	10360	1358
MG50	2400	
MG500	4100	
MG5000	11000	1067
K50	9430	
K500	10450	
K5000	22890	3339
NA50	660	
NA500	2530	
NA5000	15550	994

[1] See Table 1 for description of test solutions.

Filtrate, aside from showing obvious differences due to treatment concentrations, showed differences and trends characteristic of interactions among these cations. For example, the largest concentration of filtrate Ca^{++} in the Mg^{++}, K^+, and Na^+ treatments always occurred at the 5,000 ug/g concentration level; the least Ca^+ was always in the 50 ug/g solutions (data not shown). Although the differences were not significant, the cation concentration trends were consistent and suggest that higher concentrations of Mg^{++}, K^+, or Na^+ caused some efflux of Ca^{++} from seeds.

The cation treatments affected imbibition and other growth parameters; however, only imbibition had a significant interaction between cations and concentration. The highest imbibition was in CA500, which averaged 3.07 g moisture/g seed dry weight (Table 5). MG5000 and K5000 were second and averaged 3.01 g/g. Except for Mg^{++}, the lowest imbibition occurred at the lowest cation concentration (Table 5). Imbibition among Na^+ solutions had a pattern similar to that among Ca^{++} solutions.

Germination, seedling moisture content and hypocotyl length were significantly affected by differences in cation concentration (Table 6). Germination was greater at the 500 ug/g level than at 0, 50, or 5,000 ug/g (Note that data for the 0 ug/g level are from Experiment 4). Seedling moisture was reduced, and hypocotyl lengths probably ($P \leq 0.10$) reduced by 5,000 ug/g concentrations. Among treatment solutions the greater hypocotyl elongation occurred with NA500, which averaged 28.5 mm. The low was K5000 (17.72 mm). No significant changes were detected in seedling dry weight due to treatment with cations solutions.

Table 5. Interaction of cation species and concentrations on weight of imbibed winterfat seeds. Data are grams of moisture per gram of seed dry weight.

Cation concentration of imbibed solution	Cation species in imbibed solution			
	Ca^{++}	Mg^{++}	K^+	Na^+
(ug/g)	(g/g)			
50	2.32	2.79	2.44	2.43
500	3.07	2.40	2.67	2.94
5000[1]	2.56	3.01	3.01	2.59
L.S.D.$_{.05}$ = 0.60 g/g[2]				

[1] The Ca^{++} solution was saturated at 2,914 ug/g (Table 1).
[2] Protected at $P = 0.057\%$.

Table 6. Germination of threshed winterfat seeds, and subsequent seedling growth as affected by cation concentration[1].

Cation concentration of imbibed solution	Mean germination	Mean moisture content of seedlings	Mean hypocotyl length
(ug/g)	(%)		(mm)
0 (deionized)	62	88.16	22.0
50	64	89.88	24.2
500	72	88.93	24.6
5000[2]	57	88.12	21.5
	L.S.D.$_{.05}$ = 6	L.S.D.$_{.05}$ = 1.34	L.S.D.$_{.10}$= 2.4[3]

[1] Averaged across cations in Experiment 3. Data for the 0 concentration are from Experiment 4 and are not included in calculations of experimental error for L.S.D.s.
[2] The Ca solution was saturated at 2,914 ug/g (Table 1).
[3] The L.S.D.$_{.10}$ is protected at $P = 0.10$.

Experiment 4

Seed treated with NA500 had 73% germination, which agrees with the results of Experiment 3 (Table 6). Seedling hypocotyl lengths from seed treated in NA500 did not differ significantly from those of diaspores soaked in deionized water, but were significantly longer than hypocotyls from seeds soaked in deionized water (Table 7). Seedlings from diaspores had significantly higher ($P \leq 0.01$) dry weights (3.8 mg) than seedlings from seeds soaked in either NA500 (2.0 mg) or deionized water (2.0 mg).

Table 7. Mean 10-day seedling hypocotyl lengths from winterfat diaspores and seeds.

Treatment	Length	Mean Standard Dev.
	(mm)	
Diaspores soaked in deionized water	32	20.0
Seeds soaked in NA500	28	18.3
Seeds soaked in deionized water	22	15.3
	L.S.D.$_{.05}$ = 4.7 mm	

Discussion and Conclusions

The evidence from Experiment 1 verified that there is a concentration gradient of Ca^{++}, and sometimes of other cations, between the diaspore bracts and seed. Other workers have also demonstrated that high concentrations of cations exist in the bracts of Chenopod diaspores (Eddleman and Romo 1987, Khan et al. 1987). The indicated potential for cation movement, and the imbibitional increases in seed cation concentrations that were demonstrated in Experiments 2 and 3, support the postulation that cations in diaspore bracts move into the seed during imbibition. [It is acknowledged that cations can also move out of the seed during imbibition (Bewley and Black 1978, page 117; Table 3)].

Experiments 3 and 4 demonstrated that increases in seed cations affect seed germination and seedling growth (Tables 6 and 7). Because of the known function of Ca^{++} in cell membranes (Mengel and Kirkby 1982, page 114; Poovaiah 1985, Chowdhury and Choudhuri 1986), the increase in seed imbibition detected for the CA500 treatment of Experiment 3 (Table 5) was not unexpected. The effects of the other ions are not as well understood, but they must make the osmotic potential of the cells more negative and/or improve tightness of the cell membrane and wall. Seed imbibition in 5,000 ug/g treatments appears to have exceeded that in 50 ug/g treatments (Table 5); however, 5,000 ug/g treatments also resulted in seedlings with significantly lower moisture compared to seedlings from 50 ug/g treatments (Table 6). This may indicate some salt damage to cell membranes at the higher concentration.

Seed treated with 500 ug/g solutions germinated better than seed exposed to lower cation concentrations. This is consistent with Hilton's (1941) observation that winterfat seeds germinated better in 0.5% NaCl solution (1966 ug of Na^+/g of solution) than in distilled water. A beneficial influence of Na^+ and of Ca^{++} to seedling growth has also been discussed for other species (El-Sheikh and Ulrich 1970, Chowdhury and Choudhuri 1986, Romo and Haferkamp 1987, Eddleman and Romo 1987).

Cell extension usually accounts for most of the growth that produces germination and initial soil penetration (Bewley and Black 1978, page 120). Cell extension requires water absorption. This increases turgor pressure and drives expansion during cell wall loosening (Bewley and Black 1978, page 116; Nonami and Boyer 1987). Turgor pressure develops if cell water potential is lower than the potential of the water source. The lower the cell water potential, the greater the capability of cells to take on water, to expand cell walls, and to elongate the radicle.

Osmotic potential, which is a part of the cell water potential, occurs because cells accumulate relatively high concentrations of solutes into their vacuoles (Salisbury and Ross 1969, page 186; Bewley and Black 1978, page 106). Osmotic potential is a colligative property depending upon concentration, and is made more negative by all particles (cationic or organic) in the solution (Masterton and Slowinski 1978, page 309). This means the greater the total solute concentration, the greater the attractive force to water. Cosgrove (1987) has argued that cell wall relaxation is the primary motive force leading to water uptake during cell extension, since wall yielding tends to reduce cell turgor pressure and water potential. If we accept Cosgrove's argument, then the data from these studies suggest that increases in cell cation concentration increase the efficiency of water absorption during wall relaxation.

This is not to say that radicle elongation is independent of the nature of the cations in cell solutions. It is not. There are several physiological functions that are cation specific and that contribute to radicle elongation (Burstrom 1968, Mengel and Kirkby 1982, page 14, Devlin and Witham 1983, page 6). This was demonstrated in Study 3 for imbibition by the significant interaction between cations and concentration (Table 5). However, the differences seen in Experiment 3 for germination, seedling moisture content, and hypocotyl length (Table 6) were due to cation concentration. Differences due to cation species were not significant. Likewise, differences seen in Experiment 4 are more easily attributed to cation concentration than to the influence of any given cation. Therefore, the observed growth differences appear to be due to a colligative property of the cell solution. The suggested growth mechanism from the influx of cations into the seed is a more negative cell osmotic potential, which resulted in a higher base line moisture content and an increased rate of cell extension.

Cationic improvement of radicle elongation may not be the only bract contribution to seedling vigor. Seedlings from the threshed seed treatments of Experiment 4 had significantly lower dry weights than seedlings from the diaspore treatment. This may be due to increased respiration in seeds caused by unbalanced cell cation concentrations during treatment with either NA500 or deionized water (Carafoli and Penniston 1985). More likely, the difference is due to lower respiration rates of diaspore seeds, since wet bracts and utricle walls may restrict oxygen flow to the seed. If high respiration during imbibition and early growth wastes seed reserves, then factors which lower respiration during this period would benefit vigor. Low temperature (0° C) during seed imbibition reduces seed respiration and is known to improve seed germination and seedling vigor (Hilton 1941, Strickler 1956, Booth and Schuman 1983). Wet seed coverings may also reduce seed respiration.

From these experiments, the previously unrecognized chemical-storage function of winterfat diaspores, and its effect on seed germination and early seedling growth, have been described. The importance of these phenomena to seedling establishment and survival, within the variety of habitats occupied by winterfat, is not known. Some may suggest that movement of diaspore cations into seeds is inconsequential relative to soil cations contained in imbibed moisture. This may be true for some saline sites. However, A horizon electrical conductivity (EC) from 14 rangeland soils in southeastern Wyoming, including soils that will support winterfat ranged from grazing, ranged from 0.63 to 0.42, and averaged 0.55, dS/m (Stevenson et al. 1984). This compares to 2.08 and 2.39 dS/m for the most successful Ca and Na treatments used in Experiment 3 (Table 1). Further, snow melt, which creates the cool, saturated, soil surface environment characterizing optimum germination conditions for winterfat (Gasto 1969, page 73), can be expected to have a lower EC than the underlying soil. Hence, the nutrients stored in diaspore bracts appear as an important factor in winterfat seedbed ecology over most of its range.

It is concluded that cations, particularly Ca^{++}, in the bracts of winterfat diaspores move into the seed during imbibition. This increase in cation concentration in the seed improves water absorption, germination, and subsequent seedling growth (hypocotyl elongation). The bracts of winterfat diaspores are known to function in seed dispersal (Hilton 1941), in seed protection (Stevens et al. 1977), and in seed fixation or anchoring (Booth and Schuman 1983). They also function as nutrient reservoirs.

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