Dormancy factors in beardless wildrye (Elymus triticoides) seed
by Allen Dale Knapp

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Agronomy
Montana State University

Abstract:
The use of beardless wildrye (Elymus triticoides) as a forage grass is limited by slow germination and stand establishment. Overcoming these problems would increase the usefulness of this grass for seeding in wetlands and saline-alkaline areas. The purpose of these studies was to define the factors contributing to the slow germination of beardless wildrye. Studies were conducted to determine the effect of imbibition temperature and high oxygen concentrations on imbibition and germination; and the effects of stratification, embryo excision, seed size, scarification and hormones on germination. Stratifying seeds for five days at SC increased germination compared to non-stratified seeds by 10%. This increase indicated that beardless wildrye seed is dormant. Temperature did not affect total imbibition. However, imbibition at 30 and 2O°C induced greater germination at 15-25°C than imbibition at 10 or 1.5C. High oxygen concentrations did not affect total imbibition. However, the application of oxygen induced the greatest germination response of all treatments (57%). Excised embryos germinated rapidly. The response to oxygen and the rapid germination of excised embryos indicated that dormancy in beardless wildrye is imposed by the outer coverings of the seed. Certain combinations of gibberellic acid, benzyladenine and indole-3-acetic acid, enhanced germination. The average increase in germination due to hormones was 17%, indicating that the role of hormones in the dormancy of this species is not dominant. Germination was not influenced by seed size, mechanical scarification or ultrasonic scarification for 20 or 30 minutes.

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by

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A thesis submitted in partial fulfillment
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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The use of beardless wildrye (Elymus triticoides) as a forage grass is limited by slow germination and stand establishment. Overcoming these problems would increase the usefulness of this grass for seeding in wetlands and saline-alkaline areas. The purpose of these studies was to define the factors contributing to the slow germination of beardless wildrye. Studies were conducted to determine the effect of imbibition temperature and high oxygen concentrations on imbibition and germination; and the effects of stratification, embryo excision, seed size, scarification and hormones on germination. Stratifying seeds for five days at 5C increased germination compared to non-stratified seeds by 10%. This increase indicated that beardless wildrye seed is dormant. Temperature did not affect total imbibition. However, imbibition at 30 and 20C induced greater germination at 15-25C than imbibition at 10 or 1.5C. High oxygen concentrations did not affect total imbibition. However, the application of oxygen induced the greatest germination response of all treatments (57%). Excised embryos germinated rapidly. The response to oxygen and the rapid germination of excised embryos indicated that dormancy in beardless wildrye is imposed by the outer coverings of the seed. Certain combinations of gibberellic acid, benzyladenine and indole-3-acetic acid, enhanced germination. The average increase in germination due to hormones was 17%, indicating that the role of hormones in the dormancy of this species is not dominant. Germination was not influenced by seed size, mechanical scarification or ultrasonic scarification for 20 or 30 minutes.

INTRODUCTION

Beardless wildrye is a native, rhizomatous, perennial grass, commonly found on moist saline-alkaline soils from Texas and California, northward to Washington and Montana (1,27). It is highly cross-pollinated (61) and strains vary in vigor of rhizomes, height, leafiness, leaf coarseness and resistance to leaf rust, stem rust and ergot. Hafenrichter (27) describes two main types: "(1) tall, coarse, leafy, vigorous rhizomes, fair seed production and (2) short, fine stems, narrow leaves, small heads, poor seed production."

The potential of beardless wildrye as a forage is derived from its adaptation to adverse soil conditions. It may be of value in the vegetation of the discharge areas of saline or saline-alkaline seeps and of areas subject to periodic flooding (14). Establishing a good forage in these areas could provide a good agronomic return from otherwise wasted acreage. However, the seed of beardless wildrye germinates slowly and seedlings do not compete well with weeds or cultivated crops. Good stands are therefore difficult to obtain. The purpose of these studies was to define the factors contributing to the slow germination of beardless wildrye.

LITERATURE REVIEW

Description and Definition of Seed Dormancy

Dormancy is an important survival mechanism that allows seeds to maintain viability for an extended period of time and permits species to initiate germination and growth under favorable environmental conditions (68). Villiers (70) defined dormancy as "the state of arrested development whereby the organ or organism, by virtue of its structure or chemical composition, may possess one or more mechanisms preventing its own germination." This definition takes into account the two major dormancy types; those imposed by the actual physical structure of the species, and those imposed by the physiological state related to the species' chemical composition.

Vegis (68) states that "truly dormant shoot apices and seed embryos cannot by any means be induced to immediate normal growth." He implies that even optimum conditions for development will not induce germination of a truly dormant species. This concept helps to delineate the meaning of dormancy and quiescence. Quiescence is the state of arrested development caused by the lack of one or more environmental factors necessary for germination (46, 70). Therefore, the application of the required

environmental factors will induce immediate growth of a quiescent species but not a dormant one. Dormant species require a period of time during which some physical or physiological requirement must be satisfied before germination can proceed.

Dormancy in a seed develops in three general stages (68). The first stage or pre-dormancy is the developmental stage and is evidenced by the narrowing of the range of environmental conditions within which germination will occur. During the pre-dormancy stage some external environmental factor(s) are required which are not normally prerequisite to germination. The sensitivity to environmental factors increases until the seed enters the second stage or true dormancy. Germination cannot be achieved by any means during true dormancy (68). During the third stage or post-dormancy, the physical or physiological blocks preventing germination begin to deteriorate. As post-dormancy progresses the seed becomes less sensitive to environmental conditions until they will germinate in any range of environmental conditions not considered detrimental to growth. When the seed reaches this point, it is non-dormant.

If the above stages occur during seed maturation and dormancy is present at dispersal, the dormancy is termed primary (42). Primary dormancy is, then, the result of an inherent genetic potential as influenced by the environment. Dormancy that develops after primary dormancy has been broken is termed secondary dormancy.

Imbibition by Seeds

The imbibition of water is the primary process in the succession of events leading to germination (46). Imbibition is necessary for the initiation of many physiological functions within the seed. These functions include enzyme activation (43) and protein synthesis (45).

Temperature affects the rate of imbibition. The Q_{10} for the rate of imbibition is less than that of a chemical reaction and greater than the Q_{10} of a physical reaction (55). This implies that both physiological and physical processes are involved in the uptake of water by seeds. The physical process of water uptake is considered to be a special osmotic situation combined with a colloidal interaction with water (55). The evidence indicating the participation of a physiological reaction in the imbibitional process is not conclusive (17,55).

Temperature affects the rate of imbibition and subsequent germination. Alfalfa (Medicago sativa L.), red clover (Trifolium pratense, L.), aslike clover (Trifolium hybridum, L.), and ladino clover (Trifolium repens, L.) imbibe water faster and germinate better at 25C than at 6.7C (21). Higher temperatures, within the optimum temperature range (20), usually induce faster germination of non-dormant species. However, certain dormant species require a period of cool temperature imbibition before complete germination will occur.

Stratification of Seeds

The exposure of seeds to a period of cool temperature imbibition is called stratification or after-ripening (46). Stratification influences germination of certain dormant species and ensuing seedling growth. Flemion and De Sylva (23) exposed dormant peach (Prunus persica) seeds to stratification at 5C for varying periods of time. Those seeds which germinated without a prechill treatment were physiologically dwarfed as were those exposed to a 28-day chilling period followed by exposure to 25C for 14 days. Semi-dwarf seedlings were produced by exposing seeds to a 28-day chilling period, then 14 days at 25C followed by 5C for 35 days. Exposing seeds to 5C for 85 days enhanced

germination and normal seedling growth. Secondary dormancy was induced by chilling the seeds for 4-6 weeks and then transferring them to 25C. Flemion and De Sylva (23) found that the quantity of amino acids and phosphates was greater in seed which had been chilled for 77 days than in those exposed to a 42-day chilling period. The application of some of the amino and organic acids that increased with chilling enhanced germination but others had no effect. It is therefore impossible to state whether these changes were primary or secondary factors in the enhancement of germination.

Other changes may occur during stratification including embryo growth and increased oxygen (O_2) uptake by the embryo axis (54). Hormone levels also change during chilling.

Specific Seed Dormancy Types

Impermeability of the seed coat. Many species, especially members of the Leguminosae, possess a dormancy mechanism imposed by the seed coat's impermeability to water (46). Impermeability of the seed coat of soybeans to water is attributed to a large quantity of fat between palisade cell walls and high lignification between the palisade cell base and spool cell top (4). Development of

impermeable seed coats may vary within a species due to variety and maturation temperature of the seed.

The seed coat may also retard germination by restricting gaseous exchange. Crocker (15) has shown that increased O_2 tensions could induce 100% germination of dormant intact upper seeds of Xanthium species. Cutting the seed coat gave similar results, indicating that the seed coat restricts the supply of O_2 to the embryo. Dormancy can be induced in sorghum (Sorghum spp.) by artificially drying the seed to a low moisture content (47). Only high germination temperatures or cutting the integument can break this dormancy. Nutile (47) inferred that drying the seed caused a physical change in the structure of the integument which restricted the O_2 supply to the embryo. High temperature apparently made more O_2 available.

The seed coat membranes of Cucurbita pepo are restrictive to gaseous exchange (9). The inner membrane was shown to be about five times as permeable to carbon dioxide (CO_2) and ten times as permeable to O_2 as the outer membrane. Nitrogen diffusion rates were not significantly different from O_2. Both membranes were more permeable to CO_2 than to O_2 or nitrogen. Although the outer membrane was less permeable to gases than the inner membrane, Brown

(9) feels that the inner membrane controls the supply of gases to the embryo. The permeability of the inner membrane is apparently related to its physical structure and state of hydration.

Oxygen generally enhances germination while CO_2 usually induces dormancy. Thornton (66) found that seeds of Xanthium would not germinate in 100 percent CO_2. Complete germination could be obtained in 80-100 percent O_2. Thornton's work exemplifies the general response of seeds to O_2 and CO_2. However, certain species do not follow this rule. Seed of subterranean clover (Trifolium subterraneum) germinates best in an atmosphere of between 0.3 and 5% (by volume) CO_2 (6).

Immaturity of Seed Embryos

The state of maturity of an organ or organism is usually achieved by the progress of two related factors: (1) complete morphological differentiation; and (2) attainment of the maximum size allowed by the genetics and environment. Immaturity of the embryos of certain dormant species can be attributed to one or both factors. Holly (Ilex opaca) seed possess immature embryos (31). At dispersal, the embryos are nothing more than a spherical mass of tissue. Following dispersal, continuous embryo growth begins

and requires 8-12 months to reach maturity. The seed of Heracleum sphondylium L. develops from a mass of tissues making up 0.4 percent of the dry seed weight at dispersal compared to a complete embryo comprising 30 percent of the dry seed weight just before germination (64). In this case the maturation of the embryo involves both an increase in size and differentiation. At the opposite end of the spectrum, the embryos of Fraxinus excelsior are morphologically complete at dispersal. However, during imbibition the embryo will double in length (69). Steinbauer (63) found a great deal of variation in the degree of embryo maturity in Fraxinus seed at dispersal.

In contrast, the seeds of smooth brome (Bromus inermis) possess embryos capable of germination five days after anthesis (26). In species with mature embryos at seed dispersal, dormancy may be due to a hormonal imbalance.

Hormonal Control of Seed Dormancy

Certain hormones are known to play an important role in arrested development, initiation of growth (including germination) and the state of dormancy.

Gibberellins are probably the most widespread germination promoting hormones. Gibberellins and

gibberellin-like substances have been isolated from many different plants including: Phleum pratense L., Lolium perenne L., Dactylis glomerata L., Festuca pratensis and Hordeum vulgare (33).

Gibberellins (GA) replace many germination requirements in various dormant species. GA will replace the light requirement and reverse the dark-osmotic inhibition of the germination of lettuce (Latuca spp.) seed (38). GA also replaces light inhibition (11) in Phacelia tanacetifolia seed and light osmotic inhibition of germination (12) in the seed of Nemophylia insignis. In addition it will replace stratification requirements (7,19,24), overcome dormancy at low temperatures (35,36,37), and dormancy due to high temperature pretreatment (39).

Although the ability of GA to enhance germination is well documented, its specific effect on the physiology of dormant seeds is unknown. Frankland and Wareing (25) studied the changes in endogenous gibberellins in two species. Gibberellins were detectable in Corylus avellana only after six weeks of chilling. Fagus sylvatica seed contains gibberellin-like substances but differences were found in the chromatographic activity of substances isolated from chilled versus unchilled seed.

The content of neutral gibberellin-like substances remains unchanged during the maturation of bean (Phaseolus spp.) seed (28) but increases greatly in mature seed. The increase is accompanied by a corresponding decrease in the acid fraction of gibberellin-like substances. Hashimoto (28) proposed that the neutral gibberellin-like fraction constitutes a reserve form of GA in dry seed.

GA applied to the endosperm of barley seed stimulates the production of reducing sugars and protein. The Q_{10} values of this reaction indicates the formation or activation of enzymes (49). Paleg (49,50) hypothesized that GA is contained in the embryo but that its primary function is in the endosperm. The release of reducing sugars is not considered to be the direct mode of action of GA but the result of the initial hormone response (49,50). Varner (67) found that α-amylase activity is dependent on GA and is the result of in-vivo synthesis of the enzyme. Similar results on the relationship of GA and α-amylase activity have been reported by Chrispeels and Varner (13). They postulated that GA activity is controlled at the gene level. GA increases RNA synthesis in aleurone cells of barley (10). This increase is assumed to be related to α-amylase formation. Dormant seed treated with GA germinated in 11 days

and had seven times the amount of RNA synthesis compared with untreated controls, after 66 hours (32). The increased RNA synthesis was attributed to a greater amount of available DNA template in GA treated seed.

The application of GA will also increase the level of endogenous auxins (53), and increase cell wall plasticity (44) in a manner analogous to that of the auxin indole-3 acetic acid (65).

Cytokinin is a term used to encompass a group of chemically heterogeneous substances possessing kinetin-like activity (60). Kinetin-like activity can be generally classified as, the promotion of cytokinesis in cells, altered metabolic rates and enzyme activation (60). Cytokinins also break dormancy in seeds (58), and their activity increases during the breaking of dormancy in the buds of Betula and Populus (18).

Benzyladenine is a synthetic derivative of kinetin and induces kinetin-like physiological responses (60). Benzyladenine enhances the germination of apple seeds (5) but, as with most phytohormones, its specific mode of action is unknown. There are, however, certain metabolic changes known to occur in the presence of this cytokinin.

Benzyladenine will increase proteolytic activity when applied to excised squash (Cucurbita spp.) cotyledons (52). GA has no effect on this process (51). In addition, benzyladenine delays the degradation of starch by hindering the development of α-amylase activity (62). GA cannot counteract this effect (51,52).

Amen (3) believes that all forms of dormancy are controlled by the balance of inhibitor and promoter substances within the seed. However, no one is able to document the interactions that occur between inhibitors and promoters during the onset or dissolution stages of dormancy. Khan (40,41) proposed an interesting theory of hormonal interactions to describe this phenomenon. He assigns cytokinins the permissive role in seed germination. In other words, cytokinins negate the effects of inhibitors within dormant seed and "permit" gibberellins to promote germination processes. Khan (40,41) believes that gibberellins are necessary for germination and that even in the absence of inhibitor substances, germination will not occur without the presence of sufficient levels of gibberellins.

Combination of Dormancy Types

Crocker (16) defined dormancy as resulting from "the inhibition of one or more of the processes preceding or

accompanying germination." He discusses the changes occurring in the embryo in conjunction with the physical characteristics of the seed coat that may result in dormancy. Thus, dormancy in certain species may require more than one stimulus to induce germination.

A well documented example of a seed dormancy type involving more than one factor is found in Fraxinus excelsior (69). Fraxinus seeds possess rudimentary embryos and require long imbibition periods during which the embryos grow in size. Fully grown embryos of Fraxinus seeds will not germinate, however, and require a stratification period before germination will occur.

Amen (2) defines a seed using thermodynamics. His definition helps to conceptualize the complexity and the order in the maintenance of seed viability through structure. He describes the seed as an "autonomous living system," maintaining a dynamic homeostatic condition within its environment. The seed must possess specialized mechanisms allowing it to maintain germinability over time. With the aid of Amen's (2) systems approach, germinability and dormancy can be summarized in the following manner.

The seed coat is the first system. It provides a "buffer" between the environment, the endosperm and embryo.

Its physical structure determines the accessibility of environmental factors to the interior of the seed. These environmental factors may be required for the stimulation of growth. If so, the result is dormancy imposed by the seed coat. If the excluded environmental influences are detrimental to function, the result is protection of the seed's structural integrity.

The second system required to maintain viability is an energy reserve (the endosperm). The breakdown of the endosperm results in energy. If the energy can be utilized, the result is growth. If the energy cannot be utilized, the result is an increase in entropy indicating the deterioration of structure. The seed embryo utilizes the energy from the endosperm. It also controls the metabolic capabilities of the seed unit. Thereby comprising the third system.

By dividing the seed unit into sub-systems, it becomes easy to define and visualize the system interactions which determine the destiny of the seed. Dormancy could theoretically be imposed at any point or combination of points within or between systems. How dormancy is imposed determines the complexity of the treatment(s) necessary to induce germination.

GENERAL MATERIALS AND METHODS

Seed Sources

These studies were conducted with eight lots of beardless wildrye seed, representing three accessions. Seed lots were obtained from the SCS Plant Materials Center at Bridger, Montana (Table 1). The seed lots varied by accession and/or by the environment in which the seed was produced. These conditions could result in different dormancy levels and differential response to treatments. Because of these variables, a composite of the eight seed lots was made in which each accession was represented equally by weight. This composite was used in all but four studies.

Germination

All germination tests were conducted in the dark at an alternating temperature of 15-25C (71). Seeds to be germinated were placed in plastic germination boxes on blotters moistened with distilled water. Seeds were considered germinated if they produced a normal coleoptile and radicle. Germinated seeds were counted at 7, 14, and 21 days of germination. Seeds were treated with a fungicide, Spurgon, to reduce microbial activity.

Table 1. Seed lots used in studies of dormancy in beardless wildrye grown at Pullman, Washington or Bridger, Montana

Lot No.	P. No.	Harvest site	Year of harvest
1	Wy-5, P-15594	Freemont County, Wyoming	Ca. 1960
2	P-2741	Plant Materials Center Pullman, Washington (PPMC)	1961
3	P-2741	Pullman Plant Materials Cen.	1963
4	Wy-4, P-15593	Bridger Plant Materials Cen.	1964
5	P-15593	Bridger Plant Materials Cen.	1965
6	P-15593	Bridger Plant Materials Cen.	1966
7	P-2741	Pullman Plant Materials Cen.	1969
8	P-15594	Bridger Plant Materials Cen.	1973

Tetrazolium

The viability of seed lots and the composite was determined by a tetrazolium (TZ) test on the ungerminated seeds remaining at the end of 21 days. Individual seeds were cut longitudinally and half of each seed placed in a 0.1% TZ solution for staining. After four hours the seeds were classified as viable or non-viable. The number of germinated seeds were added to the number of viable ungerminated seeds to give the number of viable seeds per lot. Dormant seed percentages were determined by subtracting the germination percentages from the viability percentages. TZ tests were performed on dry seeds after soaking them in distilled water for 2 1/2 hours.

Imbibition

Imbibition levels were determined as follows. Seeds were removed from the germination boxes at 24 hour intervals blotted with paper towels, air-dried for five minutes and weighed. Imbibed water was expressed as a percentage of wet weight.

Analysis

All studies were conducted in a randomized complete block design. Significant differences among means were determined by Duncan's New Multiple Range Test.

THE EFFECTS OF STRATIFICATION ON SEED GERMINATION

Materials and Methods

Six groups of 50 seeds from each of the eight lots were used in this study. Three groups of 50 seeds from each lot were placed on moist blotters in plastic boxes and stratified at 5C for five days. The remaining three groups were then placed on moist blotters in plastic boxes and placed in the germinator at the same time as stratified seeds.

Results and Discussion

Stratification enhanced the germination of beardless wildrye (Table 2). The increased germination may have been due to the longer imbibition period (five days) or to the effects of stratification on the physiological and physical status of the embryo. In either case the enhancement of germination by stratification, indicates that some form of dormancy is contributing to the low germination of beardless wildrye.

Seed lots varied with respect to germination, viability and response to prechill (Table 2). Lots 2, 3, and 7 are from accession P-2741 and were harvested in Pullman, Washington in 1961, 1963, and 1969, respectively. The

germination of lot seven (80%) was almost twice that of lot two (48%) and over six times that of lot three (13%). Of the eight lots tested, lot seven had the highest germination, lot two the second highest and lot three the lowest germination percent. The variation among lots may be due to several factors.

Table 2. Mean germination of eight lots of beardless wildrye at 21 days.

Lot No.	Percent germination	
	Prechill	No prechill
7	80 a[1/]	62 a
2	48 b	36 b
6	30 c	17 c
8	30 c	18 c
5	24 cd	9 cd
1	16 de	16 c
4	16 de	13 c
3	13 e	3 d
Mean	32 a[2/]	22 b

[1]Means in the same column followed by a common letter do not differ ($P < .05$).

[2]Prechill vs no prechill differ ($P < .05$).

The environments associated with different harvest years may have modified the expression of genetic potentials for dormancy. Also, the quality of the seed lots

may vary, depending on the cultural practices and harvest techniques. The expression of these factors on the quality of the seed lots would be expressed through the lot's storability and viability. The contribution of seed quality to the variation among lots is indicated by the viability of the lots, which ranged from 49 percent (lot 5) to 80 percent (lot 7) (Appendix Table 1). The confounded nature of these factors makes it impossible to delineate the effects of accession, environment and cultural practices on dormancy.

THE EFFECT OF SEED SIZE ON THE GERMINATION OF BEARDLESS WILDRYE

Materials and Methods

The effect of seed size on germination were studied with seed from lot number eight (Table 1). Seeds were sized with screens and air separation to obtain three size classes. The small, medium, and large seeds weighed 137.2, 217.4, and 277.4 mg/100 seeds, respectively. The check was randomly selected from the original seed lot and weighed 205.9 mg/100 seeds. Three groups of 100 seeds from each size class were germinated.

Results and Discussion

Seed size did not influence the germination percentage at seven days (Table 3). The smallest seeds had a higher germination percentage than the check at 14 days and the largest seeds had a higher germination percentage than the check at 23 days. However, the germination of the large and small seeds were equal throughout the germination period.

Seed size did not affect the dormancy of this lot of beardless wildrye. These data indicate that dormancy was not affected by seed size.

Table 3. Mean germination of beardless wildrye at 7, 14, and 23 days as affected by seed size.

Seed size	% Germination by Days		
	7	14	23
Small	8.00 a[1/]	25 a	39 ab
Medium	5.00 a	21 b	37 b
Large	5.00 a	22 ab	41 a
Check	5.00 a	19 b	36 b

[1/] Means in the same column followed by a common letter do not differ significantly ($P < .05$).

EXCISION OF EMBRYOS FROM THE SEED OF BEARDLESS WILDRYE

Materials and Methods

Embryos were excised from beardless wildrye seed to determine if they were dormant. Seeds imbibed water for 16 hours at room temperature on blotters moistened with distilled water (22,29). The lemma and palea were removed and an incision made behind the embryo to allow removal of the testa. Three groups of 25 embryos were excised and placed in a germinator for five days. The embryo was too small to remove all of the testa or endosperm or to determine whether or not it had been damaged during the excision procedure. Therefore, embryos were considered germinated when the coleoptile and radicle had elongated. A TZ test was performed on three groups of 25 dry seeds to determine seed viability. A chi-square analysis was used to compare the percent germination of excised embryos with TZ test results.

Results and Discussion

The germination percentage of excised embryos was equal to the viability of the seed lot ($x^2 = 2.5$, $P > 5\% < 10\%$). Therefore, the dormancy of beardless wildrye does not originate in the embryos and must be associated with the characteristics of the seed coat and endosperm.

THE EFFECT OF TEMPERATURE ON SEED IMBIBITION AND GERMINATION OF BEARDLESS WILDRYE

Materials and Methods

The imbibition rate of beardless wildrye seed was studied at four temperatures. Six groups of 50 seeds were used in each treatment. The treatments consisted of four imbibition temperatures; 1.5, 10, 20, and 30C. Imbibition levels were determined as described in the General Materials and Methods section. Seeds were left in the imbibition chambers until it became apparent that the imbibition levels were no longer increasing. Seeds were then placed in a germinator to determine the effect of imbibition temperature on germination. The imbibition level was also determined at the first sign of germination.

Results and Discussion

Imbibition temperature did not affect the total amount of water imbibed (Fig. 1) but did influence the rate of imbibition. Maximum imbibition levels were reached in three days at 20 and 30C, in six days at 10C and in 10 days at 1.5C (Appendix Table 2).

The imbibition temperatures did not affect the percent germination at seven days (Fig. 2). Seeds which had imbibed water at 30 and 20C had a greater germination

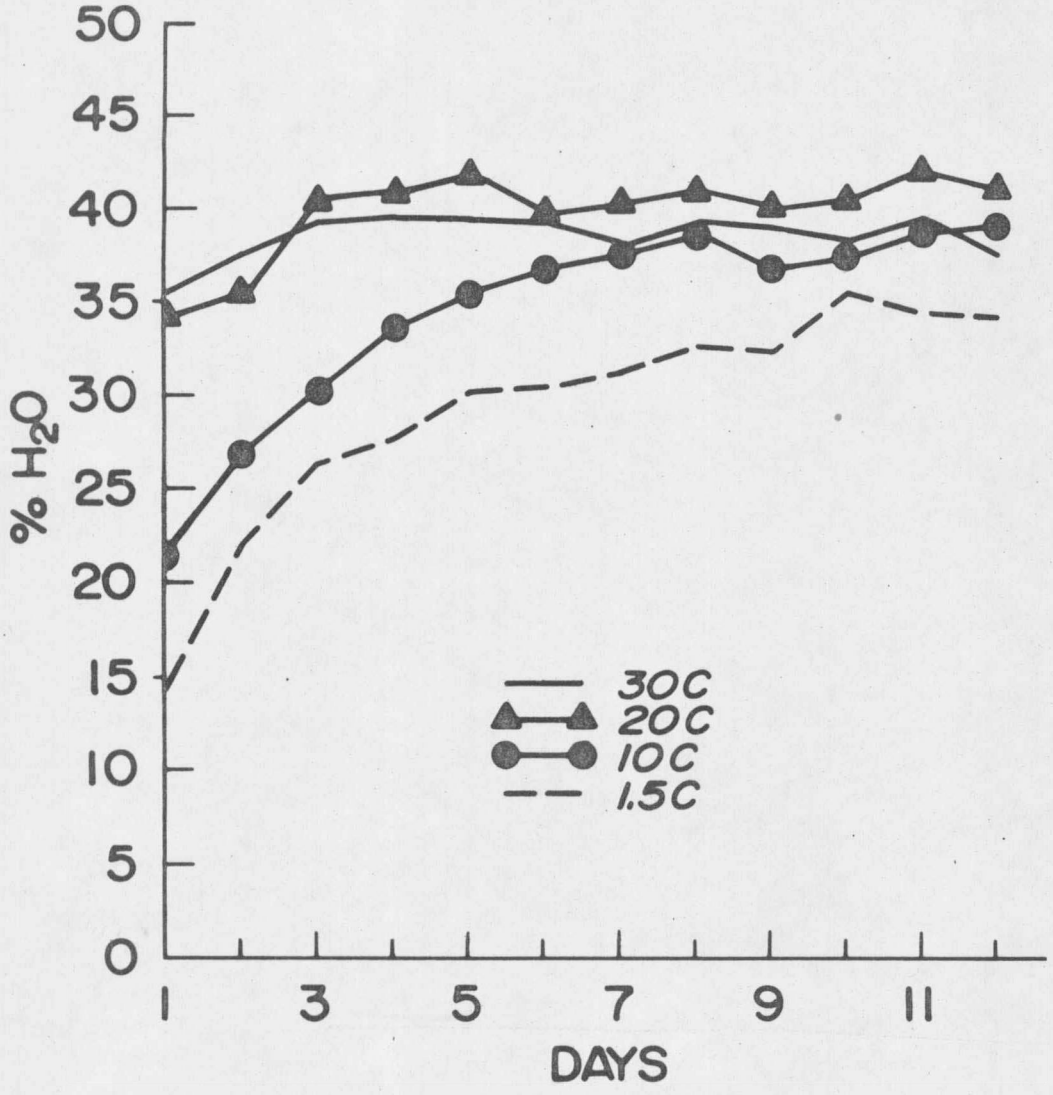

Fig. 1. The effect of temperature on the imbibition of beardless wildrye seed.

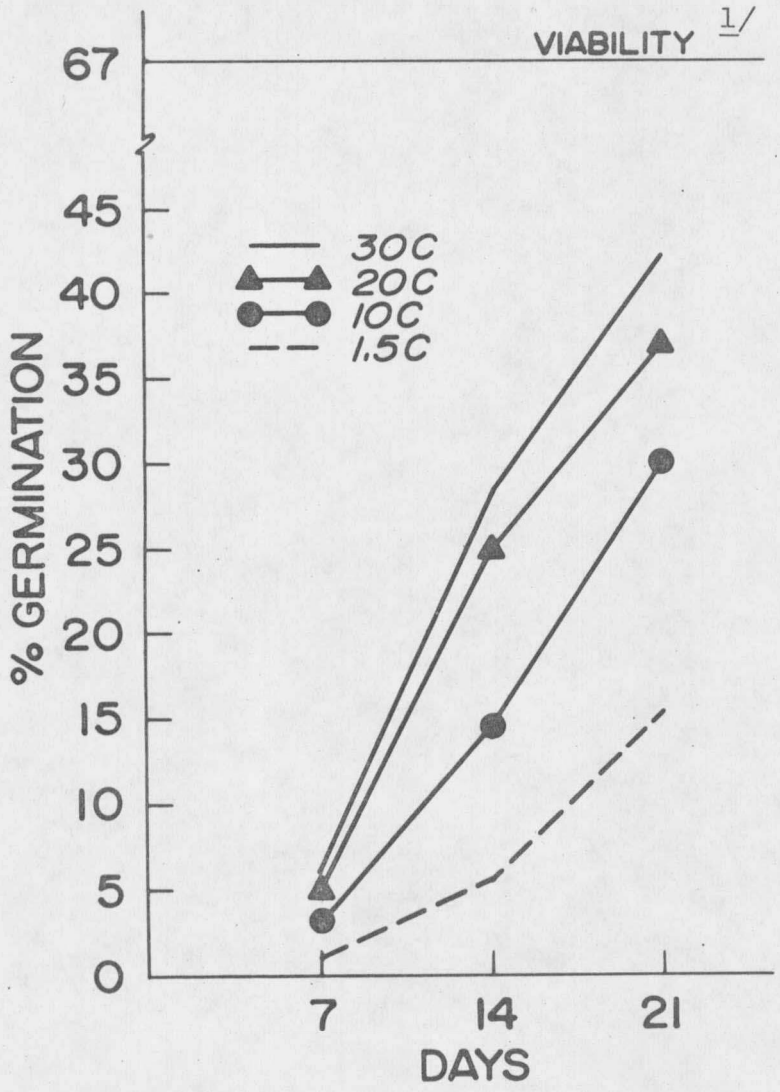

Fig. 2. Germination of beardless wildrye seed at 15-25C subsequent to imbibition at four temperatures.

1/ As determined by a tetrazolium test on ungerminated seeds remaining after the germination test was completed.

percentage than those seed imbibed at 10 and 1.5C at both 14 and 21 days. The germination percents of the 30 and 20C treatments were equal (Appendix Table 3). Seed exposed to 1.5C during imbibition had the lowest germination percentage. Imbibition at this temperature may have been physiologically detrimental to the seed. A TZ test on the ungerminated seeds at 21 days showed only 39% viable seeds for the 1.5C treatment as compared to 52% for seeds imbibed at 10, 20, and 30C.

Fully imbibed seeds did not germinate; therefore, the attainment of maximum imbibition is not the sole requisite for germination. Some other physiological requirement must be met before germination can occur.

THE EFFECT OF THE SEED COAT AND OXYGEN ON THE IMBIBITION AND GERMINATION OF BEARDLESS WILDRYE SEED

Materials and Methods

Four treatments were used to study the effect of the seed coat and oxygen (O_2) on the imbibition and germination of beardless wildrye seed: (1) seed cut, 100% O_2, (2) seed cut, normal atmosphere, (3) seed uncut, 100% O_2 and (4) seed coat uncut, normal atmosphere. Six replications of 50 seeds were germinated for each treatment. In treatments one and three, seeds were cut laterally 0.2 cm from the embryo end. Half the cut seeds were placed in an atmosphere of 100% O_2. The other half was placed in atmosphere of normal composition. Six hundred uncut seeds were placed in 100 percent O_2 and an atmosphere of normal composition. The 100% O_2 environment was maintained by pumping O_2 into germination boxes while they were in the germinator. After each imbibition weighing and germination count, the boxes were flushed by increasing the O_2 pressure for two minutes. The flow rate was then reduced. A pressure of 2.5 pounds was maintained on the tank gauge. Air of normal composition was pumped into the germination boxes of those seeds not receiving high O_2 treatments.

In this study the imbibition temperature was the same as the germination temperature (15-25C). Imbibition

levels were determined until the initiation of germination. Procedures for the determination of imbibition and germination are described in the General Materials and Methods section.

Results and Discussion

The cut treatments had a higher imbibition level than the uncut treatments at day one of the imbibition period (Fig. 3). The imbibition levels of all treatments were equal at day three (Appendix Table 4). The uncut treatments had a significantly higher imbibition level at day seven than the cut treatments. The difference between the uncut seed and cut seeds was probably due to the apparent loss of structural integrity of the cut seeds in the latter stages of the imbibition period.

The germination percentages due to treatments were similar after seven days of germination (Fig. 4). After 14 and 21 days the uncut seeds in 100% O_2 had a higher germination percentage than both of the cut seed treatments (Appendix Table 5). The germination percentages of the cut seed treatments were equal throughout the germination period.

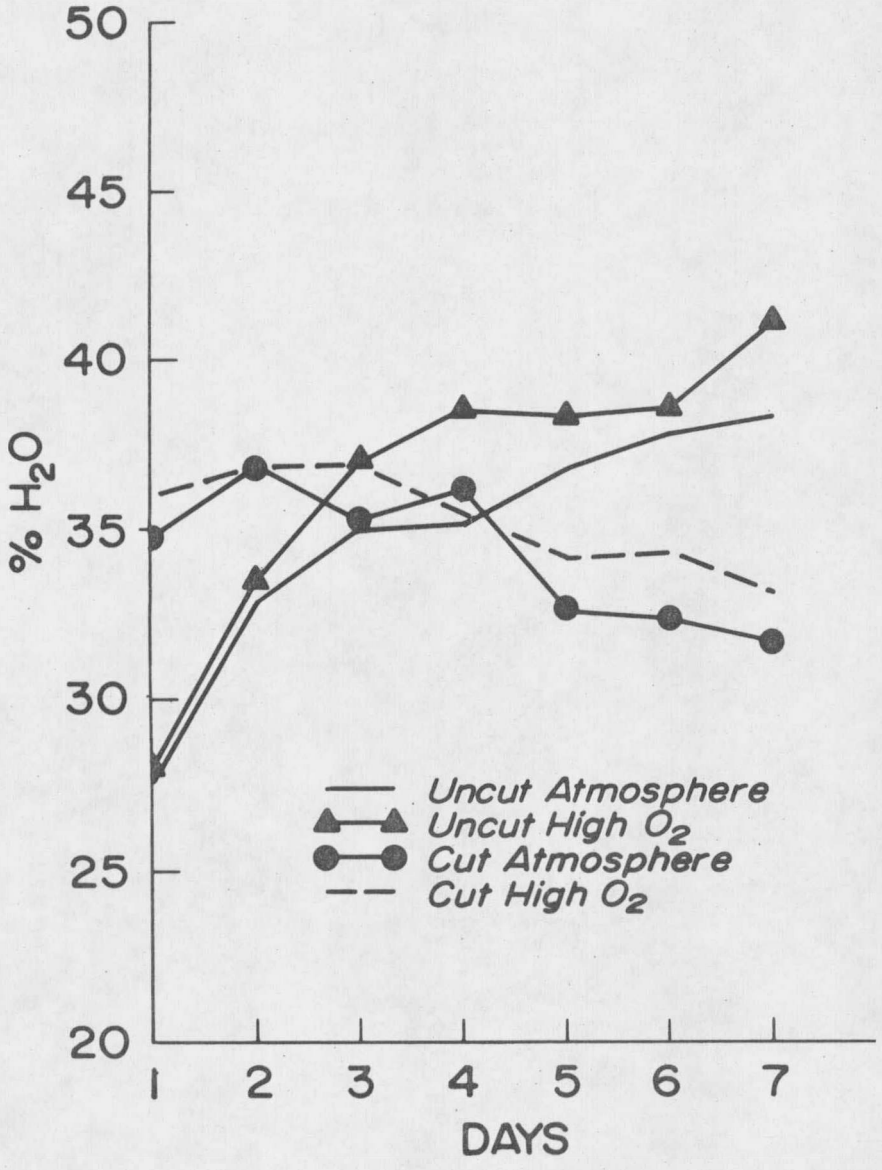

Fig. 3. The effect of cutting and high oxygen concentrations on the imbibition of beardless wildrye at 15-25C.

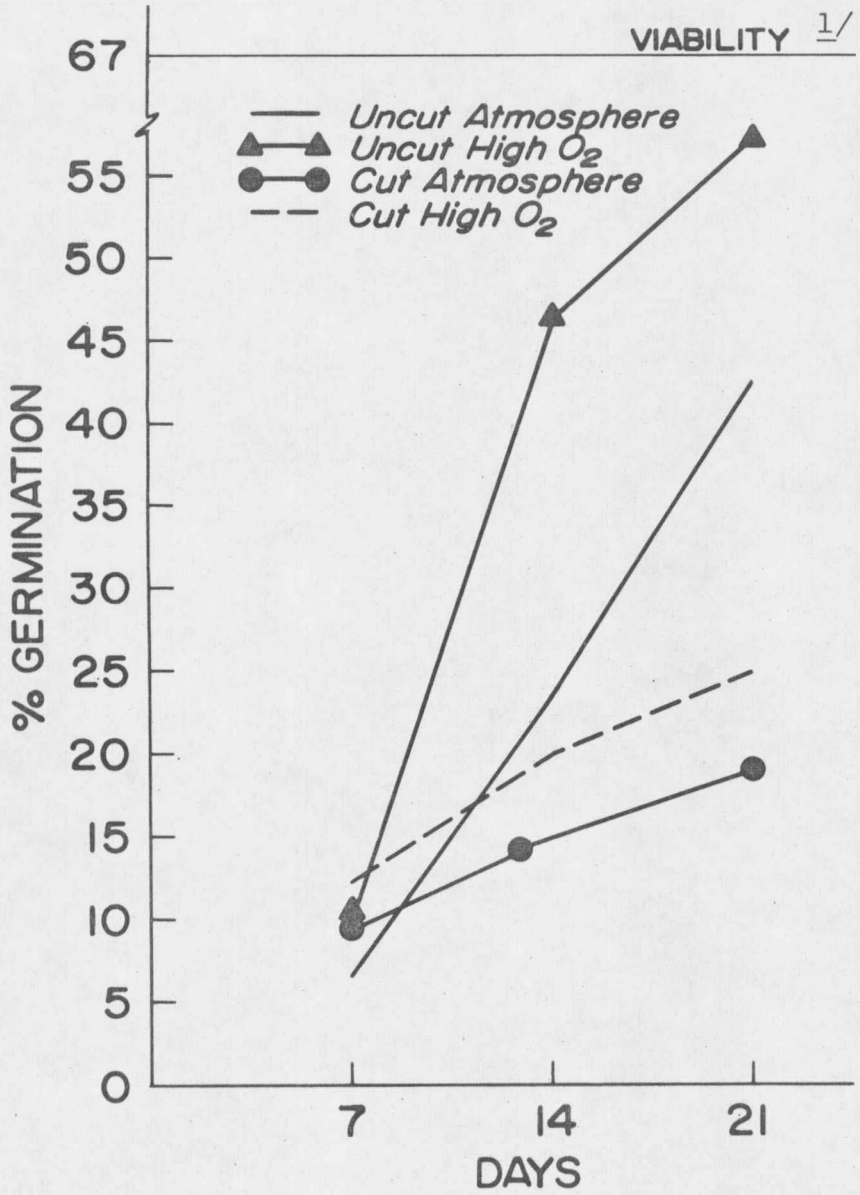

Fig. 4. Germination of beardless wildrye seed at 15-25C as affected by cutting and high oxygen concentrations.

1/ As determined by a tetrazolium test on ungerminated seeds remaining after the germination test was completed.

Oxygen enhanced the germination of dormant seeds. It did not induce germination equal to the viability as determined by TZ. It did, however, produce the highest germination percentage of any method used in this study. The mode of action of O_2 has not been determined. Wareing and Foda (72) proposed that increased O_2 concentrations cause the breakdown of inhibitor substances. The breakdown is thought to be due to the action of an oxidase present in germinating embryos. Simmonds and Simpson (56,57) have shown that increasing oxygen tensions altered the metabolism of seeds resulting in germination. This alteration is proposed to be a shift from the glycolytic-Kreb's cycle pathways to the pentose-phosphate pathway. The pentose-phosphate pathway is thought to produce precursors for the full production of energy and the substrates necessary for germination. High O_2 concentrations are required for the function of the pentose-phosphate pathway because this pathway is not able to compete with the Kreb's cycle for O_2 in conditions of limited O_2 supply. Simmonds and Simpson (56) also found that GA stimulated the activity of the pentose-phosphate pathway. Based on these hypotheses, it appears that the application of promoter substances may enhance the germination of dormant beardless wildrye seed.

THE EFFECT OF GIBBERELLIC ACID, BENZYLADENINE AND ABSCISIC ACID ON SEED GERMINATION OF BEARDLESS WILDRYE

Materials and Methods

The effects of gibberellins and a cytokinin on the germination of beardless wildrye were studied with seed from lot eight. The study consisted of nine treatments; eight hormonal concentrations and a check. All hormones were applied as an aqueous solution. The following concentrations were used: Gibberellic acid $_3$(GA_3) at 100 and 200 ppm and Benzyladenine (BA) at 1 and 5 ppm. Two drops of 6N HCl were added to solubilize BA. Hormones were applied individually and in all possible combinations by moistening the germination blotters with the appropriate hormonal solution.

In a second study the effect of abscisic acid (ABA) on the germination of beardless wildrye seed was determined. ABA was applied in the same manner as GA_3 and BA. The concentrations of ABA used were 1 and 10 ppm. Three groups of 100 seeds were germinated for each treatment in both studies.

Results and Discussion

Seed dormancy was reduced when seeds were germinated on blotters moistened with 200 ppm GA_3 and with the

combination of 200 ppmGA-5 ppmBA (Table 4). Other hormonal applications did not reduce dormancy.

Table 4. The effect of GA_3 and Benzyladenine on the germination percentage of beardless wildrye seed.

	ppm GA_3		
	0	100	200
0	15 b [1]	18 ab	20 a
Benzyladenine 1(ppm)	14 b	18 ab	14 b
Benzyladenine 5(ppm)	13 b	11 b	20 a

[1] Means in the same column followed by a common letter do not differ ($P < .05$).

ABA induced dormancy. ABA at 10 ppm was more effective in increasing dormancy than 1 ppm ABA (Table 5).

Table 5. The effect of abscissic acid (ABA) on the germination percentage of beardless wildrye seed.

Check	15 a [1]
ABA 1 ppm	10 b
ABA 10 ppm	8 c

[1] Means followed by the same letter do not differ ($P < .05$).

These data indicate that hormones will affect the germination capability of beardless wildrye. Further studies should be conducted using higher concentrations of GA_3.

Benzyladenine was used in this study to determine if Khan's (40,41) theory on the action of cytokinins is applicable to beardless wildrye. In those treatments receiving BA, there was an apparent stunting of the roots. This stunting resulted in the classification of several germinated seeds as abnormals. Skoog (59) has shown that a high cytokinin to auxin ratio induces shoot development in tobacco pith cultures. A low cytokinin to auxin ratio induces root development. The application of BA may, therefore, cause a hormonal imbalance within the seed resulting in impaired root development. The application of an auxin in conjunction with BA may induce normal germination.

THE EFFECT OF GA_3, BA AND INDOLE-3-ACETIC ACID ON THE GERMINATION OF BEARDLESS WILDRYE SEED

Materials and Methods

The effects of three hormones on the germination of beardless wildrye seed were studied. The following concentrations were used: GA_3 at 400 and 600 ppm, BA at 1 and 5 ppm and indole-3-acetic acid (IAA) at 3 and 5 ppm. Each hormone was applied individually and in all possible combinations. All hormones were applied as aqueous solutions. Three groups of 100 seeds were germinated for each treatment.

Results and Discussion

Hormones did not induce germination equal to the viability. However, certain treatments enhanced germination.

The highest level of GA_3 (600 ppm) enhanced germination when applied in a three-way combination with BA and IAA (Table 6). Four hundred ppm GA_3 enhanced germination when applied in a three-way combination with 1 ppm BA and IAA at both 3 and 5 ppm. The only two-way combination that enhanced germination was 1 ppm BA with 5 ppm IAA. Five ppm BA and 3 ppm IAA enhanced germination when applied

individually. The germination enhancement of the above treatments was similar.

Table 6. The effect of GA_3, Benzyladenine and Indole-3-acetic acid, alone and in combination on the seed germination of beardless wildrye.

ppm	ppm GA_3		
	0	400	600
0	12 GH [1/]	20 d-h	25 a-g
BA 1	25 a-g	26 a-g	20 d-h
BA 5	28 a-d	22 d-h	18 e-h
IAA 3	27 a-d	21 c-h	24 a-g
IAA 5	24 a-g	15 h	21 b-h
BA1-IAA3	26 a-g	32 a	30 ab
BA1-IAA5	32 a	29 a-c	29 a-c
BA5-IAA3	18 e-h	26 a-g	28 a-d
BA5-IAA5	22 b-h	24 a-g	27 a-f

[1/] Means followed by any common letter do not differ significantly ($P < .05$).

It appears that higher levels of GA_3 are needed when applied with high levels of BA. The interpretation of the results of this study with inference to Khan's (40,41) theory would indicate that GA_3 is not the limiting hormone in the germination in this composite of beardless wildrye. The activity of hormones within the seed may be limiting germination rather than the quantity of hormones.

THE EFFECT OF SCARIFICATION ON THE GERMINATION OF BEARDLESS WILDRYE SEED

Materials and Methods

Five treatments were used to study the effect of scarification on the germination of lot number eight of beardless wildrye (Table 1). The first treatment consisted of mechanically scarifying 1 gram of seed for 5 seconds with a Forbes model 388 scarifier. Other seeds were scarified in a Di-Sontegrator system 40, ultrasonic cleaning device. Thirty-six grams of seed were placed in the cleaning tank which was filled with acetone. Approximately six grams of seed were removed at each of three time intervals; 10, 20, and 30 minutes. An unscarified check was included. Three groups of 100 seeds were germinated for each treatment.

Results and Discussion

None of the treatments increased germination. Ultrasonic scarification for 10 minutes inhibited germination. Mechanically scarified seed and seed exposed to ultrasonic waves for 30 minutes had a greater germination than seeds exposed to ultrasonic waves for 10 minutes (Table 7).

Table 7. The effect of scarification on the seed germination of beardless wildrye.

Scarification method	% germination
Mechanical	30 a [1]
Ultrasonic waves 30 minutes	28 ab
Unscarified	27 ab
Ultrasonic waves 20 minutes	25 b
Ultrasonic waves 10 minutes	20 c

[1] Means followed by a common letter do not differ ($P < .05$).

Because the scarification method caused germination differences, more work should be done with scarification procedures.

GENERAL DISCUSSION

These data indicate that dormancy in beardless wildrye is imposed by the outer coverings of the seed and that the availability of oxygen is the major factor limiting the germination of dormant seeds. These conclusions are supported by the results of the embryo excision study and the oxygen study. The scarification study and the imbibition temperature study illustrate that imbibition processes may affect the availability of oxygen to the embryo.

The relationship of seed hydration to the availability of oxygen is not clear. Brown (9) has shown that the inner membrane of Curcurbita pepo becomes more permeable to oxygen following hydration. He feels that two factors may be involved: (1) the removal of some impermeable constituent of the membrane in solution; (2) the provision of a medium in which gases can dissolve. However, Ohmura (48) has shown that adding water to tissues of soybeans (Glycine max var. Ronoake), corn (Zea mays) and barley (Hordeum vulgare) markedly decreases oxygen uptake.

The effect of temperature on oxygen availability is also unclear. Thornton (66) has proposed that high temperatures reduce the oxygen requirement of cocklebur (Xanthium canadense) seed. In contrast, Heydecker (30)

postulates that low temperatures increase the availability of oxygen and reduce the requirements for oxygen.

The availability of oxygen to a seed embryo, under conditions of increased temperature and hydration, is probably related to the following factors: (1) the permeability of the seed coat to oxygen and water, (2) the hydrophilic nature of the seed, and (3) the physiological state of the seed. The classification of beardless wildrye seed within the above criteria cannot be concluded from these data.

SUMMARY AND CONCLUSIONS

Eight lots of seed were used to study the factors contributing to the slow germination of beardless wildrye. Studies were conducted to determine the effect of imbibition temperature and high oxygen concentrations on imbibition and germination; and the effects of stratification, embryo excision, seed size, scarification and hormones on germination.

Beardless wildrye seed is dormant. Dormancy was reduced most when seed was germinated in an atmosphere of 100% oxygen. Excised embryos germinated rapidly. The response to oxygen and the rapid germination of excised embryos indicates that dormancy is imposed by the outer coverings of the seed.

Imbibition at 30C induced greater germination at 15-25C than imbibition at 10 or 1.5C. GA_3, BA and IAA reduced dormancy. The low level of response to these hormones suggested that the role of hormones in the seed dormancy of this species is not dominant. Hormone applications in conjunction with high oxygen treatments may be necessary to obtain complete germination of dormant seed.

The seed scarification techniques used in these studies did not enhance germination. More research is

needed to evaluate scarification in conjunction with other treatments.

Seed size was not related to dormancy in lot eight.

Additional work is needed before rapid establishment of beardless wildrye can be realized. Within a long range program the following steps should be initiated:

(1) Develop treatment and/or storage techniques utilizing oxygen, hormones, and scarification.

(2) Correlate lab results with greenhouse and field studies.

(3) Develop seed production techniques to increase seed yield and quality.

(4) Study the environmental parameters influencing the development of dormancy.

APPENDIX

Appendix Table 1. The germination, dormancy and viability of eight lots of beardless wildrye prechill (P.C.) versus no prechill (N.P.C.).

Lot No.	Year of Harvest	Percent Germination				After 21 Days Germination					
		Prechill		No Prechill		Total Germination		Dormant		Viability[1/]	
		14 Days	21 Days	14 Days	21 Days	P.C.	N.P.C.	P.C.	N.P.C.	P.C.	N.P.C.
1	App 1960	5	11	3	13	16	16	47	49	63	65
2	1961	19	29	12	24	48	36	25	35	73	71
3	1963	3	10	0	3	13	3	30	45	43	48
4	1964	3	13	1	12	16	13	34	42	50	55
5	1965	9	15	0	9	24	9	22	40	46	49
6	1966	11	19	3	14	30	17	37	47	67	64
7	1969	53	27	32	30	80	62	9	18	89	80
8	1973	7	23	4	14	30	18	32	51	62	69
Mean		14	18	7	15	32	22	30	41	62	63

[1/] As determined by TZ test on ungerminated seeds after 21 days of germination.

Appendix Table 2. Mean percent imbibition of beardless wildrye as affected by temperature

	% Wet Weight											
	Days											
Temp	1	2	3	4	5	6	7	8	9	10	11	12
30 C	35.1a[1/]	37.5a	39.1a	39.5ab	39.4ab	39.3a	38.2a	39.3a	38.7ab	38.2a	39.6a	37.5a
20 C	34.1a	35.5a	40.3a	40.7a	41.9a	39.6a	40.2a	41.0a	40.0a	40.6a	42.2a	41.1a
10 C	21.3b	26.8b	30.1b	33.6bc	35.4bc	36.7a	37.5a	38.6ab	36.7ab	37.4a	38.8a	39.7a
1.5C	14.3c	22.2b	26.3b	27.8c	30.1c	30.4b	31.5b	32.8b	32.5b	35.5a	34.8b	34.7a

[1/] Means in the same column followed by a common letter do not differ significantly ($P < .05$).

Appendix Table 3. Mean germination of beardless wildrye seed at 15-25 C as affected by imbibition temperature.

Imbibition temperature	% Germination by Day		
	7	14	21
30 C	6 a [1/]	28 a	42 a
20 C	5 a	25 a	37 a
10 C	3 a	15 b	30 b
1.5 C	1 a	6 c	15 c

[1/] Means in the same column followed by a common letter do not differ significantly ($P < .05$).

Appendix Table 4. Mean imbibition at 15-25 C of beardless wildrye seed as affected by cutting and high oxygen concentrations.

Treatment	% Wet Weight by Day		
	1	2	3
cut high O_2	36.0 a [1/]	36.9 a	37.0 a
cut ATM	34.8 a	35.3 ab	36.9 a
uncut O_2	27.9 b	33.5 ab	35.3 a
uncut ATM	27.6 b	32.9 b	35.0 a

[1/] Means in the same column followed by a common letter do not differ significantly ($P < .05$).

Appendix Table 5. Mean germination at 15-25 C of beardless wildrye seed as affected by cutting and high oxygen concentrations.

Treatment	% Germination by Day		
	7	14	21
uncut high O_2	10.0 a [1]	45.0 a	56 a
uncut ATM	6.0 a	23.0 b	42 b
cut high O_2	11.0 a	19.0 bc	24 c
cut ATM	9.0 a	14.0 c	18 c

[1] Means in the same column followed by a common letter do not differ significantly ($P < .05$).

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