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Imbibition temperatures affect bitterbrush seed dormancy and seedling vigor

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Bitterbrush first-year seedling survival is low. To determine whether imbibition temperatures affected seedling vigor, I compared post-imbibition seed weight, germination, and early growth among untreated, thiourea-treated, and cool-moist-treated seeds from three collections. Seedling axial lengths from untreated seeds averaged 28 mm among all imbibition temperatures. This compared to 31 mm from thiourea-treated seeds, 68 mm from seed held at 5°C for 14 days, and 118 mm from seeds held at 2°C for 28 days. There was no imbibition temperature for untreated or thiourea-treated seeds that compensated for the lack of a cool-moist treatment. Seed treatments or seedbed conditions which fully remove dormancy and reduce dormant-seed respiration appear likely to increase seedling survival during the first growing season.

Keywords: seed-weigh; germination; seed testing; seedling survival; re-vegetation

Introduction

Bitterbrush (*Purshia tridentata* DC.) is a deciduous or evergreen, intricately branched shrub of the rose family occurring in North America from California eastward through the Rocky Mountains and from British Columbia south to Baja California. It is particularly valued for its contribution to the diets of wild herbivores and rangeland livestock. Its seeds are dormant and the dormancy mechanism is not well understood (Young & Evans, 1976, 1981; Meyer & Monsen, 1989; Booth, 1992). The seed requires 14 or more days of cool-moist conditions to germinate (Young & Evans, 1976; Meyer & Monsen, 1989) or germination can be induced with a 1–3% solution of thiourea (Pearson, 1957; Young & Evans, 1981).

Pearson (1957) acknowledged that seedling emergence and survival from spring sowing of thiourea-treated seeds was 'erratic', and Everett & Meeuwig (1975) observed that such seedings were often unsuccessful, though they did not speculate why. Others (N. Shaw, pers. comm.) report the practice can be used successfully.

Cool-moist treatments can also produce variable results. Booth & Morgan (1993) suggested residual seed dormancy after cool-moist treatment might explain differences in post-germination growth, and Dennis (1994) has commented that in general

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'... embryo dormancy is a quantitative phenomenon; growth of ... partially dormant seeds is often sluggish compared with that of chilled embryos'.

Thiourea is a carcinogen and not likely to be used for future field seedings; however, by comparing the imbibition-temperature effects on dormancy and seedling vigor among untreated, thiourea-treated, and cool-moist-treated seeds, it was aimed to clarify the interactions between bitterbrush seed dormancy, seedling vigor, and imbibition temperature. Seed and seedling vigor are conditions of active good health that permit germination and early growth to proceed rapidly under a wide range of conditions (Justice & Bass, 1978; Young & Young, 1986). It was hypothesized that imbibition temperature would influence growth of bitterbrush seeds and, that there would be at least one imbibition temperature where growth of thiourea-treated seeds would not be different from growth of cool-moist-treated seeds.

Materials and methods

Plant material

I tested three accessions of bitterbrush from the western U.S. and used a 20-seed count in each experimental unit. All accessions were supplied by the same commercial seed collector. A Utah source, lot # 9–2001, was received 23 January 1991. The bag weight for 20 seeds was 436 ± 22 mg (mean ± SD). The lot had a tetrazolium chloride test (TZ) of 98%. A California source, stock #309, lot # XS-180, was received 18 December 1991, TZ = 85%, and the 20-seed bag weight was 429 ± 36 mg. The third lot was an Oregon collection, stock #473, Lot # 5834, which was also received 18 December 1991. The TZ = 93% and the 20-seed bag weight was 492 ± 44 mg.

Treatments used in experiments A and B

Thiourea

Seeds treated with thiourea were soaked in a 3% solution for 30 minutes at room temperature (Young & Evans, 1981), dried at room temperature for at least 24 h, then counted into sample groups and weighed. Untreated seeds were counted into sample groups and weighed directly from the bag.

Imbibition temperatures

Thiourea-treated and untreated seeds were imbibed on slant boards (Jones & Cobb, 1963) at 5, 10, 15, 20, 25, 30, 35, and 40°C for 4 days for experiment A. Cool-moist-treated seeds were held on slant boards at 5°C for 14 days, or at 2°C for 28 days (Young & Evans, 1976) for experiment B. Imbibition temperature means the temperature at which water was initially absorbed by the seed.

Procedure used in experiments A and B

Groups of 20 seeds were weighted to 0·01 mg, dried at 35°C for seven days, re-weighed, and the amount of moisture lost during drying calculated. This procedure was repeated for samples of thiourea-treated seeds. Seeds were then held in a closed chamber above water (humidity chamber) at 2°C until average seed moisture exceeded 20% as determined by periodic weighing. Seed moisture after humidification was 22·0, 23·9, and 23·5% for the California, Oregon, and Utah accessions. Humidification time was 6 days for all accessions. This equilibrated seed moisture and reduced the possibility of imbibitional injury (Pollock, 1969; Vertucci & Leopold, 1984). The seeds were then mounted on slant boards (Jones & Cobb, 1963) using 10 seeds per board. After 4 days of imbibition at treatment temperature (experiment A) or after cool-moist treatment (experiment B), one seed group at each temperature was removed, dried as previously, and weighed. The remaining seeds were placed at 20°C in a dark germinator for 14 days. On days 10, 12 and 14 the axial length of seedlings was measured with a digitizing tablet and used as an indication of seed and seedling vigor (Booth & Griffith, 1994). Since day 14 represented maximum growth for all treatments and accessions, only those data were used in the analysis.

Experimental design used in experiments A and B

The thiourea-treated seeds were tested in one experiment and seeds held at cold-moist conditions in a second experiment. This allowed a precise comparison among the more similar treatments, yet allowed between-experiment comparisons of dissimilar treatments. The dependent variables in both experiments were dry-weight loss during imbibition (experiment A: 5 to 30°C only), germination percentage, and seedling length after 14 days. Seed groups were randomly assigned to treatments. The order of temperature treatments was also randomly assigned since not all temperatures could be tested at one time. Seed collections were tested together. The experiments were repeated three times in succession. The experimental designs were randomized complete blocks, with time as the blocking factor and the sequence of seed treatments random within blocked time periods. Analysis of variance (ANOVA & GLM, SAS, 1992) were used to test for significant differences among dependent variables. Germination and seedling-axial-length data were analysed separately by treatment because of the large differences in germination and numbers of seedlings among thiourea treatments.

Experiment C

The experiments described above did not answer: (i) what is the effect on seedling growth of combining thiourea and cool-moist treatments, and (ii) what effects does the Association of Official Seed Analysts (AOSA) (1990) germination protocol for bitterbrush have on seedling growth? The AOSA (1990) protocol is for seeds to be imbibed at 20 to 22°C followed by a 28-day wet pre-chill at 2°C. It was questioned whether dormant bitterbrush seeds should be imbibed at warm (20 to 22°C), or at cold (2 to 5°C) temperatures prior to quality testing. For these reasons experiment C was conducted using the following seven treatments:

(i) Thiourea (seeds were treated as described above).
(ii) Thiourea + cool-moist treatment at 2°C for 28 days.
(iii) Thiourea + cool-moist treatment at 5°C for 14 days.
(iv) Cool-moist at 2°C for 28 days.
(v) Cool-moist at 5°C for 14 days.
(vi) Soak at 20°C for 24 h + cool-moist treatment at 2°C for 28 days.
(vii) Soak at 20°C for 24 h + cool-moist treatment at 5°C for 14 days.

As in experiments A and B, the California, Oregon, and Utah accessions were tested with 20 seeds per experimental unit and with three replications. The experimental design was a randomized complete block with time as the blocking factors. Seed treatments were timed so that all seeds of a replication were incubated together using the same incubation conditions and procedures as in earlier experiments. Seeds were

Table 1. *Effect of imbibition temperature on dry weight loss after 4 days of imbibition by untreated and thiourea-treated bitterbrush seeds. Data are averaged across the Utah, California, and Oregon accessions*

	Weight loss ± SD	
Temperature (°C)	Untreated (mg/20 seeds)	Thiourea (mg/20 seeds)
5	21 ± 17	17 ± 6
10	28 ± 6	60 ± 49
15	47 ± 34	68 ± 57
20	44 ± 7	49 ± 12
25	58 ± 9	54 ± 8
30	58 ± 7	72 ± 48

incubated for 15 days and axial length measured with the digitizing tablet (Booth & Griffith, 1994). Axial lengths were analysed with a one-way AOV for each accession and treatments separated using LSD.

Results and discussion

The effect of thiourea and imbibition temperature on post-imbibition seed dry-weight

Mean dry-weight loss (DWL) during 4 days of imbibition varied by imbibition temperature ($p < 0{\cdot}001$), and by an accession × thiourea-treatment interaction ($p = 0{\cdot}015$). The least DWLs were at 5°C and the greatest losses were at 30°C (Table 1).

The accession × treatment interaction appears due to the response of the Oregon accession which averaged 38 ± 19 (mean ± SD) mg/20 seeds DWL from the untreated seeds, and 68 ± 48 mg/20 seeds from thiourea-treated seeds. This compares to DWLs of 45 ± 19 and 40 ± 19, and 46 ± 28 and 49 ± 38 mg/20 seeds for the Utah and California accessions respectively.

Possible reasons for DWL include exudation during early imbibition, and seed respiration. Pre-treatment humidification and gradual hydration from the slant boards (as opposed to hydration through partial immersion) are believed to significantly reduce exudation due to imbibitional injury (Vertucci & Leopold, 1984; Spaeth, 1986). Therefore, the most likely reason for weight loss was respiration.

Dormant seeds respire. Bewley & Black (1982, p. 200–204) review the evidence that oxygen uptake is similar among germinable and dormant seeds of wild oat (*Avena fatua* L.) and lettuce (*Lactuca sativa* L.). Booth & Sowa (submitted) found no difference in CO_2 evolution from imbibed-but-dormant and germinating bitterbrush seeds. Therefore, the differences in DWLs appear due to a correlation between seed respiration and imbibition temperature.

A small, but measurable loss in seed weight occurred as a result of treating California seeds with thiourea. This did not influence the analysis of imbibition effects since the baseline seed weight was taken after treatment with thiourea and before the 4-day imbibition period.

The effect of cool-moist treatment on post-imbibition seed dry-weight

Dry weight loss for seeds held at 5°C/14 and 2°C/28 days was 37 ± 7 and 35 ± 4 mg/20 seeds. The difference is not significant ($p = 0{\cdot}474$). There were no differences

Table 2. *Germination percentage of untreated and thiourea-treated bitterbrush seeds as influenced by accession. Means are averaged across imbibition temperatures. The number of observations for each mean is 24 20-seed groups*

Accession	Germination percentage ± SD	
	Untreated	Thiourea
Utah	4 ± 7	87 ± 13
California	2 ± 5	74 ± 18
Oregon	10 ± 11	75 ± 17

by accession ($p = 0{\cdot}678$), nor was the interaction significant ($p = 0{\cdot}399$). Weight losses by accession were; California = 37 ± 4, Oregon = 37 ± 8, and Utah = 34 ± 4 mg/20 seeds. Overall, DWL averaged 36 mg/20 seeds.

Germination of untreated and thiourea-treated seeds

Data for untreated seeds at imbibition temperatures above 15°C contained many zeros, so the AOV was limited to the 5–15°C treatments. Mean germination percentage of untreated seeds ranged from < 1 to 28%, and varied by accession ($p = 0{\cdot}001$) and by temperature ($p = 0{\cdot}005$). The accession × temperature interaction was not significant ($p = 0{\cdot}489$).

Among accessions, the Oregon source was the least dormant (Table 2), having some germination at all temperatures tested. It also had over 20% germination of untreated seed at 5 and 10°C imbibition temperatures, whereas the other collections had no untreated seed germinate greater than 15% for any of the imbibition temperatures (data not shown).

The trend among all accessions for untreated and thiourea-treated seeds was toward greater germination at the colder imbibition temperatures (Table 3). Germination of thiourea-treated seeds ranged from 56 to 91%, and seeds from all accessions had better

Table 3. *Germination percentage of untreated and thiourea-treated bitterbrush seeds as influenced by imbibition temperature. Means are averaged across the Utah, California, and Oregon accessions. The number of observations for each mean is 9 20-seed groups*

Temperature (°C)	Germination percentage ± SD	
	Untreated	Thiourea
5	14 ± 13	88 ± 8
10	16 ± 10	88 ± 9
15	3 ± 5	91 ± 5
20	<1 ± 2	86 ± 12
25	4 ± 7	83 ± 9
30	1 ± 2	73 ± 9
35	1 ± 2	63 ± 19
40	<1 ± 2	56 ± 21

Table 4. *Germination percentage of Utah, California, and Oregon accessions of bitterbrush seeds held at 5°C for 14 days or at 2°C for 28 days. The number of observations for each mean is 3 20-seed groups*

Accession	Germination percentage ± SD	
	5°C/14 days	2°C/28 days
Utah	33 ± 10	82 ± 8
California	18 ± 3	83 ± 13
Oregon	47 ± 12	73 ± 10

than 70% germination. The accession × temperature interaction for thiourea-treated seeds was not significant ($p = 0{\cdot}450$).

Germination of cool-moist treated seeds

The 2°C/28-day treatment averaged 79 ± 10% germination, significantly ($p = 0{\cdot}001$) greater than the 33 ± 15% from the 5°C/14-day treatment. There was no difference among accessions (Table 4).

The effect of imbibition temperature on axial length of untreated seeds

The mean axial length for untreated seeds across all accessions and imbibition temperatures was 28 mm (76 observations from 2840 seeds). Seeds imbibed at 5, 10 and 15°C appeared to have greater axial length than seeds imbibed at warmer temperatures ($p = 0{\cdot}074$), but the number of observations for treatments above 15°C was low.

The effect of imbibition temperature on axial length of thiourea-treated seeds

The mean axial length for thiourea-treated seeds, across all accessions and imbibition temperatures was 31 mm (1006 observations from 2840 seeds). Although the accession × imbibition temperature interaction was significant ($p \leq 0{\cdot}005$), the response pattern (Fig. 1) suggests the overall mean can be used as a general reference point for axial elongation from thiourea-treated seeds in this study. Accession responses were different but generally followed similar trends, although growth from the Oregon seeds, the least dormant of the accessions, varied less by imbibition temperature than did the other accessions (Fig. 1). Maximum, or near maximum, axial growth occurred after imbibition at 30°C. This does not seem to have resulted from faster germination since all treated seeds germinated in less than 2 days for all temperatures except 35 or 40°C (data not shown).

A curious fact is that the greatest germination of thiourea-treated seeds occurred at 15°C (Table 3); and, the greatest growth of these seeds was measured from Utah and California seeds imbibied at 30°C (Fig. 1). That 15 and 30°C are optima temperatures is evident in Table 1 (untreated , 15°C; thiourea-treated, 15 and 30°C), Table 2 (thiourea-treated, 15°C), and Fig. 1. While this is the first report of this phenomenon in bitterbrush, the occurrence of biological anomalies near 14 to 16°C, and at 15°C increments thereafter (within the range of active metabolism), has been reported in at

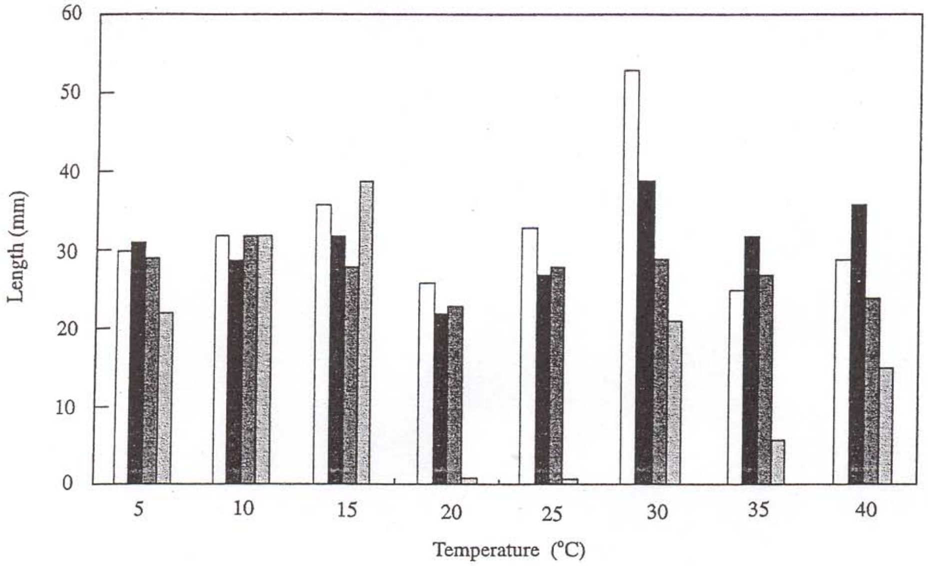

Figure 1. Mean axial length by imbibition temperature for all untreated, and by accession for thiourea-treated, bitterbrush seeds: □, Utah; ■, Califernia; ▩, Oregon; ▤, all untreated

least 25 papers and for a variety of plant and animal species (Drost-Hansen & Singleton, 1992*a*)

The cause of biological anomalies at 15°C increments has been attributed to changes in the physical properties of water when it is adjacent to surfaces (Clegg & Drost-Hansen, 1991; Dorst-Hansen & Singleton, 1992*a,b*). The layer of water molecules is referred to as vicinal or interfacial water (not to be confused with chemical 'bounded' water directly on the surface) and within a cell includes water associated with cell membranes, macromolecules (including enzymes), cell ultra-structure, and cell metabolites. Vicinal water has been found to exhibit thermal anomalies at 15°C intervals, but no direct cause and effect has been demonstrated between the thermal anomalies of vicinal water and the biological anomalies that occur at comparable temperatures (Clegg & Drost-Hansen, 1991; Drost-Hansen & Singleton, 1992 *a,b*).

If the physical anomalies of vicinal water are the cause of the biological anomalies that occur at comparable temperatures, then the increases in germination and growth observed for bitterbrush at 15 and 30°C were (a) the result of disrupting a competitive metabolic inhibitor, or (b) caused by a switch in metabolic pathways. Since there was an increase in germination or growth at both 15 and 30°C, I favor the speculation that vicinal water anomalies at 15 and 30°C reduced inhibitor-substrate binding during the 15 and 30°C imbibition-temperature treatments, and this led to an increase in germination and growth at those temperatures relative to other treatment temperatures.

The effect of cool-moist treatment on axial length

The seeds held at 5°C/14 and 2°C/28 days had radicles which averaged at 68 and 118 mm ($p < 0{\cdot}001$). Axial length was not different among seed collections and the mean axial length across accessions and cool-moist temperatures was 104 mm (202 observations from 360 seeds). Considering the lack of an observed difference in dry weight after cool-moist treatment (35 *vs.* 37 mg/20 seeds), the difference in axial length may indicate a lingering influence of seed dormancy on growth of seeds held at 5°C. That agrees with the earlier speculation by Booth & Morgan (1993) that residual dormancy may influence seedling growth, and with Dennis (1994) that embryo dormancy is quantitative.

Experiment C

Cool-moist treatment at 2°C/28 days produced the greatest axial length for the Utah and California accessions, and ranked second to the 5°C/14-day treatment for the Oregon accession (Table 5). Thiourea (only) consistently produced the least growth. The soaking treatments (AOSA 1990) were not different to the optimum for the California accession, but for the other accessions they ranked significantly lower than the two cool-moist treatments that did not use the soak (Table 5).

Implications of results

Imbibition temperature had a significant influence on the growth of thiourea-treated and untreated seeds, and also on post-imbibition seed weight and germination; however, there was no imbibition temperature at which the growth of thiourea-treated seeds was equal to that of cool-moist-treated seeds. The seed treatments used in this study, for which there were more than 20 observations, produced seedling axial-length means which ranged from 22 mm (Calif., Thiourea, 20°C) to 152 mm (Calif., cool-moist at 2°C, Table 5). Thiourea induced germination, but post-germination growth was, as Dennis (1994) observed, 'sluggish' compared with that of 'chilled' seeds.

The differential performance of untreated, thiourea-treated, and the cool-moist-treated seeds, the occurrence of growth optima at 15 and 30°C for untreated and thiourea-treated seeds, and the rankings of thiourea treatments in Table 5, imply that growth from thiourea-treated seed was inhibited by a chemical factor of dormancy and by significant DWLs during imbibition. To a lesser extent, the same is true for other treatments that produced axial lengths significantly less than those of the first-rank treatments. Dormancy and DWLs limited post-germination growth; and, because seedlings must maintain root growth ahead of the drying front from the soil surface, dormancy and DWLs can also limit stand establishment.

Conclusions and recommendations

No reason was found to reject the hypothesis that imbibition temperature influences seedling vigor as measured by early growth of bitterbrush seeds. There was a significant influence on both germination and seedling growth, and this extended to the current AOSA (1990) bitterbrush germination protocol. The protocol should be changed, calling for seeds to be imbibed at 2°C, rather than 20 or 22°C (AOSA 1990).

The hypothesis that there is an imbibition temperature where seedling growth of thiourea-treated seeds is not different from growth of cool-moist treated seeds is rejected. Seeds held at 2°C for 28 days repeatedly had much greater axial length than did any thiourea-treated seeds or seeds treated with thiourea + cool-moist conditions.

Untreated and thiourea-treated seeds had germination and growth optima at 15 and 30°C which may suggest reduced inhibitor-substrate binding at those temperatures. Also, the differences in axial lengths of seedlings among treatments suggest a residual effect of dormancy on post-germination growth and an effect from DWLs during warm-temperature imbibition.

Table 5. *Mean seedling axial length by treatment after 15 days incubation of Utah, California, and Oregon bitterbrush seeds, and treatment means averaged across accessions. The number of observations for each mean is indicated in parentheses. The germination percentage is equal to the number of observations divided by 60*

Treatment description	California			Oregon (mm)			Utah			Mean
Moist @ 2°C/28 days	(52)	152	a	(30)	125	a	(44)	139	a	141
Moist @ 5°C/14 days	(21)	129	b	(16)	137	a	(18)	129	a	131
Soak 20°C/24 hours + moist @ 5°C/14 days	(16)	135	ab	(17)	71	b	(15)	68	bcd	91
Soak 20°C/24 hours + moist @ 2°C/28 days	(41)	136	a	(32)	41	c	(35)	76	bc	88
Thiourea + moist @ 2°C/28 days	(38)	104	c	(30)	54	bc	(31)	83	b	82
Thiourea + moist @ 5°C/14 days	(29)	76	d	(17)	60	b	(23)	56	cd	66
Thiourea	(46)	57	e	(28)	38	c	(33)	47	d	49

Means followed by the same letter within columns are not significantly different at $p \leq 0{\cdot}05$ using LSD.

It is concluded from these findings that stand establishment can be increased by: (i) sowing bitterbrush in late fall or early winter since seeds sown too early are at risk of imbibing at warm temperatures; (ii) mixing vermiculite with the seed to reduce seed drying in the soil and promote dormancy removal (Booth, 1980); or (iii) holding moist seeds at 2°C for 28 days, then sowing in spring by fluid drilling (Booth, 1985). These methods offer the most logical means of increasing stand establishment because they increase post-germination root elongation and therefore, the number of seedlings capable of surviving the first growing season.

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