

AN ABSTRACT OF THE THESIS OF

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Title: EFFECTS OF ENVIRONMENTAL CONDITIONS ON GERMINATION AND

EARLY SEEDLING DEVELOPMENT IN AGROPYRON SPICATUM

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Richard F. Miller

This research evaluated the germination and early seedling development response of two sources of bluebunch wheatgrass (Agropyron spicatum) to a wide range of environmental conditions. Seeds collected near John Day, Oregon and Secar seed obtained from the Soil Conservation Service were used in the investigations.

Evaluation of the germination response to conditions of controlled temperature and moisture stress revealed similarities and differences between the two sources. Seed of both John Day and Secar germinated over the widest range of water potentials at 20 C. In all temperature regimes, rate of germination and total percent germination declined as moisture stress increased. As temperature moved away from the optimum 20 C, seeds were less able to germinate at increasing levels of moisture stress. Secar seed germinated better than John Day seed at higher levels of moisture stress when temper-

atures were favorable. At high temperatures (30 C), germination of Secar was suppressed at all levels of moisture stress, where John Day germinated well at 30 C and lower levels of moisture stress.

The effects of several soil moisture regimes on seedling development of the two sources of bluebunch wheatgrass were studied in a greenhouse trial. Soil moisture conditions were the same for all treatments through the emergence period, and John Day seedlings emerged faster than Secar seedlings. Since moisture was adequate at the onset of the study, all seedlings had an opportunity for initial growth and to develop good seminal root systems. Since John Day seedlings emerged first, they had a longer period for growth which resulted in larger herbage and root biomass production than in Secar. As soil moisture decreased, however, the rate and amount of seedling growth for both sources was suppressed. When seedlings were in the three-leaf stage and exposed to surface soil moisture above field capacity, adventitious roots were initiated. Secar seedlings developed adventitious roots sooner than John Day seedlings and produced significantly more and longer adventitious roots than John Day seedlings. Subsurface soil moisture above field capacity provided a favorable environment for rapid extension of adventitious roots once initiation had occurred.

Secar seedling development was also related to soil moisture and air temperature in a field study, and findings were similar to the results of the greenhouse study. Seedlings subjected to several weeks of dry soil conditions did not develop well. Most seedlings did not develop three leaves until the tenth week after planting when rainfall

increased soil moisture to field capacity. This moisture also stimulated initiation of adventitious roots. However, at the end of the 10 week study adventitious root system length averaged only 5.6 cm, and at this depth these roots would be very susceptible to drying conditions.

Effects of Environmental Conditions on Germination
and
Early Seedling Development in Agropyron spicatum

by

Angela G. Evenden

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Professor of Rangeland Resources in charge of major

Redacted for Privacy

Head of department of Rangeland Resources

Redacted for Privacy

Dean of Graduate School

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Typed by Angela G. Evenden

DEDICATION

This thesis is dedicated, with all my love to my parents,
Frederick G. Evenden (1921-1982) and Mildred J. Evenden (1922-1982).
I thank you both for your love and support through all the wonderful
years we had together, and for sharing with me your love of learning
and appreciation for the natural world around us.

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CONTRIBUTION OF AUTHORS

Dr. Richard F. Miller, major professor, and Dr. Marshall R. Haferkamp, committee member, greatly aided in consultation throughout all stages of this research, from set-up of the studies to review of the manuscripts.

EFFECT OF ENVIRONMENTAL CONDITIONS ON GERMINATION
AND
EARLY SEEDLING DEVELOPMENT IN AGROPYRON SPICATUM

INTRODUCTION

Bluebunch wheatgrass (Agropyron spicatum (Pursh) Scribner and Smith), a long-lived, cool season perennial bunchgrass, is considered an important native forage species (Sampson 1924). At one time it was the dominant bunchgrass in many plant communities of eastern Oregon. This bunchgrass has been reduced or eliminated in many areas due to poor management practices. In some of these areas artificial revegetation is necessary to reintroduce bluebunch wheatgrass. Managers in the past have generally not included bluebunch wheatgrass in range seeding mixtures due to difficulty in seedling establishment, and the availability of hardy, introduced, cool season perennial grasses. Until recently, only the Whitmar cultivar of the awnless variety of bluebunch wheatgrass has been commercially available. Increased interest in native forages for use on semiarid rangelands has resulted in an effort to locate ecotypes adapted to adverse environments. The Soil Conservation Service has recently released Secar, a selection of bluebunch wheatgrass chosen for these qualities (USDA 1981). Little information, however, is available on this new selection regarding the germination and seedling development response to harsh environmental conditions, and on its ability to establish under field conditions.

Sites in need of revegetation often host a harsh environment for seedling establishment. Moisture is the most limiting environmental

factor affecting plant establishment on semiarid rangelands (Brown 1977). In addition, the effect of moisture and temperature interactions may stress the developing plant. Seed germination and early seedling development are highly susceptible to adverse conditions and are the most critical periods in determining seedling establishment (Mayer and Poljakoff-Mayber 1975).

An understanding of seed germination and seedling development response to a range of environmental conditions can be useful for planning successful seedings. The primary objective of this research was to evaluate the response of seed germination and early seedling development for two sources of bluebunch wheatgrass to a range of environmental conditions. The two sources chosen for study were the Secar cultivar and a collection made from native stands on the John Day Fossil Beds National Monument in eastern Oregon. The following evaluations were performed in controlled environments and in the field to meet the general objective:

1. Evaluation of seed germination response of the Secar and John Day sources of bluebunch wheatgrass to a range of temperature and moisture stress conditions.
2. Evaluation of the influence of different soil moisture regimes on early seedling development of the Secar and John Day sources of bluebunch wheatgrass.
3. Evaluation of the response of Secar bluebunch wheatgrass to spring growing conditions in the field.

LITERATURE REVIEW

GERMINATION

The sequence of steps in which a quiescent seed imbibes water, exhibits an increase in metabolic activity and initiates the formation of a seedling, is known as seed germination (Mayer and Poljakoff-Mayber 1975). A seed will germinate only when provided adequate levels of moisture, temperature, gases and in some cases light (Koller 1972). Specific requirements of these environmental variables vary with species and variety and are largely determined by hereditary factors as well as conditions which prevailed during seed formation (Mayer and Poljakoff-Mayber 1975). The proper combination of moisture and temperature is probably the most critical environmental factor in determining germination of seeds in the soil. When considering a species for range seeding, it is necessary to identify what environmental conditions are needed for seed germination to occur. Evaluation of seed germination under a range of temperature and moisture regimes can help identify these requirements.

Germination Response to Temperature

Germination in controlled environments is a common method of evaluating the effect of temperature on seed germination. In testing germination over a range of temperatures there is usually an optimum temperature, below and above which germination is delayed, but not prevented (Mayer and Poljakoff-Mayber 1975). McDonough (1977) suggested

optimum temperatures for range species generally fall midway or lower (10 to 20 C) between 0 and 70 C extremes. The optimal temperature and width of temperature range was dependent on the length of incubation period (Koller 1972). He suggests as incubation is prolonged and more germination occurs, optimum temperatures may decrease and the overall temperature range may increase.

Germination response to temperature has been studied in several cool season perennial grasses, including Agropyron spicatum. Young et al. (1981) conducted 4-week germination tests on several sources of A. spicatum at 55 constant and alternating temperature regimes. The sources included a Nevada ecotype, several numbered accessions from the USDA, Soil Conservation Service, and the awnless cultivar, Whitmar. Their results indicated A. spicatum has the potential to germinate and to be highly germinable over a wide range of temperatures. Optimum germination for the numbered accessions consistently occurred at 15 temperatures ranging from an alternating 5/15 C through a constant 25 C. The SCS accession number P-6409 they tested was released in 1981 as Secar. Seed of this accession, approximately 2 years old, germinated well over a wide range of temperatures. High levels of germination (>90%) occurred in over one-half of the temperature regimes with less than 10% germination occurring in 4% of the temperature regimes. Percent germination at constant temperatures of 2, 5 and 10 C was 30, 50 and 76%, respectively. Even though germination percentages were small at the lower temperature extremes, they may be of practical importance. On rangelands in eastern Oregon these lower temperatures often coincide with an adequate moisture supply for seed germination.

Young et al. (1981) observed no readily apparent advantage to alternating versus constant temperatures. The advantage of alternating versus constant temperatures varied with the relative range of temperatures. In one analysis alternating temperature regimes produced greater germination at low temperatures, 0 through 10 C, approximately equal germination at moderate temperatures, 15 and 30 C and lower germination at 35 C. Earlier work by Plummer (1943) showed higher germination of A. spicatum under alternating temperatures when compared to constant temperature regimes.

Recently, Young and Evans (1982) investigated the germination response of cool season grass cultivars belonging to four genera (Agropyron spp., Elymus spp., Festuca spp. and Poa spp.) to 55 constant and alternating temperature regimes. For each plant material source a germination temperature profile was generated using quadratic response surface analysis. In addition, a germinability index was developed and germination response was related to seedbed temperatures. Their investigations included six sources of A. spicatum previously evaluated (Young et al. 1981). Of all the A. spicatum sources tested, Secar ranked the highest with a mean germination of 57% for all temperature regimes. The germination response of Secar was best at moderate seedbed temperatures, lowest at colder temperatures and intermediate at widely fluctuating and warmer temperatures.

Germination Response to Moisture Stress

The effect of simulated moisture stress on seed germination has been evaluated for numerous species. Several studies have documented

the trend of a decrease in germination rate with a decrease in water potential (Knipe and Herbel 1960; Kaufman and Ross 1970; and Sharma 1973). Hadas and Russo (1974) found more negative values of external water potential affect the rate of water uptake, but not percent germination. Each seed has a minimum water level below which germination does not occur (McDonough 1977). Total germination was not affected as long as the critical water content was reached (Hadas and Russo 1974).

Choudhuri (1968) investigated soil salinity effects on A. spicatum and found that seed germinated well at stress levels to -0.54 MPa. A different response was noted for Agropyron smithii when germination was significantly reduced by stress levels greater than -0.1 MPa (Knipe 1973).

Germination Response to Temperature-Moisture Stress

The interaction between temperature and water stress have been examined in many studies. Tadmor et al. (1969) reported final germination percentages for six range species were dependent on the temperature-water potential interaction. The further the temperature diverged from optimum, the greater the inhibitory effect of the moisture stress. Water uptake and rate of germination increased with higher temperatures and less negative soil water potentials (Wanjura and Buxton 1972; Sharma 1976).

McGinnies (1960) investigated the effect of moisture stress and temperature on Agropyron desertorum, A. intermedium, A. inerme, Bromus inermis, Elymus junceus, Bouteloua gracilis and Eragrostis

trichodes. As moisture stress increased germination was delayed and total germination was reduced. At high moisture stress levels, all species germinated better at the optimum 20 C than at 10 or 30 C.

Temperature-water stress interactions of Bouteloua gracilis, Buchloe dactyloides and Agropyron smithii were examined by Bokhari et al. (1975). They found rate of germination decreased with increasing water stress, especially at lower temperatures. For all temperature regimes examined, an increase in water stress resulted in a decrease of total germination. Germination of A. smithii was inhibited at water potential levels of -1.1 MPa or lower for all temperatures.

Few studies have investigated the effect of temperature and moisture stress combinations on seed germination in Agropyron spicatum. Harris (1967) germinated seeds of A. spicatum at 10, 20 and 30 C and water potential levels of -.62 and -1.14 MPa. At the end of 6 days germination was highest for all water potentials at 20 C. Germination percentages for 0 and -.62 MPa were higher at 30 C than at 10 C. Germination response of A. spicatum to a range of water potential-temperature conditions needs to be evaluated for longer periods of time.

Methodology for Moisture Stress Germination Studies

Several considerations should be made when conducting germination tests with osmotic solutions and artificial substrates. In the past, solutes used to simulate water stress have included sodium chloride, glucose, sucrose, mannitol and polyethylene glycol (PEG). Mannitol and high molecular weights of polyethylene glycol are the most widely used osmotic agents since they do not penetrate the seed coat (Manohar 1966) and they simulate drought effectively (Sharma 1973).

The osmotic potential of PEG 6000 MW and PEG 20,000 MW solutions of a given concentration vary with temperature. Michel and Kaufmann (1973) found the osmotic potential of solutions at a given concentration of PEG 6000 MW increased linearly with temperature. They propose a method of calculating water potentials from known PEG concentrations over a wide range of temperatures. Inconsistencies in osmotic potentials for known concentrations of PEG 20,000 MW have been reported in the literature (Thill et al. 1979). They suggest that these differences may be due to variation in molecular weight between lots and sources of PEG. Therefore they recommend that the relationship between concentration and osmotic potential be determined for each lot and source of PEG.

Another concern in using osmotic solutions is stability of the solution and maintenance of the desired water potential over time. Thill et al. (1979) reported incubation temperature of 10, 20 and 30 C had no effect on the stability of PEG 20,000. Solutions with higher concentrations of PEG 20,000 had more stable osmotic potentials than the dilute solutions. No change was observed in the water potentials of 30 and 40g/100ml water PEG solutions over time, however, water potentials of 20 and 25g/100ml water solutions decreased $-.06$ and $-.07$ MPa, respectively, between days 9 and 14. Berkat and Briske (1982) recommend vapor seals or a vapor saturated atmosphere be utilized to prevent solution evaporation and thereby a reduction in water potential.

Although water potential of the PEG solutions is known, the substrate water potential may be different and should be measured at

the beginning and periodically throughout the germination study (Berkat and Briske 1982). They evaluated the use of PEG 20,000 with three germination substrates. For long duration germination studies they recommend utilizing a substrate with a solution reservoir, such as foam floating in PEG solution.

Finally, care should be taken in relating the results of simulated water stress germination tests to performance in the field. Results of these tests are useful in assessing the general response of a species to a wide range of conditions. However, germination in the soil may be hindered by factors not present with the use of artificial substrates, including lack of soil-seed contact, limited water flow properties of the soil and harmful microbial growth (Sharma 1973).

SEEDLING DEVELOPMENT IN PERENNIAL GRASSES

Favorable environmental conditions necessary for successful seedling development and establishment, include appropriate levels of water, light, temperature, oxygen, carbon dioxide and minerals (Koller 1972). On semiarid rangelands water and solar energy are probably the most important environmental components affecting plant establishment. Of all the resources needed for plant growth, the supply of water is often the least reliable (Harper 1977).

In semiarid environments seedlings developing rapidly when moisture is available and those exhibiting the ability to grow under restricted moisture supply are the most likely to survive. Seedling vigor as evidenced by a rapid rate of germination and growth, and early achievement of adequate leaf and root area can be an advantage in

seedling establishment (McKell 1972; Johnson et al. 1982). In a study of early development of twelve range grasses, Plummer (1943) attributes the initial success or failure of establishment to total root development prior to summer drought. Seedling establishment depends on rates of root elongation that keep part of the root in moist soil ahead of the drying front (Daubenmire 1970).

Two types of root systems exist in perennial grasses. Seminal roots begin development with germination and are characteristically small in diameter and are finely branched. The other system is composed of adventitious roots that develop from lower nodes of the main shoot or tillers. The survival of perennial grasses appears to depend ultimately on the development of adventitious roots (Hyder 1974). Two main types of grass seedlings are reported, those with an elongated subcoleoptile internode and short coleoptile (ie. Bouteloua gracilis) and those with a long coleoptile and no elongation in the subcoleoptile internode (ie. Agropyron desertorum). Seedlings with an elongated subcoleoptile internode initiate adventitious roots at or near the soil surface, where adventitious roots in seedlings with no subcoleoptile elongation develop near the depth of planting. In semiarid environments adventitious root development would be enhanced in deeper and moist environments.

Recent investigations of Lolium perenne and Phalaris aquatica, suggested adventitious root development can be delayed or prevented when surface sowing places the seed in the rapidly drying soil (Cornish 1982). The delay in root development is related to soil moisture and not directly to surface sowing. Boatwright and Ferguson (1967) found

adventitious roots of wheat failed to grow in dry soil. Under field conditions the probability of adventitious root development will relate to the frequency and duration of periods of adequate water supply. Cornish (1982) suggested the soil surface must be moist for 3 days before L. perenne and P. aquatica produce adventitious roots.

A few studies have evaluated seedling development of Agropyron spicatum. Harris (1967) monitored root growth of A. spicatum in the field after fall germination. Roots grew slowly until mid-November when growth ceased almost entirely until spring. At the onset of warmer temperatures in the spring rapid root growth was observed. He reported minimum soil temperatures of 8 to 10 C were needed for rapid root growth. By mid-May adventitious roots were relatively abundant and averaged 20 cm in length. He noted the adventitious roots were heavier in structure, less branched and had fewer hairs than seminal roots.

Agropyron spicatum seedlings must often compete with introduced annual species such as Bromus tectorum and Taeniatherum asperum for soil moisture. Harris and Wilson (1970) studied rates of root elongation in A. spicatum, B. tectorum, T. asperum and Agropyron desertorum, under controlled temperatures. Seedlings of A. spicatum and B. tectorum grown in intraspecific competition for 6 weeks at 10 C extended roots 14 cm and 27 cm, respectively. When A. spicatum and B. tectorum seedlings were grown together at 2 C, the rapidly elongating roots of B. tectorum penetrated the soil ahead of A. spicatum roots and used available moisture. Under field conditions A. spicatum is often subjected to low levels of soil moisture since annual grasses

exhaust upper profile moisture supplies to depths beyond the reach of developing A. spicatum roots (Harris 1977; Harris and Goebel 1976).

DeWitt (1969) examined seedling root growth in A. spicatum from 51 locations in the western United States and Canada, and found significant differences in rate of root growth between sources. From the 51 sources he took six representative sources and tested root growth under soil temperatures of 2, 5, 8, 11, 14 and 17 C and again found significant differences between sources.

Since significant variation in root growth potential exists between sources of A. spicatum, it is necessary to evaluate the response of new selections independently. Information relating to root development of the Secar cultivar of A. spicatum in different environmental conditions is needed.

SECTION I

INFLUENCE OF TEMPERATURE AND MOISTURE STRESS ON GERMINATION
OF TWO SOURCES OF BLUEBUNCH WHEATGRASS (AGROPYRON SPICATUM)

Angela G. Evenden
Richard F. Miller
Marshall R. Haferkamp

INFLUENCE OF TEMPERATURE AND MOISTURE STRESS
ON GERMINATION OF TWO SOURCES OF BLUEBUNCH
WHEATGRASS (AGROPYRON SPICATUM)

ABSTRACT

Germination response to a range of moisture stress and temperature conditions during a 30-day period was observed in two sources of bluebunch wheatgrass. Seeds collected near John Day, Oregon and Secar, a newly released cultivar, were evaluated. Seeds were incubated in the dark at constant temperatures of 10, 20 and 30 C, and water potentials from 0 to -2.2 megapascals (MPa) were simulated with polyethylene glycol 6000. Seeds of both sources germinated over the widest range of water potentials at 20 C. In all temperature regimes, rate of germination and total percent germination declined as moisture stress increased. Germination rate and total percent germination of John Day and Secar were similar at moderate temperatures (10 and 20 C) and low levels of moisture stress. However, as moisture stress increased at these temperatures Secar germinated faster and with larger amounts of total percent germination than John Day. In the high temperature regime, 30 C, John Day consistently germinated faster and with a greater amount of total percent germination than Secar. Since Secar is able to germinate well under high levels of moisture stress at moderate temperatures, it may show promise as a useful cultivar for reseeding deteriorated bluebunch wheatgrass communities.

INTRODUCTION

Bluebunch wheatgrass (Agropyron spicatum (Pursh) Scribner and Smith), a long-lived, cool season perennial bunchgrass, is an important native forage species on western rangelands (Sampson 1924). This bunchgrass has been greatly reduced or eliminated in many areas due to its low tolerance to grazing and poor management practices. In some of these areas artificial revegetation is necessary to reintroduce bluebunch wheatgrass.

Seeding practices in the past have generally not included bluebunch wheatgrass due to difficulty in seedling establishment, and the availability of hardy introduced cool season species. Until recently, only the Whitmar cultivar of the awnless form of A. spicatum has been commercially available. Interest in native forages for use on semiarid rangelands has resulted in an effort to locate ecotypes adapted for establishment in adverse environments. The Soil Conservation Service has recently released, Secar, a cultivar of bluebunch wheatgrass selected for these qualities (USDA 1981).

In semiarid environments limited soil moisture and unfavorable temperatures can restrict seed germination and plant establishment. An understanding of moisture and temperature requirements for germination of bluebunch wheatgrass can be useful in selecting appropriate cultivars or ecotypes for use in range seedings. The objective of this study was to compare the germination characteristics of Secar and a collection of bluebunch wheatgrass from eastern Oregon in response to varying temperature and moisture conditions.

MATERIALS AND METHODS

Two sources of bluebunch wheatgrass, a collection from John Day, Oregon and the released cultivar, Secar, were investigated. In the following text, seed collected near John Day will be referred to as John Day and the released cultivar as Secar. The John Day seed was hand collected from stands on the John Day Fossil Beds National Monument in eastern Oregon. Seed of Secar was obtained from the USDA, Soil Conservation Service, Plant Material Center in Pullman, WA. Prior to use, all seed was stored in paper bags at room temperature. Selection of the filled seed used in the germination trials was accomplished with a seed blower and backlighting of seed on a light table. Seeds were dusted with Captan to prevent fungal development.

John Day seed approximately 1 year old and 2 year old Secar seed were germinated in the dark for 30 days in controlled temperature chambers at 10, 20 and 30 C. At each temperature seeds of both John Day and Secar were subjected to a range of osmotic potentials from 0 MPa to approximately -2.0 MPa.

Osmotic solutions of polyethylene glycol (PEG, molecular weight 6000) were prepared to simulate the moisture stress conditions. A control treatment was prepared using distilled water. Required concentrations for each water potential and temperature combination were prepared following the technique described by Michael and Kaufmann (1973). Prior to use, water potentials of the PEG solutions were measured using sample chamber psychrometers (Wescor model C-52) with a microvoltmeter (Wescor model HR-33T). The dew point mode was used, and readings were taken after a 2 minute equilibration period. Sample chambers were calibrated with standard NaCl solutions prior to

measurement. Based on the initial determinations some solution water potentials were adjusted to the desired levels (Appendix C). Substrate water potentials were determined at the beginning of the incubation period and again 2 weeks later. The two sets of water potential determinations were averaged for use in the analysis.

The germination tests were conducted in covered petri dishes, sealed in plastic sacks. Seeds were imbibed on two filter paper discs supported by cellulose pads (Kimpak). Adequate distilled water and PEG solutions were added to the dishes to saturate the germination substrate. Four replications of 25 seeds for John Day and Secar were used for each water potential.

Petri dishes were arranged in a randomized block design within each temperature chamber. Germination was recorded daily, and a seed was considered germinated when both the radicle and plumule had extended 5 mm. Abnormal germination activity was also recorded, and abnormal germination was considered any amount of radicle and plumule development not meeting the germination criteria. Ungerminated seeds were tested for filled caryopses at the end of the trials, and total germination percentages were based on the number of filled seed only.

Analysis of Variance was used to test significance of germination data for each of the three temperatures. An arcsin transformation was performed on data for total germination percentage before analysis, however, untransformed data are presented in the figures. To reduce bias, data were omitted from the analyses at moisture stress levels where germination was mainly zero. Where significant differences were found, Tukey's test was employed to separate treatment means at the .05 level of significance. Polynomial regression was used

to generate an equation and response curve to best characterize total percent germination as a function of water potential at each temperature.

RESULTS AND DISCUSSION

Germination Response at 10 C

Seeds of John Day and Secar incubated at 10 C were slow to germinate, with no germination occurring in the first 10 days (Fig. 1). Rates of germination were fastest and total percent germination was highest at the lower levels of moisture stress (Figs. 1 and 2). Some John Day and Secar seed in the control treatment (0 MPa) germinated by day 12, and days to 50% of final germination were 13 and 17 days, respectively. John Day and Secar seed germinated 80% or greater at water potentials between 0 and -0.7 MPa (Fig. 2). John Day seed germinated faster and had larger amounts of total % germination ($p \leq .05$) than Secar at the lowest levels of moisture stress.

As moisture stress increased, rate of germination and total percent germination declined significantly ($p \leq .05$) for both John Day and Secar. At water potentials less than -1.2 MPa Secar seed germinated somewhat faster and had a significantly ($p \leq .05$) higher total percent germination than John Day seed. Thirteen percent of the Secar seed germinated normally at -1.6 MPa, where 44% of the seed initiated germination but failed to extend both plumules and radicles 5mm in length (Appendix B). No normal germination occurred in John Day seed at -1.6 MPa, however, 70% of the seed developed radicles. As moisture stress increased to -2.2 MPa, radicle development was observed

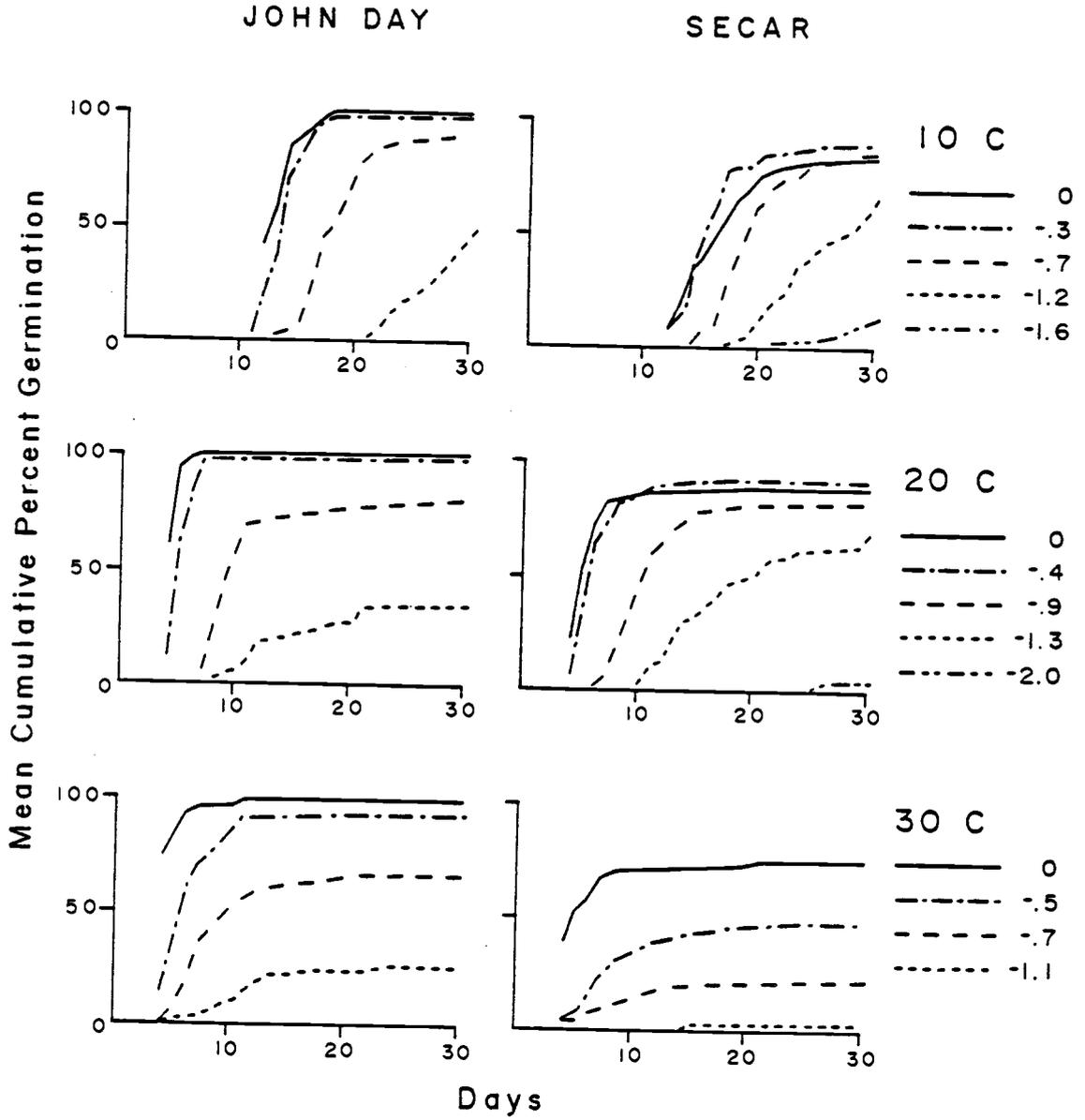


Fig. I.1. Germination response of John Day and Secar at 10, 20 and 30 C and a range of water potentials.

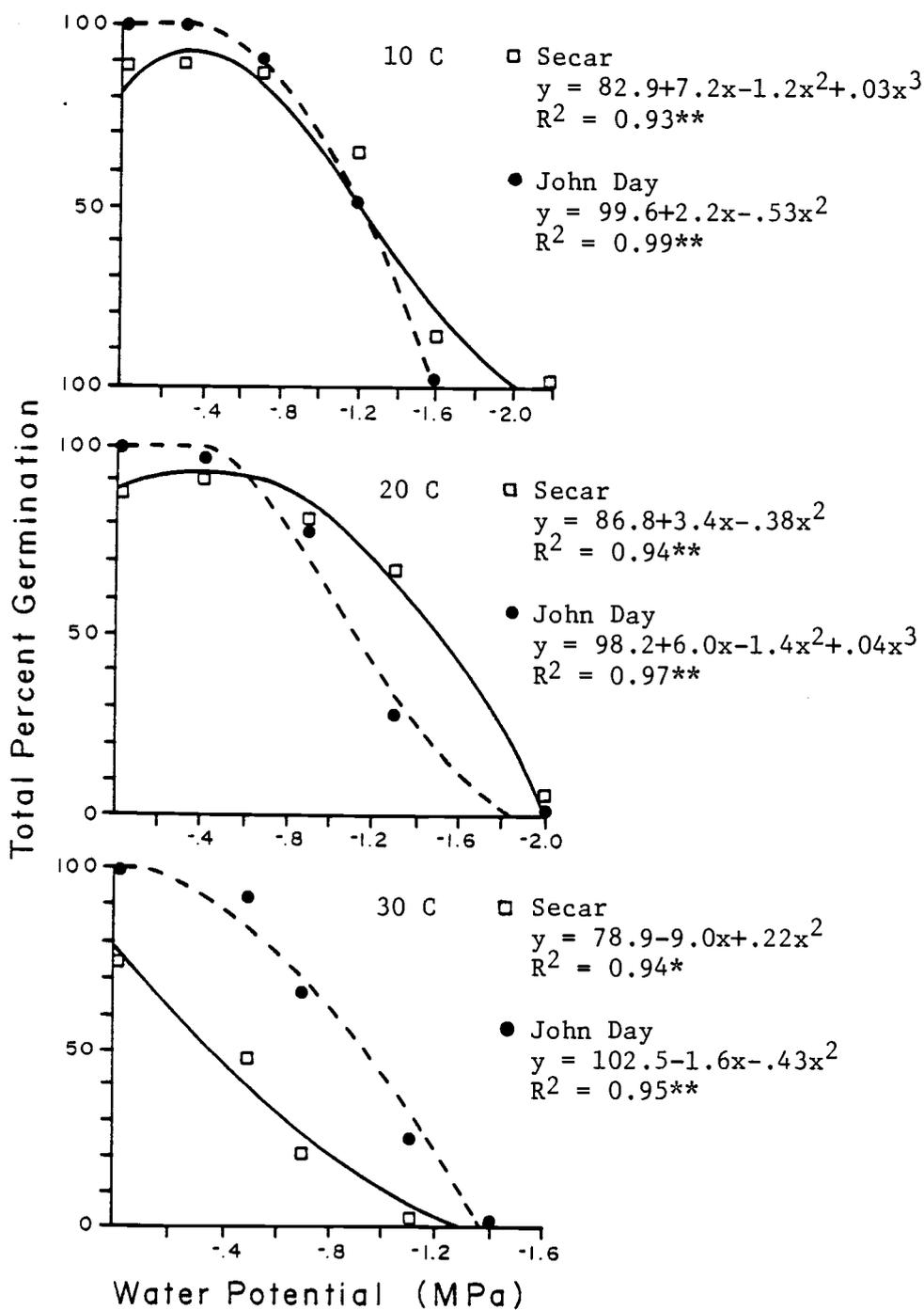


Fig. I.2. Total percent germination of John Day and Secar as affected by water potential at constant temperatures 10, 20 and 30 C.
*,** significant at the .05 and .01 level of probability.

in 11% of the Secar seed, but no signs of germination activity were observed in the John Day seed.

Germination Response at 20 C

The overall germination responses of John Day and Secar seed exposed to the range of water potentials at 20 C were similar ($p \geq .05$). Maximum rates of germination and total percent germination occurred at the highest water potentials (low moisture stress) (Figs. 1 and 2). Germination proceeded rapidly in the control treatment, and 50% of total germination had occurred by days 4 and 5 for John Day and Secar, respectively. As moisture stress increased, total percent germination and rate of germination in Secar and John Day declined. At stress levels of -1.3 MPa or greater Secar germinated significantly faster and with higher total percent germination than John Day ($p \leq .05$). At -1.3 MPa, 68% of the Secar seed germinated normally, compared to 29% normal germination of John Day seed (Appendix B). Abnormal germination was evident at the higher moisture stress levels. As moisture stress increased to -2.0 MPa, normal germination only occurred in 9% of the Secar seed, where abnormal germination occurred in 34% of the seed. No normal germination was observed in John Day seed under the same conditions, however, 67% of the seed had formed radicles.

Germination Response at 30 C

Germination response of John Day and Secar seed differed significantly ($p \leq .05$) to the range of water potentials at 30 C. Although rate of germination and total percent germination in both

John Day and Secar seed declined with increasing water stress, John Day seed consistently germinated better than the Secar seed (Figs. 1 and 2). Maximum germination for both sources occurred in the control treatment. These seeds germinated rapidly at 0 MPa where 50% of final germination was attained in 4 and 5 days for John Day and Secar, respectively. John Day seed tolerated moderate levels of moisture stress better than Secar seed, and after 30 days at -0.5 MPa, 95% of the John Day seed germinated compared to 48% of the Secar seed. At 30 C, high levels of moisture stress suppressed germination activity significantly ($p \leq .05$). As moisture stress increased to -1.4 MPa, no normal germination occurred in either John Day or Secar, however, 35% of the John Day seed developed radicles compared to 5% of the Secar seed (Appendix B). At the highest level of stress, -2.2 MPa, Secar seed exhibited no germination activity whereas 11% of the John Day seed developed radicles.

Summary and Conclusions

The optimum temperature regime appears to be 20 C for both sources. McGinnies (1960) observed cool season grass seeds germinated fairly well under relatively high levels of moisture stress if the temperature was favorable. Our data for both John Day and Secar seed agree with his findings, since both sources germinated faster and with higher total percent germination over a wider range of stress levels at 20 C than at 10 or 30 C. Similar germination responses to temperature, and combinations of temperature and moisture stress, have been reported for other cultivars and ecotypes of bluebunch wheatgrass by Young *et al.* (1981), Young and Evans (1982) and Harris (1967).

Speed of germination has long been considered an important factor for evaluation of seedling vigor (Maguire 1962). The faster a seed germinates the greater the potential for successful seedling establishment (Harper 1977). In semiarid regions this factor is especially important since temperatures favorable for germination and subsequent growth of bluebunch wheatgrass often coincide with limited supplies of soil moisture. At the optimum temperature, 20 C, Secar seed germinated faster than John Day seed at moderate to high moisture stress levels, suggesting that Secar may have better chances for establishment under field conditions with favorable soil temperatures and moderate soil moisture stress. However, one must keep in mind that at higher temperatures (30 C) the performance of Secar deteriorates. High temperatures in the field are most often accompanied by decreased soil moisture, and therefore an unfavorable environment for seedling development. It appears that the success of seed germination and subsequent seedling development at high temperatures would probably be dependent on the receipt of precipitation. Under sufficient moisture conditions at soil temperatures of 30 C, the John Day seed would probably germinate faster.

SECTION II

EARLY SEEDLING DEVELOPMENT OF TWO SOURCES OF BLUEBUNCH WHEATGRASS
(AGROPYRON SPICATUM) GROWN IN SIX SOIL MOISTURE REGIMES

Angela G. Evenden
Richard F. Miller
Marshall R. Haferkamp

EARLY SEEDLING DEVELOPMENT OF TWO SOURCES OF
BLUEBUNCH WHEATGRASS (AGROPYRON SPICATUM)
GROWN IN SIX SOIL MOISTURE REGIMES

ABSTRACT

Research was conducted to evaluate the effects of six soil moisture regimes on early seedling development in two sources of bluebunch wheatgrass (Agropyron spicatum). Seeds collected near John Day, Oregon and Secar, a newly released cultivar were planted and grown for 6 weeks in the greenhouse in moisture regimes representing patterns of soil wetting and drying. John Day seedlings emerged faster than Secar seedlings and due to an increased opportunity for growth, John Day seedlings developed the largest leaf areas and root systems. With adequate moisture conditions in all regimes at the onset of the study seedlings of both sources developed good seminal root systems. As soil moisture decreased, however, the rate of seedling growth for both sources was suppressed. When seedlings were in the three-leaf stage and exposed to surface soil moisture greater than field capacity (-0.033 MPa) adventitious roots were initiated. Secar seedlings developed adventitious roots sooner than John Day seedlings and at 36 days after planting these seedlings had produced significantly more and longer adventitious roots than John Day seedlings. Subsurface soil moisture above field capacity provided a favorable environment for rapid extension of adventitious roots once initiation had occurred.

INTRODUCTION

Bluebunch wheatgrass (Agropyron spioatum (Pursh) Scribner and Smith) is an important forage species that once dominated many of the bunchgrass communities in eastern Oregon. Low resistance to grazing and poor management practices have reduced or eliminated bluebunch wheatgrass in many areas, and revegetation programs are often needed to reestablish bluebunch wheatgrass on these areas. Thus adapted varieties and seeding prescriptions are necessary for effective establishment of stands.

Many factors influence the potential success of seedling establishment in semiarid regions. One of the most limiting environmental factors affecting growth and establishment of range plants is the availability of water (Brown 1977). Rangelands are characterized by low annual rainfall, received at irregular intervals. Rooting vigor is of primary importance when evaluating the ability of native species to establish in harsh environments (Eddleman 1980; Johnson 1982). Seedlings of bluebunch wheatgrass usually germinate in the fall and must produce a long root system if they are to effectively utilize the soil moisture (Harris and Goebel 1976). This root system must include development and extension of adventitious roots if the seedlings are to become established (Hyder 1974).

The purpose of this study was to compare early seedling growth of two sources of bluebunch wheatgrass and to assess the response of bluebunch wheatgrass seedlings exposed to different soil wetting and drying regimes.

MATERIALS AND METHODS

Two sources of bluebunch wheatgrass, a native collection from John Day, Oregon and a released cultivar, Secar, were investigated. In the following text, seed from the native collection will be referred to as John Day and the released cultivar as Secar. Secar seed obtained from the USDA, Soil Conservation Service, Plant Material Center in Pullman, WA was harvested in 1980 at Pullman. The John Day seed was hand collected from stands on the John Day Fossil Beds National Monument in eastern Oregon in July 1981. Prior to use, all seed was stored in paper bags at room temperature. Selection of filled seed was accomplished by backlighting seed on a light table.

Seeds were germinated and seedlings were grown in six moisture regimes for a 6 week (43 day) period. Individual seedlings were grown in super cell tubes (20cm x 4cm) filled with 164 g of an autoclaved soil mixture containing 60% sand, 20% loam and 20% peat. One cotton ball was placed in the bottom of each tube to prevent soil leakage. Approximately 24 hours before planting, soil moisture in each tube was adjusted to a level above field capacity. Two seeds were then planted in each cell and covered with 5 mm of soil. The first seedling to emerge in each tube was used in the experiment, and all other seedlings were thinned when they emerged.

Watering treatments were selected to cover a range of conditions from high levels of soil moisture for seedling growth to drier conditions which would stress seedlings (Table 1). Treatments 1 and 2 represent the most mesic conditions of the six treatments examined. Both treatments received water twice after onset of the study. The

TABLE II.1. Watering scheme for six soil wetting and drying treatments in the greenhouse study. Checks indicate when soil moisture levels were increased to above field capacity.

Treatment	Days After Planting			
	13	28	35	40
1	✓	✓		
2		✓	✓	
3	✓			
4		✓		
5			✓	
6				✓

most xeric conditions occurred in treatments 5 and 6, which were allowed to dry for 35 and 40 days respectively, between the initial and second watering. Treatments 3 and 4 represented intermediate moisture stress conditions. Moist soil conditions prevailed in treatment 3 for the first 4 weeks of the study, after which soil moisture decreased steadily. Treatment 4 was allowed to dry down 4 weeks before moisture was added.

Tubes were arranged in a randomized complete block design with four replications. Each block included three observations per treatment and source of bluebunch wheatgrass, for each of five sampling dates. Eighty-four tubes per block were prepared without seeds for soil water determinations.

Seedling response to the six wetting and drying regimes was determined by measuring seedling emergence, leaf number, total leaf length, leaf oven-dry weight, rooting depth (length of longest seminal root), total oven-dry root weight (includes both seminal and adventitious root systems), adventitious root number, and total length of adventitious roots. Leaf and root measurements were taken on days 15, 22, 29, 36 and 43 after planting. Roots were washed free of soil particles and leaf and root samples were oven-dried 48 hours at 60 C and weighed.

Soil moisture was determined gravimetrically for three soil depths, surface (0-1 cm) and subsurface (2-7 cm and 8-17 cm) on 14 dates. A moisture retention curve was constructed with four points; -0.033 , -0.1 , -0.5 , and -1.5 MPa (Richards 1954), and soil water potential was determined using the moisture retention curve.

Analysis of variance was used to analyze seedling growth parameters for each of five dates. Tukey's test was employed to test

significance between water treatments and source means. The mean of the three observations per treatment, within a block, was used in the analysis. Soil moisture data were analyzed with the analysis of variance across all dates. Significant differences referred to in this paper are at or greater than the .05 level. Comparisons of John Day and Secar refer to seedling response averaged across water treatments. When relating seedling development of bluebunch wheatgrass to soil moisture the response of Secar and John Day have been combined. Due to the large percentage of zero values for adventitious root number on day 35 an arcsin transformation was performed. The analysis was run with the transformed values, but untransformed data are presented in the text.

RESULTS AND DISCUSSION

Soil Moisture - Emergence

Soil moisture was increased to above field capacity in the surface and subsurface depths of all tubes with the initial watering (Figs. 1 and 2). Soil moisture was sufficient for seed germination as both John Day and Secar seedlings began emerging on the 6th day after planting, and emergence was completed by the 12th day (Table 2). Over 90% of the total emergence had occurred for both John Day and Secar by day 9. John Day seedlings, however, emerged at a faster rate and achieved greater total emergence than Secar seedlings.

By day 13 surface soil moisture in all treatments was approaching wilting point (-1.5 MPa), but subsurface moisture remained well above field capacity. Watering of treatments began on day 13 resulting in the varying wetting and drying regimes represented in Figs. 1 and 2.

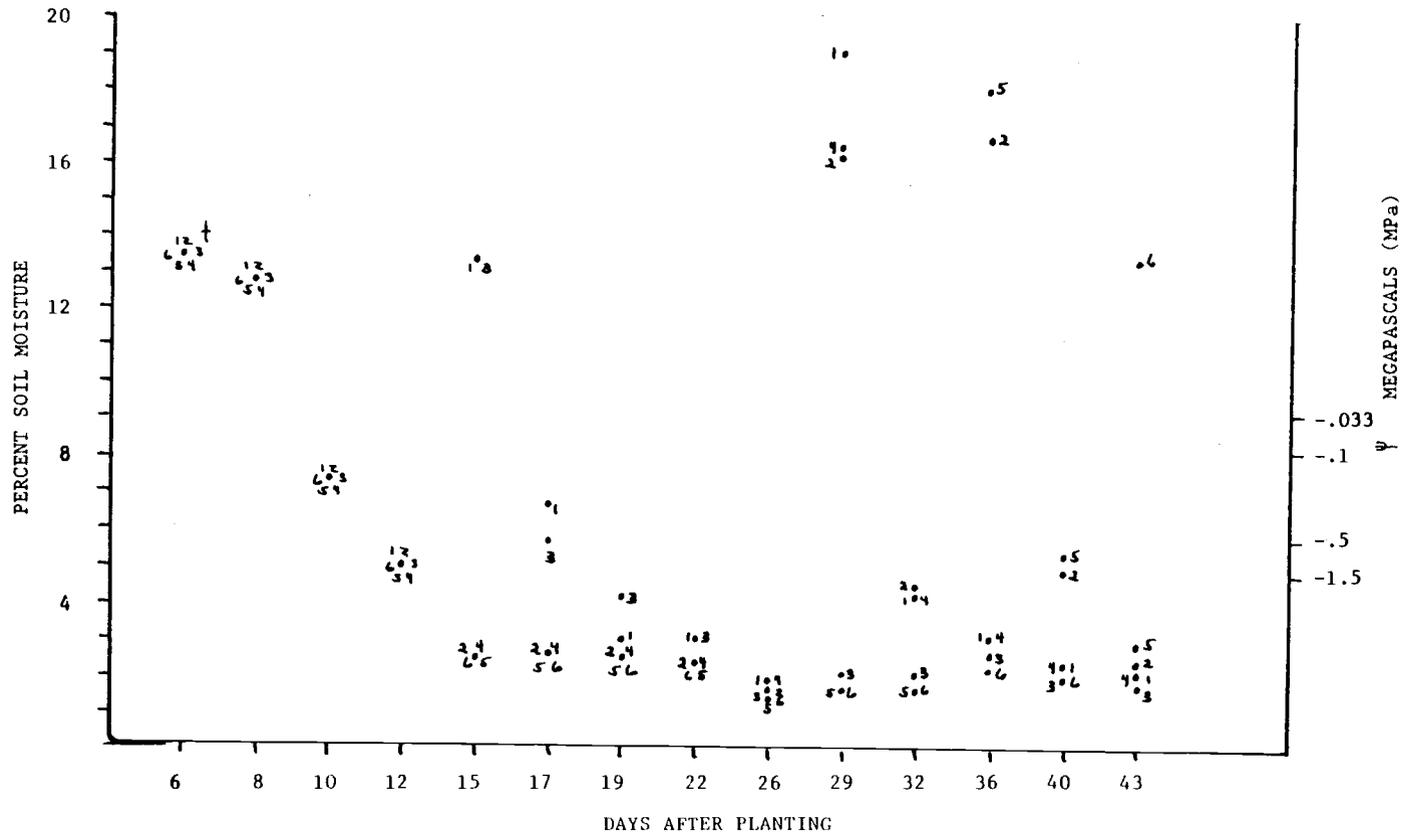


Fig. II.1. Percent surface (0-1 cm) soil moisture and corresponding soil water potential (Ψ) for six water treatments on 14 dates.

†Numbers adjacent to dots on each date refer to the water treatments.

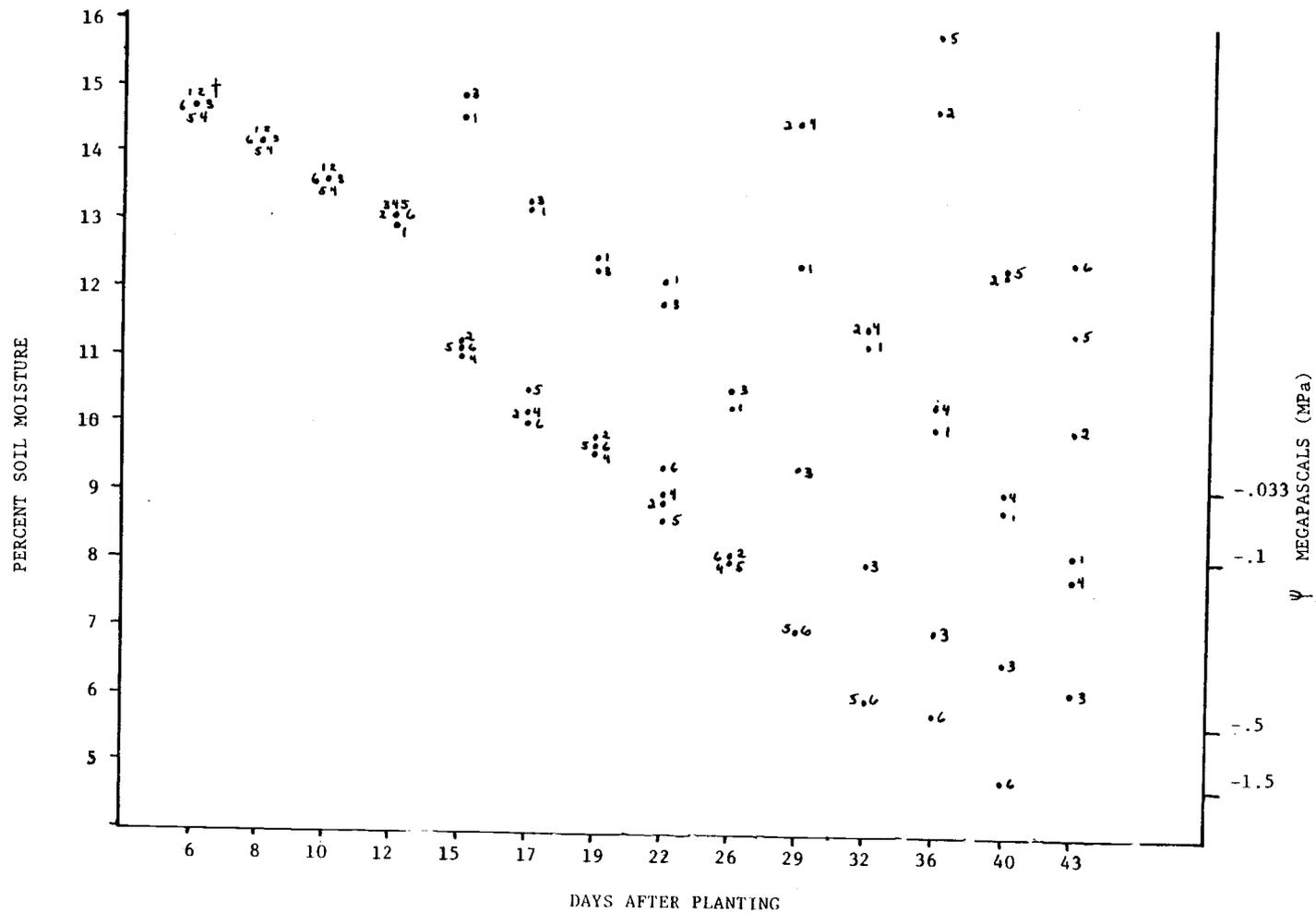


Fig. II.2. Percent subsurface (2-20 cm) soil moisture and corresponding soil water potential (Ψ) for six water treatments on 14 dates.

†Numbers adjacent to dots on each date refer to the water treatments.

Table II.2. Cumulative mean percent emergence, based on final emergence of John Day and Secar seedlings.

Days After Planting	John Day	Secar
6	62.0	46.0
7	84.0	68.0
8	92.0	82.0
9	98.0	94.0
10	99.0	98.0
11	100.0	99.0
12	100.0	100.0

The addition of water always increased soil moisture to above field capacity but drying of the surface centimeter began immediately and proceeded rapidly after each watering. Drying of the subsurface soil proceeded more slowly.

Seedling Development Response of John Day and Secar

John Day seedlings developed more rapidly and produced significantly more leaves than Secar seedlings through the 2.8 leaf stage (Table 3). Although leaf length was significantly longer in the John Day seedlings on days 15 and 22 (Table 4), leaf weights did not reflect this difference (Table 5). It is possible that John Day and Secar seedlings differed in leaf thickness. After day 29, John Day seedlings had both longer leaves and a heavier leaf weight than Secar seedlings.

Soil moisture early in the study was adequate to allow rapid development of seminal roots and by day 29 both Secar and John Day seedlings had extended roots the full depth of the cells (Table 6). Root weights between sources did not differ initially, however, on day 29 John Day seedlings had significantly heavier seminal roots than Secar seedlings (Table 7).

Both John Day and Secar initiated adventitious roots when seedlings were in the three-leaf stage (Tables 3 and 8). Secar seedlings, however, developed adventitious roots at a faster rate than John Day seedlings as evidenced by the higher adventitious root number and length on day 36 (Tables 8 and 9). Although differences were not significant on day 43, Secar seedlings continued to have larger adventitious root systems. Root weights on day 36 and after included

Table II.3. Main effect means and standard deviations for seedling leaf number for two sources of bluebunch wheatgrass and six soil moisture treatments.

Main Effect	Days After Planting				
	15	22	29	36	43
<u>Source</u>					
John Day	1.8±.3b [†]	2.2±.4b	2.8±.3b	2.9±.3a	3.2±.3a
Secar	1.4±.3a	2.0±.2a	2.3±.3a	2.8±.5a	3.1±.4a
<u>Treatment</u> ‡					
1	1.7±.3a	2.4±.4a	2.9±.2a	3.2±.3b	3.1±.4ab
2	1.6±.5a	2.1±.3a	2.4±.4a	3.0±.1ab	3.5±.4b
3	1.6±.3a	2.0±.1a	2.7±.4a	3.0±.1ab	2.9±.1a
4	1.6±.3a	2.1±.4a	2.5±.4a	3.0±.1ab	3.2±.2ab
5	1.5±.4a	2.1±.2a	2.5±.4a	2.5±.4a	3.0±.2a
6	1.5±.4a	2.1±.3a	2.4±.4a	2.5±.5a	2.9±.2a

[†]Means in columns within source and treatment, with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

[‡]Treatment numbers 1 through 6 represent the following soil moisture regimes: mesic, treatments 1 and 2; intermediate, treatments 3 and 4; and xeric, treatments 5 and 6.

Table II.4. Main effect means and standard deviations for seedling total leaf length for two sources of bluebunch wheatgrass and six soil moisture treatments.

Main Effect	Days After Planting				
	15	22	29	36	43
<u>Source</u>	cm				
John Day	12.0±1.6b [†]	20.0±3.4b	23.0±3.8b	25.9±5.5b	27.7±3.5b
Secar	8.9±2.0a	17.0±4.0a	19.5±4.4a	23.5±4.2a	25.0±4.3a
<u>Treatment</u> ‡					
1	10.7±2.7a	21.7±4.1a	26.8±4.3c	29.2±3.8c	29.3±3.6b
2	10.2±1.8a	17.6±5.0a	19.7±3.1ab	23.1±5.3ab	29.1±2.9b
3	10.5±2.7a	19.5±4.4a	23.3±3.6bc	27.7±3.3c	26.9±3.1b
4	11.2±3.1a	17.2±3.3a	19.8±2.7ab	27.5±3.3bc	26.1±3.0b
5	10.1±2.1a	17.6±3.2a	18.0±3.0a	20.0±3.1a	25.3±4.4ab
6	10.0±2.1a	17.4±2.9a	20.2±3.8ab	20.5±1.9a	21.6±2.8a

[†] Means in columns within source and treatment, with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

‡ Treatment numbers 1 through 6 represent the following soil moisture regimes: mesic, treatments 1 and 2; intermediate, treatments 3 and 4; and xeric, treatments 5 and 6.

Table II.5. Main effect means and standard deviations for seedling leaf weight for two sources of bluebunch wheatgrass and six soil moisture treatments.

Main Effect	Days After Planting				
	15	22	29	36	43
<u>Source</u>	mg				
John Day	2.5±0.8a [†]	4.5±1.1a	8.4±1.8b	10.4±2.4b	11.2±3.0b
Secar	2.2±0.8a	4.0±1.0a	7.0±1.6a	8.4±1.9a	9.1±2.3a
<u>Treatment</u> [‡]					
1	2.3±0.8a	4.2±1.1a	9.8±1.8b	11.0±2.5b	11.8±2.3cd
2	2.0±0.5a	4.3±1.5a	7.5±1.4a	8.8±2.0ab	12.4±2.4d
3	2.1±1.2a	4.4±1.0a	8.4±1.8ab	10.6±2.1b	11.4±3.4bcd
4	2.4±0.6a	4.0±0.7a	7.4±1.5a	10.6±2.2b	9.5±1.8abc
5	2.5±1.1a	4.3±1.1a	6.5±1.5a	7.4±1.9a	8.7±1.6ab
6	2.6±0.4a	4.2±1.1a	6.9±1.5a	8.1±1.0a	7.1±1.1a

[†] Means in columns within source and treatment, with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

[‡] Treatment numbers 1 through 6 represent the following soil moisture regimes; mesic, treatments 1 and 2; intermediate, treatments 3 and 4; and xeric, treatments 5 and 6.

Table II.6. Main effect means and standard deviations for seedling rooting depth for two sources of bluebunch wheatgrass.

Source	Days After Planting				
	15	22	29	36	43
	cm				
John Day	13.9±2.2b [†]	16.6±1.3a	17.0±0.6a	16.8±1.0a	17.1±0.6a
Secar	12.6±2.5a	15.9±1.7a	16.8±1.2a	16.7±1.2a	17.0±0.8a

[†] Means in columns with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

Table II.7. Main effect means and standard deviations for seedling root system weight for two sources of bluebunch wheatgrass and six soil moisture treatments.

Main Effect	Days After Planting				
	15	22	29	36	43
<u>Source</u>	mg				
John Day	1.3±0.5a [†]	2.9±0.7a	6.2±1.4a	8.0±2.1a	10.0±2.6a
Secar	1.2±0.6a	2.6±0.6a	5.1±1.3b	6.8±1.8b	8.6±2.6b
<u>Treatment</u> ‡					
1	1.1±0.5a	2.6±0.4a	6.1±1.3a	8.8±2.7c	11.2±3.0cd
2	1.0±0.4a	2.7±1.0a	5.9±1.3a	7.0±2.6abc	12.3±1.0d
3	1.2±0.7a	2.6±0.8a	5.6±1.6a	7.5±1.5abc	8.7±2.1ab
4	1.4±0.6a	2.6±0.5a	5.9±1.5a	8.6±1.1bc	9.3±1.7bc
5	1.3±0.5a	2.9±0.7a	5.2±1.0a	6.3±1.3ab	7.9±1.5ab
6	1.4±0.6a	2.9±0.8a	5.4±1.8a	6.1±0.7a	6.4±1.1a

[†] Means in columns within source and treatment, with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

[‡] Treatment numbers 1 through 6 represent the following soil moisture regimes: mesic, treatments 1 and 2; intermediate, treatments 3 and 4; and xeric, treatments 5 and 6.

Table II.8. Main effect means and standard deviations for seedling adventitious root number for two sources of bluebunch wheatgrass and six soil moisture treatments.

Main Effect	Days After Planting	
	36	43
<u>Source</u>		
John Day	.47 ± 0.4a [†]	.92 ± 0.6a
Secar	1.0 ± 0.6b	1.18 ± 0.7a
<u>Treatment</u> ‡		
1	.93 ± 0.6b	1.0 ± 0.3abc
2	.92 ± 0.6b	1.90 ± 0.5c
3	.29 ± 0.3a	.32 ± 0.5a
4	.75 ± 0.8ab	1.12 ± 0.5abc
5	0 #	1.34 ± 0.4bc
6	0	.72 ± 0.7ab

[†] Means in columns within source and treatment, with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

‡ Treatment numbers 1 through 6 represent the following soil moisture regimes: mesic, treatments 1 and 2; intermediate, treatments 3 and 4; and xeric, treatments 5 and 6.

A trace or less of adventitious root development occurred in treatment 5 on day 36 and therefore zero values are being reported for this date.

Table II.9. Main effect means and standard deviations for seedling adventitious root system length for two sources of bluebunch wheatgrass and six soil moisture treatments.

Main Effect	Days After Planting	
	36	43
<u>Source</u>	cm	
John Day	3.4 ± 3.3a [†]	6.2 ± 5.4a
Secar	6.5 ± 4.1b	7.7 ± 6.6a
<u>Treatment</u>		
1	6.8 ± 4.2b	7.9 ± 3.1c
2	5.8 ± 3.8ab	15.9 ± 5.0d
3	1.9 ± 3.6a	1.5 ± 3.6ab
4	5.3 ± 3.0ab	9.1 ± 7.0c
5	0 [#]	6.2 ± 2.2bc
6	0	1.0 ± 1.5a

[†] Means in columns within source and treatment, with the same letter are not significantly different at the 0.05 level according to Tukey's Test.

[‡] Treatment numbers 1 through 6 represent the following soil moisture regimes: mesic, treatments 1 and 2; intermediate, treatments 3 and 4; and xeric, treatments 5 and 6.

[#] A trace or less of adventitious root development occurred in treatment 5 on day 36 and therefore zero values are being reported for this date.

both seminal and adventitious root systems. Since total root weights remained greater in John Day seedlings (Table 7), this would indicate that John Day seedlings had developed larger seminal root systems than Secar seedlings.

The more rapidly emerging John Day seedlings had an extended opportunity for growth and therefore the larger biomass of herbage and seminal roots produced by this ecotype was not unexpected. Adequate development of an adventitious root system, however, is the key to perennial grass establishment (Hyder 1974). Ecotypes or selections that are able to initiate and extend adventitious roots quickly should show promise for use in range seedings. It appears that seedlings of the Secar cultivar, when compared to the John Day collection would have the greatest potential for establishment since they developed adventitious roots at a faster rate.

Seedling Development Response of Bluebunch Wheatgrass to Soil Moisture

Initial seedling development was similar for all water treatments, since subsurface soil moisture for all treatments remained above or near field capacity for 3 weeks following planting (Fig. 2). This resulted in sufficient moisture for rapid development of seminal roots which had extended the full depth of the cells in all treatments by day 29. Leaf development was similar among treatments through day 22 when seedlings were in the two-leaf stage with an average total leaf length of 18 cm (Tables 3 and 4).

The patterns of soil wetting and drying represented by the six soil moisture regimes showed a variable effect on seedling development

after day 29. Higher levels of soil moisture resulted in larger amounts and faster rates of leaf and root development. By day 36, seedlings of the mesic and intermediate treatments had developed three leaves and total leaf lengths greater than 23 cm, compared to seedlings of the dry treatments which had only produced 2.5 leaves and a total leaf length of 20 cm (Tables 3 and 4). By the final sampling date leaf number, leaf length and leaf weight were generally similar for most treatments (Table 3, 4 and 5). The driest treatment however, still had the shortest leaves and therefore the lightest leaf weights, and leaf weights were largest in the most mesic treatments.

Soil moisture also affected the development of adventitious roots, which were first observed in the mesic and intermediate treatments on day 36 when seedlings were in the three-leaf stage (Tables 3 and 8). A moist surface soil was required for initiation of adventitious roots and a moist subsurface soil was necessary for their extension. Surface soil moisture is critical since this is the zone in which initiation of adventitious roots in bluebunch wheatgrass occurs. Seedlings exposed to surface and subsurface soil moisture above field capacity during the 5th week produced .75 or more adventitious roots with a total length greater than 5 cm (Tables 8 and 9). Surface moisture in the intermediate treatment, that received water early in the study, was below wilting point (-1.5 MPa) after the third week, and as a result only .29 adventitious roots per seedling were initiated by day 36 (Fig. 1, Table 8). Although a trace of adventitious root development was observed on day 36 in the dry treatments most of these seedlings showed no signs of adventitious root initiation. Surface soil moisture in these treatments had been below wilting point since the second week,

and subsurface moisture was below -0.1 MPa after the fourth week (Figs. 1 and 2). These dry conditions prevented seedlings from developing as quickly as in the moister soil regimes, and leaf number on day 36 was only 2.5. Since seedlings of other treatments did not develop adventitious roots until the three-leaf stage, it was not surprising that adventitious roots were not formed in these seedlings.

Clearly surface soil moisture below -1.5 MPa prevented initiation and extension of adventitious roots. Once seedlings of the dry treatments were exposed to surface and subsurface soil moisture above field capacity, leaf number increased and adventitious root development proceeded rapidly. By the final sampling date seedlings watered on day 35 averaged 1.34 adventitious roots and total system length was 6.2 cm (Tables 8 and 9). Other seedlings were exposed to sufficient soil moisture for initiation of adventitious roots, however, when surface moisture decreased below -1.5 MPa and subsurface moisture below -0.1 MPa the roots failed to grow.

These results agree with the findings of Boatwright and Ferguson (1967) in their studies of wheat, that adventitious roots fail to grow in dry soil. Recent investigations by Cornish (1982) reported surface drying prevented adventitious root extension in Lolium perenne and Phalaris aquatica, although plants otherwise had sufficient moisture.

The most favorable treatment for seedling leaf and root development was the mesic treatment receiving water during the fifth and sixth weeks. Surface soil moisture was above field capacity during the fifth week and subsurface soil moisture was above field capacity after the first watering (Figs. 1 and 2). These seedlings produced an average

of 1.9 adventitious roots and a total adventitious root system length of 15.9 cm, which was significantly longer than in any other treatment (Tables 8 and 9). Total root weights in these seedlings were heavier than in any other treatment, reflecting the largest amount of adventitious root development (Table 7).

These data suggest that the development of John Day and Secar bluebunch wheatgrass seedlings is dependent on soil moisture being available at critical morphological stages. It appears that John Day and Secar seedlings must be in the three-leaf stage before they are capable of initiating and extending adventitious roots. Since development of adventitious roots is essential for seedling establishment, periods of surface and subsurface soil moisture above field capacity need to be provided when seedlings are in the three-leaf stage, to assure development of adventitious roots.

SECTION III

EARLY SEEDLING DEVELOPMENT OF SECAR, BLUEBUNCH WHEATGRASS
UNDER SPRING GROWING CONDITIONS IN EASTERN OREGON

Angela G. Evenden

Richard F. Miller

Marshall R. Haferkamp

EARLY SEEDLING DEVELOPMENT OF SECAR BLUEBUNCH WHEATGRASS
UNDER SPRING GROWING CONDITIONS IN EASTERN OREGON

ABSTRACT

The purpose of this study was to relate the development of Secar bluebunch wheatgrass (Agropyron spicatum) seedlings to soil moisture and air temperature under spring growing conditions on a site in eastern Oregon. Soil moisture was adequate for 80% of total emergence to occur by 22 days after planting. Following emergence, limited rainfall and rising air temperatures resulted in dry conditions which suppressed seedling growth. Most seedlings did not develop three leaves until the tenth week after planting when rainfall increased soil moisture to field capacity (-.033 MPa). This moisture also stimulated initiation of adventitious roots. However, at the end of the 10 week study adventitious root system length averaged only 5.6 cm, and at this depth these roots would be very susceptible to drying conditions.

INTRODUCTION

Bluebunch wheatgrass (Agropyron spicatum (Pursh) Scribner and Smith), is an important forage species that once dominated many of the bunchgrass communities in eastern Oregon. This bunchgrass has been reduced or eliminated in many areas due to a low resistance to grazing and poor management practices. Artificial seeding practices are often necessary to reintroduce bluebunch wheatgrass, however, in many areas revegetation efforts are hindered by steep and rocky terrain and a harsh environment. The rough topography often prevents the use of conventional seeding equipment. Therefore seed must be broadcast into unprepared or chemically prepared seedbeds. These seeds are exposed to extremes in moisture and temperature, and competition from other plants.

Species or ecotypes used for reseeding must be adapted to establish under these harsh environments. Secar, a new cultivar of bluebunch wheatgrass, was released by the USDA, Soil Conservation Service in 1980. Secar is noted for superiority in drought tolerance, ability to establish, and production of crown and roots in areas receiving less than 350 mm of precipitation annually (USDA 1981). Information, however, is needed to determine how Secar performs in the harsh environments of deteriorated communities in eastern Oregon. This study was designed to relate soil moisture and air temperature to the development of Secar seedlings under spring growing conditions on a steep and rocky site in eastern Oregon.

STUDY AREA AND METHODS

Secar seedlings were grown in PVC tubes from April to June, 1982 on an Artemisia tridentata/Agropyron spicatum habitat type (Daubenmire 1970), situated on west and southwest exposures, on the John Day Fossil Beds National Monument in eastern Oregon. Annual precipitation averaging 300 mm is received primarily in the winter and spring. Soils are a stony clay loam belonging to the Simas series (USDA 1981), and elevation is approximately 700 meters.

Five exclosures were fenced to exclude livestock grazing from the study area. Within each exclosure 20 tubes made from 20 cm lengths of 4.4 cm PVC pipe, were placed into holes augered into the soil. Tubes were arranged in a randomized complete block design with exclosures being replications. The tubes facilitated recovery of entire seedlings. Soil collected from the top 20 cm of the soil horizon on the site was dried at room temperature and mixed after removing rocks and other large debris. Soil was placed into the tubes and a 2 week equilibration period was permitted before planting. On April 2, 1982 five Secar seeds, obtained from the Soil Conservation Service Plant Material Center, Pullman, WA, were placed on the soil surface in each tube and covered with 3 mm of additional soil. To prevent seed predation from birds or small rodents, 20-cm lengths of vexar tubing were secured over each tube, and Paradichlorobenzene crystals were spread around the tubes.

Seedling response to environment was monitored by determining rooting depth (length of longest primary root), adventitious root number,

total length of the seedling adventitious root system, leaf number, total leaf length, number of tiller per seedling, number of leaves per tiller and total leaf length per tiller. Seedlings were harvested on six different dates following planting (Table 1).

Table III.1. Seedling harvest dates and days following planting.

Seedling Harvest Date	Days Following Planting
May 6, 1982	35
May 12, 1982	41
May 21, 1982	50
May 26, 1982	55
June 4, 1982	64
June 9, 1982	69

Low numbers of seedling emergence occurred in two of the five replications, thus they were combined into one replication, and all analyses were performed using four replications. Analysis of variance was used to analyze seedling growth parameters through time. An arc-sin transformation was performed on percentage of seedlings with tillers data before analysis, but untransformed data are presented in the tables. Treatment means were separated and significant differences at $p \leq 0.05$ were determined by Tukey's test.

Environmental conditions occurring during the study were monitored on or near the research area. Daily air temperatures were obtained from a weather station located at the Monument. Soil temperatures were

measured on a limited number of dates using a soil probe and psychrometers with a microvolt meter. Mid-day soil moisture outside the tubes was determined gravimetrically at the 0-1 cm, 2-7 cm and 8-20 cm depth, on 24 dates, and soil moisture was determined inside the tubes on each harvest date. A moisture retention curve was constructed with six points; -0.033 , -0.05 , -0.1 , -0.2 , -0.5 and -1.5 MPa (Richards, 1954), and soil water potential was determined using the soil moisture curve.

RESULTS AND DISCUSSION

Environmental conditions of 20 mm rainfall and average maximum and minimum temperatures of 17 and 1 C (Fig. 1), respectively, during the 5 weeks following planting were adequate to allow germination and seedling emergence. Most of the precipitation fell during the first 3 weeks and resulted in soil moisture above field capacity (-0.033 MPa) on or before day 13. A drying trend followed and soil moisture decreased to between -0.1 and -1.5 MPa on day 15. With these conditions, over 80% of the total emergence had occurred by day 22 (Table 2), and seedlings had emerged from about 20% of the seeds planted during the entire study. Following emergence, seedlings continued to grow and produced 2.3 leaves per seedling by day 35, with an average total leaf length of 7.6 cm (Table 3). Seminal roots were initiated and had extended to a depth of 8.8 cm (Table 3). The lowest minimum soil temperature, 12 C, recorded during the first 3 weeks was well above the 8 to 10 C required for root growth in A. spicatum (Harris 1967).

Precipitation during the day 35 to 41 period totaled 4.1 mm and maximum air temperature averaged 18 C. This small amount of precipitation may have increased soil moisture for a brief period but by

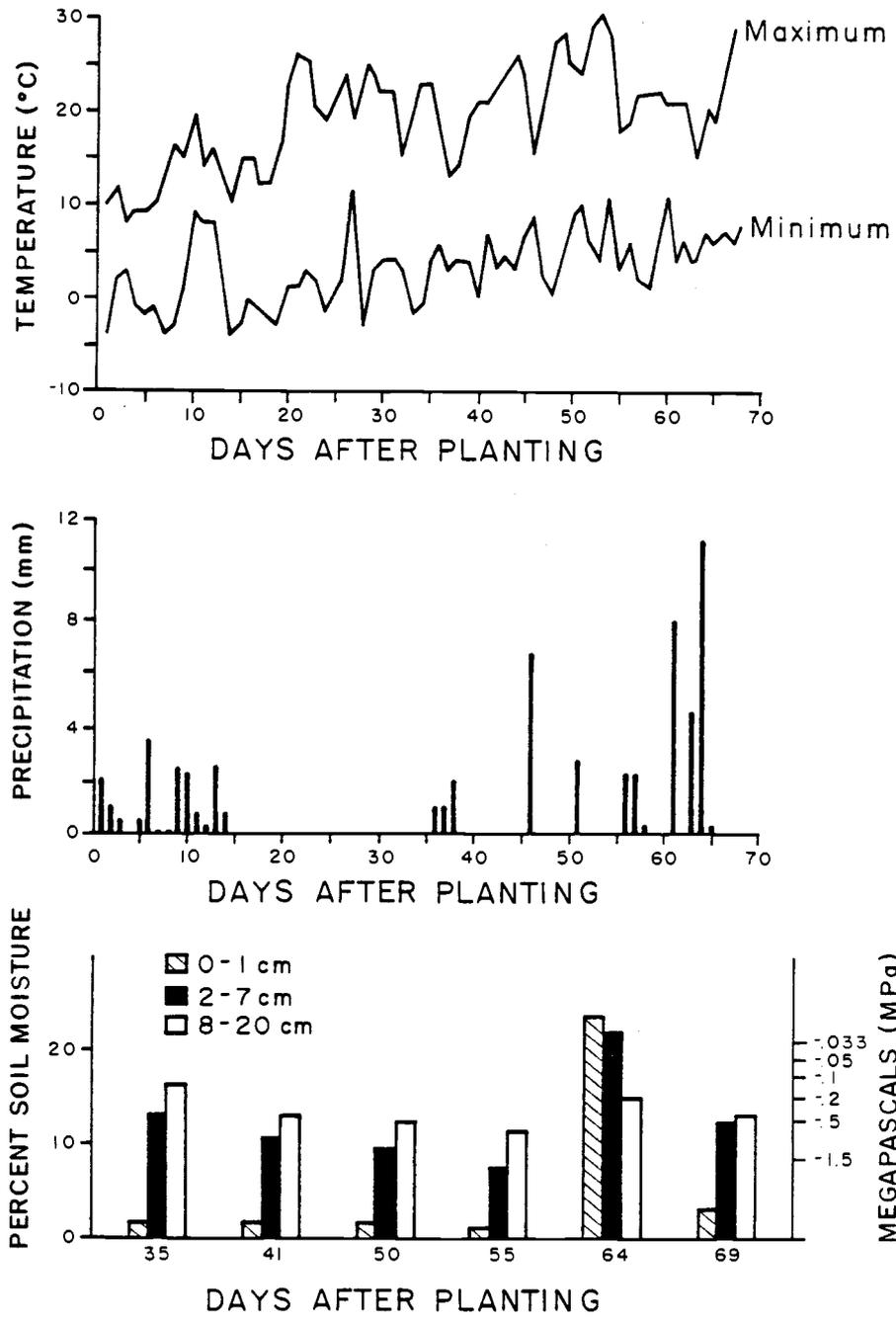


Fig. III.1. Minimum and maximum air temperature, precipitation and percent soil moisture at three soil depths, for the 69-day field trial.

Table III.2. Cumulative mean percent emergence for Secar bluebunch wheatgrass.

Days After Planting	Percent Emergence of Seeds Planted	Percent of Final Emergence
22	21.8 ± 10.3†	86.0
25	23.6 ± 10.0	93.0
29	24.6 ± 10.9	97.0
31	24.6 ± 10.9	97.0
35	24.6 ± 10.9	97.0
50	25.4 ± 10.6	100.00

†Mean ± standard deviation, n=4.

Table III.3. Means and standard deviations for seedling parameters of Secar measured during the 69-day field study.

Days After Planting	Leaf Number	Total Leaf Length (cm)	Rooting Depth (cm)	Adventitious Root Number	Adventitious Root Length (cm)	Percent Seedlings with Tillers	Number of Tillers per Seedling	Tiller Leaf Number	Total Tiller Leaf Length (cm)
35	2.3±.5a [†]	7.6±3.4a	8.8±3.3a	-	-	-	-	-	-
41	2.5±.5a	8.5±3.4a	10.5±3.3a	1.0±.5ab	0.3±1.2a	-	-	-	-
50	2.8±.5ab	9.7±3.4a	14.4±3.3ab	0.4±.5a	0.3±1.2a	37.6±24a	1.0±.7a	1.6±1.1a	4.7±2.5a
55	2.8±.5ab	10.3±3.4a	15.6±3.3ab	0.3±.5a	0.1±1.2a	41.8±24a	1.0±.7a	1.6±1.1a	3.9±s.5a
64	3.2±.5ab	10.0±3.4a	18.3±3.3b	0.8±.5ab	0.7±1.2a	42.9±24a	1.1±.7a	1.7±1.1a	4.5±2.5a
69	3.7±.5b	14.2±3.4a	18.8±3.3b	1.8±.5b	5.6±1.2b	68.5±24a	2.2±.7a	2.4±1.1a	7.8±2.5a

[†] Means in columns with the same letter are not significantly different at the .05 level according to Tukey's Test.

day 41 surface and subsurface soil moisture levels were below -1.5 MPa and approximately $-.5$ MPa respectively. Seedling leaf number, total leaf length and rooting depth did not increase during this period (Table 3), but with the small amount of rainfall, adventitious roots were initiated in some seedlings, and roots grew an average of 0.3 cm (Table 3). Further extension of adventitious roots, however, was probably prevented by the dry surface soil conditions.

Soil moisture was recharged only one time between days 41 and 50 when 6.9 mm of precipitation was received on day 46 (Fig. 1). This resulted in subsurface soil moisture levels between $-.5$ and -1.5 MPa on day 50 (Fig. 1). Average maximum air temperature during this period was 22 C. These conditions were adequate for growth as seedling leaf number, total leaf length and rooting depth continued to increase over time (Table 3), and tiller development was first observed on seedlings on day 50 (Table 3). Dry surface soil conditions, however, prevented an increase in adventitious root number and length. Herbage development appeared to be hindered by the hot and dry conditions, for leaf growth appeared stunted and leaf tips were brown and wilted.

A total of 17.8 mm of rainfall fell during the period from day 55 to 64 and increased water potential in the surface and subsurface soil to the 7 cm depth to above field capacity ($-.033$ MPa). Soil water potential below 8 cm was less than $-.1$ MPa. Seedling growth continued with the increase in soil water potential and on day 64 seedlings averaged 3.0 leaves each, totaling 10.0 cm in length. Seminal rooting depth increased to 18.3 cm, and small increases in adventitious root length were noted (Table 3).

During the period from day 64 to day 69 precipitation totaled 12.7 mm and maximum temperatures averaged 21 C. Soil moisture inside the tubes on day 69 was below -1.5 MPa in the surface layer and approximately -.5 MPa below the surface (Fig. 1). Soil moisture increase during this period resulted in increased seedling growth immediately prior to day 64. On the final sampling date (day 69) average leaf number per seedling was 3.7 and average total leaf length was 14.2 cm (Table 3). The number of seedlings with tillers increased to almost 70%. Seedlings with tillers averaged 2.3 tillers each and each tiller averaged 2.4 leaves with a total tiller leaf length of 7.8 cm (Table 3).

Adventitious root initiation and extension were also substantial during this period (days 64 to 69). The average number of adventitious roots per seedling increased to 1.8 and average total adventitious root system length increased 4.9 cm. Root growth during this period was seven times greater than in any previous period.

CONCLUSIONS

Extension of adventitious roots is one of the most important factors determining perennial grass establishment (Hyder 1974). These roots must be able to penetrate the soil profile at a rate to keep roots ahead of the wetting front. Adventitious root systems of 10-week old Secar seedlings penetrated only the upper soil horizon which placed these roots in a zone susceptible to drying. It appears that periods of soil moisture above field capacity would be necessary to assure further extension of these roots. Precipitation received late in the study increased soil moisture to above field capacity and

resulted in a significant increase in adventitious root development. Prior to receipt of this precipitation, surface soil moisture was well below -1.5 MPa and adventitious roots did not grow. These results agree with findings of Boatwright and Ferguson (1967) that adventitious roots of wheat failed to grow in dry soil.

It appears from the overall lack of vigor exhibited in Secar seedlings during this study that a more favorable environment is needed for growth. Possible solutions for enhancing or increasing the period of available moisture under field conditions might include an earlier planting date or use of mulching treatments. Additional research is needed to adequately describe Secar's adaptability to varying environmental conditions, with different dates of planting or mulching treatments.

SUMMARY AND CONCLUSIONS

Bluebunch wheatgrass sites in need of revegetation frequently host a harsh environment for seedling establishment. Cultivars of bluebunch wheatgrass used in seedings must be able to germinate and establish under conditions of limited moisture. Secar, a newly released cultivar, was selected for its ability to establish and grow in adverse environments. The evaluations performed in this thesis were intended to provide an understanding of the seed germination and seedling development response of John Day and Secar bluebunch wheatgrass to a range of moisture stress and temperature conditions.

Both Secar and John Day bluebunch wheatgrass were able to germinate and grow well under a wide range of temperature and moisture stress conditions. Rate of germination, total percent germination, and rate and amount of seedling development, however, decreased as moisture stress increased. Seeds of both sources germinated best over the widest range of moisture stress levels at 20 C.

John Day seed germinated faster than Secar at moderate temperatures and low moisture stress. This same trend was apparent in the greenhouse study where John Day seedlings emerged at a faster rate than Secar seedlings. A fast rate of development can be an advantage when adequate amounts of soil moisture follow germination and emergence. However, if soil moisture in the surface layer were adequate for germination but moisture in the subsurface layer was limiting, a rapid rate of germination could be detrimental and result in seedling mortality. Due to rapid emergence rates, John Day seedlings

had an extended opportunity for growth when compared to Secar seedlings. This resulted in higher herbage and root biomass in John Day seedlings.

Secar seeds germinated better than John Day seed at moderate temperatures and moderate to high levels of moisture stress. This could be an advantage on many sites, where by the time temperatures are favorable for growth in the spring, moisture is already limiting. Secar seedlings also exhibited the ability to initiate and extend adventitious roots at a faster rate than John Day seedlings. The importance of adventitious root development and extension, as a necessity for perennial grass establishment has been stressed by Hyder (1974). From the results of the greenhouse and field studies, it appears that bluebunch wheatgrass seedlings must be in or near the three-leaf stage before they are capable of developing adventitious roots. Both sources initiated adventitious roots when most seedlings were in the three-leaf stage and surface soil moisture was increased to above field capacity. Subsurface soil moisture above field capacity provided a favorable environment for adventitious root extension. The faster rate of adventitious root development and the larger adventitious root systems of Secar seedlings could be valuable for establishment in harsh environments. When soil moisture is available, Secar would be able to develop adventitious roots more rapidly.

In comparing the germination and seedling development response of Secar and John Day, the Secar cultivar appears to have an advantage for establishment in harsh environments. The two characteristics which appear to be beneficial for Secar are its ability to germinate under

higher levels of moisture stress at moderate temperatures, and a faster rate of adventitious root development. With these considerations in mind, Secar may show promise for use in revegetation in the harsh environments of deteriorated bluebunch wheatgrass sites.

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APPENDICES

APPENDIX A. Analysis of Variance and two-way interaction means for total percent germination of two sources of bluebunch wheatgrass for a range of moisture stress conditions at three constant temperatures.

A-1. Analysis of Variance for total percent germination of two sources of bluebunch wheatgrass at five levels of water potential and 10 C.

Source	df	Mean Square
Total	29	799.37
Block	2	17.08
Source	1	49.54
Water Potential	4	5153.09**
Source x Water Potential	4	512.20**
Error	18	24.27

**Significant at the 0.01 level.

A-2. Two-way interaction means for total percent germination of two sources of bluebunch wheatgrass at five levels of water potential and 10 C.

Source	Water Potential (MPa)				
	0	-0.3	-0.7	-1.2	-1.6
John Day	100d†	100d	91c	49b	0a
Secar	86c	88c	86c	66b	13a

†Means in a row followed by the same letter are not significantly different at the 0.05 level according to Tukey's Test.

A-3. Analysis of Variance for total percent germination of two sources of bluebunch wheatgrass at five levels of water potential and 20 C.

Source	df	Mean Square
Total	39	942.75
Block	3	43.56
Source	1	23.84
Water Potential	4	8332.37**
Source x Water Potential	4	493.02**
Error	27	48.56

**Significant at the 0.01 level.

A-4. Two-way interaction means for total percent germination of two sources of bluebunch wheatgrass and five levels of water potential at 20 C.

Source	Water Potential (MPa)				
	0	-.4	-.9	-1.3	-2.0
John Day	100d†	97d	79c	29b	0a
Secar	89c	92c	82bc	68b	9a

†Means in a row followed by the same letter are not significantly different at the 0.05 level according to Tukey's Test.

A-5. Analysis of Variance for total percent germination of two sources of bluebunch wheatgrass at four levels of water potential and 30 C.

Source	df	Mean Square
Total	31	641.61
Block	3	17.13
Source	1	5469.01**
Water Potential	3	4334.80**
Source x Water Potential	3	127.04
Error	21	46.86

**Significant at the 0.01 level.

A-6. Two-way interaction means for total percent germination of two sources of bluebunch wheatgrass at four levels of water potential and 30 C.

Source	Water Potential (MPa)			
	0	-.5	-.7	-1.1
John Day	99c†	93c	67b	26a
Secar	76c	48b	22a	3a

†Means in a row followed by the same letter are not significantly different at the 0.05 level according to Tukey's Test.

APPENDIX B. Summary of total germination activity at the end of a 30 day period for two sources of bluebunch wheatgrass germinated at a range of water potentials and three constant temperatures.

B-1. Summary of germination activity at the end of a 30 day period for two sources of bluebunch wheatgrass germinated at seven levels of water potential and 10 C.

Water Potential (MPa)	John Day			Secar		
	Normal Germination	Abnormal Germination		Normal Germination	Abnormal Germination	
	Radicle & Plumule (each 5mm)	Radicle & Plumule 5mm	Radicle Only	Radicle & Plumule (each 5mm)	Radicle & Plumule 5mm	Radicle Only
0	100 ± 0†	-	-	86 ± 4.5	2 ± 2.8	3 ± 2.6
-.3	100 ± 0	-	-	88 ± 6.2	3 ± 2.8	3 ± 2.6
-.7	91 ± 2.3	-	4 ± 0	86 ± 11.1	2 ± 2.8	3 ± 2.6
-1.2	49 ± 8.1	7 ± 4.6	39 ± 10.3	66 ± 13.6	6 ± 2.6	16 ± 9.5
-1.6	-	3 ± 4.6	70 ± 9.6	13 ± 1.0	11 ± 7.6	33 ± 5.1
-2.2	-	-	-	-	-	11 ± 11.5
-2.7	-	-	-	-	-	-

†Mean percent germination ± standard deviation, n=3.

B-2. Summary of germination activity at the end of a 30 day period for two sources of bluebunch wheatgrass germinated at five levels of water potential and 20 C.

Water Potential (MPa)	John Day			Secar		
	Normal Germination	Abnormal Germination		Normal Germination	Abnormal Germination	
	Radicle & Plumule (each 5mm)	Radicle & Plumule 5mm	Radicle Only	Radicle & Plumule (each 5mm)	Radicle & Plumule 5mm	Radicle Only
0	100 ± 0†	-	-	89 ± 3.8	-	2 ± 4.5
-0.4	97 ± 3.8	-	2 ± 4.0	92 ± 9.8	-	1 ± 2.0
-0.9	79 ± 8.5	-	20 ± 10.0	82 ± 6.9	-	2 ± 2.3
-1.3	29 ± 6.8	-	70 ± 7.6	68 ± 13.0	2 ± 2.6	13 ± 8.3
-2.0	-	-	67 ± 4.0	9 ± 12.1	5 ± 6.1	29 ± 20.0

†Mean percent germination ± standard deviation, n=4.

B-3. Summary of germination activity at the end of a 30 day period for two sources of bluebunch wheatgrass germinated at seven levels of water potential and 30 C.

Water Potential (MPa)	John Day			Secar		
	Normal Germination	Abnormal Germination		Normal Germination	Abnormal Germination	
	Radicle & Plumule (each 5mm)	Radicle & Plumule 5mm	Radicle Only	Radicle & Plumule (each 5mm)	Radicle & Plumule 5mm	Radicle Only
0	99 ± 2.0†	-	1 ± 2.0	76 ± 5.7	-	5 ± 0.6
-0.5	93 ± 8.9	1 ± 2.0	2 ± 2.3	48 ± 6.4	3 ± 4.5	4 ± 2.5
-0.7	67 ± 1.9	2 ± 2.3	24 ± 10.0	22 ± 12.8	1 ± 2.0	17 ± 7.8
-1.1	26 ± 3.0	5 ± 4.1	35 ± 9.4	3 ± 2.9	5 ± 5.5	14 ± 8.5
-1.4	-	1 ± 2.0	35 ± 9.9	-	-	5 ± 5.5
-2.2	-	-	11 ± 7.4	-	-	-
-2.7	-	-	-	-	-	-

†Mean percent germination ± standard deviation, n=4.

APPENDIX C. Concentrations of Polyethylene glycol (PEG) used and adjustments made for prepared water potential solutions, for use at three constant temperatures.

C-1. Concentrations of Polyethylene glycol (PEG) used and adjustments made for prepared water potential solutions for use at 10, 20 and 30 C.

Water Potential (MPa)	gm PEG/500 ml H ₂ O [†]	Adjustments		X Final Water Potential
		gm PEG Added	ml H ₂ O Added	
<u>10 C</u>				
-0.3	64.5			-0.3
-0.6	98.0	17.0		-0.7
-0.9	123.9	28.0		-1.2
-1.2	146.0	25.0		-1.6
-1.5	165.3	38.0		-2.2
-1.8	183.0	44.0		-2.7
<u>20 C</u>				
-0.3	72.0			-0.4
-0.6	107.0	26.8		-0.9
-1.2	157.0			-1.3
-1.5	177.3	19.7		-2.0
<u>30 C</u>				
-0.3	80.3			-0.5
-0.6	117.3		91.7	-0.7
-0.9	145.9		55.6	-1.1
-1.2	170.0		62.5	-1.4
-1.5	191.0			-2.2
-1.8	210.3		66.7	-2.7

[†]PEG(6000 MW) concentrations and corresponding water potentials according to Michel and Kaufman (1973).

APPENDIX D. Analysis of Variance for seedling leaf and root measurements for two sources of bluebunch wheatgrass grown under six moisture regimes.

D-1. Analysis of Variance for seedling leaf number on five sampling dates.

Source	df	Mean Square Day 15	Mean Square Day 22	Mean Square Day 29	Mean Square Day 36	Mean Square Day 43
Total	47	.12	.10	.14	.16	.10
Blocks	3	.30	.11	.08	.14	.14
Source	1	1.33**	.68**	2.48**	.18	.11
Water Treatment	5	.08	.14	.28**	.74**	.43**
Source x Water Treatment	5	.03	.06	.05	.09	.07
Error	33	.09	.08	.07	.08	.05

**Significant at the 0.01 level.

D-2. Analysis of Variance for total seedling leaf length on five sampling dates.

Source	df	Mean Square Day 15	Mean Square Day 22	Mean Square Day 29	Mean Square Day 36	Mean Square Day 43
Total	47	5.55	16.14	19.41	24.79	16.67
Blocks	3	7.71	21.85	20.70	26.96	15.81
Source	1	113.47**	112.85**	144.11**	66.04*	85.60**
Water Treatment	5	1.51	25.42	82.02**	124.43**	63.09**
Source x Water Treatment	5	1.78	7.03	8.02	13.67	2.12
Error	33	3.27	12.66	7.75	9.92	9.83

*,**Significant at the 0.05 and 0.01 levels, respectively.

D-3. Analysis of Variance for seedling total leaf weight on five sampling dates.

Source	df	Mean Square Day 15	Mean Square Day 22	Mean Square Day 29	Mean Square Day 36	Mean Square Day 43
Total	47	.64	1.17	3.47	5.53	8.00
Blocks	3	3.66	.82	2.18	6.03	6.96
Source	1	1.27	2.85	24.51**	47.01**	50.02**
Water Treatment	5	.41	.15	10.98**	17.98**	33.55**
Source x Water Treatment	5	.65	1.08	.38	3.57	2.26
Error	33	.38	1.32	2.29	2.64	3.82

**Significant at the 0.01 level.

D-4. Analysis of Variance for seedling rooting depth on five sampling dates.

Source	df	Mean Square Day 15	Mean Square Day 22	Mean Square Day 29	Mean Square Day 36	Mean Square Day 43
Total	47	5.85	2.34	.84	1.15	.50
Blocks	3	4.59	9.71	.69	2.84	.81
Source	1	19.51*	6.31	.40	.03	.15
Water Treatment	5	19.18**	.66	1.96*	1.07	.88
Source x Water Treatment	5	3.77	1.41	.47	.30	.50
Error	33	3.85	1.94	.75	1.18	.42

*,**Significant at the 0.05 and 0.01 levels respectively.

D-5. Analysis of Variance for seedling root system weight on five sampling dates.

Source	df	Mean Square Day 15	Mean Square Day 22	Mean Square Day 29	Mean Square Day 36	Mean Square Day 43
Total	47	.30	.50	1.99	4.01	7.02
Blocks	3	1.92	.27	.47	9.77	8.88
Source	1	.09	1.17	15.08**	16.92*	21.47**
Water Treatment	5	.23	.13	1.00	10.00**	36.98**
Source x Water Treatment	5	.09	.46	1.41	.79	1.20
Error	33	.20	.56	1.98	2.68	2.76

*,**Significant at the 0.05 and 0.01 levels, respectively.

D-6. Analysis of Variance for seedling adventitious root number on two sampling dates.

Source	df	Mean Square Day 36	df	Mean Square Day 43
Total	31	288.64	47	332.04
Blocks	3	452.62	3	115.79
Source	1	1749.36**	1	449.58
Water Treatment	3	737.46**	5	1442.27**
Source x Water Treatment	3	149.59	5	122.47
Error	21	151.40	33	211.67

**Significant at the 0.01 level.

D-7. Analysis of Variance for seedling adventitious root system length on two sampling dates.

Source	df	Mean Square Day 36	df	Mean Square Day 43
Total	31	15.63	47	35.98
Blocks	3	9.55	3	2.41
Source	1	76.66*	1	29.08
Water Treatment	3	36.71*	5	242.26**
Source x Water Treatment	3	19.62	5	12.99
Error	21	10.01	33	11.47

*,**Significant at the 0.05 and 0.01 levels, respectively.

APPENDIX E. Soil temperature and moisture measurements taken for three soil depths on the study area at the John Day Fossil Beds National Monument in eastern Oregon.

E-1. Mean Soil Temperatures ($^{\circ}\text{C}$) taken at three soil depths on assorted dates.

Days After Planting	Date	Soil Depth		
		0 - 1 cm	2 - 7 cm	8 & below
13†	4/14/82	12.1	12.8	12.3
15	4/16/82	23.7	17.8	11.6
18	4/19/82	23.9	17.8	13.0
20	4/21/81	32.2	22.8	15.6
52	5/23/82	42.1	25.8	22.6
53	5/24/82	45.5	27.8	24.0
54	5/25/82	25.2	20.8	19.3
55	5/26/82	41.0	26.3	23.3
57	5/28/82	35.6	24.2	20.0
58	5/29/82	31.2	23.6	18.1
61	6/ 1/82	21.5	20.1	18.5
64	6/ 4/82	20.7	18.3	16.5
65	6/ 5/82	17.4	17.1	16.5
67	6/ 7/82	24.8	22.7	20.3

†Temperature measurements on days 13, 15, 18 and 20 were taken using a soil probe, all others were taken with psychrometers and a micro-voltmeter, at mid-day.

E-2. Percent soil moisture at three depths for the study area on the John Day Fossil Beds National Monument in eastern Oregon.

Days After Planting	Date	Soil Depth		
		0 - 1 cm	2 - 7 cm	8 cm & below
13	4/14/82	26.3 ± 1.7†	23.7 ± 1.5	23.1 ± 1.1
15	4/16/82	11.9 ± 2.0	24.1 ± 2.0	23.0 ± 1.9
18	4/19/82	4.5 ± 3.2	19.6 ± 2.9	19.7 ± 1.3
20	4/21/82	7.8 ± 1.5	20.1 ± 4.2	20.3 ± 2.9
22	4/23/82	9.2 ± 1.9	17.8 ± 2.7	17.3 ± 1.5
25	4/26/82	9.9 ± 5.0	16.9 ± 3.8	16.7 ± 2.5
27	4/28/82	8.6 ± 3.0	14.5 ± 1.2	16.7 ± 2.1
29	4/30/82	7.9 ± 4.5	13.4 ± 2.3	15.8 ± 0.5
31	5/ 2/82	5.6 ± 3.1	12.9 ± 1.9	14.7 ± 1.1
37	5/ 8/82	1.9 ± 0.8	7.6 ± 1.3	9.8 ± 1.8
39	5/10/82	6.2 ± 0.9	6.4 ± 0.8	8.6 ± 0.9
40	5/11/82	3.9 ± 1.5	6.5 ± 1.0	8.5 ± 0.5
45	5/16/82	1.1 ± 0.2	5.9 ± 0.5	7.8 ± 1.3
46	5/17/82	19.2 ± 2.4	9.6 ± 1.0	9.0 ± 1.0
47	5/18/82	15.5 ± 1.6	10.4 ± 1.1	10.0 ± 0.6
51	5/22/82	2.2 ± 1.2	6.4 ± 0.2	6.6 ± 0.8
53	5/24/82	0.4 ± 0.1	4.9 ± 0.7	5.8 ± 0.8
54	5/25/82	0.8 ± 0.5	4.6 ± 0.6	5.8 ± 0.8
57	5/28/82	9.0 ± 1.0	7.8 ± 0.5	11.5 ± 4.0
58	5/29/82	6.8 ± 1.4	7.6 ± 0.5	9.6 ± 0.5
61	6/ 1/82	1.9 ± 1.0	13.5 ± 2.0	10.9 ± 0.2
65	6/ 5/82	21.9 ± 2.0	20.5 ± 1.2	19.0 ± 0.8
67	6/ 7/82	16.6 ± 0.3	18.3 ± 1.4	18.2 ± 1.0

†Mean ± standard deviation.

E-3. Percent soil moisture and corresponding water potentials for soil on study area at the John Day Fossil Beds National Monument.

	Water Potential (MPa)					
	-0.03	-0.05	-0.1	-0.2	-0.5	-1.5
Percent Soil Moisture	20.9	19.4	17.4	15.0	12.2	9.3