

Seedbed ecology of winterfat: effects of mother-plant transpiration, wind stress, and nutrition on seedling vigor

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Abstract

The upward movement of absorbed salts within a plant is influenced by the transpiration stream. This study tested the hypothesis that transpiration by winterfat mother plants affects seedling vigor. Mature plants, growing in a greenhouse, were exposed to forced air and measurements were made on water loss from the plants, concentrations of Ca^{++} , Mg^{++} , Na^+ , and K^+ in the diaspores, and on offspring growth parameters. The diaspores produced by the plants were germinated and grown under 2 identical temperature regimes, except that 1 regime included 1 hour of dark-period freezing stress. The forced-air treatment had no detectable effect on mother plants, including no significant ($P \leq 0.05$) effect on water loss or on cation concentrations in the diaspore. However, it did significantly decrease offspring vigor. Analysis of the total test-plant population revealed significant, linear relationships between water loss and: diaspore yield, Ca^{++} and K^+ concentrations in the diaspore, seedling dry weight, and seedling hypocotyl length. Linear relationships between seedling variables and covariables provided evidence that Ca^{++} , K^+ and Na^+ influence seedling weight, moisture, and hypocotyl length. It is concluded that mother-plant transpiration, windstress, and nutrition affect offspring vigor.

Keywords: calcium, magnesium, potassium, sodium, freezing, growth model, environmental stress, seed production

"...one must become at the same time a comparative morphologist, a comparative physiologist, and an ecologist." G. Ledyard Stebbins (1974) on seedling ecology.

Germination characteristics of winterfat [*Eurotia lanata*¹ (Pursh) Moq.; *Ceratoides lanata* (Pursh) J.T. Howell], vary among genetic populations (Workman and West 1967), among locations (Wilson 1931, Asay 1959, Moyer and Lang 1976), and from year to year at a given location (Springfield 1968, 1972, Dettori et al. 1984). Nongenetic variation has been attributed to general environmental conditions (Springfield 1972), but specific cause-and-effect relationships are not well understood.

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

The influence of the mother-plant environment on seed germination and/or subsequent seedling growth has been noted for such species as winter wheat [*Triticum aestivum* variety Knox, (Riddell and Gries 1958)], plantain [*Plantago aristata*, (Stearns 1960)], and for *Ononis sicula* [a legume native to the Negev desert (Evenari et al. 1966)]. In reviewing maternal effects on seed germination, Gutterman (1980) commented on the environmental stimuli of day length, temperature, and position. He cited evidence that these stimuli affect the plant hormonal system, and subsequently the level of hormones in seeds. Poovaiah (1985) has reviewed the functions of Ca^{++} in plant cells, including the role of that ion in cellular response to external and internal (hormones) stimuli. This, and other evidence (Booth 1989), indicate that Ca^{++} , and perhaps other cations, influence seed germination.

The upward movement of absorbed salts, especially Ca^{++} , within a plant is influenced by, among other things, the transpiration stream (Biddulph et al. 1961, Mengel and Kirkby 1982, Devlin and Witham 1983). This study was conducted to test the hypothesis that transpiration by winterfat mother plants affects seedling growth by influencing cation concentrations in the diaspores. Diaspores are the seed-containing units of a plant which function in seed dispersal and in promoting the establishment and survival of the seedlings (Booth 1987). The study also provided the opportunity to separate effects on the offspring of mother-plant transpiration and mother-plant wind stress.

Methods

Plant Material

Forty seed-producing winterfat plants were collected at Cheyenne, transplanted into 7.4 liter pots, and grown in the greenhouse where daytime temperatures were 40–45° C. Aluminum foil caps were fitted over the top of the pots and around the base of the plants to reduce soil evaporation. In separate tests the foil caps reduced soil evaporation by 63% in unshaded pots, and by 74% in unshaded pots exposed to forced air treatments. The tests used a simulated shrub stem with soil at field capacity.

Beginning 8 July 1985, 20 of the 40 plants were randomly selected to be exposed once a week for 15 weeks to 8 hours of forced air (3.3 m/s). Treatment starting date was selected to avoid, as much as possible, treatment interference with seed set, and yet to be in effect throughout the period of diaspore growth and maturation. During the treatment period all pots were weighed weekly. Pots with treated plants were also weighed immediately before and after exposure to forced air. After each weighing, lost moisture was

replaced with Hoaglands solution so that nutrients would not be a limiting factor in plant growth or cation accumulation in diaspores. At diaspore maturity (Nov. 1985), diaspore yield (weight of all diaspores harvested), total aboveground plant weight, and leaf weight were obtained for each plant. Diaspores were separated from seed stalks, allowed to afterripen at room temperature for about 2 months, and stored under refrigeration (Springfield 1974) until used in 1986. Diaspores were used in seedling growth tests and were analyzed for Ca^{++} , Mg^{++} , Na^+ , and K^+ . There is some bias in this study because low producing plants did not provide enough material for analysis.

Seedling Growth

Diaspores harvested from treated and untreated plants were used to compare seedling growth under 2 temperature regimes. Each diaspore sample (100 diaspores representing 1 plant) was weighed, mounted on Cobb-Jones germination plates (Jones and Cobb 1963), then imbibed for 2 days at $0 \pm 2^\circ \text{C}$ (Booth and Schuman 1983). Germination plates and reservoirs were isolated by sample. Diaspores were cultured for 10 days in germinators at: (a) 15°C with light for 12 hours and at 5°C without light for 12 hours or (b) as in (a), but with a mid-dark cycle temperature drop to -5°C for 1 hour. Light readings at germination plate positions averaged 63 and $74 \mu\text{E/s/m}^2$ for the freezing and nonfreezing runs, respectively. Samples were rotated daily to minimize variation due to location in the germinator. Samples with 60 or fewer diaspores were randomly assigned to 1 of the 2 temperature regimes rather than splitting the available diaspores between the 2 regimes. Data were collected for each mother plant on seedling hypocotyl lengths, and on seedling dry and fresh weights. Seedling samples were oven dried at 60°C for 24 hours.

Cation Analysis

Dried samples were ground, weighed, then ashed at 550°C (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, K^+ , Mg^{++} , and Na^+ were determined on the ash digest by atomic absorption spectrophotometry.

Statistical Analysis

Analysis of variance and analysis of covariance were used to test whether cation concentration was related to water loss and to analyze the relationship between seedling variables and cation concentration in diaspores (Table 1). Analysis of variance, using data from plants represented in both freezing and nonfreezing regimes (paired analysis), compared seedling growth variables (Table 1) with respect to the forced-air treatment of mother plants and to germination temperature regimes. Covariate analysis for seedlings used all data available from each temperature regime.

The F-ratio probability value is reported as the Observed Significance Level (OSL). The term "significant" is applied throughout this paper to findings with an $\text{OSL} \leq 0.05$. However, that level is recognized as an arbitrary point on a continuous scale.

Steel and Torrie (1980) describe analysis of covariance as, using the concepts of both analysis of variance and of regression with 2 or more measured variables, where any measured independent variable is not at predetermined level (i.e., water loss). Covariate analysis has been used here to control error and increase precision of tests, to adjust treatment means of dependent variables for differences in values of corresponding independent variables, and to detect relationships between dependent and independent variables that are approximately linear. It has been particularly useful for separating effects of the forced-air treatments from water loss effects and for detecting relationships with water loss that exist across treatments and would otherwise be obscured by plant to plant variability.

A significant regression line implies that x is of value in explaining the variability in y . The amount of variation in y that is explained by x is estimated by the coefficient of determination (r^2). This coefficient is usually not reported in an analysis of covariance because the model contains factors from noncontinuous variables. For example, forced air was not a continuous variable since plants were either treated or not treated. However, in cases where treatment effects are not significant, and where the treatment sums of squares (SS_{treat}) contribute an insignificant amount to the total sums of squares (SS_{total}), a valid r^2 can be calculated for a significant regression term. This paper will report some r^2 values together with the associated ratio of treatment to total sums of squares.

Results and Discussion

Effect of Forced-air Treatment on Mother-plant Variables

Exposing mother plants to forced air did not cause significant changes in mother-plant water loss, total plant weight, leaf weight, yield of diaspores, average weight of diaspores, or cation concentrations in diaspores (Table 2). This was true even when the covariates were included in the analysis. This indicates that the measured variables were not affected by factors associated with the treatments, such as watering with Hoaglands solution. Lack of treatment differences is believed to be due to a stoma-closing response to wind by treated plants and to the variability in water loss. Water loss ranged from 3,300 to 11,200 g for the forced-air treated plants and from 5,100 to 11,800 g for the untreated plants.

Since the forced-air treatment did not induce water-loss differences between treated and untreated plants, regression analysis of variables with covariables for all plants (i.e., across both treatments) was used for testing the hypothesis that transpiration by the mother plants affected cation concentrations in the diaspores. The

Table 1. Winterfat variables and covariables used for evaluating the effects of air movement and transpiration on the cation concentration in diaspores and on offspring vigor.

Mother-plant variables	Mother-plant covariables for cation concentration	Seedling variables	Seedling covariables
Forced air by:	Water loss	Forced air on mother plant, and temperature regime,	Concentration in the diaspore of:
Water loss	Total plant weight	by:	Ca^{++}
Total plant weight	Leaf weight	Seedling dry weight	Mg^{++}
Leaf weight	Diaspore yield	Seedling moisture	Na^+
Diaspore yield		Hypocotyl length	K^+
Diaspore weight		S.D. hypocotyl length	Water loss
Concentration in diaspore of:			All combinations of above.
Ca^{++}			
Mg^{++}			
Na^+			
K^+			

Table 2. Means for mother-plant variables as affected by forced-air treatment.

Variable	Untreated	Forced air treated	OSL ¹
Water-loss (g)	6954	6777	.821
Total plant wt (g)	12.8	12.8	.969
Leaf weight (g)	4.28	3.69	.951
Diaspores (g/plant)	2.49	2.54	.951
Diaspores (mg/diaspore)	4.8	4.4	.851
Cation concentration in diaspores (ug/g)			
Calcium	6686	7493	.374
Magnesium	2296	2425	.473
Potassium	22543	21406	.139
Sodium	596	646	.473

¹Observed Significance Level

effectiveness of regression analysis as a statistical test is enhanced by the range of water loss found to exist in the total test-plant population.

Relationships between Mother-plant Variables and Covariables

Covariate analysis across treatments revealed significant linear relationships between water loss and concentrations of Ca^{++} and of K^+ in diaspores (Table 3). Calcium in diaspores increased by 0.544 ug/g, and K^+ increased by 0.352 ug/g of water used by the plant. The concentrations of Mg^{++} and of Na^+ in the diaspores were not significantly related to water loss. Water loss was also significantly related to diaspore yield and to leaf weight (Table 3). Both increased by 0.4 mg/g of water lost.

Table 3. Statistics describing significant relationships between winterfat mother-plant variables and covariables.

Variable	Covariable	OSL ¹	r ²	SS _{treat} /SS _{total} ²
Water loss	Ca^{++}	0.003	21.5	2.7
	K^+	0.027	12.5	5.4
	diaspore yield	0.012	16.5	0.1
	leaf weight	0.008	18.4	1.6
	Mg^{++}	0.010	17.2	1.4
Total plant weight				

¹Observed Significance Level

²Values indicate the degree of influence on r² by noncontinuous factors of the covariance model.

Diaspore yield is related to the amount of carbon assimilated by the seeds and to the number of diaspores produced. The relationship between water loss and yield is significant because transpiration and yield are both related to photosynthesis. Since green diaspore bracts contain stomata (personal observation), these bracts, and other axillary bracts and leaves associated with developing diaspores, add to the photosynthetic capacity of the plant, to water loss, and to the significant relationship between water loss and yield. Also, phloem sap is probably 75 to 95% water (Salisbury and Ross 1969, Biddulph 1969, Hall and Baker 1972) and diffusion of water through diaspore epidermis may have contributed to water loss. Potassium enhances translocation of assimilates and is the most abundant cation in the phloem (Mengel and Kirkby 1982). The concomitant linear relationships of yield and K^+ with water loss is indicative of the link between transpiration, photosynthesis/translocation, and yield.

Total plant weight, leaf weight, and diaspore yield were used in covariate analysis of cation concentrations in diaspores. Usually the greater the plant or leaf weight the lower the diaspore cation concentration, indicating a dilution effect from plant material.

This relationship was significant between total plant weight and Mg^{++} (Table 3). Magnesium decreased by 39 ug/g of plant material. The relationship between Mg^{++} and leaf weight was not significant (OSL = 0.094) and there were no significant relationships between diaspore weight and the concentration of any cation.

Effect of Forced-air Treatment on Seedling Variables

Offspring were significantly affected by the forced-air treatment of mother plants. Analyzed over both temperature regimes (using only paired data), the forced-air treatment resulted in a significant decrease in the dry weight and in the moisture content of seedlings. The OSLs for these variables were not improved by covariate analysis (Table 4). Also, the forced air probably (OSL = 0.109) decreased hypocotyl length (Table 4). The probability that the observed hypocotyl decrease was real is strengthened by the lack of treatment differences (OSL = 0.329) for the standard deviations of hypocotyl length (Table 3).

Table 4. Winterfat seedling characteristics as affected by forced-air treatment of mother plants.

Variable	Untreated	Forced air treated	OSL ¹
Seedling dry weight (g)	0.1472	0.1172	0.004
Seedling moisture (g)	1.4882	1.1066	0.002
Hypocotyl length (mm)	41	37	0.109
SD hypocotyl length (mm)	12.846	12.194	0.329

¹Observed Significance Level

Covariate analysis made no improvement in the OSL of treatment means with respect to hypocotyl length under the freezing regime; under the nonfreezing regime, treatment means adjusted for Na^+ resulted in an OSL of 0.047. Further improvement was realized by using the best combination: $\text{Ca}^{++} + \text{K}^+ + \text{Na}^+ + \text{water loss}$ (OSL = 0.017). This indicates the importance of these factors to seedling growth. Since the forced-air treatment was not severe enough to produce real differences in water loss or in concentrations of cations in diaspores, the detrimental effects of forced-air on the offspring must be ascribed to factors not measured.

The most likely reason for reduced vigor of offspring from treated mother plants is lower seed mass (as opposed to diaspore mass). This could result from interrupted photosynthesis if stomata closed during forced-air treatments. Although no difference was detected between treatments in the mean weight per diaspore (Table 2), it is likely that seed coverings, which are relatively inexpensive for the plant to produce, hid differences in seed mass. Lack of experimental material precluded measurement of seed mass.

The threshold for wind-induced stoma closure is probably not uniform among winterfat ecotypes. Plants collected from Sterling, Colo. (1,220 m), Cheyenne, Wyo. (1,890 m), and Sheep Mountain near Laramie, Wyo. (2,440 m), averaged 18,700, 14,800 and 11,400 g of water loss, respectively, under a forced-air treatment similar to that described for this study (Booth, unpublished data). Perhaps adaptation to higher, windier habitats was accomplished by changes in the balance between photosynthetic potential and water conservation. We may speculate that a breeze which closes stomata and interrupts transpiration and photosynthesis in the Sheep Mountain or Cheyenne ecotypes might have no effect on stomata in plants from Sterling.

Analysis of covariance for seedlings, which used all the data available from each temperature regime, will be discussed for the freezing and nonfreezing regimes with respect to each variable. The linear models showing significant relationships with growth parameters differ by temperature regime (Table 5). This difference might be indicative of real phenomenon, but could also be the

Table 5. Effects of a 1-hour diurnal freeze on linear models¹ of winterfat seedling variables with covariables.

Variable	Model without freeze	OSL ²	Model with freeze	OSL
Dry weight	K ⁺ Na ⁺ water loss	0.010	Ca ⁺⁺ +water loss	0.035
Moisture	Ca ⁺⁺ +Mg ⁺⁺ +Na ⁺	0.008	Ca ⁺⁺ +water loss	0.019
Hypocotyl length	Ca ⁺⁺ +K ⁺ +Na ⁺ water loss	0.038	Mg ⁺⁺	0.145

¹These are the best models for each variable as judged by the OSL of the models.

²Observed Significance Level

result of nonlinear responses caused by the abrupt temperature changes in the freezing regime. Water loss was found to be an important covariable with all seedling variables. Its significance in these analysis appears best explained by assuming (1) that it is correlated with Ca⁺⁺ concentrations in the diaspore, and (2) that it is an indirect measure of photosynthesis. The latter is a valid assumption under arid conditions since leaf water potential has predominate control over stomatal aperture.

Seedling Weight

Covariate analysis revealed a significant (OSL = 0.039), positive, linear relationship between seedling dry weight under the nonfreezing temperature regime, and water loss by the mother plant. Since carbon fixation by a 10-day-old seedling is relatively small, seedling dry weight is primarily a function of the original seed weight. Therefore it is not surprising, given the significant relationship between water loss and diaspore yield, that water loss was related to seedling dry weight. The linear relationship was improved when the K⁺+Na⁺ concentrations in the diaspore were considered in the model with water loss (OSL = 0.010 – Table 5). Potassium accounts for most of this improvement in the significance level. These findings support the interpretation that the forced-air treatment lowered seed mass by interrupting photosynthesis and the translocation of photosynthate. Under the freezing regime Ca⁺⁺ became important, and Ca⁺⁺ + water loss was the only covariable combination that was significantly (OSL = 0.035) related to seedling dry weight.

Seedling Moisture

Diaspore concentrations of Ca⁺⁺ and of Na⁺ were most closely correlated with seedling moisture; the covariable combination Ca⁺⁺+Mg⁺⁺+Na⁺ gave the best linear relationship under the nonfreezing regime (OSL = 0.008). The importance of Ca⁺⁺ to seedling moisture content is explained by the known relationship between Ca⁺⁺ and membrane integrity (Mengel and Kirkby 1982, Poovaiah 1985). The importance of Na⁺ in the seedling-moisture model is supported by the findings of Booth (1989) and by the work of others (El-Sheikh and Ulrich 1970, Romo and Haferkamp 1987, Eddleman and Romo 1987), who have shown in other species of Chenopodiaceae that Na⁺ has a positive effect on the water regime of the plant. In this model, both Ca⁺⁺ and Na⁺ were positively related to seedling moisture, while Mg⁺⁺ was negatively related. Under the freezing regime Ca⁺⁺ + water loss was the best model (OSL = 0.019).

Hypocotyl Length

The best linear relationships among single covariables were with water loss (OSL = 0.059) and with Na (OSL = 0.169); the best combination was, Ca⁺⁺+K⁺+Na⁺+water loss. The OSL of the combination model was 0.038 (Table 5). Under the freezing regime, Mg was the only covariable (single or combination) that showed a linear relationship with hypocotyl length (OSL = .145). The relationship was negative.

Standard Deviations of Hypocotyl Length

Sodium was significantly related to standard deviations of

hypocotyl lengths (OSL = 0.024), and the best combination, Na⁺+water loss was a slightly better model with OSL = 0.022. This indicates that the concentration of Na⁺ in the diaspore and water loss from the mother plants account for a significant amount of the variation in hypocotyl length. It adds to the evidence of this study, and others (Hilton 1941, Booth 1989), that Na⁺ concentrations in the seed influence seedling moisture and hypocotyl length. Under the freezing regime only water loss was significant (OSL = 0.053).

Conclusions and Recommendations

Increased transpiration, as indicated by water loss, increased diaspore concentrations of Ca⁺⁺ and K⁺ but not of Na⁺ and Mg⁺⁺. Evidence cited by Mengel and Kirkby (1982) support the conclusion of a direct relationship between transpiration and the Ca⁺⁺ concentration in the diaspores. The relationship between K⁺ concentration in the diaspores and transpiration may be indirect, such as the fact that both transpiration and K⁺ concentration are related to photosynthesis and to translocation of photosynthate. It may be argued that the significant relationships of Ca⁺⁺ and K⁺ concentrations with transpiration are due to the fact that these cations were added in proportion to water loss. However, Na⁺ and Mg⁺⁺ were also added in proportion to water loss. Therefore, it is concluded that the volume of water transpired by winterfat mother plants significantly affected seedling vigor by influencing, among other things, the diaspore concentration of Ca⁺⁺.

Wind stress on winterfat mother plants which occurred after seed set decreased offspring vigor. This occurred at a relatively mild, but steady, wind speed and is assumed to be due to an interruption of photosynthesis when stomata closed. The negative effects of wind stress were seen in reduced seedling dry weights, moisture, and hypocotyl lengths.

Analysis of the relationships between seedling variables and covariables has provided specific evidence of the importance of Ca⁺⁺, K⁺, and Na⁺ to winterfat seedling growth. These findings are an indication to seed producers, seed collectors, and to students of seedling growth, of the importance of mother plant nutrition with respect to these cations. Producers may wish to pay particular attention to soil Na⁺, since this cation accounted for most of the variability in seedling hypocotyl length. The study also raised questions about the role of Mg⁺⁺, particularly during seedling freezing stress.

The maintenance of plant transpiration emerged as the single most important factor in seed production. Not only is transpiration a factor in moving Ca⁺⁺, and possibly K⁺, into the diaspore, but also interruptions to transpiration, as in stoma-closing responses to wind, will usually decrease yields (Waggoner 1969, page 356). For this reason seed producers and collectors may wish to avoid winterfat ecotypes that readily close their stoma, or, if wind tolerant ecotypes are needed, that seed be produced or collected in protected places.

A predictive model of early seedling growth will have at least 3 major components: genetic effects, maternal effects, and effects of the seed environment during dormancy and early growth. If we apply to winterfat Gutterman's (1980) list of environmental stimuli that may cause maternal effects (day length, temperature, and seed position), then to the list can be added transpiration, wind stress, and nutrition.

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