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Responses of winterfat seeds and seedlings to desiccation

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Abstract

Winterfat [*Krascheninnikovia lanata* (Gueldenstaedt) syn. *Ceratoides lanata* (Pursh) J.T. Howell, syn. *Eurotia lanata* (Pursh) Moq.] is a native shrub of mixed prairie of North America. A large portion of hydrated seeds and seedlings can be killed when exposed to seedbed desiccation. Winterfat seeds and young seedlings subjected to varying levels of desiccation were studied to measure the influence of this stress. Germination was unaffected (P>0.05) when seeds were exposed for 0 to 10 hydration-desiccation cycles (2 hours hydration and 22 hours desiccation cycle^{-1} at 20 to 30% relative humidity and 20°C). Linear increases in germination rate (0.6% day^{-1} hydration-desiccation cycle^{-1}), seedling length (0.1 mm hydration-desiccation cycle^{-1}), and seed decay (1.5% hydration-desiccation cycle^{-1}) occurred with an increasing number of hydration-desiccation cycles. Seedling survival following desiccation decreased 10.4% mm^{-1} as seedling length increased from <2mm to 10–15 mm. Seedling survival was positively correlated with relative humidity and negatively correlated with duration of desiccation. The difference (P≤0.05) in survival between 0 and 90% relative humidity was 62% for seedlings 4–6-mm in length and 70% for seedlings 9–11-mm in length. Seedlings from seeds that germinated rapidly were more tolerant of desiccation than those from seeds germinating slowly. After desiccation in 30% relative humidity, survival of seedlings from seeds germinating on the first day of incubation was 40% greater than those from seeds germinating on the third day of incubation. Electrolyte leakage indicated that desiccation damaged cells. Establishment of winterfat seedlings will be favored by seedbed conditions that protect seedlings from severe and prolonged desiccation and allow fast entry of the radicle into soil.

Key Words: *Krascheninnikovia lanata* (Gueldenstaedt), *Ceratoides lanata* (Pursh) J.T. Howell, *Eurotia lanata* (Pursh) Moq., restoration, seed germination, seed hydration, seedbed ecology.

Resumen

"Winterfat" [*Krascheninnikovia lanatai* (Gueldenstaedt) syn. *Ceratoides lanata* (Pursh) J.T. Howell syn. *Eurotia lanata* (Pursh) Moq.] es un arbusto nativo de las praderas mixtas de Norte América. Un gran proporción de semillas y plántulas hidratadas pueden morir cuando se exponen a la desecación de la cama de siembra. Se estudiaron semillas y plántulas de "Winterfat" sometidas a diferentes niveles de desecación para medir la influencia de este estrés. La germinación no fue afectada (P>0.05) cuando las semillas se expusieron de 0 a 10 ciclos de hidratación-desecación (2 horas de hidratación y 22 horas desecacion ciclo^{-1} y de 20 a 30% de humedad relativa y 20°C). Incrementos lineales en la tasa de germinación (0.6% día-1 ciclo hidratación-desecación^{-1}), longitud de la plántula (0.1 mm ciclo hidratación-desecación^{-1}) y decadencia de la semilla (1.5 ciclo hidratación-desecación^{-1}) ocurrieron con un número creciente de ciclos de hidratación-desecación. La sobrevivencia de plántulas después de la desecación decreció 10.4% mm^{-1} conforme la longitud de la plántula incrementó de <2 mm a 10–15 mm. La sobreviviencia de las plántulas fue positivamente correlacionada con la humedad relativa y negativamente correlacionada con la duración de la desecación. La diferencia en sobrevivencia (P≤0.05) entre 0 y 90% de humedad relativa fue 62% para plántulas de 4–6-mm de longitud y 70% para plántulas de 9–11-mm de longitud. Las plántulas provenientes de semillas que germinaron rápidamente fueron más tolarantes a la desecación que aquellas provenientes de semillas que germinaron lentamente. Después de una desecación del 30% de la humedad relativa la sobrevivencia de plántulas de semillas que germinaron el primer día de incubación fue 40% mayor que aquellas de semillas que germinaron el tercer día de incubación. La fuga de electrolitos indicó que la desecación daño las células. El establecimiento de plántulas de "Winterfat" sería favorecido por condiciones de la cama de siembra que portejan las plántulas de una desecación severa y prolongada y que permitan la entrada rápida de la radícula en el suelo.

Winterfat [*Ceratoides lanata* (Pursh) J.T. Howell, syn. *Eurotia lanata* (Pursh) Moq., syn. *Krascheninnikovia lanata* (Gueldenstaedt)] is a long-lived, native shrub of northern mixed prairie in North America (Coupland 1950, Romo et al. 1995). Winterfat provides excellent forage (Clarke and Tisdale 1945, Smoliak and Bezeau 1967) and contributes to the structural diversity of rangeland ecosystems (Romo et al. 1995). High seedling mortality has been identified as a major obstacle to seedling establishment (Booth 1992), and desiccation may be an important factor causing seedling death.

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On northern mixed prairie, winterfat diaspores are shed mid-September through October (Romo et al. 1995). Diaspores must after-ripen, and thus do not germinate until the following spring. Many diaspores lodge in plant litter above the soil surface while others lie on the soil surface (Booth 1987, Booth and Haferkamp 1995). Diaspores germinating in early spring during moist conditions (Woodmansee and Potter 1971) may be exposed to alternating periods of desiccation and rehydration. Environmental factors such as litter, microtopography, and neighboring plants can influence moisture conditions immediately surrounding a diaspore or seedling (Fowler 1986, Cheplick and Quinn 1987). Diaspores and seedlings on different microsites may, therefore, experience a wide range of desiccation stress. Response of germinating seeds or seedlings to desiccation varies with developmental stages (Hassanyar and Wilson 1979, McKersie and Tomes 1980, Friedman et al. 1981, Senaratna and McKersie 1983, Hong and Ellis 1992, Allen et al. 1993, Debaene-Gill et al. 1994), implying that biological timing of desiccation is an important aspect of this stress.

Other factors besides desiccation may be responsible for winterfat seedling mortality, including freezing (Hou and Romo 1997, Bai et al. 1998a) and fungal infection. It is, however, difficult to separate these causes in the field. The purpose of this study was to evaluate impacts of desiccation on germinating seeds and young seedlings of winterfat. These experiments characterized effects of: 1) repeated seed hydration-desiccation cycles on winterfat germination and seedling growth; 2) desiccation on survival of different size seedlings, and; 3) desiccation duration and relative humidity during desiccation on subsequent growth and survival of seedlings.

Materials and Methods

Seed collection

Winterfat diaspores were collected in late September 1995 at the University of Saskatchewan, Matador Research Station (50°42'N, 107°43'W, elevation 685 m). This northern mixed prairie has been described by Romo et al. (1995). Diaspores were air dried to about 3–5% water content at room temperature for about 30 days and then stored in plastic bags at –15°C until used.

Experiment I—Effects of hydration-desiccation cycles on seed germination and seedling growth

The hypothesis that repeated hydration and desiccation of diaspores of winterfat reduces germination was tested by exposing diaspores to 0 to 10 hydration-desiccation cycles. Several hundred diaspores were placed on moistened germination paper over plastic slant-boards, and covered with 1 layer of cellulose tissue (Jones and Cobb 1963). Slant-boards were then placed in closed germination boxes (25 x 40 x 20 cm), which were filled with distilled water to a 3-cm depth. These boxes were placed in incubators at 20°C in darkness for 2 hours. One-half of the diaspores were then removed and placed in dry germination boxes with 20 to 30% relative humidity for 22 hours at 20°C, completing 1 hydration-desiccation cycle. These hydration-desiccation cycles were repeated 9 times more giving a range of 0 to 10 cycles. After each hydration-desiccation cycle, water content (dry-weight basis) of 10 hydrated and 10 desiccated diaspores was measured using tin capsules as described by Booth and Bai (1998). Following each cycle, 20 desiccated diaspores were incubated on slant-boards at 20°C in 12 hours light and 12 hours darkness for 7 days, prepared as above. Germination was checked daily between 1 and 7 days, and diaspores were considered germinated if the radicle of seedlings was ≥2 mm. The number of diaspores not germinating, but decaying, was determined for each hydration-desiccation cycle. Germination rate was calculated as the sum of total germinated diaspores day^{-1} divided by total germination and multiplied by 100 (Maguire 1962). At the end of the 7-day-incubation period, seedling axial length was determined using a digitizing tablet (Booth and Griffith 1994).

Experimental design was a randomized-complete-block with the 11 hydration-desiccation cycles applied to 4 blocks separated by 1-day intervals. Percentage data were transformed into arcsin angles and subjected to analysis of variance (Snedecor and Cochran 1980). Regression analyses were performed and best-fit models ($P \leq 0.05$) were selected (Snedecor and Cochran 1980). Untransformed data are presented.

Experiment II—Effects of desiccation on survival of different size seedlings

This experiment was conducted to test the effects of desiccation on seedlings of different sizes. Seeds, removed by hand from diaspores, were soaked in a 600 mM ethanol solution at room temperature for 4 hours, then thoroughly washed in distilled water. This ethanol treatment ensured fast and synchronous germination (Hou and Romo 1998). After ethanol treatment about 300 seeds were placed in 32 x 21 x 7 cm plastic boxes lined with 6 layers of germination paper wetted with 120 ml distilled water, and incubated at 18°C in darkness. On the fourth day of incubation seedlings were removed from the boxes in which seeds were germinated, and seedling axial length was measured.

Seedlings were grouped according to those that were <2, 2–4, 4–6, 6–8, 8–10, or 10–15 mm in length. These seedlings were then placed in desiccators at 20% relative humidity and 24°C for 14 days. Relative humidity was controlled by filling desiccators with 350 ml of calcium chloride ($CaCl_2$) solution prepared according to Stokes (1949). Upon completion of the desiccation treatment, 3 blocks each containing 10 seedlings were selected, blotted dry on paper tissues and weighed. These seedlings were oven-dried at 80°C for 48 hours, weighed, and water content determined. Three more blocks of 20 seedlings for each seedling length group were rehydrated in 100 x 15 mm Petri dishes lined with 2 layers of No. 1 Whatman filter paper moistened with 4 ml distilled water, and incubated at 18°C in darkness for 7 days. Seedling survival was determined on the seventh day by examining root hair development; seedlings developing root hairs were considered live.

Reliability of using root hairs as the criterion of seedling survival in the following experiments was tested by randomly selecting seedlings from each seedling-length group, scoring root hairs, and transplanting them into 125 x 125 x 100 mm pots filled with wet 'Redi-earth' potting media. Seedling cotyledons were covered with about 5 mm of media. Pots were placed in a growth chamber at 15°C with light (220 $\mu mol\ m^{-2}\ sec^{-1}$) for 14 hours and 10°C darkness for 10 hours. Pots were watered every 2 days, and seedling sur-

vival was recorded after 21 days. Survival, judged by growth of root hairs provided a slightly high estimate of seedling emergence ($Y = 7.8+0.93X$ where Y is seedling emergence from soil (%) and X is seedling survival (%) judged by the presence of root hairs, $R^2 = 0.99$, $P < 0.001$).

Root hair development was used to assess seedling survival in Experiments II through IV. These experiments were repeated twice with 3 blocks per run in a randomized-complete-block design. Regression analyses were used to relate seedling survival and seedling length when desiccated with the best-fit model ($P \leq 0.05$) selected (Snedecor and Cochran 1980). Mid-points of seedling length classes were used as independent variables.

Experiment III—Effects of relative humidity on seedling survival

This experiment was conducted to test the hypothesis that relative humidity during desiccation affects seedling survival. Seeds were pretreated in a 600 mM ethanol solution and washed in water as in Experiment II. About 300 of these seeds were placed in 32 x 21 x 7 cm plastic boxes lined with 6 layers of germination paper wetted with 120 ml distilled water then incubated 4 days at 18°C in darkness. Seedlings were removed from the boxes, axial length measured, and seedlings were grouped into those that were 4-6 or 9-11 mm in length. Three blocks of 20 seedlings for each seedling-length group were placed in desiccators containing 350 ml $CaCl_2$ solution (Stokes 1949) prepared to create 30, 45, 60, 75, and 90% relative humidity. Calcium chloride powder, oven dried at 120°C for 48 hours, was used for 0% relative humidity. Desiccators were placed in an incubator at 25°C in darkness for 7 days. Upon completion of the desiccation treatment, 3 blocks each containing 10 seedlings were selected and weighed. These seedlings were oven-dried at 80°C for 48 hours, weighed, and water content determined.

This experiment was repeated twice with 3 blocks per run in a randomized-complete-block design. Percentage data were transformed into arcsin angles and subjected to analysis of variance (Snedecor and Cochran 1980). Regression analyses were performed and best-fit models ($P \leq 0.05$) were selected (Snedecor and Cochran 1980) for untransformed data.

Experiment IV—Effects of varying lengths of desiccation on seedling survival

This experiment was conducted to test the hypothesis that the duration of desiccation affects seedling survival. Several hundred seeds were pretreated in ethanol and incubated as described in Experiment II. Twenty seedlings that were 7–10 mm long were desiccated at 20°C for 1, 4, 7, 10, 13, or 16 days over a $CaCl_2$ solution prepared to create 30% relative humidity. After the specified length of desiccation 20 seedlings were removed from the desiccator, rehydrated as in Experiment II, and incubated for 5 days at 18°C in darkness. On the fifth day, survival of seedlings for each desiccation treatment was determined.

Another lot of seeds was incubated as above, and on the fifth day seedlings were measured and grouped as being 2–5 or 7–10 mm long. These seedlings were desiccated in darkness for 7 days at 20°C in desiccators with $CaCl_2$ solutions prepared to create 30 or 90% relative humidity. Control was 100% relative humidity in sealed germination boxes with wet germination paper. Seedlings were removed from dessicators and germination boxes and placed in 100 x 15-mm Petri dishes lined with 2 layers of No.1 Whatman filter paper moistened with 4 ml distilled water. These seedlings were incubated at 18°C in darkness for 7 days and the lengths of 40 seedlings measured.

These tests, conducted in a randomized-complete-block with 3 blocks, were repeated twice. Relationships between days of desiccation and seedling survival were determined with regression analysis and the best-fit model ($P \leq 0.05$) was selected (Snedecor and Cochran 1980). In the second aspect of this study, analysis of variance was used, and means were separated with Least Significant Difference ($P \leq 0.05$).

Experiment V—Effects of desiccation on seedlings of different ages

Several hundred seeds were prepared and incubated in germination boxes as in Experiment I. One, 2, and 3 days after beginning incubation, seedlings that were 7–10 mm in length were removed from germination boxes and desiccated for 7 days at 25°C over $CaCl_2$ solutions prepared to create 30% relative humidity. Upon completion of the desiccation treatment, seedlings were rehydrated in 100 x 15-mm Petri dishes lined with 2 layers of No. 1 Whatman filter paper moistened with 4 ml distilled water, and incubated at 18°C in darkness for 7 days. Seedling survival was determined on the seventh day by examining root hair development; seedlings developing root hairs were considered live.

This experiment was repeated twice with 3 blocks per run in a randomized-complete-block design. Percentage data were transformed into arcsin angles and subjected to analysis of variance (Snedecor and Cochran 1980). Means were with separated with Least Significant Difference ($P < 0.05$); untransformed data are presented.

Experiment VI—Effects of varying periods of desiccation and relative humidity on electrolyte leakage from seedlings

Seeds were pretreated with ethanol and germinated as described in Experiment II. Seedlings of <2, 4–6, or 9–11-mm lengths were placed in desiccators containing $CaCl_2$ solutions with 30 or 90% relative humidity at 20°C for 7 days. Control seedlings were placed in sealed germination boxes with wet germination paper to create 100% relative humidity. Three blocks, each containing 7 seedlings from each length category and humidity treatment, were soaked in 3 ml distilled water at room temperature. Electrical conductivity of the soaking solution was measured at 15, 30, 45, 60, 90, 120, 150, 180, 240, 300, 360, 420, or 480 minutes of soaking with a YSI Model 32 conductance meter. Three new blocks were used for each period of soaking. The number of seedlings and water volume were determined in preliminary experiments so measurements fell into the range of the instrument.

This experiment was repeated twice in a randomized-complete-block design with 3 blocks per run. Best-fit regression equations were selected ($P \leq 0.05$) (Snedecor and Cochran 1980) to describe relationships between soaking time and electrical conductivity for each size class of seedlings and relative humidity.

Results

Effects of hydration-desiccation cycles on seed germination and seedling growth

Initial seed water content was about 5%. Water content peaked at about 35% on the second hydration-desiccation cycle and decreased as the number of hydration-desiccation cycles increased from 2 to 10 (Y = 36.1–0.06X, where Y is water content (%) and X is the number of hydration-desiccation cycles; R^2 = 0.55, P≤0.05). Water content of dehydrated seeds did not change after the first cycle and averaged 13.4% (SE = 0.4). When rehydrated for 24 hours after the hydration-desiccation cycles, water content of seeds averaged 141% (SE = 1.9).

Total germination percentage varied among hydration-desiccation cycles, but was not correlated (P>0.05) with the number of cycles and averaged 66% (SE = 1.5). Seeds germinated faster with exposure to increasing number of hydration-desiccation cycles (Y = 37.3 + 0.6X, where Y is germination rate (% day^{-1}) and X is the number of hydration-desiccation cycles, R^2 = 0.33, P≤0.05). Of the seeds that did not germinate, seed decay increased about 1.5% with each hydration-desiccation cycle (Y = 16.2+1.5X, where Y is seed decay (% of seeds incubated), and X is the number of hydration-desiccation cycles, R^2 = 0.53, P≤0.05). Axial length of seedlings increased with increasing number of hydration-desiccation cycles (Y = 34.7+0.05X, where Y is seedling axial length (mm) and X is the number of hydration-desiccation cycles, R^2 = 0.44, P≤0.05).

Effects of desiccation on survival of different size seedlings

Seedling survival after 14 days of desiccation at 20% relative humidity declined as seedling length increased (Y = 113.9–10.04X where Y is seedling survival (%) X is seedling length (mm), R^2 = 0.90, P = 0.004). Final water content of desiccated seedlings ranged from 4.9 to 5.5%, but was not correlated (P>0.05) with survival.

Effects of relative humidity on seedling survival

Survival of desiccated seedlings 4-6 or 9-11 mm in length increased as relative humidity increased (Fig. 1). The difference in survival between 0 and 90% relative humidity was 62% for 4–6 mm seedlings and 70% for 9–11 mm ones. Survival of 4–6 mm seedlings was 20 to 45% higher than that of 9–11 mm seedlings after desiccation. As expected, water content of desiccated seedlings also increased with increasing relative humidity (Fig. 1). After desiccation at 75 and 90% relative humidity, 9–11 mm seedlings contained more water than those that were 4–6 mm long.

Effects of varying lengths of desiccation on seedling survival and growth

Seedling survival decreased curvilinearly as the length of desiccation increased from 1 to 16 days (Fig. 2). Seedling survival was about 67% for seedlings desiccated 1 day compared to 31% for those desiccated 16 days. Water content of desiccated seedlings was similar (P>0.05) after different lengths of desiccation, averaging 7.5% (SE = 1.1).

Desiccation at 30 and 90% relative humidity produced similar effects on growth of seedlings that survived, even though survival differed with relative humidity. Growth was reduced for 7–10 mm long seedlings that survived 7 days of desiccation, but growth of 2–5 mm long seedlings was not affected by desiccation (Fig. 3). Abnormal growth, twisted or sharply curved radicles, was observed among seedlings that survived desiccation.

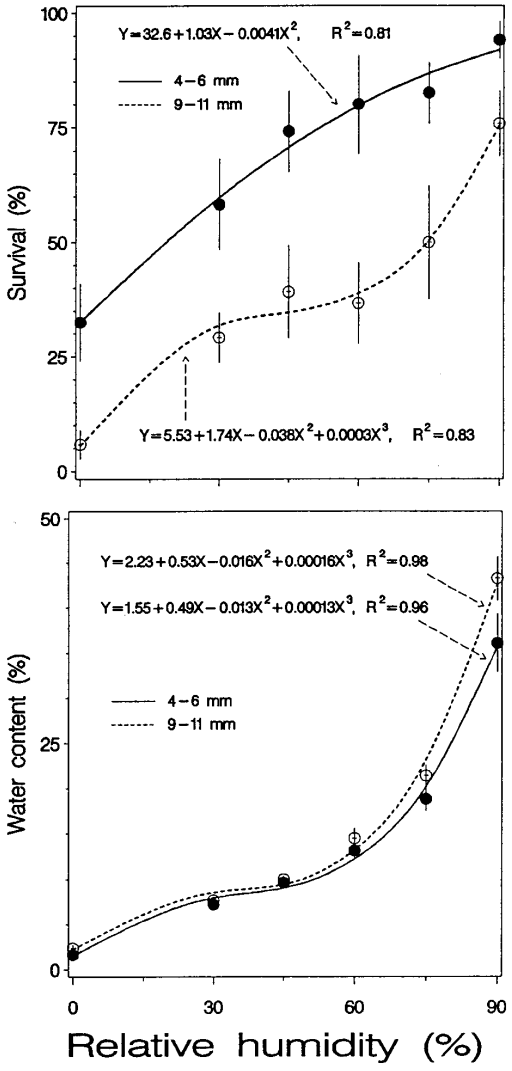

Fig. 1. Fitted regression lines for survival and water content in winterfat seedlings of 4–6 mm and 9–11 mm lengths after 7 days of desiccation at relative humidities between 0 and 90%. Each value is the mean±SE of 6 replicates of 20 seedlings. If no vertical bar is evident, SE is less than the size of the symbol.

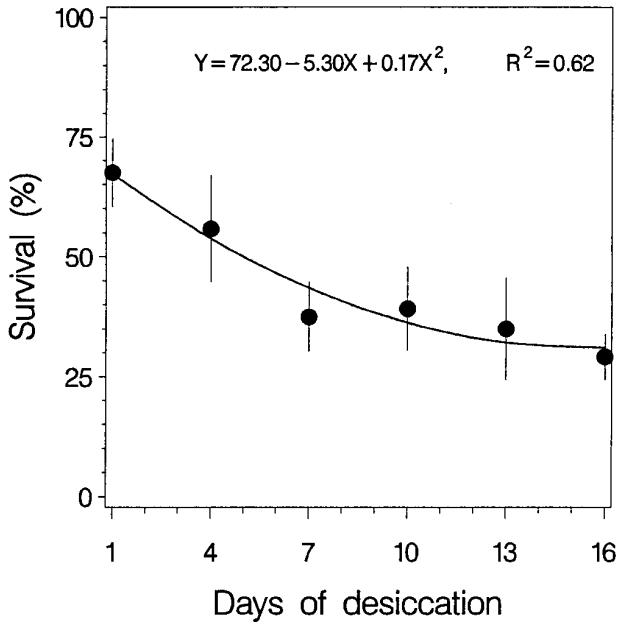

Fig. 2. Fitted regression lines for survival of 7–10 mm long winterfat seedlings after desiccation at 20°C and 30% relative humidity for 1 to 16 days. Each value is the mean±SE of 6 replicates of 20 seedlings.

Effects of desiccation on survival of seedlings of different ages

Survival of desiccated seedlings varied among times of seed germination. Desiccated seedlings from seeds germinating on the first day averaged 64% (SE±3.5) compared to 40% (SE±4.3), and 23% (SE±2.1) on the second and third days, respectively.

Effects of varying lengths of desiccation and relative humidity on electrolyte leakage from seedlings

Decreasing relative humidity and increasing seedling length contributed to greater electrolyte leakage from seedlings (Fig. 4, Table 1). Leakage increased faster at earlier than later stages of soaking.

Discussion

Seeds are generally tolerant of wetting and drying (Hegarty 1978, Hassanyar and Wilson 1979, Friedman et al. 1981, Hong and Ellis 1992). Lack of correlation between germination and number of hydration-desiccation cycles, as observed in this study, indicates that germination of viable winterfat seeds is not likely impaired or favored by repeated moisture fluctuations in the field. This response contrasts with forage kochia (*Kochia prostrata*) (Haferkamp et al. 1990) and spiny hopsage (*Grayia spinosa*) (Shaw et al. 1994) in which germination is increased by wetting and drying cycles under field conditions. Germination rate and seedling growth of winterfat actually increased after hydration-desiccation treatments, and may be attributed to the well-known effect of priming (Hegarty 1978). Germination rate of forage kochia and spiny hopsage also increases following periods of wetting and drying (Haferkamp et al. 1990, Shaw et al. 1994). Increased seed decay in ungerminated seeds after hydration-dehydration treatments suggests some seeds were damaged by wetting and drying, but this damage apparently did not affect germination during the test period. It could, however, be expected that such damage over prolonged periods of moisture fluctuations may eventually reduce the viable seed population, and hence germination of winterfat in the field. Booth et al. (1999) discovered significant deterioration of mitochondria in 6-month-old winterfat seeds at 20°C and 50% moisture, a relatively high water content for seeds. This deterioration did not occur at 5°C, and they attributed the deterioration at 20°C to a lack of translocation of food reserves within partially hydrated seeds with high respiration rates.

Survival and growth of winterfat seedlings can be negatively affected by desiccation, depending on seedling growth stage, and intensity and duration of desiccation. Tolerance and avoidance are mechanisms of resisting stress in

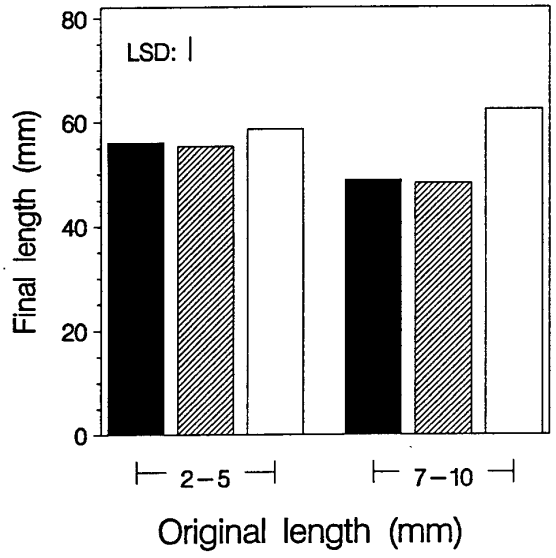

Fig. 3. Growth of winterfat seedlings that were 2–5 or 7–10 mm in length and survived 7 days of desiccation at 20°C, 30, 90, or 100% relative humidity. The final length was measured 7 days after rehydrating and incubating seedlings at 18°C in darkness. Desiccation treatments were 30 (solid bar) or 90% relative humidity (hatched bar), and control (empty bar) (100% relative humidity in sealed germination boxes). Each bar is the mean of 40 seedlings. LSD is least significant difference among means (P<0.05).

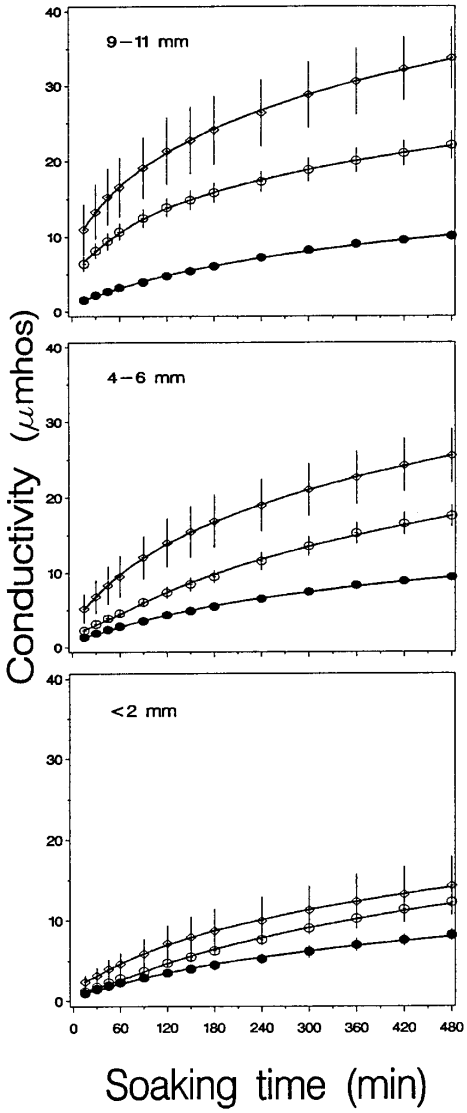

Fig. 4. Fitted regression lines for electrolyte leakage from winterfat seedlings of different lengths after desiccation at 30, 90, or 100% relative humidity. In each graph the upper, middle and lower lines are for desiccation at 100, 90 and 30% relative humidity, respectively. Each value is the mean±SE of 6 replicates. If no vertical bar is evident, SE is less than the size of the symbol. Regression equations are presented in Table 1.

plants (Levitt 1980). Results of this study indicate that desiccation tolerance in winterfat seedlings is high at early stages of growth and diminishes as growth progresses. Similar changes in desiccation tolerance were reported for *Agropyron desertorum* and *Psathyrostachys juncea* (Hassanyar and Wilson 1979), *Anastatica hierochuntia* (Friedman et al. 1981), *Glycine max* (Senaratna and McKersie 1983), *Hordeum vulgare*, and *Vigna radiata* (Hong and Ellis 1992). Electrolyte leakage measurements support the argument that collapse of enlarged cells, and membrane injury, are primary causes of increased sensitivity to desiccation (Senaratna and McKersie 1983). As soils dry, mortality of 1- to 4-day old seedlings of winterfat is high (Waddington and Shoop 1995). Thus, once desiccation tolerance is lost, winterfat seedlings must avoid stress if they are to survive. A wet seedbed for 2 days is needed for emergence and growth of winterfat seedlings that can survive subsequent drying conditions (Waddington and Shoop 1995). Germination near 0°C (Hilton 1941, Booth 1987, Bai et al. 1998a) may allow root growth before warm temperatures dry the soil surface. Winterfat seeds do not germinate in the fall in the northern reaches of northern mixed prairie; however, seeds shed during the previous fall, germinate at low temperatures in early spring (Hou and Romo 1997). Water content of the soil surface is usually high at this time (Evans and Young 1970, Booth 1992). Seedlings grow slowly at low temperatures (Hou and Romo 1997), and they may tolerate desiccation. Desiccation alone is not, therefore, likely to threaten survival of winterfat seedlings in early spring. It is possible, however, that radicles of seedlings may not be able to penetrate frozen soil, and seedlings may desiccate.

As temperatures increase and seedlings grow, their survival will be increasingly threatened by freezing temperatures (Hou and Romo 1997, Bai et al. 1998b) and desiccation. Litter or soil cover may increase seedling establishment because of high soil moisture retention (Evans and Young 1970, Springfield 1971, Fowler 1986, Cheplick and Quinn 1987). Evans and Young (1970) reported a diurnal range of relative humidity between 60 and 95% under plant litter in the field, compared to relative humidity below 30%

Table 1. Regression equations for electrolyte leakage from winterfat seedlings <2, 4–6, and 9–11 mm in length and desiccated at 30, 90, or 100% relative humidity at 20°C for 7 days. Y = electrical conductivity (μmhos), X = soaking time (15 to 480 minutes). Fitted curves are presented in Figure 4.

Seedling length	Relative humidity	Regression equation	R^2
(mm)	(%)		
<2	30	$Y= 7.48–4.15\ln X+0.85\ln X^2$	0.65
	90	$Y=11.00–6.42\ln X+1.07\ln X^2$	0.95
	100	$Y= 5.98–3.43\ln X+0.61\ln X^2$	0.93
4-6	30	$Y= 9.71–5.03\ln X+1.23\ln X^2$	0.78
	90	$Y=14.89–8.43\ln X+1.44\ln X^2$	0.96
	100	$Y= 6.46–3.65\ln X+0.67\ln X^2$	0.98
9-11	30	$Y=13.60–4.17\ln X+1.20\ln X^2$	0.70
	90	$Y= 5.84–1.65\ln X+0.69\ln X^2$	0.91
	100	$Y= 6.03–3.41\ln X+0.66\ln X^2$	0.97

during the day on bare soil. The current study indicates that chances of survival in winterfat can be substantially higher when relative humidity is within the range of 60 to 90%. Seedlings developing from seeds that germinate on, versus under litter (including diaspore aggregations), may not benefit from improved moisture conditions because they may not be exposed to high humidity and large amounts of litter can prevent radicles from reaching the soil (Fowler 1986, Booth 1987, Booth and Haferkamp 1995). Desiccation of winterfat seedlings with radicles exposed in air is detrimental, as demonstrated by 100% mortality in seedlings >10 mm in length. On the other hand, entry of the radicle into soil from diaspores on the surface may be favored by loose soil, high soil moisture, and increased heterogeneity of the soil surface (Campbell and Swain 1973). Diaspores may germinate during a 1- to 4-day period of high moisture (Waddington and Shoop 1995), but many seedlings will likely die if their roots do not reach a stable water supply.

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