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Title: TEMPERATURE PRECONDITIONING OF RYEGRASS (LOLIUM SP.) SEED DORMANCY

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The purposes of this study were to determine the effects of temperature, nutrients, growth regulators, and culm detachment during seed development on ryegrass seed dormancy and weight. The effects of storage temperature on seed dormancy were also studied.

Seed dormancy of annual (Lolium multiflorum Lam.) and perennial (Lolium perenne L.) ryegrass was evaluated by observing germination in the dark at 30, 25, 20, 15, and 15-25C. Dormant ryegrass seeds failed to germinate at 30 and 25C, but as after-ripening occurred seeds became insensitive to germination temperature.

Field-grown ryegrass varieties were found to differ in degree of seed dormancy when grown under the same environment. 'Gulf', 'Florida Rust Resistant', and 'Magnolia' annual and 'NK-100', 'Manhattan', 'Atempo', 'Petra', and 'Pelo' perennial ryegrass varieties were considered dormant. 'Oobahikari' annual and 'Verna Pajbjerg'

and 'Linn' perennial ryegrass varieties were nearly nondormant.

Dormancy patterns of greenhouse-grown Manhattan perennial ryegrass seed differed from those of field grown Gulf annual ryegrass. Dormancy of Manhattan was reduced when seeds reached maximum dry weight; whereas, Gulf seeds were dormant at all stages of maturity.

A detached culm technique was used in growth chamber and greenhouse studies to determine the effects of nutrients, growth regulators and temperature on seed weight and dormancy. The dormancy response of Gulf seed produced on detached culms was similar to that of seeds from intact plants; lending validity to the use of the detached culm technique in studying seed dormancy.

Development of Gulf seed in solutions deficient in nitrogen, phosphorus, and potassium did not significantly reduce dormancy. Phosphorus deficiency was more detrimental to seed weight than deficiencies of nitrogen or potassium.

Production of Gulf seed on detached culms in gibberellic acid, benzyladenine and sucrose reduced dormancy. Seed developed in sucrose on culms cut at the soil surface produced the largest seeds. However, these seeds were not equal in size to seeds from intact culms. Gibberellic acid had no effect on seed size, while benzyladenine solution significantly reduced seed weight.

Ryegrass seed dormancy and weight were affected by temperature during seed development. Gulf seeds developed at low

temperature were dormant; whereas, seeds developed at high temperature were nondormant. The duration of exposure to different temperatures and the stage of development at which the seeds were exposed to high or low temperature also influenced the degree of dormancy. Exposure to one week of low temperature during the ripening stage increased seed dormancy, while the same duration of exposure to high temperature immediately after anthesis reduced seed dormancy.

Extended periods of low temperature during seed development increased seed weight, while seed weight was decreased if low temperature preconditioning was delayed until later stages of development. The greatest reduction in seed weight occurred when seeds were exposed to high temperatures during the second week of seed development.

In storage studies with seven ryegrass varieties, dormancy was quickly overcome at storage temperatures of 30 and 20C, but storage at 5 and -18C increased dormancy.

Temperature Preconditioning of Ryegrass (*Lolium* sp.) Seed Dormancy

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INTRODUCTION

Ryegrass seed is produced on more acres in Oregon than any other grass seed crop. Annual and perennial are the two main ryegrass species grown. A native of the Mediterranean region, annual ryegrass was first cultivated in Northern Italy and has been referred to as Italian ryegrass. Annual ryegrass has been used as a hay crop, temporary pasture, and for quick ground cover when establishing permanent pastures or lawns. In the Southern part of the United States annual ryegrass has been used for fall seeding on permanent lawns to maintain a green lawn throughout the winter.

Perennial ryegrass occurs naturally in all of temperate Asia and in Northern Africa. It is a short-lived perennial which is usually used in permanent pastures with other more permanent grasses. Perennial ryegrass starts growth early in the spring and provides grazing while the more permanent grasses are becoming established.

Plantings of ryegrass seed are made either in the fall or spring depending on the climatic conditions. In areas where winters are severe plantings are usually made in the spring, but in the warm southern regions fall seedings are more successful.

One of the main reasons for seeding ryegrass is its ability to establish a stand quickly. However, if seeds fail to germinate due to

seed dormancy this advantage is lost. The advent of new and improved varieties has complicated the seed dormancy situation. Seed lots which appear nondormant in the seed laboratory may be dormant under stress conditions of moisture, temperature and light in the soil. The general consensus has been that after-ripening takes place during shipment of the seed to the consuming areas; however, this may not be true today with improved means of transportation and more dormant varieties. Consequently, these factors need to be more thoroughly understood before ryegrass plantings can reach maximum effectiveness.

Most ryegrass seed grown in Oregon is processed, bagged and labeled immediately after harvest and shipped to the ultimate consumer. Labeling requirements necessitate the identification of ryegrass species and the determination of pure seed and germination percentages. In order to make these determinations, seed dormancy must be overcome. Germination procedures for freshly harvested ryegrass seed require pre-chilling for at least five days prior to germination. These procedures increase the time required for determining germination and species purity of dormant seed and delay the shipment of seed.

If the genetic potential for seed dormancy of a variety and the effect of the environment on that potential were known, it may be possible to predict the level of dormancy present in freshly harvested

seed lots and modify testing procedures accordingly.

The main objectives of this study were to determine the genetic potential for seed dormancy of ryegrass varieties and to determine the modifying effects of temperature on dormancy. The effects of maturity, nutrients, growth regulators, and culm detachment on seed development and dormancy were also studied.

LITERATURE REVIEW

Concepts of Seed Dormancy

Numerous attempts have been made to define the concept of seed dormancy. Evenari (12) stated: "There are few cases in biology where one and the same concept has been defined in so many different ways as the term dormancy." He defines dormancy as "control of germinability," meaning to restrict germination to special conditions of temperature, light, and composition of atmosphere.

Mayer and Poljakoff-Mayber (39) define seed dormancy as a condition of the seed in which germination does not occur when it is placed under normal conditions favorable to germination. Dormant seeds are viable and can be induced to germinate by using special treatments.

Vegis (62) describes dormancy as a gradual decrease in growth activity. As growth activity starts to decrease some seeds of a sample germinate rapidly, while others are delayed in germination. A continued decrease in growth activity causes all seeds to become sluggish in germination and require longer periods of time for germination. The decreasing growth activity is accompanied by the narrowing of the temperature range in which germination will occur. Some seeds continue to decrease in growth activity until germination is not possible at any temperature--this, according to Vegis, is true

dormancy. Vegis uses the term "relative dormancy" to describe the dormancy present in seeds that will germinate when exposed to a favorable narrow temperature range.

Wareing (56) states

> Many seeds will not germinate when sown under apparently favorable conditions of temperature, moisture, and aeration, although they will readily germinate under the same conditions after they have received certain pre-treatment.

Wareing concluded that dormancy in some seeds could be due to the absence of germination promoters, rather than to the presence of germination inhibitors. This concept could be applied to seeds which are stimulated to germinate by addition of gibberellic acid, but would not apply to seeds stimulated to germinate by leaching. Therefore, Wareing suggests that dormancy and germination are controlled by a balance of promoter and inhibitor.

Amen (1) defines seed dormancy as an endogeneously controlled or environmentally imposed temporary suspension of growth and reduced metabolic activity.

Effects of the Environment on Seed Dormancy

The seeds of many plants are known to be dormant at maturity. These plants possess a genetic potential for dormancy, but expression of this potential is determined by the environment. The effect of environment on morphological and physiological characteristics of a

plant or seed has been termed environmental preconditioning. Kidd and West (31, 32) stated that

> During the course of germination, seedling development, and periods of dormancy, the potentialities of plants may be affected by actions which only subsequently produce visible results. These results appear during the later stages of development without reference to the conditions then existing.

The importance of studying the effects of environment on plant performance was expressed by Rowe (47) when he stated

> Intensive studies of preconditioning by ecologists, physiologists, and geneticists, are merited, to find when and in what part the organism is sensitive to environmental signals that entrain directing rhythms or set the patterns of future development. There is evidence that the times of initiation and formation of seeds, buds, and growing points often following a dormant or resting stage, are particularly sensitive to environmental preconditioning.

There is a great deal of evidence indicating that the environment affects seed dormancy as seeds develop on the plant. Wentland and Holm (59) studied the effects of day-length on seed dormancy of lambsquarters.[1] A higher percentage of dormant seed was produced under long photoperiods (17 hours) than under short photoperiods. Junges and Ludwig (25) studied the influence of water, fertilizer, and light on seed dormancy of balsam. The dormancy of freshly harvested seed was strongly influenced by water supply acting in conjunction with nutrient supply. The effects of light intensity on seed dormancy were not as important as were the effects of water and nutrients. Seed

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[1] The scientific names of all seeds or plants referred to in this thesis are presented in Appendix Table 1.

dormancy of balsam increased when the water supply was increased without increasing the nitrogen supply. Seed dormancy was decreased when the increase in water was combined with an increase in nitrogen. They also showed that as weight of balsam seed increased, seed dormancy increased, unless dormancy was influenced by nitrogen.

Kienitz (33) and Kamra and Simack (27) have studied the effects of the environment on seed dormancy as related to elevation of seed production. Kienitz, in 1879, expressed the fact that seeds of Norway spruce from high elevations germinated better at 7C than did seed from trees at lower elevations, while the opposite was true at a 19C germination temperature. He also found that seed from trees on north-facing mountain slopes could germinate at lower temperatures than seed from trees on south-facing slopes. However, Kamra and Simack found the opposite effect when germinating seeds of Scots pine collected from different elevations in Sweden. Germination percentages of seed samples from northern latitudes were equal at all germination temperatures, while seed samples from southern latitudes germinated higher at 20C and lower at 25C than at 20-30C. From these data, they concluded that seed samples from southern latitudes or lower elevations were more sensitive to the germination temperature than were the seeds from samples obtained from northern latitudes or higher elevations.

Variations in temperatures during seed development have been

shown to affect dormancy of seed in several species, although there are some seed plants which are not affected. Gelmond and Nakamura (14) and Dotzenko (11) studied seed dormancy of peanuts and Russian wildrye, respectively, and found that temperature during seed development had no effect on subsequent germination.

Chang (6), when studying the length of dormancy in cereal crops, observed that high temperatures during the 1939 experiments may have accounted for the dormant periods being longer than in the previous year.

Koller (34) found that conditions of light and temperature during maturation of lettuce seed affected the temperature response of germination. An increase in temperature during seed maturation improved subsequent germination, both in continuous and in interrupted darkness (opening of containers for one minute).

Von Abrams and Hand (63) have indicated that dormancy of rose seed will vary depending upon the climatic conditions. A high correlation was found between germination and mean average daily temperature of the 30 days preceding harvest. The mean average daily temperatures during the 30 days preceding harvest in 1950, 1951, 1952, and 1953 were as follows: 10.7, 12.2, 14.9, and 12.9C. The germination percentages of rose seed harvested during these years were: 0.0, 6.2, 42.3, and 13.2%. These results indicate that the higher temperatures during 1952 caused rose seeds to be less

dormant. Harrington and Thompson (19) obtained similar results when studying lettuce seed. Lettuce seed produced in areas of high temperature germinated better in the dark at 26C than seed produced in areas of low temperature.

Lipp and Ballard (37) studied germination patterns of light sensitive seeds of scarlet pimpernel. High temperatures during seed development increased the promoting effect of continuous red light on seed germination. High temperatures also reduced the time period required for after-ripening of dormant seeds of this species.

Stearns (50) allowed seeds of bracted plantain to develop to maturity at constant temperatures of 15, 21, and 27C under a 16-hour photoperiod. The seeds that matured at 27C produced larger and more vigorous seedlings. The increase in growth of seedlings from seeds preconditioned at 27C could not be attributed to larger seed size.

Laude (36) and Dotzenko (11) studied the effects of temperature stress during anther extrusion and seed maturation of 'White Wonder' millet. Results of their studies showed that heat stress of White Wonder millet during seed development induced a dormancy which was more persistent than in seed not heat stressed. Laude, in the same study, found that heat stressing of barley produced results similar to those obtained with White Wonder millet. Seedling emergence of barley seeds heat stressed at 18 and 25 days after awn emergence remained low when tested 51 days after harvest. Seedling emergence

of non-heat stressed seed increased rapidly and seed dormancy had disappeared 27 days after harvest. He also found that barley seed, heat stressed 25 days after awn emergence, showed greater emergence from the soil than seeds heat stressed 18 days after awn emergence. These results suggest that a temperature sensitive gradient exists during the maturation period. In a second study of heat stress effects, Khan and Laude (30) observed that a heat stress at 19 and 22 days after awn emergence greatly increased seed germination. Heat stress at 21 days after awn emergence reduced the thickness of the lemma and palea and increased the rate of water imbibition over non-heat stressed seeds. Heat stressing seeds seven to ten days after awn emergence was very detrimental to seed viability.

Laude (35) also studied the effect of heat stressing of seedlings on seed dormancy. Seed dormancy of red brome was increased when seedlings in the two leaf stage were subjected to air temperatures of 54C for three to five hours. An increase in the duration of the heat stress increased red brome seed dormancy.

Effect of Maturation on Seed Dormancy

Hardesty (17) and Wellington (58) report the effects of maturity on seed dormancy of cereals. Hardesty found that within the same wheat spike, florets which reached anthesis first were slower to germinate. Wellington showed that separation of wheat seeds from the

plant during the early stages of ripening caused an earlier reduction in the moisture content and an earlier increase in germinability of seeds of dormant wheat varieties. Seed germination of nondormant wheat varieties was not affected by time of separation from the plant.

Delouche (10) found the reverse to be true for Kentucky bluegrass seed. Degree of seed dormancy was associated with seed moisture--the higher the moisture content at time of harvest, the higher the seed dormancy. He also stated: "It is of interest that seeds from the 1954 harvest were less dormant at equivalent stages of maturity and intervals after harvest than those harvested in 1953." This statement would suggest that dormancy of Kentucky bluegrass varies with year of production. Kearns and Toole (28) observed that immature and mature fescue seed required a lower temperature for germination than did dead ripe seed.

Schaaf and Rogler (48) and Wiesner and Kinch (60) demonstrated that seed dormancy in green needlegrass is not affected by stage of maturity as dormancy was found to be present in all maturity classes.

Effect of Storage Temperature on Seed Dormancy

When studying seed dormancy it is important to have a continuous and lasting supply of dormant seeds. Roberts (45) found that storage of dry rice seeds at 3C considerably delayed the breaking of dormancy.

When dormant seeds were removed from storage, breaking of dormancy followed the normal pattern. Moisture level of stored seed was found to be important--if rice seeds were moist when stored at low temperature, dormancy was broken faster than when stored at high temperature. The storage of rice seeds in oxygen accelerated the breaking of dormancy and low temperature storage enhanced the effect of oxygen. Carbon dioxide and nitrogen had no effect on rice seed dormancy except through the indirect effect of excluding oxygen. Roberts (46), in a later study with rice, found a negative relationship between storage temperature and log mean dormancy period over the temperature range of 27 and 57C.

In contrast to work by Roberts, Brown et al. (5) found that the relative humidity level was not a critical factor when storing freshly harvested oats and barley seeds at 2C. Oats and barley seeds when stored in a relatively high humidity remained dormant for a period of three years. Freshly harvested seeds of these crops germinated readily at temperatures slightly above freezing, but seeds failed to germinate at 30C. Storage at high temperatures (24 to 40C) increased germination at 30C.

Ryegrass Seed Dormancy

Researchers have shown that dormancy of ryegrass seed may be determined by the surrounding environment. In Mediterranean

areas where winters are favorable for plant growth and summers are hot and dry, cultivated perennial ryegrass seeds germinate immediately after ripening, but Wimmera ryegrass, a winter annual, has dormant seeds (9). In Northern European areas where winter cold is a limiting factor to survival, seed dormancy prevents autumn germination and in the intermediate maritime areas where neither winter cold nor summer drought are limiting factors, the growing season extends over most of the year and no strong dormancy mechanisms have been developed.

Ryegrass seed dormancy, according to Jensen and Pierpoint (24), appears to be influenced by environmental and genetic factors. They observed that dormancy varies with season and area of production, as well as with species, being more pronounced and persistent in annual ryegrass than in perennial ryegrass.

Justice (26), in a report to the Association of Official Seed Analysts, recommended the following method for germination of freshly harvested ryegrass seed: Pre-chill seed for five days at 10C prior to germination at 15-25C in the light on blotters moistened with 0.2% potassium nitrate (KNO_3). Post-chilling from the 15th through the 17th day was suggested for seeds which were still dormant after 14 days of testing and the germination test should then be continued for a total of 21 days. This recommendation was based on work done by Colbry et al. (8).

In 1951, Weisner and Kanipe (57) reported that Oregon-grown annual ryegrass seed produced during 1936-39 showed varying degrees of dormancy. Twenty-eight to 49 days were normally required for satisfactory germination at 20-30C. However, seed harvested in 1937-38 required 76 days for satisfactory germination. Other reports (3, 21, 41) have been published describing similar variations in ryegrass seed dormancy and have discussed ways to overcome dormancy.

Buried seed studies have pointed out some important factors concerning dormancy and persistence of ryegrass seed. In reference to seed persistence and dormancy, Harris (20) stated

> . . . the results of this experiment indicate that there may be more danger in contaminating (soil) by perennial ryegrass than by Italian ryegrass (annual) since a higher percentage of perennial ryegrass seeds were unaccounted for at the end of the first autumn.

The viability of seeds remaining in the soil was not determined in this study. Rampton and Ching (43, 44), in their studies of buried ryegrass seed, obtained results which could not support the findings of Harris. Buried seed of 'Linn' perennial ryegrass retained a trace of viability into the fourth year, whereas some Oregon annual ryegrass seeds remained viable for at least seven years. Schafer and Chilcote (49) obtained similar results in buried seed studies of perennial and annual ryegrass. Annual ryegrass seed was found to contain a high degree of persistence among buried seeds. Dormancy was induced in annual ryegrass when seeds were buried in cold, wet soil. The

varieties of annual and perennial ryegrass used in this experiment were not stated.

Seed Development on Detached Culms

Detaching of seed culms and its effect on seed size has been studied by several workers. Harlan and Pope (18) observed that immature barley kernels continued to grow for at least eight days when kept moist on the culm after detaching. Barley kernels allowed to air-dry on the culm also continued to grow for at least eight days, but the final length of the kernel was approximately 40% less than when culms were kept moist. Immature kernels dried in the glumes developed equally in size to seeds dried on the culms. No growth occurred when kernels were removed from the culm, separated from the lemma and palea, and air-dried.

Keller (29) found that viable seed could be produced on detached grass culms when culms were detached at anthesis; however, the quantity and weight of seed produced on detached culms was reduced.

McWilliams and Wardlaw (40) compared production of seed on detached and intact harding grass culms from anthesis to maturity. The growth curve for seed developed on intact culms was sigmoid and seeds were mature 30 days after anthesis. Detaching of culms at anthesis caused a small reduction in growth rate during the first 18 days of development. There was a sudden decline in growth rate and

a premature maturation of seed approximately 24 days after anthesis. The final weight of seed produced on detached culms was 20% lower than seed from intact culms and the number of seeds per head was significantly reduced by detaching.

The ability of flowering culms to produce viable seed when detached at anthesis indicates that the developing seed obtains the necessary food for development either from active photosynthesis or from products stored in the tissues of the culm or both. To study this aspect of seed development, McWilliams and Wardlaw shaded and removed parts of harding grass culms. The removal of all or some of the leaves had no significant effect on seed set or weight. The removal of entire internodes caused a reduction in seed set and seed weight, and resulted in more rapid senescence of the remaining culm parts. Shading of the inflorescence greatly reduced seed set. The photosynthetic ability of detached culms was not reduced during the first two weeks after detaching but senescence in detached culms became evident later and a drop in the photosynthetic ability of all parts of the culm was noted.

Studies conducted by McWilliams and Wardlaw (40) using intact culms and labeled CO_2 indicated that only those assimilates produced by photosynthesis in the inflorescence and upper part of the stem were utilized for seed development. These experiments also indicate that seed culms can be virtually independent of the root with respect to the

supply of assimilates and nutrients to the developing seed.

Pope (42) was able to cross two-row 'Hannchen' barley with other barley varieties using pollen from culms of Hannchen barley detached before the pollen was ripe and placed in flasks containing distilled water. The seeds produced on detached culms of Hannchen barley were harvested 29 days after detaching. The average air-dry weight of the seed was 19 milligrams, while the weight of intact Hannchen barley seed was 53 milligrams.

Stoddart (51) used ryegrass species to study the effect of culm detachment on total soluble carbohydrates (TSC) and uptake of sugars. When darnel seed culms were detached early in the maturation period, the final TSC content was within 1% of that obtained when culms were detached late in the maturation period, in spite of initial contents ranging from 5 to 23%. Therefore, he concluded that free sugar loss due to respiration or incorporation into polysaccharides takes place during the final stages of seed maturation on detached culms. Stoddart also presented evidence which suggests that endosperm protein and starch formation were able to proceed after culms were detached.

Infiltration studies conducted by Stoddart (52) using C^{14} sucrose and detached seed culms, showed that sugar was readily incorporated into polysaccharides but the degree of uptake was directly proportional to the developmental stage of the seed at time of detachment. In an earlier study Stoddart (51) found that sugar uptake was highest during

the period prior to the TSC maximum and that during most of the maturation phase a low but stable requirement existed. The TSC maximum for ryegrass occurred eight to 13 days after anthesis.

Black and Naylor (4) were able to prevent the onset of seed dormancy of seed produced on detached culms of wild oats. Wild oats seed culms were detached at the milk stage and placed in flasks containing 200 milliliters of gibberellic acid. Treatment of seed culms with 100 or 1000 ppm of gibberellic acid resulted in the production of nondormant wild oats seed. Seed dormancy was evaluated by germinating seeds in the dark at 20C. Lippert et al. (38) were also able to prevent dormancy in white potatoes with a foliar application of gibberellic acid four weeks prior to harvest.

MATERIALS AND METHODS

General Procedures

Seed viability was determined by pre-chilling seeds for five days at 5C on blotters moistened with 0.2% potassium nitrate (KNO_3), then placing them to germinate at 15-25C with light.[2] Preliminary counts were made after seven days and final counts after 14 days.

Sensitivity of seed to germination temperature was determined by germinating seed in the dark at various temperatures (usually 30, 25, 20, 15, and 15-25C) in plastic boxes on blotters moistened with tap water. Dark germination conditions were obtained by wrapping plastic boxes in heavy-duty aluminum foil. Germination counts were made at seven and 14 days. Percentage seed dormancy, as defined in this thesis, was usually determined by subtracting the percentage germination at 25C from the percentage viability.

Seed moisture content was determined by placing approximately 10 grams of seed in a weighing bottle and oven-drying at 100C for 24 hours. Percentage seed moisture was calculated on a wet weight basis using the following formula:

$$\text{Percent moisture} = \frac{\text{Weight of water removed}}{\text{Initial weight of seed}} \times 100$$

Weight of seed was determined by weighing 4 X 100 seeds of each

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[2] 15-25C - refers to an alternating temperature with 16 hours at the low temperature and eight hours at the high temperature.

treatment on a Mettler balance. The number of observations and seeds per observation was reduced when amount of seed was limiting.

All seed samples were cleaned to remove sticks and sterile florets before seed size and dormancy determinations were made. The Oregon Continuous Blower or the Dakota Blower were used for cleaning seed samples.

Techniques for Characterization of Ryegrass Seed Dormancy

A study was conducted to develop a technique for evaluating ryegrass seed dormancy. Two lots of Gulf seed that varied in degree of seed dormancy were germinated at temperatures of 30, 25, 20, and 15-25C. Two X 100 seeds were germinated at each temperature.

In a second study the effect of after-ripening on seed dormancy was determined. Two X 50 seeds of freshly harvested Gulf were germinated 1, 9, 18, 27 and 36 weeks after harvest at 30, 25, 20 and 15C.

Varietal Differences in Seed Dormancy

Annual and perennial ryegrass varieties were evaluated for seed dormancy characteristics in 1969 and 1970.

In 1969, seed of four annual (Gulf, Magnolia, Florida Rust Resistant, and Tetila Vertas) and three perennial (Linn, Manhattan, and Norlea) varieties was collected approximately two weeks after

harvest from seed fields in Linn county, Oregon. All seed lots were air-dried, cleaned, and tested for moisture content. Dormancy was evaluated by germinating 2 X 50 seeds at 30, 25 and 15C.

In 1970, these studies were extended to include 12 annual and 11 perennial varieties. Seed was hand harvested from plots established at Hyslop Farm on October 15, 1969, from breeders or certified seed stocks. Annual varieties were harvested July 3, 1970 and perennial varieties were harvested July 17, 1970. Moisture content of the seed was determined immediately after harvest. Seed dormancy was evaluated by the same procedures as in 1969.

Effect of Maturity on Seed Dormancy

Seed maturation studies were conducted to determine if seed dormancy of Manhattan and Gulf varied with stage of development. Plants of Manhattan perennial ryegrass were transplanted from a certified seed field into pots and placed in a 21C greenhouse on February 17, 1969. The plants started to head 25 days after being placed in the greenhouse and peak anthesis occurred 18 days after heading. Seed collections were made at three-day intervals beginning at peak anthesis and continuing for 42 days. Each seed collection consisted of five spikes randomly selected from each of 20 randomly selected plants. Seed collections were air-dried and hand threshed. Fifty-seed weight, seed viability, and seed dormancy determinations

were made for each collection. Dormancy was determined by germinating 2 X 25 seeds at 30 and 25C.

In a second experiment, seed maturity of Gulf annual ryegrass was studied. A planting of Gulf was made October 15, 1969 at Hyslop Farm. On May 29, 1970, 3,888 individual florets with anthers extruded were identified using the following system:

1. Individual seed culms with open florets were tagged.
2. Spikelets with open florets were identified by number counting upward from the lowest spikelet.
3. Open florets were identified by number starting with the lowest floret of each spikelet.
4. All identification numbers were recorded in a field book.

Seed collections of 100 seeds each were made at four-day intervals for the first 12 days after anthesis and at two-day intervals for the next 24 days. For each collection, tagged seed culms were selected at random and all identified florets on those culms were removed and placed in a plastic bag. When at least 100 florets were collected, the plastic bag was sealed and brought to the laboratory for fresh weight determinations. Each seed collection was dried in a desiccator over anhydrous calcium sulphate (Drierite) for seven days and re-weighed. Dormancy was determined seven days after harvest by germinating 3 X 10 seeds at 30 and 25C. The remaining seeds were used for seed viability determinations.

Effect of Nutrients, Growth Regulators and Temperature on Seed Dormancy and Seed Weight

Greenhouse and growth chamber studies were conducted to determine the effect of nutrients, growth regulators and temperature on dormancy of Gulf annual ryegrass seed. For the greenhouse study, Gulf plants were transplanted from a certified seed field February 17, 1969 and placed in a 21C greenhouse.

A detached culm technique similar to that used by Keller (29) was used to study the effect of the environmental variables. Eighteen days after heading, randomly selected seed culms were detached and placed in green and brown beverage bottles filled with 250 milliliters of distilled water or nutrient solution. The four nutrient solutions used were complete Hoagland's solution[3], and Hoagland's solution minus nitrogen, phosphorus or potassium. The bottles containing detached culms and the pots containing intact culms were completely randomized on a greenhouse bench.

Twenty-seven days after detaching of culms, seeds were hand harvested, air-dried, cleaned and evaluated for size, number per treatment and dormancy. Dormancy was determined by germinating 2 X 25 seeds at 30, 25, 20, 15 and 15-25C.

A growth chamber study was conducted to determine the effect

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[3]Chemical composition of Hoagland's solution is shown in Appendix Table 12.

of temperature, distilled water and Hoagland's solution on seed dormancy and seed weight. Detached culms of Gulf were used for this study. Culms were cut from a certified seed field at peak anthesis and immediately placed in water. Ten randomly selected seed culms were placed in bottles containing either Hoagland's solution or distilled water. Bottles with seed culms were placed in growth chambers at 15 and 30C. Light in both growth chambers was maintained at approximately 1200 ft-c and humidity controls were turned off. At one-week intervals, groups of five bottles were removed from the 15 and 30C chambers and placed in another growth chamber at 21C for the remainder of the experiment.

After preconditioning for seven weeks, seed of all treatments was hand harvested, air-dried, and cleaned. Seed was evaluated for size and dormancy. Seed dormancy was determined 20 days after harvest by germinating 2 X 100 seeds at 30, 25, 20 and 15-25C.

Effects of sucrose and growth regulators on seed size and dormancy were studied in growth chambers. Ten randomly selected Gulf seed culms were placed in bottles containing 250 milliliters of 1.0% sucrose, distilled water, 100 ppm gibberellic acid, or 100 ppm benzyladenine. Seed from intact Gulf culms was used as the control. Seed culms were preconditioned in growth chambers for 44 days at 15C. Light in the growth chamber was maintained at 600 ft-c and the relative humidity was low. Seed was evaluated for size, percent

moisture, and dormancy. Seed dormancy was determined 12 days after harvest by germinating 2 X 25 seeds at 30, 25 and 20C.

A study was also conducted to determine the critical period during seed development when temperature most affects dormancy. Ten randomly selected seed culms were detached from field-grown Gulf plants at peak anthesis and immediately placed in bottles containing 250 milliliters of distilled water. The bottles containing the detached culms were placed in a growth chamber at 21C. At weekly intervals, two groups of five bottles were removed from the 21C chamber and transferred to either a 15 or 27C chamber. These bottles remained in the 15 or 27C chamber for seven days and then were returned to the 21C chamber for the remainder of the experiment. For controls, one group of five bottles was allowed to remain in each of the three growth chambers for the four week duration of the experiment. Seeds were hand harvested and evaluated for percentage moisture, dormancy and 50-seed weight. Seed dormancy was determined by germinating 2 X 50 seeds at 30, 25 and 20C.

A summation of accumulated heat units was made to determine if heat units were associated with dormancy of seed developed in controlled environment chambers. The number of accumulated heat units from peak anthesis until harvest were determined using the remainder index method (22, 61). Heat units for the constant temperature growth chambers were determined by subtracting the base

temperature of 45F from the mean average daily temperature, the remainder being the number of heat units for the day. Total accumulated heat units were determined by summation of daily heat units. The base temperature of 45F was determined by estimating the temperature which would produce 100% dormant seed of Gulf.

Accumulative heat units were also determined for field-grown Gulf seed in 1969 and 1970. Temperature records[4] were obtained from the Oregon State University weather station (54, 55) and Gulf seed was harvested from fields in the Corvallis area. Seed dormancy was determined by germinating 2 X 50 seeds at 30, 25 and 15C.

Effect of Reduced Photosynthetic Area on Seed Weight

A study was conducted to determine the importance of leaves and stem to seed development of Gulf annual ryegrass when using the detached culm technique. Seed culms were cut from a certified field of Gulf. At the time of detachment, each culm had three leaves. Varying amounts of photosynthetic area were obtained by removing leaves and stems as follows: (1) all leaves removed, (2) all leaves removed except the top leaf, (3) all leaves present, and (4) all leaves and stems removed except for a short portion of stem which remained inside the bottle. Ten similarly treated culms were placed

[4] Maximum and minimum daily temperatures for 1969 and 1970 are presented in Appendix Table 11.

in each brown beverage bottle containing 200 milliliters of distilled water. Seed culms with and without parts removed were preconditioned for six weeks at temperatures of 15 and 30C. After preconditioning, the seeds were hand harvested, air-dried, threshed, cleaned and 4 X 50 seeds weighed.

Effect of Storage Temperature on Seed Dormancy

Seed storage studies were conducted to determine a suitable storage temperature for maintaining ryegrass seed dormancy. Seed for the study consisted of four annual and three perennial ryegrass varieties obtained from seed fields in Linn county, Oregon, approximately two weeks after harvest. Seed of each variety was placed in sealed quart jars and stored at 30, 20, 5 and -18C. Seed dormancy was determined at the beginning of storage and after 7, 14, 28 and 45 weeks for annual ryegrass varieties, and after 6, 13, 27 and 44 weeks for perennial ryegrass varieties. Seed dormancy was determined by germinating 2 X 50 seeds at 30, 25 and 15C. Seed viability was determined at the beginning and end of storage.

Statistical Analysis of Data

Most experiments conducted herein were set up as completely randomized designs. A completely randomized block design was used for two studies: (1) the effect of sucrose and growth regulators on

seed weight and dormancy, and (2) the critical stage during maturity when seed dormancy and weight were most affected by temperature preconditioning.

In general, most studies were analyzed as a factorial analysis or a simple analysis of variance.

RESULTS

Techniques for Characterization of Ryegrass Seed Dormancy

Dormancy of ryegrass seed was determined by germinating seeds over a range of temperatures. By observing the percentage seed dormancy at several temperatures it was possible to distinguish differences between seed lots which were not evident when germinated at a single temperature. This concept is illustrated in Figure 1. When the two seed lots were germinated at 30 and 15-25C, dormancy appeared quite similar. However, germination at 25 and 20C indicated that there were wide differences in seed dormancy between the two seed lots.

In the experimental results which follow, seed dormancy data are presented only for the temperature which best characterized dormancy differences between treatments (usually 25C). Percentages of seed dormancy for the remaining temperatures are presented in Appendix Tables 13 through 22. The statistical analyses of seed dormancy differences are shown in Appendix Tables 2 through 10.

The temperature range over which germination was possible widened as seeds after-ripened, necessitating the use of the multi-temperature technique for the duration of the research period. Germination of Gulf seeds one week after harvest, for example, occurred only at 20 and 15C (Figure 2). Thirty-six weeks after

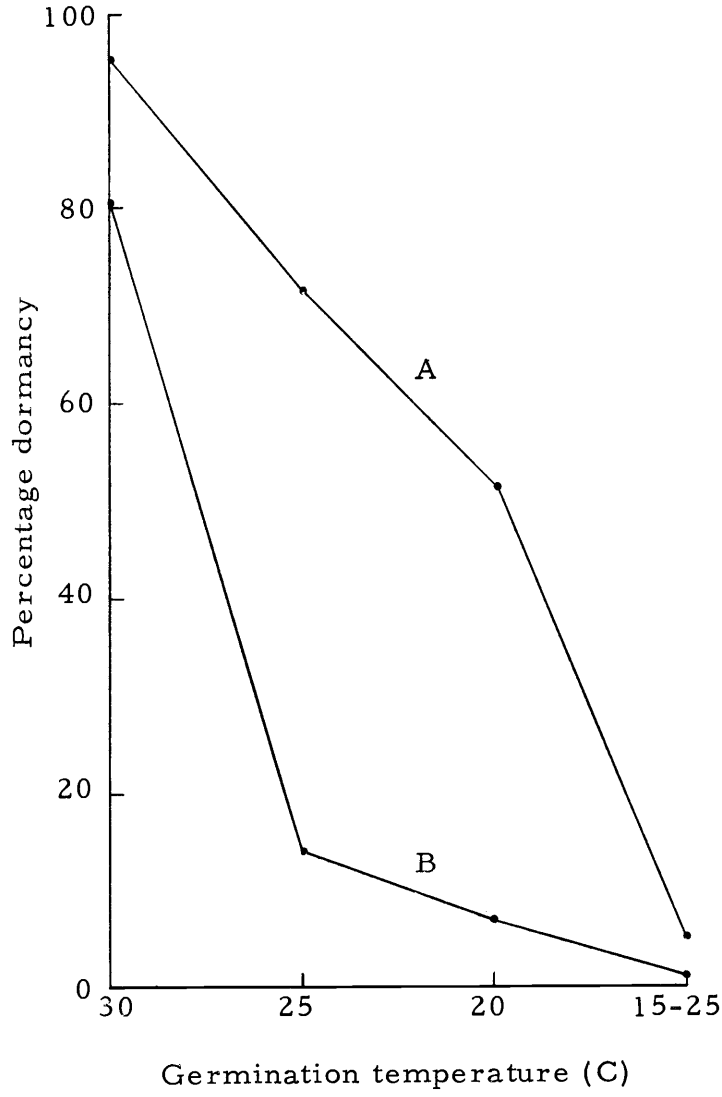

Figure 1. Dormancy of two Gulf annual ryegrass seed lots when germinated at four temperatures.

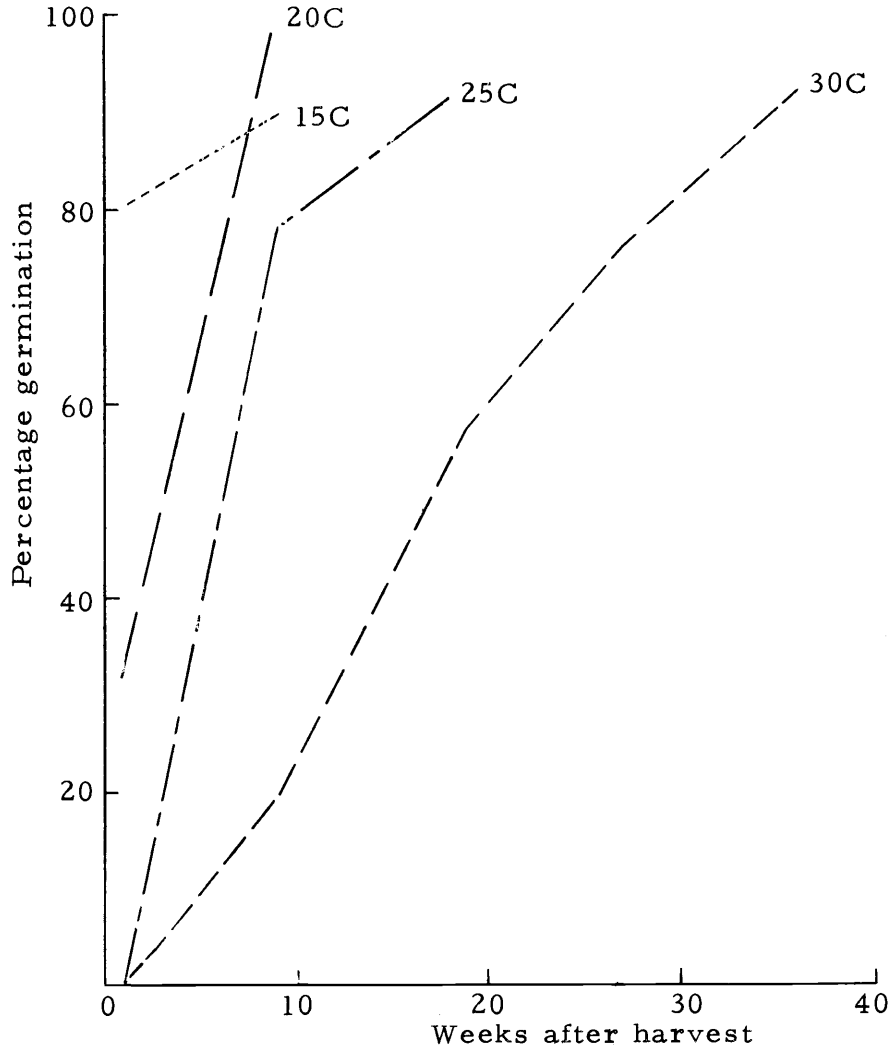

Figure 2. Germination of ryegrass seed at four temperatures following various periods of after-ripening at 21C.

harvest, however, maximum germination occurred at 30C.

Varietal Differences in Seed Dormancy

Varieties of both annual and perennial ryegrass differed in degree of seed dormancy when grown in the field under uniform environmental conditions. The 1969 studies (Table 1) showed that among the seven varieties tested, Gulf was the most dormant annual variety, with Manhattan the most dormant perennial variety.

Table 1. Differences in seed dormancy of seven ryegrass varieties grown in 1969.

Varieties	Seed germination (%)	Seed viability (%)	Seed dormancy (%)
Annuals			
Gulf	27	97	70
Tetila Vertas	33	94	61
Florida R.R.	54	99	45
Magnolia	59	96	37
Perennials			
Manhattan	32	100	68
Norlea	74	96	22
Linn	85	92	7
$LSD_{.01}$	-	-	13

The 1970 studies (Table 2) showed that several other varieties also were dormant. Of 12 annual varieties tested, four showed over 50% dormancy, while eight of 11 perennial varieties were over 50% dormant when germinated at 25C. 'Linn' perennial was the least dormant variety tested, being nearly nondormant in both 1969 and

Table 2. Differences in seed dormancy of 23 ryegrass varieties grown in 1970.

Varieties	Seed germination (%)	Seed viability (%)	Seed dormancy (%)
Annuals			
Florida Rust Resistant	31	100	69
Gulf	34	97	63
Magnolia	42	98	56
Tetila	45	98	53
Tetila Vertas	46	93	47
Tetrone	47	94	47
Tetila Barmultra	54	100	46
Tetila Sceempter	50	94	44
St. Tottori	57	100	43
Tetila Tetrone	52	94	42
Waschikari	54	96	42
Oobahikari	70	97	27
$LSD_{.01}$	-	-	25
Perennials			
NK-100	7	94	87
Manhattan	13	98	85
Atempo	12	97	85
Petra	14	94	80
Pelo	34	99	65
Brabantia Gazon-en-sporteveldtype	33	95	62
Norlea	38	96	58
Taptoe	46	99	53
R. V. P. (pasture type)	50	95	45
Verna Pajbjerg	82	98	16
Linn	90	97	7
$LSD_{.01}$	-	-	14

1970. Seed dormancy of six 'Tetila' varieties was not significantly different when tested in 1970 (Table 2). The seed dormancy of these six genetically similar varieties ranged from 53% to 42%.

Effect of Seed Maturation on Dormancy

Changes in seed weight, moisture content, viability, and dormancy of Gulf annual and Manhattan perennial ryegrasses during the developmental period are shown in Figures 3 and 4.

Dormancy patterns of greenhouse-grown Manhattan ryegrass seed differed from those of field-grown Gulf. Manhattan seed dormancy decreased from 92% 18 days after anthesis to 44% nine days later (Figure 3). From this point onward, dormancy gradually increased to 94% at 45 days after anthesis. The point of minimum dormancy (44%) coincided with the attainment of maximum dry weight 27 days after anthesis. Seed of Manhattan attained 90% viability 15 days after anthesis.

Field-grown Gulf seeds were dormant at all stages of maturity (Figure 4). Ninety percent seed viability was reached 12 days after anthesis when moisture content was 61%, while maximum seed weight was not attained until 30 days after anthesis when moisture content was 31%. The moisture content of the seed decreased slowly until 26% moisture was reached 34 days after anthesis. After this point, loss of moisture was accelerated until a moisture content of 5% was

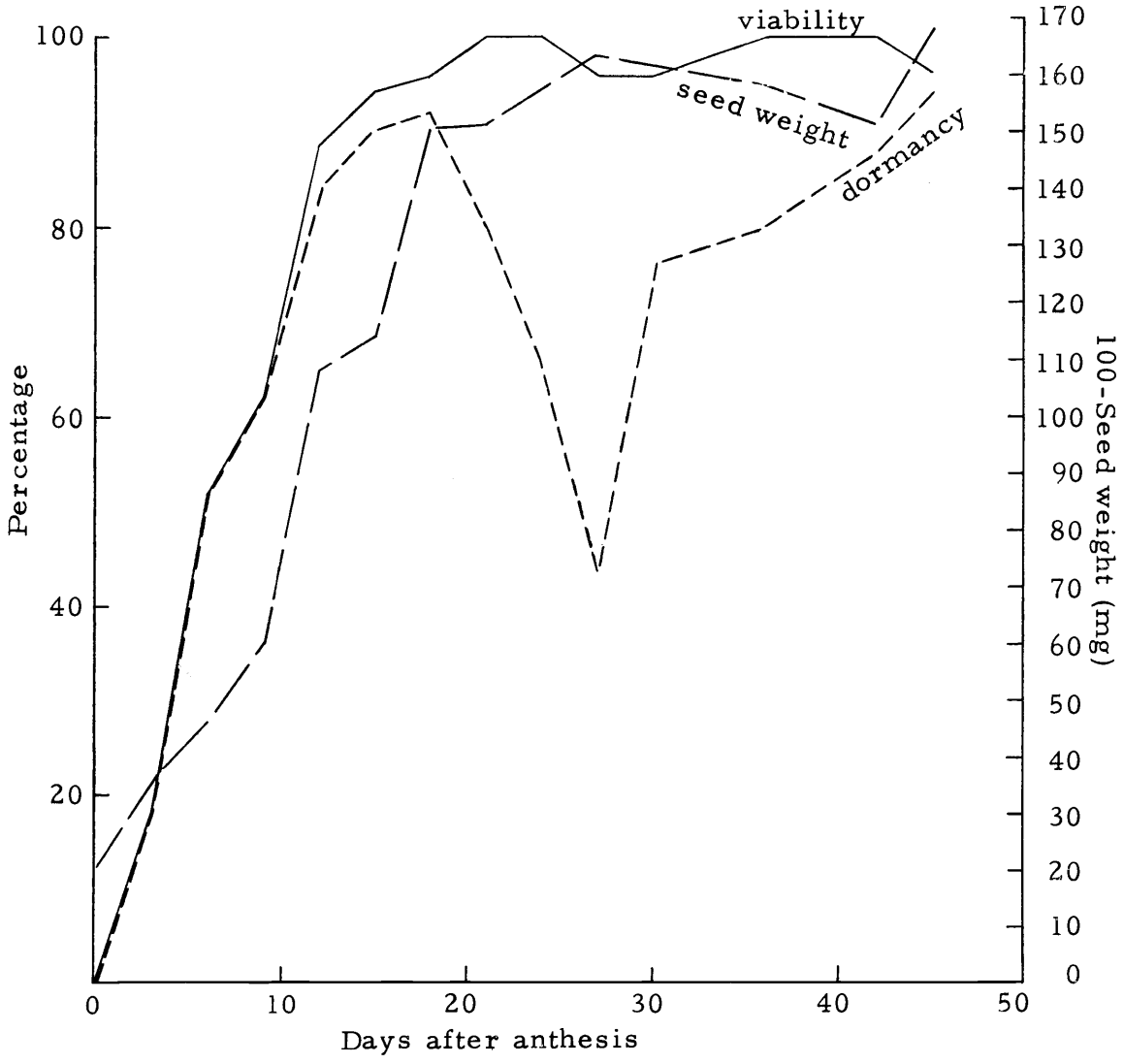

Figure 3. Changes in seed weight, viability, and dormancy of greenhouse-grown Manhattan perennial ryegrass.

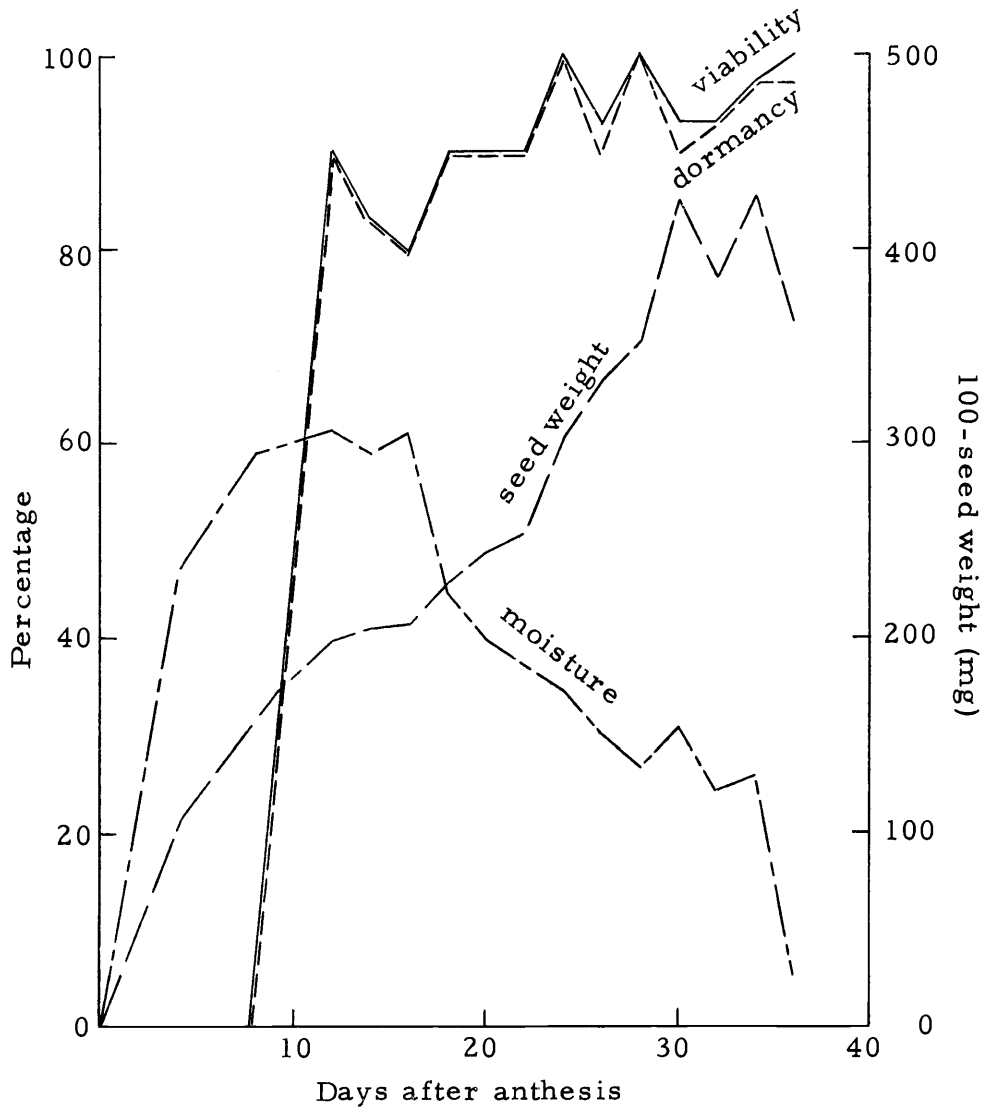

Figure 4. Changes in seed weight, viability, moisture and dormancy of field-grown Gulf annual ryegrass.

reached. The rapid loss in moisture at this time was associated with hot dry weather, the mean average daily temperature for this period being 23.17C.

Effect of Culm Detachment on Seed Dormancy and Weight

The dormancy response of Gulf seeds developed on detached culms was nearly identical to that of seeds from intact plants, as indicated by the response of seeds when germinated over a range of temperatures (Figure 5). These results lend validity to the use of the detached culm technique in studying seed dormancy.

Removal of photosynthetic area of detached Gulf seed culms reduced seed weight (Table 3). Greatest reduction in seed weight occurred when only the seed head was placed in distilled water. When the stem and top leaf remained attached, seed weight was not reduced at 15C, but reduction did occur at 30C. Removal of all leaves reduced seed weight at both temperatures.

Table 3. Effect of photosynthetic area on 50-seed weight of ryegrass seed produced on detached culms preconditioned at 15 and 30C.

Plant parts present	Preconditioning temperature	
	15C (mg)	30C (mg)
Head only	62.3	64.1
Head and stem	76.6	63.4
Head, stem and top leaf	92.3	66.3
Head, stem and all leaves	91.6	83.3

$L.S.D._{.01}$ - 7.4

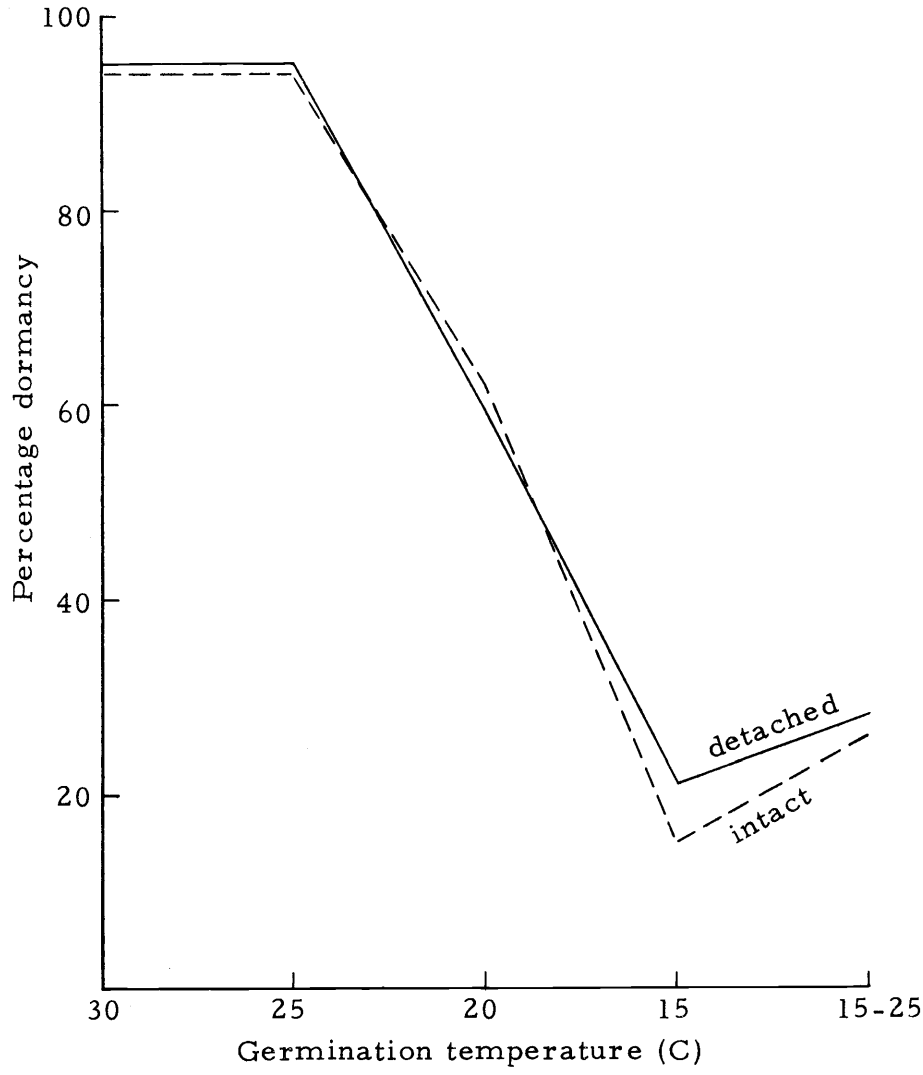

Figure 5. Dormancy of seed produced on detached and intact Gulf annual ryegrass culms when evaluated at five temperatures.

Effect of Nutrients and Growth Regulators on Seed Dormancy

As shown in Table 4, dormancy of Gulf seeds developed on detached culms was not affected when nutrients were added to the medium. Dormancy was similar regardless of whether culms were immersed in Hoagland's solution, Hoagland's minus N, P, or K, or in distilled water.

Distilled water and Hoagland's solution were also shown to have equivalent effects on seed dormancy in a second experiment (Table 5). These results show that the Hoagland's solution and distilled water produced similar levels of dormancy irregardless of temperature or length of preconditioning period.

Addition of gibberellic acid to the medium reduced seed dormancy by 25%, while benzyladenine and sucrose caused a 12% reduction (Table 6).

Seeds produced in a gibberellic acid solution were also significantly lower in dormancy than seeds produced on culms attached to the plant. Neither benzyladenine nor sucrose had this effect.

Effect of Nutrients and Growth Regulators on Seed Weight

Weight of seed from intact culms was significantly higher than weight of seed developed on detached culms in nutrient solutions and

Table 4. Effect of nutrient solutions on ryegrass seed production, size and dormancy of seed developed on detached and intact culms.

Treatments	Total seed weight (gr)	100-seed weight (mg)	Seed dormancy (%)
Detached culms in:			
Hoagland's - P	3.932	129.2	54
Hoagland's - K	4.240	133.6	46
Hoagland's solution	4.153	136.0	51
Hoagland's - N	4.254	140.4	52
Distilled water	4.303	144.6	59
Intact culms	5.671	231.6	59
$LSD_{.01}$	--	11.4	ns

Table 5. Effect of Hoagland's solution and length of temperature of preconditioning on dormancy of ryegrass seeds produced on detached culms.

Weeks of preconditioning	Preconditioning temperatures					
	15C			30C		
	Distilled water (%)	Hoagland's solution (%)	Ave. (%)	Distilled water (%)	Hoagland's solution (%)	Ave. (%)
1	30	37	33	41	20	30
2	47	43	45	12	8	10
3	51	35	43	19	11	15
4	64	71	67	23	17	20
5	72	64	68	14	5	9
7	86	81	83	6	11	8
$\bar{X}$	58.3	55.2	56.5*	19.2	12.0	15.3*

Grand mean of distilled water - 38.75.
Grand mean of complete nutrient - 33.58.
*$LSD_{.01}$ - 11.9.

Table 6. Effect of benzyladenine, gibberellic acid and sucrose on ryegrass seed development on detached culms.

Treatments	100-Seed weight (mg)	Seed dormancy (%)
Detached culms in:		
Benzyladenine	116	44
Gibberellic acid	144	31
Distilled water	153	56
Sucrose	181	44
Intact culms	218	53
$LSD_{.01}$	20	9

distilled water (Table 4). A phosphorus deficiency was more detrimental to seed weight than deficiencies of nitrogen or potassium. Intact culms produced the largest yield of seed per ten culms, followed by distilled water, Hoagland's solution minus nitrogen, Hogaland's solution minus potassium, complete Hoagland's solution, and Hoagland's solution minus phosphorus.

When preconditioned at 15C, seeds in distilled water were significantly larger than seeds developed in Hoagland's solution (Table 7). Similar results were obtained when seeds were developed at 30C. The longer the detached culms remained in distilled water at 15C before being transferred to 21C, the heavier the seeds were at harvest. At 30C, however, seeds developed in distilled water or complete nutrient solution did not significantly increase or decrease in seed weight with longer exposures.

Table 7. Effect of Hoagland's solution and length and temperature of preconditioning on 100-seed weight of ryegrass seeds produced on detached culms.

Weeks of preconditioning	Preconditioning temperature			
	15C		30C	
	Distilled water (mg)	Hoagland's solution (mg)	Distilled water (mg)	Hoagland's solution (mg)
1	158	148	148	134
2	159	150	151	131
3	192	184	147	136
4	200	178	146	134
5	185	166	135	118
7	201	168	140	122
$\overline{X}$	183	166	144	129

Grand mean of distilled water - 163
Grand mean of complete nutrient - 147
$LSD_{.01}$ - 3

Sucrose added to the medium increased seed size by 18% while benzyladenine decreased size by 24% (Table 6). Gibberellic acid had no effect on seed size. As was the case with nutrient solutions, seeds produced on intact culms were considerably larger than seeds produced on detached culms in solutions containing growth regulators. Seeds produced in benzyladenine were 18% lower in viability than the average of the other treatments.

Effect of Temperature on Seed Dormancy

Dormancy of Gulf seed was affected by temperature of preconditioning (Table 5). As the duration of temperature preconditioning

increased, the greater were the effects. Seeds developed at 15 or 30C for one week before being transferred to 21C were similar in dormancy (33 and 30%, respectively, when germinated at 25C). However preconditioning for seven weeks at 15C increased dormancy to 83% and preconditioning for the same duration at 30C decreased dormancy to 8%. The effects of preconditioning temperature when evaluated over a range of germination temperatures are shown in Figures 6 and 7.

Gulf seeds are also sensitive to short periods of high or low temperatures at various stages during seed development and ripening (Table 8). Preconditioning of Gulf seed culms at 15C during the early stages of seed development did not change dormancy from that resulting from a continuous exposure to 21C, but exposure to 15C during the ripening stage (4th week) increased dormancy. Preconditioning of Gulf seed culms at 27C for seven days immediately after anthesis reduced dormancy in comparison to the 21C control. Seed dormancy was also reduced when culms were preconditioned at 27C during the ripening stage, but not as much as exposure immediately after anthesis.

Accumulated heat units were associated with the level of dormancy when Gulf seeds were developed in controlled environment chambers. Seeds were dormant when germinated at 25C if they received less than 1449 heat units during seed development and ripening (Figure 8).

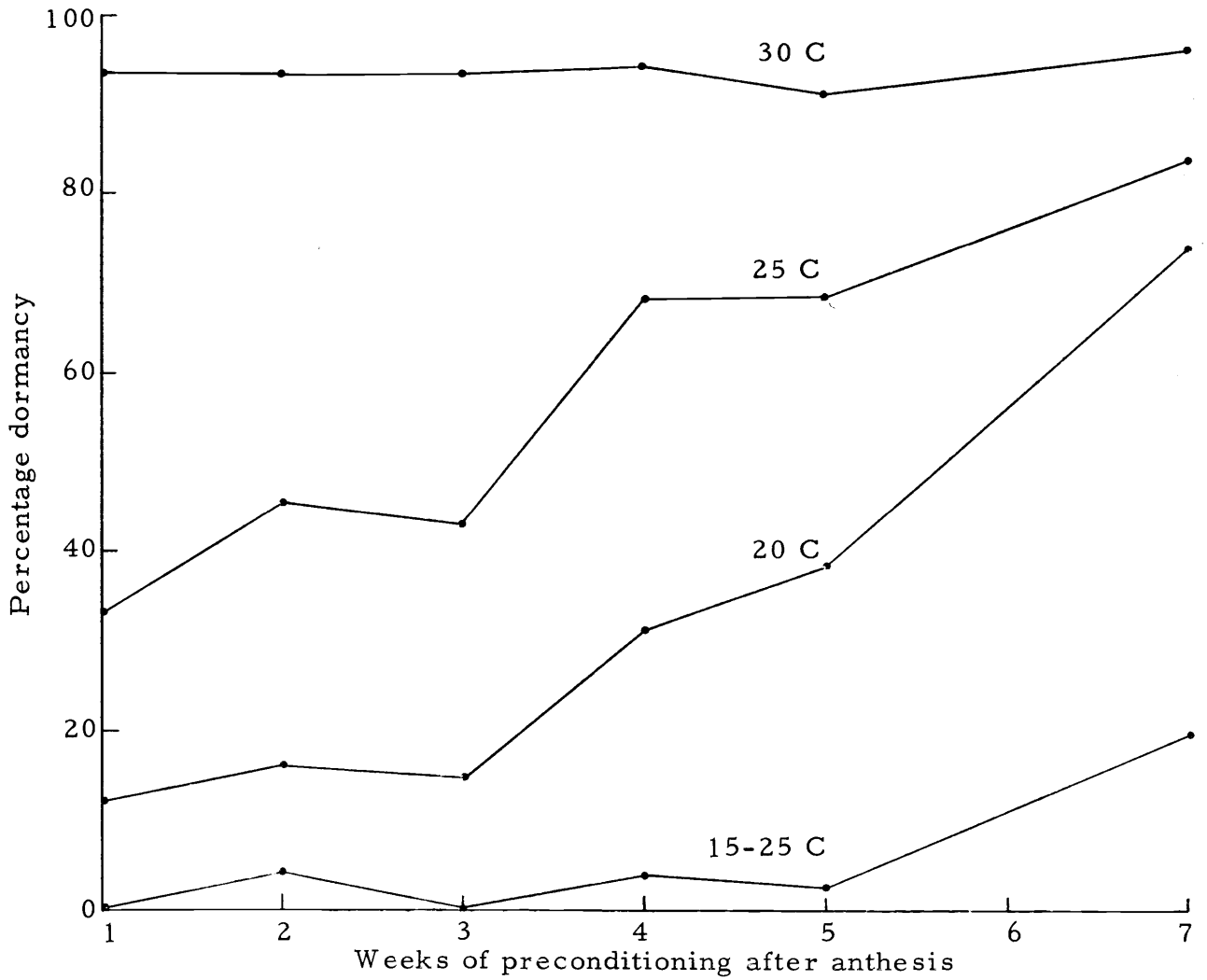

Figure 6. Dormancy of ryegrass seed when evaluated at four temperatures following preconditioning periods of one to seven weeks at 15 C.

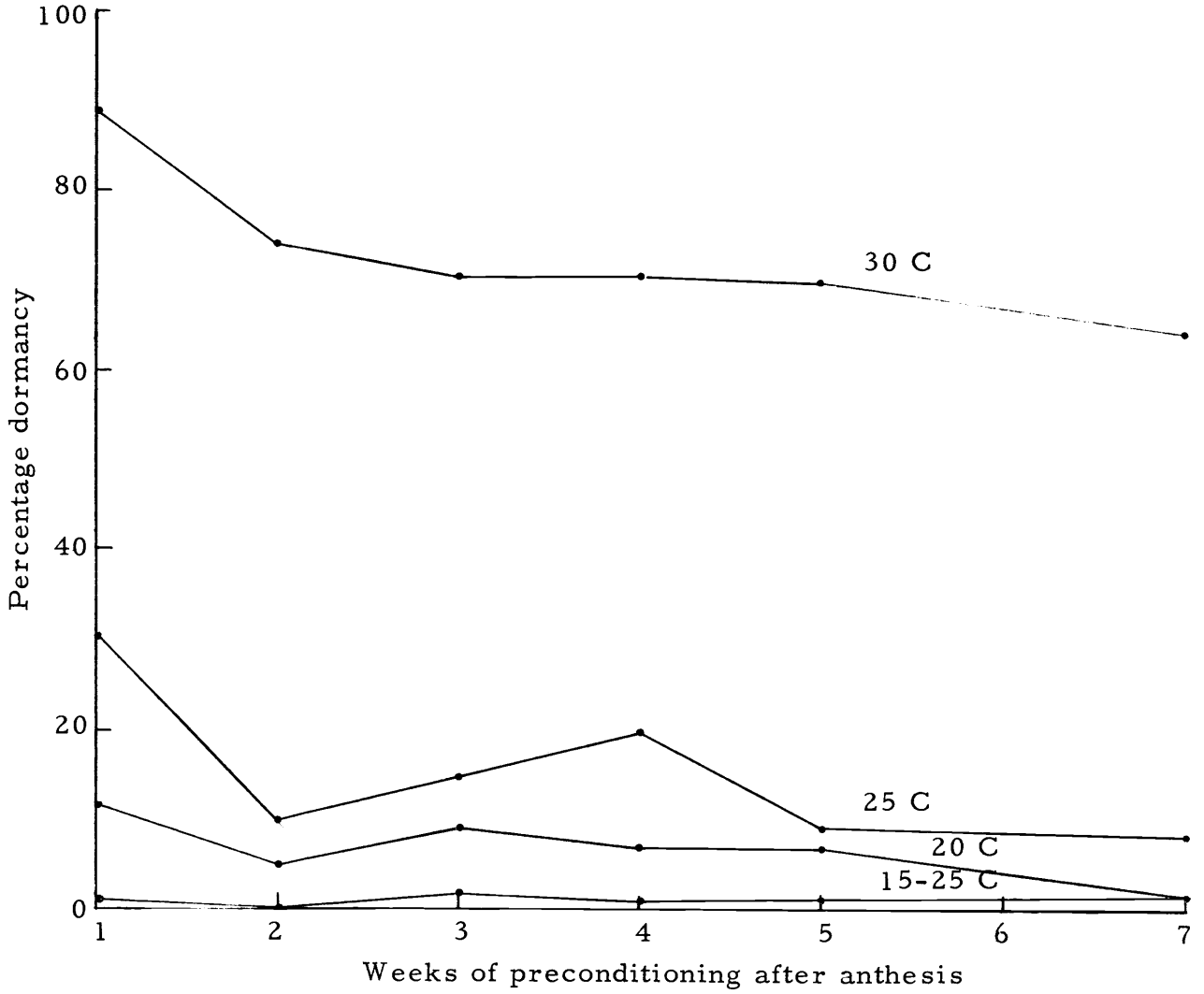

Figure 7. Dormancy of ryegrass seed when evaluated at four temperatures following preconditioning periods of one to seven weeks at 30 C.

Table 8. Effect of preconditioning at 15 and 27C for one week intervals during development on weight and dormancy of ryegrass seed. Seeds produced on detached culms.

Preconditioning regime*		50-seed weight (mg)	Seed dormancy (%)
Weeks after anthesis	Temp. (C)		
Continuous (4 wk)	21	81.1	35
1st	15	84.8	29
2nd	15	77.8	37
3rd	15	75.7	36
4th	15	73.7	46
Continuous (4 wk)	15	97.1	58
1st	27	75.6	14
2nd	27	65.0	30
3rd	27	78.7	27
4th	27	75.0	25
Continuous (4 wk)	27	73.7	24
$LSD_{.01}$	-	5.1	9

*Seed culms were held at 21C before and after preconditioning.

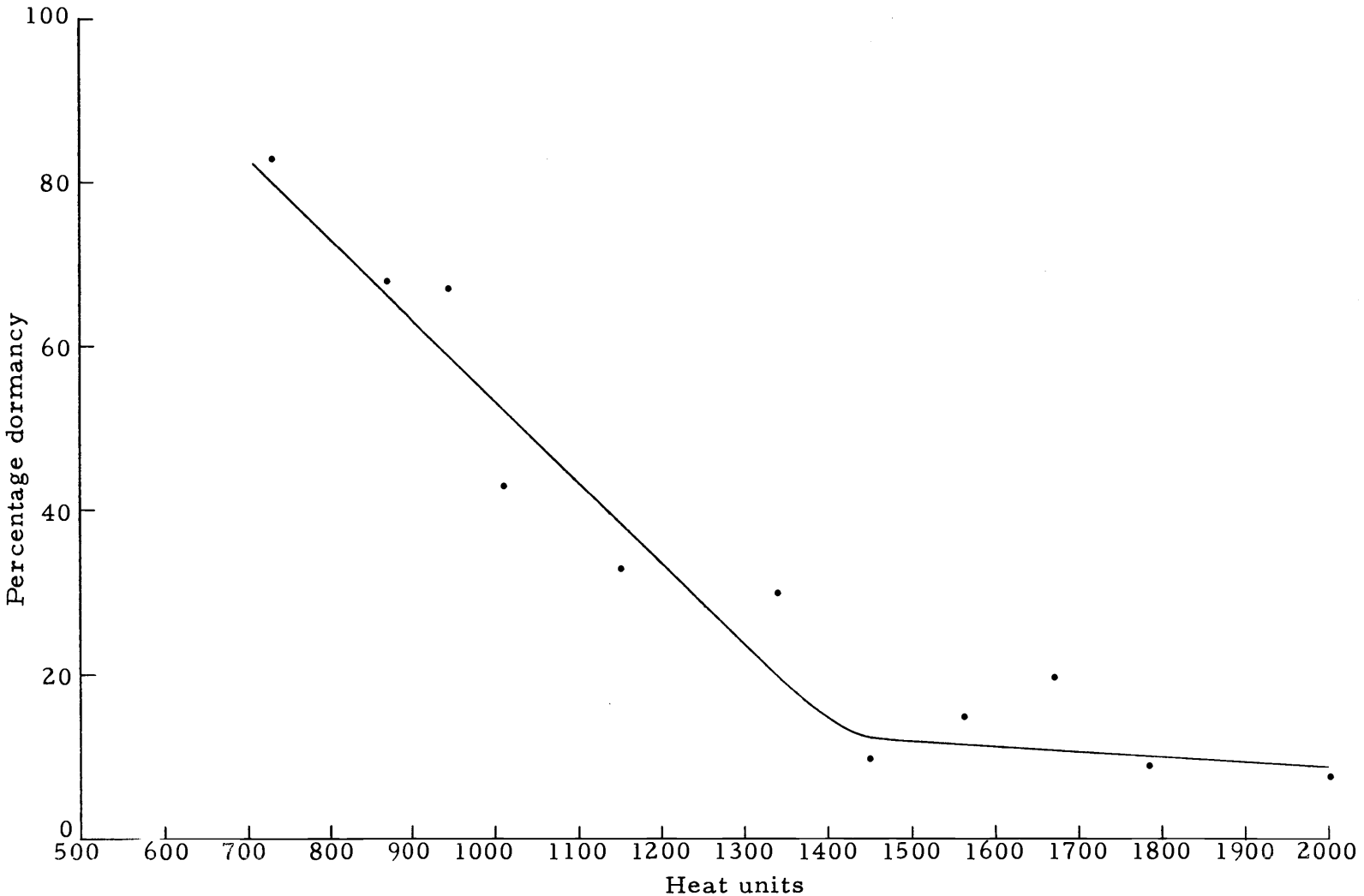

Figure 8. Comparison of seed dormancy and accumulated heat units during seed development on detached Gulf annual ryegrass culms in growth chambers.

Gulf seed growing in the Corvallis, Oregon area during 1969 and 1970 received approximately 539 and 541 heat units, respectively, and were 70 and 63% dormant.

Effect of Temperature on Seed Weight

Seed size was affected by the duration of preconditioning at 15 and 30C before being transferred to 21C (Table 7). Extended periods of low temperature preconditioning increased seed weight, while seed weight was decreased when preconditioning at 15C was delayed until later stages of development (Table 8). The heaviest seeds were produced with four weeks continuous preconditioning at 15C. High temperature preconditioning reduced seed weight as duration of preconditioning increased. The greatest reduction in seed weight occurred when seeds were exposed for one week to high temperature during the second week of development. Seed weight was also significantly reduced with exposure to high temperature during the first and fourth weeks after anthesis (Table 8).

Effect of Storage Temperature on Seed Dormancy

Seed storage temperatures affected dormancy of ryegrass seed (Figures 9, 10, 11, and 12). Dormancy of all varieties decreased rapidly during storage at 30C (Figure 9). Germination of all varieties exceeded 80% after six and seven weeks of storage, except for Gulf,

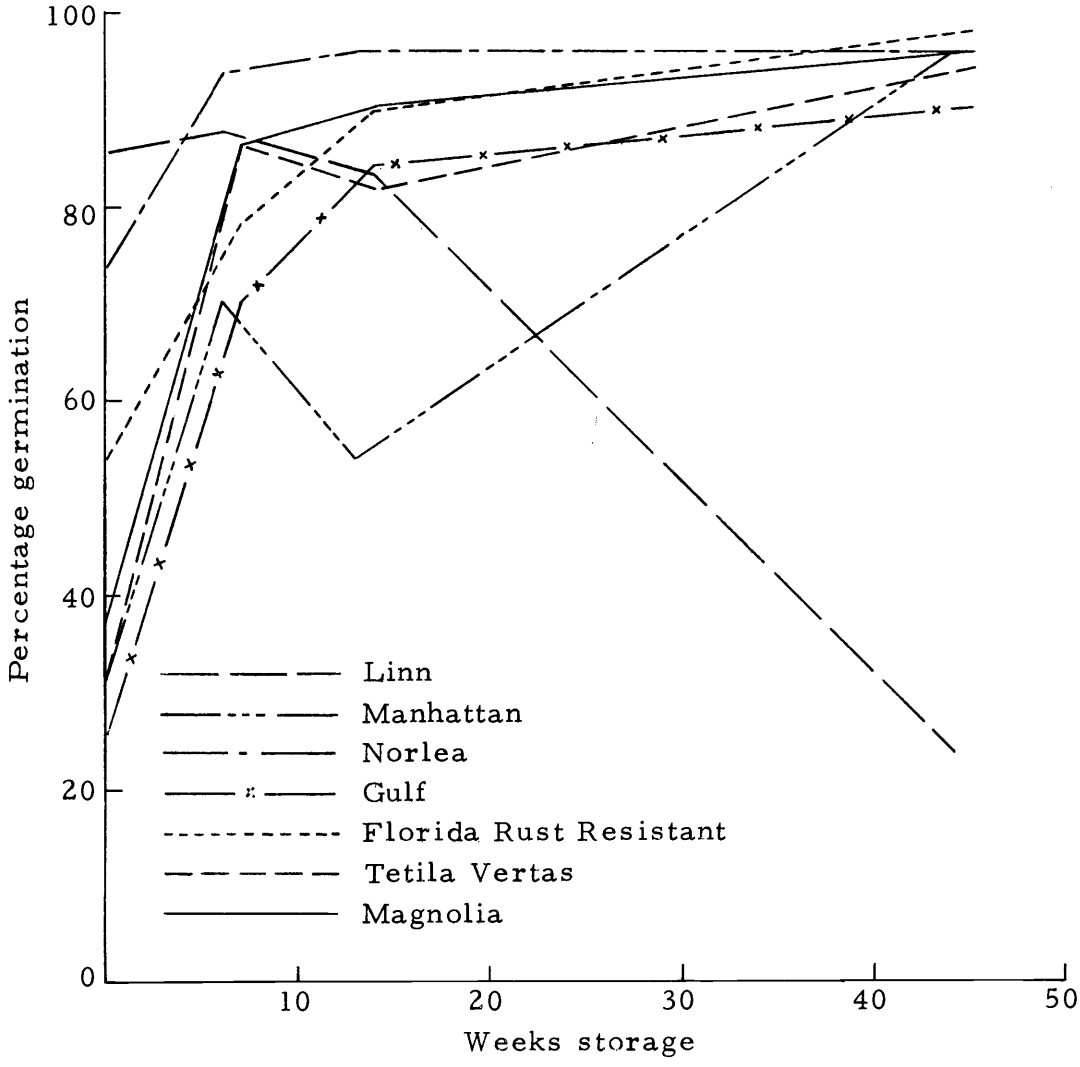

Figure 9. Germination of seven ryegrass varieties after storage at 30C (germinated in the dark at 25C).

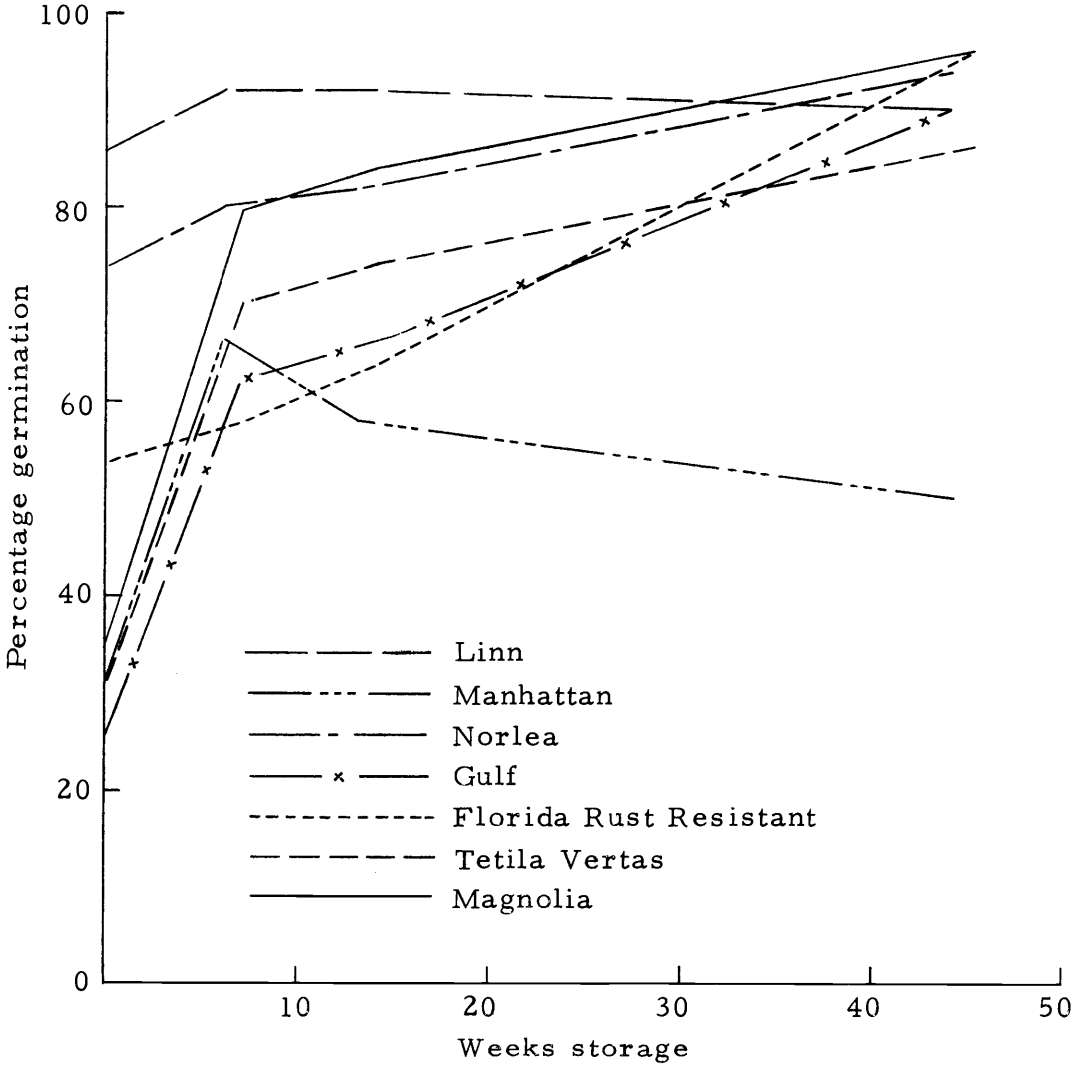

Figure 10. Germination of seven ryegrass varieties after storage at 20C (germinated in the dark at 25C).

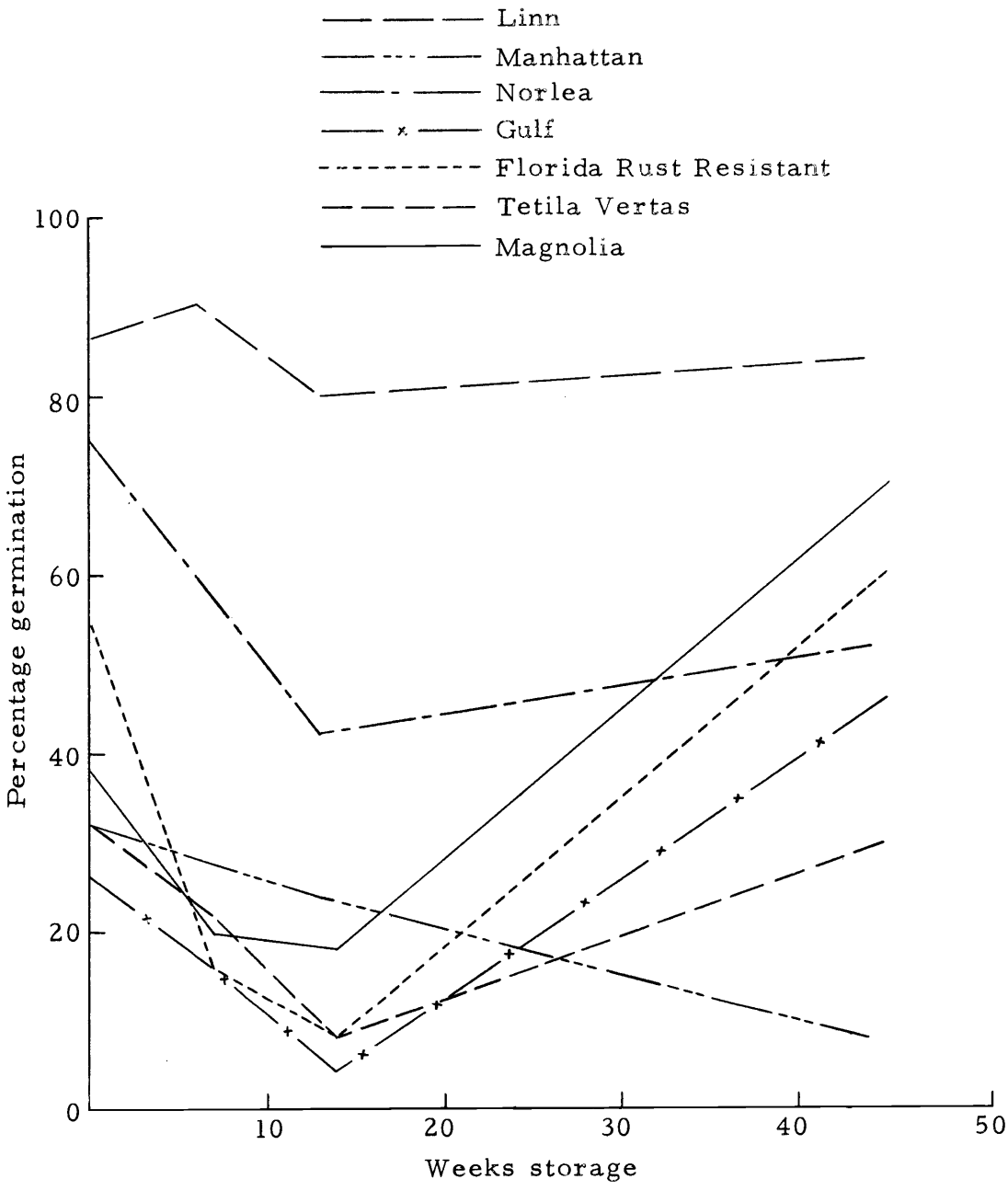

Figure 11. Germination of seven ryegrass varieties after storage at 5C (germinated in the dark at 25C).

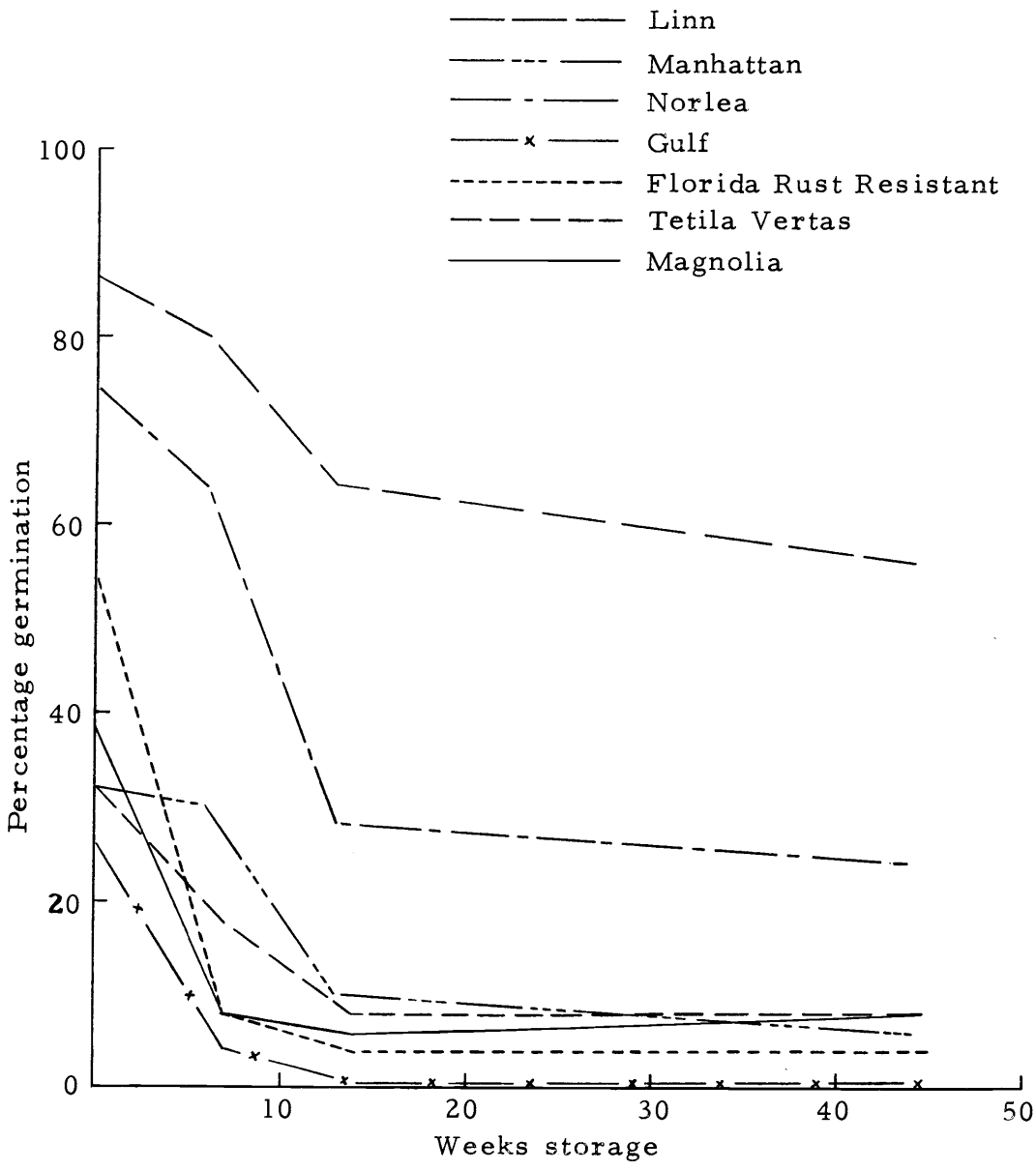

Figure 12. Germination of seven ryegrass varieties after storage at -18C (germinated in the dark at 25C).

'Florida Rust Resistant', and Manhattan. Linn perennial seed began to lose viability after six weeks of storage at 30C; whereas, Manhattan perennial became more dormant.

Dormancy decreased slowly when seeds were stored at 20C (Figure 10). Gulf, 'Tetila Vertas', and Manhattan varieties had still not reached maximum germination after 44 and 45 weeks of storage at 20C. Manhattan perennial seed became more dormant during storage at 20C.

Storage of seed at 5C increased seed dormancy during the first 14 weeks of storage (Figure 11), but the dormancy was not maintained. The degree of dormancy remaining after 44 and 45 weeks of storage at 5C was about the same as the dormancy present at the beginning of storage. Manhattan perennial seed stored at 5C continued to increase in dormancy and after 44 weeks of storage, germinated only 8%.

Seed dormancy was induced in all varieties by storage at -18C and this dormancy was maintained for the duration of the study (Figure 12). Dormancy of Linn perennial seed was much less affected by storage temperatures of 5 and -18C than were the other varieties.

Viability of stored seed remained high at all temperatures except for seed of Linn stored at 30C (Table 9). Linn seed viability after 44 weeks of storage at 30C was reduced to 32%. Percentage moisture of all varieties increased somewhat during storage (Table 10).

Table 9. Effect of storage temperatures on seed viability of seven ryegrass varieties.

Variety	Before storage (%)	After storage			
		30C (%)	20C (%)	5C (%)	-18C (%)
Gulf	96	92	98	98	96
Florida Rust Resistant	98	94	98	96	98
Magnolia	96	90	98	96	94
Tetila Vertas	94	90	98	94	100
Manhattan	100	98	98	100	94
Norlea	96	94	96	94	94
Linn	88	32	82	86	80

Table 10. Effect of storage temperatures on seed moisture of seven ryegrass varieties.

Variety	Before storage (%)	After storage			
		30C (%)	20C (%)	5C (%)	-18C (%)
Gulf	11.30	13.29	12.21	12.33	12.37
Florida Rust Resistant	10.36	11.95	12.70	11.64	11.68
Magnolia	10.75	12.12	11.72	11.83	11.96
Tetila Vertas	9.01	11.89	11.30	10.97	10.71
Manhattan	5.76	8.04	6.80	7.79	7.39
Norlea	8.39	7.38	9.43	9.47	9.88
Linn	7.33	11.14	13.04	12.80	12.99

DISCUSSION

Dormancy of ryegrass seed is expressed by differential sensitivity to germination temperatures. Nondormant ryegrass seeds will germinate over a wider range of temperatures than dormant seeds. When ryegrass seed lots were dormant, no germination occurred at temperatures of 30 and 25C, but seeds did germinate at 20 and 15C. Upon after-ripening, germination occurred at 25 and 30C as well as at 15 and 20C. This type of dormancy fits Vegis' (62) description of "relative dormancy" and substantiates his concept of dormancy that as seeds after-ripen the temperature range for germination widens.

Ryegrass varieties have different genetic potentials for seed dormancy, but the expression of these potentials is influenced by temperature. This temperature influence was evident in growth chamber studies in which seeds developed in cool environments were more dormant than seeds developed in warmer environments. This would lead one to expect that similar trends would occur in the field. Most annual varieties, in fact, did appear to follow this trend--early maturing varieties (Gulf and Florida Rust Resistant) which received lesser amounts of high temperature during seed development were more dormant than later maturing varieties.

The association of field temperatures and dormancy was not as evident in the perennial varieties tested. Linn and Verna Pajbjerg, early maturing varieties which were exposed to cooler temperatures,

were nondormant when harvested. These varieties, however, do not appear to have a genetic potential for seed dormancy and were not affected by the relatively cool temperatures.

Thus it appears that a variety which does not have a genetic potential for seed dormancy cannot become dormant when grown in an environment which stimulates dormancy. The varieties Gulf, Florida Rust Resistant, NK-100, Manhattan, Atempo, Petra, and Pelo have genetic potentials for seed dormancy and produced dormant seeds when developed in a favorable environment for dormancy.

The differences found in degree of seed dormancy among ryegrass varieties parallel the findings of other researchers in regard to dormancy of wheat varieties. Everson and Hart (13) found dormancy differences among wheat varieties when germinated at 10C, and Toole (53) stated that freshly harvested wheat and other grains are sensitive to germination temperatures. The findings of Everson and Hart and Toole have been strengthened by work of several other researchers (7, 9, 15, 16, 25).

Buried seed studies comparing Linn perennial and Oregon annual ryegrass seed (43, 44, 49) have indicated that annual ryegrass seed was more persistent in the soil than perennial ryegrass seed. These results are consistent with the findings of the present study which indicate that Linn perennial ryegrass is a nondormant variety and would not have the genetic potential for persistence in the soil.

Although Oregon annual was not tested, it apparently is a dormant variety of annual ryegrass and would be expected to persist longer than Linn. It is possible to speculate that if seed of a dormant perennial ryegrass variety such as Manhattan was buried, persistence of the perennial ryegrass would equal or even exceed that of certain annuals.

The finding of varietal differences in seed dormancy has practical application in the setting of field history standards in ryegrass seed certification programs. According to the 1970 Oregon Certification Standards a field must not have grown or been seeded to annual or perennial ryegrass species during the five previous years. Results of these studies suggest that varietal differences in seed dormancy should be considered when establishing field history requirements, rather than differentiating only between annual and perennial species. For example, field history requirements for Linn perennial could be reduced because it is a nondormant variety, but the requirements for Manhattan perennial should be similar to those of dormant annual varieties.

Consideration of the seed dormancy potential of ryegrass varieties may also be used to advantage when germinating freshly harvested seed in the laboratory. Pre-chilling of freshly harvested ryegrass seed could be confined to those varieties known to be dormant. Elimination of the five-day pre-chilling period on nondormant varieties

would substantially reduce the time required for completion of the germination test.

Seed maturation characteristics of Manhattan and Gulf were similar to those reported by Hyde et al. (23) when studying other ryegrass varieties. For example, these workers reported that maximum seed weight of annual ryegrass seed was reached 30 days after anthesis as compared to 28 days for Gulf. Ninety percent seed viability of Manhattan was obtained 13 days after anthesis compared to the 14 days reported by Hyde in his study with another variety of perennial ryegrass. The changing pattern of dormancy observed in Manhattan during seed development was not found in Gulf. Further investigation is required before the reason for these differences can be explained.

The use of detached culms is a desirable research technique in that it requires less space in growth chambers and allows more flexibility in applying environmental variables to the plants. Viable seed of ryegrass was produced on detached culms, but seed weight was reduced in comparison to seed from intact culms. The dormancy response of Gulf seeds was not altered by detaching seed culms; therefore, the use of the detached culm technique appears to be justified.

The amount of photosynthetic area present on detached culms had an appreciable effect on seed weight. Largest seeds were

produced when culms were cut at the soil surface. When only the top leaf remained attached, the seeds produced at 15C were equal in size to seed from culms with all leaves attached. When preconditioning occurred at 30C, seed weight was significantly reduced by removing plant parts, including the top leaf. Perhaps removal of plant parts did not affect seed size at 15C because maturation was slower and photosynthate produced per given area was increased.

In some species nutrient deficiencies have affected seed dormancy, but that was not true for Gulf ryegrass as deficiencies of nitrogen, potassium and phosphorus did not increase or decrease dormancy. It was also found that dormancy of Gulf seed was not affected by development of culms in distilled water or Hoagland's solution. Preconditioning temperatures of 15 and 30C did not interact with solutions used for seed development of detached culms.

Growth regulators and sucrose reduced seed dormancy when Gulf culms were developed in solutions containing these chemicals. Gibberellic acid reduced seed dormancy 25% and benzyladenine and sucrose each reduced dormancy 12%. These results agree with the published data of Black and Naylor (4) and Lippert et al. (38) who showed that dormancy of wild oat seeds and potato tubers, respectively, was reduced by an exogeneous application of gibberellic acid.

The genetic potential for dormancy of Gulf seed was modified by the degree and distribution of temperature received during seed

maturation and ripening. Low temperatures during seed development increased dormancy of Gulf seeds, while high temperatures immediately after anthesis reduced dormancy.

Temperature affected dormancy, not only during the seed development period, but also during storage. Low temperature is commonly used for seed storage to maintain viability. Many kinds of seed are sealed in air-tight containers when the seed moisture is low and placed in refrigerated storage. These storage conditions maintained or induced dormancy in ryegrass, and if these methods were used commercially, could result in stand establishment problems. For example, seed dormancy was maintained at original levels when seeds were stored at 5C, but dormancy was greatly increased at -18C.

Dormancy of freshly harvested Gulf seed developed in growth chambers was associated with the total accumulated heat units received during seed maturation and ripening. If during seed development and ripening 1449 accumulated heat units were received, Gulf seed was nondormant. However, if less than 540 accumulated heat units were received, all seeds were dormant. Field application of the heat unit concept for predicting seed dormancy appears possible, although other factors such as fluctuation in temperature and variety of ryegrass must be considered. Extreme high or low temperatures during critical stages of seed development may hinder the practical application of the accumulative heat unit index for prediction of seed

dormancy.

No explanation can be given for the reduced size of seed developed in Hoagland's at 15 and 30C as compared to seeds developed in distilled water. It would seem, however, that the nutrients were interfering with normal growth and development in distilled water.

Other workers (40) found that detached culms maintained full photosynthetic ability for two weeks after detaching, but senesced more rapidly than intact culms. Stoddart (51) determined that free sugar uptake of Lolium sp. was greatest prior to the total soluble carbohydrate maximum. Thereafter, free sugar requirements were low. Considering these findings, we would not expect weight of seed from detached culms to equal weight of seed from intact culms unless culms were detached after the total soluble carbohydrate maximum was reached. Stoddart has determined the total soluble carbohydrate maximum for Lolium sp. to occur eight to 13 days after anthesis.

In this experiment, leaves on culms developed at 30C began to senesce earlier than did leaves of culms developed at 15C. Therefore, the larger size of seeds developed at low temperature could be due to the ability of the culms to continue photosynthesis for a longer time than at 30C.

SUMMARY AND CONCLUSIONS

Seed dormancy of ryegrass was evaluated by germinating seeds in the dark at temperatures of 30, 25, 20, 15 and 15-25C. The germination response of ryegrass seeds to these temperatures indicates the degree of dormancy present in the seed. Dormant seeds will produce some germination at the cooler temperatures but will fail to germinate at the warmer temperatures. As seeds after-ripen, germination will occur at all of these temperatures.

Varieties of annual and perennial ryegrass differ in degree of seed dormancy. Some varieties such as Florida Rust Resistant, Gulf, NK-100, Manhattan and Atempo were dormant; whereas, Oobahikari, Verna Pajbjerg and Linn were practically nondormant. There was no relationship between seed dormancy and species as had been previously assumed by several researchers.

Seed dormancy of Manhattan perennial ryegrass was related to stage of development, and dormancy was reduced when seeds attained maximum seed weight. Gulf annual ryegrass, however, was not affected by stage of development and was dormant throughout the maturation period.

A detached culm technique was developed to study the effects of temperature, nutrients and growth regulators on ryegrass seed dormancy. Seed developed on detached Gulf culms possessed the same

degree of dormancy as seeds developed on intact culms, although seed weight was reduced.

Dormancy of seed was not influenced by deficiencies of nitrogen, phosphorus and potassium, but phosphorus deficiencies did reduce seed weight.

Gibberellic acid, benzyladenine and sucrose reduced seed dormancy. Sucrose solution increased seed weight over that of seeds developed on culms in distilled water.

Temperature had the greatest influence on seed dormancy. Seeds allowed to develop for seven weeks at 15C were 83% dormant as compared to 8% dormancy when developed at 30C. The timing of the exposure to high or low temperatures also affected seed dormancy. Dormancy was reduced when seeds were exposed to high temperature during the milk or ripening stage. Exposure of seeds to low temperatures during the ripening stage increased dormancy. The effects of temperature on seed dormancy of Gulf annual ryegrass were accumulative, although during certain stages of development extremes in temperature may alter the accumulative effect.

Under constant temperatures in a growth chamber over 1400 heat units were required during seed development to produce non-dormant Gulf annual ryegrass seeds. Field application of the heat unit concept appears possible for predicting seed dormancy. However, more information on the effects of temperature fluctuation and varieties

is necessary before the concept can be used to predict dormancy of field-grown ryegrass seed.

Temperature not only affects dormancy during seed development but also during storage. Storage of seven ryegrass varieties at 5 and -18C induced seed dormancy and at the lower temperature the high level of dormancy was maintained.

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APPENDIX

Appendix Table 1. Common and scientific names of plants referred to in this thesis.

Common name	Scientific name
Balsam	Impatiens balsamina L.
Barley	Hordeum vulgare L.
Bluegrass, Kentucky	Poa pratensis L.
Brome, Red	Bromus rubens L.
Darnel	Lolium temulentum L.
Fescue	Festuca sp. L.
Harding Grass	Phalaris tuberosa L.
Lambsquarters	Chenopodium album L.
Lettuce	Lactuca sativa L.
Millet, White Wonder	Setaria italica (L.) Beauv.
Needlegrass, Green	Stipa viridula Trin.
Oats	Avena sativa L.
Oats, Wild	Avena fatua L.
Peanuts	Arachis hypogaea L.
Pimpernel, Scarlet	Anagallis arvensis L.
Pine, Scots	Pinus sylvestris L.
Plantain, Bracted	Plantago aristata M.
Potatoes	Solanum tuberosum L.
Rice	Oryza sativa L.
Rose	Rosa sp. L.
Ryegrass, Annual (Italian)	Lolium multiflorum Lam.
Ryegrass, Perennial	Lolium perenne L.
Ryegrass, Wimmera	Lolium rigidum Gaudin.
Spruce, Norway	Picea excelsa Link.
Wheat	Triticum aestivum L.
Wildrye, Russian	Elymus junceus Fisch.

Appendix Table 2. Analysis of variance of seed dormancy for four annual and three perennial ryegrass varieties in 1969.

Source of variation	df	SS	Mean square
Between	6	6886.857	1147.809**
Error	7	104.000	14.857
Total	13	6990.857	

**Significant difference at 1% level.

Appendix Table 3. Analysis of variance of seed dormancy for 12 annual ryegrass varieties in 1970.

Source of variation	df	SS	Mean square
Between	11	2628.500	238.954*
Error	12	790.000	65.833
Total	23	3418.500	

*Significant difference at 5% level.

Appendix Table 4. Analysis of variance of seed dormancy for 11 perennial ryegrass varieties in 1970.

Source of variation	df	SS	Mean square
Between	10	14809.454	1480.945**
Error	11	238.000	21.636
Total	21	15047.454	

**Significant difference at 1% level.

Appendix Table 5. Mean squares of seed dormancy and seed weight for Manhattan perennial ryegrass seed maturation study.

Source of variation	df	Mean squares	
		Seed dormancy	Seed weight
Between	13	1637.508*	1441.023**
Error	14	57.179	6.502
Total	27		

*Significant difference at 5% level.
**Significant difference at 1% level.

Appendix Table 6. Mean squares of seed dormancy and seed weight for seed produced on detached culms developed in various nutrient solutions.

Source of variation	df	Mean squares	
		Seed dormancy	Seed weight
Between	5	122.880^{Ns}	7637.953**
Error	24	249.814	207.983
Total	29		

^{Ns}Nonsignificant
**Significant difference at 1% level.

Appendix Table 7. Mean squares of seed dormancy and seed weight for seed produced on detached culms developed in solutions containing sucrose, distilled water and growth regulators.

Source of variation	df	Mean squares	
		Seed dormancy	Seed weight
Between	4	465.600*	7411.060**
Error	20	129.200	623.295
Total	24		

*Significant difference at 1% level.
**Significant difference at 5% level.

Appendix Table 8. Analysis of variance for seed weight of seeds developed on culms with various plant parts removed.

Source of variation	df	SS	Mean square
Between	7	4536.584	648.084**
Error	24	338.555	14.106
Total	31	4875.139	

**Significant difference at 1% level.

Appendix Table 9. Mean squares for seed dormancy and seed weight of seed preconditioned at 15 and 30C for one to seven weeks. Detached seed culms were developed in distilled water and Hoagland's solution.

Source of variation	df	Mean squares	
		Seed dormancy	Seed weight
Temperatures	1	10168.167*	8400.042**
Durations	5	243.767^{Ns}	253.375^{Ns}
Solutions	1	160.167^{Ns}	1520.042**
T x D	5	630.667	362.642
T x S	1	24.000	3.375
D x S	5	24.267	34.042
T x D x S	5	51.100	22.375
Total	23		

^{Ns}Nonsignificant
*Significant difference at 5% level.
**Significant difference at 1% level.

Appendix Table 10. Mean squares for seed dormancy and seed weight of seed preconditioned for one week intervals at 15 and 27C.

Source of variation	df	Mean squares	
		Seed dormancy	Seed weight
Between	10	693.120**	647.216**
Error	44	132.410	182.580
Total	54		

**Significant difference at 1% level.

Appendix Table 11. Maximum, minimum and average daily temperatures for the 30 day period prior to seed harvest in 1969 and 1970.

1969			1970		
Max	Min	Ave	Max	Min	Ave
66	55	60.5	93	54	73.5
72	55	63.5	75	51	63.0
77	59	68.0	43	48	60.5
67	56	61.5	87	50	68.5
67	55	61.0	79	43	61.0
77	57	67.0	74	47	60.5
71	54	62.5	61	51	56.0
76	54	65.0	64	49	56.5
80	51	65.5	64	44	54.0
81	50	65.5	62	46	54.0
93	58	75.5	75	49	62.0
97	54	75.5	70	54	62.0
85	54	69.5	64	53	58.5
75	57	66.0	67	51	59.0
71	52	62.0	69	41	55.0
76	52	64.0	80	46	63.0
68	56	62.0	86	50	68.0
66	53	59.5	89	57	73.0
61	51	56.0	94	60	77.0
64	48	56.0	88	50	69.0
62	50	56.0	87	53	70.0
62	51	56.5	88	52	70.0
58	52	55.0	86	58	72.0
72	49	60.5	90	53	71.5
79	50	64.5	84	51	67.5
79	56	67.5	62	47	54.5
68	55	61.5	66	41	53.5
69	46	57.5	64	48	56.0
73	52	62.5	66	52	59.0
74	49	61.5	75	52	63.5

Appendix Table 12. Chemical composition of modified Hoagland's solution.[1]

Stock solution	Complete	-K	-N	-P
1M $Ca(NO_3)_2$	10	10	--	10
1M KNO_3	10	--	--	10
1M $MgSO_4$	4	4	4	4
1M KH_2PO_4	2	--	2	--
$FeCl_3$*	2	2	2	2
Micronutrients**	2	2	2	2
1M $NaNO_3$	--	10	--	--
1M NaH_2PO_4	--	2	--	--
1M $CaCl_2$	--	--	10	--
1M KCl	--	--	10	--
Distilled water	1970	1972	1972	1974

*Each ml of the $FeCl_3$ stock solution contains 5 mg of Fe.

**The micronutrient stock solution contains 2.86 g of H_3BO_3, 1.81 g of $MnCl_2 \cdot 4H_2O$, 0.11 g of $ZnCl_2$, 0.05 g of $CuCl_2 \cdot 2H_2O$, and 0.025 g of $Na_2MoO_4 \cdot 2H_2O$ per liter.

[1]Table taken from Plants in Action by L. Machlis and J. G. Torrey.

Appendix Table 13. Percentage seed dormancy of annual and perennial ryegrass varieties in 1969.

Varieties	Germination temperature	
	30C (%)	15C (%)
Annuals		
Gulf	97	72
Tetila Vertes	90	48
Florida Rust Resistant	99	57
Magnolia	94	46
Perennials		
Manhattan	100	16
Norlea	90	12
Linn	48	6

Appendix Table 14. Percentage seed dormancy of annual and perennial ryegrass varieties in 1970.

Varieties	Germination temperature	
	30C (%)	20C (%)
Annuals		
Florida Rust Resistant	100	40
Gulf	97	31
Magnolia	97	24
Tetila	97	42
Tetila Vertas	91	24
Tetrone	91	27
Tetila Barmultra	98	13
Tetila Sceempter	92	7
St. Tottori	97	10
Tetila Tetrone	93	14
Wasehikari	92	7
Oobahikari	95	5
Perrenials		
NK-100	93	80
Manhattan	98	12
Atempo	97	3
Petra	93	12
Pelo	98	9
Brabantia Gazonen-sportveldtype	92	5
Norlea	96	2
Taptoe	97	3
R. V. P. (pasture type)	93	0
Verna Pajbjerg	93	2
Linn	72	0

Appendix Table 15. Percentage seed dormancy of Manhattan perennial ryegrass at various stages of maturity and ripening.

Days after anthesis	Germination temperature 25C (%)
0	0
3	20
6	48
9	46
12	72
15	50
18	28
21	12
24	8
27	8
30	4
33	-
36	2
39	-
42	0
45	0

Appendix Table 16. Percentage seed dormancy of Gulf annual ryegrass at various stages of maturity and ripening.

Days after anthesis	Germination temperature 30C (%)
4	0
8	0
12	90
14	83
16	80
18	90
20	90
22	90
24	100
26	90
28	100
30	90
32	93
34	97
36	100

Appendix Table 17. Percentage dormancy of seed developed on detached culms in distilled water, Hoagland's solution, Hoagland's minus nitrogen, Hoagland's minus phosphorus and Hoagland's minus potassium compared to seed from intact culms.

Treatments	Germination temperatures			
	30C (%)	25C (%)	15C (%)	15-25C (%)
Hoagland's solution	96	96	24	32
Hoagland's - N	96	96	24	32
Hoagland's - P	96	96	12	32
Hoagland's - K	96	96	12	20
Distilled water	96	96	20	32
Intact culms	96	96	16	28

Appendix Table 18. Percentage dormancy of seed developed on detached culms in benzyladenine, gibberellic acid, sucrose and distilled water compared to seed developed on intact culms.

Treatments	Germination temperatures	
	30C (%)	25C (%)
Benzyladenine	74	74
Gibberellic acid	92	86
Sucrose	94	93
Distilled water	93	93
Intact culms	90	90

Appendix Table 19. Percentage dormancy of Gulf seed preconditioned at 15 and 30C for one to seven weeks.

Weeks of preconditioning	Germination temperature		
	30C (%)	20C (%)	15-25C (%)
	Preconditioning at 30C		
1	88	12	1
2	74	5	0
3	71	9	2
4	71	8	1
5	70	7	1
7	64	3	2
	Preconditioning at 15C		
1	94	14	0
2	94	17	4
3	94	15	0
4	94	32	4
5	93	38	3
7	96	74	20

Appendix Table 20. Percentage dormancy of seeds preconditioned at one week intervals after anthesis at 15 and 27C.

Preconditioning regime			Germination temperature	
Initiation	Duration (wks)	Temp. (C)	30C (%)	25C (%)
Continuous	4	21	97	92
At anthesis	1	15	95	89
Anthesis + 1 wk	1	15	96	92
Anthesis + 2 wk	1	15	96	91
Anthesis + 3 wk	1	15	91	88
Continuous	4	15	96	96
At anthesis	1	27	90	81
Anthesis + 1 wk	1	27	93	84
Anthesis + 2 wk	1	27	96	90
Anthesis + 3 wk	1	27	95	86
Continuous	4	27	95	84

Appendix Table 21. Percentage germination at 15 or 30C of three perennial ryegrass varieties after various lengths of storage at temperatures of 30, 20, 5 and -18C.

Storage temp.	30C					20C					5C					-18C				
	Weeks of storage					Weeks of storage					Weeks of storage					Weeks of storage				
	0	6	13	27	44	0	6	13	27	44	0	6	13	27	44	0	6	13	27	44
									Germination temperature 30C											
Manhattan	0	4	14	20	74	0	0	2	2	10	0	0	0	0	0	0	0	0	0	0
Norlea	6	60	76	94	94	6	20	20	62	84	6	4	0	0	10	6	0	0	0	2
Linn	44	84	76	78	24	44	76	76	80	84	44	62	62	74	74	44	28	14	16	36
									Germination temperature 15C											
Manhattan	84	90	92	94	98	84	74	96	94	94	84	92	86	84	84	84	84	90	86	78
Norlea	84	90	96	98	94	84	88	94	96	96	84	76	76	88	86	84	86	74	78	74
Linn	86	92	86	80	36	86	88	92	84	92	86	92	86	88	84	86	90	86	88	86

Appendix Table 22. Percentage germination at 15 and 30C for four annual ryegrass varieties after various lengths of storage at temperatures of 30, 20, 5 and -18C.

Storage temp.	30C					20C					5C					-18C				
	Weeks of storage					Weeks of storage					Weeks of storage					Weeks of storage				
	0	7	14	28	45	0	7	14	28	45	0	7	14	28	45	0	7	14	28	45
										Germination temperature 30C									
Gulf	0	36	58	90	86	0	14	20	62	90	0	0	0	0	42	0	2	0	0	2
Magnolia	2	74	80	92	96	2	24	50	74	96	2	0	0	14	56	2	0	0	0	4
Florida Rust Resistant	0	40	66	90	98	0	14	18	36	96	0	0	0	2	20	0	0	0	0	6
Tetila Vertas	54	72	84	90	90	4	12	22	78	80	4	6	6	6	5	4	4	2	0	12
										Germination temperature 15C									
Gulf	26	92	88	98	92	26	88	90	98	96	26	62	84	92	82	26	56	60	72	42
Magnolia	50	96	92	96	98	50	86	92	98	96	50	72	84	82	88	50	74	74	84	58
Florida Rust Resistant	42	96	96	98	94	42	92	88	100	92	42	72	64	86	88	42	76	66	64	64
Tetila Vertas	46	94	96	94	90	46	88	92	94	94	46	88	84	98	88	46	84	74	92	82