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SEED DORMANCY OF SIDEOATS GRAMAGRASS, *BOUTELOUA CURTIPENDULA* (MICHX.) TORR.

by

Roger Lee Major

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF AGRONOMY AND PLANT GENETICS

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN AGRONOMY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Roger Lee Major

entitled SEED DORMANCY OF SIDEOATS GRAMAGRASS, BOUTELOUA CURTIPENDULA (MICHX.) TORR.

be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

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ABSTRACT

The objectives of this study were to determine the pattern, duration, and causes of seed dormancy in sideoats gramagrass. Investigations were pursued to identify and characterize seed dormancy and to relate seed dormancy characteristics to stand establishment under natural conditions.

Germination experiments were conducted in a laboratory germinator on five relatively dormant and five relatively nondormant seed sources. The germination procedure for all experiments was standard except the factor under evaluation was varied.

Post-harvest dormancy was present in all sources, but disappeared after four to six months dry storage following harvest. Long-term dormancy persisted for five years in the relatively dormant seed, with no decrease in viability. Long-term dormancy was almost completely removed by removing the lemmas, paleas, and glumes from the caryopses. Post-harvest dormancy was evidently due to factors within the caryopses, while long-term dormancy was conditioned primarily by the spikelet appendages enclosing the caryopsis.

Germination in soil, alternating moisture conditions, enriched-oxygen atmosphere, and sodium hypochlorite

treatment were effective in breaking dormancy. Prechilling, light treatments, leaching with water, sodium carbonate, and hydrogen peroxide were less effective in relieving dormancy. Characteristics associated with seed dormancy included 30% less caryopsis weight, a low molecular-weight protein, apomixis, and coumarin-like compounds in the spikelet appendages. The mechanism of seed dormancy appeared to involve interactions among low seed weight, impermeable seedcoats, and the presence of inhibitory materials.

The emphasis of these investigations was directed toward the potential advantages of seed dormancy in rangeland and stand establishment. The determination of the relationship between seed dormancy and field establishment would allow the development of selection criteria associated with desirable seed dormancy characteristics.

INTRODUCTION

Large portions of the desert grasslands of the southwestern United States have been invaded with undesirable woody and nonwoody species. Overgrazing by livestock and cessation of fires appear to be the principal factors responsible for degeneration in species composition. Sideoats gramagrass, Bouteloua curtipendula (Michx.) Torr., is a desirable rangeland grass from the standpoint of forage, seed production, and drouth tolerance as an established plant. However, attempts at establishing sideoats gramagrass on depleted rangelands or abandoned croplands in the Southwest have been commonly characterized by erratic and disappointing results.

There is considerable variation in degree of dormancy among seed sources of sideoats gramagrass collected at various locations. Some degree of seed dormancy may be of advantage to a species where establishment must occur under conditions of limited and sporadic rainfall. Factors responsible for dormancy may interact with environmental variables and allow germination to occur in a series of flushes. Successive surges of germination would expose a species to a broader array of environments in time and space and enhance the probability of establishment. Considering the potential advantages of seed dormancy, it

would be desirable to investigate the characteristics of seed dormancy and germination of sideoats gramagrass seed. An understanding of seed dormancy may give the plant breeder practical tools to select germplasm with desirable stand establishment qualities.

This research was partially supported by grant funds from Western Regional Marketing Research Project (WM-35). The principal objectives of the Regional Project are assessment of seed quality factors and evaluation of growth performance potential of seed. Methods are needed to evaluate the field establishment potential of sideoats gramagrass in relation to seed quality factors, such as dormancy.

The objectives of this study were:

1. To evaluate the duration and pattern of seed dormancy in available genetic sources.
2. To locate and identify dormancy conditioning factors.
3. To associate dormancy-related characteristics with performance under field conditions.
4. To determine mode of reproduction of sources chosen for detailed dormancy investigations.

REVIEW OF LITERATURE

Origin and Use

Sideoats gramagrass, B. curtipendula (Michx.) Torr., is one of our most important and widely adapted range grasses and is a key species of most Arizona grasslands (Gould, 1959; Humphrey, Brown, and Everson, 1956). It is a medium size, perennial bunchgrass that occurs from approximately 3000 to 7000 feet on rocky open slopes, woodlands, forest openings over most of the state, and in various forms from southern Canada to South America (Freter and Brown, 1955; Humphrey et al., 1956). The desirable forage and seed producing characteristics and drouth tolerance as a mature plant make sideoats gramagrass a desirable species to establish on depleted rangelands and abandoned croplands. However, few successful stands have been established by artificial seeding in southern Arizona (Anderson et al., 1953; Jordan, 1971). Greater success in stand establishment has apparently been achieved in the central and southern Great Plains (Dudley and Holt, 1963; Launchbaugh and Owensby, 1970; and Newell et al., 1962). The role and management of sideoats gramagrass as a component of established rangelands has been quite well documented (Schmutz, 1971; Sims, Ayuko, and Hyder, 1971; Waldrip, 1965).

Reproduction and Breeding

Extensive cytological and taxonomic studies have been made on sideoats gramagrass (Freter and Brown, 1955; Fults, 1942; Gould and Kapadia, 1964; Harlan, 1949). Gould (1959) observed a remarkable variation in morphological characteristics and found that cytological variation was equally striking. Kapadia and Gould (1964a) separated the species B. curtipendula into three taxonomic varieties based on origin and chromosome numbers. Diploid and tetraploid plants of Mexico are referred to as var. tenuis with 2n = 20, and 40 to 42. Tetraploid and rhizomatous aneuploid plants of the United States and Canada comprise the var. curtipendula with 2n = 40, and 41 to 64. Caespitose (non-rhizomatous) plants with high chromosome numbers (2n = 58 to 103) are referred to as var. caespitosa, and have probably arisen through hybridization of many different combinations of diploids and tetraploids. It is believed that plants with chromosome numbers greater than 2n = 52 are largely obligate apomicts (Gould, 1959).

Some effort has been made toward breeding to improve stand establishment and plant characteristics (Harlan, 1950; Newell et al., 1962; Voigt and Brown, 1969). Breeding of sideoats gramagrass is made more difficult by the fact that a great many of the plant types found in the Southwest are apomictic. Olmsted (1962) found that sideoats gramagrass exhibited a wide range of photoperiodic responses and

cautioned the breeder that a given strain may be so differentiated in its photoperiodic adjustments and requirements that its growth habit in one environment is not predictable in another environment.

General Considerations of Seed Dormancy

Seed dormancy will be discussed here as the reversible failure of seed to germinate even when normally optimum conditions of moisture, temperature, and oxygen are present. Dormancy and germination are opposite responses which are separated by one or more of various external and internal factors. A considerable volume of literature has accumulated concerning seed dormancy. Excellent reviews are available on numerous aspects, including the ecological value of seed dormancy (Koller, 1969; Wright, 1971), factors responsible for dormancy imposition (Barton, 1965a, 1965b; Lang, 1965; Wareing, 1965), factors associated with the breaking of dormancy (Black, 1969; Evenari, 1965a; Lang, 1965; Marcus, 1969; Stokes, 1965), and models to explain dormancy phenomena (Amen, 1968; Black, 1970; Evenari, 1965a; Kelly, 1969; Khan, 1971; Roberts, 1969; Vegis, 1964; Wareing and Saunders, 1971).

Ecological Significance of Seed Dormancy

The environment under desert conditions presents a large "uncertainty factor." The more predominant the

uncertainty the more important it becomes for germination to be controlled by precise perception of the environment. Koller (1969) stated that it is not surprising that germination regulating mechanisms exist in most species to insure that the whole reproductive capacity is not exhausted in one habitat, except where and when the probability of survival is maximal. He discussed a number of species which react with various conditions of temperature, light, and water in such a way that they respond only to environmental situations in which they are most likely to succeed. In addition, some species are adapted for metering out their reproductive units systematically over time in response to specific environmental conditions.

Steiner (1968) differentiated between germination polymorphism and germination polyphenism, where the former is used to classify germination flushes in response to genetically controlled differences in seed morphology. In contrast, germination polyphenism refers to differences in germination over time which can be attributed to phenotypic differentiation. In either case, the adaptive value of successive surges of germination lies in the opportunity of a species to exploit a greater array of environments in both time and space. Flushes of germination occurring at different times greatly enhance the chance of ultimate survival and reproduction, and minimize the possibility of stand failure due to a single large flush of germination

followed by a catastrophic natural event, such as severe drouth during the seedling stage.

Wright (1971) reviewed the role of seed dormancy in relation to stand establishment under semiarid and arid environments. A number of cases have been reported of a positive association between degree of seed dormancy and plant establishment and performance under limited moisture conditions (Amen, 1966; Coukos, 1944; Logan, Hoveland, and Donnelly, 1969; Marshall and Jain, 1970; Sumner et al., 1959; Went, 1961; Winkworth, 1971). Dormancy may also be advantageous where other environmental extremes, such as temperature, are encountered (Bell and Amen, 1970; Burrows, 1970; Koller, 1969; Steiner, 1968). Many weed populations are apparently able to maintain themselves through control of rate of germination of buried seed (Schafer and Chilcote, 1970; Taylorson, 1970; Young et al., 1970). Koller (1962) pointed out that cultivated species, in which dormancy has been selected against, require constant reseeding, while most wild species, in which regulated germination has been naturally selected for, are hard to eradicate by any single treatment.

Factors Imposing Dormancy

Various causes of seed dormancy have been recognized (Amen, 1968), including rudimentary embryos, physiologically immature embryos (inactive enzyme systems),

mechanically resistant seed coats, impermeable seed coats, and presence of germination inhibitors. Sumner and Cobb (1962) obtained evidence that dormancy in fresh seed of sideoats gramagrass was controlled by the embryo, but after 43 to 74 days the presence of germination inhibitors in the appendages enclosing the caryopsis was largely responsible for the maintenance of prolonged dormancy. No attempt was made to identify the inhibitory compounds.

Seed dormancy appears to be induced during the ontogeny of the seed. Genes and the environment interact during seed maturation to lead to the onset of dormancy. This interaction could be considered a potential genetic response that is activated and regulated by physiological influences. Black (1970) postulated that seed may become dormant while still on the mother plant because of inhibitors accumulated during seed maturation. The question then arises as to whether the inhibitors are synthesized in the seed themselves or are derived from the mother plant. Inhibitors synthesized in the leaves are responsible for the onset of bud dormancy (Wareing, 1969) and it may be that seed dormancy is also induced this way. One significant finding is that dormancy in Avena fatua L. seed can be prevented by treating mother plants with gibberellic acid (Black, 1970). Since environmental factors such as day-length and temperature do influence the development of seed dormancy, it is possible that environmental control of

dormancy is partially exerted through the gibberellic acid content of the mother plant. It has been shown repeatedly that gibberellins and other growth promoting substances decrease during seed maturation (Hashimoto and Rappaport, 1966; Pillay, 1966; Black and Naylor, 1959). In contrast, inhibitory materials build up during the onset of dormancy (Hashimoto and Rappaport, 1966; Jansson, 1969; Roberts, 1964).

Dormancy is often considered an hereditary characteristic with the length and degree of the dormant condition genetically determined. Vegis (1964) cautioned that the properties of dormancy are not genetically transmitted, but only the way in which the species may respond to environmental conditions. Evenari (1965b) raised the question of whether the maturation environment alone determines dormancy or if the environment of the mother plant even before anthesis influences the germinability of the seed to be formed. Another aspect is presented by workers who have observed endogenously-controlled cyclic variations in seed germinability over time (Kummerow, 1965; Sweeney, 1963; Maguire, 1969). A possible explanation for these cycles is that they are imparted to the seed from the mother plant and represent a continuation of the rhythmic growth fluctuations which were inherent in the life cycle of the mother plant. The condition of the mother plant during reproduction is one of progressive growth reduction (Amen, 1968),

and it appears logical that whatever is responsible for loss in plant growth rate may also be imparted to the seed. In addition to build-up of inhibitory materials, Evenari, Koller, and Gutterman (1966) found that in Ononis sicula L. the environment to which the mother plant is exposed influences the germinability of its seed progeny by affecting seed coat permeability to water.

Regardless of the particular manner in which they may be laid down, dormancy-related growth inhibitors have been found in the seed of many species (Black, 1959; Black and Wareing, 1959; Bradbeer, 1968; Edwards, 1968; Fendall and Canode, 1971; Stoltz, 1968; Takahashi, 1968; Westra and Loomis, 1966). The main natural inhibitors that are known are phenolic compounds and abscisic acid (Hathway, 1969; Kefeli and Kadyrov, 1971; Pridham, 1965; Wareing, 1965). Abscisic acid may be classified as a plant growth regulator and is effective at concentrations 100 to 1000 times less than phenolics. Sumner and Lyon (1967) found that absciscic acid was inhibitory to germination in sideoats gramagrass but it did not destroy seed viability irreversibly. Wareing (1965) noted that chemical and physiological studies of seed dormancy were associated in very few instances. Thus, in many cases where the chemical nature of inhibitors is known, evidence is lacking whether they function in seed dormancy regulation. Conversely, where physiological

evidence suggests a role in seed dormancy, the chemical nature of the inhibitors has often not been determined.

The mechanical and permeability blocks involved with the presence of the seed coat have been studied quite extensively (Esahi and Leopold, 1968; Fendall and Carter, 1965; Frank and Larson, 1970). The physical influence of the seed coat is intimately associated with the presence of inhibitory substances in the regulation of dormancy. A classical example of this interaction is shown in Xanthium pensylvanicum L. Esahi and Leopold (1968) found that dormant seed of Xanthium lacked adequate mechanical force in the embryo to rupture the seed coat. Crocker and Barton (1953) considered dormancy in Xanthium to be due to impermeability of the testa to oxygen. Inhibitory materials have also been found in Xanthium seed (Wareing and Foda, 1957). It now appears that the seed coat acts mainly by preventing the leaching of germination inhibitors from the embryo, and that increased oxygen tensions accelerate enzymic oxidation of these inhibitors to inactive forms (Roberts, 1969). Seed dormancy in Avena fatua functions in a similar manner (Black, 1959; Andrews and Simpson, 1969).

Breaking of Seed Dormancy

Dormant seed can be induced to germinate in a variety of ways, depending on the factors involved in the

imposition of dormancy. Scarification or removal of the seed coat, moist low-temperature treatment (chilling or stratification), alternating temperatures, maintenance in dry storage (after-ripening), light, leaching to remove inhibitors, high oxygen tension, application of exogenous growth promoters, and application of certain respiratory inhibitors are all reported to be effective in breaking dormancy under certain conditions (Amen, 1968; Roberts, 1969). A few pertinent examples are discussed.

In species where dormancy is imposed by the seed coat, relief is obtained by removal of the structures surrounding the embryo. A number of grass species are characterized by seed-coat imposed dormancy (Baskin, Schank, and West, 1969; Canode, Horning, and Maguire, 1963; Fendall and Carter, 1965; Frank and Larson, 1970; Geng and Barnett, 1969; Sumner and Cobb, 1962). The role of the seed coat may be complex, as indicated previously in the cases of Xanthium and Avena. Leaching of inhibitors, increased oxygen tension, and seed coat scarification may have effects similar to seed coat removal.

Low temperature treatment presents an interesting example in overcoming dormancy. The beneficial effect of moist chilling is probably similar to that which regulates the time which germination may occur in the springtime (Black, 1970). In most species that have a requirement for chilling, the embryo or tissues immediately surrounding

it (e.g., endosperm) are responsible for dormancy, rather than the seed-coat. The physiological factors involved in low temperature breaking of dormancy are not well understood (Amen, 1968).

Many dormant seed will germinate when exposed to light. Light may control germination through the photoreversible pigment phytochrome (Black, 1969). A classical example of light-controlled germination is that of 'Grand Rapids' lettuce (Evenari, 1965a). The red light spectrum changes with depth in the canopy, and the phytochrome system may function in regulation of the timing of germination, in relation to the life cycle of the plant. The interactions of light and other dormancy-conditioning factors, especially light and temperature, are likely to exert precise control over germination and insure the greatest chances for survival (Koller, 1969).

A number of chemical compounds stimulate germination when applied exogenously, including gibberellins (Naylor, 1965; Simpson, 1965; Svedarsky and Kucera, 1970), cytokinins (Ketring and Morgan, 1971; Khan, 1971; Khan and Waters, 1969), ethylene (Ketring and Morgan, 1969, 1970), nitrates (Ahring, Dunn, and Harlan, 1963; Amen, Carter, and Kelly, 1970; Maguire and Steen, 1971), thiorea (Lipp and Ballard, 1970), and, in certain cases, respiratory inhibitors (Black, 1970; Major and Roberts, 1968a; Roberts, 1969). Gibberellins have been the most widely studied

compounds and most species respond to them. They have been strongly implicated as an integral part of the natural promoter-inhibitor complexes controlling growth (Amen, 1968; Black, 1970). Experiments using exogenous growth regulators have been useful since the endogenous levels of certain growth hormones are often too low to detect and follow.

The biochemical changes that take place during breaking of dormancy have been followed quite extensively. It is believed that, regardless of the treatment used to break dormancy, the end result is achievement of a balance of promoters and inhibitors that is favorable to growth (Amen, 1968; Black, 1970). An increase in gibberellins and other growth promoting substances in association with relief of dormancy has been noted (Frankland and Wareing, 1966; Simpson, 1965; Villiers and Wareing, 1965). Likewise, inhibitory materials may disappear during breaking of dormancy (Lipe and Crane, 1966; Sondheimer, Tzou, and Galson, 1968; Villiers and Wareing, 1965). An increased capacity for nucleic acid synthesis has been observed in relation to the breaking of dormancy (Jarvis, Frankland, and Cherry, 1968a, 1968b; Khan, 1966; Tuan and Bonner, 1964). Nucleic acid synthesis will be discussed further in the next section.

Models to Explain Dormancy Phenomena

Amen (1968) has developed a model which attempts to integrate many apparently diverse dormancy phenomena under one common system of control. He envisioned that all forms of seed dormancy are controlled by endogenous promoter-inhibitor complexes, and that the differences lie in how these complexes may be triggered to allow or prevent growth. The control mechanism was divided into four stages: inductive, maintenance, trigger, and germination.

The induction of seed dormancy is preset during the ontogeny of the seed and, as mentioned in an earlier section, may be accompanied by a buildup of inhibitors, a decrease in promoters, or both. This would throw the promoter-inhibitor complex in favor of dormancy. Esahi and Leopold (1969) found a requirement in Begonia tubers for a nucleic acid and protein synthesis for induction of dormancy, which implies that entry into the dormant state was a consequence of synthetic events programmed in the genome.

The maintenance phase of seed dormancy is characterized by reduced metabolic activity due to specific blocks. Dormancy is apparently maintained because inhibitors interfere with the synthesis or action of growth-promoting hormones. Villiers (1968) concluded that abscisic acid was antagonistic to gibberellic acid and that it maintained dormancy in Fraxinus seed by inhibiting the production of specific types of messenger RNA. Amen (1968)

expressed doubt that the endogenous production of growth inhibitors is closely linked with the gene-specified hormone-enzyme systems associated with growth promotion. He concluded, rather, that growth inhibitors are coincidental byproducts of unrelated metabolic activities, but which have, when interacting with specific hormone-enzyme systems, conferred in the form of seed dormancy some adaptive advantage to certain species.

Germination of a dormant seed can only take place if the promoter-inhibitor balance is shifted in favor of promoters. Factors that can cause this shift are called triggering agents, and include the dormancy breaking treatments previously mentioned, such as light, chilling, and seed coat removal (Amen, 1968).

After exposure to the triggering agent, the continuing presence of a germination agent is required for germination to occur. The germination agents presumably are hormones, of which gibberellins have been most widely implicated. Available evidence indicates that gibberellins are closely associated with food reserve degradation and mobilization. It appears that gibberellins are able both to activate preformed latent hydrolytic enzymes and to initiate de novo enzyme synthesis via RNA control (Akazawa, 1965; Chrispeels and Varner, 1967b). As indicated previously, an increase in nucleic acid synthesizing capacity has been observed in association with breaking of dormancy.

The implication is that growth hormones derepress genetic sites and allow synthesis of enzymes necessary to initiate germination. Tuan and Bonner (1964) observed that the genetic material of buds of dormant potato tubers was largely in a repressed state and that the breaking of dormancy was accompanied by derepression of the genetic material. A similar situation may exist in seed dormancy, although some work indicates that chromatin in dormant seed is equal or better than nondormant in its ability to synthesize RNA (Roberts, 1969).

Respiratory inhibitors have been effective in relieving dormancy in some cases. Roberts (1969) has advanced an hypothesis which explains why respiratory inhibitors may break dormancy and which also assigns a different role to other dormancy-breaking factors, such as gibberellins and oxygen. Roberts postulated that, as a prerequisite to germination, seed must partition a considerable proportion of their initial respiratory metabolism through the pentose-phosphate pathway, and that in dormant seed this ability is restricted. Thus, any factor tending to divert respiration toward the pentose-phosphate pathway would be a dormancy breaking agent. Conventional respiration is a strong competitor for oxygen and probably interferes with oxidation reactions necessary to make the pentose-phosphate pathway operative in dormant seed. Thus, respiratory inhibitors and increased oxygen would have

similar effects by increasing the supply of oxygen available to the pentose-phosphate system. Gibberellic acid also promotes the breakdown of sugar through the pentose-phosphate pathway. The requirement for pentose-phosphate metabolism during early germination is not fully understood.

Amen (1968) expressed confidence that resolution of the problems of seed dormancy will play a significant role in formulating a general theory of growth regulation, and that investigators of seed dormancy, spore and bud dormancy, insect diapause, mammalian hibernation, and even of cysts and tumors share a common problem.

MATERIALS AND METHODS

Seed Sources

Sideoats gramagrass seed was obtained from a nursery established by Dr. L. N. Wright at the Tucson Plant Materials Center, Soil Conservation Service, Tucson, Arizona, in cooperation with the Arizona Agricultural Experiment Station, The University of Arizona. From 159 sources in the nursery, which were collected at sites ranging from the northern Great Plains to Argentina, five relatively dormant and five relatively nondormant sources were chosen on the basis of laboratory germination of one-year-old seed and increased. Origins of the ten sources are given in Table 1.

Nursery seed was obtained in 1966, 1967, and 1968. Increase seed was harvested in October of 1969, 1970, and 1971. All harvesting was accomplished by hand stripping, since mechanical harvest may cause scarification and thus influence seed dormancy. The seed unit of sideoats gramagrass is actually a spike containing one to many spikelets with the associated glumes, lemmas, paleas, and caryopses. Seed were fumigated with methyl bromide after harvest and stored in cloth bags at 5 C and 10 to 20% relative humidity.

Table 1. Source numbers and origins of Bouteloua curtipendula seed used in these investigations.

ARS[a] source no.	TPMC[b] accession no.	P. I.[c] no.	Origin and remarks
		Dormant	
84	--	216266	Mexico
72	--	216224	Mexico
99	--	216818	Texas
27	16495	--	Texas--Texas P.M.C., PM-T-56, Orange Grove
88	--	216274	Mexico
		Nondormant	
63	3603	--	New Mexico--'Vaughn,' Tucson P.M.C. lot 3196
104	--	216826	Texas
10	16481	--	Oklahoma--crossing block W1, Woodward, 1958 seed
141	--	279525	Argentina
6	16461	--	Nebraska--'Trailway,' Woodward, Okla. seed

[a]Agricultural Research Service, Tucson, Arizona.

[b]Tucson Plant Materials Center, Tucson, Arizona.

[c]Plant Introduction, Washington, D. C.

Germination Procedure

Seed dormancy was evaluated in a Cleland Model 1000 FAAT germinator. Most germination experiments were conducted at alternating 20 and 30 C temperatures with 16 hours of darkness at 20 C and 8 hours of light at 30 C. Relative humidity within the germination chamber was maintained at 75 to 85%. Disposable plastic petri dishes (9 cm) were used as germination containers. Substrate was two circles of Eaton and Dikeman No. 617 filter paper moistened with 10 ml distilled water. Sample size was 0.4 gm spike material (intact seed units) per petri dish. Number of caryopses per gram of spike material was determined by hand threshing four samples to calculate germination percentage. Germination counts were taken after 14 days exposure on the basis of the number of green shoots observed. The experimental design was randomized complete blocks with one or more tray blocks arranged from top to bottom in the germinator. Four blocks per treatment were used. This germination procedure will be referred to as the standard procedure. In various dormancy conditioning experiments designed to test the influence of factors such as light, substrate, moistening agent, and physical and chemical treatments on germination, the standard procedure was maintained with variable treatments of the factors under study.

All sources were evaluated for germination in soil. Seed were placed on moist soil (80% field capacity) in 90 by 50 mm crystallizing dishes, covered with 3/16 inch of moist soil, and placed in the germinator. The effect of alternating soil moisture conditions on germination was tested by exposing the seed to moist soil and alternately desiccating the soil for 48 hours at 37 C in a forced-air oven.

Dormancy Conditioning Procedures

Dehulling

Seed units were dehulled to caryopses to evaluate germination without the presence of the associated spikelet appendages. Caryopses were removed from the seed units with forceps to avoid scarification. Four replications of 25 caryopses were placed on filter paper in petri dishes with 4 ml of distilled water for germination. The loose spikelet appendages were added back to part of the samples to evaluate the effect on germination of caryopses in the presence of the spikelet parts. Another portion of the samples was allowed to imbibe water for 48 hours before the caryopses were hand removed by forceps.

Spike Clipping

The basal end of the spikes was clipped off with a razor blade to expose the embryo end of the caryopses prior to germination.

Prechilling

Seed samples of 0.4 gm were prepared for germination in the standard way. Seed were then prechilled for 14 days at 5 C. After prechilling, lids were removed from the petri dishes and samples were allowed to air-dry at room temperature for 72 hours. The filter paper substrate was then remoistened and samples were germinated by the standard procedure.

Nutrient Solution

A complete nutrient solution (Hoagland and Arnon, 1950) was substituted for distilled water as the substrate moistening agent.

Wetting and Drying

Seed samples were prepared for germination on filter paper. Petri dishes were put on a laboratory bench with lids off and allowed to dry. The substrate was remoistened each time it was observed to be dry. New shoots were counted and removed each day. After 7 days the substrate was remoistened, lids were replaced, and the samples were placed in the germinator the remaining 7 days.

Leaching

Various leaching treatments were imposed on intact seed units. Seed were placed in small cloth bags for treatment. One set of seed samples was exposed only to 24

hours of running distilled water at 25 C. Other treatments were accomplished as follows:

1. Five minutes in 0.2% alconox.
2. Five minutes in distilled water.
3. Thirty minutes in: (a) 5% sodium carbonate (w/v), (b) 5.25% sodium hypochlorite (w/v), (c) 5% hydrogen peroxide (v/v), or (d) 2% activated charcoal (w/v).
4. Six hours running distilled water rinse at 25 C.
5. Forty-eight hours of air-drying prior to germination.

Light Experiments

Seed were allowed to imbibe the first 48 hours of the germination period in darkness for one evaluation. Another treatment was a red cellophane filter over the germinator light source during the first seven days of germination to evaluate the effect of red light on germination.

Enriched-Oxygen Atmosphere

A thirty-two liter plexiglass chamber, illustrated in Fig. 1, was built to fit into the germinator compartment. Bottled oxygen was bubbled into the chamber through 10 cm of water at a rate of 500 ml per min and exhausted through a 1/4 inch port. Gas distribution was achieved uniformly by

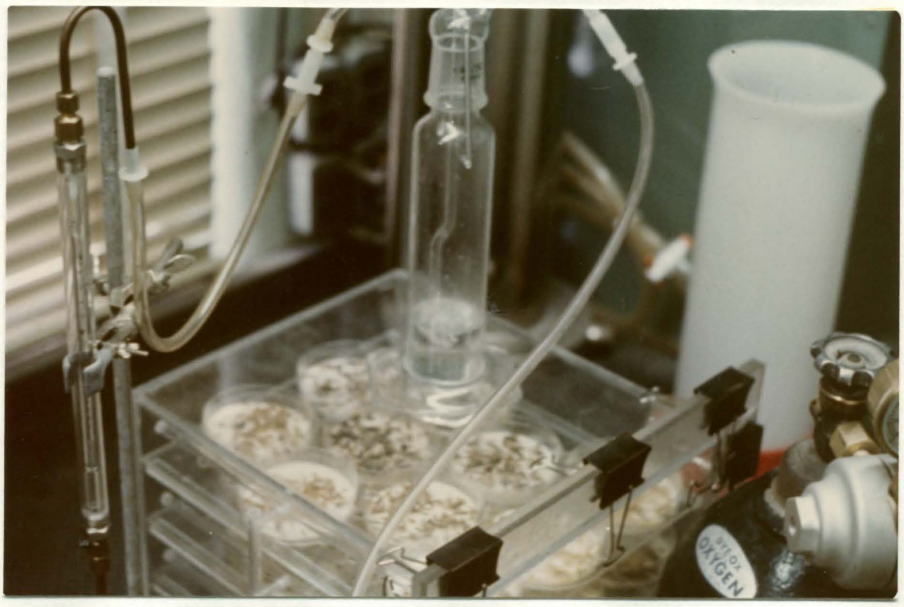

Fig. 1. Plexiglass chamber used to germinate seed in enriched oxygen atmosphere.

a manifold having input at four levels and depths of the chamber. The chamber accommodated forty, 9-cm petri dishes.

Electrophoretic Studies

Gel electrophoresis was used to determine patterns of protein extracted from caryopses, hulls, and 48-hour old coleoptiles of dormant and nondormant sources. Five mg of caryopses or hulls, or eight coleoptiles were ground in a reducing buffer (Mutwakil, 1971) and proteins were separated by electrophoresis according to McDaniel (1970).

Chemical Inhibitors in Spikelet Appendages

Extraction Procedure

Seed units were threshed with a hammer-mill until most of the caryopses were free. Caryopses were removed from the spikelet appendages by a combination of screening and air cleaning in a Dakota blower. Spikelet material was ground to pass through a 2 mm screen on a Wiley mill. Caryopses were saved for subsequent bioassays. Sources 84 and 27 (dormant) and 63 and 141 (nondormant) were used in the extraction experiments.

Ten grams of ground spikelet material were submitted to two extractions in 100 ml of 1.0% sodium hypochlorite (w/v) for two hours at 25 C with periodic shaking. The samples were filtered with suction on Whatman No. 2 filter paper after each extraction and the filtrates were combined. The filtrate was adjusted to pH 3.0 with 6 N

HCl, refrigerated overnight, and refiltered on Whatman No. 5 paper to remove any precipitate. The filtrate was extracted four times with diethyl ether (15% of filtrate volume) in a separatory funnel and the aqueous phase was discarded. Some emulsion formed at the ether-aqueous interface, but it was readily broken up with a few drops of methanol. The ether fractions were combined, reduced to 5 ml on a warm hot plate, and stored in vials at -10 C.

Ethanol (80%) was also used to extract ground spikelet material. Ten grams of material were extracted twice for 30 minutes with stirring in 100 ml of boiling 80% ethanol and filtered. The filtrates were combined, adjusted to pH 3.0, refrigerated overnight, refiltered, and evaporated to a moist residue. The residue was taken up in 200 ml water at 70 C and extracted 4 times with ether. The ether phases were combined, evaporated to a residue, and dissolved in 5 ml of 100% ethanol for chromatography.

Purification of Extracts

The ether concentrates were purified using the techniques of paper chromatography. Whatman No. 1 chromatography paper was cut into 9 by 22 inch strips to fit a "chromatocab" chromatography chamber. All paper was washed with isopropanol, ammonia, and water (8:1:1) for 48 hours and with distilled water for 24 hours to remove

contaminants that might interfere with chromatography or bioassay.

Initial purification was accomplished as follows.

1. Two hundred microliters of the ether concentrates were spotted on washed Whatman No. 1 chromatography paper. Six spots 1.5 inches apart were accommodated per strip.
2. Strips were developed in isopropanol, ammonia, and water (8:1:1, v/v/v) by descending chromatography. One hundred ml of the solvent was placed in the bottom of the chromatography chamber, and a blank strip was placed in solvent at least 4 hours before development of the chromatogram, so that the chamber could be thoroughly saturated with the vapor of the developing solvent.
3. Specific regions of these chromatograms were selected on the basis of a bioassay using root elongation of germinating sideoats gramagrass caryopses. These regions were eluted with 20 ml of acetone, chloroform, and water (67:30:3, v/v/v) and the eluates were reduced to 2 ml.

These eluates were further purified according to the following procedure.

1. Four hundred microliter samples were spotted on washed Whatman No. 1 chromatography paper.

2. Strips were developed in ethanol and water (80:20, v/v) by descending chromatography and bioassayed.

Specific inhibitory regions from these chromatograms were eluted and chromatographed in silica gel on thin layer plates using benzene and acetone (90:10, v/v) or benzene, acetic acid, and water (100:70:30, v/v/v) as developing solvents.

The ethanol concentrates from the ethanol extraction were spotted on Whatman No. 1 chromatography paper and chromatographed in isopropanol, ammonia, and water (8:1:1, v/v/v). These chromatograms were used for qualitative detection only.

Bioassay Procedure

The chromatograms from the purification procedures were cut into 1.5 by 1.5 inch squares and bioassayed in 60 by 15 mm plastic disposable petri dishes with 0.75 ml distilled water as the moistening agent. The bioassay consisted of measuring root elongation of germinating sideoats gramagrass caryopses of the same seed sources from which the extracts were made according to the following procedure.

1. Caryopses were germinated in rows on 8 by 11 inch filter paper between two panes of plate glass at 25 C.

2. After 30 hours five seedlings having roots 10 mm (± 1 mm) long were removed and placed in each test solution. Seedlings were oriented in the direction the solvent originally moved across the chromatogram.
3. Root length was remeasured after 24 hours in the germinator at 25 C.

Detection of Compounds

Location reagents were (1) long wave ultra-violet light before and during the application of ammonia vapor, (2) diazotized sulfanilic acid reagent (Krebs, Heusser, and Wimmer, 1969), (3) methanolic potassium hydroxide (Krebs et al., 1969), and (4) bromcresol green (Krebs et al., 1969).

Synthesized phenolic compounds, including coumarin and coumarin derivatives, were chromatographed and/or bioassayed in the same systems as the extracts for check purposes.

Cytologic Investigations

Heads of all sideoats gramagrass were collected and fixed in ethanol and acetic acid (3:1) when the heads were approximately one-half extruded from the boot and again when the anthers began to extrude. Anthers were macerated in acetocarmine for microscopic observation. Chromosome numbers were determined from observation of

first division metaphase configurations of meiotic pollen mother cells in the younger anthers. Pollen size was determined from the mature anthers. Diameters of 50 thick-walled, well-developed, deeply-stained pollen grains were measured at 450X from three different plants of each source.

Field Investigations

A seedling establishment study was planted in March, 1970, near Bowie, Arizona, in cooperation with Dr. G. L. Jordan, Department of Watershed Management, The University of Arizona. Seed from two dormant and two non-dormant sources was hand seeded in duplicate, 45 by 200 ft plots at a rate of 100,000 seed per acre. Small basins were formed in the plots prior to seeding with a rotating-drum pitting machine to improve the soil moisture-holding capacity. Plants established per 100 sq ft were counted in October, 1970.

A further planting was made in July, 1971, at the Santa Rita Experimental Range south of Tucson. Sources were seeded in 6 by 8 ft pits using a randomized complete blocks design with four replications. Established plants were counted in October, 1971.

Statistical Procedures

Steel and Torrie (1960) served as a guideline for statistical procedures. Most statistical analyses were

performed by computer through the Statistics Laboratory, College of Agriculture, The University of Arizona.

RESULTS AND DISCUSSION

Data for the five sources within each of the dormant and nondormant classifications were combined. In general, significantly different responses among sources within classifications were not found. Since the five sources of each classification represented the extremes of dormancy of the 159 sources that were originally evaluated, little source variation was expected. Attention will be directed to the instances when significant deviations among sources were found.

Germination and Dormancy Patterns

Average germination percentage of one-year-old seed from dormant and nondormant sources for five harvest years showed the spread in germination percentage between dormant and nondormant seed was 36% or more for all years except 1970 (Fig. 2). It should be noted that the classifications of dormancy are only relative, since nondormant seed did not exhibit 100% germination. The 1970 seed apparently had a prolonged period of post-harvest dormancy, which will be discussed further in the section on dormancy breaking treatments. The classification of seed sources as dormant or nondormant (Table 1) remained constant from year to year, except for 1970,

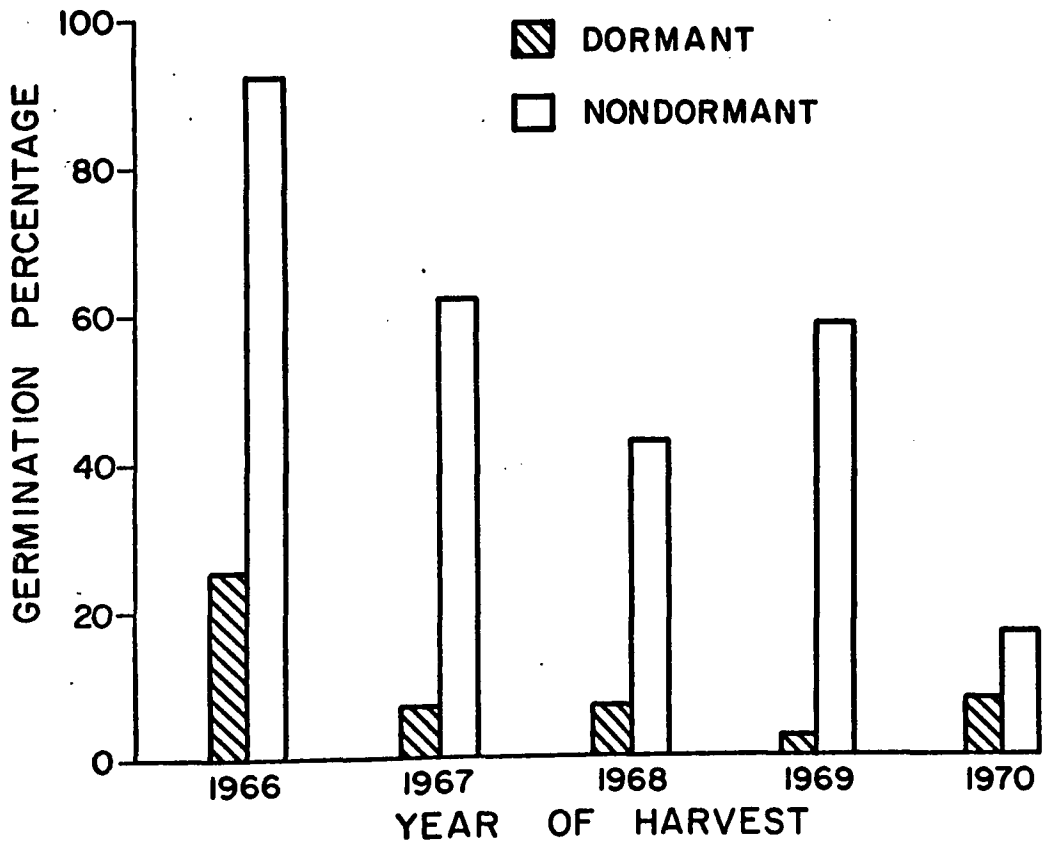

Fig. 2. Germination percentage of one-year-old seed from five dormant and five nondormant sources of Bouteloua curtipendula for five harvest years.

which suggests that the dormancy response in sideoats gramagrass is heritable. There was a significant year to year variation in degree of dormancy, which suggests that dormancy was conditioned by the environment. This is in agreement with the hypothesis of Vegis (1964) that genetics and environment both contribute to the ultimate expression of dormancy. Some research has indicated that the environment during seed formation and maturation plays the foremost role in determining seed germinability (Koller, 1969). Seed dormancy in sideoats gramagrass appeared to be largely determined by heritable traits, including the genetic ability to respond to environmental conditions in specific ways that lead to the onset of dormancy. The seed used in these investigations was produced under irrigated conditions, whereas the environmental impact on dormancy might be more significant under the natural desert environment. However, seed used for grassland seeding will largely be produced under irrigated conditions, and these results are realistic in relation to the expected dormancy response.

The spread in germination percentage between dormant and nondormant sources remained nearly constant for five years in 1966 seed (Fig. 3). One-year-old nondormant seed exhibited a significantly higher germination than it did in subsequent years. This high germination percentage followed by a decline and leveling off was not

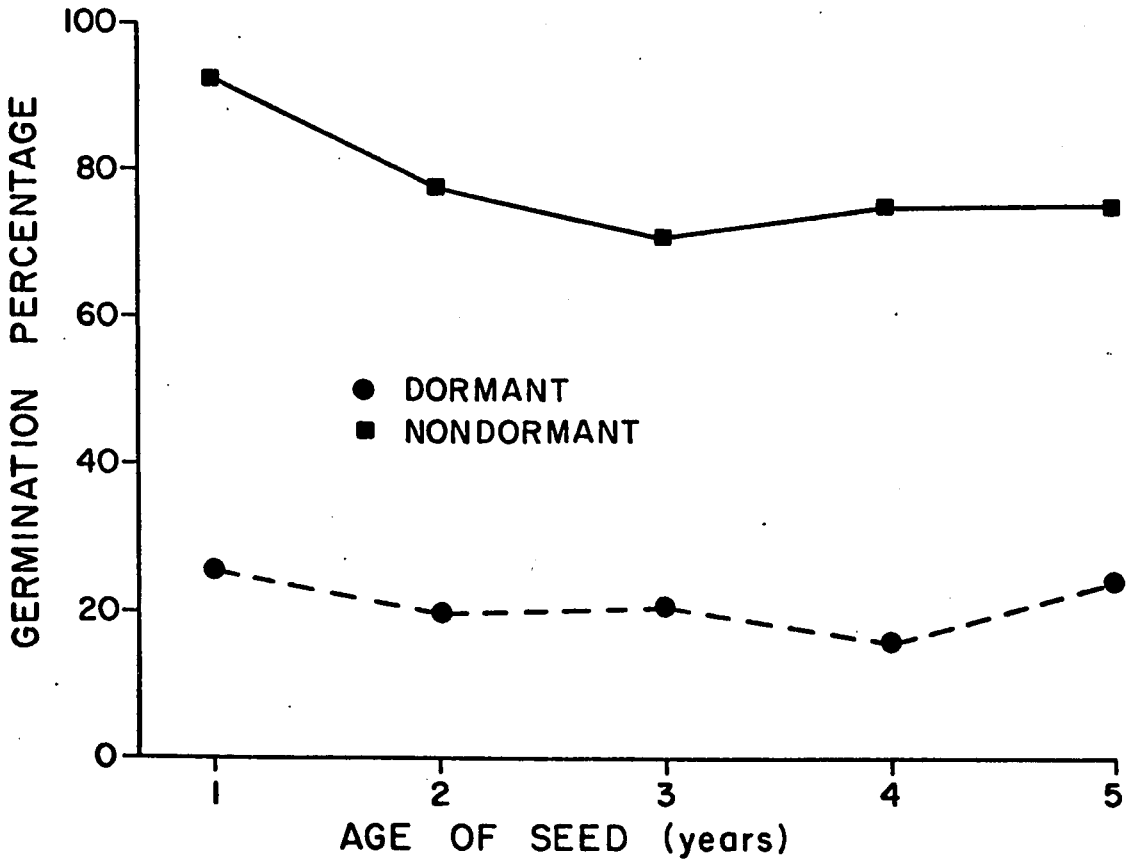

Fig. 3. Germination percentage of 1966 seed from five dormant and five nondormant sources of Bouteloua curtipendula for a five year period.

observed in any of the seed from subsequent harvest years (Table 2). Seed dormancy in sideoats gramagrass remained intact for at least five years, with no significant decline in viability.

The pattern of germinability for 1969 seed from harvest through 24 months is presented in Fig. 4. The 4 to 6 month period following harvest was characterized, most obviously in nondormant seed, by post-harvest dormancy which gradually disappeared over this period. The post-harvest dormancy was evidently imposed by factors within the caryopsis, since removal of the spikelet appendages (lemma, palea, and glumes) did not improve germination. This agrees with the findings of Sumner and Cobb (1962) for sideoats gramagrass. After the post-harvest dormancy period, germination of nondormant sources remained relatively high in comparison to dormant sources. There was some indication of a cyclic fluctuation in germinability of nondormant seed. Evidence has been found in seed of certain species of endogenously-controlled germinability fluctuations of varying lengths (Kummerow, 1965; Maguire, 1969; Sweeney, 1963). The length of the cycle shown in Fig. 4 was greater than one year, which makes it difficult to reconcile in terms of being set in motion by some natural or environmental cycle.

Table 2. Germination percentage of seed from five dormant and five nondormant sources of Bouteloua curtipendula over time for five harvest years.

Year of harvest	Class[1]	Age of seed (years) 1	2	3	4	5
1966	Dormant	25.7 a	20.0 a	20.6 a	15.9 a	19.4 a
	Nondormant	92.5 b	77.5 a	71.2 a	74.9 a	74.7 a
1967	Dormant	2.5 a	3.3 a	3.0 a	3.8 a	
	Nondormant	62.4 a	57.1 ab	46.1 b	63.5 a	
1968	Dormant	6.8 a	4.9 a	9.7 a		
	Nondormant	42.6 a	35.0 a	41.3 a		
1969	Dormant	2.7 a	4.3 a			
	Nondormant	58.8 a	62.5 a			
1970	Dormant	7.9				
	Nondormant	17.1				

[1]Values within classes not followed by the same letter are significantly different at the 5% level.

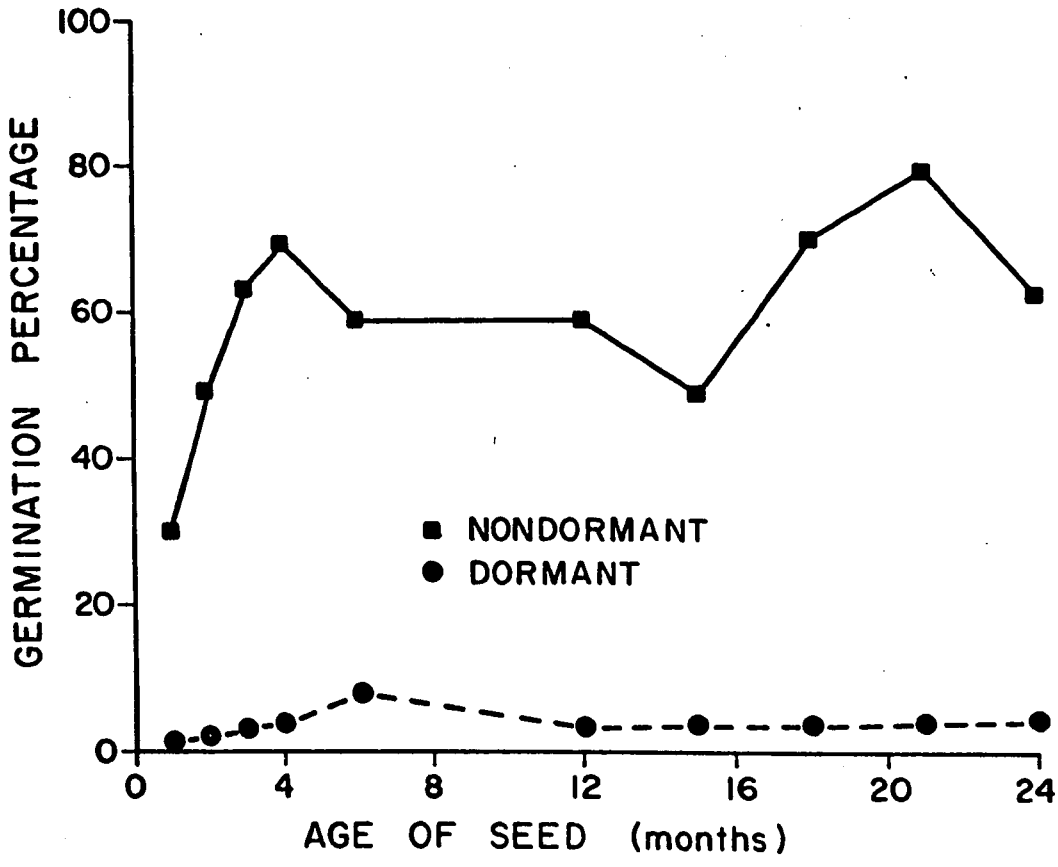

Fig. 4. Germination percentage of 1969 seed from five dormant and five nondormant sources of Bouteloua curtipendula for a 24 month period.

Dormancy Breaking Treatments

Physical Treatments

The effects of several physical treatments on average germination percentage of dormant and nondormant 1969 seed were summarized (Table 3). Treatments were imposed at different times, so the control values for germination of intact seed units varied slightly among experiments. Hand removal of the caryopses from spikelet appendages allowed almost complete emergence from the dormant state in all sources. This coincides with the work of Sumner and Cobb (1962) for sideoats gramagrass and is similar to the dormancy situation in other grasses (Baskin et al., 1969; Fendall and Carter, 1965; Frank and Larson, 1970). Thus, it can be concluded that the germination potential of sideoats gramagrass caryopses, which have passed through the post-harvest dormancy period, is at least 90%. Incubating the hand threshed caryopses in the presence of their loose spikelet appendages did not reduce germination in comparison with caryopses alone. If intact seed units were allowed to imbibe water for 48 hours prior to dehulling, germination percentage was significantly reduced in comparison to the control, which consisted of caryopses which were threshed dry (Table 3). Reduction of germination was greatest in dormant sources. Clipping the basal ends of the spikelets with a razor blade, so that gas

Table 3. Effects of physical dormancy conditioning treatments on germination percentage of 1969 seed from five dormant and five nondormant sources of Bouteloua curtipendula.

Treatment	Dormant		Nondormant	
	Treated	Control	Treated	Control
Dehulling	89.7**[a]	4.3	90.0**	65.3
Caryopses plus loose hulls	85.6**	4.3	88.0**	65.3
Imbibition before dehulling	32.0**	91.0	61.0**	95.0
Spikelet clipping	52.2**	4.1	80.0	79.5
Prechilling	12.2	4.2	78.7	78.5
Alternating moisture on filter paper	30.4**	4.9	81.2	66.4
Soil	66.9**	2.7	91.8**	58.8
Activated charcoal	9.8	6.0	82.7**	71.5
Nutrient solution	6.0	5.3	57.8	58.7

[a]Paired values within dormant or nondormant classifications are significantly different at the 1% level.

exchange between the caryopsis and the atmosphere was less restrictive, resulted in a significant break in dormancy for dormant sources, but germination did not reach the 90% potential (Table 3). These results suggested that, although the glumes, lemma, and palea of sideoats gramagrass may limit gas exchange, intimate contact between the caryopsis and its enclosing structures produced an inhibitory effect on germination greater than could be explained by gas exchange impairment alone. Thus, the presence of chemical inhibitors either on the surface of the caryopsis or in the spikelet appendages was implicated. In either case germination would be inhibited in the intact spikelet where inhibitory materials would be held in close proximity to the embryo.

Exposure of intact seed units to moist, low temperature conditions (prechilling) prior to germination was ineffective in relieving dormancy (Table 3). Two of the five dormant sources (99 and 27) responded slightly to prechilling, which made the average show a trend toward improvement in germination percentage. Black (1970) indicated that, in general, dormancy that could be broken by chilling was embryo or endosperm imposed. Since long-term dormancy in sideoats gramagrass is apparently seedcoat imposed, it is logical that prechilling would be relatively ineffective in improving germination.

Germination in soil at a moisture content of 80% of field capacity was quite effective in breaking dormancy (Table 3). The basis of improved germination in soil is not fully understood, but certain mechanisms may be postulated. The microorganisms in soil may be effective in scarification of the seedcoat (Shankar, 1968). This effect was probably minimal in the present investigation, because germination in steam sterilized soil was nearly as high as in nonsterile soil. Soil colloids may function in adsorbing inhibitory materials, thus reducing the concentration of inhibitors in the immediate proximity of the embryo. It is believed that adsorption or removal of inhibitors represented a considerable part of the dormancy breaking action of soil because of some preliminary germination tests in other media. Germination was best in soil, followed by vermiculite, perlite, sand, and filter paper, in that order. This suggested that media with greater areas of adsorptive sites were more effective in breaking dormancy. Activated charcoal, which has a high adsorptive capacity, was relatively ineffective in improving germination when used in a pregermination soak (Table 3). Certain ions or nutrients found in the soil solution may stimulate germination. However, germination on filter paper in a complete nutrient solution did not improve germination (Table 3).

Since germination of dormant sources was so much better in soil than on the standard filter paper, there was some concern that the seed dormancy phenomenon observed was partially a laboratory generated artifact. Koller (1964) has pointed out some of the pitfalls in drawing conclusions about adaptation of plants in nature from laboratory experiments on germination. However, there was a 25% differential in germination percentage between dormant and nondormant seed, even in soil at a constant moisture of 80% of field capacity (Table 3). The next step was to test germination under conditions that more nearly approximated the natural establishment environment.

Alternate wetting and drying on filter paper allowed a significant increase in germination in both dormant and nondormant sources (Table 3). One factor involved may have been a scarifying action from the physical forces of wetting and drying so that permeability through the spikelet parts was improved. Wetting and drying may also increase the susceptibility of inhibitors to oxidation. Alternating moisture conditions represent a typical part of the desert environment during establishment.

Cumulative germination percentage under alternating soil moisture conditions is presented in Figs. 5 and 6. Exposure to 24 or 48 hour cycles of moisture at 80% of soil field capacity gave significantly less total germination than 96 hour or constant exposure to moisture in both

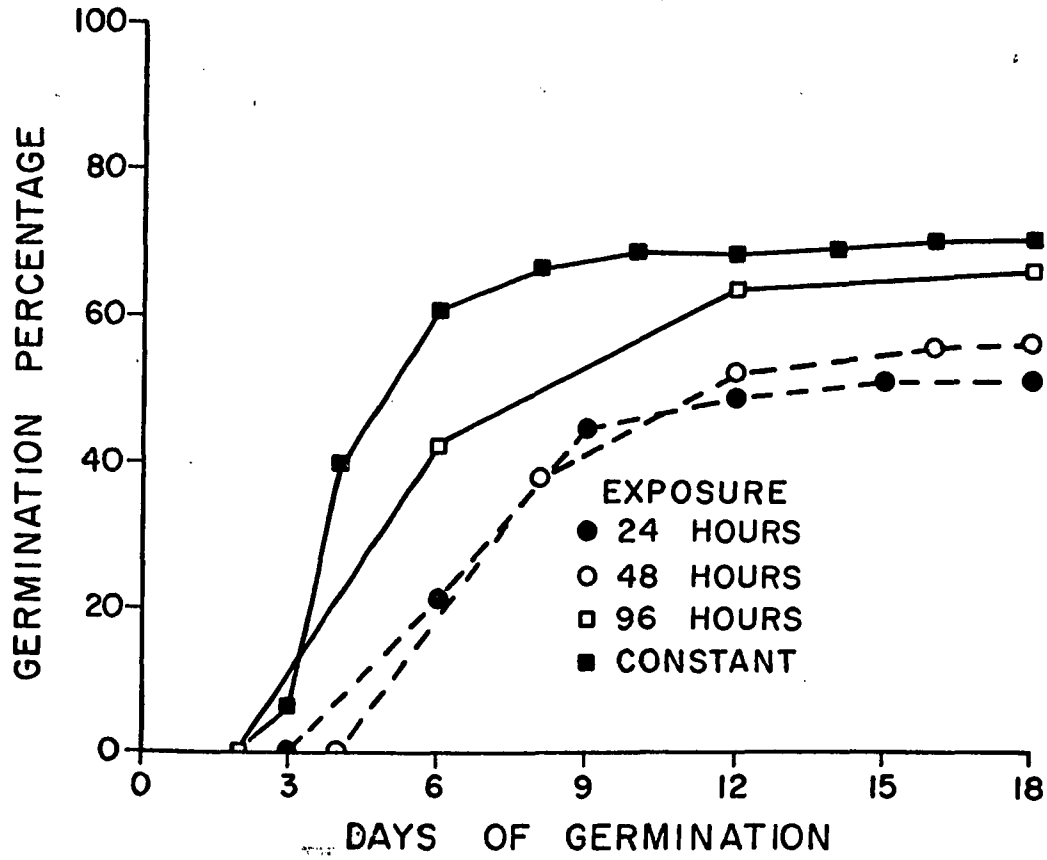

Fig. 5. Cumulative germination percentage of 1969 seed from five dormant sources of Bouteloua curtipendula under alternating soil moisture conditions.

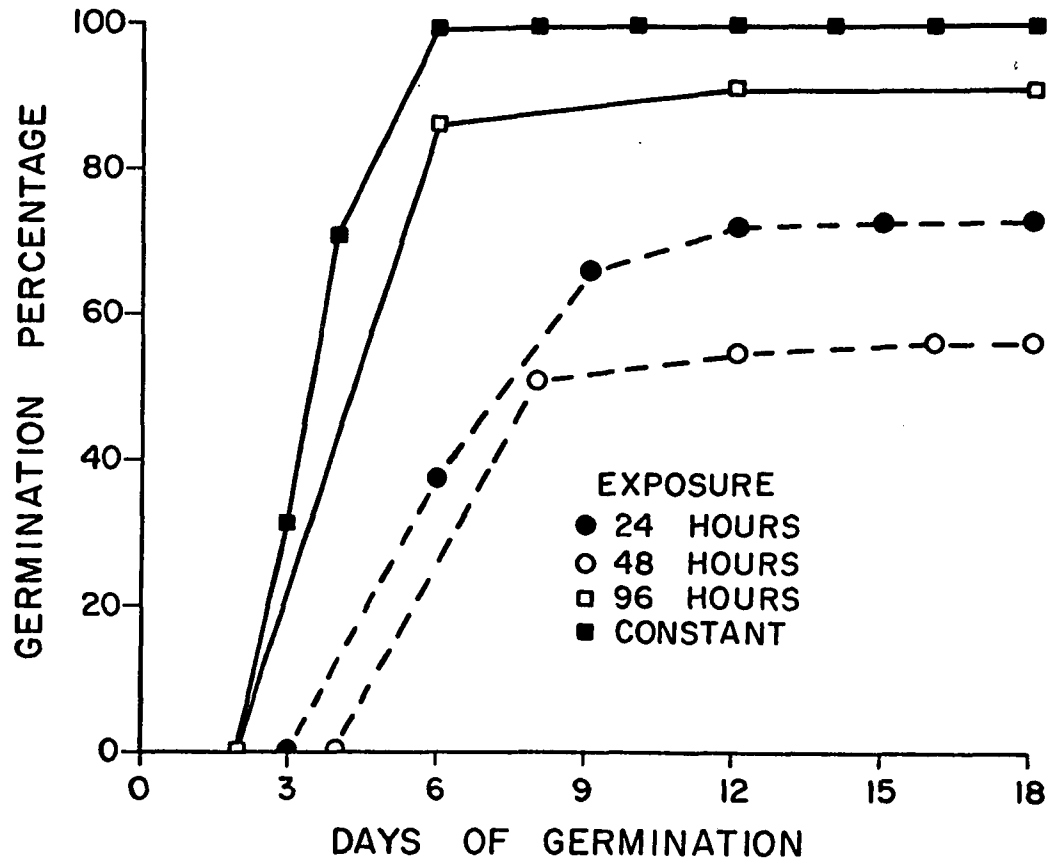

Fig. 6. Cumulative germination percentage of 1969 seed from five nondormant sources of Bouteloua curtipendula under alternating soil moisture conditions.

dormant and nondormant sources (Table 4). Nondormant sources germinated less under the 48-hour moisture regime than under the 24 hour cycles, whereas dormant sources showed the opposite pattern. The significance of these data with respect to the possible role of dormancy in stand establishment is not fully understood. It was apparent that the moist period needed to be over 48 hours in duration for the full potential of germination to be realized. This concurs with the observations of Jordan (1971) for sideoats gramagrass and other species, that moist periods of less than 72 hours were insufficient for seedling survival under field conditions.

Table 4. Germination percentage of five dormant and five nondormant sources of Bouteloua curtipendula after eighteen days exposure to four alternating soil moisture regimes.

	Germination %[1]	
Exposure period	Dormant	Nondormant
24 hours	51.0 b	70.0 c
48 hours	56.9 b	56.2 d
96 hours	65.4 a	90.7 b
Constant	69.9 a	99.8 a

[1]Values within a column not followed by the same letter are significantly different at the 5% level.

No experiments were conducted to study the effects of temperature variations on breaking of dormancy. However, Cole (1971) evaluated two of these sources (27 and 141) for optimum germination temperature conditions, and found response to temperature to be quite variable between sources. This may reflect adaptations to the environment at the particular sites where the various sources were collected. Thus, dormancy may be partially temperature-induced when seed are germinated at temperatures other than the optimal temperature range.

Light, Leaching, and Enriched-Oxygen Atmosphere

The effects of various light, leaching, and enriched-oxygen atmosphere treatments on germination in 1969 seed of sideoats gramagrass were summarized (Table 5). A 48-hour dark imbibition period prior to the regular light regime had no effect on germination. Dark imbibition has been effective in breaking dormancy in some light-sensitive species (Brauen, 1967). Exposure to red light during the early part of the germination period increased the germination percentage of nondormant sources to their 90% potential. Exposure to red light had little effect on dormant sources (Table 5). The promotive effects of red light on germination are closely associated with the photoreversible pigment phytochrome (Black, 1969). Sideoats gramagrass is known to exhibit a wide range of photoperiodic effects

Table 5. Effects of light, leaching, and enriched-oxygen atmosphere treatments on germination percentage of 1969 seed from five dormant and five non-dormant sources of Bouteloua curtipendula.

Treatment	Dormant		Nondormant	
	Treated	Control	Treated	Control
Dark imbibition	4.3	6.7	49.6	51.6
Red light	9.6*[a]	4.9	86.5**	66.4
Water leach	4.1	4.2	73.3	78.5
Sodium carbonate leach	7.1	6.0	80.6	71.5
Sodium hypochlorite leach	32.2**	4.0	91.9**	74.4
Hydrogen peroxide leach	15.0*	4.1	85.6	79.5
Oxygen	49.6**	4.9	89.8**	70.9
Sodium carbonate plus oxygen	53.6**	6.0	90.0**	71.5
Sodium hypochlorite plus oxygen	89.6**	4.3	97.3**	68.3

[a]Paired values within dormant or nondormant classifications are significantly different at the 5% (*) and 1% (**) levels.

(Olmsted, 1962), and it is possible that these sources possess a phytochrome system which functions to some degree in germination control.

Leaching of intact seed units in running distilled water for 24 hours did not improve germination (Table 5). This indicated that, if inhibitory materials were present, they were either insoluble in water or inaccessible to removal by water leaching in intact seed units. It was necessary to air dry seed for at least 24 hours prior to germination following any of the pregermination wet treatments. Germination percentage was drastically reduced unless this was done. Roberts (1969) described "water sensitivity" in barley which was the inability to germinate in supraoptimal moisture conditions. It was proposed that the main effects of excess water were reduction in the oxygen entry rate and competition for available oxygen by microflora. Water sensitivity may partially account for the drying requirement in sideoats gramagrass following wet pregermination treatments.

A dilute solution of sodium carbonate may be a better solvent of inhibitory chemicals than water (Jordan, 1962). However, soaking intact seed units in sodium carbonate did not increase germination in sideoats gramagrass (Table 5). Sodium hypochlorite (chlorox) has been found to be an effective dormancy relieving agent in some grass species (Sumner and Cobb, 1962; Burton, 1969; Frank

and Larson, 1970). Sodium hypochlorite was also effective in increasing germination in dormant and nondormant seed of sideoats gramagrass (Table 5). The dormancy breaking action of sodium hypochlorite has been attributed to partial degradation of the lemma and palea, reduction in seed borne fungi, and to solubilization and removal of inhibitors (Sumner and Cobb, 1962; Frank and Larson, 1970). Sodium hypochlorite is also an oxidizing agent with the release of oxygen into the solution the basis of the bleaching action. Thus, it may also inactivate inhibitors by oxidation. However, hydrogen peroxide, a strong oxidizing agent, was much less effective in relieving dormancy than sodium hypochlorite (Table 5). This finding suggested that sodium hypochlorite had a more complex action than simple oxidation.

Incubation in a 100% oxygen atmosphere for 7 days resulted in a highly significant increase over standard atmospheric conditions in germination of both dormant and nondormant sources (Table 5). Similar findings were reported by Black and Wareing (1959), Frank and Larson (1970), and Major and Roberts (1968a). Increased germination obtained by oxygen-enriched conditions may be related to a mechanical barrier or to impermeability of the seed coat. If oxygen were limited by these barriers, respiration and growth would be inhibited. Increasing the oxygen supply would then result in an increase in germination.

Black and Wareing (1959) reported that the loss of dormancy involved with increased oxygen tensions was by oxidation of inhibitors to inactive forms. Roberts (1969) proposed that the early stages of germination were characterized by the occurrence of a major part of respiration through the pentose-phosphate pathway. Dormant seed with a low capability for pentose-phosphate metabolism could be induced to germinate with increased oxygen. Certain oxidation reactions were evidently necessary to switch the respiratory system toward a greater proportion of pentose-phosphate reactions. The theory proposed by Roberts (1969) explains the influence of an oxygen-enriched atmosphere on increasing germination in sideoats gramagrass more adequately than mechanical or permeability barriers to oxygen uptake. There was no observable barrier to water uptake in dormant seed units. Thus, it is difficult to understand that a gas exchange barrier could exist which could impose the level of dormancy observed.

The sodium carbonate and sodium hypochlorite pregermination treatments were combined with enriched-oxygen conditions during germination (Table 5). Sodium carbonate plus oxygen was no better than oxygen alone. These results complement the earlier observation that sodium carbonate was not effective in breaking dormancy in sideoats gramagrass. However, sodium hypochlorite and oxygen had a synergistic effect, which allowed germination

of both dormant and nondormant sources to reach its 90% or greater potential. Sodium hypochlorite may have increased the permeability of seed units to oxygen, or it may have rendered inhibitory compounds more susceptible to oxidation. The combination of sodium hypochlorite treatment with enriched-oxygen atmosphere appeared to be an effective way to determine the germination potential of dormant seed of sideoats gramagrass.

Dormancy Conditioning Treatments for 1970 Seed

The potential of a prolonged period of post-harvest dormancy of 1970 seed was introduced previously. Dehulling, germination in soil, and enriched-oxygen atmosphere, which are largely related with seed coat imposed dormancy, were less effective in increasing germination of 1970 seed (Table 6) than in 1969 seed. Prechilling, which was associated with embryo imposed dormancy, was more effective in increasing germination of 1970 seed. Data for 1969 seed suggested that long-term dormancy in sideoats gramagrass was primarily related to the spikelet material surrounding the caryopsis, while post-harvest dormancy was associated with factors of the caryopsis. A considerable portion of the dormancy in 1970 seed existed in the dehulled caryopsis, suggesting embryo imposed or post-harvest dormancy. The environment during seed maturation must have induced this

Table 6. Effects of dormancy conditioning treatments on germination percentage of 1970 seed from five dormant and five nondormant sources of Bouteloua curtipendula.

	Dormant		Nondormant	
Treatment	Treated	Control	Treated	Control
Dehulling	62.8**[a]	12.2	39.4**	11.3
Soil	44.6**	10.0	40.2**	12.9
Prechilling	14.8	10.0	30.0**	12.9
Oxygen	28.4**	11.7	41.3**	14.8

[a]Paired values within dormant or nondormant classifications are significantly different at the 1% level.

prolonged period of post-harvest dormancy, but the mechanism is unknown.

Characteristics Associated with Seed Dormancy

Seed Unit Factors

Weight of caryopses, number of caryopses per gram of seed units, and hull weight of 100 caryopses are presented in Table 7 for all harvest years. The most consistent differential between dormant and nondormant sources was in caryopsis weight. Dormant seed had 30% less weight than nondormant seed for all years. Associations among the three seed-unit parameters and germination

Table 7. Weight of caryopses, number of caryopses per gram of seed units, and hull weight per one hundred caryopses of five dormant and five nondormant sources of Bouteloua curtipendula for six harvest years.

Year of harvest	Weight of caryopses mg/100		Caryopses per g seed units		Hull weight mg/100 caryopses	
	Dormant[1]	Nondormant	Dormant	Nondormant	Dormant	Nondormant
1966	56.3 b	80.0 b	256.2 ab	121.4 d	472.0 c	873.3 a
1967	52.5 d	76.3 c	116.4 e	118.5 d	1223.3 a	789.3 ab
1968	54.5 c	78.8 b	263.8 a	181.0 ab	479.3 c	442.8 c
1969	58.6 a	82.0 a	222.8 c	166.1 bc	519.5 c	801.4 ab
1970	51.2 d	72.2 d	244.4 b	187.6 a	435.8 c	510.6 c
1971	51.1 d	64.1 e	172.1 d	169.5 b	682.8 b	660.2 b
Mean[2]	54.0**	76.6	212.6**	157.4	635.5	679.6

[1]Values within a column not followed by the same letter are significantly different at the 5% level.

[2]Dormant mean was significantly different from the nondormant at the 1% level.

percentage of one-year-old seed are shown in Table 8. There was a significantly positive r-value between weight of caryopses and germination percentage for 1969 and for the combination of all years, while the r-value for other years approached significance. A significantly negative r-value was found between the number of caryopses per gram of seed units and germination percentage. Hull weight per 100 caryopses was not related to germination percentage. These results suggested that caryopsis weight was associated with seed dormancy of sideoats gramagrass, although a causal relationship was not established. However, certain causal relationships may be proposed from literature dealing with seedling vigor. Wright (1971) reviewed the role of seed food reserves on seedling vigor and found that a positive relationship existed between seed weight, germination, and initial growth for a number of species. McDaniel (1969) established a physiological basis for vigor differences due to seed size, showing that seedling mitochondrial protein and mitochondrial respiratory activity were positively associated with seed weight of barley (Hordeum vulgare L.). If the greater weight of nondormant seed of sideoats gramagrass is indicative of greater seedling vigor and biochemical activity, nondormant seed might be expected to have the ability to perform better in the presence of dormancy imposing factors such as inhibitory chemicals. Thus, heavy seed may be able to overcome the

Table 8. Values of correlation coefficients for weight of caryopses, number of caryopses per gram of seed units, and hull weight per one hundred caryopses with germination percentage of one-year-old seed from five dormant and five nondormant sources of Bouteloua curtipendula for five harvest years.

Year of harvest	Constituents		
	Weight of caryopses and germination %	Caryopses per g and germination %	Hull weight and germination %
1966	0.624	-0.698*[a]	0.600
1967	0.651	-0.234	-0.379
1968	0.514	-0.530	0.357
1969	0.766**	-0.524	0.461
1970	0.403	-0.125	-0.402
All years	0.557**	-0.390**	0.221

[a]Significant at the 5% (*) and 1% (**) levels.

effect of inhibitors through superior growth rate or extra production of growth promoting substances, whereas light seed would be retarded because of low vigor. Therefore, the quantity of inhibitors present may be less important in determining dormancy than the ability to overcome their effects. However, the interactions between stress environments and both nondormant and dormant seed are emphasized. The presence of seed dormancy which would gradually disappear in response to environmental fluctuations may be of advantage in stand establishment.

Proteins

A relatively low molecular weight protein (arrows, Fig. 7) was found in the electrophoretic patterns of caryopsis proteins of dormant sources 84, 72, 99, and 27 which was not observed in the other sources. No attempt was made to characterize the protein. The relationship of this protein with dormancy is not known. Seed dormancy of sideoats gramagrass appears to be heritable, which implies coding for the synthesis of proteins associated with dormancy. No differences in coleoptile proteins between dormant and nondormant seed were observed. The techniques used were not sufficiently sensitive to determine the protein patterns of the spikelet appendages.

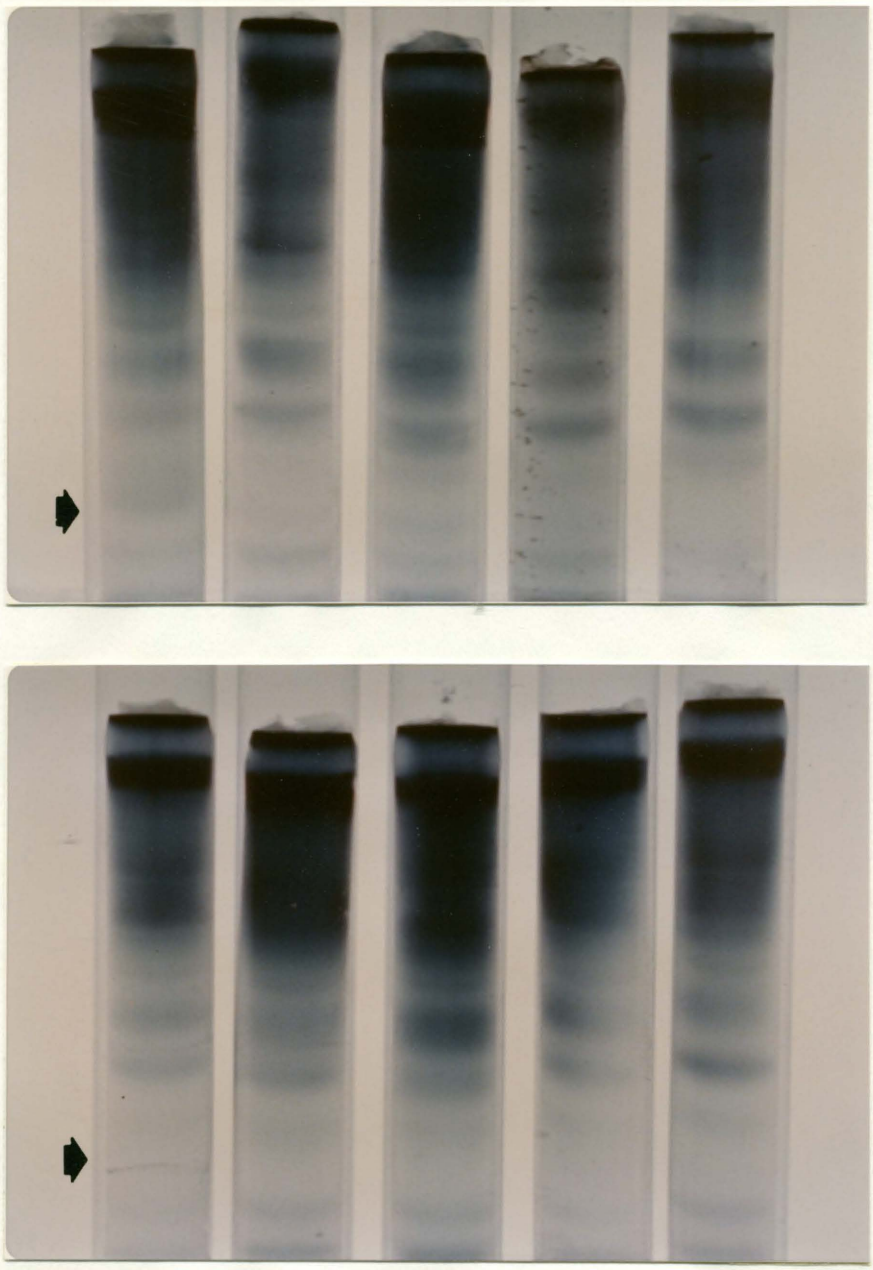

Fig. 7. Electrophoretic characterization of caryopsis proteins of Bouteloua curtipendula sources -- Top (L to R), dormant sources: 84, 72, 99, 27, and 88. Bottom (L to R), nondormant sources: 63, 104, 10, 141, and 6.

Cytology

Classification of the mode of reproduction for all sources was made on the basis of chromosome numbers and pollen size distribution (Table 9). Gould (1959) concluded that most sideoats gramagrass plants with chromosome numbers greater than 2n = 52 were obligate apomicts. Gould studied the distribution of pollen size for a large number of types of sideoats gramagrass plants and found that, in general, sexual types had quite uniform pollen size, while apomicts showed considerable variation in pollen size. The pollen size distribution for apomictic types was characterized by a high frequency of small and large pollen and a low frequency of intermediate sizes. Microsporogenesis of apomictic plants of sideoats gramagrass is characterized by unequal first division which results in pollen of variable size (Kapadia and Gould, 1964a). The pollen size distribution of sexual and apomictic types used in these investigations were similar to those found by Gould (Fig. 8). The significance of apomixis in relation to seed dormancy in sideoats gramagrass is not understood, although it is an associated characteristic in four of the five dormant sources. All the apomictic types are from Mexico and Texas, and probably fit into the taxonomic var. caespitosa because of the high chromosome numbers (Gould and Kapadia, 1964). It should be noted that source 27, the only dormant sexual

Table 9. Chromosome numbers, pollen size, and probable mode of reproduction of five dormant and five nondormant sources of Bouteloua curtipendula.

Source no.	Chromosome no. 2n =	Range of pollen size microns	Mode of reproduction
		Dormant	
84	ca 84	34.1-55.3	Apomictic
72	ca 102	32.5-65.0	Apomictic
99	ca 84	32.5-60.1	Apomictic
27	54	26.0-40.6	Sexual
88	ca 96	32.5-66.1	Apomictic
		Nondormant	
63	40	29.3-39.0	Sexual
104	54	27.6-42.3	Sexual
10	40	22.8-39.0	Sexual
141	32	27.6-37.4	Sexual
6	40	26.0-37.4	Sexual

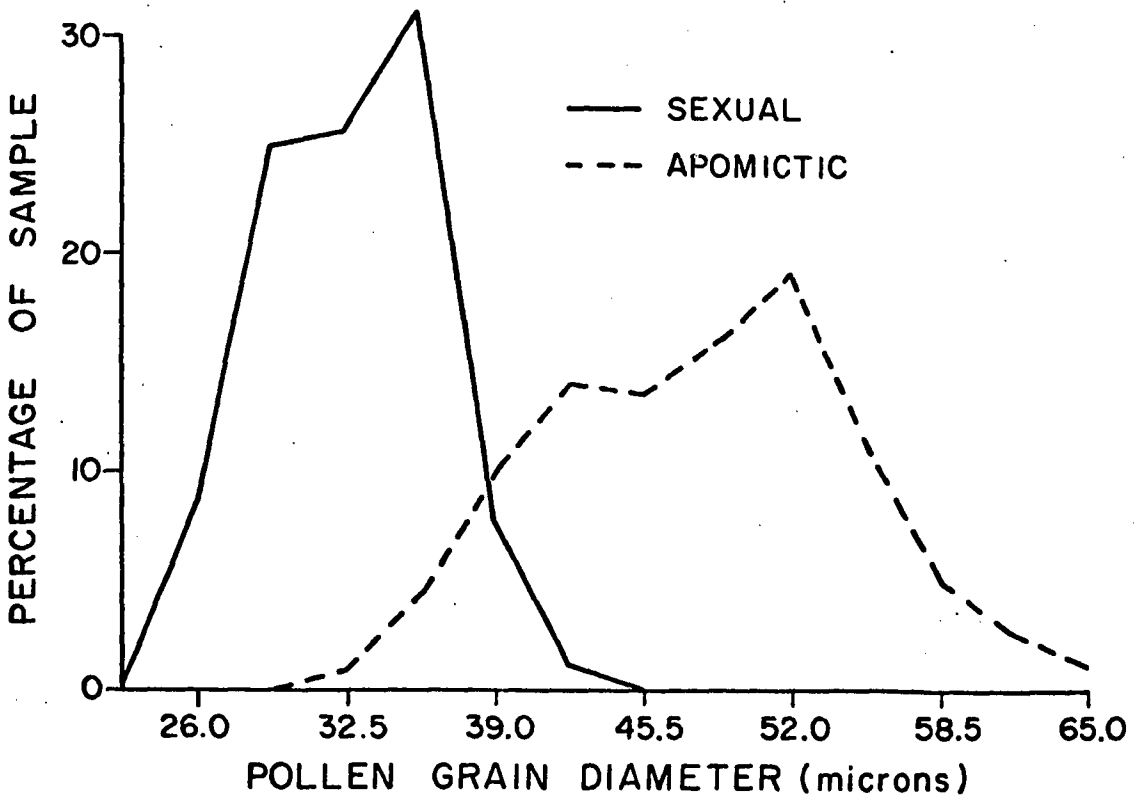

Fig. 8. Pollen size distribution of four apomictic and six sexual sources of Bouteloua curtipendula.

type in this study, showed the least degree of dormancy of the dormant sources. A number of dormancy breaking treatments were effective for source 27 and not for other dormant types. The existence of apomixis complicates breeding procedures that could be used to incorporate desirable traits into improved cultivars.

Inhibitory Materials in Spikelet Appendages

Previous data and the literature suggested the presence of inhibitory materials in the spikelet appendages of sideoats gramagrass. These materials might partially explain the differential in seed dormancy observed among sources. Attempts were made to isolate and identify these inhibitors in ground spikelet material. Figure 9 shows the results of a bioassay of consecutive fractions of a paper chromatogram from sodium hypochlorite extracts using isopropanol, ammonia, and water, as a developing solvent. Root elongation of germinating sideoats gramagrass caryopses was used as a measure of inhibition. Fractions six, seven, and eight were the most inhibitory, although little differential inhibition between dormant (84 and 27) and non-dormant (63 and 141) sources was found.

Fractions six, seven, and eight were eluted from the paper and rechromatographed using 80% ethanol as a developing solvent. The bioassay for this chromatogram is shown in Fig. 10. Fraction nine (Fig. 10) contained

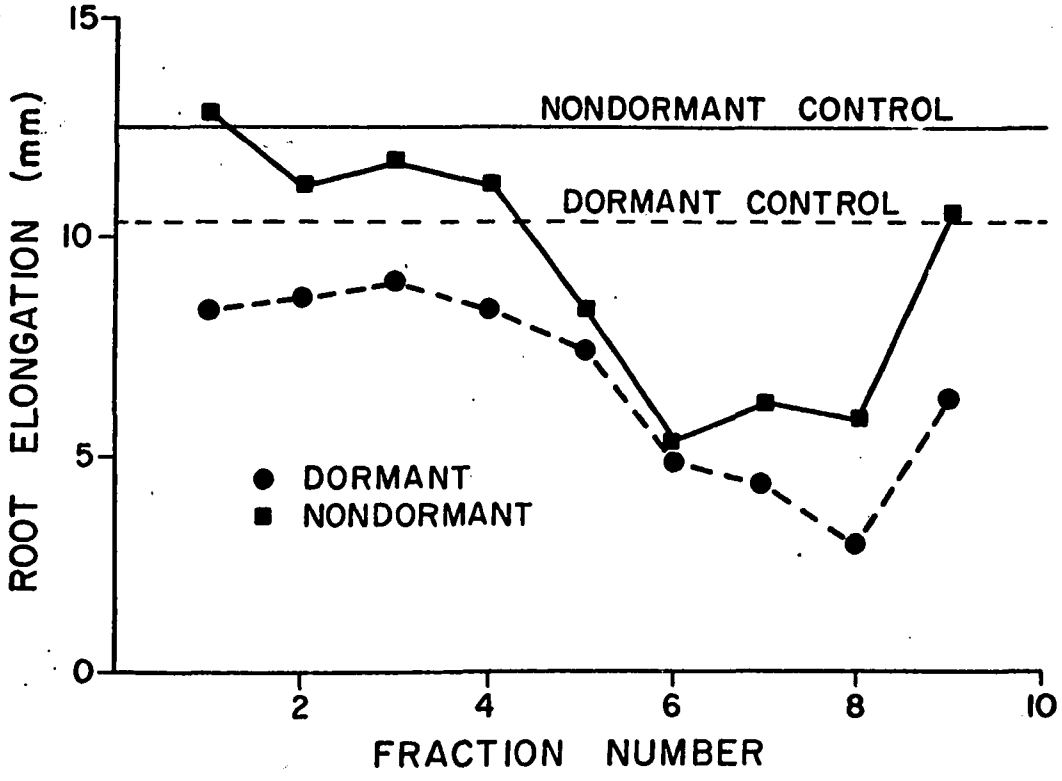

Fig. 9. Root elongation of germinating caryopses as affected by sodium hypochlorite extracts of spikelet appendages of Bouteloua curtipendula.

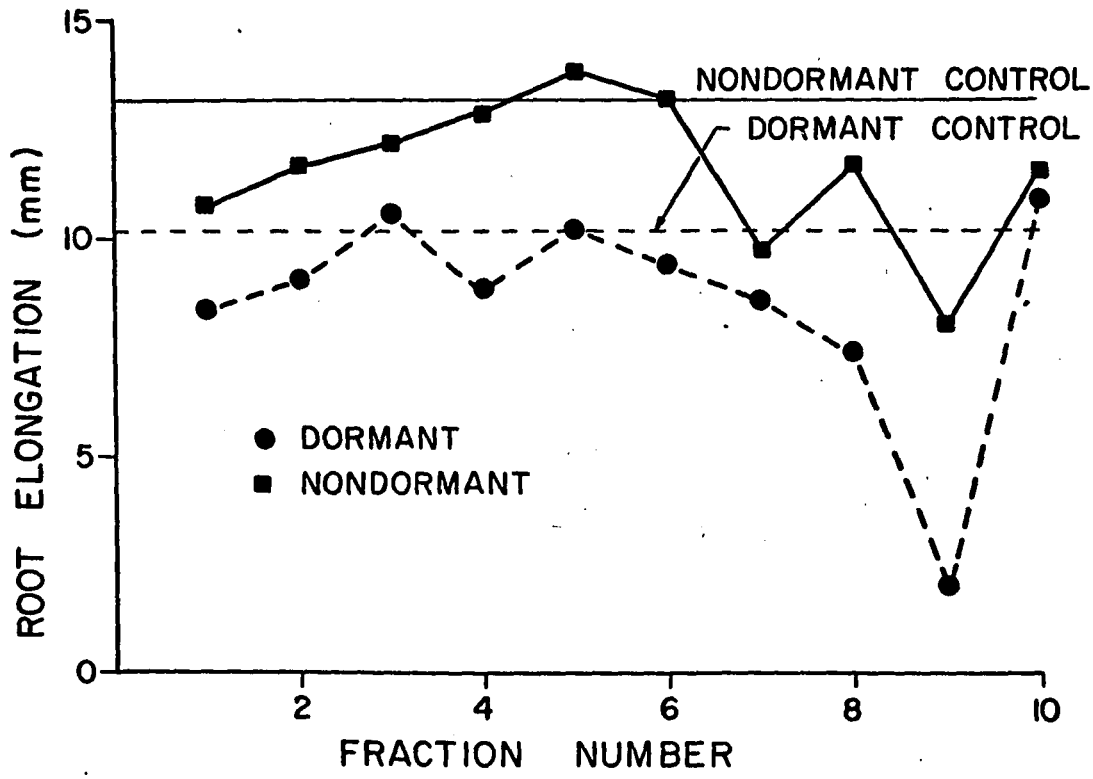

Fig. 10. Root elongation of germinating caryopses as affected by purified sodium hypochlorite extracts of spikelet appendages of Bouteloua curtipendula.

factors responsible for differential inhibition between dormant and nondormant sources. Wareing and Saunders (1971) have pointed out the limitations regarding the significance of bioassays of partially fractionated extracts, including incomplete separation of compounds, nonlinear response over a range of concentrations, and interactions of two or more components. However, on the basis of Rf values and comparison with standards, coumarin or derivatives of coumarin were indicated as major constituents of fraction nine. Since coumarin has been quite widely reported as a germination inhibitor (Lerner, Mayer and Evenari, 1959; Mayer and Evenari, 1952; Sivan, Mayer, and Poljakoff-Mayber, 1965; Wareing, 1965), further measures were taken to confirm or disprove the presence of coumarin-like compounds.

Fraction nine (Fig. 10) was eluted and chromatographed on silica gel using thin layer chromatography. The compounds did not separate out distinctly when compared to coumarin and a few of its derivatives, so confirmation of the identity of the compounds was in doubt. Phenolic compounds are subject to oxidation under alkaline conditions (Hathway, 1969). The conditions during initial extraction in these experiments were pH 10.5 with oxygen being released into the solution from sodium hypochlorite. Therefore, there was the possibility of oxidation of side groups, polymerization of ring compounds, or both. The

extent of compound alteration during the extraction procedure was undetermined; however, the brownish color of the concentrated extracts indicated that some polymerization of phenolic units may have occurred. Dilute, aqueous sodium hypochlorite was initially chosen as an extractant in preference to an organic solvent because it would more closely approximate the natural soil solution and it was known to relieve dormancy in sideoats gramagrass. In addition to solubilizing properties, sodium hypochlorite may have been important as an oxidant of inhibitors. Therefore, a different extraction system was developed to help resolve the possible artifacts generated by sodium hypochlorite, and to determine whether coumarin or its derivatives occurred differentially between dormant and nondormant seed.

Ground spikelet material was extracted with 80% ethanol and the compounds were separated with paper chromatography using isopropanol, ammonia, and water as a developing solvent. The Rf values, UV fluorescence, and color reactions of compounds which occurred differentially between dormant (84) and nondormant (63) sources, and of standard compounds which had similar characteristics are shown in Table 10. A number of other phenolic compounds were identified which occurred about equally in the dormant and nondormant sources. Two spots (one and three) were present in the extract of the dormant source which were not

Table 10. R_f value, UV fluorescence, and color reactions of compounds occurring differentially between dormant (84) and nondormant (63) sources of Bouteloua curtipendula and of pure coumarin derivatives.

	Compound	R_f value	UV Fluorescence: Before spraying	UV Fluorescence: Methanolic KOH	UV Fluorescence: Sulfanilic acid
Dormant (84)	1	54	br-Bl[a]	br-Bl	Gr-Bn
	2	70	br-Bl	br-Bl	Gr-Bn
	3	79	Absent	Absent	R-Bn
Nondormant (63)	1	Not present			
	2	70	f-Bl	f-Bl	f-Gr
	3	Not present			
	Esculetin	55	br-Bl	br-Bl	Y-G
	Scopoletin	54	br-Bl	br-Bl	V
	Umbelliferone	70	br-Bl	br-Bl	Y-O
	Coumarin	80	Absent	Aq	f-Bn

[a]Abbreviations indicate the following shades and colors: br = bright; f = faint; Bl = blue; Aq = aqua; Gr = grey; Bn = brown; R = red; Y = yellow; G = green; V = violet; O = orange.

detected in the nondormant source. Spot two was present in a much smaller amount in the nondormant source. Coumarin and its substitution derivatives umbelliferone (7-hydroxycoumarin), esculetin (6,7-dihydroxycoumarin), and scopoletin (7-hydroxy-6-methoxycoumarin) are commonly found in plant tissue (Hathway, 1969). The Rf values and UV fluorescence patterns of these compounds compare rather well with the unknown spots, while the colors from spray reagents fit less conclusively. Other compounds in the crude extracts may have interfered with the reactions of spray reagents and given colors which were not true to the pure compounds. With these reservations, spot one could have been esculetin or scopoletin or both, spot two could fit the pattern of umbelliferone, and spot three may have been coumarin. While the identification of these compounds is not absolute, it appeared that coumarin or some of its substitution derivatives occurred differentially between these dormant and nondormant sources.

The effect of pure coumarin on root elongation of germinating sideoats gramagrass caryopses is shown in Table 11. A significant reduction in root growth was observed at concentrations of coumarin of 10 μg/ml or greater. Umbelliferone, esculetin, and scopoletin were not bioassayed for their effects of sideoats gramagrass germination. Mayer and Evenari (1952) found that substitution on the coumarin molecule resulted in partial or

Table 11. Root elongation of germinating caryopses of dormant (84) and nondormant (63) sources of Bouteloua curtipendula as affected by levels of pure coumarin.

Source	Coumarin (µg/ml)						
	0	1	10	25	50	100	200
84 (dormant)[1]	9.9 a	8.7 a	5.5 b	5.2 b	0.9 c	0.4 c	0.0 c
63 (nondormant)	16.3 a	13.2 ab	11.1 b	6.9 c	5.1 c	2.3 d	2.1 d

[1]Horizontal values not followed by the same letter are significantly different at the 5% level.

complete loss of inhibitory activity in lettuce and wheat seed germination. However, Wareing (1965) concluded that the inhibitory activity of seed extracts may be due, in some instances, to the cumulative effects of a number of relatively weak inhibitory compounds. These results tended to corroborate the results from the sodium hypochlorite extracts that coumarin-like compounds function in imposing dormancy in sideoats gramagrass seed. This preliminary work appears to offer an approach by which a chemical index could be developed to differentiate among dormant and nondormant seed sources and used as a selection tool in a breeding program.

Field Establishment

The 1970 field planting of sideoats gramagrass was a failure because of severe moisture stress at the Bowie, Arizona site. The early summer moisture in 1971 was very erratic in the Santa Rita Experimental Range south of Tucson, and no differential in stand establishment between dormant and nondormant sources was observed in 1971. Fairly large, replicated plots at a number of sites will probably be necessary to determine the association between plant establishment and seed dormancy characteristics.

CONCLUSIONS

This research results in the following conclusions.

1. Caryopses of all the sideoats gramagrass sources were dormant for 4 to 6 months following harvest. Post-harvest dormancy was evidently due to factors within the caryopses.
2. Dormancy appeared to be a heritable characteristic, although conditioned by the environment during seed maturation.
3. Long term dormancy was imposed by the spikelet appendages (lemma, palea, and glumes) enclosing the caryopsis. Seed units of some sources were dormant for at least 5 years.
4. Dehulling, germination in soil, sodium hypochlorite, and enriched-oxygen atmosphere were efficient breakers of dormancy.
5. Prechilling, red light, water leaching, hydrogen peroxide, and activated charcoal were less effective in breaking dormancy.
6. Pregermination treatment with sodium hypochlorite plus a seven day exposure to a 100% oxygen atmosphere appeared to yield a reliable estimation of germination potential in sideoats gramagrass.

7. Dormancy was positively associated with caryopsis weight, apomixis, the presence of a low molecular weight caryopsis protein, and coumarin-like inhibitors in the spikelet appendages.
8. The mechanism of dormancy was considered to be a combination of oxygen impermeability, inhibitory materials, and seedling vigor reduction due to lower caryopsis weight. Interactions between these and unstudied factors may lead to a complex system for germination control.
9. Caryopsis weight, mode of reproduction, differences of caryopsis proteins, and inhibitors in the spikelet appendages may be useful as selection criteria for improvement of sideoats gramagrass.
10. The association between performance of dormant and nondormant sources under field conditions and seed dormancy characteristics has not been established for sideoats gramagrass.

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