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Germination-Regulating Mechanisms of Giant Foxtail *(Setaria faberii)*

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CONTENTS

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D. James Morre' and O. Hale Fletchall

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The subject of seed germination is an often investigated and little understood area of plant physiology. It is a reasonably safe assumption that few plant investigators have never become fascinated by at least one of its many aspects. A number of experiments were performed during the years 1954 through 1959 in an attempt to illucidate the germination-regulating mechanisms of giant foxtail *(Setaria faberii),* an annual grass. Most of the experiments are necessarily of an exploratory nature, but serve to illustrate the control mechanisms which dictate whether or not, at a given time, a particular seed will germinate and produce a viable seedling.

INTRODUCTION

Giant foxtail *(Setaria faberii* Herrm.) is believed to have been introduced into the United States during the early 1930's as a contaminant of Chinese millet (8, 9). In the less than 30 years since its introduction, giant foxtail has proven such a successful competitor that it is regarded by many as the most serious annual weed ever to threaten the farmers of the cornbelt.

A tetraploid (10), giant foxtail often attains a height of six feet, and occasional specimens exceeding seven feet have been observed in well-fertilized corn fields. Giant foxtail is a serious competitor of row crops and finds optimal conditions for growth in tilled soil. Individual plants isolated in fence rows, although seldom growing over three or four feet high, branch profusely and produce as many as 20 tillers with a total of 30 or more individual panicles (seed heads). Giant foxtail will persist even when grown in the presence of a dense stand of alfalfa (13). In addition, depauperate fruiting forms less than three inches high have been observed where repeated mowing was sought as a means of preventing seed production (13).

Giant foxtail is a member of the foxtail millets and is a close relative of *Setaria italica,* the common or German millet (8). In form, growth habits and seed structure, it most closely resembles *S. viridis,* the common green foxtail of gardens and roadsides. Giant foxtail is usually taller and more robust and can be easily recognized by the rough pubescent leaves and a conspicuously nodding panicle.

The spikelet of *S. faberii* is subtended by an involucre of three to six bristles (8). Dehiscence is normally above the bristles so they seldom appear in carefully harvested seed. As in the closely allied genus *Panicum,* the thin and papery first glume of *Setaria* is reduced (about three-fourths the length of the second glume). The longer second glume and sterile lemma are of like texture and the caryopsis is enclosed in a much hardened lemma and palea. The lemma is roughened with coarse, closely-spaced transverse ridges. The entire spikelet is about 2.5 to 3 mm long and narrowly elliptic in outline. Color ranges from dark brown (nearly black) to yellowish green. Since the complete spikelet, including glumes and sterile lemma, is the natural dispersal unit of *S. faberii,* this structure will be referred to as the seed (or dispersal unit when it is necessary to emphasize that experiments involved use of the complete spikelet).

The germination characteristics of giant foxtail were first studied by King in 1952 (9). His observations with mature seed revealed that germination seldom exceeded 20 to 34 percent. In addition to studying the depth from which seeds would germinate, he also investigated the conditions under which seed would germinate in the laboratory. Culturing in association with soil, treatment with potassium nitrate and sodium thiocyanate, alternating temperatures (21° to 37°C) and moist storage at 21°C all resulted in increased germination. King (9) suggested that alternate wetting and drying of the soil also stimulated germination by the partial removal of growth inhibiting substances. The presence of germination inhibitors was indicated from filter paper absorption experiments.

PROCEDURES

Seed depths for emergence.—The first of two experiments to investigate the depth from which giant foxtail seedlings would emerge from the soil was initiated March 12, 1955 and conducted in the greenhouse at the University of Missouri.

After several unsuccessful attempts to germinate harvested seed, a source of seed that would germinate was obtained by removing the surface one-inch of soil from several locations on an area where giant foxtail was abundant the previous season. The soil was screened and thoroughly mixed. A one-inch layer of the seed-bearing soil was placed in each of seven two-gallon crockery pots eight inches in diameter, so that each container represented a different germination zone extending stepwise from the surface to seven inches below the surface. The experiment was replicated four times. Filler soil, screened and mixed, was also added in weighed, one-inch incruments. After the last addition, the pots contained 8 ± 0.5 inches of soil.

Daily counts of emerging seedlings were obtained for about one month after planting. Germination or, more correctly, emergence is defined as the number of seedlings appearing above the soil surface. Seedings were removed from the containers as they emerged. Soil moisture was kept near field capacity. Greenhouse temperature was maintained above 20° to 25°C from March 12 to April 8, 1955 when the minimum temperature was raised to 30°C. The initial experiment was terminated April 18, 1955.

A similar test was conducted under existing weather conditions starting with the zone placed from two inches to three inches below the surface. Soil was removed from an area twelve inches deep and twelve inches in diameter located in a well-drained site. Seed-bearing and filler soil was added as above. The test was initiated March 18, 1955 and the first seedlings appeared April 4, 1955. The test was terminated May 14, 1955.

Germination over a five-year period.—The containers from the greenhouse seed depths for emergence experiment were held at greenhouse temperatures from March 16, 1955 to September 1, 1956. At that time the zero- to one-, one-to two-, and two- to three-inch depths were transferred to existing weather conditions for further observations on seed viability.

Filler soil was removed step-wise by one-inch layers on April 19, June 1, June 24, September 1, October 3, and November 19, 1956 until the seed layers were exposed at the surface in all containers. Pots containing filler soil over the seed-bearing layer had not produced seedlings for at least two weeks prior to removal of the next layer of filler soil. Daily counts of emerging seedlings were recorded during extended periods of germination. With sequences of diminished germination, observations were limited to two- or three-day intervals.

Soil cores were removed January 3, 1956 from one-fourth of the containers using a laboratory cork borer of one-half inch diameter. The seeds were recovered by washing over a fine screen and examined for signs of deterioration.

Light, temperature, and conditions of storage.—Much of the information concerned with light, temperature and storage conditions was obtained coincidental to other experiments. Constant temperature rooms provided temperatures of 7°, 15° and 24°C. The 30°C temperature was maintained in a small light germinator. The effect of light was determined by germinating seeds in both light and dark germinators and in soil by covering the containers with transparent or opaque polyethylene plastic.

Natural dormancy of seed contained in the soil.—As a means of investigating the dormancy of seeds in the soil, seed sources were obtained by removing the surface one-inch of soil from several locations randomly selected in an area of *ca.* 30 square feet. The samples were mixed and transferred to containers fashioned for this purpose from half-gallon paraffined milk cartons, providing a germination area of *ca.* 30 square inches. A one-inch layer of seed soil was placed in each container. Samples were removed from the field at approximately one-week intervals. Greenhouse temperatures were maintained between 25° and 30°C during germination. Three experiments were conducted—at the University of Missouri in 1957 and at Purdue University in 1958 and 1959.

Germinability as a function of seed maturity.—Since previous experiments with freshly harvested seed indicated a close correlation between ability to germinate and date of harvest, an experiment was conducted in 1957 and 1958 to quantitate this relationship. The most highly developed panicles from several plants were collected August 1, August 15, September 1, October 1, and November 15, 1957 from a single location adjacent to the Purdue University Agronomy Farm. A sample was tested immediately and the remainder was stored at 24°C for 30 days. At that time the dispersal units were shattered from the panicle, cleaned and weighed. Each month following harvest an additional 100-unit sample stored at 24°C was submitted to test until October 1958. The test procedure consisted of placing 100 dispersal units on moistened Whatman Number 1 filter paper in a 10 X 100 mm petri plate. Germinations were conducted at 24°C for a period of 30 days.

Extracts from dispersal units.—Material for these experiments was obtained in quantity from a location in White County, Indiana. When submitted to test, less than two percent germination was obtained and the dispersal units were considered to be in a dormant condition. Preparation of extracts is described along with a tabulation of data under discussion of results. Seeds of cultivated millet *(Setaria italica)* and Vermillion wheat were used as a bioassy for inhibitory substances. The assay was conducted on extracts applied to Whatman Number 1 filter paper and contained in 10 X 100 mm petri plates.

Special techniques applied to specific problems have been omitted here. Additional details of materials and methods are included in discussion of results to facilitate interpretation of the data.

RESULTS AND DISCUSSION

Seed depths for emergence

In the greenhouse studies, 45 percent of the seedlings emerging in the first month were recorded from the surface one inch of soil (figure 1). The daily emergence rate from the first inch varied considerably as compared to the other depths and was most noticeably affected by environmental factors. For example, the number of seedlings emerging rose sharply on each third day after watering, even though the soil was kept near field capacity during the entire test.

Emergence from the one-inch to two-inch zone was comparable to the surface to one-inch depth and accounted for 37 percent of the total. Daily emergence from this depth was relatively constant and less affected by time of watering.

The number of emerging seedlings began to drop off sharply beginning with the two-inch to three-inch zone which produced only 13 percent of the total. Many seedlings emerged from this depth with a foliate leaf extended through the coleoptile and appeared less vigorous than seedlings from shallower zones.

The critical depth, however, appeared to be the zone between three inches and four inches below the surface. Only three percent of the seedlings emerged

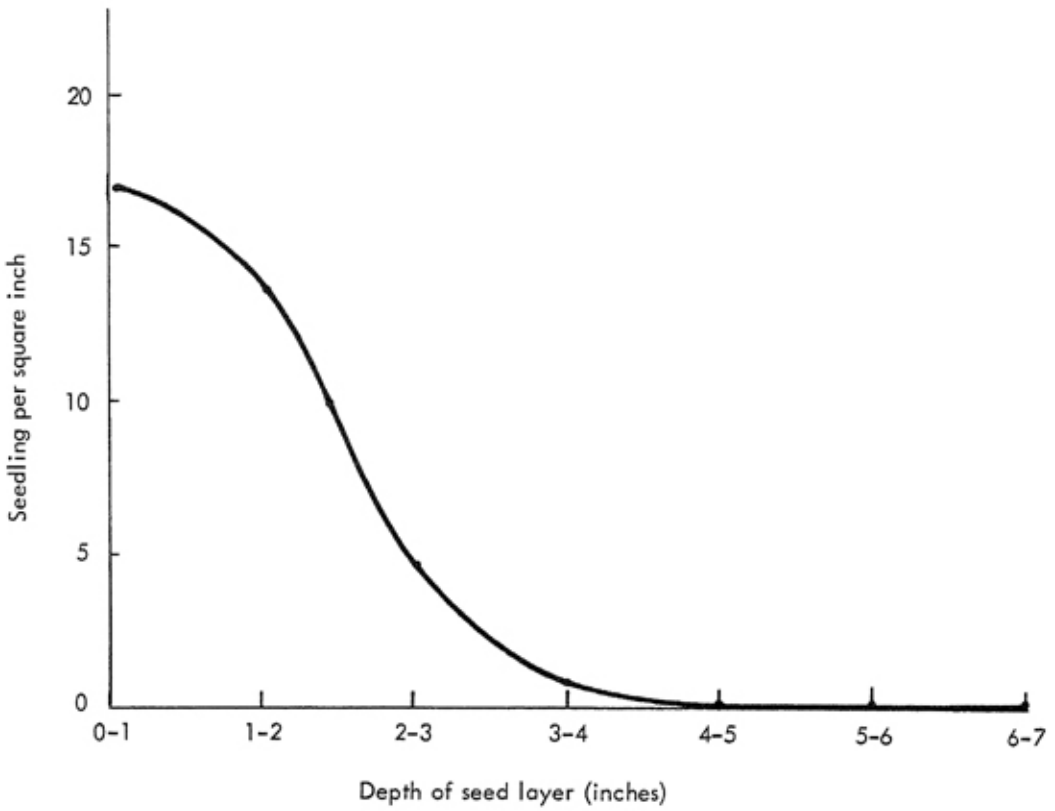

Figure 1. The number of plants per square inch emerging from seed-bearing soil placed in one-inch zones at varying depths. Greenhouse, March 16 to April 18, 1955.

from this layer. The emergence pattern of the remaining depths was found to parallel that of the control and it is doubtful if any seedlings actually emerged from a depth greater than four inches.

When a similar experiment was conducted under field conditions, the zone from four inches to five inches below the surface accounted for six times as many seedlings as either the five to six inch zone or the six to seven inch zone and possibly represents emergence from that depth (figure 2). Particularly in the field experiment, it was difficult to avoid contamination of filler soil during preparation of the test sites due to seed bearing soil adhering to the sides of the test holes.

In studying the behavior of giant foxtail in the field, Slife and coworkers (14) found no seedlings that emerged from a depth below three inches. However, they suggested that a small percentage may emerge from as deep as five inches under greenhouse conditions. These results, therefore, confirm those reported by King (9) where giant foxtail seed germinated and emerged from a depth of no more than three cm in compact soil. When the soil was loose and well aerated, they emerged from a depth of 12 cm.

On April 22, 1955, emerged foxtail seedlings were examined in the field to

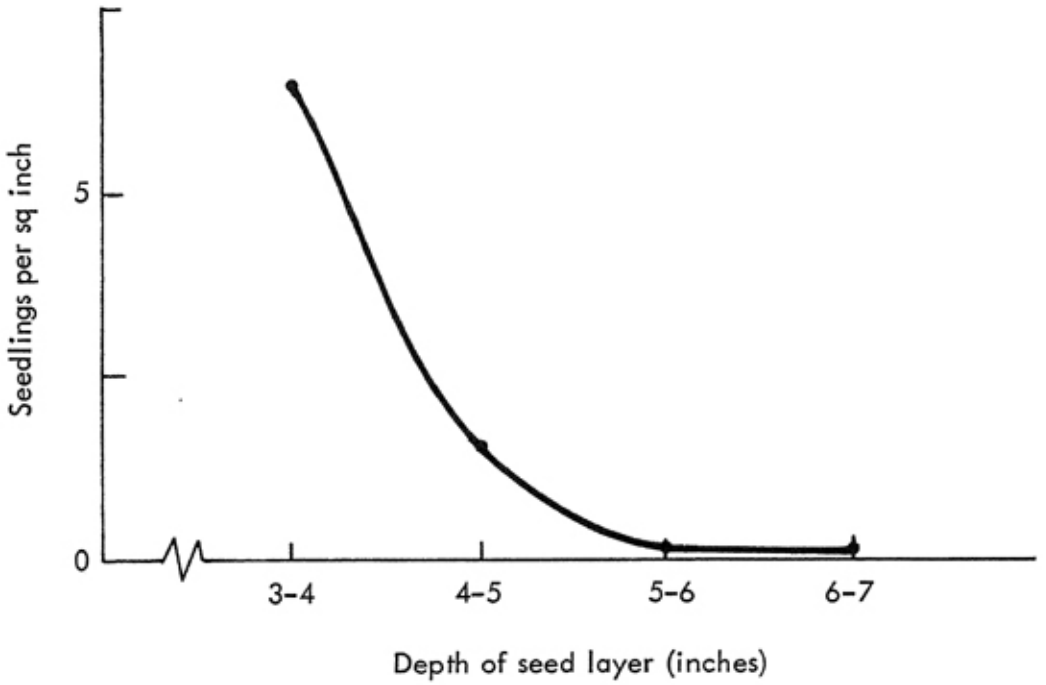

Figure 2. The n mber of plants per square inch emerging from seed-bearing soil placed in one-inch zones at varying depths. Existing weather conditions, April 4 to May 14, 1955.

determine the normal distribution of germination depth. Seedlings from 200 one square inch samples from two locations were measured and grouped into six classes (table 1). Although the sample is small, the data do tend to substantiate the greenhouse results—that most seedlings emerge from the surface inch of soil. The tendency for surface and near surface germination was greatly accelerated, however, since seed matured the previous fall was concentrated in this area. The maximum depth of germination recorded was just over two inches.

It is the mesocotyl that must compensate for differences in depth of germination, and in the field studies few plants were encountered with a mesocotyl over five centimeters in length. However, in the greenhouse, occasional plants germinating through cracks in the soil were able to produce sturdy mesocotyls over eight centimeters in length. Germination was consistently higher around the edge of the pots than in the center with all except the surface to one inch depth. These and other observations indicate that aeration or soil compaction may be a factor seriously limiting the depth at which seeds will germinate and from which seedlings will emerge. Experiments to induce germination of dormant seeds through increased aeration or to reduce emergence through application of external force were, for the most part, unsuccessful.

TABLE 1 - SEED DEPTH FOR EMERGENCE OF GIANT FOXTAIL SEEDLINGS UNDER FIELD CONDITIONS. AN AVERAGE OF 200 ONE SQUARE INCH SAMPLES FROM TWO LOCATIONS, COLUMBIA, MISSOURI, APRIL 22, 1955.

Seed Depth for emergence (mm)	Percentage of total
Surface	55
1-10	38
11-20	2
21-30	1
31-40	2
41-56	2
> 56	0

Germination over a five-year period

The germination of giant foxtail seeds contained in seed-bearing soil is represented schematically in figure 3 for the period March 16, 1955 to September 1, 1956. The first seedlings were observed March 17, 1955 and over 600 seedlings per day were recovered between March 19 and March 28, with a maximum of 975 on March 23, 1955. Germination then decreased steadily and from May 15 to July 22, 1955, only 20 seedlings were produced. Secondary peaks of germination were recorded between July 22 and July 30, 1955 and between October 27 and November 6, 1955.

A germination peak occurred again in April and May of 1956, the second year after initiation of the experiment. Between March 27 and June 5, 1957, seedlings were also produced; a total of 166 for the third season. During the summer of 1957 no seedlings were recorded, but a significant number appeared in the spring of 1958. Observations were continued through June of 1959 with no further germination being evident.

The results of the 5-year seed viability experiment further demonstrate the ability of a small percentage of the giant foxtail seeds to remain dormant in the soil for at least 4 years (the spring following seeding being considered as the first year) and to continue to produce repeated infestations from a single seeding. This viability is not unduly high since the life of bristly foxtail in dry storage is estimated at 20 years and that of yellow foxtail is said to exceed 30 years (4).

The removal of filler soil had no marked effect on the rate of emergence. Distinct increases in rate of emergence occurred at approximate intervals of three months with lesser fluctuations during the interum. Attempts to correlate the increases with daily fluctuations in temperature or solar radiation were unsuccessful.

When the soil cores removed January 3, 1956 were examined, it became evident that the central layers contained only a small fraction of the seeds origi-

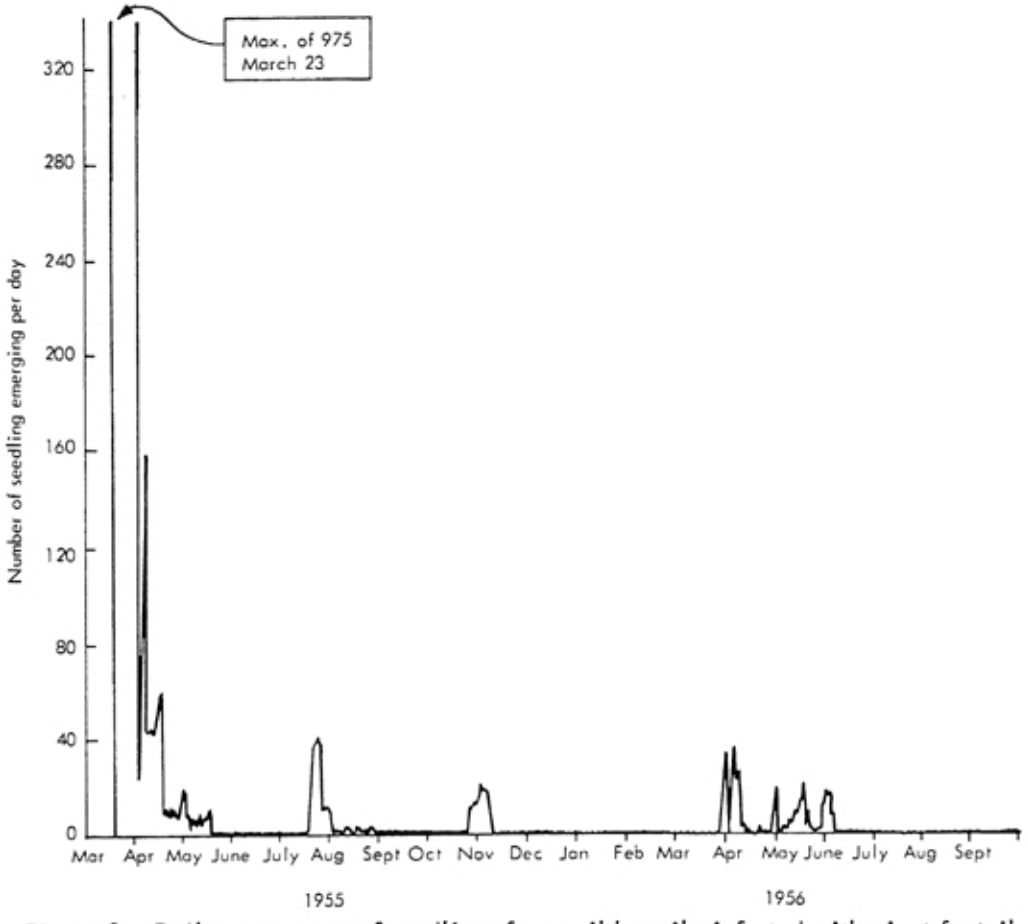

Figure 3. Daily emergence of seedlings from soil heavily infested with giant foxtail seeds (March 16, 1955 to Sept. 1, 1956).

nally present (summarized in figure 4). The surface and bottom layers contained the greatest number of apparently intact seeds (although far fewer germinations were recorded from the basal layers even after removal of filler soil). Since the containers were in equilibrium with the atmosphere at both top and bottom, it is evident that zones with comparable oxygen tensions retained comparable numbers of intact dispersal units. The bottom layers would be expected to represent slightly more anaerobic conditions due to an increased water content. On this basis it is suggested that destruction of the dispersal units which imbide water but do not germinate or emerge is through the action of soil organisms, certain of which are favored by anaerobic conditions.

Effect of temperature, light and conditions of seed storage

Germination percentages were comparable at various temperatures between 15° and 30°C and in most experiments germination was regarded as being relatively insensitive to small temperature fluctuations, but not germination occurred at 7°C. The highest germination percentage recorded (90%) was obtained at 24°C.

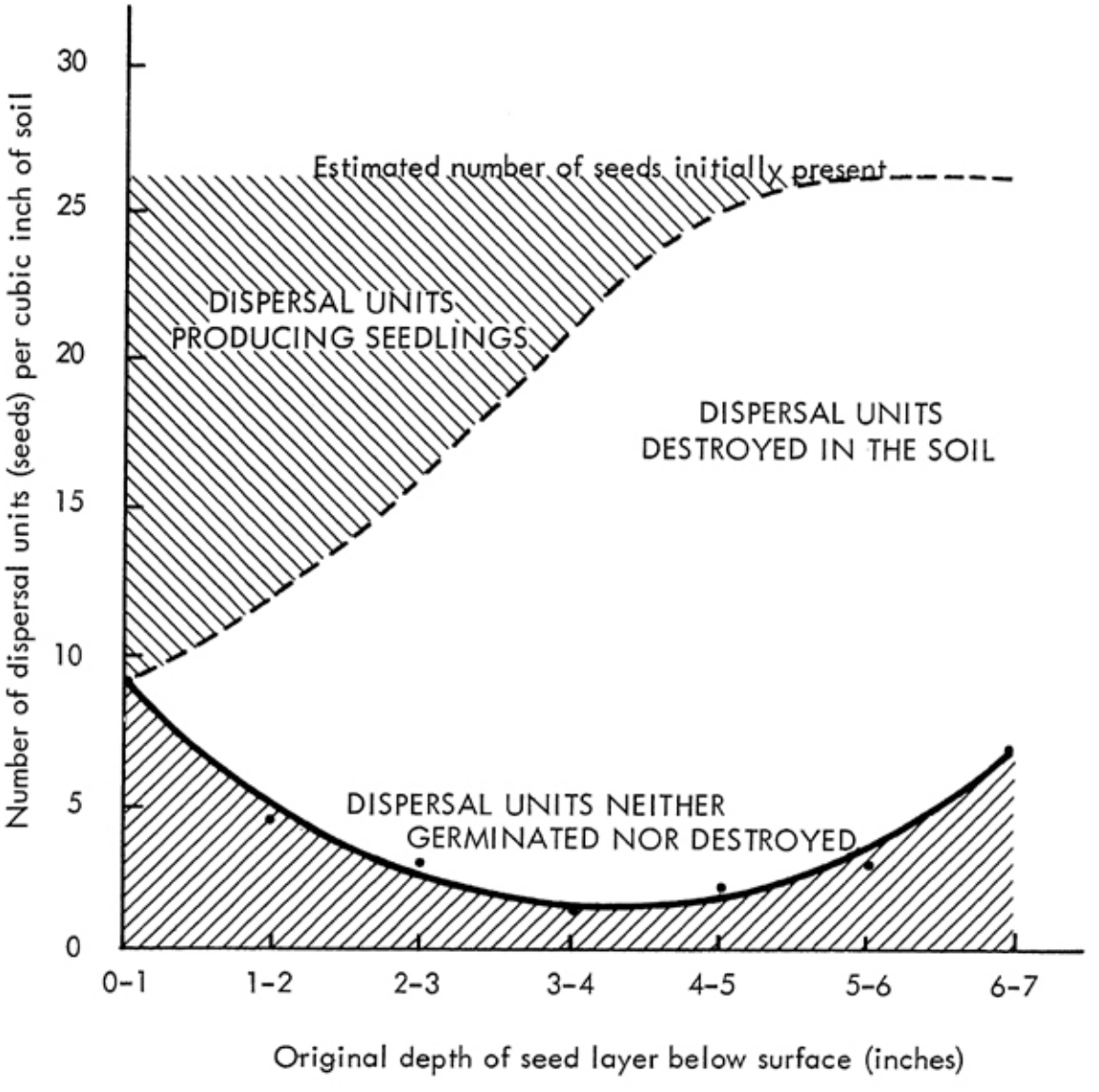

Figure 4. Schematic diagram showing the number of apparently undamaged dispersal units recovered at each depth (plotted points) in relation to the number producing seedlings (area above the broken curve). The difference between the two curves is taken to be an indication of the number of dispersal units destroyed in the soil.

using mature seed. Light was included as a variable in a number of experiments without effect.

The influence of storage conditions on the germination of freshly harvested dispersal units was not sufficiently critical to cause noticeable fluctuations in the results, except for weeds stored for long periods of temperatures exceeding 30°C. Temperatures alternating between below freezing and room temperature for two and four weeks during the February following harvest was found to be ineffective in hastening germination of either dry or imbibed seeds previously stored at room temperature. Alternate wetting and drying of seeds mixed with soil was also found to be ineffective contrary to the suggestion of King (9).

Slife's group (14) found that after storage for two years, giant foxtail seed was completely dormant regardless of conditions. They apparently obtained satisfactory results in restoring germinability by alternating the temperatures every other day between below freezing and 50°F for 8 weeks in the case of ***P. aneeps*** (5) and for one week or less in the case of ***P. antidotale*** (11).

Influence of enveloping structures on germinability

Improvement of germination by disorganization or removal of enveloping structures (scarification) is normally considered to result from improved permeability. In the case of giant foxtail, dispersal units, standard sulfuric acid treatment and sand paper scarification (in the manner for legume seeds) proved ineffective. However, by careful disruption of the bracts in the region of the seed apex (distal to the embryo), germination could be increased by 5% in the case of dormant seeds (0% control germination) and as much as 10% using seed predisposed toward germination. Results from experiments employing various methods of disrupting the eveloping structures of the caryopsis are summarized in table 2. It is interesting to note that germination could be increased by merely pricking the intact dispersal unit with a fine needle.

A treatment effective in the case of low-germinating samples, consisted of making a longitudinal cut along the apical one-third of the dispersal unit (just through the pericarp of the caryopsis). However, in April and May when many seeds germinated without special treatment, this method became progressively less effective.

The slight improvement in germinability resulting from mechanical treatment apparently does not result from a mechanical alteration of the caryopsis. Thus, germination could be most effectively increased by removing only the apical portion of the bracts, those which extend beyond the caryopsis, and without disturbing the pericarp.

It is important to note that scarification methods involving a minimum disturbance of the point of attachment of the bracts seem to offer the greatest stimulatory response. If the bracts were removed completely, the embryos were observed to swell but did not germinate. Caryopses of giant foxtail also failed to germinate when cultured on an agar surface or imbedded in the agar surface under asceptic conditions. By way of a procedural control, isolated caryopsis of cultivated millet ***(S. Italica),*** grown under identical conditions, resulted in a

TABLE 2 - SUMMARY OF EXPERIMENTS INVOLVING DISRUPTION OF STRUCTURES ENVELOPING THE CARYOPSIS, 1957.

Method of disruption	Sample Size No. of Seeds	Germination Percentage[1/]
none	900	16
bracts cut with razor blade on apex (penetrating pericarp)	900	16
bracts broken with forceps (apical region)	200	20
bracts removed completely	200	0
apical portion of bracts extending beyond endosperm removed with razor blade	200	23
apical portion of bracts removed as above to include the apical tip of the endosperm (penetrating pericarp)	200	11
sand paper scarification (broken dispersal units discarded)	100	16
prick units with fine steel needle		
in apical region distal to embryo	100	22
in dorsal region distal to embryo	100	2
prick units with coarse steel needle		
in apical region distal to embryo	100	5
in dorsal region distal to embryo	100	1

[1/] Standard deviation ± 2 percent.

germination percentage of 50%, slightly greater than the intact dispersal units. Dissection of the giant foxtail embryo was also ineffective in inducing germination.

Aqueous extracts prepared from isolated bracts prevented browning of the embryos and retarded growth of mold in the case of caryopses grown under nonsterile conditions. However, the ability of the caryopsis to germinate was not restored by addition of either the extracts or a finely ground powder prepared from isolated bracts.

Properties of extracts prepared from dispersal units.

Since seeds of cultivated millet *(S. italica)* do not exhibit a condition of

winter dormancy in the sense of giant foxtail *(S. faberii)*, it was possible to utilize cultivated millet as a bioassay of germination inhibitors extracted from giant foxtail seeds. The data presented in table 3 show that petroleum ether and ethanol were completely ineffective in extracting any sort of inhibitory substance from the dispersal units. The water extracts were, however, definitely in-

TABLE 3 - GERMINATION OF CULTIVATED MILLET (S. ITALICA) AS INFLUENCED BY EXTRACTS PREPARED FROM DORMANT GIANT FOXTAIL SEEDS[1/]

Extraction solvent[2/]	percent germ. of millet	inhibition of wheat root growth
none	43	none
petroleum ether	39	none
absolute ethanol	50	none
water	1	severe

1/ cg. 2% germination. Twenty-five grams of intact seeds were extracted 12 hours in the cold with 50 ml of extraction solvent. Extract corresponding to 5 grams of seed was evaporated onto filter paper in a 10 X 100 mm petri plate. Twenty-five wheat seeds and 25 millet seeds per plate were utilized in the bioassay. Each plate received 5 ml of water following solvent evaporation.

2/ In no instance did over 2% of the giant foxtail seed germinate following extraction.

hibitory to both millet seed germination and growth of wheat root. The osmotic concentration of the extract was excessive as indicated by plasmolysis experiments and contributed to the inhibition observed.

The inhibitory fraction is localized in the caryopsis as shown by the data in table 4. Soluble inhibitors could be detected in comparable extracts prepared from bracts of the giant foxtail dispersal unit (includes glumes, sterile and fertile lemma and palea). A dilution of extract from the caryopsis was then utilized which did not inhibit the growth of wheat roots over a 72 hour period but which still inhibited the germination of cultivated millet seed (table 4).

Germination of seeds over activated charcoal merely served to reduce an already scarcely perceptible germination rate. If charcoal was effective in removing any inhibitors, the beneficial effects were completely counter-balanced by removal of essentialities for germination.

One might argue that the inhibition of germination of *S. italica* seeds by water extracts prepared from *S. faberii* seeds is positive evidence for an inhibitor germination-regulating mechanism as suggested by King (9). But the fact remains that none of the extraction procedures were effective as a means of increasing the germination of *S. faberii* even with prolonged extraction (7 days). Until such evidence is obtained, any definitive conclusion regarding the physiological importance of such inhibitors is questionable.

TABLE 4 - GERMINATION OF CULTIVATED MILLET (S. ITALICA) AS AFFECTED BY A WATER EXTRACT OF DORMANT GIANT FOXTAIL SEEDS (S. FABERII) [1]

Extracted Material	Germination Percentage
none	44
intact dispersal units	33
bracts [2]	48
caryopsis [3]	33

[1] ca. 2% germination. One gram of plant material was extracted with 5 ml of deionized water for 6 hours. The extract was filtered and submitted to test without further dilution. Four tests utilizing 100 millet seeds each were utilized in the bioassay.
[2] glumes, sterile lemma, fertile lemma and palea
[3] embryo, endosperm and pericarp

Dormancy of seeds overwintered in the soil

Seed-bearing soil removed from the field on March 16, 1955 yielded up to 20 plants per square inch from a one-inch layer during the month following transfer to the greenhouse. However, the following year when seed soil was collected from the same area on January 1, less than one plant per square inch was obtained. It seemed reasonable to suppose that seeds of giant foxtail might exhibit some sort of cold requirement for germination. Samples of seed-bearing soil from the University of Missouri South Farm were collected at weekly intervals between February 4 and March 13, 1957 and transferred to the geeenhouse for observation (figure 5). An analagous experiment was conducted in 1958 at Lafayette, Indiana, with samples collected at weekly intervals from January 12 to March 23, 1958 (figure 6). The Indiana experiment was repeated in 1959 with nearly identical results.

The data presented in figures 5 and 6 are analagous in that germination increased sharply over a one-week interval in mid-February or early March to a relatively constant value. Prior to this sharp rise, germination did not proceed, nor did any of the samples collected before the critical period produce seedlings during the time that the later collections were germinating. This phenomenon may well fit yet another concept, that of secondary dormancy (3). However, one should be hesitant to classify a seed as dormant unless at some later time it is observed to germinate. It is perhaps more realistic to suggest that the bulk of the imbibed seeds in which after-ripening has not proceeded sufficiently to permit germination, fall prey to attack by soil organisms at the elevated greenhouse temperatures. As a first consideration, the germination control appears best interpreted as being the result of a critical cold requirement. However, an absolute cold requirement in the usual sense becomes untenable with further experimentation.

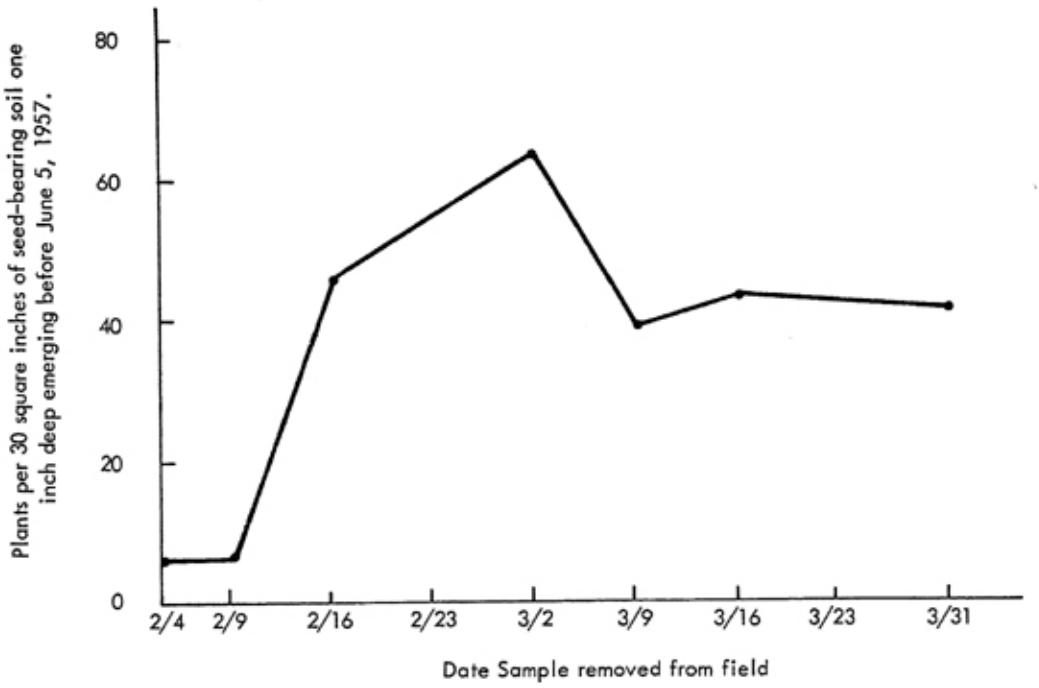

Figure 5. Emergence of giant foxtail plants in the greenhouse from seed-bearing soil removed form the field on different dates. University of Missouri South Farms, Columbia, Missouri, 1957.

Germinability as a function of seed maturity

The germination percentages of each of the twelve monthly trials following and including the month of harvest were averaged and are presented as figure 7. It is evident that germinability as a function of the date of seed harvest increases almost linearily with time. Dispersal units harvested in August, while still green, did not germinate. Maximum germinability was not attained until after senescence and death of the parent plant. It is important to mention that shattering from the panicles occurred by August 1, and by October 1 sufficient dispersal units had dropped to make further observations on seed production useless. The November 15 collection, which eventually attained 90% germination (figure 8) was harvested after frost and after essentially all dispersal units had shattered except from an occasional panicle protected from the wind.

The weight per 1000 seeds increased rapidly between August 15 and October 1, decreasing only slightly with the November 15 collection (figure 9). It becomes apparent after comparison of figures 7 and 9 that germinability is not a direct function of seed weight. The period of maximum weight coincides with the date of the first killing frost implying that translocation of storage materials is not a factor limiting germinaton.

None of the seeds germinated immediately following harvest and significant

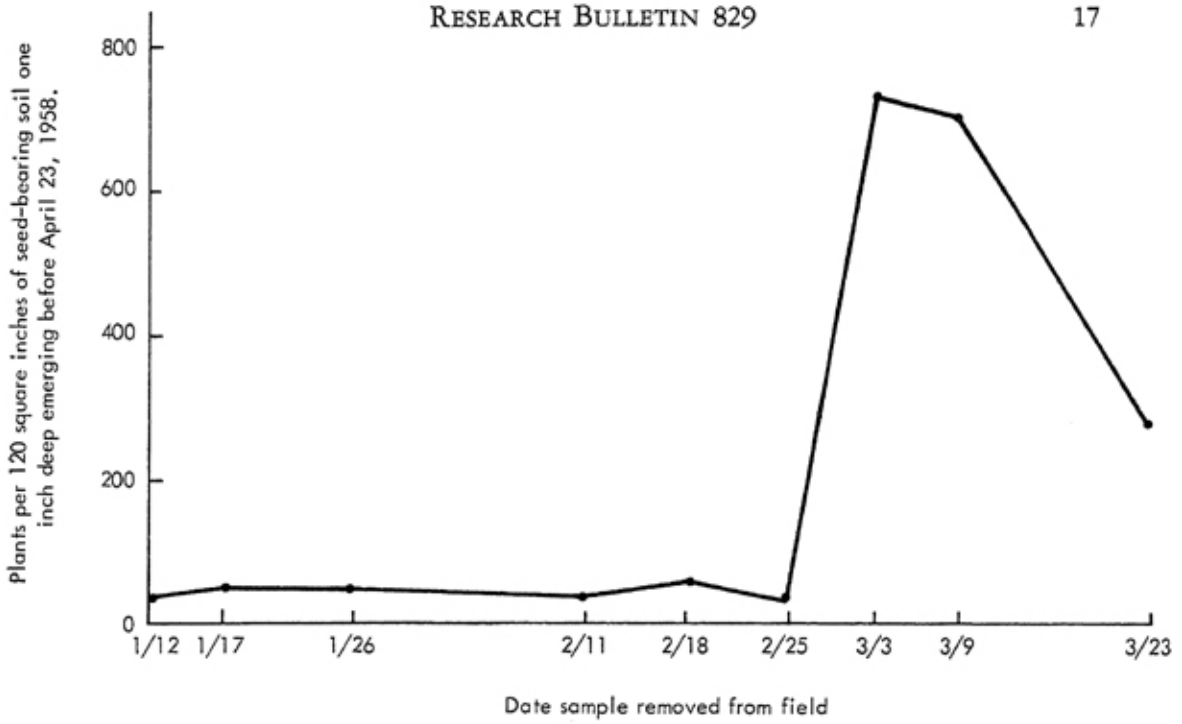

Figure 6. Emergence of giant foxtail plants in the greenhouse from seed-bearing soil removed from the field on different dates. Purdue University Agronomy Farm, Lafayette, Indiana, 1958.

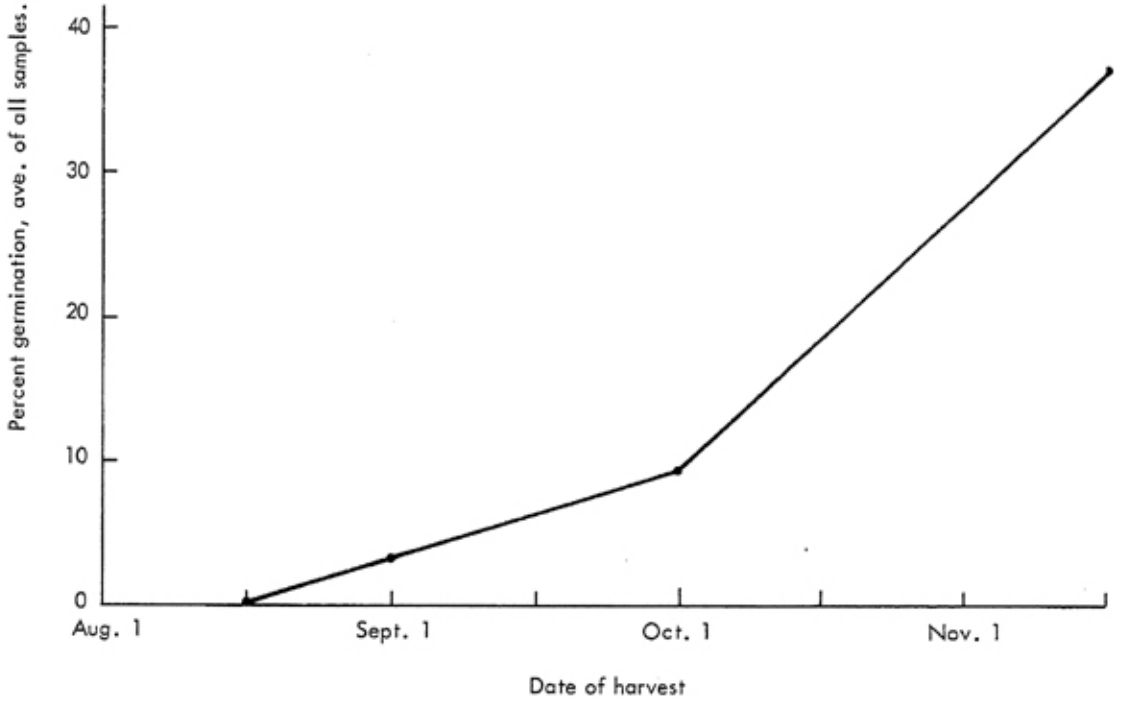

Figure 7. Average germination percentage over a twelve-month period following harvest as a function of date of harvest. Dispersal units stored and germinated at 24°.

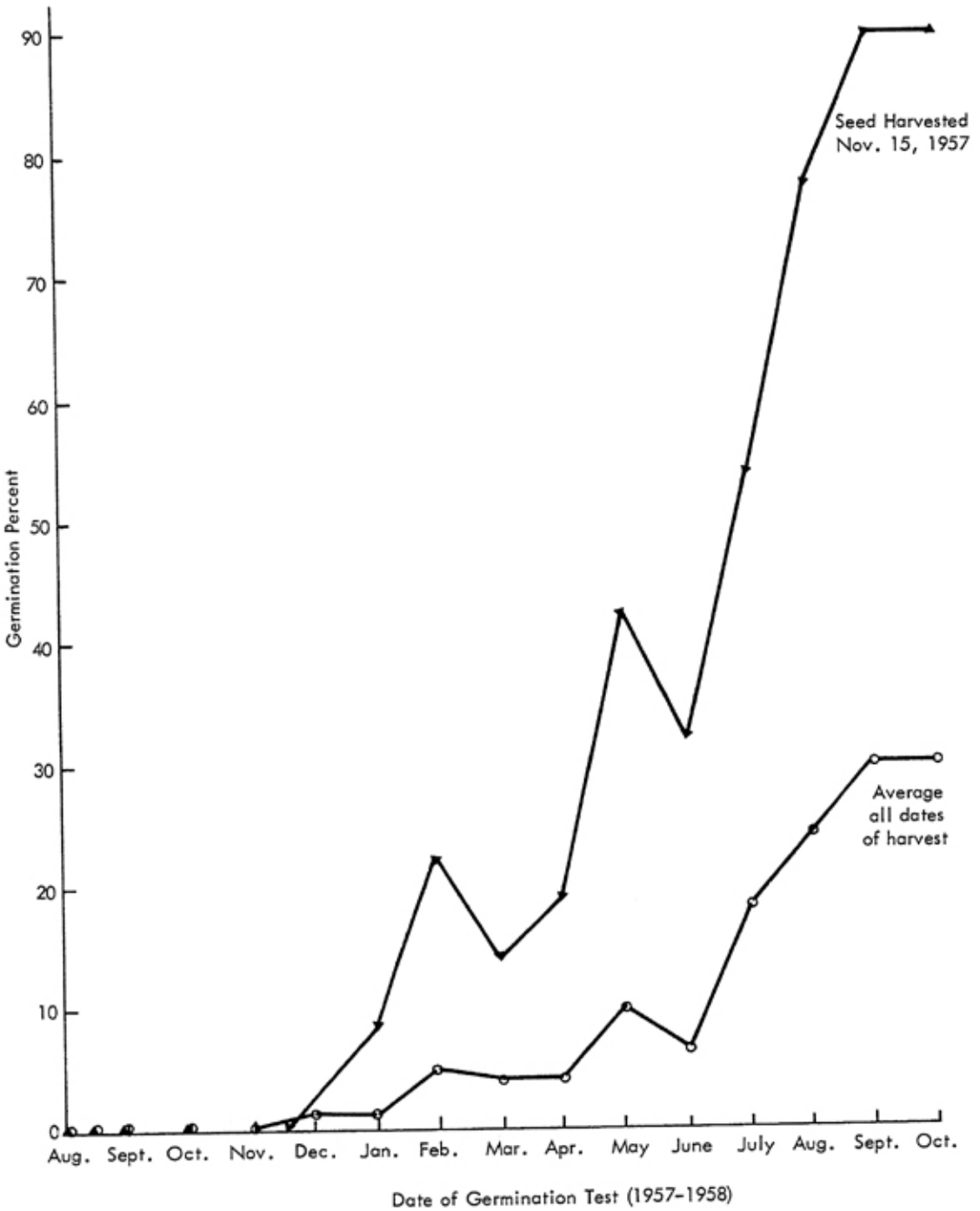

Figure 8. Monthly germination of dispersal units harvested November 15, 1957 (triangles) and the average monthly germination of all dates of harvest (circles). Units stored and germinated at 24°.

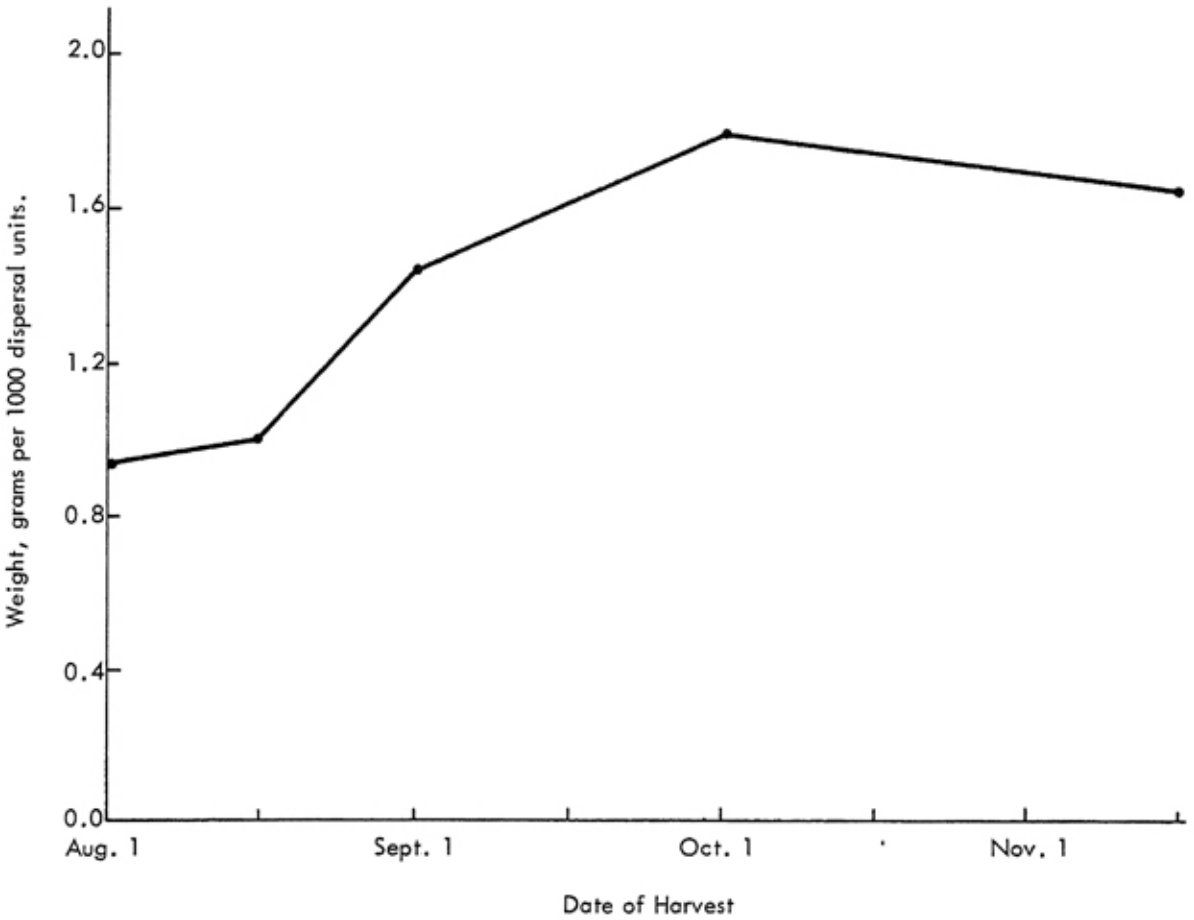

Figure 9. Average weight per 1000 dispersal units as a function of date of harvest.

germination percentages were not recorded until February coinciding with the time germination was found to occur in samples from the field (figure 8). Since germination proceeded in the absence of a cold treatment, the data are more suggestive of the phenomenon embryo dormancy (3). Germination then remained constant throughout April, rising in May and falling in June to again coincide with data obtained from field experiments (figures 3, 5 and 6). However, beginning with the July sample, germination increased steadily to attain a maximum in Sepember and October. This information, combined with that of the previous section, is perhaps best interpreted as embryo dormancy which would normally require a period of cold treatment for maximum efficiency in reverting to an embryo that can resume growth. Crocker and Barton (3) conclude that this type of dormancy is often associated with effects of dry storage at moderate temperature as presented in figure 8. Although the data presented are an average of all dates of harvest, each sample behaved in an analagous manner, reaching a constant value during the last two or three months of testing. This would suggest that seeds harvested prematurely have reached a state of development insufficient to allow germination even under conditions where embryo dormancy would otherwise be overcome.

A chemical difference in immature seeds is revealed by the fact that aqueous

extracts of freshly harvested seeds reoxidized methylene blue chloride previously reduced over excess sodium thiosulfate; a property which might occur, for example, as the result of large quantities of peroxides. Furthermore, the ability of freshly prepared seed extracts to oxidize pyrogallol was found to be a function of date of harvest, being most pronounced with the August collections and decreasing thereafter.

In the same experiment, seeds of giant foxtail plants treated in mid-August with dalapon (2,2-dichloropropionic acid) were also tested for germinability. Seeds were collected September 1, 1957 from plants showing about 50% neucrosis. Maximum germination was six percent as compared to 19 percent for untreated seed collected the same date. The resulting seedlings were weak and deformed and seed weight was reduced approximately 50 percent by the dalapon treatment.

A useful index for estimating germination potential

An early observation indicated that seeds with dark-colored (brown to black) inner bracts (lemma and palea) were among the first to germinate in any given test and in most instances were the only seeds to germinate. The data of figure 10 illustrates the close correlation between the percentage of "brown seeds" and maximum germination percentage recorded from each date of harvest. A parallel relationship is maintained until the final date of harvest when the germination percentage exceeded the percentage of "brown seeds". The data serve as a useful guide for determining the physiological age at which a mowing treatment would effectively reduce a giant foxtail infestation. If the most fully developed heads contained less than 10 percent "brown seeds", mowing to prevent seed production could still be employed as an effective control measure.

The weight per 1000 seeds and the total weight of seed from a given number of heads when combined with the data on the number of heads per plant made it possible to provide an accurate estimate of the potential seed production of a single giant foxtail plant. Data from 70 individual panicles collected between August 1 and September 1 contained an average of 870 seeds per panicle. The number of tillers per plant varied from 1 to 20 and the number of heads varied from 1 to 33 depending on stand density, competition and a number of other factors. An average value obtained for plants collected from a fence row indicates that a single plant may produce 20,000 or more seeds with an average of about 7,500. These results have already been presented in summary form (12).

GERMINATION-REGULATING MECHANISMS

Giant foxtail seeds, therefore, appear to undergo a period of after-ripening during which one would anticipate that the embryo becomes "of age" and continues the maturation process underway at the time of harvest. Seeds harvested early in the reproductive cycle seem to require additional direction from the parent plant in order for the embryo to eventually resume active growth. Such seeds have never been observed to after-ripen even under conditions which in-

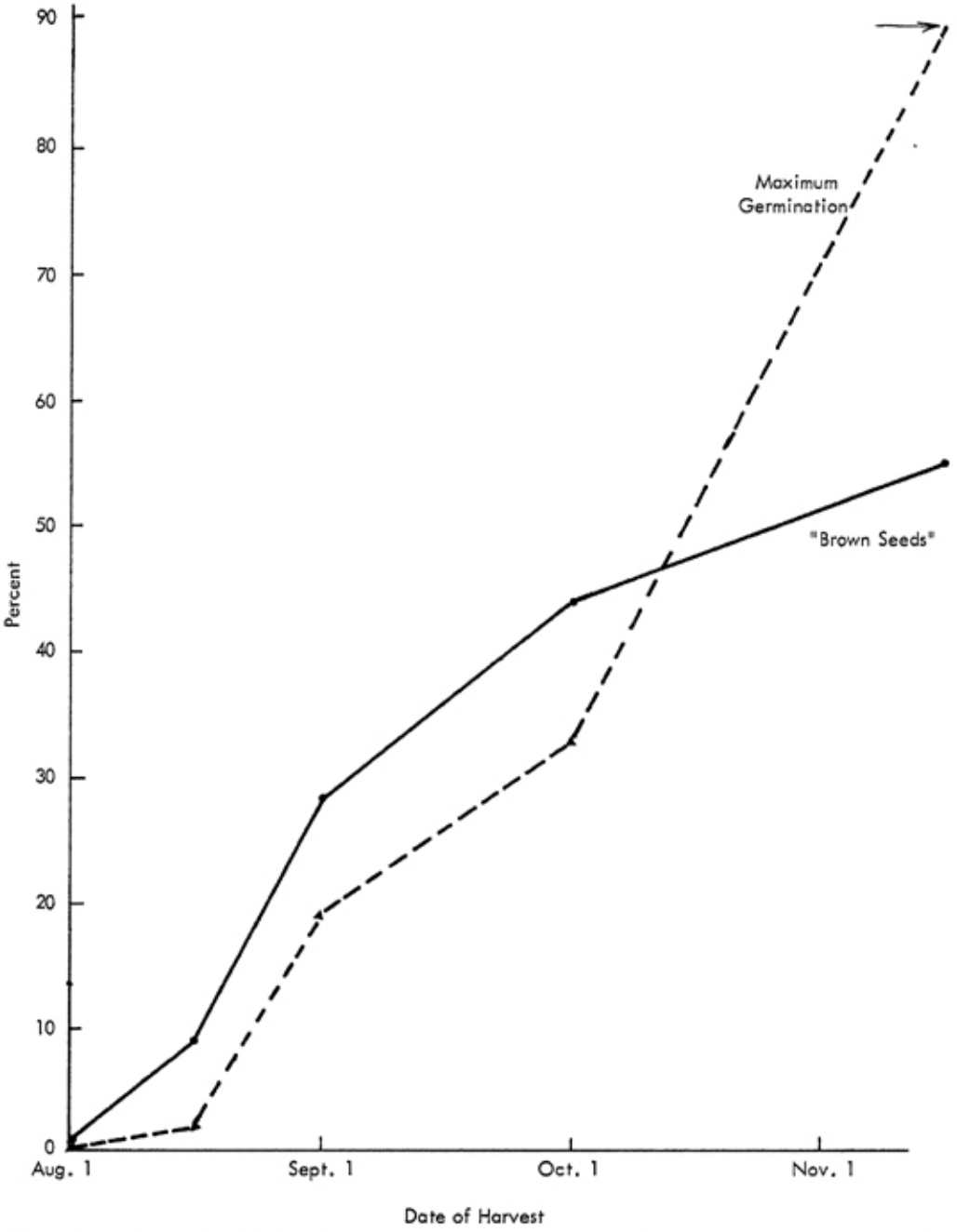

Figure 10. The relationship between maximum germination percentage over a twelve-month period following harvest and the proportion of "brown seeds" for each date of harvest.

sure the germination of other embryo dormant seed. As the panicle matures, more and more of the members of the seed population acquire the ability to develop mature embryos. For some reason, seed maturation is accompanied by change in coloration of the bracts from green to brownish black. Such an index provides an easy evaluation of germinability of a given seed sample. An associated chemical change is a decrease in the ability of aqueous extracts to oxidize

pyrogallol, a finding, for example, that might be indicative of large quantities of peroxides in immature seeds.

Seeds requiring a period of after-ripening can usually be induced to germinate by a moist treatment at low temperature to break the dormancy of the embryo (3). Seeds stratified in the soil under field conditions begin germinating in late February or early March, the actual time varying less than a week at the same location in two successive years. If such a dormancy condition does exist in seeds of giant foxtail, it would most likely be of the type overcome by a period of dry storage at room temperature. That this is so is suggested by the fact that seed populations stored at 24°C began germinating at approximately the same time as those in the field. Maximum germination, however, does not occur until the following season. Therefore, certain of the after-ripening processes appear as timing mechanisms to ensure germination under favorable conditions. Although not completely independent of temperature, after-ripening may proceed in at least some members of the population over a wide range of conditions, in both embibed and dry seeds.

Most of the seeds swell rapidly upon contact with water or in moist soil but are protected from decomposition in the field until after-ripening occurs by reduced temperatures and natural water soluble inhibitors of microbial growth contained in the bracts. These materials would be slowly leached out, eventually allowing ungerminated seeds to fall prey to destruction by soil microorganisms.

Oxygen supply is known to be a critical factor for seed germination in the soil (3) and in the case of both greenhouse and field studies, maximum emergence of seedlings was obtained from dispersal units contained in the surface inch of soil. The zone located between one inch and two inches below the surface compared favorably to the surface inch. In both field and greenhouse experiments, the critical depth for emergence was encountered between three and four inches below the surface. It is doubtful if any emergence occurs below a depth of four inches except through cracks in the soil. When emergence was investigated in a natural population of giant foxtail, 95 percent of the seedlings resulted from surface or near surface germinations.

Seeds unable to germinate or emerge as a result of being buried in the soil for a month or longer did not produce seedlings when the overlying layers were removed. The bulk of the buried seeds are apparently destroyed by soil organisms but invariably, a small percentage of the dispersal units appear to neither germinate nor decay. These seeds could at some later time account for what is commonly termed delayed germination or periodically occurring secondary peaks in the sense of the five-year viability experiment and produce yearly reinfestations. It is suggested that these seeds correspond to the "hard seed" fraction which responds to increase permeability through scarification. Although aeration appears to be a controlling factor in regulating the germination of nondormant seeds, attempts to induce germination of dormant seeds in the soil by various treatments to increase oxygen tension were unsuccessful.

In general, the properties which render certain seeds resistant to decomposi-

tion are not completely understood although impervious enveloping structures appear to contribute. In the cases of Johnsongrass *(Sorghum halapense),* the inner integument and certain layers of the pericarp have been suggested to contain tannin compounds which decrease their permeability (7). Increased deposition of tannins in these layers would account for the existance of "hard seed" in Johnsongrass as would increased lignification. Dispersal units of Johnsongrass also represent a situation where germination is benefited by a period of after-ripening (6).

A water soluble inhibitor of millet seed germination was found to be located in the caryopsis of the giant foxtail dispersal unit. Extracts prepared from dormant seeds inhibit germination under conditions where growth is unaffected. Since extraction of the inhibitor failed to increase the germination of dormant foxtail seeds, the water soluble inhibitor fails to fulfill a necessary requirement as a control mechanism. The bracts of the dispersal unit, although apparently free of substances inhibitory to germination, inhibit the growth of microorganisms and, in laboratory experiments, function as an early defense mechanism against decomposition.

Neither isolated caryopses nor isolated embryos from giant foxtail could be induced to germinate. A possible explanation lies in the fact that any scarification treatment that disturbs the point of attachment of bracts and caryopsis near the embryo, serves to drastically reduce germination, presumably through mechanical damage to the embryo.

In addition to the initial embryo dormancy and possible secondary dormancy induced by environmental extremes, giant foxtail seed germination appears to follow a circa-annum rhythm. Germination maxima occur each spring following harvest virtually independent of external conditions. A striking example is provided in figure 3 in that a strong secondary peak of germination occurred in the spring following almost five months of inactivity and in the absence of any cold treatment or conscious alteration of environmental conditions. Evidence for long-range biological clocks regulating seed germination is available for other species (2) and experimentation will undoubtedly reveal more.

The problem of periodicity in germination of seeds is adequately expressed by Warington (15) who states, "External factors alone, however, cannot provide the full explanation . . . neither can it be solely a matter of the seeds needing a definite period of after-ripening, or (in the case of Alchemilla) one would expect a continuous spell of germination with a gradual falling off after the rush in autumn whereas actually the decrease is fairly sharp and is followed by a second maximum in the following autumn without any fresh seed having been introduced."

SUMMARY

1. The factors that regulate the germination of giant foxtail *(Setaria faberii)* dispersal units are attributed primarily to embryo dormancy as quantitatively influenced by the maturity of the seed at the time of dispersal. Embryo dormancy is broken in late February or early March by stratification in the soil under field conditions. After-ripening of a portion of the seed populations stored at room temperature is accomplished at approximately the same time but maximum germination does not occur until the following season.

2. Nondormant seeds germinate over a wide range of temperatures (15° to 30°C; optimum 20° to 25°C) in both light and dark.

3. Whereas the bulk of the dispersal units are apparently permeable to water, permeability may limit germination in certain seeds in which germination is induced by scarification.

4. The critical depth for emergence of giant foxtail seedlings was encountered between three and four inches below the soil surface. It is doubtful if any emergence occurred from below a depth of four inches. When emergence was investigated in a natural population of giant foxtail on tilled soil, 55 percent of the seedlings were found to result from surface germinations with near surface germinations accounting for much of the remainder.

5. Many of the buried seeds which do not germinate or emerge are eventually destroyed by soil organisms. Some remain viable for at least four years producing yearly reinfestations.

6. Freshly harvested dispersal units are resistant to attack by microorganisms, a feature restricted to the bracts.

7. The caryopses of the dispersal unit contain a water soluble germination inhibitor absent from the bracts. Since extraction of the inhibitor failed to increase germination, the significance of this finding remains uncertain.

8. Germinability is a linear function of maturation time on the parent plant although the pattern of after-ripening is not changed appreciably. Coloration of the inner bracts (lemma and palea) provides an accurate index of seed maturity which should prove useful in scheduling mowing treatments to reduce seed production.

9. Seed production is estimated to be 870 seeds per panicle or an average of about 7,500 per plant. A single isolated plant growing on fertile soil may produce in excess of 20,000 seeds.

10. In general, germination of giant foxtail dispersal units is a cyclic phenomenon with maximum germination occurring in the spring independent of external conditions.

LITERATURE CITED

1. **Bass, C. M.,** Viability of injured weed seed. Proc. Assoc. Off. Seed Anal. N. Amer. 52-57 (1938)
2. **Barton, L. V.,** Respiration and germination studies of seeds in moist storage, Ann. New York Acad. Sci. 46:185-208 (1945)
3. **Crocker, W. and L. V. Barton,** Physiology of Seeds, Chronica Botanica, Waltham, Mass. 267 pp. (1953)
4. **Darlington, H. T.** The 50-year period for Dr. Beal's seed viability experiment, Amer. Jour. Bot. 38:370-381 (1951)
5. **Garman, H. R. and L. V. Barton,** Germination of seeds of **Panicum anceps** Michx, Contrib. Boyce Thompson Inst. 14:117-122 (1946)
6. **Harrington, G. T.,** Germination and viability of Johnsongrass seed, Proc. Assoc. Off. Seed Anal. No. Ama. 1916-1917 (1918)
7. **Harrington, G. T. and W. Crocker,** The pericarp and integument of Johnsongrass seed in relation to its physiology, **J. Agr. Res.** 23:193-222 (1923)
8. **Hitchcock, A. S.,** Manual of the grasses of the United States, 2nd ed., rev. by Agnes Chase, U.S.D.A. Misc. Publ. 200, 1051 pp. 1950 (1951)
9. **King, L. J.,** Germination and chemical control of the giant foxtail, Contrib. Boyce Thompson Inst. 16:469-487 (1952)
10. **Kishimoto, E.,** Chromosomenzahlen in den Gattungen **Panicum** und **Setaria.** I. Chromosomenzablen einiger **Setaria**-Arten, Cytologia 9:23-27 (1937)
11. **Koller, D. and M. Negbi,** Hastening the germination of **Panicum antidotale** Retz., Bull. Res. Council of Israel 5D:225-238 (1957)
12. **Lee, O. C., B. J. Rogers, and D. J. Morre',** Giant foxtail invades Indiana farms, Purdue University Ag. Ext. Circ. 457 (1959)
13. **Morre', D. J., O. H. Fletchall, and D. L. Klingman,** The Control of giant foxtail by the use of alfalfa, alone and in combination with herbicides, unpublished annual report of the Noxious Weed Control Projects of the Missouri Agricultural Experiment Station, Columbia, Missouri (1954)
14. **Slife, F. W.,** Private communication
15. **Warington, K.** The effect of constant and fluctuating temperature on the germination of the weed seeds in arable soil, **J. Ecol.** 24: 185-204 (1936)