AN ABSTRACT OF THE THESIS OF

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Title: The Influence of Certain Environmental and Edaphic Factors on Germination and Emergence of *Bromus tectorum* L.

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Dr. Arnold P. Appleby

The influence of certain environmental and edaphic factors on the germination and emergence of downy brome (*Bromus tectorum* L.) was investigated in the laboratory. A preliminary study was conducted to determine the osmotic stability of mannitol and polyethylene glycol 20,000 (PEG) solutions, which are commonly used to simulate water stress in seed germination studies, and to compare osmotic versus matric potential effects on the germination of winter wheat (*Triticum aestivum* L.). Lacking a weed seed source of known genetic uniformity and high percentage germination, wheat, which has both of these traits, was used as the test plant. Solutions of mannitol, PEG, and KCL (standard), with water potentials ranging from -3.5 to -18.0 bars, were incubated at 10, 20, and 30 C and analyzed periodically for water potential using thermocouple psychrometry. In addition, percentage and rate of germination of wheat seeds placed in moist soil or in 27-day-old or freshly prepared solutions of mannitol and PEG were compared. The osmotic

potential of the different mannitol solutions and the -9.1 and -17.4 bar PEG solutions did not change with time. However, the osmotic potential of the -4.0 and -6.4 bar PEG solutions decreased about 1.0 bar. Percentage and rate of germination of winter wheat was the same in the 27-day-old and freshly prepared mannitol and PEG solutions; but at equal potentials, the germination rate was most rapid in the mannitol solutions. Wheat emergence rate from watered soil was linearly related to germination rate in PEG, but not mannitol solutions. Hence, the slight instability of PEG solutions appears to be of no biological consequence in seed germination studies.

The interactive influence of soil matric potential and temperature on the percentage of downy brome seedling emergence was determined using soil ranging in matric potentials from -2 to -16 bars, and incubated at alternating and constant mean temperatures from 5.1 to 20 C. The interactive effects of soil bulk density, ranging from 0.9 to 1.3 g $cm^{-3}$, and soil matric potentials, from -2 to -13 bars, on the percentage of seedling emergence was also examined.

Reductions in soil matric potential markedly reduced the percentage of emergence. Overall, emergence was better at constant than at alternating temperatures. At higher matric potentials, downy brome emerged faster at warmer temperatures, while at very low matric potentials the percentage of seedling emergence was least restricted at

cooler temperatures. Cold soil temperatures markedly reduced emergence at all levels of soil moisture. Soil matric potentials did not affect the percentage of emergence of seedlings grown from seed lots harvested during climatologically diverse years. Emergence, but not germination, was inhibited by increased levels of soil compaction. No significant soil compaction x moisture interaction was observed as measured by final seedling emergence.

Under rangeland and wasteland conditions, the successful seedling establishment of downy brome is probably most limited by warm, dry soils or very cold soils (subzero temperatures for part of the day). All other moisture-temperature conditions appear intermediate to these two extremes in effect on establishment. Under cultivated field conditions soil compaction appears to be the major factor controlling successful seedling establishment.

The effect of high-temperature on overcoming initial postharvest dormancy, and the possible occurrence of natural endogenous germination rhythms in downy brome seeds were investigated. Afterripening temperatures from 0 to 50 C, for periods of 0 to 28 days, had little effect on downy brome germination in petri dishes at 15 and 20 C incubation temperature. However, at 30 C germination temperature, the percentage of germination was significantly increased by short periods of afterripening at 50 C. Similar results occurred at 20 to 40 C afterripening after 14 to 28 days exposure. In general, high-temperature afterripening

conditions (40 to 50 C) initially increased downy brome germination at 30 C incubation temperature, with prolonged exposure tending to decrease germination. No endogenously controlled germination rhythms were observed in downy brome seeds.

# The Influence of Certain Environmental and Edaphic Factors on Germination and Emergence of *Bromus tectorum* L.

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III and IV. "The Influence of Soil Moisture, Temperature, and Compaction on the Germination and Emergence of *Bromus tectorum* L." and "Influence of Afterripening Temperature on the Germination of *Bromus tectorum* L." These two chapters were prepared using Weed Science manuscript format, and will be submitted for publication in Weed Science.

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# The Influence of Certain Environmental and Edaphic Factors on the Germination and Emergence of *Bromus tectorum* L.

## I. INTRODUCTION

Seed germination and emergence under undisturbed and cultivated field conditions is extremely complex. A multitude of environmental effects, soil physical and biological factors, and inherent seed characteristics ultimately determine the success or failure of seedling establishment.

Downy brome (*Bromus tectorum* L.), an annual grass widespread throughout Western rangelands, wasteways, and cultivated fields, can be a desirable forage or a serious weed pest. The ubiquitous nature of downy brome indicates it has the ability to adapt easily and competitively to a wide range of ecological conditions. Since the reproduction of this species is solely by seed it is essential to know the requirements for germination of the seeds in order to (a) better understand its ability to adapt to many ecological conditions, and (b) to develop new cultural and chemical control methods. Two major components of any ecosystem that influence seed germination are moisture and temperature. A third factor of importance in cultivated ecosystems is soil compaction.

In order for seed germination to occur when ecological conditions are favorable, the seeds must be

physiologically ready to germinate, i.e., endogenous and/or exogenous conditions must be suitable for overcoming any dormancy within the seeds. In downy brome, the principal types of dormancy are postharvest and later, acquired overwinter dormancy. When postharvest afterripening requirements in downy brome are overcome, seeds will successfully germinate over a wide range of ecological conditions. Overwinter dormancy allows for a carryover of seeds from one year to the next to assure the continuation of the species.

This thesis attempts to (a) determine a methodology for studying the influence of water potential on seed germination; (b) assess the importance of temperature, soil moisture- and soil compaction, alone and in combination with one another, on the germination and emergence of downy brome; (c) determine the role of short durations of high temperature on accelerated afterripening on recently matured downy brome seeds; and (d) investigate the role of endogenous germination rhythms on overwinter dormancy in downy brome seeds.

# II. OSMOTIC STABILITY OF MANNITOL AND POLYETHYLENE GLYCOL 20,000 SOLUTIONS USED AS SEED GERMINATION MEDIA

## Introduction

Research on the effect of moisture conditions on seed germination has spanned several decades (Doneen and MacGillivery, 1943; Ayers, 1952; Collis-George and Sands, 1961; Hadas, 1977). During this period, various solutes, such as NaCl (Uhvits, 1946; Manohar, 1966; Sharma, 1976), glucose, sucrose (Wiggans and Gardner, 1959), mannitol (McGinnies, 1960; Helmrich and Pfeifer, 1954; Muchena and Grogan, 1977), and polyethylene glycol (PEG) (Jackson, 1962; Sharma, 1976; Heydecker et al., 1975; Hadas, 1977) have been used to simulate drought conditions during seed germination. Mannitol and PEG are the most widely used osmotic agents in germination studies, because they are chemically inert, nontoxic (Parmar and Moore, 1966), and do not penetrate seed coats (Manohar, 1966) with the high molecular weight (6,000 to 20,000) PEG used predominantly. Mannitol is used less often because of possible movement of the solute into the germinating seeds (Manohar, 1966). Recently, Hadas (1977) suggested that PEG solutions be used in standard germination tests to estimate seed germination performance under field conditions.

With the use of PEG and mannitol as osmotic agents in seed germination experiments, knowledge about their

osmotic stability with time is needed. The osmotic potential of a PEG 1540 solution does not change with time (Greenway et al., 1968). Osmotic data for mannitol or high molecular weight PEG's that have different physical and chemical properties than the lower molecular weight PEG's (Manohar, 1966) are not available. In most drought studies, seeds are exposed to the germination media for extended periods of time. If the solutions are not osmotically stable over time, the germination results could be erroneous and subsequent interpretations misleading.

The objectives of this study were to determine the osmotic stability of PEG 20,000 and mannitol solutions with time and to test the subsequent biological significance of any osmotic potential changes. Also, the percentage and rate of germination of winter wheat (*Triticum aestivum* L., 'Nugaines') in PEG and mannitol soltuions were compared to each other and to the rate of seedling emergence from soil media in order to determine the solutions' capacity to simulate "true" drought conditions.

## Materials and Methods

*Solution Osmotic Potentials.* Solution concentrations ranging from 0.1 to 0.8 molal for mannitol and 10 to 45 g/100 ml distilled water for PEG 20,000 were prepared and stored overnight in the laboratory at 24 ± 0.5 C. Thermocouple psychrometer (Wescor Inc., Model HR-33) measurements were made the following day at 24 ± 1 C.

Duplicate measurements were made on mannitol solutions, while four observations were made on all PEG solutions. In addition to psychrometric measurements, the osmotic potentials of different strength molal solutions of mannitol were calculated according to Van't Hoff's equation.

*Osmotic Stability*. The osmotic stability of mannitol and PEG 20,000 solutions, as a function of time, temperature, and solute concentration, was determined using thermocouple psychrometry. Solution concentrations were 0.60, 0.44, 0.29, and 0.14 molal for mannitol and 40.0, 30.0, 25.2, and 20.0 g/100 ml distilled water for PEG. Standard KCl solutions of 0.4, 0.3, 0.2, and 0.1 molality were also prepared to determine the psychrometer variation with time. The average coefficient of variation for all KCl measurements was 4.6%. Four 100-ml samples of each solution were incubated at 10, 20, and 30 C in rubber-stoppered, 125-ml erlenmeyer flasks. One hour before psychrometric measurements, the flasks were removed from the incubators and allowed to equilibrate to laboratory temperature (25 ± 1 C) where the psychrometer was located. Measurements were made 2, 6, 9, 14, and 19 days after the solutions were prepared. Samples from each solute treatment (i.e., mannitol, PEG, and KCl) were analyzed separately as a completely randomized design.

*Solution Comparisons*. The rate and percentage germination of winter wheat were measured in freshly prepared and 28-day-old solutions of mannitol and PEG 20,000.

Solution osmotic potentials were determined at the time of seed placement using a thermocouple psychrometer. Twenty-five seeds were placed on two Whatman No. 2 qualitative filter paper disks in petri dishes 9-cm diameter x 1.2 cm high. Ten milliliters of PEG or 7.5 ml of a mannitol solution were added to each petri dish. Germinated seeds were counted and removed when 0.5 cm of root had extended through the seed coat. A check treatment (0 bars osmotic potential) consisted of seeds germinated in 7.5 ml of distilled water.

The rate and percentage of emergence of winter wheat from soil were also determined. Various water potentials of a methyl bromide fumigated Ritzville silt loam soil (calciorthidic Haploxerall) were prepared by mixing air-dried sieved soil (2-mm mesh) and water together in an 8-liter twin-shell blender equipped with an agitator for complete mixing. After mixing, the soils were sealed in double plastic bags and stored for a week or more at 10 C to allow for further moisture equilibration and to avoid the initial surge of microbial activity that occurs when an air-dried soil is wetted. Soil water potential was determined at the time of seeding using thermocouple psychrometers. A 150-g equivalent of air-dried soil of each soil water potential level was placed in a 250-ml disposable beaker and packed to a uniform soil bulk density of 1.26 $g/cm^3$. Fifteen seeds were placed on the "seed bed," covered with an additional 20-g equivalent of

air-dried soil, and packed to a final bulk density of 1.26 g/cm$^3$. The beakers were sealed with a clear, plastic film. Seedlings were counted when the coleoptile emerged through the soil surface.

All beakers and petri dishes were incubated in the dark at a constant temperature of 20 C for the duration of the experiment. The experiment was a completely randomized design with four replications per treatment.

## Results and Discussion

*Solution Osmotic Potentials.* Mannitol solutions behaved in accordance with the Van't Hoff equation (Fig. 1). Psychrometrically measured and calculated data were the same except for small differences in slope and intercept values, which agreed with previous reports (Manohar, 1966). The relationship between osmotic potential and concentration of higher molecular weight PEG deviates from predicted values (Lagerwerff et al., 1961; Jackson, 1962; Manohar, 1966), necessitating experimental determination of this information. The osmotic potential of PEG 20,000 was found to be curvilinearly related to concentration (Fig. 2), as also shown by Williams and Shaykewich (1969) and Michael and Kaufmann (1973). However, at similar concentrations of PEG 20,000 the osmotic values shown by Williams and Shaykewich (1969) were quite different from those reported here. Dissimilarities between concentration and potential for PEG 6000 were also noted in the literature (Hegarty, 1977;

Waldron and Manbeian, 1970; Michel and Kaufmann, 1973). The differences may have been caused by variations in molecular weight between different lots and sources of PEG. For example, the results reported by Williams and Shaykewich (1969) were for PEG molecular weight 15,000 to 20,000, whereas the molecular weight was approximately 20,000[1] for the PEG used in this investigation. Thus, the relationship between concentration and osmotic potential apparently must be determined for each lot and source of PEG because values reported in the literature cannot be relied on.

*Osmotic Stability*. The osmotic stability of PEG 20,000 and mannitol solutions was determined periodically over a 19-day period. Incubation temperature (10, 20, and 30 C) had no effect on the osmotic stability of any of the solutions tested, and the values reported are the average of the observation means summed over temperatures (Table 1). As expected, the KCl solution osmotic potentials did not change with time, indicating minimal instrument error. Likewise, there was no variation with time for any of the mannitol solutions or for the 30- and 40-g/100 ml PEG 20,000 solutions. However, the osmotic potential of the 20- and 25-g/100 ml water PEG solutions decreased 0.6 and 0.7 bars, respectively, between 9 and 14 days but did not decline further during the measurement period (Table 1).

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[1]Polyethylene glycol purchased from Sigma Chemical Company with molecular weight listed as approximately 20,000.

The magnitude of the decline between 2 and 14 days was 1.0 bar in both solutions.

The observed decline in osmotic potential of the most dilute PEG 20,000 solutions may have been due to a reorientation of the molecular configurations with time. Michel and Kaufmann (1973) cited a personal communication from D. G. Stafford and reported that PEG 6000 molecules existed as rigid helical segments occasionally disrupted by disorder and folding in aqueous solutions, and that most hydrogen bonding of water molecules occurred at ether oxygens exposed at the sites of disorder and folding. It was further stated that there was little disorder in dilute solutions, whereas in concentrated solutions the disorder was great and each added increment of PEG 6000 had a greater effect in reducing the water potential. Since water potential was not a linear function of PEG concentration, a small increase in disorder and folding with time might produce a more obvious reduction in osmotic potentials in dilute solutions (20 to 25 g/100 ml $H_2O$) than in concentrated solutions (30 to 40 g/100 ml $H_2O$).

*Solution Comparisons.* The biological significance of the osmotic instability of dilute PEG 20,000 solutions was determined by germination of winter wheat seeds in media of freshly prepared and 28-day-old solutions of mannitol and PEG 20,000. Differences in the percentage (Table 2) or rate of germination between 28-day-old and freshly prepared mannitol and PEG 20,000 solutions at all concentrations

tested were not significant. However, the rate of germination in isotonic solutions of mannitol and PEG 20,000 was quite different, with germination progressing more rapidly in mannitol than in PEG 20,000 (Fig. 3). This could have resulted from the differential permeability of the seed coat to low molecular weight solutes (Manohar, 1966), which would have allowed movement of mannitol but not PEG into the germinating seed, thus reducing the true drought effect of the mannitol solution.

The percentage and rate of germination in mannitol and PEG 20,000 were further compared to seedling emergence from a soil media. At soil water potentials below -11 bars, the percentage emergence from the soil was much less than the percentage germination in either aqueous solution (Table 2). As expected, the emergence rate from soil was much slower than the germination rate in mannitol and PEG 20,000 at all water potentials tested (Fig. 3). The slower rate and lower percentage of emergence in the soil media were probably related to the hydraulic conductivity and wetted seed contact area (Hadas and Russo, 1974). The net result was a reduced rate of water uptake, which in drier soils will delay attainment of seed's critical hydration level and thus postpone or prevent germination and emergence (Hadas and Russo, 1974). A comparison of germination

and emergence rate indices[2] at a constant temperature of 20 C showed that the emergence rate from this particular soil system was linearly correlated to the germination rate in PEG 20,000 (Fig. 4). However, it appears that the germination rate in mannitol was more curvilinearly than linearly related to the emergence rate from soil. This would further indicate that PEG's of high molecular weights may be used to simulate true drought more effectively than other low molecular weight solutes (Manohar, 1966; Sharma, 1973).

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[2]Calculated by dividing the percentage germination or emergence occurring during the counting interval by accumulative time from time 0 and summing the values over all counting intervals.

13. McGinnies, W. J. 1960. Effect of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-162.

14. Michel, B. E. and M. R. Kaufmann. 1973. The osmotic potential of polyethylene glycol 6000. Plant Physiol. 51:914-916.

15. Muchena, S. C. and C. O. Grogan. 1977. Effect of seed size on germination of corn (*Zea mays*) under simulated water stress conditions. Can. J. Plant Sci. 57:921-924.

16. Parmar, M. T. and R. P. Moore. 1966. Effect of simulated drought by polyethylene glycol solutions on corn (*Zea maize* L.) germination and seedling development. Agron. J. 58:391-392.

17. Sharma, M. L. 1973. Simulation of drought and its effect on germination of five pasture species. Agron. J. 65:982-987.

18. -------. 1976. Interaction of water potential and temperature effects on germination of three semi-arid plant species. Agron. J. 68:390-394.

19. Ehvits, R. 1946. Effects of osmotic pressure on water absorption and germination of alfalfa seeds. Am. J. Bot. 33:278-285.

20. Waldron, L. J. and T. Manbeian. 1970. Soil moisture characteristics by osmosis with polyethylene glycol: A simple system with osmotic pressure data and some results. Soil Sci. 110:401-404.

21. Wiggans, S. C. and F. P. Gardner. 1959. Effectiveness of various solutions for simulating drought conditions as measured by germination and seedling growth. Agron. J. 51:315-318.

22. Williams, J. and C. F. Shaykewich. 1969. An evaluation of polyethylene glycol (PEG) 6000 and 20,000 in osmotic control of soil water matric potential. Can. J. Soil Sci. 49:397-401.

Table 1. Osmotic stability of PEG 20,000 and mannitol with time compared with a standard KCl solution. All measurements were made at 24 C using thermocouple psychrometry.

| Solution | Solution strength† | Osmotic potential, Time, days | | | | |
|---|---|---|---|---|---|---|
| | | 2 | 6 | 9 | 14 | 19 |
| PEG | 40* | 17.4a | 17.5a | 16.8a | 16.9a | 17.3a |
| | 30 | 9.1a | 9.6a | 9.2a | 9.7a | 10.0a |
| | 25 | 6.4a | 6.6a | 6.8ab | 7.4b | 7.3b |
| | 20 | 4.0a | 4.1a | 4.3a | 5.0b | 5.2b |
| Mannitol | 0.6 | 15.2a | 15.4a | 15.1a | 15.0a | 15.1a |
| | 0.44 | 11.1a | 11.4a | 11.0a | 11.0a | 11.1a |
| | 0.29 | 6.9a | 7.2a | 7.1a | 6.9a | 7.1a |
| | 0.14 | 3.4a | 3.6a | 3.6a | 3.5a | 3.2a |
| KCl | 0.4 | 17.6a | 17.9a | 17.7a | 18.0a | 18.0a |
| | 0.3 | 13.6a | 13.5a | 13.3a | 13.3a | 13.4a |
| | 0.2 | 8.9a | 9.0a | 8.8a | 8.8a | 8.7a |
| | 0.1 | 4.3a | 4.4a | 4.5a | 4.4a | 4.0a |

*Means within rows followed by like letters are not significantly different at the 5% level of probability according to Tukey's HSD range test.

†PEG 20,000 concentrations expressed as g solute/100 ml of water. Mannitol and KCl solution concentration expressed as molality. Values expressed as the average of the observation means summed over temperatures.

Table 2. Final percentage germination in 28-day-old and freshly prepared mannitol and PEG 20,000 solutions and emergence from soil of winter wheat incubated at a constant temperature of 20 C and varying water potentials.

| Treatment | Water potential | | Germination or emergence* | |
|---|---|---|---|---|
| | 28-day-old | Freshly prepared | 28-day-old | Freshly prepared |
| | -bars | | % | |
| Mannitol | 3.9 | 3.7 | 97 a | 96 a |
| | 7.4 | 7.2 | 97 a | 97 a |
| | 11.0 | 11.4 | 96 a | 96 a |
| | 15.5 | 15.7 | 92 a | 93 a |
| PEG 20,000 | 4.3 | 4.3 | 97 a | 97 a |
| | 6.3 | 6.9 | 98 a | 99 a |
| | 9.3 | 9.3 | 95 a | 92 a |
| | 16.9 | 17.3 | 0 c | 0 c |
| Soil | | 4.1 | | 95 a |
| | | 7.4 | | 86 a |
| | | 11.4 | | 42 b |
| | | 16.7 | | 7 c |
| Check† | | 0.0 | | 98 a |

*Means followed by like letters are not significantly different at the 5% level of probability according to Tukey's HSD range test.

†Seeds germinated for 14 days on moistened blotter paper in petri dishes.

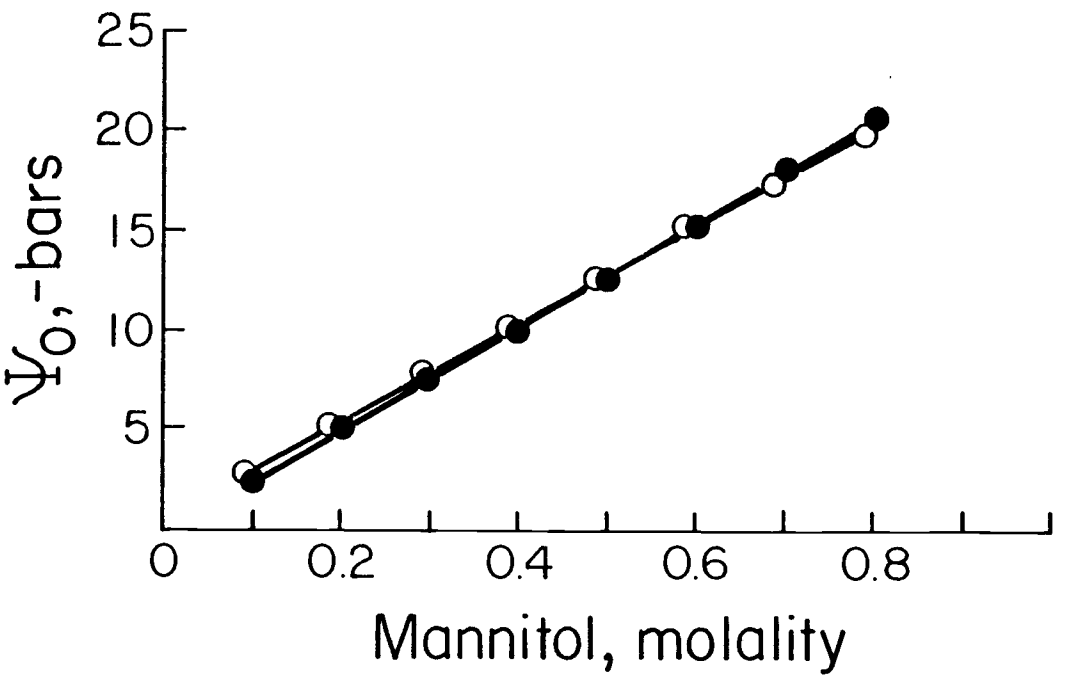


Figure 1. The relationship between mannitol concentration and osmotic potential ($\Psi_o$) (● measured, o calculated). Regression coefficients for both measured and calculated data = 0.99, and $\hat{y}$ measured = 0.44 + 25.96 X.

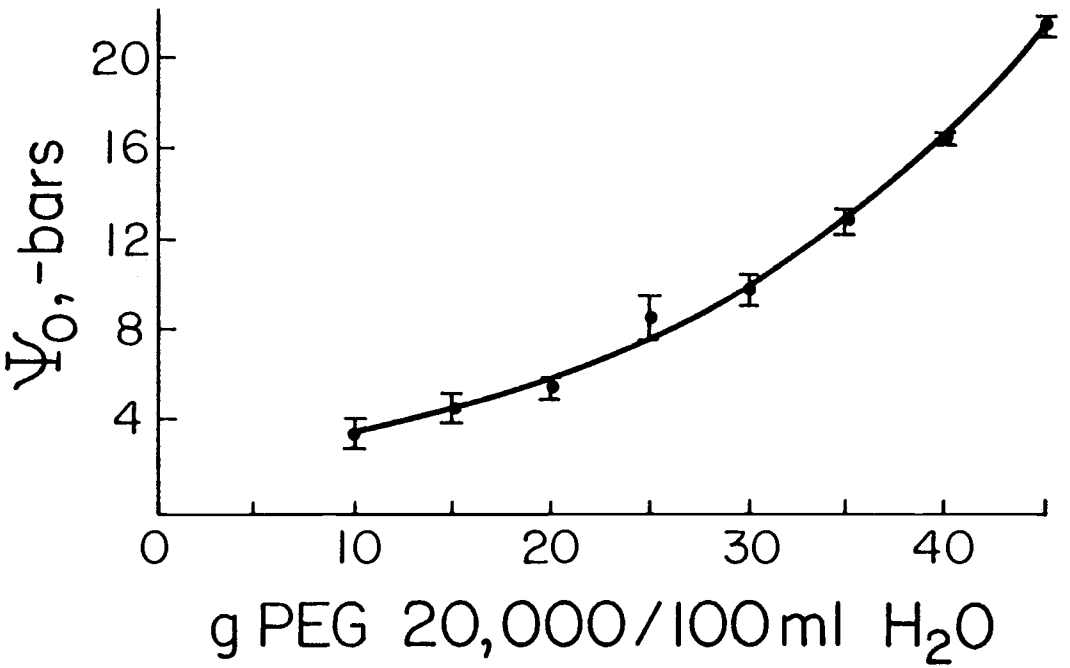


Figure 2. The relationship between PEG 20,000 concentration and osmotic potential ($\Psi_o$). Vertical bars indicate the confidence intervals at the 5% level of probability.

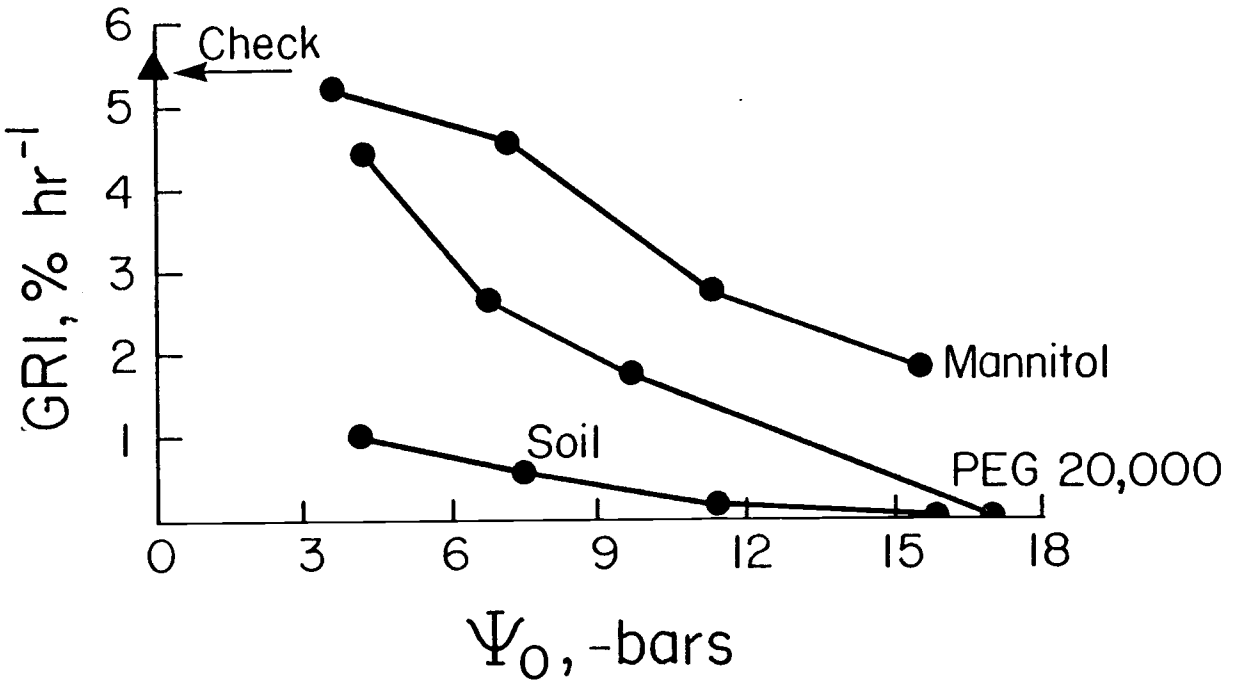


Figure 3. Germination or emergence rate indices (GRI) for winter wheat in mannitol, PEG 20,000, and soil media measured at various osmotic potentials ($\Psi_o$).

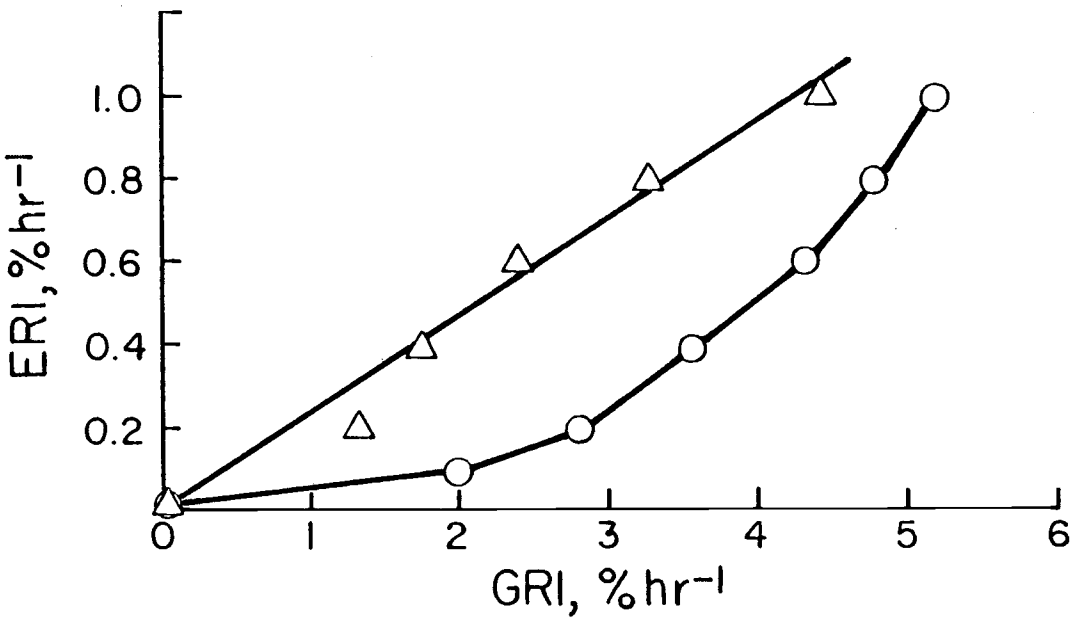


Figure 4. Germination rate indices (GRI) in PEG 20,000 (Δ), and mannitol (O) vs. emergence rate (ERI) in soil at isopotentials. $r^2$ = 0.98 and 0.85 for PEG and mannitol, respectively. $\hat{y}$ = -0.03 + 0.24 X for PEG 20,000.

# III. THE INFLUENCE OF SOIL MOISTURE, TEMPERATURE, AND COMPACTION ON THE GERMINATION AND EMERGENCE OF *BROMUS TECTORUM* L.

## Introduction

Downy brome, an annual plant introduced from Eurasia about a century ago, is widespread in many of the semi-arid parts of the Western United States, particularly in the Great Basin and Columbia Basin. Some consider it an important forage because it provides most of the early spring grazing for all classes of stock on millions of hectares in the West (11). However, it also is considered a troublesome weed in rangeland (19), winter wheat (16), several other crops, and non-cropland.

The ubiquitous nature of the species and its dual role as a serious weed and important forage has resulted in the generation of a substantial amount of literature on downy brome, which was reviewed by Steward and Hull (19) and Klemmendson and Smith (11). A great deal of taxonomic and autecological information (7, 9), life cycle data (4), and soil type and planting depth effects (22), also have been reported for downy brome.

Extensive Studies on certain factors controlling germination and emergence of downy brome have been reported. These include the influence of afterripening (18), temperature (3, 9), light (9), and soil moisture and microsites (3, 27). However, there is limited information on the

interactive influence of soil moisture and temperature (6), and none on the interactive effects of soil moisture and soil compaction on germination and emergence of downy brome. The importance of the interaction of simulated moisture stress and temperature has been demonstrated for many plant species (2, 10, 17, 23). In most cases moisture-temperature interactions were found to significantly influence seed germination. Likewise, significant interactive effects of soil moisture and soil compaction on seed germination and emergence have been shown (5, 8, 15).

The objectives of these studies were to (a) determine the interaction of soil moisture stress and temperature on the germination and emergence of downy brome, (b) determine if downy brome seeds produced during different years and under widely varying climatic conditions exhibit similar patterns of emergence when subjected to varying levels of soil moisture stress, and (c) assess the importance of soil bulk density and soil moisture stress interactions on the germination and emergence of downy brome.

## Materials and Methods

Mature downy brome seeds were collected near Pullman, Washington, during July of 1976, 1977, and 1978. The seeds were hand harvested, cleaned with vibrating screens and forced air blower, and stored in sealed containers at 21 ± 1 C. Prior to the initial experiment, the seeds were allowed to afterripen for a minimum of 8 weeks.

In all experiments reported, the effect of soil water potential on the percentage of downy brome emergence was determined using soil media. The soil was prepared and the water potential was determined in a manner previously reported (21).

*Temperature-Moisture Studies.* The effect of soil moisture and temperature on the percentage of downy brome seedling emergence was determined in the laboratory by placing premoistened soil (150 g air dry equivalent) in 250-ml beakers and packing it to a uniform bulk density of 1.0 g $cm^{-3}$. Fifteen seeds were placed on the soil surface and covered approximately 5 mm deep with an additional 20 g equivalent of air dry soil and packed to a final bulk density of 1.0 g $cm^{-3}$. The beakers were sealed with a clear plastic film. Soil water potential values ranged from -1.9 to -16.5 bars. Emergence was recorded when the coleoptile penetrated through the soil surface.

A control treatment (0 bars water potential and no soil) was established by germinating 15 seeds on saturated filter paper disks in sealed 237-ml jars. The saturation was maintained by placing two Whatman No. 2 filter paper disks on the surface of 160 $cm^3$ of heat sterilized, water-saturated sand. Germinated seeds were counted and removed when 5 mm of radicle had extended through the seed coat.

Four replications of each moisture level were incubated in the dark at 10, 15, and 20 C constant temperature and -2.5 to 12.5, -1.5 to 17.5, and 7.5 to 28 C alternating

temperatures. Alternating temperatures were produced by modified constant temperature baths designed to produce approximate sine wave, diurnal temperature curves. The integrated mean temperatures for the alternating temperature treatments were 5.1, 9.3, and 16.4 C for -2.5 to 12.5, -1.5 to 17.5, and 7.5 to 28 C, respectively.

Germination and emergence counts were made at 2-4 day intervals for a period of 27 days. After 27 days, the seeds from treatments with little or no emergence were washed from the soil. Seeds which had germinated but not emerged were counted and discarded. All other nongerminated seeds were placed on moist filter paper disks in petri dishes and incubated at 20 C constant temperatures for an additional 10 days. Germinated seeds were counted and removed at periodic intervals during this period.

The experiment was conducted once using the 1976 seed lot and twice using the 1977 seed lot. Each experiment was analyzed separately as a completely randomized design with four replications per treatment. An arcsin transformation was performed on the percentage germination and emergence data, and all subsequent statistical analyses were conducted using the transformed data. The reported percentage germination and emergence values are for the nontransformed data.

*Moisture-Seed Lot Studies.* Downy brome seeds from lots collected in 1976 through 1978, were compared to determine if variation in climatic conditions during seed

production affected percentage of emergence under different soil moisture regimes. Climatically, the three collection years were quite diverse. The 1976 growing season can be classified as normal in terms of the 30-year average, 1977 hot and dry, and 1978 cool and wet (Table 3). The 1,000 seed weight of the three seed lots were 2.61, 2.32, and 7.76 g for 1976, 1977, and 1978, respectively.

The method used to test the effect of soil water potential on emergence percentage of the three seed lots was the same as that described in the preceding section. Soil water potential values ranged from -1.8 to -14.3 bars. Control treatments (0 bars water potential) for each seed lot were established by germinating 25 seeds in petri dishes on germination blotter paper saturated with distilled water. Germinated seeds were counted and removed when 5 mm of radicle had extended through the seed coat.

Petri dishes and beakers were incubated in the dark at 20 C constant temperature. Germination and emergence counts were made at 3-5 day intervals for a period of 28 days.

The experiment was conducted once with five replications per treatment and analyzed as a completely randomized design.

*Moisture-Compaction Study.* Interactive effects of soil moisture and soil compaction on the percentage of emergence of downy brome were determined in the laboratory by differentially packing soil, ranging in water potential

from -1.7 to -12.8 bars, into 250-ml beakers. The soil bulk density levels used were 0.9, 1.0, 1.1, 1.2, and 1.3 g $cm^{-3}$. For each soil compaction level, a predetermined amount of soil at each water potential was weighed into each beaker, and packed with a hand-operated press to a 150-$cm^3$ volume. Fifteen seeds were placed on the seedbed in each beaker, covered with additional soil, and packed to a bulk density equal to that of the seedbed. The depth of seed coverage was 5 mm for all treatments. A clear plastic film was used to seal the beakers. Emergence was recorded when the coleoptile penetrated through the soil surface.

A control treatment (0 bars water potential and no compaction) was established by germinating 25 seeds in petri dishes as previously described.

All beakers and petri dishes were incubated in the dark at 20 C constant temperature. Germination and emergence counts were made at 2-5 day intervals for a period of 27 days. After 27 days, the seeds from all treatments were washed from the soil and the number of seeds germinated but not emerged was determined.

The experiment was conducted twice using the 1977 seed lot and once with the 1976 seed lot. Each experiment, minus the check treatment, was analyzed separately as a completely randomized design with four replications per treatment.

## Results

*Temperature-Moisture Study*. Soil matric potential and temperature and their interactions significantly influenced percentage of emergence of downy brome ($P < 0.01$) (Table 4).

In most cases, downy brome seedling emergence declined with decreasing matric potential. When summed over all temperatures and experiments, emergence declined nonlinearly from a high of 61% at 0 bars to a low of 10% at -15.6 to -16.5 bars matric potential. The level of matric potential at which emergence ceased varied with temperature and experiment.

Downy brome emergence withstood more negative matric potentials at constant than at alternating temperature (Table 4). Emergence, when summed over all matric potentials and experiments, was 53, 49, 48, 37, 25, and 16% for 15, 10, 20, 16.4, 9.3, and 5.1 C temperature treatments, respectively. At very low matric potentials (-15.6 to -16.5 bars), emergence was least suppressed at 10 and 15 C.

The emergence rate of downy brome declined in a manner similar to emergence percentage with decreasing matric potential (data not shown). In general, at higher matric potentials, emergence was accelerated by warmer mean temperatures, except where 15 C constant temperature was superior to 16.4 alternating temperature. At matric potentials at or below -15.6 bars, the emergence rate was faster at 10 and 15 C than at warmer or cooler mean temperatures.

Germination recorded after the 27-day standard incubation period for the 5.1 and 9.3 C treatments showed the combined average seeds germinated but not emerged to be 37, 40, 17, and 1% for the increasing levels of matric potential. The average combined delayed germination of the nongerminated seeds placed on saturated filter papers in petri dishes was 1, 5, 21, and 23% for the increasing levels of matric potential. The average combined delayed germination of the nongerminated seeds for all other temperature treatments at the highest matric potential was 17%. In all cases, the seeds that did not germinate after 10 additional days in petri dishes were totally colonized with microorganisms.

Multiple linear regression analysis performed on transformed data showed the equation $\hat{Y} = 46.28 + 2.83\ X_1 - 4.33\ X_2$ (where $\hat{Y}$ is the predicted emergence in percentage for transformed data, $X_1$ is the temperature in C, and $X_2$ is the absolute value of soil matric potential) did not satisfactorily predict emergence, thus indicating a more complex relationship between temperature, moisture, and seedling emergence. The data were transformed to a percentage of the 0 bars, 20 C treatment for each experiment to standardize the data.

*Moisture-Seed Lot Study*. The percentage of emergence of seeds collected during each of the 3 years decreased in a similar manner with decreased soil matric potential (Table 5).

*Moisture-Compaction Study*. Soil bulk density was the only parameter in this experiment that consistently and significantly ($P < 0.01$) influenced seedling emergence. However, soil matric potential was influential at intermediate levels of soil compaction (Table 6). Little difference in emergence was noted between levels of soil matric potential when summed over all levels of bulk density and over all experiments. The range of seedling emergence was 23.8% at -6.4 to -7.8 bars to 32.7% at -3.5 to -3.7 bars. All other values were intermediate. A simple linear regression analysis of soil bulk density, summed over matric potentials, versus emergence percentage yielded a straight line relationship ($\hat{Y} = 279.10 - 214.33\ X$, where $\hat{Y}$ = percentage seedling emergence and X = soil bulk density in g $cm^{-3}$; $r^2 = 0.88$ and $n = 15$).

Emergence restriction of germinated downy brome seedlings increased with increasing soil compaction (Table 7). The average emergence restriction for each level of soil compaction was 8, 22, 28, 52, and 60% at 0.9, 1.0, 1.1, 1.2, and 1.3 g $cm^{-3}$ bulk density, respectively. Soil matric potential had little or no effect on the emergence restriction of germinated downy brome seedlings (Table 7).

The total percentage downy brome germination was determined by summing the emergence percentage (Table 6) and percentage which germinated but did not emerge (Table 7) for each treatment. When percentage final germination was summed over soil matric potentials or soil bulk density, no significant difference between treatments was observed.

## Discussion

When summed over all experiments, the optimum temperature requirements for the emergence of downy brome in the present study were 15 to 20 C at 0 bars, but shifted to 10 to 20 C constant temperature when summed over all levels of matric potential. Under zero moisture stress conditions, reported optimum temperatures ranged from 5 to 25 C (3, 9). Alternating temperatures above zero but below 30 C influenced germination no differently than comparable mean constant temperatures (3). The percentage of emergence was least affected by matric potentials at 10 and 15 C. This shows that low levels of soil moisture reduce downy brome emergence more at warm than at cool soil temperatures. This shift in optimum temperature with decreasing water potential is contrary to previous reports for downy brome (6), other cool-season grasses (14), and three Australian semi-arid species (17) where germination at all levels of water stress was always superior at the zero water stress optimum temperature.

No downy brome germination has been previously observed where temperatures were subzero for 16 h per day (3). The number of hours per day in this study at subzero temperatures was reduced compared to the 16 h treatment by the use of a sine wave temperature regulator, and under these conditions some germination occurred. The methodology used herein approximates natural diurnal temperature patterns more closely than standard square wave temperature

regulators and should provide a better estimate of potential seed germination under periodic subzero temperature conditions that usually occur during late-fall to early-spring germination periods in much of the western habitat of downy brome.

Moisture and temperature are the two most important environmental parameters controlling seed germination, with wide variation in the response of various species to these factors. Based on work with mannitol solutions, several workers have suggested that germination and drought relationships for perennial grasses (14, 20) were sensitive to temperature but those for wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) were not affected (20). With polyethylene glycol solutions, the effects of temperature and water potential on germination were significant for lettuce (*Lactuca sativa*) (10) and three Australian semi-arid species (17). In the present study, the moisture-temperature interactions show that downy brome has the potential to adapt to a wide range of environmental conditions. Cold temperatures and, as previously discussed, warm dry soils limit rapid and successful seedling emergence. During germination, the metabolic processes required to solubilize seed reserves and to develop an effective osmotic component within the seed (12) probably are related to temperature with suboptimal temperatures reducing metabolism, thus resulting in the reduced percentage of downy brome emergence. At optimum temperatures (20 to 22 C), the

internal water potential of germinating downy brome seeds has been shown to decrease rapidly to -16 bars between 20 to 60 hr after the start of imbibition, which has resulted in its classification as a rapidly and vigorously germinating species (13). In our studies, some seeds slowly germinated at high levels of soil matric potential in the colder soils, but failed to emerge.

The seed lot-water potential study showed no significant difference in response to drought for the three downy brome seed lots tested. Therefore, one would expect the response to soil moisture to cause only minor variation in germination from year to year. However, care should be taken in expanding this extrapolating conclusion to include seeds produced at widely different geographical locations where different selections or varieties may occur. Young et al. (26) have reported that the germination of various medusahead (*Taeniatherum asperum* (Sim.) Nevski) selections, which occupy many of the same habitats as downy brome, differ in their response to water stress.

For seedlings to emerge, they must not only germinate, but also penetrate through overlying soil layers. Therefore, soil compaction must be considered as a factor influencing seedling emergence. Under most rangeland conditions, soil compaction probably plays a minor role in influencing the final emergence of downy brome because most seeds are located in the surface litter (24). Under cultivated conditions, soil compaction could play an important role in

the ability of downy brome to compete with cultivated crops, such as wheat. Our findings show that the emergence, but not the germination, of downy brome was inhibited by increased levels of soil compaction. Therefore, under favorable conditions, seeds will germinate, but may or may not emerge depending on the extent of soil compaction. If used properly as a crop management tool, the net result could be a reduction in the potential level of infestation of downy brome in a planted crop. For example, at a soil bulk density level of 1.1 g $cm^{-3}$, the downy brome emergence is predicted to be reduced by 57% and the rate of emergence reduced by 80% compared with germination potential in a standard petri dish test. In comparison, wheat seedling percentage and rate of emergence were virtually unaffected at soil bulk density levels ranging from 1.2 to 1.3 g $cm^{-3}$ depending on soil type (5). Hence, under cultivated field conditions where most downy brome seedlings must emerge from the soil, slight compaction may suppress potential downy brome emergence but not adversely influence the seedling establishment of such crops as wheat.

Under laboratory conditions our experiments show that downy brome is adopted to a wide range of temperature and moisture conditions, limited mostly by cold soil temperatures or warm dry soil. The ubiquitous nature (9), rapid germination with late summer and early fall rains (11), and role as an early succession species in disturbed sites (1),

support these findings. Under cultivated conditions where seedlings must emerge through soil layers, soil compaction becomes a major factor determining the successful establishment of downy brome.

## Liturature Cited


1. Daubenmire, R. 1970. Steppe vegetation of Washington. Wash. Agric. Expt. Sta. Bull. 62:80-82.

2. El-Sharkawi, H. M. and I. Springuel. 1977. Germination of some crop plant seeds under reduced water potential. Seed Sci. Technol. 5:677-688.

3. Evans, R. A. and J. A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. Weed Sci. 20:350-356.

4. Finnerty, D. W. and D. L. Klingman. 1962. Life cycles and control studies of some weed bromegrasses. Weeds 10:40-47.

5. Hanks, R. J. and F. C. Thorp. 1956. Seedling emergence of wheat as related to soil moisture content, bulk density, oxygen diffusion rate, and crust strength. Soil Sci. Soc. Am. Proc. 20:307-310.

6. Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol. Monogr. 37:89-111.

7. Hinds, W. T. 1975. Energy and carbon balances in cheatgrass: An essay in autocology. Ecol. Monogr. 45:367-388.

8. Hudspeth, E. B. and H. M. Taylor. 1961. Factors affecting seedling emergence of Blackwell switchgrass. Agron. J. 53:331-335.

9. Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Monogr. 25:181-213.

10. Kaufmann, M. R. and K. J. Ross. 1970. Water potential, temperature and kinetin effects on seed germination in soil and solute systems. Am. J. Bot. 57: 413-419.

11. Klemmedson, J. D. and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). Bot. Rev. April-June:226-262.

12. Koller, D. 1972. Environmental control of seed germination, pp. 1-101 *In* T. T. Kozlowski, Ed. Seed Biology, Vol. 2. Academic Press, New York.

13. McDonough, W. T. 1975. Water potential of germinating seeds. Bot. Gaz. 136:106-108.

14. McGinnies, W. J. 1960. Effect of moisture stress and temperature on germination of six range grasses. Agron. J. 52:159-162.

15. Parker, J. J., Jr. and H. M. Taylor. 1965. Soil strength and seedling emergence relations. I. Soil type, moisture tensions, temperature, and planting depth effects. Agron. J. 47:289-291.

16. Rydrych, D. J. 1974. Competition between winter wheat and downy brome. Weed Sci. 22:211-214.

17. Sharma, M. L. 1976. Interaction of water potential and temperature effects on germination of three semi-arid plant species. Agron. J. 68:390-394.

18. Steinbauer, G. P. and B. H. Grigsby. 1957. Field and laboratory studies on the dormancy and germination of seeds of chess (*Bromus secalinus* L.) and downy brome-grass (*Bromus tectorum* L.). Weeds 5:1-4.

19. Stewart, G. and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)--an ecological intruder in southern Idaho. Ecology 30:58-74.

20. Tadmor, N. H., Y. Cohen, and Y. Harpez. 1969. Interactive effects of temperature and osmotic potential on the germination of range plants. Crop Sci. 9:771-774.

21. Thill, D. C., R. D. Schirman, and A. P. Appleby. 1979. The osmotic stability of mannitol and polyethylene glycol 20,000 solutions used as seed germination media. Agron. J. 71:105-108.

22. Wicks, G. A., O. C. Burnside, and C. R. Fenster. 1971. Influence of soil type and depth of planting on downy brome seed. Weed Sci. 19:82-86.

23. Wright, D. L., R. E. Blaser, and J. M. Woodrull. 1978. Seedling emergence as related to temperature and moisture tension. Agron. J. 70:709-712.

24. Young, J. A. and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. Weed Sci. 23:358-364.

25. Young, J. A., R. A. Evans, and R. E. Eckert, Jr. 1969. Population dynamics of downy brome. Weed Sci. 17:20-26.

26. Young, J. A., R. A. Evans, R. O. Gifford, and R. E. Eckert, Jr. 1968. Germination of medusahead in response to osmotic stress. Weed Sci. 16:364-368.

27. Young, J. A., R. A. Evans, and B. L. Kay. 1971. Germination of caryopses of annual grasses in simulated litter. Agron. J. 63:551-555.

*Table 3.* The departure of seasonal (September 1 through August 31) precipitation, and mean, maximum, and minimum temperatures from the long-term average at Pullman, Wash.

| Meterorological parameter | Long-term average | Mean seasonal departure | | |
|---|---|---|---|---|
| | | Year | | |
| | | 1976 | 1977 | 1978 |
| Precipitation (mm) | 520 | -6.0 | -238 | +42.0 |
| Mean maximum temperature (C) | 57.4 | -1.6 | +1.3 | - 1.5 |
| Mean minimum temperature (C) | 36.3 | -0.6 | +0.6 | + 0.8 |

*Table 4.* The influence of temperature and soil matric potential on seedling emergence of *Bromus tectorum* L.

| Soil matric potential -bars | Percent emergence[a] | | | | | |
|---|---|---|---|---|---|---|
| | Integrated temperature, C | | | | | |
| | 5.1[b] | 9.3[b] | 10.0 | 15.0 | 16.4[b] | 20.0 |
| | *1976 Seed, experiment 1* | | | | | |
| 0.0 | 70.0a | 65.0a-c | 61.7a-d | 73.4a | 61.7a-d | 68.3ab |
| 1.9 | 41.7d-f | 58.3a-d | 66.7a-c | 68.4ab | 55.0a-e | 66.7a-c |
| 3.3 | 21.7g | 46.7b-f | 55.3a-3 | 51.7a-3 | 45.0c-f | 56.7a-d |
| 8.8 | 5.0h | 20.0g | 61.7a-d | 56.7a-d | 33.3e-g | 61.7a-d |
| 16.5 | 0.0h | 0.0h | 46.7b-f | 53.3a-e | 1.7h | 30.0fg |
| | *1977 Seed, experiment 2* | | | | | |
| 0.0 | 8.3ef | 55.0a-c | 66.7ab | 66.7ab | 70.0a | 68.3a |
| 2.2 | 6.7f | 18.3de | 46.7c | 60.0a-c | 46.7c | 48.3bc |
| 5.0 | 0.0g | 0.0g | 45.0c | 51.7a-c | 43.3c | 46.7c |
| 9.4 | 0.0g | 0.0g | 43.3c | 53.3a-c | 13.3d-f | 26.7d |
| 15.7 | 0.0g | 0.0g | 11.7ef | 11.7ef | 0.0g | 0.0g |
| | *1977 seed, experiment 3* | | | | | |
| 0.0 | 61.7a-c | 61.7a-c | 41.7cd | 73.4a | 61.7a-c | 66.7ab |
| 2.0 | 11.7f-h | 16.7e-g | 61.7a-c | 63.3a-c | 46.7b-d | 56.7a-c |
| 3.6 | 11.7f-h | 18.4ef | 60.0a-c | 56.7a-c | 50.0b-d | 63.3a-c |
| 6.3 | 0.0i | 5.0g-i | 55.0a-c | 46.7b-d | 30.0de | 55.0a-c |
| 15.6 | 0.0i | 1.7i | 18.4e-g | 5.0hi | 0.0i | 1.7i |

[a]Mean within experiments followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test ($S_{\bar{x}}$ = 3.98, 3,50, and 4.11 for experiments 1, 2, and 3, respectively; n = 4 in all cases.)

[b]Sine wave alternating temperature.

*Table 5.* The influence of soil moisture on the emergence of *Bromus tectorum* L. seed produced in 1976, 1977, and 1978.

| Seed lots | Emergence[a] | | | |
|---|---|---|---|---|
| | Soil matric potential, -bars | | | |
| | 1.8 | 3.3 | 7.5 | 14.3 |
| | % | | | |
| 1976 | 80.5 ab | 81.6 ab | 48.7 d | 1.7 e |
| 1977 | 72.4 a-c | 65.8 b-d | 57.0 cd | 1.9 e |
| 1978 | 92.1 a | 64.4 b-d | 46.8 d | 0.0 e |

[a]Emergence is expressed as a percentage of the 0 bars water potential treatment for each year's seed lot. Mean percentage germination was 71.2, 60.8, and 91.2 for the 1976, 1977, and 1978 seed lots, respectively. Means followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test ($S_{\bar{x}}$ = 7.32 and n = 5).

*Table 6.* The influence of soil moisture and soil bulk density on emergence of *Bromus tectorum* L.

| Soil matric potential -bars | Percent emergence[a] | | | | |
|---|---|---|---|---|---|
| | Soil bulk density, g $cm^{-3}$ | | | | |
| | 0.9 | 1.0 | 1.1 | 1.2 | 1.3 |
| | *1976 Seed, experiment 1* | | | | |
| 2.1 | 65.0ab | 63.3a-c | 45.0e | 30.0g | 6.7g |
| 3.7 | 61.7a-d | 61.7a-d | 55.0b-e | 10.0g | 8.3g |
| 7.4 | 60.0a-e | 45.0e | 46.7de | 6.7g | 1.7g |
| 12.8 | 70.0a | 58.4a-e | 48.3c-e | 0.0g | 0.0g |
| | *1977 Seed, experiment 2* | | | | |
| 1.7 | 58.4a | 33.3b-e | 23.4de | 15.0ef | 1.7f |
| 2.8 | 45.0a-c | 28.4c-e | 31.7b-e | 31.7b-e | 1.7f |
| 6.4 | 55.0a | 40.0a-d | 23.4de | 5.0f | 0.0f |
| 7.8 | 50.0ab | 26.7c-e | 16.7ef | 3.3f | 0.0f |
| | *1977 Seed, experiment 3* | | | | |
| 2.1 | 51.7ab | 41.7b | 38.3b | 13.3c-e | 6.7de |
| 3.5 | 63.3ab | 38.3b | 21.7c | 6.7de | 0.0d |
| 7.0 | 51.7ab | 21.7c | 23.4c | 0.0e | 0.0e |
| 11.2 | 51.7ab | 45.0b | 16.7cd | 3.4de | 0.0e |

[a]Means within experiments followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test ($S_{\bar{x}}$ = 4.86, 5.91, and 4.70 for experiments 1, 2, and 3, respectively. n = 4 in all cases). The average percentage germination in a standard germination test at 20 C = 69, 69, and 62% for experiments 1, 2, and 3, respectively.

*Table 7.* Emergence restriction of *Bromus tectorum* L. as influenced by soil moisture and soil bulk density.

| Soil matric potential, -bars | Percent germinated but not emerged[a] | | | | |
|---|---|---|---|---|---|
| | Soil bulk density, g $cm^{-3}$ | | | | |
| | 0.9 | 1.0 | 1.1 | 1.2 | 1.3 |
| | *1976 Seed, experiment 1* | | | | |
| 2.1 | 3.4fg | 8.3d-g | 20.0de | 45.0c | 60.0ab |
| 3.7 | 6.7e-g | 8.8d-g | 13.3d-g | 51.7bc | 56.7a-c |
| 7.4 | 0.0g | 16.7d-f | 15.0d-g | 70.0a | 58.3a-c |
| 12.8 | 3.3fg | 6.7e-g | 23.4d | 66.7a | 63.6a |
| | *1977 Seed, experiment 2* | | | | |
| 1.7 | 1.7f | 20.0ef | 33.4a-e | 48.4a-c | 60.0a |
| 2.8 | 21.7c-f | 30.0b-e | 30.0b-e | 45.0a-d | 58.3a |
| 6.4 | 11.7ef | 33.4a-e | 26.7b-f | 46.7a-d | 58.3a |
| 7.8 | 13.4ef | 30.0b-e | 30.0b-3 | 53.4ab | 56.7a |
| | *1977 Seed, experiment 3* | | | | |
| 2.1 | 5.0j | 18.3h-j | 36.7d-g | 45.0c-e | 50.0b-d |
| 3.5 | 3.3j | 23.3f-i | 30.0d-g | 48.4b-d | 63.3a-c |
| 7.0 | 10.0h-j | 36.7d-g | 40.0d-f | 60.0a-c | 65.0ab |
| 11.2 | 10.0h-j | 26.7e-h | 41.7d-g | 38.3d-f | 71.7a |

[a]Mean within experiments followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test ($S_{\bar{x}}$ = 4.70, 8.17, and 6.13 for Experiments 1, 2, and 3, respectively. n = 4 in all cases).

# IV. INFLUENCE OF AFTERRIPENING TEMPERATURE ON THE GERMINATION OF DOWNY BROME

## Introduction

The potential germinability of downy brome seeds is reported to be influenced by post harvest (2, 4, 6), and environmentally acquired dormancy (1, 9, 10).

Initial dormancy at supraoptimum germination temperatures encountered in recently harvested downy brome seeds can be overcome during an afterripening period. This may be accomplished by prechilling moistened seeds at 5 C for 1 week (6). Recently, accelerated afterripening induced by high temperature has been reported for several annual grass weeds by Taylorson and Brown (8). They found that initial dormancy could be overcome by pretreatment of dry seeds at 50 C for 14 days or less. In all instances, the net result is an increase in optimum and maximum germination temperatures and germination percentage.

Under field conditions, downy brome seeds mature in early summer, disarticulate, and fall to the ground by early August. I have observed germination to occur in mid-August with the onset of sufficient summer rain when soil temperatures were still supraoptimum, and when previously reported afterripening requirements had not yet been fulfilled. This early germination suggests that downy brome seeds also undergo accelerated afterripening.

Evans and Young (1) found when the afterripening requirements were fulfilled, downy brome seeds were non-dormant; however, those seeds that did not germinate in the fall acquired a dormancy while overwintering in the field. In spring, the seeds assumed a continuous germination pattern, as contrasted to a simultaneous pattern that occurred in the fall (9). This germination cycle appeared to be environmentally controlled because different rangeland microsites varied in environmental extremes of moisture and temperature and thus influenced the number of downy brome seeds that acquired dormancy (9). However, endogenously produced rhythmic phenomena of this type can also occur in seeds (5, 7).

The objectives of this study were to (a) examine the effectiveness of high temperature in overcoming the initial postharvest dormancy in downy brome seeds, and (b) to determine if natural endogenous germination rhythms occur in downy brome seeds.

## Materials and Methods

*Afterripening*. Mature seeds of downy brome were hand harvested at Pullman, Washington and cleaned with vibrating screens and forced air blower on 21 July 1978. Immediately after processing (time zero), a subsample was removed to determine the initial postharvest percentage of germination. Next, the collection was equally divided into six lots with each lot further subdivided into four additional subsamples.

Subsamples were sealed in 60-$cm^3$ glass jars and incubated at 0, 10, 20, 30, 40, or 50 ± 1 C constant storage temperatures for 4, 7, 14, or 28 days. At the end of each storage interval, one jar was removed from each temperature regime to determine the seed germination percentage for the different afterripening conditions. Six replicates of 25 seeds each were placed on two distilled water-saturated Whatman number 2 filter paper disks in 9-cm diameter petri dishes and incubated for 27 days at 10, 20, or 30 ± 1 C constant temperature in the dark. Germinated seeds were counted and removed at 3- to 7-day intervals when a minimum 5 mm of radicle extended through the seedcoat.

The entire experiment, minus the time zero germination test, was analyzed as a completely randomized design with a factorial arrangement of treatments.

*Endogenous Rhythm*. Mature seeds of downy brome were hand-harvested at Pullman, Washington in mid- to late-July of 1977 and 1978 and cleaned as described above. Each year's seed lot was divided in half, and stored in tightly closed glass containers (one-half at 0 and one-half at 20 ± 1 C). Commencing shortly after harvest, germination of the 1977 seed lot was measured for 1 year at 1- to 2-month intervals. The germination of the 1978 seed lot was measured monthly for 6 months. The germination percentage was determined by placing 25 seeds in petri dishes as above and incubating in the dark at 15 and 20 ± 1 C constant temperature for 21 days.

Both experiments were analyzed as completely randomized designs with four and eight replications per treatment for the 1977 and 1978 seed lots, respectively.

## Results and Discussion

*Afterripening*. The germination percentage of freshly harvested downy brome seeds at 15 and 20 C germination temperature was initially high (time 0), and essentially unaffected by the temperature and duration of afterripening (Table 8). Freshly harvested downy brome seeds are reported to have high germination initially at 15 C, but reduced levels of germination at 20 constant and 20 to 30 C alternating temperature (6). The germination at the two higher temperatures was reported to improve with age after harvest. The high germination at 20 C immediately after harvest in our experiment is contrary to all previous reports. Apparently the seeds had partially afterripened on the plants, in the field prior to the harvest. However, at the 30 C germination temperature, the percentage of germination after 6 days incubation was markedly influenced by the temperature and duration of afterripening (Table 8). After 4 and 7 days storage, germination increases 23 and 28%, respectively, at 50 C when compared to 0 C afterripening temperature (Table 8). Similar results occurred after 14 days and 28 days storage at 20 to 40 C afterripening temperature. Taylorson and Brown (8) have reported similar

results for 12 other species of annual grass exposed to 50 C afterripening temperature for 14 days or less, and they have referred to the process as accelerated afterripening.

After 4, 7, and 14 days storage, the germination percentage at 30 C tended to increase with increasing afterripening temperature, while after 28 days storage, the germination percentage initially increased with increasing afterripening temperature and then declined at the higher storage temperatures (Table 8). Prolonged high temperature afterripening treatments have also caused germination impairment in several other annual grasses (8).

After a germination period of 28 days, more than 79% had germinated in all treatments except one (data not shown). Germination in the 50 C, 28-day afterripening treatment incubated at 30 C was partially suppressed by severe fungal infection in three of the six replicates. If the contaminated dishes were excluded from the average, the germination percentage increased from 60 to 80%.

Extensive downy brome germination has been observed in the field in August under suitable moisture conditions. This is prior to the previously reported afterripening period required for the germination of downy brome seeds (4, 6). Mean maximum air temperature at Pullman, Washington exceeds 27 C in August, with maximum soil surface temperatures above 60 C during this same period. According to previous reports, little or no germination of new seeds of

downy brome occurs above 15 C (3). The data presented herein indicate that high temperature can cause accelerated afterripening in new downy brome seeds, which rapidly reduces the initial level of postharvest dormancy and broadens the temperature range at which successful germination can occur under otherwise suitable germination conditions.

*Endogenous Rhythm*. In all cases except one, no significant cyclic germination rhythms were observed for downy brome seeds (Tables 9 and 10). Germination in the 1978 seed, 0 C storage, and 20 C germination temperature appeared to have a cyclic germination pattern. However, the amplitude of the response was less than 10%, and no rhythmic germination pattern was observed in the same seed lot germinated at 15 C. Both test periods were of adequate length to determine if reported winter dormancy (1) was related to endogenous stimuli. Our results indicate that germination cycles in downy brome seeds are not controlled by endogenous factors.

## Literature Cited


1. Evans, R. A. and J. A. Young. 1975. Enhancing germination of dormant seeds of downy brome. Weed Sci. 23:354-357.

2. Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Monogr. 25:181-213.

3. Klemmedson, J. O. and J. G. Smith. 1964. Cheatgrass (*Bromus tectorus* L.). Bot. Rev. April-June:226-262.

4. Laude, H. M. 1956. Germination of freshly harvested seeds of some western range species. J. Range Manage. 9:126-129.

5. Maguire, J. D. 1969. Endogenous germination rhythms in seeds. Proc. Assoc. Off. Seed Anal. 59:95-100.

6. Steinbauer, G. P. and B. H. Grigsby. 1957. Field and laboratory studies on the dormancy and germination of the seeds of chess (*Bromus secalinus* L.) and downy bromegrass (*Bromus tectorus* L.). Weeds 5:1-4.

7. Sweeney, B. M. 1969. Rhythmic phenomena in plants. Exp. Bot., An. Internat'l Series of Mongr., Vol. 3. Academic Press, New York. p. 89-90.

8. Taylorson, R. B. and M. M. Brown. 1977. Accelerated after-ripening for overcoming seed dormancy in grass weeds. Weed Sci. 25:473-476.

9. Young, J. A. and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. Weeds Sci. 23:358-364.

10. Young, J. A., R. A. Evans, and R. E. Eckert, Jr. 1969. Population dynamics of downy brome. Weed Sci. 17:20-26.

*Table 8.* The influence of afterripening temperature and duration on the germination percentage of *Bromus tectorum* L.

| Afterripening temperature C | Germination percentage after 6 days incubation[a] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Days at afterripening temperature | | | | | | | | | | | |
| | 4 | | | 7 | | | 14 | | | 28 | | |
| | Germination temperature, C | | | | | | | | | | | |
| | 15 | 20 | 30 | 15 | 20 | 30 | 15 | 20 | 30 | 15 | 20 | 30 |
| 0 | 91a-c | 87a-e | 51mn | 89a-d | 81b-g | 50mn | 91a-c | 85a-f | 50mn | 87a-e | 85a-f | 49n |
| 10 | 80c-g | 81b-g | 60j-m | 85a-f | 85a-f | 56l-n | 87a-e | 86a-e | 57l-n | 91a-c | 87a-e | 55l-n |
| 20 | 86a-e | 85a-f | 58k-n | 87a-e | 80c-g | 68h-l | 89a-d | 84a-f | 69h-j | 92ab | 88a-e | 73g-i |
| 30 | 81b-g | 86a-e | 58k-n | 90a-c | 84a-f | 74f-i | 91a-c | 87a-e | 81b-g | 88a-e | 93a | 82a-g |
| 40 | 85a-f | 86a-e | 64i-l | 91a-c | 88a-e | 65i-l | 93a | 86a-e | 82a-g | 88a-e | 87a-e | 69h-j |
| 50 | 91a-c | 89a-d | 74f-i | 89a-d | 89a-d | 78d-h | 84a-f | 87a-e | 77e-h | 87a-e | 88a-e | 65i-l |

[a]Means followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test ($S_{\bar{x}}$ = 3.23 and n = 6). Mean germination at 0 days after harvest = 84, 91, and 57% for germination temperatures of 15, 20, and 30 C, respectively.

*Table 9.* Germination percentage of 1977 seeds of *Bromus tectorum* L. at various intervals after harvest

| Days after harvest[a] | Storage temperature, C | | | |
|---|---|---|---|---|
| | 0 | | 20 | |
| | Germination temperature, C | | | |
| | 15 | 20 | 15 | 20 |
| | % | | | |
| 5 | 51 c[b] | | 53 b | |
| 42 | 51 c | 46 c | | |
| 102 | 56 bc | 48 c | 68 a | 58 a |
| 161 | 58 a-c | 46 c | 70 a | 65 a |
| 176 | | | 67 ab | 68 a |
| 204 | 70 ab | 63 ab | 70 a | 74 a |
| 253 | 73 a | 58 bc | 65 ab | 67 a |
| 294 | 66 a-c | 65 ab | 59 ab | 71 a |
| 322 | 69 ab | 73 a | 59 ab | 71 a |

[a]Seeds harvested on July 20, 1977.

[b]Means within columns followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test.

*Table 10*. Germination percentage of 1978 seeds of downy brome at various intervals after harvest

| Days after harvest[a] | Storage temperature, C | | | |
|---|---|---|---|---|
| | 0 | | 20 | |
| | Germination temperature, C | | | |
| | 15 | 20 | 15 | 20 |
| | % | | | |
| 0 | 89 ab[b] | 92 ab | 89 ab | 92 a |
| 41 | 93 a | 93 a | 86 b | 91 a |
| 68 | 91 ab | 88 a-c | 88 ab | 88 a |
| 96 | 87 ab | 83 c | 91 ab | 91 a |
| 126 | 85 b | 86 bc | 88 ab | 89 a |
| 147 | 89 ab | 92 ab | 93 a | 89 a |

[a]Seeds harvested July 21, 1978.

[b]Means within columns followed by like letters are not significantly different at the 5% level of probability according to Duncan's New Multiple Range Test.

# APPENDIX

# I. PRELIMINARY EXPERIMENTS

## Introduction

Several preliminary experiments were conducted in order to develop suitable techniques to test the influence of drought and temperature on downy brome seed germination. Parameters studied included the use of mannitol as an osmotic agent to produce germination media of varying osmotic potentials, the use of different soil moisture contents to produce germination media of various matric potentials, and the use of laboratory vs. freezer-stored downy brome seeds.

## Materials and Methods

*Mannitol study.* Solutions of mannitol, ranging in osmotic potential from 0 to -14.9 bars, were prepared according to the Van't Hoff equation. A solution volume of 7.5 ml was added to each 9-cm diameter petri dish, which contained two filter paper disks. In addition, each plant contained 50 ppm of PCNB (parachloronitrobenzene) plus 50 ppm of streptomycin sulfate to suppress fungal and bacterial growth, respectively. Twenty-five freezer-stored (-17 C) downy brome seeds (1977 seed lot) were counted into each petri dish. Petri dishes of each osmotic solution were incubated at 7, 14, 21, and 28 C constant temperature, and 5 to 10, 15 to 25, and 20 to 30 C alternating

temperature. The diurnal cycle for the alternating temperatures was 8 h in the light at the high temperature, and 16 h in the dark at the low temperature. Germination counts were made at 2- to 5-day intervals for 28 days. Seeds were considered germinated when 5 mm of radicle extended through the seedcoat. The experiment was analyzed as a completely randomized design with four replications per treatment.

*Soil Study.* Soils of various soil matric potential were prepared as previously described in Chapter II. The soil matric potential ranged from -4.1 to -16.7 bars. Wax-coated paper cups, of approximately a 240-ml volume, were filled to within 2 cm of the top with 260 g equivalent of air dry soil, and packed to a bulk density of 1.26 g $cm^{-3}$. Fifteen freezer-stored downy brome seeds were evenly distributed on the seedbed, covered with 20 g equivalent of air dry soil, and packed to a final bulk density of 1.26 g $cm^{-3}$. The cups were covered with parafilm and plastic lids.

A 0-bar water potential treatment was established by germinating 25 seeds on two distilled water-saturated filter paper disks in 9-cm diameter petri dishes.

The cups and petri dishes were incubated in the dark at 10, 15, and 20 C constant temperature, and 0 to 10, 0 to 15, and 10 to 25 C alternating temperature. The diurnal cycle for the alternating temperatures was 8 h at the high temperature, and 16 h at the low temperature.

Seeds were considered germinated when 5 mm of radicle extended through the seed coat and were considered emerged when the coleoptile emerged through the soil surface. Observations were made at 2- to 5-day intervals for a period of 39 days.

The experiment was analyzed as a completely randomized design with four replications per treatment.

*Laboratory vs. Freezer-Stored Seed.* This experiment was run concurrently with the soil study. Laboratory-stored (20 ± 1 C) seeds of downy brome were placed in petri dishes and incubated in a manner identical to the 0-bar water potential treatment described in the preceding section.

## Results and Discussion

*Mannitol Study.* The results of the mannitol solution study are presented in Table 11. Analyses of variance invariably showed the effect of mannitol solutions, temperature, and their interactions to be highly significant ($P < 0.01$). However, mannitol was not used in any subsequent experiment because of excessive fungal and bacterial contamination even when PCNB and streptomycin sulfate were used to suppress their growth. In addition, the relatively low molecular weight and small molecular size of mannitol can allow the solute to move into the germinating seed and reduce the true drought level of the solution.

*Soil Study*. This experiment was conducted to determine the interactive effect of soil matric potential and temperature on downy brome seedling emergence. The data are presented in Table 12.

Three severe complications developed in this experiment which did not allow a reliable interpretation of the data. First, the volume of soil placed in the cups did not allow adequate head space for the emerging seedlings, which at times punctured the parafilm seal. Second, the soil bulk density proved to be a major factor limiting seedling emergence. This was determined at the termination of the experiment when many seeds were found to have germinated but not emerged through the compacted surface layer. Third, the lids and parafilm seal on the cups had to be removed at each observation time. This allowed some loss of moisture from the cups and promoted the subsequent drying of the soil surface. Thus, the major contribution of this experiment was in the development of suitable techniques for subsequent studies.

*Laboratory vs. Freezer-Stored Seed*. The objective of this study was to determine if the germination potential of laboratory-stored seeds was greater than that of freezer-stored seed. The average germination percentage (Table 13) summed over the six temperature treatments, of the laboratory-stored seed was slightly greater than that of the 0-bar treatment of the freezer-stored seeds in Table 12

(58% vs. 51%). We decided to use the laboratory-stored seed in all subsequent experiments.

*Table 11.* The influence of temperature and osmotic potential on the germination of freezer-stored *Bromus tectorum* L.

| Temperature, C | Germination[a] Mannitol osmotic potential, -bars | | | | |
|---|---|---|---|---|---|
| | 0 | 1.9 | 3.9 | 7.7 | 14.9 |
| | % | | | | |
| 7 | 66.7 a | 38.3 c-3 | 15.0 ij | 19.2 g-i | 2.5 kl |
| 14 | 50.8 b | 40.0 b-d | 50.8 b | 25.0 f-i | 13.4 i-k |
| 21 | 31.7 d-f | 30.0 d-g | 21.7 f-i | 2.5 kl | 0.0 kl |
| 28 | 20.9 f-i | 13.3 l-k | 5.8 j-l | 0.0 kl | 0.0 kl |
| 5 to 10 | 40.8 b-d | 39.2 b-e | 40.0 b-d | 19.2 g-i | 0.0 kl |
| 15 to 25 | 30.8 d-g | 27.5 e-h | 6.7 j-l | 0.0 kl | 0.0 kl |
| 20 to 30 | 47.5 bc | 29.2 d-g | 15.9 h-j | 1.7 kl | 0.0 kl |

[a]Means followed by like letters are not significantly different at the 5% level of probability according to Duncan's new multiple range test ($S_{\bar{x}}$ = 3.74, with n = 4).

*Table 12.* The influence of temperature and soil moisture on the germination and emergence of freezer-stored *Bromus tectorum* L.

| Temperature, C | Germination or emergence[a] Soil matric potential, -bars | | | | |
|---|---|---|---|---|---|
| | 0 | 4.1 | 7.4 | 11.4 | 16.7 |
| | % | | | | |
| 10 | 54.0 a | 23.3 c-f | 25.0 c-e | 20.0 d-f | 1.7 gh |
| 15 | 56.0 a | 30.0 cd | 16.7 d-f | 3.4 gh | 0.0 h |
| 20 | 48.0 ab | 10.0 e-h | 10.0 e-h | 1.7 gh | 0.0 h |
| 0 to 10 | 52.0 a | 36.7 bc | 25.0 c-e | 6.7 gh | 0.0 h |
| 0 to 15 | 45.0 ab | 51.7 ab | 10.0 e-h | 0.0 h | 0.0 h |
| 10 to 25 | 52.0 a | 13.4 e-h | 8.4 f-h | 0.0 h | 0.0 h |

[a]Means followed by like letters are not significantly different at the 5% level of probability according to Duncan's new multiple range test ($S_{\bar{x}}$ = 4.85 with n = 4). Soil bulk density = 1.26 g $cm^{-3}$.

*Table 13.* The effect of temperature on the germination of laboratory-stored *Bromus tectorum* L.

| Temperature | Germination[a] |
|---|---|
| | —— % —— |
| 10 | 59.0 a |
| 15 | 68.0 a |
| 20 | 58.0 a |
| 0 to 10 | 52.0 a |
| 0 to 15 | 52.0 a |
| 10 to 25 | 59.0 a |

[a]Means followed by like letters are not significantly different at the 5% level of probability according to Duncan's new multiple range test ($S_{\bar{x}}$ = 6.12, with n = 4).

# II. LONGEVITY OF *BROMUS TECTORUM* L. SEEDS IN SOIL

## Introduction

The reported longevity of viable downy brome seeds in the soil varies widely. Hulbert (3) and Klemmedson and Smith (4) assumed because of the rapid and high percentage germination of freshly harvested seeds that all available seeds would germinate when conditions were suitable and no viable but ungerminated seeds would remain in the soil. On the other hand, other investigators showed that viable downy brome seeds do persist in the soil for one or more reasons (5, 2).

The purpose of this study was to determine if viable downy brome seeds do persist in the soil for at least one season.

## Materials and Methods

*Field Planting Study.* On 3 October 1977, downy brome field plots were established at the Land Management and Conservation Farm approximately 5 km north of Pullman, Washington. The plots were 1.0 $m^2$ with four planted rows spaced 20 cm apart. Fifty seeds were planted 2 cm apart within each row. Treatments included rototilling 10 cm deep, an undisturbed bare soil surface with all existing wheat straw residue removed, and an undisturbed surface

without residue removed. Seeds collected during July 1977 were planted 1.3 cm deep in the rototilled plots, planted 0.1 cm deep in the undisturbed bare soil treatment, and laid on the existing straw residue and covered loosely with 4.0 metric tons (approximately 4 cm deep) of fresh wheat straw in the undisturbed straw plots. To prevent the added straw from blowing away, the straw-added plots were covered with polypropylene netting.

Emergence counts were made periodically for 1 year. Seedlings were considered emerged when the coleoptile emerged through the soil surface.

On 12 May 1978, all plots were sprayed with 0.56 kg $ha^{-1}$ (a.e.) of glyphosate (N-(phosphonomethyl)glycine) to prevent seed formation and to dessicate the existing downy brome plants. The plots were hand weeded throughout the summer. In late October, the final emergence observations were made, and the experiment was terminated.

*Seed Burial*. Downy brome seeds were collected during July 1977 and stored in the laboratory at 20 ± 1 C until burial. In early October, 400 10.2-$cm^2$ nylon mesh packets of 100 seeds each were buried approximately 20 cm deep in the field at the Land Management and Conservation Farm. The germination potential of the seedlot was determined just prior to burial by placing 25 seeds on two filter paper disks in four 9-cm diameter petri dishes and incubating in the dark at 15 and 20 C constant temperature. Seeds were

considered germinated when 0.5 cm of radicle extended through the seedcoat. The germination period was 28 days.

Twenty seed packets were exhumed 85 days after burial and returned to the laboratory. The packets were washed free of soil, and the number of seeds germinated during burial was determined. The viability of the nongerminated seeds was determined using the standard germination test previously described. The duration of the test was 45 days. The remaining seed packets were stored at 0 C.

One hundred ninety-eight days after burial, 30 more seed packets were exhumed. An attempt was made to count the germinated seeds per packet, but natural deterioration in the soil and the washing procedure prevented reliable determinations. A standard germination test at 15 C constant temperature was conducted on eight replicates of the cold-stored 85-day-old seed and the freshly exhumed 198-day-old seed. Ten packets of the 198-day-old seed were stored in the laboratory at 20 ± 1 C, and at 0 C.

Both the laboratory and cold-stored 198-day-old seeds were incubated at 20 C constant temperature in a solution of 0.1 mmole $KNO_3$ + 0.14 mmole $GA_3$ 218 days after burial. It had been reported that this solution could enhance the germination of dormant downy brome seeds (1). Observations were made periodically for 28 days.

## Results

*Field Planting Study.* Final percentage of emergence in the bare soil with the straw-removed treatment was more than twice that in the rototilled plots (Table 14). No seedling emergence was noted in the straw-added treatment. The number of seedlings emerged was initially higher in the rototilled plots, but did not change appreciably with time. The seedling emergence in the straw-removed plots increased throughout the month of November and then leveled off. The slight decline in cumulative emergence overwinter was probably due to seedling mortality. After the spring application of glyphosate, no emergence was observed in any treatment.

*Seed Burial.* The average number of seeds germinated per packet during 85 days of burial was 49% (s = 5.9 and n = 4). The percentage germination of the seed lot prior to burial was 68 and 59% at 15 and 20 C, respectively.

In all subsequent germination tests on the 85 and 198-day-old seeds, no germination was observed.

Seeds exhumed 198 days after burial were studied under a 10X binocular microscope. In most instances, the seeds were found to have severely deteriorated or entirely missing embryos, and lacked endosperms.

## Discussion

The results of the seed burial experiments at Pullman, Washington, indicate that viable downy brome seeds do not

persist in the soil from one season to the next. This is in agreement with Hulbert (3), and Klemmedson and Smith (4). Some seeds that germinated during burial may have expired due to depth of burial, and adverse or unfavorable environmental, microbial, or soil conditions. Viable seeds which did not germinate in the soil were possibly subjected to microbial attack. However, under natural conditions, seeds near the soil surface may acquire an environmentally induced winter dormancy that would allow part of the seed population to survive from one season to the next (1).

## Literature Cited

1. Evans, R. A. and J. A. Young. 1975. Enhancing germination of dormant seeds of downy brome. Weed Sci. 23:354-357.

2. Finnerty, D. W. and D. L. Klingman. 1962. Life cycles and control studies of some weed bromegrasses. Weeds 10:40-47.

3. Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Mono. 25:181-213.

4. Klemmedson, J. O. and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). The Bot. Review, Apr-June:226-262.

5. Young, J. A., R. A. Evans, and R. E. Eckert, Jr. 1969. Population dynamics of downy brome. Weed Sci. 17:20-26.

*Table 14.* Average seedling emergence percentage of *Bromus tectorum* L. in the field

| Date | Cumulative seedling emergence | | |
|---|---|---|---|
| | Rototilled | Bare, no straw | Bare, straw added |
| | % | | |
| 20 October 1977 | 8.0 | 4.9 | 0.0 |
| 25 October | 8.8 | 6.1 | 0.0 |
| 28 October | 8.3 | 6.1 | 0.0 |
| 2 November | 8.5 | 6.5 | 0.0 |
| 7 November | 8.8 | 9.4 | 0.0 |
| 15 November | 9.3 | 15.8 | 0.0 |
| 29 November | 9.3 | 20.8 | 0.0 |
| 18 January 1978 | 8.9 | 19.9 | 0.0 |
| 31 March | 8.4 | 18.5 | 0.0 |
| 12 May | 8.4 | 17.4 | 0.0 |
| Sprayed[a] | | | |
| 31 October | 0.0 | 0.0 | 0.0 |

[a]Plots sprayed with 0.56 kg $ha^{-1}$ glyphosate on 12 May 1978.

## III. WATER POTENTIAL EFFECTS ON SEED GERMINATION: BIBLIOGRAPHY

Akalehiywot, T. and J. D. Bewley. 1977. Promotion and synchronization of cereal grain germination by osmotic pre-treatment with polyethylene glycol. J. Agric. Sci. 89:503-506.

Aldon, E. F. 1969. Alkali Sacaton Seedlings: Germination and survival in an agar medium. USDA. Forest Service Research Note RM-156. 1-3.

Ayers, A. D. 1952. Seed germination as affected by soil moisture and salinity. Agron. J. 44:82-83.

Cleland, R. 1967. A dual role of turgor pressure in auxin-induced cell elongation in *Avena coleoptiles*. Planta (Berl.) 77:182-191.

Collis, George N., and J. B. Hector. 1966. Germination of seeds as influenced by matric potential and by the area of contact between the seed and soil water. Aust. J. Soil Res. 4:145-164.

Collis, George N., and J. E. Sands. 1959. The control of seed germination by moisture as a soil physical property. Aust. J. Agric. Res. 10:628-636.

Collis, George N., and J. E. Sands. 1961. Moisture conditions for testing germination. Nature 190:367.

Collis, George N., and J. E. Sands. 1962. Comparison of the effects of the physical and chemical components of soil water energy on seed germination. Aust. J. Agric. 13:575-584.

Collis, George N., and J. Williams. 1968. The comparative influence of matric potential and effective isotropic stress on germination of *Lactuca sativa*. Aust. J. Soil Res. 6:179-192.

Dasberg, S. 1971. Soil water movement to germinating seeds. J. Exp. Bot. 22:999-1008.

Dasberg, S., and Mendel, K. 1971. The effect of soil water and aeration on seed germination. J. Exp. Bot. 22:992-998.

Doneen, L. D. and J. H. MacGillivery. 1943. Germination (emergence) of vegetable seeds as affected by different soil moisture conditions. Plant Physiol. 18: 524-529.

Esashi, Y. and A. C. Leopold. 1968. Physical forces in dormancy and germination of *Xanthium* seeds. Plant Physiol. 43:871-876.

Gingrich, J. R. and M. B. Russel. 1956. Effect of soil moisture tension and oxygen concentration on the growth of corn roots. Agron. J. 48:517-521.

Greenway, H. R., R. G. Hiller, and T. Flowers. 1968. Respiration inhibition in chlorella produced by purified polyethylene glycol 1540. Science 159:984-985.

Hadas, A. 1969. Effects of soil moisture stress on seed germination. Agron. J. 61:325-327.

Hadas, A. 1970. Factors affecting seed germination under soil moisture stress. Israel J. Agr. Res. 20:3-14.

Hadas, A. 1976. Water uptake and germination of leguminous seeds under changing external water potential in osmotic solutions. J. Exp. Bot. 27:480-489.

Hadas, A. 1977. A simple laboratory approach to test and estimate seed germination performance under field conditions. Agron. J. 69:582-587.

Hadas, A. 1977. Water uptake and germination of leguminous seeds in soils of changing matric and osmotic water potential. J. Exp. Bot. 28:977-985.

Hadas, A. and D. Russo. 1974. Water uptake by seeds as affected by water stress, capillary conductivity, and seed soil water contact. I. Experimental Study. Agron. J. 66:643-647.

Hadas, A. and D. Russo. 1974. Water uptake by seeds as affected by water stress, capillary conductivity, seed soil water content. II. Analysis of Experimental Data. Agron. J. 66:647-651.

Hadas, A. and E. Stibbe. 1973. An analysis of soil water movement towards seedlings prior to emergence. *In* A. Hadas et al. (ed.) Physical aspects of soil water and salts in ecosystems. Ecological studies. Vol. 4: 97-106. Springer-Verlag, Heidelberg.

Hagon, M. W. and C. W. Chan. 1977. The effects of moisture stress on the germination of some Australian native grass seeds. Aust. J. Exp. Agric. Ani. Husb. 17:86-89.

Halitligil, Mahmut Basri. 1975. Effect of soil moisture, temperature, bulk density, and texture on emergence of three wheat varieties (*Triticum aestivum*, L.) MS Thesis. Oregon State University, Corvallis, OR.

Harper, J. L. and R. A. Benton. 1966. The behavior of seeds in the soil. II. The germination of seeds on the surface of a water supplying substrate. J. Ecol. 54:151-166.

Hegarty, T. W. 1977. Seed activation and seed germination under moisture stress. New Physiol. 78:349-359.

Helmrich, R. H. and R. P. Pfeifer. 1954. Differential varietal response of winter wheat germination and early growth to controlled limited moisture conditions. Agron. J. 46:560-562.

Heydecker, W., J. Higgins, and R. L. Gulliver. 1973. Accelerated germination by osmotic seed treatment. Nature 246:42-44.

Hillel, D. 1972. Soil moisture and seed germination. *In* Water deficits and plant growth. T. T. Kozlowski (ed.) Vol. III, pp. 65-69. Academic Press, N.Y.

Hoveland, C. S. and G. A. Buchanan. 1973. Weed seed germination under simulated drought. Weed Sci. 21:322-324.

Hunter, J. R. and A. E. Erickson. 1952. Relation of seed germination to soil moisture tension. Agron. J. 44: 107-110.

Jackson, W. T. 1962. Use of carbowaxes (Polyethylene Glycols) as osmotic agents. Plant Physiol. 37:513-519.

Kaufmann, M. 1969. Effect of water potential in germination of lettuce, sunflower, and citrus seeds. Canad. J. Bot. 47:1761-1764.

Kaufmann, M. R. and A. N. Eckard. 1971. Evaluation of water stress control with polyethylene glycols by analyses of guttation. Plant Physiol. 47:453-456.

Kaufmann, M. R. and A. N. Eckard. 1977. Water potential and temperature effects on germination of Englemann Spruce and Lodgepole Pine seeds. For. Sci. 23:27-33.

Kaufmann, R. R. and K. J. Ross. 1970. Water potential, temperature and kinetin effects on seed germination in soil and solute systems. Am. J. Bot. 57:413-419.

Kneebone, W. R. 1957. Selection for seedling vigor in native grasses under artified moisture stress. Agron. Abstracts.

Koller, D. 1972. Environmental control of seed germination. *In* T. T. Kozlowski (ed.) Seed Biology. Vol. 2. Academic Press, New York.

Lagerwerff, J. V., G. Ogata, and H. E. Eagle. 1961. Control of osmotic pressure of culture solutions with polyethylene glycol. Science 133:1486-1487.

Lazenby, A. 1955. Germination and establishment of *Juncus effusus*. II. The interaction effects of moisture and competition. J. Ecol. 43:595-605.

Lewak, S. and A. A. Khan. 1977. Mode of action of gibberlic-acid and light on lettuce seed germination. Plant Physiol. 60:575-577.

Malik, R. S. 1975. Note on the relative seed germination under simultaneous action of matric and osmotic tension. Indian J. Agric. Res. 9:217-219.

Manohar, M. S. 1966. Effect of "osmotic" systems on germination of peas (*Pisum sativum* L.) Planta (Berl.) 71:81-86.

Manohar, M. S. 1966. Measurement of water potential of intact tissues. III. The water potentials of germinating peas (*Pisum sativum* L.). J. Exp. Bot. 17: 231-235.

Manohar, M. S. and W. Heydecker. 1964. Effect of water potential on germination of pea seeds. Nature, Lond. 202:22-24.

Maguire, J. D. 1972. Physiological disorders in germinating seeds induced by the environment. *In* W. Heydecker (ed.) Seed Ecology. The Pennsylvania St. Univ. Press, Univ. Park.

McDonough, W. T. 1975. Water potential of germinating seeds. Bot. Gaz. 136:106-108.

McGinnies, W. J. 1960. Effect of moisture stress and temperature on germination of six range grass. Agron. J. 52:159-162.

McWilliam, J. R. and P. J. Phillips. 1971. Effect of osmotic and matric potentials on the availability of water for seed germination. Aust. J. of Biol. Sci. 24:423.

Mexal, J., J. T. Fisher, J. Osteryoung, and C. P. P. Reid. 1975. Oxyten availability in polyethylene glycol solutions and its implications in plant-water relations. Plant Physiol. (Lancaster) 55:20-24.

Michel, B. E. 1970. Carbowax 6000 compared with mannitol as a suppressant of cucumber hypocotyl elongation. Plant Physiol. 45:507-509.

Michel, B. E. 1971. Further comparison between Carbowax 6000 and mannitol as suppressants of cucumber hypocotyl elongation. Plant Physiol. 48:513-516.

Michel, B. E. 1972. Solute potential of sucrose solutions. Plant Physiol. 50:196-198.

Michel, B. E. and M. R. Kaufmann. 1973. The osmotic potential of polyethylene glycol 6000. Plant Physiol. 51:914-916.

Muchena, S. C. and C. O. Grogan. 1977. Effect of seed size on germination of corn (*Zea mays*)under simulated water stress conditions. Can. J. Plant Sci. 57:921-924.

Nabors, M. W. and A. Lang. 1971. The growth physics and water relations of redlight-induced germination in lettuce seed. I. Embryos germinating in osmoticum. Planta (Berl.) 101:1-25, by Springer-Verlag.

Nabors, M. W. and A. Lang. 1971. The growth physics and water relations of red-light-induced germination in lettuce seeds. II. Embryos Germinating in Water. Planta (Berl.) 101:26-42, by Springer-Verlag.

Parmar, M. T. and R. P. Moore. 1966. Effect of simulated drought by polyethylene glycol solutions on corn (*Zea maize* L.) germination and seedling development. Agron. J. 58:391-392.

Pawloski, M. C. and C. F. Shaykewich. 1972. Germination of wheat as affected by soil water stress. Can. J. Plant Sci. 52:619-623.

Scifres, C. J. and J. H. Broct. 1969. Seed soaking as a presowing drought hardening in wheat and barley seedlings. Agron. J. 60:179-182.

Sedgley, R. H. 1963. The importance of liquid-seed contact during germination of *Medicago tribuloides*. Aust. J. Agric. Res. 14:646-653.

Sharma, M. L. 1973. Simulation of drought and its effects on germination of five pasture species. Agron. J. 65: 982-987.

Sharma, M. L. 1976. Interaction of water potential and temperature effects on germination of three semi-arid plant species. Agron. J. 68:390-394.

Sharma, M. L., D. K. McBeath, and W. H. Vanden Born. 1977. Studies on the biology of wild oats. Part 2: Growth. Can. J. Plant. Sci. 57:811-818.

Srivastava, A. K. and G. Singh. 1975. Ecology of germination of wheat and triticale seeds in relation to temperature and moisture stress. Indian J. Ecol. 2: 132-138.

Stiles, I. E. 1949. Relation of water to the germination of bean seeds. Plant Physiol. 25:540-545.

Tao, K. L. and A. A. Khan. 1977. Biochemical changes during osmotic conditioning of lettuce seeds. Plant Physiol. 59:86.

Thimann, K. V., G. M. Loos, and E. W. Samuel. 1960. Penetration of mannitol into potato discs. Plant Physiol. 35:848-853.

Thompson, P. A. 1977. A note on the germination of Narciscus-bulbocadium. New Phytol. 79:287-290.

Uhvits, R. 1946. Effects of osmotic pressure on water absorption and germination of alfalfa seeds. Am. J. Bot. 33:278-285.

Waldon, L. J. and T. Manbeian. 1970. Soil moisture characteristics by osmosis with polyethylene glycol: A simple system with osmotic pressure data and some results. Soil Sci. 110:401-404.

Wiggans, S. C. and F. P. Gardner. 1959. Effectiveness of various solutions for simulating drought conditions as measured by germination and seedling growth. Agron. J. 51:315-318.

Williams, J. and C. F. Shaykewich. 1969. An evaluation of polyethylene glycol (PEG) 6000 and 20,000 in the osmotic control of soil water matric potential. Can. J. Soil Sci. 49:397-401.

Williams, J. and C. F. Shaykewich. 1971. Influence of soil water potential and hydraulic conductivity on germination of rape (*Brassica napus* L.). J. Expt. Bot. 22:386-397.

Wilson, A. M. 1970. Incorporation of $^{32}P$ in seeds at low water potential: Evaluation of microbiological contamination. Plant Physiol. (Lancaster) 45:524.

Wilson, A. M. and G. A. Harris. 1968. Phosphorylation in crested wheatgrass seeds at low water potentials. Plant Physiol. (Lancaster) 43:61.

Wood, M. K., R. W. Knight, and J. A. Young. 1976. Spiny hopsage germination. J. Range Manage. 29:53-56.

Woods, L. K. and H. A. MacDonald. 1971. The effect of temperature and osmotic moisture stress on germination of *Lotus corniculatus*. J. Expt. Bot. 1031-1032.

Yaklich, R. W. and Orzolek, M. D. 1977. Effect of polyethylene glycol 6000 on pepper seed. Hort. Sci. 12: 263-264.

Young, J. A. and R. A. Evans. 1972. Germination and establishment of *Salsola* in relation to seedbed environment. I. Temperature, after ripening, and moisture relations of *Salsola* seeds as determined by laboratory studies. Weed Science 64:214-218.

Young, J. A. and R. A. Evans. 1976. Stratification of Bitterbrush seeds. J. Range Manage. 29:421-425.

Young, J. A., R. A. Evans, R. O. Gifford, and R. E. Eckert, Jr. 1968. Germination of Medusahead in response to osmotic stress. Weed Sci. 16:364-368.

Young, J. A., R. A. Evans, R. O. Gifford, and R. E. Eckert, Jr. 1970. Germination characteristics of three species of *Cruciferse*. Weed Sci. 18:41-47.

# IV. *BROMUS TECTORUM* L.: A BIBLIOGRAPHY

Al-Ansary, M. M. and D. C. Smith. 1976. Variation in seed and seedling characters of smooth bromegrass, *Bromus intermis*, in relation to environment. Euphytica 25: 549-558.

Bleak, A. T. and W. Keller. 1972. Germination and emergence of selected forage species following preplant seed treatment. Crop Sci. 12:9-13.

Bovey, R. W., D. LeTourneau, and L. C. Erickson. 1961. The chemical composition of medusahead and downy brome. Weeds 9:307-311.

Bruns, V. F., W. W. Heinemann, and D. L. Oldemeyer. 1959. Control of downy brome in alfalfa and related studies. U. S. Dept. of Agr. Tech. Bull. No. 1197:29.

Canode, C. L., W. C. Robocker, and T. J. Muzik. 1962. Grass seed production as influenced by chemical control of downy brome. Weed Sci. 10:216-218.

Cline, J. F. and W. H. Rickard. 1973. Herbage yields in relation to soil and water and assimilated nitrogen. J. Range Manage. 26:296-298.

Cline, J. F., D. W. Uresk, and W. H. Rickard. 1977. Comparison of soil water used by a wagebrush-bunchgrass and a cheatgrass community. J. Range Manage. 30:199-201.

Day, T. L. 1975. Cheating a cheater. *Bromus tectorum* in competition with *Agropyron spicatum*. Wash. St. Ag. Exp. Sta. Advance 12:4-5.

Eckert, R. E., Jr., J. E. Asher, M. D. Christensen, and R. A. Evans. 1974. Evaluation of the atrazine-fallow technique for weed control and seedling establishment. J. Range Manage. 27:288-292.

Eckert, R. E., Jr., and R. A. Evans. 1963. Responses of downy brome and crested wheatgrass to nitrogen and phosphorus in nutrient solutions. Weeds 11:170-174.

Eckert, R. E., Jr. and R. A. Evans. 1967. A chemical-fallow technique for control of downy brome and establishment of grasses on rangeland. J. Range Manage. 20:35-41.

Eckert, R. E., Jr., G. J. Klomp, J. A. Young, and R. A. Evans. 1970. Nitrate-nitrogen status of fallow rangeland soils. J. Range Manage. 23:445-447.

Evans, R. A. 1961. Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. Weeds 9:216-223.

Evans, R. A., R. E. Eckert, Jr., and B. L. Kay. 1967. Wheatgrass establishment with paraquat and tillage on downy brome ranges. Weeds 15:50-55.

Evans, R. A., R. E. Eckart, Jr., B. L. Kay, and J. A. Young. 1969. Downy brome control by soil-active herbicides for revegetation of rangelands. Weed Sci. 17:166-169.

Evans, R. A., H. R. Holbo, R. E. Eckert, Jr., and J. A. Young. 1970. Functional environment of downy brome communities in relation to weed control and revegetation. Weed Sci. 18:154-162.

Evans, R. A., B. L. Kay, and J. A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. Hilgardia 43:79-102.

Evans, R. A. and J. A. Young. 1970. Plant litter and establishment of alien annual species in rangeland communities. Weed Sci. 18:697-702.

Evans, R. A. and J. A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. Weed Sci. 20:350-356.

Evans, R. A. and J. A. Young. 1975. Enhancing germination of dormant seeds of downy brome. Weed Sci. 23:354-357.

Evans, R. A. and J. A. Young. 1977. Weed control-revegetation systems for big sagebrush-downy brome rangelands. J. Range Manage. 30:331-336.

Fenster, C. R. 1976. Cheatgrass-*Bromus tectorum*. Control in small grains. Montana St. Univ. Coop. Ext. Serv. Bull. 1132:222-224.

Fenster, C. R., L. A. Morrow, M. K. McCarty. 1974. Downy brome control in native grass. Proc. Annual Meeting North Cent. Weed Control Conf. 29th, 52-53.

Fenster, C. R., G. A. Wicks, and L. R. Robison. 1970. Know and control downy brome. Univ. of Nebraska Agr. Ext. Serv. Circ. 70:188.

Finnerty, D. W. and D. L. Klingman. 1962. Life cycles and control studies of some weed bromegrasses. Weeds 10:40-47.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol. Monogr. 37:89-111.

Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. J. Range Manage. 30: 172-177.

Harris, G. A. and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. Ecology 41:530-534.

Haupt, H. F. 1956. Nitrogen loss from granitic soils on cheatgrass brome range. Forest Sci. 2:269-272.

Hinds, W. T. 1973. Small lysimeters for measurement of water use and herbage yield. J. Range Manage. 26:304-306.

Hinds, W. T. 1974. An ecological assessment of energy and carbon pathways in swards of *Bromus tectorum* L., BNWL-1882, Battelle, Pacific Northwest Laboratories, Richland, WA, 134 pp.

Hinds, W. T. 1975. Energy and carbon balances in cheatgrass: An essay in autecology. Ecol. Monographys 45: 367-388.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecol. Monographs 25: 181-213.

Hull, A. C., Jr. 1949. Growth periods and herbage production of cheatgrass and reseeded grasses in Southwestern Idaho. J. Range Manage. 2:183-186.

Hull, A. C., Jr. 1963. Competition and water requirements of cheatgrass and wheatgrasses in the greenhouse. J. Range Manage. 16:199-204.

Hull, A. C., Jr. 1964. Emergence of cheatgrass and three wheatgrasses from four seedling depths. J. Range Manage. 17:32-35.

Hull, A. C., Jr. and W. Theron Hansen, Jr. 1974. Delayed germination of cheatgrass seed. J. Range Manage. 27: 366-368.

Hull, A. C., Jr. and J. F. Pechanec. 1947. Cheatgrass--a challenge to range research. J. Forestry 45:555-564.

Hull, A. C., Jr. and G. Stewart. 1948. Replacing cheatgrass by reseeding with perennial grasses in Southern Idaho ranges. Soc. Agron. J. 40:694-703.

Kay, B. L. and R. A. Evans. 1965. Effects of fertilization on a mixed stand of cheatgrass and intermediate wheatgrass. J. Range Manage. 18:7-11.

Klemmedson, J. O. and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). The Bot. Review, April-June: 226-262.

Kline, L. G. and C. M. McKell. 1974. Bromegrass *(Bromus tectorum)* productivity in relation to precipitation, canopy cover, and soil nitrogen content. In Sectional Papers International Grassland Congress 12th (Sect. 4), 79-84.

Knowles, P. F. 1944. Interspecific hybridizations of *Bromus*. Genetics 29:128-140.

Kreitlow, L. W. and A. T. Bleak. 1964. *Podosporiella verticillate*, a soil-borne pathogen of some western Gramineae. Phytopathology 54:355-357.

LaTourrette, J. E., J. A. Young, and R. A. Evans. 1971. Seed dispersal in relation to rodent activities in seral big sagebrush communities. J. Range Manage. 24: 118-120.

Massee, T. W. 1976. Downy brome control in dryland winter wheat with stubble-mulch fallow and seeding management. Agron. J. 68:952-955.

Morrow, L. A., C. R. Fenster, and M. K. McCarty. 1977. Control of downy brome on Nebraska rangeland. J. Range Manage. 30:293-296.

Murray, R. B. 1971. Grazing capacity, sheep gains: Cheatgrass, bunchgrass ranges in Southern Idaho. J. Range Manage. 24:407-410.

Newman, E. I. 1963. Factors controlling the germination date of winter annuals. J. Ecol. 51:625-639.

Raguse, C. A., J. A. Young, and R. A. Evans. 1977. Germination of California annual range plants in response to a summer rain. Agron. J. 69:327-329.

Rickard, W. H., J. F. Cline, and R. O. Gilbert. 1973. Soil beneath shrub halophytes and its influence upon the growth of cheatgrass. Northwest Sci. 47:213-217.

Robocker, W. C. 1961. The influence of perennial vegetation and precipitation on occurrence of *Halogeton glomeratus* and *Bromus tectorum* in arid and semi-arid regions. J. Range Manage. 14:28-34.

Robocker, W. C. 1973. Production potential of four winter annual grasses. J. Range Manage. 26:69-70.

Robocker, W. C. and C. L. Canode. 1965. Effects of litter, incorporated organic matter, soil type, and selective herbicides on seedlings of downy brome. Weed Sci. 13: 8-10.

Robocker, W. C., D. H. Gates, and H. D. Kerr. 1965. Effects of herbicides, burning, and seeding date in reseeding on arid range. J. Range Manage. 18:114-118.

Rummel, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. Ecology 27:159-167.

Rydrych, D. J. 1974. Competition between winter wheat and downy brome. Weed Sci. 22:211-214.

Savage, D. E., J. A. Young, and R. A. Evans. 1969. Utilization of medusahead and downy brome caryopses by Chukar partridges. J. Wildlife Manage. 33:975-978.

Steinbauer, G. P. and B. H. Grigsby. 1957. Field and laboratory studies on the dormancy and germination of the seeds of chess (*Bromus secalinus* L.) and downy bromegrass (*Bromus tectorum* L.). Weeds 5:1-4.

Stewart, G. and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.): An ecologic intruder in Southern Idaho. Ecology 30:58-74.

Stewart, G. and A. E. Young. 1939. The hazards of basing permanent grazing capacity on *Bromus tectorum*. Am. Soc. Agron. J. 31:1002-1015.

Swan, D. G., M. M. Oveson, and A. P. Appleby. 1974. Chemical and cultural methods for downy brome control and yield of winter wheat. Agron. J. 66:793-795.

Warg, S. A. 1938. Life history and economics studies on *Bromus tectorum*. Unpubl. M.S. thesis, State Univ. of Montana, Missoula.

Wicks, G. A., O. C. Burnside, and C. R. Fenster. 1971. Influence of soil type and depth of planting on downy brome seed. Weed Sci. 19:82-86.

Wilson, A. M. 1966. Fertilization of mixed cheatgrass-bluebunch wheatgrass stands. J. Range Manage. 19: 134-137.

Wilson, A. M., D. E. Wondercheck, and C. J. Goebel. 1974. Response of range grass seeds to winter environments. J. Range Manage. 27:120-122.

Young, J. A. and R. A. Evans. 1972. Conversion of medusa-head to downy brome communities with diuron. J. Range Manage. 25:40-43.

Young, J. A. and R. A. Evans. 1973. Downy brome: Intruder in the plant succession of big sagebrush communities in the Great Basin. J. Range Manage. 26:410-415.

Young, J. A., R. A. Evans, and B. L. Kay. 1971. Germination of caryopses of annual grasses in simulated litter. Agron. J. 63:551-555.

Young, J. A., R. A. Evans, and R. E. Eckert, Jr. 1969. Population dynamics of downy brome. Weed Sci. 17: 20-26.

Young, J. A. and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. Weed Sci. 23: 358-364.

Young, J. A., R. A. Evans, and B. L. Kay. 1973. Temperature requirements for seed germination in an annual-type rangeland community. Agron. J. 65:656-659.

Young, J. A., R. A. Evans, and R. A. Weaver. 1976. Estimating potential downy brome competition after wildfires. J. Range Manage. 29:322-325.