

A STUDY OF DORMANCY IN SEEDS OF
BEAKED PANICUM, PANICUM ANCEPS MICHX.

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A STUDY OF DORMANCY IN SEEDS OF
BEAKED PANICUM, PANICUM ANCEPS MICHX.

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INTRODUCTION

Although seed dormancy is very common among grasses, the phenomenon is often difficult to study because dormancy may be lost within a matter of a few months and it is virtually impossible to repeat an experiment with a given lot of seed. Beaked panicum (Panicum anceps Michx.) has proved to be useful for such studies since seed lots may retain dormancy for a matter of several years. The grass has a potential value as a soil cover below pond dams and, in wet, water logged and frequently flooded areas. It has been used very little in seedings to date because of its extreme dormancy and information on breaking dormancy would be of considerable practical value. The studies reported in this paper were designed to find practical methods for breaking dormancy and to learn something about the nature of the physiological mechanisms involved.

LITERATURE REVIEW

The inability of viable seeds to germinate except under special environmental conditions is commonly called "dormancy", although as Koller et al. (1962) have pointed out "the significance of this term is vague and often misleading because of its indiscriminate use and lack of established criteria." Primary dormancy is that of the ripe dispersal unit at the time of dispersal or harvest, while secondary or induced dormancy is that appearing in the mature dispersal unit when imbibed under conditions unfavorable for germination. Primary dormancy is of survival value for the species and induced dormancy is important for survival and longevity of seed (Koller et al. 1962).

Because dormancy has survival value, a wide variety of mechanisms has evolved and the phenomenon is widespread throughout the Spermatophytes from conifers to Compositae and Gramineae. In one class of seeds, the embryos are immature when the seed is shed and a period of growth and development must follow before germination is possible. In some cases, the embryos are small, relatively undifferentiated masses of cells which must undergo considerable development during after-ripening. In other cases, the embryos are almost complete but still require a period of maturation before germination (Crocker and Barton 1957). In other classes of seeds, the embryos are mature and ready to grow, but germination is prevented by other means. Some of the more common mechanism affecting germination of seeds with nondormant embryos are

given below.

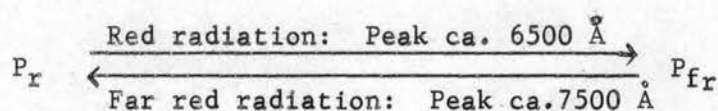
1.) Hard or impervious seed coats. The most extreme case on record of dormancy due to hard seed coats is that of Manchurian lotus (Nelumbo). The seeds were collected by Ichiro Ohga in a peat layer exposed by erosion in the Pulantien valley of South Manchuria. Ohga germinated several hundred seeds either by filing through the thick outer shell or by soaking in concentrated sulfuric acid for up to 5 hours. The age of the seeds was determined by W. F. Libby (1951) by the C^{14} method as 1040 ± 210 years. While this is an extreme example, many species have hard seed coats that prevent imbibition of water and/or gas exchange. This method of controlling dormancy is especially common in the Leguminosae. Mechanical or chemical scarification are usually effective in breaking dormancy of this kind. This may be done by piercing with a needle, filing with emerypaper or a steel file, violent shaking, scratching or abrading the seed coat, or soaking in strong acids or alkalis.

In some cases, the seed coats do not prevent imbibition of water but do act as semipermeable membranes preventing exchange of gasses or other materials required for germination. Examples are Xanthium, Triticum, Avena, or Hordeum (Crocker and Barton 1957). Increasing the oxygen pressure in the atmosphere greatly increased the germination at room temperature of partially after-ripened wheat (Harrington 1923). Waxy or oily substances in enclosing appendages may play a similar role, for example in Buchloë dactyloides (Ahring unpublished).

2). Light. The role of light in promoting or preventing germination is complex and not thoroughly understood. One of these is the

red-far red reaction of phytochrome. The action spectrum of light was first studied by Evenari and later more intensively by S. B. Hendricks, H. A. Borthwick and their associates at the Plant Industry Station, Beltsville, Maryland (Toole et al. 1956, Van der Veen and Meyer 1959, Koller et al. 1962, and Mohr 1962). In small, light sensitive seeds such as Lactuca and Lepidium, it was found that red light of 6000-6800 Å promotes germination while for far red light of 7000-7800 Å prevents germination. Imbibed seeds can be alternately shifted from red to far red light and back again any number of times and will respond according to the last radiation dosage received.

Phytochrome is a soluble chromoprotein in the cytoplasm and can be isolated in rather pure form. It behaves like an enzyme involved in a chain of biochemical processes directing the development of the plant. Since a small dose of radiation is needed to produce a measurable effect on the phytochrome system, it is a low energy reaction and can be illustrated as follows:



Phytochrome in the P_R form absorbs red light and is converted to the P_{FR} form. Upon absorbing far red light the P_{FR} form is changed back to P_R . The quantum efficiency for the conversion of P_R to P_{FR} is three times as great as that of P_{FR} to P_R (Mohr 1962).

P_R is stable in the dark while P_{FR} slowly changes back to P_R in the dark at physiological temperatures and in the presence of oxygen. In natural, white sunlight, both wave-length zones are present, but the

effect of red light usually predominates over the far red and P_{fr} dominates in imbibed seeds exposed to sunlight. In seeds inactivated by sunlight, the reverse effect takes place and the P_r phytochrome predominates, preventing germination. The relative radiant energies required to produce a given response in light sensitive seeds is influenced by many factors such as age of seed, storage conditions, temperatures during germination, oxygen supply and other factors (Toole et al. 1956).

Although the red-far red mechanism has been found to operate in most light sensitive seeds studied, it is probably not the only mechanism involved.

Some seeds show a photoperiodic response. Betula pubescens, for example, has "long day seeds" and seeds of Nemophila insignis are stimulated by short days (Koller et al. 1962). In some cases, the photoperiodic response seems to be confounded by the red-far red reaction, while in others the seeds behave as typical long day or short day plants. In Begonia evansiana, for example, germination is obtained at all photoperiods longer than 12 hours including continuous light, while photoperiods shorter than 8 hours inhibit. Interruption of the dark periods permits germination even with short photoperiods (Koller et al. 1962).

3). Temperature. Many seeds respond to a diurnal alternation of temperatures (Harrington, 1923a; Toshitaro, 1926). The mechanisms are far from being understood, but the phenomenon is so general that the rules for testing many species of agricultural and weed seeds include specifications for alternating temperatures (Assoc. Official Seed Analysis, 1960). Since the specifications were usually developed in temperate regions, they generally call for 8 hours of light at 30° C. and 16

hours of dark at 20° C. Other cycles were explored by Ahring (unpublished) for tropical species of grasses. Twelve hour cycles were found to have no marked advantage over the 8-16 hour cycle, but temperatures as low as 20° C. were sometimes detrimental (Ahring and Harlan 1961, 1961a).

High temperature shocks have been used to break dormancy in a few species (Evans 1952). Seeds of Eragrostis trichodes were found to respond even to temperatures of 100° C. for 40 minutes (Ahring et al. 1963). Drying seeds at 45-50° C. for 24 hours was found effective in breaking dormancy in Dichanthium annulatum (Ahring and Harlan 1961a).

One of the commonest methods of breaking dormancy, however, is moist low temperature storage, often called "prechilling". Storage temperature is usually about 5° C. and duration of treatment varies from a few days to several months depending on the degree of dormancy. The mechanisms are not at all well understood, but studies by Wareing and Villiers (1961) on Fraxinus excelsior suggest at least one mode of operation. Fraxinus has dormant embryos that must after-ripen. This can be done at either low temperature or at temperatures suitable for germination, although the embryos mature more rapidly at the higher temperatures. When after-ripening is complete, the seeds still will not germinate unless chilled for up to 6 months. The dry seeds do not contain a growth inhibitor, but after the seeds have imbibed water for 24 hours, a water soluble inhibitor is produced which effectively prevents germination. Under moist, low temperature storage, growth promoters are gradually produced and eventually accumulate in sufficient quantities to overcome the inhibitor. The inhibitor does not break

down and is found in approximately constant concentration throughout 6 months of prechilling. Apparently the reactions that produce the growth promoters are able to take place, although very slowly, at low temperatures while at temperatures suitable for germination, the inhibitor is produced more rapidly than the growth promoters. Thiourea promotes germination of unchilled seeds, but does not reduce the inhibitor. There may well be other kinds of mechanisms involved in moist low temperature storage, but it seems likely that some reactions are able to proceed at lower temperatures than others and that the prechilling treatments that break dormancy control opposing sets of reactions. One set of reactions, whatever it may be, promotes germination, and the other set prevents germination.

4). Chemical. Dormancy may be broken and germination promoted by a variety of chemicals added to the substrate. One of the most commonly used is KNO_3 at dilutions of about 0.2%. Ahring et al. 1963 demonstrated that the response in Eragrostis trichodes came from the NO_3^- ion and not from the potassium which could actually cause damage to the seedlings under some conditions. Calcium nitrate was just as effective and less likely to damage the seedlings. The use of KNO_3 is standard procedure for the germination of many species. The mechanism involved is not known.

Another class of germination promoters is the gibberellins. Gibberellic acid is most frequently used and is most often effective on light sensitive seeds. The acid may promote germination in the dark or reduce the light requirement. It may alter the photoperiodic requirement and is often most effective in combination with salts like KNO_3 (Koller et al. 1962). Kinetin has been found to reduce light requirements

and overcome certain kinds of induced dormancy. Several 6-substituted purines have been found effective as germination promoters and auxins have been reported as effective under certain conditions. Thiourea is another compound effective on a variety of seeds.

Evidence of germination inhibitors is widespread, but only a few chemicals have been incriminated. According to Barton and Solt (1949), there are three general groups of inhibitors known, essential oils such as those found in Brassica and Juniperus, alkaloids such as cocaine, quinine, caffeine and physostigmine, and glucosides such as those found in Amygdalus and Prunus. Inhibitors have been extracted but not identified in a wide variety of seeds (Barton and Solt 1949, Barton 1957, Koller et al. 1962, Ahring and Harlan 1961, Wareing and Villiers 1961, Wareing and Foda 1957, etc.). In some cases the inhibitors can be leached out, in most cases they break down with time, and they can often be removed with the seed appendages. Strong acids, alkalis, alcohol and organic solvents have been found effective in some cases.

According to Crocker and Barton (1957), factors affecting respiration of seeds are as follows: 1) seed coat, 2) moisture content, 3) temperature, 4) concentration of oxygen and carbon dioxide, 5) light, 6) embryo versus endosperm respiration, 7) dormancy, 8) effects of fungi and bacteria, 9) chemical composition of the seed.

The changes in respiration activity of seed during the initiation of germination are used as an indicator of the metabolism of the seed. According to Umbreit (1964) respiration quotients (RQ) are defined as the ratio of CO₂ produced / O₂ consumed, and serve to indicate the nature of the metabolism. However, authorities differ in their opinions on

the value of respiration quotient and in the interpretation of experimental results. Crocker and Barton (1957) stated "respiration quotients do not necessarily depend upon the principle food reserve but upon the substrate being used at a given time, and upon whether oxidation is complete," and "respiration quotient may not give an index of all the oxygen actually used or all the carbon dioxide which is released by the living tissues for some of either or both of these gasses may be held in the tissues." Just how many factors affect the relationship of one gas to the other in the exchange characteristic of living tissue is not well known. However, respiration quotients might give good information about the metabolism of the seed, if the experiment could be run properly and the respiration quotients were measured accurately.

Seed dormancy in Panicum anceps was studied by Barton and Gorman (1946) and Mathews (1947). The removal of seed coats with concentrated H_2SO_4 improved germination in one seed lot and not in another. Treatments with 71.0% H_2SO_4 , 0.2% KNO_3 , 35% $NaOH$, 50% HCl and 0.025% $HgCl_2$ were ineffective as were several concentrations of dioxygen and ether water, various temperature treatments and dry heat.

The literature in the area of seed dormancy is enormous and cannot be covered here, but of particular interest to this study is a series of papers on the biochemistry and bioenergetics of low temperature stratification (Barton and Fine 1958, 1961, and Barton 1945, 1947) published by the Boyce Thompson Institute. The review of germination inhibitors by Evenari (1949) is also pertinent. Despite a great deal of very good research in the physiology of dormancy and germination the mechanisms that promote or prevent germination are very poorly

understood. The studies conducted in this report were designed to learn something of the requirements for germination of Panicum anceps seed.

METHODS AND MATERIALS

Seed of Panicum anceps Michx. was furnished by Mr. Robert P. Lippert, Plant Materials Technician, Soil Conservation Service, Manhattan, Kansas. The age of the seed studied was: 1) less than one year, 2) one but less than two years of age, 3) two but less than three years of age, and 4) three but less than four years of age.

A Stults Da-lite germinator set for 8 hours of artificial light at 30° C. and 16 hours of darkness at 20° C. was used to provide the germinating environment. Plastic boxes 2 7/8 by 2 7/8 by 1 1/8 inches with lids were used as germinating conditioners. The substrate for all boxes was 6 thicknesses of Kimpak Tissue cut to equal size and drawn at random for each box. The moistening agent was 8 milliliters of distilled water measured accurately with a burette. One box containing 50 seeds was considered as an experimental unit. Four replications were used throughout with one replication of each treatment on each of four trays in a randomized block design with a tray being a block. Except where otherwise noted the germination period was 28 days with counts made every seven days.

The following studies were made:

1. Mechanical removal of lemma and palea. Seeds were rubbed gently on a rub-board, examined under a dissecting microscope and broken or scarred seeds discarded. Only apparently perfect caryopses were used.

2. Treatment with concentrated sodium hypochloride (household clorox).

Ten treatments were used, Table II. After each soaking period, seeds were removed and washed under running tap water for about 15 minutes before placing on moistened substrate for germination.

3. Prechill treatment. Seeds were placed in their germination boxes

with moistened substrate and then placed in a refrigerator at approximately 5° C. at various time intervals so that all treatments could be removed and germinated simultaneously, Table III. The accumulative effect of prechilling was studied in another experiment. There were six treatments each totaling ten weeks of prechill plus a no prechill check, Table IV. In one treatment, the seed was prechilled one week, germinated for two weeks, prechilled again for one week, germinated for two weeks, returned to prechill, etc. for a total of ten one-week treatments. In the second treatment, seeds were prechilled for two weeks, germinated for two weeks, etc. for a total of five two-week prechillings. Three-week, four-week, five-week and six-week treatments were also included as indicated in Table IV.

4. Leaching in running water. Seeds were leached in running tap water for 24 and 48 hours to remove water soluble inhibitors.

5. Respiration quotients during prechill treatments. Seven Warburg flasks were used, three for oxygen uptake, three for CO₂ release, and one for a thermobarometer. Each flask contained a circular piece of filter paper in the bottom, 1 ml. of distilled water and ½ gram of Panicum anceps seeds (ca. 800). Lanolin was used for sealing stopcocks and flasks. The experiment was conducted in a cold room at a constant

temperature of 5° C. Four measurements of O₂ uptake and CO₂ release were taken each week. Since lanolin became solid at 5° C., the manometers could not be closed and flasks could not be opened. The manometers and the flasks had to be moved to room temperature for five minutes, allowing the lanolin to soften, and then 1 ml. of fresh 20% KOH solution was injected into the center wells and side arms of the flasks used for measuring O₂ uptake. Next, all seven stopcocks were taken out and manometers and flasks were returned to the cold room. After an hour to stabilize the temperature, the stopcocks were replaced, the measurements were taken. The first measurement started at 3:00 p.m. and lasted until 5:00 p.m. One reading was taken every 20 minutes. After the last reading, the manometers were left closed until 9:00 a.m. of the following morning when another seven readings were taken. Next, the manometers were opened and KOH solution was removed from the flasks. Seeds were germinated as in the other experiments.

RESULTS AND DISCUSSION

1. Mechanical removal of lemmas and paleas resulted in a striking increase in germination, Table I. It is evident that we are not dealing with immature or dormant embryos. If dormancy is due to an inhibitor, it must be primarily in the lemma and palea and not in the testa, endosperm, or embryo.

Mold was a serious problem in the germination of these lots and may have reduced total germination.

TABLE I

THE EFFECT OF MECHANICAL REMOVAL OF LEMMA AND PALEA ON
GERMINATION OF PANICUM ANCEPS SEED

Age of Seed	Average Percent Germination	
	Control	Caryopses
0-1 year	0	56.6
2-3 year	8.0	50.0

2. Treatment with concentrated sodium hypochloride resulted in increasing germination almost to the maximum obtained by any method. Significant increases were obtained by three hours, and maximum results were obtained in six hours. Having established in the previous experiment that the lemma and palea are responsible for most of the dormancy, the question is raised concerning the effect of a strong oxidizing agent such as clorox. Did the chemical destroy an inhibitor? Did it weaken the lemma and palea making them more permeable to water and gasses? These questions were not answered by the experiment, but a quick and practical method of breaking dormancy was demonstrated. Upon our recommendation, Mr. Lippert, who furnished the seeds, was able to obtain a field stand for the first time by soaking beaked panicum seeds in clorox before seeding.

TABLE II
 THE EFFECT OF COMMERCIAL CLOROX ON GERMINATION
 OF PANICUM ANCEPS

Length of Time in Minutes	Average Percent Germination	
	0-1 year	1-2 year
0	0.5	3.5
30	---	10.0
60	---	10.0
90	---	12.0
120	---	14.0
180	26.5	29.0
240	28.5	30.0
300	53.0*	56.9*
360	79.5*	79.0*
420	58.0*	64.0*
480	21.0*	37.0*

*Significantly different from control at 5% level.

3. Prechill treatments were effective in breaking dormancy, Table III. The same lot of seed was studied in successive years, and there was a consistent relationship between age and the degree of dormancy. As might be expected, the fresher seed required longer storage at low temperature to reach maximum germination. Again questions are raised concerning the mechanism. Did the long soaking weaken the lemma and palea and make them more permeable? Did the treatment destroy an inhibitor? What kind of biological reaction takes place at low temperature and which does not take place at a temperature suitable for germination?

TABLE III

THE EFFECT OF VARIOUS PRECHILLING TREATMENTS ON GERMINATION
OF A SINGLE LOT OF P. ANCEPS SEED AT
DIFFERENT TIMES AFTER HARVEST

Duration of Prechill (weeks)	Average Percent Germination			
	Age of Seed			
	0-1 year	1-2 year	2-3 year	3-4 year
0	0	0	0	7.0
1	0.75	0.5	0.7	0
2	2.20	2.3	1.2	30.0
3	4.20	4.0	4.2	70.2*
4	7.20	7.2	3.0	70.0*
5	24.50	44.0*	79.0*	74.0*
6	42.75*	41.2*	64.0*	86.0*
7	32.00*	57.0*	60.0*	78.5*
8	51.50*	60.0*	60.8*	72.2*
9	65.75*	72.0*	86.0*	---
10	65.25*	77.5*	73.3*	---

*Significantly different from control at 5% level.

The accumulative prechill study, Table IV, seems to indicate that for the most part treatments can be interrupted and resumed and the seed can "remember" the previous treatments. The interrupted periods are more or less additive although ten interrupted one week periods is not as effective in breaking dormancy as some of the other treatments. In this study the 2, 3, and 4 week initial prechill treatments were much more effective than in the previous study. This is attributable to a higher degree of processing of the seed previous to the experiment, but does not alter the general conclusions.

TABLE IV

THE EFFECT OF INTERRUPTED PRECHILL TREATMENTS ON GERMINATION OF PANICUM ANCEPS SEED

Number of Prechill Treatments	Average Percent Germination Following Each Prechill Period*										Ave. Total % Germination	
	1	2	3	4	5	6	7	8	9	10		
None	12.3	---	---	---	---	---	---	---	---	---	---	12.3
10 for 1 week each	14.0	9.2	20.2	4.2	1.0	0	0.5	1.0	0	0	50.1	
5 for 2 weeks each	34.0	8.0	21.0	0	0						62.0	
3 for 3 weeks each plus 1 for 1 week	57.7	8.7	8.0	0							70.2	
2 for 4 weeks each plus 1 for 2 weeks	60.5	7.0	1.5								69.0	
2 for 5 weeks each	61.0	10.5									71.5	
1 for 6 weeks plus 1 for 4 weeks	46.7	25.2									71.9	

*Seed 2-3 years old

4. Leaching in running water had relatively little effect on germination, Table V. If an inhibitor is involved it would seem to be bound on else not very water soluble.

TABLE V

THE EFFECT OF LEACHING IN RUNNING WATER ON
GERMINATION OF P. ANCEPS SEED

Treatment	Average Percent Germination
	Seed 0-1 year old
Control	4.0
Leaching 24 hours	11.2
Leaching 48 hours	10.2

5. Respiration quotients during prechill treatments were determined on 2-3 year old seed over a 10 week period, Table VI. The curves for O_2 uptake and CO_2 release are of the same general form as the germination curves, Figures I and II. The most rapid increase in germination occurred in the fifth week of prechill and the most rapid rise in O_2 uptake was also in the fifth week. The minor fluctuations in both the respiration study and the germination study are probably not significant. Both methods point strongly to a substantial increase in metabolic activity from the fifth week onward. Apparently, the seeds are actively mobilizing their reserves of energy during low temperature storage at about this time.

It should be pointed out that the seeds did not actually sprout during the ten weeks of treatment, but metabolic activity increased at the same time that the capacity for germination increased. Obviously, low temperature storage is not required to mobilize the reserves of energy, because this can be done more rapidly at higher temperature provided the lemma and palea are removed or the seed is treated with chlorox. It would seem, therefore, that the physiological reactions within the caryopses are more or less temperature independent. The question remains: what do the lemma and palea do to prevent germination, and why do the lemma and palea lose their effectiveness as germination inhibitors under cool, moist storage?

The sudden drop in the R.Q. at three weeks suggests that substrates other than carbohydrates are being metabolized at that time. The R.Q. close to unity during the first two weeks probably means that carbohydrates only are being metabolized early in the prechill period. At

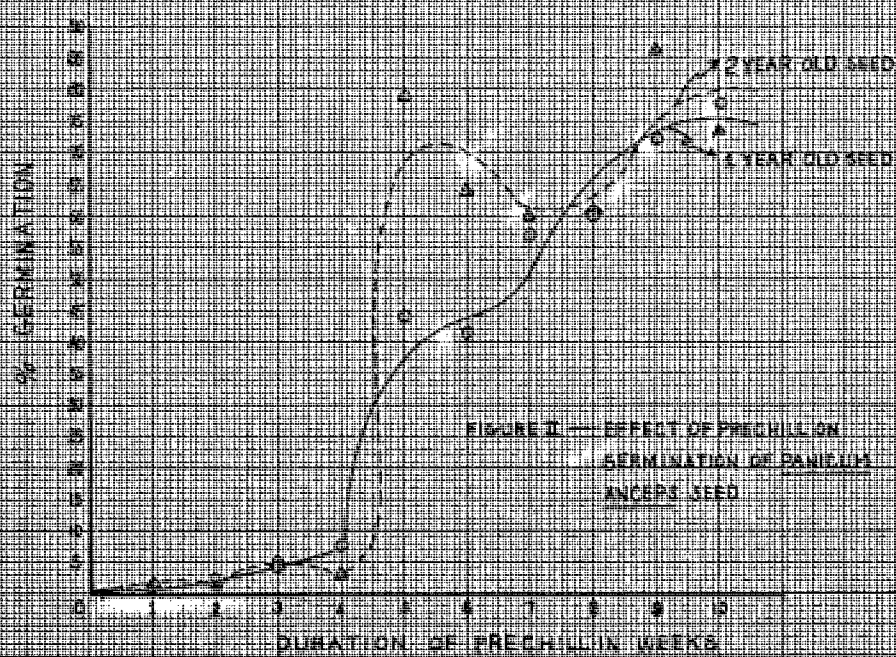
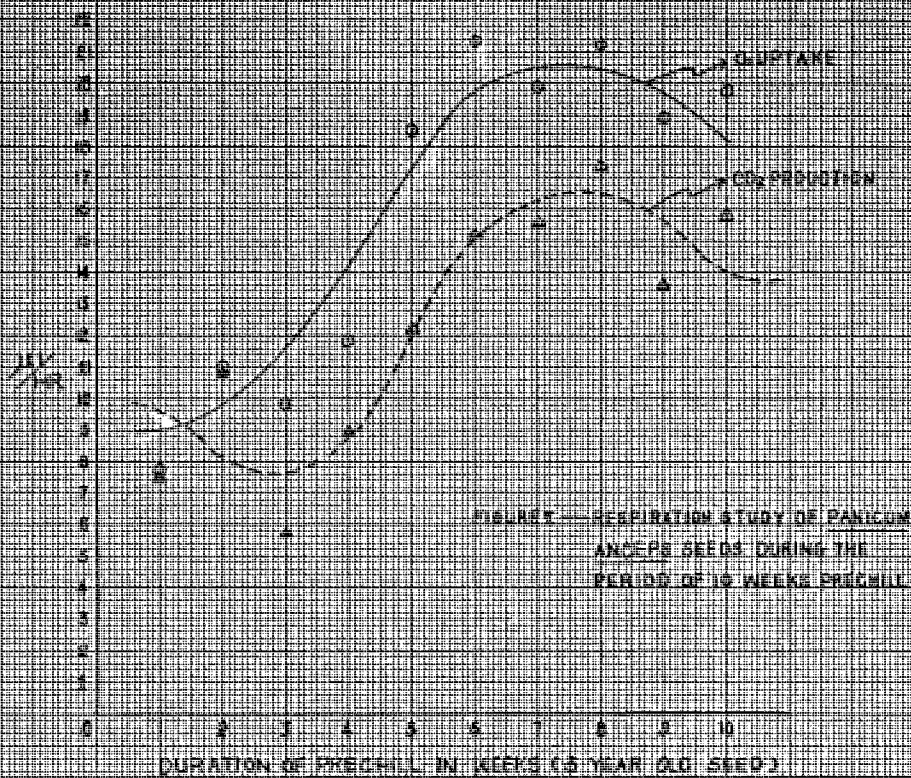
three weeks, the drop to an R.Q. of 0.60 indicates that fatty materials are being converted and utilized. This is two weeks before the first major increase in germination. The implication is that oily or waxy substances are being broken down for about two weeks before a sudden release of germinability. Since the lemma and palea are clearly incriminated in the control of dormancy, it seems likely that some of the oily or waxy substances are in the enclosing appendages and that after these substances are sufficiently broken down (about 5 weeks in prechill) the appendages are no longer able to prevent germination. Why these fatty materials are not metabolized at ordinary germination temperatures remains to be investigated.

An alternate explanation is that the fatty materials are primarily in the embryos and that they are being converted into growth promoting substances which are able to overcome the effects of inhibitors. This would be in line with the experience of Wareing and Villiers with Fraxinus.

TABLE VI
 THE STUDY OF SEED RESPIRATION DURING THE
 PERIOD OF TEN WEEKS PRECHILL

Prechill Duration (weeks)	Average O ₂ Uptake μl/hr	Average CO ₂ Release μl/hr	Respiration Quotients
1 week	7.72	7.60	0.96
2 weeks	10.96	10.79	0.98
3 weeks	9.96	5.65	0.60
4 weeks	11.84	8.94	0.76
5 weeks	18.51	12.08	0.65
6 weeks	21.37	15.06	0.70
7 weeks	19.95	15.55	0.78
8 weeks	21.16	17.38	0.92
9 weeks	18.91	13.44	0.73
10 weeks	19.73	15.74	0.80

*2-3 years old seed.



SUMMARY

- 1) Moist storage at 5° C. was found to significantly improve germination of dormant seeds of Panicum anceps. The optimum treatments were nine and ten weeks prechill at 5° C. for seeds up to three years of age and about six weeks prechill for seeds over three years old. Germination without prechill was essentially zero, while the best treatments ranged from 65% for new seeds to 86% for three year old seeds.
- 2) Presoaking seeds of P. anceps in concentrated sodium hypochloride was found to be effective in overcoming dormancy. Six hours of treatment was found to be the most effective. This treatment resulted in 79.5% and 79.0% germination for one and two year old seeds respectively. After soaking seeds in concentrated sodium hypochloride for six hours, the lemma and palea and part of the seed coat were separated from the caryopses.
- 3) Naked caryopses obtained by rubbing intact seeds on a rubber board gave 56% and 50% germination for one and two to three year old seeds respectively. High susceptibility to mold affected germination of the naked caryopses, otherwise a higher percent germination might have been obtained. This result suggested that dormancy in seeds of P. anceps is mainly due to some effect of the lemma and palea.
- 4) No increase in germination was found by leaching seeds under

running water for the periods of 24 and 48 hours.

- 5) Prechill effects on germination were found to be accumulative since seeds given various discontinuous prechill treatments brought nearly the same total germination. The interruption of 14 days germination at warm temperature seemed not to affect the prechilling effect on germination.
- 6) From the results of the study of seed respiration during the period of ten weeks prechill, it was evident that both oxygen uptake and carbon dioxide production were low for the first three weeks, and that both of them increased after the fourth week about two-fold and remained almost the same after the sixth week. It was found that the rise of respiration activity paralleled the rise of germination percentage during the period of ten weeks prechill. The respiration quotient was close to unity for the first two weeks and there was a sudden drop at the third week. It remained between 0.7 and 0.8 for the rest of the period of study. The R.Q. indicated that carbohydrates were metabolized for the first two weeks and the drop in R.Q. at the third week suggests that fatty materials were being metabolized from the third week on.

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