DORMANCY STUDIES IN *HORDEUM SPONTANEUM* SEEDS

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I. INTRODUCTION

The seed dormancy, especially of cereals, seems to be of interest from the scientific as well as the agricultural viewpoints. Many works were devoted to this problem, and it has been well established that the seed dormancy in many species is caused by the inhibitory influence of structures covering the embryo rather than by some other factors within the embryo itself. Though various interpretations have been presented, the mechanism by which the coveriug structures impose dormancy in cereal seeds is still by no means clear.

Furthermore, there is a growing body of evidence which shows that seed dormancy in many species is due to the presence of inhibitory substances in various parts of the dispersal unit. Therefore, the possibility that the effect of the covreing structures is due to their action in preventing the diffusion of inhibitors from the caryopsis seems also to be of value to study.

Moreover, increasing attention is now being paid to the effect of gibberellin in breaking the dormancy of cereal seeds.

In this study, the effects of various treatments known to be effective in inducing the germination of dormant seeds were investigated with the purpose of developing a practical method for breaking dormaney for use in breeding programmes and of finding the basic mechanism controlling the dormancy of these seeds.

Though the dispersal unit of the barley plant, used in this study, is a caryopsis surrounded by the attached husk, in the agricultural sense this is the "seed". For convenience, the word "seed" will be used in this paper.

II. MATERIAL AND METHODS

The seeds of *Hordeum spontaneum* C. Koch var. *transcaspicum* Vav. were used as plant materials, because of the very deep post-harvest dormancy (Figure 1). They were sun-dried after harvest and stored in a tin-container at ambient temperature until the experimental use.

In the germination test, 50 seeds were distributed equally between two 9 cm Petri dishes; the bottom of each Petri dish was lined with a filter paper, moistened with 5 m*l* of distilled water or of chemical solutions. The seeds were

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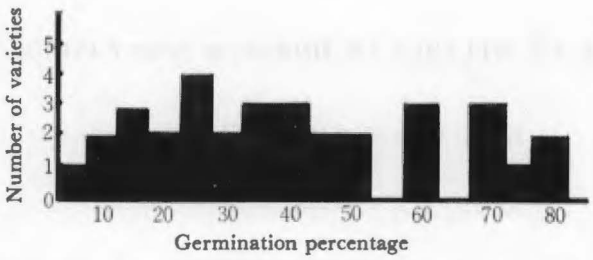

Fig. 1. Histogram showing distribution of germination percentages of 33 different varieties of *Hordeum spontaneum* C. Koch. Germination tests: 20°C for 7 days, in late July to early August. *Hordeum spontaneum* C. Koch var. *transcapsicum* Vav. seeds failed to germinate under the experimental condition.

incubated for 7 days at 20°C.

The germination of embryos was tested in Petri dishes of 5.5 cm in diameter. The seeds were surface-sterilyzed by immersing into Uspuln solution (1 : 800) for 20 minutes and then imbibed water for a day at 30°C. After imbibition, the seeds were removed and embryos were excised from them for the germination tests at 30°C. The germination test, in which twenty embryos were distributed equally between two dishes, was repeated several times and only a typical result was reported. Occasional departures from this technique are noted in the text.

In the experiments for knowing the germination of isolated caryopsis from plants treated with gibberellin, the stem was cut below the flag-leaf at various stages of maturation of seeds after anthesis, and the cut end was inserted into flasks containing gibberellin solutions of various concentrations and water as a check. After remaining them for 7 days, the spikes were dried and the caryopsis from these spikes were used for the germination tests.

The determination of water absorption was based on the increase of weight during the imbibition period with 2 samples of each 25 seeds. The seeds were placed on a filter paper in 9 cm Petri dish and 5 m*l* of distilled water was added. After having been imbibed for 2, 4, 6, 24, 48 and 72 hours at 30°C, the seeds were weighed, and the results were expressed as percentages of dry seeds.

The respiration was measured manometrically. The center well of Warburg vessel contained about 0.7 m*l* of 20% solution of potassium hydroxide and a piece of filter paper, and the amount of oxygen taken up by 25 seeds were recorded at 30°C.

For the determination of amylase activity, homogenates were prepared by grinding 10 seeds by pestle and mortar in 10 m*l* of distilled water. The reaction mixture contained 5 m*l* of 1/20 M acetate buffer (pH 5.1), 10 m*l* of 2% starch solution, 5 m*l* of distilled water and 5 m*l* of homogenate as enzyme solution. Five m*l* from the reaction mixture was pipetted into a beaker containing 5 m*l* of 0.1 N NaOH solution, to which was added 2 m*l* of 0.1 N iodine solution. After 15 minutes, the mixture was acidified by adding 10 m*l* of H_2SO_4 (1 : 4)

for its iodometric titration with 0.025 N solution of sodium thiosulfate. The same procedure was applied after incubating the reaction mixture for 4 hours at 37°C, and the difference in the amount of sodium thiosulfate solutions needed for the titrations was recorded for amylase activity of the homogenete.

For the determination of reducing-sugar, micro-Bertrand method was used.

For the test of the possibility of the presence of inhibitors, 10 g of seeds were ground into meal and extracted with ether for 48 hours at 3°C. Fatty substances were removed with petrol ether from the dried ether extract (petrol ether extract), and the residue was melted in 90% methanol (methanol extract). The seed meal, after extracting with ether, was extracted again with water, and the aqueous extract was filtered and the filtrate was precipitated with the equivalent amount of ethanol (water extract). Furthermore, the petrol and the methanol extracts were separated into water soluble and methanol soluble fractions. They were dried to 2 m*l*, and the concentrated extract was diluted with water to 20 m*l* of total volumes. For the bioassay of these extracts, non-dormant seeds of a naked cultivar., Kobinkatagi, were used.

III. EXPERIMENTAL RESULTS

1. *Effects of Structures External to the Embryo on Seed Germination*

The inhibitory effect of structures other than the embryo on germination seems to be well-known, but the possibility still exists that the effects of various surgical treatments may differ with the states of after-ripening. If the mechanism by which dormant seeds can be germinated differs with the different surgical treatments, and if the requirements for germination may differ in variously after-ripened seeds, it may be that the relative effectiveness of the various surgical treatments should differ depending upon the states of after-ripening.

In order to investigate this possibility, germination tests were carried out during after-ripening at room temperature using four treatments as follows: (1) seeds not dehusked (control); (2) seeds dehusked; (3) seeds cut in half transversely; and (4) seeds dehusked, cut in half transversely.

The results shown in Figure 2 indicate that this is not true. The relative effectiveness of these treatments was not altered by the after-ripening. Moreover, it may be said that, though the inhibitory influence of the husk is a factor in causing germination in *Hordeum spontaneum* seeds, a more important factor also exists. An excision of the distal half of the endosperm and associated pericarp and testa is more effective in causing germination than the dehusking, and the cutting in half of the dehusked seeds causes additional increase in germination; in fact, the results indicate that the effect of this treatment is more than additive of the effects of both dehusking and cutting.

Furthermore, it must be mentioned that the germination of intact seeds at 20°C was never exceeded 30% even by the prolonged storage at ambient

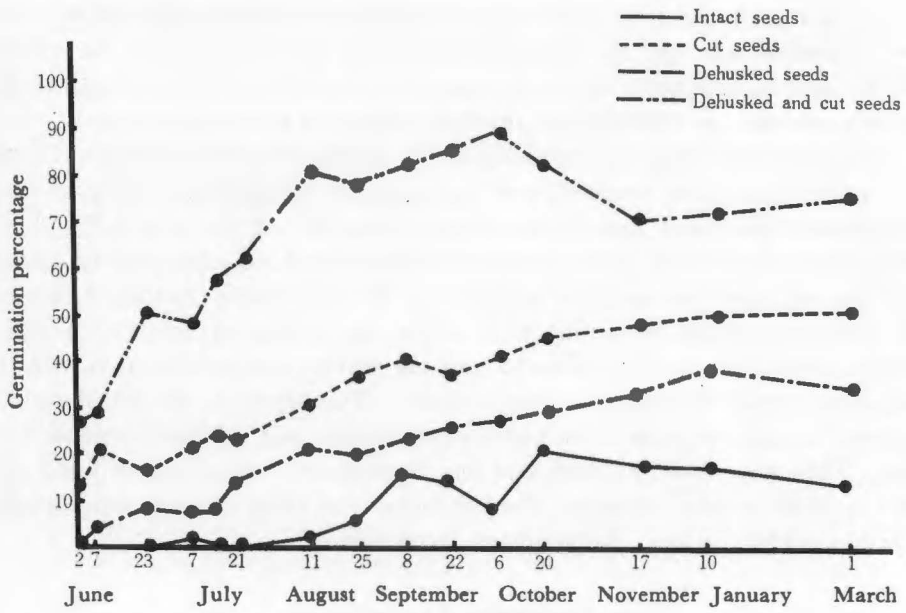

Fig. 2. Germination of variously wound seeds during after-ripening.

temperature.

That the freshly harvested seeds of cereals do not germinate at high temperature of 30°C, but they develop this faculty during a period of after-ripening has been known since the work of Atterberg (1907). It may be of interest to study whether or not the effect of the wounding on germination at different temperatures varies with the after-ripening.

An experiment was conducted in order to know the temperature effect on germination of seeds exposed to various surgical treatments. A sample of newly harvested seeds was obtained and a part of it dehusked by hand, cut in half transversely or dehusked and cut in half transversely. They were set to germinate at 5°, 20° and 30°C for 7 days and the results were compared with those of intact seeds. A comparable series of treatments on seeds which had partially broken dormancy was also carried out. The results of this experiment have been presented in Figure 3.

In the newly harvested population, maximum germination occurred at 5°C, and the dehusked and cut seeds showed almost complete germination as compared with the dehusked seeds or the cut seeds. The intact seeds failed to germinate. The rise in temperature lowered the germination, and scanty germination occurred at 30°C. Furthermore, it must be pointed out that the dehusked seeds are more sensitive to the higher temperature than the seeds cut in half. In the partially dormant population, germination occurred to some extent even at 30°C if the seeds were dehusked and cut in half transversely. Therefore, it may be said that *Hordeum spontaneum* seeds behave similarly to seeds of wheat in

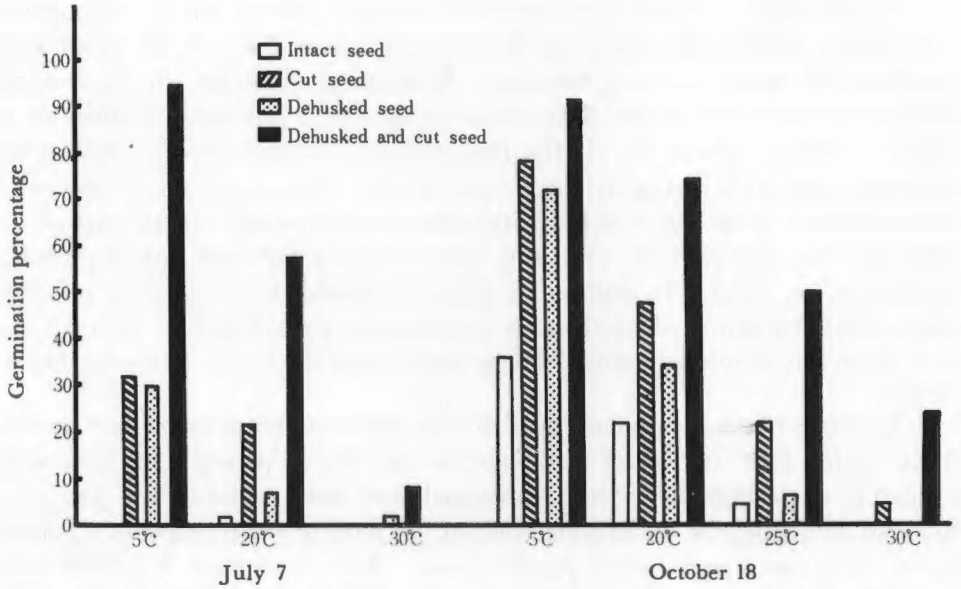

Fig. 3. Effects of various wounding treatments on germination at 5°, 20°, 25° or 30°C of dormant and partially after-ripened seeds.

the sense that germination of dormant seeds is very low at high temperature but the seeds eventually develop the ability to germinate at these temperatures.

In this study, it was found that the removal of the distal half of the endosperm is more effective in inducing germination of dormant seed than the dehusking. But the effect of cutting varies with the amount of endosperm removed from the caryopsis. This is apparent from the results of experiment shown in Table 1, in which 0, 1/4, 1/2 or 3/4 of the endosperm was removed from the intact and the dehusked seed.

TABLE 1

Effect of excision of endosperm on germination of intact and dehusked seeds

Amount of endosperm removed	Husk intact	Husk removed
Not excised (control)	6%	12%
1/4 endosperm removed	12	58
1/2 endosperm removed	46	68
3/4 endosperm removed	48	84
Embryo	100%	

It can be seen that the more the endosperm is removed, the higher is the germination and that nearly all the seeds germinate if the husk and 3/4 of endosperm are removed. Furthermore, it is very important to note that extracted embryo germinate completely under the conditions of the experiment.

As previously stated, the removal of the husk allows the germination of some seeds which would otherwise be dormant, but it does not affect all seeds and some of them remained dormant. It seems possible that the husk could form a barrier to the inward diffusion of oxygen or to the outward diffusion of some inhibiting substances. If the husk prevents the germination during the dormant period by acting as the barrier to the diffusion of some substances, then it should be possible to break dormancy by excising a small part of the husk covering the embryo. Excising other parts of the husk would probably have a similar effect. In addition, it might be possible to obtain more informations about the nature of mechanism by removing a small part of pericarp and testa from the dehusked seeds. These suggestions led to the following experiment.

In some of the treatments, half of the husk was removed at proximal or distal region from the intact seeds, and in the others, pericarp and testa were excised from the dehusked seeds at proximal or at distal region. Care was taken to avoid damaging the underlying emdryo. In some of the treatments, a portion of the seed was covered with paraffin wax. After treatments the seeds were germinated as usual, and the results are shown in Table 2, with the experimental designs.

TABLE 2
Effects of various surgical treatments on germination

Treatment No.	Treatments	Percent germination
1	Husk intact (control)	0%
2	Entire husk removed	4
3	Median region of husk incised	34
4	Median region of husk incised, proximal half of husk removed	82
5	Median region of husk incised, distal half of husk removed	42
6	Entire husk removed, paraffin placed over embryo	4
7	Seed with husk, cut in half transversely	42
8	Seed with husk, cut in half transversely, cut surface sealed with paraffin	30
9	Dehusked seed, cut in half transversely	68
10	Dehusked seed, cut in half transversely, cut surface sealed with paraffin	68
11	Dehusked seed, pericarp and testa scarified with sand paper in distal region	82
12	Dehusked seed, pericarp and testa scarified with sand paper in proximal region	82

From the results of this experiment, it may be said that there is a considerable difference in effectiveness between the removals of distal and proximal half of the husk. The removal of a part of the husk near to the embryo was more effective in breaking dormancy. In addition, the incision at median region of the husk was almost as effective as the cutting in half. Much increase in germintion was obtained by excision of a part of pericarp and testa. In this case, no difference in effectiveness could be seen between regions of excision.

The results of the treatments in which paraffin wax was used to seal are difficult to interpret because it is not known how effective the wax was as a sealing agent. Nevertheless, there is an indication that sealing of cut surface reduced the stimulating effect of the cutting of the husk intact seeds.

In addition, an experiment was conducted in order to see the effects of the surgical treatment given after a period of imbition. The seeds were dehusked, cut in half or dehusked and cut in half immediately before the germination test or after imbibition at 20°C for 7 days.

It seems certain from the results in Table 3, that the stimulatory effects of the treatments are reduced when given after imbibition period of 7 days.

TABLE 3
Relation of previous imbibition and surgical treatment in germination

Treatments	Periods of treatments	
	Immediately before germination test	After 7 days' imbibition
Intact	0%	0%
Dehusked	8	2
Cut in half	40	0
Dehusked, cut in half	68	62

Furthermore, experiment was carried out to know the effects of orientation of seeds on their germination, using filter paper or sand as substratum. A part of seed sample was placed so that embryo was in contact with water, and in the other the seed was orientated so that the embryo faced upwards and away from the substratum.

TABLE 4
Effects of orientation of seeds on germination

Seed treatments	Orientation of embryo			
	Up		Down	
	Filter paper	Sand	Filter paper	Sand
Intact	8%	8%	6%	8%
Dehusked	22	18	20	14
Cut in half	52	94	52	94
Dehusked, cut in half	94	100	92	98

It will be seen from the result in Table 4 that the orientation of the seed had no effect. But much higher values were obtained if sand was used as substratum, especially in the germination of the cut seed.

2. *Effects of Chemicals, Prechilling and Wounding on Germination*

The stimulating effect of gibberellin on seed germination of many species has been well established. In cereal seeds, Naylor and Simpson (1962) reported

the stimulatory effect of gibberellin on germination of dormant embryo of *Avena fatua* L. In the present study, the effect of gibberellin has been investigated using four concentrations with the following four treatments; (1) seeds not dehusked, (2) seeds dehusked, (3) seeds cut in half transversely, and (4) seeds dehusked, cut in half transversely. The results are presented in Table 5.

TABLE 5
Relation of various surgical treatments and gibberellin in germination

Treatments	Concns. of gibberellin (ppm)				
	0	0.5	1	10	25
Intact	0%	0%	2%	2%	6%
Dehusked	2	22	28	78	84
Cut in half	20	24	50	32	24
Dehusked, cut in half	42	82	92	86	96

It can be concluded that gibberellin stimulates the germination of dormant seeds of *Hordeum spontaneum*, but the effect varies with the treatments. The dehusked seeds responded most remarkably to the application of gibberellin, but the effect on the cut seeds with only 1/2 of endosperm was not so great.

During the course of this experiment, it has been frequently observed that seeds on gibberellin solutions suffered from the mould. The reduction of the occurrence of moulds was obtained, to some extent, by the application of gibberellin for short period without a significant lowering of germination. An experiment shown in Figure 4 illustrates this. The dehusked seeds were imbibed 0, 5, 10, 25 and 50 ppm solutions of gibberellin for 3 or 6 hours before the transfer to distilled water. As a control, seeds were kept continuously on gib-

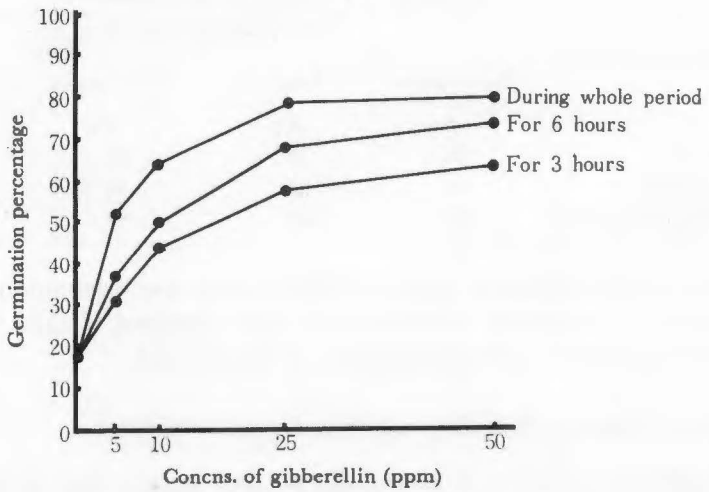

Fig. 4. Effects of gibberellin-treatments of short period on germination of dehusked seeds.

berellin solution. The results indicate that even the imbibition of as short as 3 hours has a significant effect on germination.

One of the common methods of breaking seed dormancy of many species is to subject the moist seeds to a low temperature. The effects of the prechilling on germination of *Hordeum spontaneum* seeds were investigated in the following experiment.

Half the seeds were dehusked by hand, and 0, 1/4, 1/2 or 3/4 of eodosperm was removed from each of the dehusked and the intact seeds. They were soaked in distilled water for 7 days at 3°C and then germinated at 20°C. The results are presented in Table 6, together with those obtained by seeds which had been similarly treated but not exposed to a low temperature.

TABLE 6
Relation of dehusking, removal of endosperm and prechilling in germination

Husk intact or removed	Prechilled or not	Amount of endosperm removed			
		Not removed	1/4 of endosperm removed	1/2 of endosperm removed	3/4 of endosperm removed
Husk intact	Not prechilled	0%	0%	20%	28%
	Prechilled	0	40	88	96
Husk removed	Not prechilled	4	24	32	88
	Prechilled	64	80	100	100

It can be seen that the failure of the response of intact seeds to the prechilling is modified by dehusking or the removal of endosperm. The complete germination was obtained by the prechilling of the dehusked seeds or of the cut seeds with 1/2 or less of endosperm, or of the dehusked and cut seeds.

In addtion, the results of the experiment in which the intact and the dehusked seeds were germinated on 0, 25, 50, 75 and 100 ppm solutions of gibberellin with or without 3 days' prechilling are presented in Table 7, which clearly demonstrate the high responsibility of dehusked seeds both to gibbereliin and prechilling. Thus, it seems quite apparent that a considerable number of seeds are awaken from dormancy by dehusking and subsequent application of gibberellin or prechilling.

TABLE 7
Effect of prechilling and gibberellin of various concentrations on germination of intact and dehusked seeds

Husk intact or removed	Prechilled or not	Concns. of gibberellin (ppm)				
		0	25	50	75	100
Husk intact	Not prechilled	0%	4%	10%	12%	12%
	Prechilled	4	18	20	20	16
Husk removed	Not prechilled	18	54	58	56	52
	Prechilled	78	82	88	72	84

Recently, Naylor and Simpson (1961) showed that sucrose is effective in promoting germination of dormant embryos of *Avena fatua* and that requirement for exogenous sucrose can be replaced by gibberellic acid. In the germination of *Hordeum spontaneum* seeds, effect of sucrose was slight, but considerable effect could be seen when combined with gibberellin (Table 8).

TABLE 8
Effects of sucrose, gibberellin and their combination on germination

Treatments	Chemicals			
	Water	Sucrose 0.5%	Gibberellin 25 ppm	Sucrose 0.5% plus gibberellin 25 ppm
Intact	20%	24%	34%	56%
Dehusked	64	64	80	96
Cut in half	60	68	62	64
Dehusked, cut in half	86	90	88	88

Furthermore, the recent finding of Black and Naylor (1959) seems to be interesting, who showed that the insertion of stem, from which the seeds are isolated, into the solution of gibberellin is very effective in inducing germination of dormant *Avena fatua* seeds.

The effects of stem-treatments with gibberellin were investigated with the seeds of *Hordeum spontaneum*. The stems were cut at 15, 20, 25 or 30 days after anthesis and the cut ends were inserted into 25, 50, 75 or 100 ppm solution of gibberellin. They were removed from the solutions after 7 days and then dried for 2 weeks at 35°C. The isolated seeds were collected per every spike and germinated at 30°C. The seeds from the stems which were inserted into distilled water were used as controls. The results are shown in Table 9.

TABLE 9
Germination of seeds isolated from stem which were cut at various stages of maturation and inserted for 7 days into gibberellin solutions of various concentrations

Maturity of seeds (Days after anthesis)	Concns. of gibberellin (ppm)				
	0	25	50	75	100
15	0%	20.6%	28.7%	34.1%	20.6%
20	0	38.0	34.5	40.9	50.1
25	0	15.4	41.3	21.1	49.3
30	0	14.5	19.7	15.2	38.5

From the results in Table 9, it is apparent that the treatments of stem with gibberellin solutions are more or less effective in inducing the germination of otherwise dormant *Hordeum spontaneum* seeds. But the effects depended upon the stage of maturation of seeds when the stem was cut for the treatments and the concentration of gibberellin solution into which the stem was inserted. The

treatment of immature seeds with higher concentration of gibberellin often resulted in the abnormal germination. When the seeds were more matured at the time of treatment, however, less effects were observed and it was needed to use higher concentration of gibberellin.

In addition, it must be mentioned that the seeds isolated from the treated stem were frequently covered with moulds.

Though the stem treatments with gibberellin were more or less effective in inducing germination of seeds isolated from them, it was far from obtaining the complete germination. The more complete germination was obtained by dehusking or prechilling of seeds from the gibberellin-treated stems. The stems cut 20 days after anthesis were treated with 0, 25, 50, 75 or 100 ppm solution of gibberellin. After 7 days, they were removed and dried for 10 days at 35°C.

TABLE 10

Effects of dehusking, prechilling and their combination on germination of seeds from stems cut 20 days after anthesis and inserted into 0, 25, 50, 75 or 100 ppm solution of gibberellin

Treatments	Prechilled or not	Concns. of gibberellin (ppm)				
		0	25	50	75	100
Intact	Not prechilled	0 %	12.7%	12.0%	33.0%	5.6%
	Prechilled	4.0	4.7	36.0	62.0	52.0
Dehusked	Not prechilled	2.5	54.0	61.7	56.6	46.0
	Prechilled	72.0	78.2	79.3	74.0	84.4

As seen in Table 10, the prechilling or the dehusking of seeds isolated from the gibberellin-treated stems resulted in higher germination. Furthermore, the seeds from the gibberellin-treated stems were more sensitive to dehusking than to prechilling.

TABLE 11

Effects of gibberellin and prechilling on germination of seeds isolated from stems treated with gibberellin at three different stages of maturity

Stages of maturation of seeds	Stem treatments	Prechilled or not	Substratum		
			Water	Gibberellin 50 ppm	Gibberellin 100 ppm
Early	Water	Not prechilled	0%	61%	79%
		Prechilled	39	64	72
	Gibberellin 50 ppm	Not prechilled	3	77	82
		Prechilled	65	80	78
Intermediate	Water	Not prechilled	0	42	—
		Prechilled	36	64	52
	Gibberellin 50 ppm	Not prechilled	6	54	—
		Prechilled	44	54	60
Late	Water	Not prechilled	0	48	—
		Prechilled	8	54	—
	Gibberellin 50 ppm	Not prechilled	0	54	—
		Prechilled	44	72	—

In an experiment shown in Table 11, the effects of gibberellin and prechilling on the germination of seeds isolated from stems treated gibberellin at three different stages of maturation were examined. The stems were cut at early, intermediate and late stages of maturity of seeds, and the cut ends were inserted into 50 ppm solution of gibberellin for 7 days. The seeds from these stems were dried for 10 days at 35°C, and set to germinate on 0, 50 or 100 ppm solution of gibberellin with or without prechilling.

The very remarkable effect of gibberellin was shown in seeds isolated from both gibberellin- and water-treated stems. The prechilling also increased germination, but its effect became less remarkable as the stems, from which the seeds were taken, approached to the maturity. The use of gibberellin, instead of water, as the inserting medium of stems, prevented, to some extent, the decrease of the effect of prechilling.

Effect of hydrogen peroxide was investigated in the following experiment, in which the intact, dehusked, and cut seeds were germinated on 0, 0.01, 0.1 and 1.0 per cent solutions of hydrogen peroxide. The results are shown in Figure 5.

A very striking result was obtained with hydrogen peroxide. The intact seeds showing only 6% germination on water germinated at high level as 68% on 1.0 per cent solution of hydrogen peroxide.

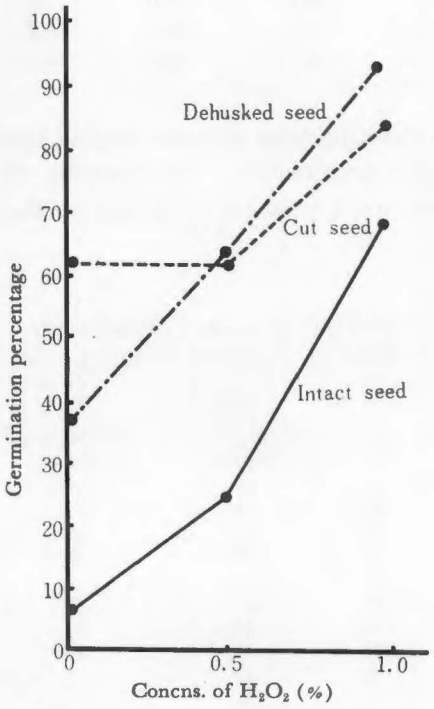

Fig. 5. Effects of hydrogen peroxide on germination.

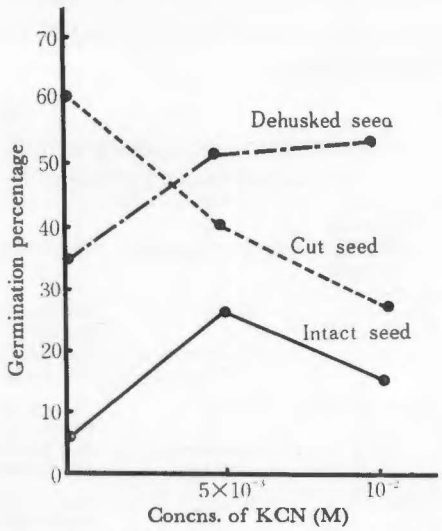

Fig. 6. Effects of potassium cyanide on germination.

TABLE 12
Effects of malonic acid on germination

Treatments	Concns. of malonic acid (M)		
	0	5×10^{-3}	10^{-2}
Intact	2%	10%	30%
Dehusked	12	44	44
Cut in half	56	46	0

Furthermore, potassium cyanide and malonic acid were more or less effective in stimulating germination (Table 12, Figure 6).

3. *Effect of Stage of Maturation on Germination*

It seems to be of importance, from the biological and practical viewpoints, to know when the seeds aquire the germinability during the process of maturation. The seeds were harvested at intervals after the anthesis. They were divided into 2 groups; one group was dried for 7 days at 30°C, but the other was subjected to the germination test immediately after harvest. In the germination test, the following four treatments were used: (1) husk intact, (2) dehusked, (3) cut in half transversely, and (4) dehusked and cut in half transversely.

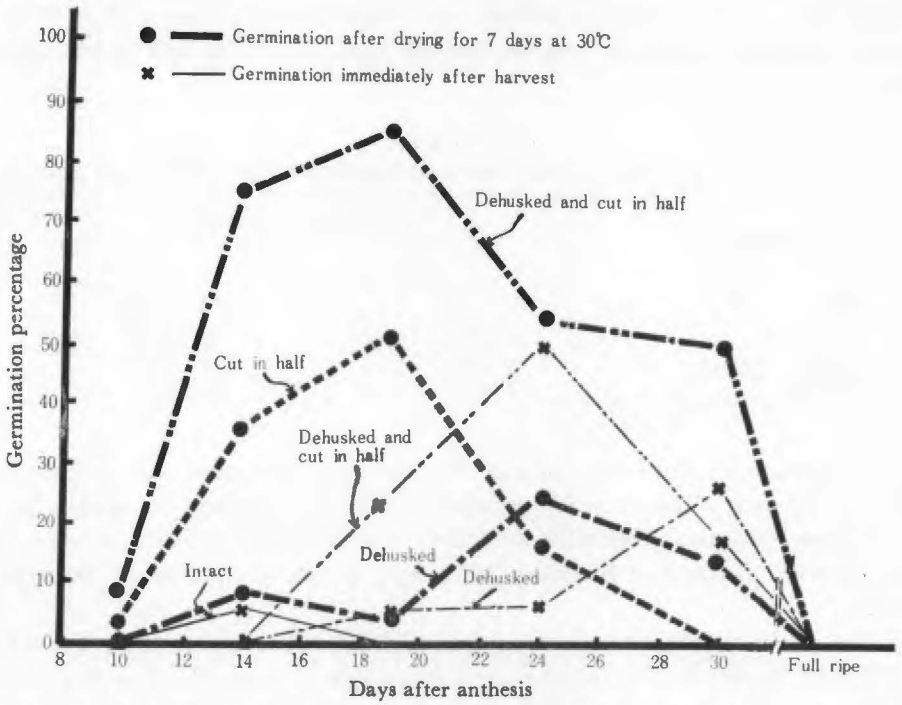

Fig. 7. Germination of immature seeds at various stages of maturity, and effects of drying and various woundings on their germination.

Figure 7 shows the significant effect of the stage of maturation of the seeds on their germination. The intact seeds and those cut in half were incapable of germination at any stage of maturation. The dehusked seeds, especially those cut in half, germinated well under the same experimental condition. Optimum germination was achieved by the dehusked seeds at 30th day, and by the dehusked and cut seeds at 24th day after the anthesis. Thereafter, however, the germination decreassed rapidly.

Figure 7 also shows that the drying out of the immature seeds improves their germinability significantly. At very early stage of maturation as 10 days after anthesis, a few seeds were germinated by the dehusking and cutting in half transversely. The increase in germinability occurred as the seeds were more matured, and the optimum germination was achieved at 20–25 days after anthesis, with subsequent reduction in germination capacity. Furthermore, as in the fresh seeds, optimum germination was achieved later by the dehusked seeds than by the dehusked and cut seeds.

4. *Germination of Excised Embryos*

It is very important to note that embryos can germinate well even at temperature of as high as 30°C, whenever they were excised from seeds during after-ripening. In the first experiment, the dormant seeds were imbibed water at 30°C for one day before embryos were excised and germinated at 30°C on various solutions including 2 % sucrose, 25 ppm gibberellin and their combination.

TABLE 13
Effect of sucrose, gibberellin and their combination on germination of embryos

Chemicals	Germination period (days)	
	1	2
Water	15%	60%
2% sucrose	75	90
25 ppm gibberellin	90	100
2% sucrose+25 ppm gibberellin	95	100

The results in Table 13 indicate that embryos themselves are not dormant and that further stimulation of germination can be obtained by application of 2 % sucrose, 25 ppm gibberellin and their combination, which is accord with the results of Naylor and Simpson (1961) with dormant embryos of *Avena fatua* seeds.

The effect of different sugars on germination of excised embryos are shown in Table 14, from which it is apparent that maltose is more effective than sucrose in promoting the germination of embryos. Glucose was relatively less effective.

Effect of hydrogen peroxide was investigated by germinating embryos on

TABLE 14
Effects of different sugars on germination of embryos

Chemicals	Germination period (days)		
	1	2	3
Water	5%	30%	75%
2% Sucrose	15	65	80
2% Maltose	60	70	80
2% Glucose	5	40	70
2% Fructose	0	60	85

TABLE 15
Effects of hydrogen peroxide on germination of embryos on wet filter paper or under water

Germinating conditions	Concns. of H_2O_2 (%)			
	0	0.01	0.1	1.0
On wet filter paper	100%	100%	100%	10%
Uhder water	0	50	100	0

wet filter paper or under 0, 0.01, 0.1 and 1.0 per cent solutions of hydrogen peroxide. For germination under water, embryos were kept at the bottom of Petri dish filled with the solution.

As seen from Table 15, hydrogen peroxide had no detectable influence upon germination on filter paper if not exceeded 0.1 per cent in concentration, in contrast to the remarkable effect on germination under water. Though embryos cannot germinate under water, perhaps due to the insufficient supply of oxygen, complete germination was recorded under the corresponding condition when water was replaced by 0.1% solution of hydrogen peroxide.

In the preliminary experiment, it was observed that the prolonged imbibition of seeds at 30°C lowered the germinability of embryos excised from them. An experiment was run to know the relation of length of time and temperatures of water imbibition, using both the intact and the dehusked seeds. The results are presented in Table 16.

It will be seen that the embryos lose their viability during the imbibition at 30°C and fail to germinate after being excised. Dehusking before the imbibition prevented the lowering of embryo viability, and the most rapid and complete germination was obtained with embryos of seeds imbibed at 5°C.

Furthermore, hydrogen peroxide is effective, at least partly, in reducing the loss of germinability of embryos as shown in the following experiment. The seeds were submerged in 0, 0.01, 0.1 and 1.0% solution of hydrogen peroxide for 2 days or kept on filter paper moistened by the same solutions for 5 days at 30°C. At the end of the experimental period, embryos were excised and germinated on filter paper moistened with distilled water.

TABLE 16
Effects of imbibition of various length of time at 30° and 5°C of intact and dehusked seeds on germination of embryos excised from them. Germinated embryos were counted after 3 days at 30°C

Length of imbibition (days)	Imbibition temperature			
	30°C		5°C	
	Husk intact	Husk removed	Husk intact	Husk removed
1	95%	90%	100%	100%
2	75	90	100	100
3	55	80	100	100
4	50	95	100	100
5	30	80	100	100

TABLE 17
Effects of imbibition on wet filter paper or of immersion under water in presence of hydrogen peroxide on germination of embryos excised from them.

Seeds, from which embryos were extracted	Concns. of H_2O_2 (%)			
	0	0.01	0.1	1.0
Immersed in solution for 2 days	0%	0%	65%	75%
Kept on wet filter paper for 5 days	55	60	70	75

From Table 17, it is clear that though the embryos are unable to germinate on filter paper when they are taken from seeds immersed in water for 2 days, but those from seeds submerged in 1.0 per cent solution of hydrogen peroxide are still able to germinate under the corresponding condition. The similar situation was seen when the seeds were kept on wet filter paper for 5 days at 30°C.

In order to know the relation of the stage of after-ripening and the loss of viability due to the prolonged imbibition at high temperature, the fresh and the partially after-ripened seeds were incubated at 30°C for 1, 3, 5, and 7 days, and the embryos from these seeds were set to germinate at 30°C.

The results in Table 18 show that the after-ripened seeds are more resistant to the prolonged imbibition at high temperature than the fresh seeds.

TABLE 18
Relation of after-ripening and loss of embryo viability after prolonged imbibition at 30°C

Length of imbibition (days)	Unafter-ripened	Partially after-ripened
1	100%	100%
3	80	80
5	40	75
7	35	75

It seemed to be of interest to know whether or not the lowered activity of embryos caused by the prolonged imbibition of seeds at high temperature can be reversed by the applicetion of chemicals. The seeds were imbibed at 30°C for 7 days, and the effects of 2% sucrose, 25 ppm gibberellin, 0.01 M KNO_3, and their combinations on germination of excised embryos were investigated. Puncturing of embryos at radicle ends was also included.

TABLE 19
Stimulation of germination of embryos excised from seeds imbibed at 30°C for 7 days by some chemicals and puncturing of embryos

Treatments	Germination period (days)	
	1	3
Water	0%	25%
2% Sucrose	10	25
25 ppm gibberellin	50	55
10^{-2}M KNO_3	20	40
2% Sucrose + 25 ppm gibberellin	35	60
2% Suceose + 10^{-2}M KNO_3	15	45
10^{-2}M KNO_3 + 25 ppm gibbrellin	40	60
Punctured at radicle end of embryo	25	40

From the results in Table 19, it seemed that gibberellin and potassium nitrate were more or less effective in increasing germination of the embryos whose activities were lowered by the prolonged imbibition at high temperature. Puncturing at radicle end was also more or less effective.

Furthermore, the fact that the embryos gradually lose their viabilities when the seeds were imbibed at unfavorable temperature as high as 30°C led the following experiment regarding the presence of the inhibitors within the seeds.

Twenty five seeds or seed parts variously treated were put in flask with 10 m*l* of distilled water and maintained for 6 days at 30°C. They were filtered and the filtrates were used in the germination tests with embryos excised from the seeds imbibed for a day. The list of treatments together with the results

TABLE 20
Effects of water extracts of various parts of seeds on germination of embryos

Medium used in germination test	Germination period (days)	
	1	2
Water (control)	75%	90%
Extract of intact seeds	60	85
Extract of dehusked seeds	75	90
Extract of proximal halves	65	90
Extract of endosperm halves	70	80
Husk extract	85	95

are shown in Table 20, and it will be seen that these results cannot be explained in terms of the presence of water soluble germination inhibitors.

5. *Water Absorption by Seeds*

The inhibition of water absorption by the impermeable seed coats is one of the factors causing dormancy in some species. It was suggested that the germination of dormant cereal seeds when the outer coverings were broken was due to the rapid intake of water. In order to test this possibility in *Hordeum spontaneum* seeds, an experiment was carried out using four treatments: (1) seeds not dehusked, (2) seeds dehusked, (3) seeds cut in half transversely, and (4) seeds dehusked and cut in half transversely. They were imbibed water at 30°C. The results are given in Figure 8, in which the curves show the increase in weight plotted against time.

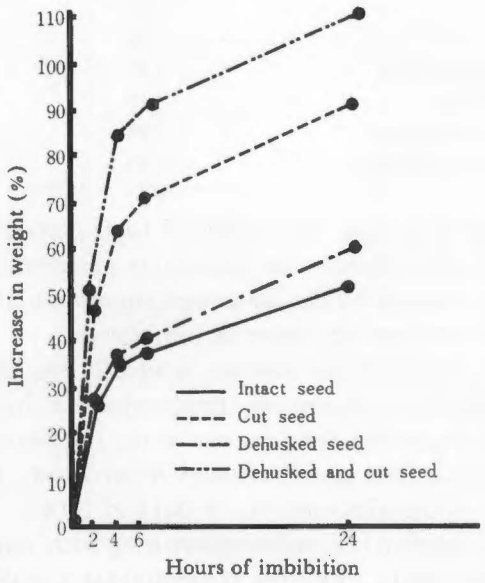

Fig. 8. Effects of woundings on water uptake by dormant seeds.

It will be seen that there are considerable differences between the four curves, and that the cutting is more effective in increasing the water absorption than the dehusking. The maximum rate was obtained by the combined treatment of dehusking and of cutting. In addition, it seems most important to note that even the intact seeds can absorb enough water without any difficulties.

6. *Respiration of Seeds During Imbibition*

The inhibition of gaseous exchange by the seed coats may be one of the causal factors of the failure of germination. The delayed germination of the

upper seeds of *Xanthium* is due to low permeability of seed coats and high oxygen requirement of embryos for germination. The possibility that the seed covers inhibit germination of *Hordeum spontaneum* seeds by restricting the oxygen uptake was investigated using four treatments. Half of the seeds were dehusked, and each of the samples of intact and dehusked seeds were cut in half transversly. They were imbibed water in Warburg vessels at 30°C, and the amount of oxygen uptake were recorded.

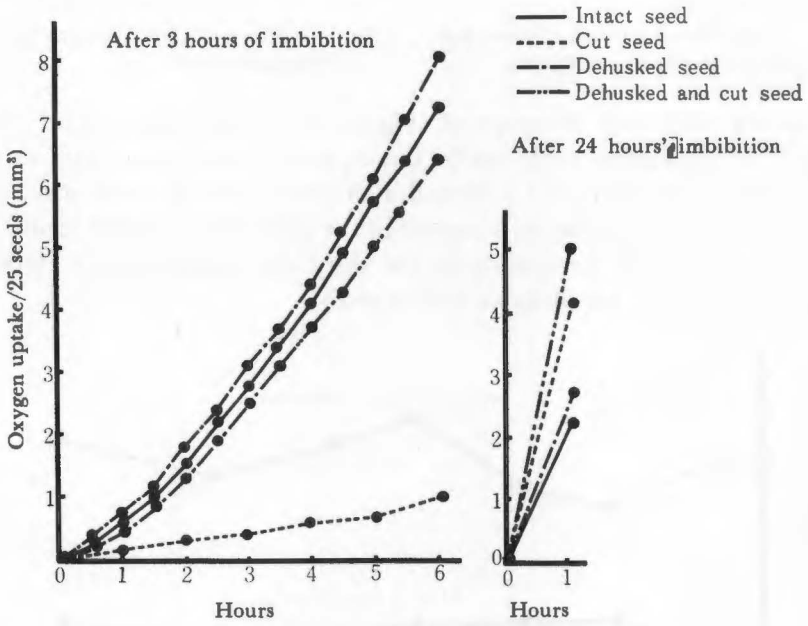

Fig. 9. Effects of various woundings on respiration.

Figure 9 shows the results. On the first day of imbibition, only slight differences can be seen between the three curves representing respiration with time of intact, dehusked, and dehusked and cut seeds. But it is very curious that the halved seeds respired only a small amount of oxygen, if they were not dehusked. On the second day of imbibition, however, the relation was quite different. The respiratory activity was much higher in the halved seeds than in the intact seeds. A stimulatory effect, though not so great, of the dehusking on respiration was also apparent.

The change in oxygen uptake was followed during the first three days of imbibition. The curves in Figure 10 show the amount of oxygen taken up for an hour by intact and dehusked seeds.

It is apparent that the respiratory activities of both the intact and the dehusked seeds were increased gradually as the imbibition period was prolonged, but began to slope downwards after about a day's imbibition at 30°C. Furthermore, in another experiment, the effect of gibberellin on the oxygen uptake by

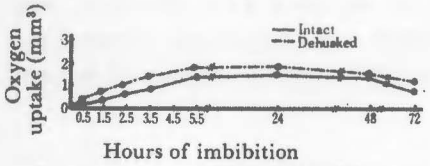

Fig. 10. Changes in respiration of intact and dehusked seeds during imbibition.

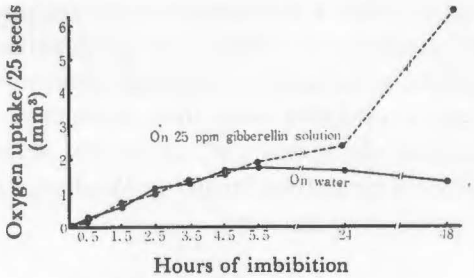

Fig. 11. Effects of gibberellin on respiration of dehusked seeds.

the dehusked seeds was investigated (Figure 11). Any stimulatory effect of gibberellin on respiration could not be found, but the respiratory rate increased rapidly under the influence of gibberellin on the second day and later, and on the third day some germination occurred in the gibberellin-treated seeds. Consequently, the increased respiration on the third day represents the respiration of a mixture of young seedlings as well as seeds.

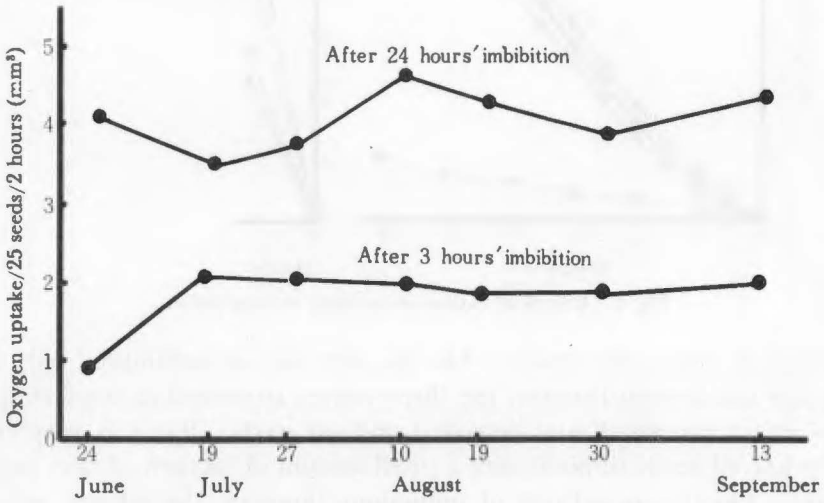

Fig. 12. Changes in respiratory activity of seeds during after-ripening.

In addition, the changes in respiratory activity of *Hordeum spontaneum* seeds during after-ripening was investigated. As shown in Figure 12, the activity was maintained at relatively uniform rate for about 3 months after harvest, though the seeds after-ripened, to some extent, during this period.

7. *Germination Inhibitor*

The presence of germination inhibitors in the husk of cereal has been shown by many authors. Attempts have been made to extract germination inhibitors

TABLE 21
Effects of various extracts from dormant *Hordeum spontaneum* seeds on germination of non-dormant seeds of naked cultivar. Kobinkatagi

Germination period (days)	Medium used in germination test					
	Distilled water	Water extract	Methanol extract water soluble	Methanol extract methanol soluble	Pet. ether extract water soluble	Pet. ether extract methanol soluble
2	60%	34%	60%	70%	68%	55%
3	84	65	79	76	77	76

from *Hordeum spontaneum* seeds, and results of the typical experiment has been presented in Table 21.

Evidence of inhibitor has been found only in the water extract.

8. *Changes in Amylase Activity and Reducing-sugar Content during Imbibition*

It seems to be interesting, from several reasons, to investigate the change in amylase activity and reducing-sugar content of imbibing seeds at different stages of after-ripening. Naylor and Simpson (1961) showed that dormancy of *Avena fatua* embryos is due to insufficient production and accumulation of sugars, and Paleg (1960) reported that gibberellic acid increased the amylase activity in barley seeds. According Yomo (1960), alpha-amylase activity in endosperm

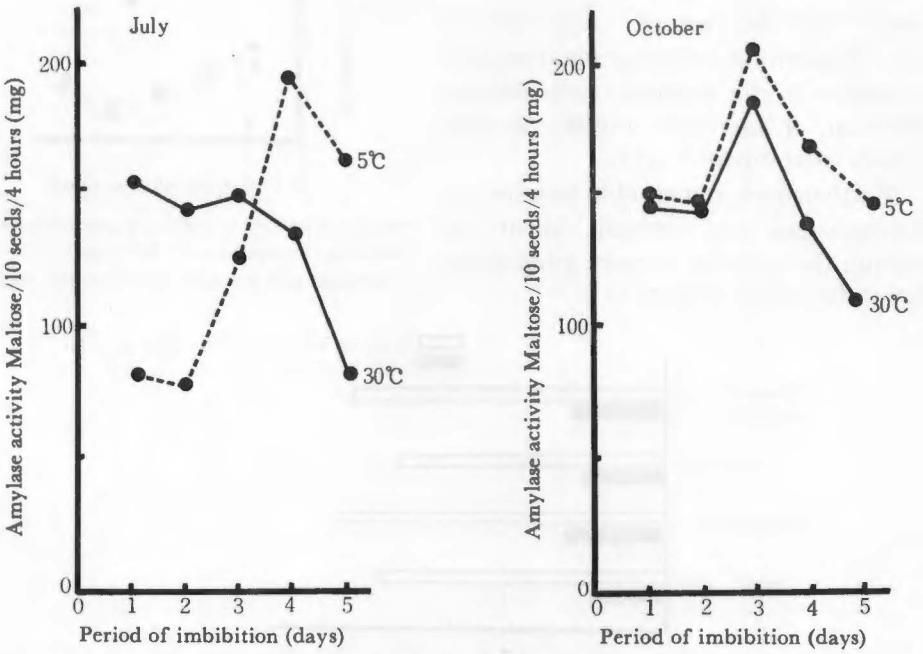

Fig. 13. Changes in amylase activity during imbibition at 30°C and 5°C of dormant and partially after-ripened seeds.

halves of barley caryopsis does not increase during imbibition on distilled water, but increases on gibberellin solution. The stimulatory effects of gibberellic acid on alpha-amylase was verified by Moro, Pomeranz and Shellenberger (1963) in wheat endosperms. In addition, the increase in alpha-amylase activity was achieved in endosperm halves of barley seeds by imbibing them in the presence of proximal halves containing embryos on distilled water (Yomo 1960).

In this study, amylase activity was measured after imbibing the fresh and the partially after-ripened seeds for 1, 2, 3, 4 and 5 days at 30°C and 5°C.

The results of this experiment, illustrated in Figure 13, show that the changes in amylase activity during the imbibition depend upon the stage of after-ripening and the imbibition temperature. In the fresh dormant seeds, if they were imbibed at 30°C, amylase activity increased faster than if they had been imbibed at 5°C. At 30°C, however, lowering of amylase activity was more rapid than at 5°C. In the partially after-ripened seeds, by contrast, amylase activity increased with about the same rate at 30°C and at 5°C, and began to decrease after maximum activity has been attained.

Changes in reducing-sugar content during the imbibition at 30°C and 5°C are illustrated in Figure 14, with the dormant and the partially after-ripened seeds. Though the reducing-sugar cannot accumulate in the dormant seeds during imbibition, it increased rapidly in the partially after-ripened seeds.

Furthermore, remarkable increase in reducing-sugar was brought about by imbibing the seeds on 25 ppm gibberellin solution for a day (Figure 15).

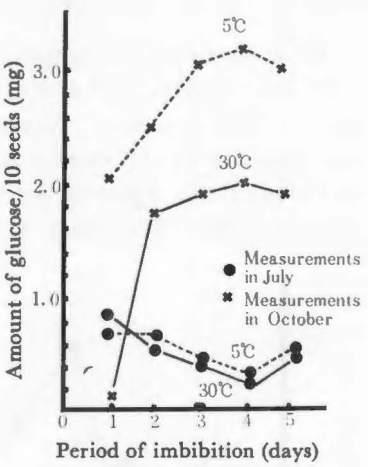

Fig. 14. Changes in reducing-sugar contents during imbibition at 30°C and 5°C of dormant and partially after-ripened seeds.

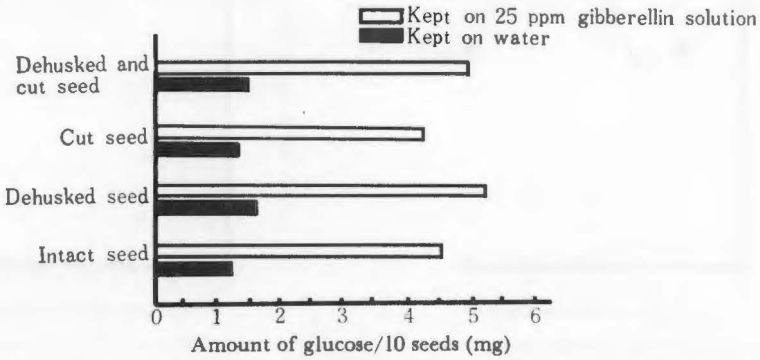

Fig. 15. Relation of gibberellin and reducing-sugar content in imbibing seeds.

9. *After-ripening of Hordeum Spontaneum Seeds*

The effectiveness of dry storage at high temperature in breaking dormancy of cereal seeds has been shown by several authors (Harrington 1923, Roberts 1961), though the problem whether the effect is attributed to drying or to high temperature is still remained. The after-ripening of *Hordeum spontaneum* seeds during the storage was investigated by storing the seeds at 35°, 30° and 5°C. They were germinated at intervals with or without 7 days' prechilling using 25°C as germinating temperature, with occasional raising to 30°C or higher during the summer time.

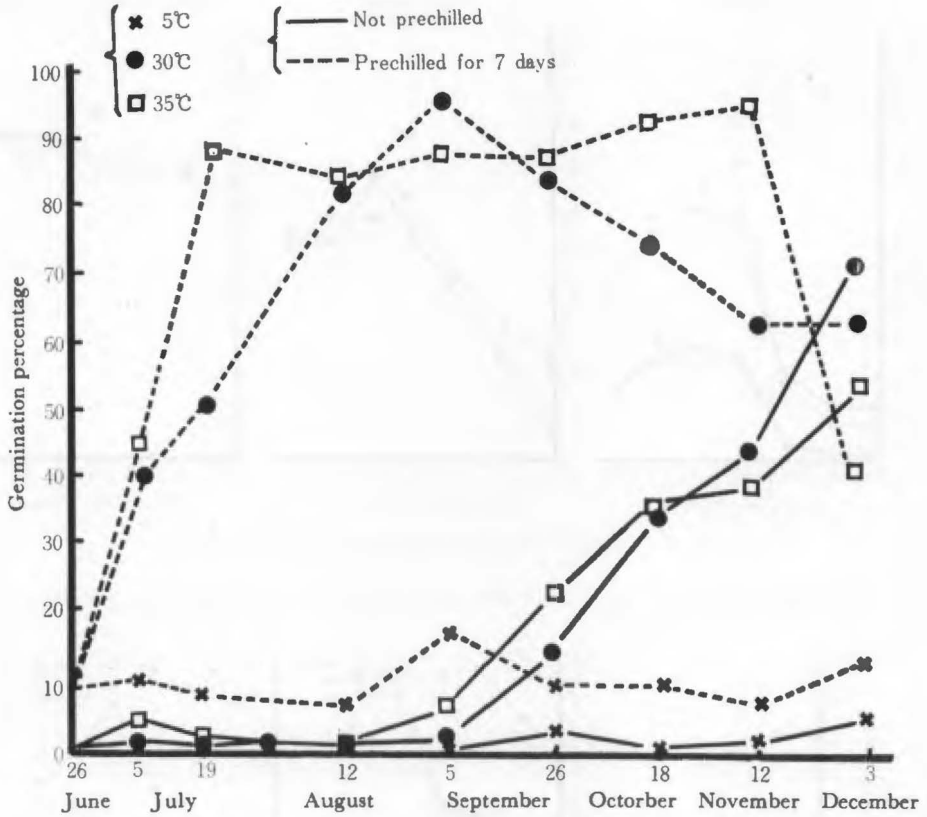

Fig. 16. Effects of dry storage at various temperatures on after-ripening.

From Figure 16, it is apparent that high temperature acts for the promotion of after-ripening, and that low temperature is effective in maintaining dormancy. Despite of failure of germination of seeds stored at 5°C, 30–40% of seeds were awaken from dormancy at the middle of November when they were stored at 30°C. When accompanied by prechilling, nearly all the seeds had the germinability at the beginning of September, whereas those stored at 5°C showed only about 10% of germination.

Though the surgical treatments as dehusking and cutting in half are effective in stimulating the germination of *Hordeum spontaneum* seeds, it is not known the extent to which these treatments influence the after-ripening. The seeds were dehusked, cut in half, or dehusked and cut in half transversely, and stored at ambient temperature. They were set to germinate at intervals during the storage, and the results were compared with those with the seeds treated immediately before each germination test.

From the results in Figure 17, the stimulating effect of these treatments on after-ripening could not be concluded. Furthermore, for a small proportion

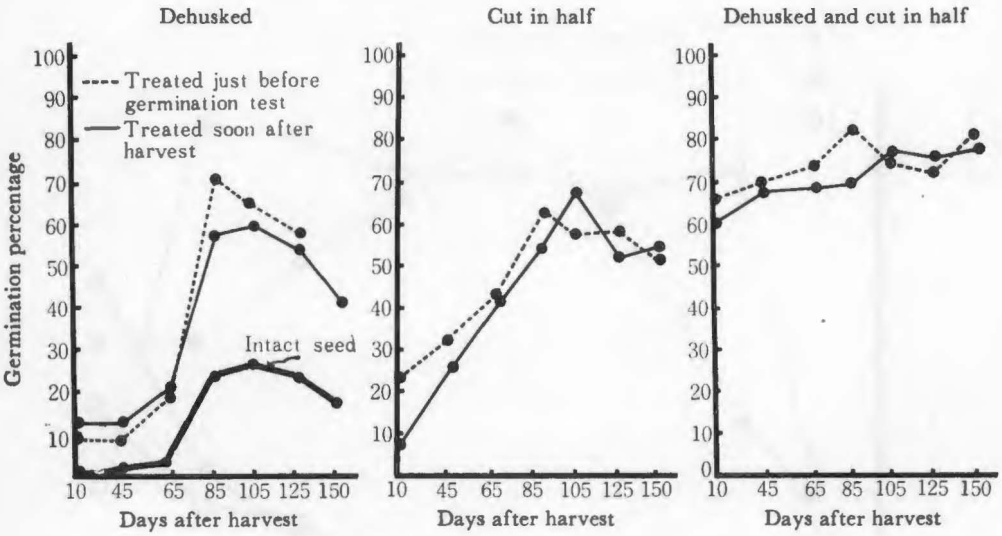

Fig. 17. Effects of various woundings on after-ripening.

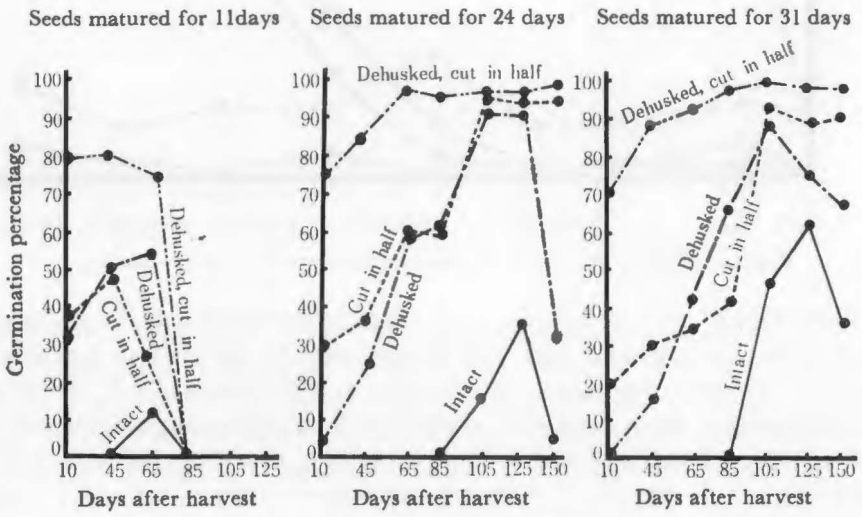

Fig. 18. Relation of stage of maturation of seeds and their after-ripening.

of the seeds cutting immediately before each test was effective in removing dormancy, whereas cutting soon after harvest was not. The same effect on dormancy of rice seeds of removing the husk has been shown by Roberts (1961).

Relation of stage of maturation and after-ripening was also investigated by harvesting immature seeds of various maturity and storing them at ambient temperature. They were tested for their germinabilities at intervals during the storage using four treatments.

It is apparent, from Figure 18, that immature seeds after-ripen faster than mature seeds but lose their viabilities more rapidly.

IV. DISCUSSION

In this study, the effects of woundings on germination of dormant seeds of *Hordeum spontaneum* have been investigated, and the stimulatory effects of dehusking, cutting in half, and their combination have been demonstrated. Moreover, it has been shown that embryos excised from dormant seeds germinate as completely as those from non-dormant seeds. These facts suggest that the embryo itself is not dormant in freshly harvested seeds of *Hordeum spontaneum* and that the dormancy is caused by the inhibitory influence of the structures covering the embryo. Furthermore, these suggestions are supported by the fact that the respiratory activity remains at relatively constant rate during the after-ripening.

Harrington (1923) suggested some of the more likely ways in which the covering structures might inhibit germination. The covering structures may prevent (1) diffusion of an inhibiting substance outwards, (2) entry of water, (3) increase in respiration or alteration in its nature, or (4) a more obscure stimulus of the living protoplasm.

In the following, these possibilities will be discussed on the basis of the experimental results.

The presence of the endogenous inhibitors have been demonstrated by several authors in wheat and *Avena fatua* seeds. Miyamoto et al. (1961) have succeeded in isolating the four inhibitors of catechin, catechin-tannin and alkaloid nature from the seed coats of wheat, and Ching and Foote (1961) also found the inhibitors in the water extract of dormant wheat seeds. Moreover, the germination inhibitors in the husk of *Avena fatua* seeds have been shown by Black (1959) and others. In this study, the fact that the germination inhibitor can be extracted by water from *Hordeum spontaneum* seeds does not necessarily imply that the inhibitory action of the husk is due to its possible content of inhibitors or that the husk acts by restricting the outwards diffusion of inhibitors. The low activity of the inhibitor supports this suggestion.

The prevention of entry of water by seed coats does not seem to be the causal factor of dormancy of freshly harvested seeds. Though the dehusking increased the water uptake by seeds, the effect is too small to explain the dormancy; in

other word, the intact seeds absorb water almost as rapidly as the dehusked seeds. Furthermore, the cutting induces the dormant seeds to germinate deponding upon the amount of endosperms; at the closer to the embryos the seeds were cut, the higher the germination. If the germination is determined only by water absorption, it is unlikely that the germination rate is proportional to the amount of endosperms removed. The different effectiveness of the removing of the proximal and the distal half of the husk in inducing germination of dormant seeds also demonstrate this.

This view is further supported by the experiment with wheat seeds. Takahashi (1938) found that the effect of wounding is affected by the temperature; the effect was greater at higher temperatures then at optimum ones for germination. It seems that this finding cannot be accounted for by the hypothesis of impermeable seed coat to water. More recently, Miyamoto, Tolbert and Everson (1961), in attempt to elucidate the varietal differences in the germination behavior of red and white wheats, state that the difference in germination rate cannot be attributed to the difference in the permeability of seed coat to water. Ching and Foote (1961) could not find any difference in the absorption rate of water by wheat seeds including both of dormant and non-dormant varieties. Wellington (1956) is of opinion that water-supply is not a determining factor in the varietal difference in germination of wheat seeds.

The possibility of the prevention of increasing the respiration is also precluded. Both the dehusking and the cutting in half are effective in inducing the germination of dormant seeds, and the results of respiration study showed that the dehusking stimulated the respiration only a small extent, and the cutting, contrary to the dehusking, decreased it during the initial period of imbibition, but stimulated at later stage. Though this is unexplainable, the suggestion that the main inhibitory action of the covering structure is not due to their prevention of gaseous exchange by seeds can be possible. Miyamoto et al. (1961) could not find any difference in respiration between dormant and non-dormant wheat seeds.

Thus, it seems to be clear that the first three possibilities cannot be applied to the dormancy of *Hordeum spontaneum* seeds. Consequently, some other interpretations must be awaited on the basis of future works. Nevertheless, a few problems will be discussed in the following.

As mentioned above, the embryos of *Hordeum spontaneum* are not dormant at harvest ripe. After attained germinability at relatively early stage of maturation, the embryos, if extracted from the caryopsis, can germinate easily regardless of the stage of maturation as well as of after-ripening of seeds. On the other hand, the germination rates of the intact and the wound seeds vary with the time during maturity and after-ripening. These facts suggest that more important change during after-ripening occur in the covering structures rather than in the embryo itself.

Moreover, the present study confirmed the finding of Naylor and Simpson (1961) about the stimulatory effects of sucrose, gibberellin and their combination on embryo germination. The dormant embryos from *Avena fatua* seeds were much sensitive to exogenous sucrose and gibberellin, as compared with the non-dormant embryos (Naylor and Simpsom 1961). Though the embryos of *Hordeum spontaneum* seeds are not dormant, thier germination was promoted by application of sucrose and/or gibberellin. Takahashi (1963) also found that embryos of rice seeds broken from dormancy by chemical treatmeat responded to exogenous sucrose. Furthermore, it was found that embryos gradually lose their viability during the prolonged imbibition of seeds at high temperature. This suggested that an inhibitor formed within seeds as the results of metabolism at unfavorable temperature inhibited germination, and eventually led to death of embryos. But this was not true, because the results of germination tests of embryos with water extracts of various parts of seeds could not be explained in terms of the hypothesis of inhibitor. Moreover, dehusking of seeds, imbibing the seeds at low temperature or on solution of hydrogen peroxide prevented, to some extent, the loss of embryo viability. It was also interesting that as the seeds are more after-ripened, the lesser extent was the loss of viability. These facts suggest that an participation of unknown metabolic activity during the after-ripening process determine the germination.

By what mechanism the covering structures controll the dormancy of *Hordeum spontaneum* seeds is difficult to interpret. Now, compare the effects of various surgical treatments. So, it will be seen that there are differences in effectiveness between the dehusking and the cutting; the latter was more effective in breaking dormancy provided the seeds were germinated on water. On gibberellin solution, however, the seed germination was higher in the dehusked seeds than in the halved seeds. In other word, the seeds were sensitized to gibberellin by dehusking. With the cut seeds, the effect of gibberellin was stimulative only at low concentration, and inhibitory at higher ones. It will be suggested that the decay from the cut surface resulted in the decrease of germination, but this was not true. The reason is that the combination of the dehusking and the cutting did not result in the failure of germination even when higher concentration of gibberellin was applied.

In any way, gibberellin was effective in breaking dormancy not only when it was applied as germinating medium but also when it was used as inserting solution of stems from which the seeds were isolated. But mould occurrence reduces its availability in the practical use. Furthermore, it seems to need detailed study about the after-effect when barley plants are grown for the experimental study on their heading times. Here, it seems to be interesting to note that hydorgen peroxide increase the germination of *Hordeum spontaneum* seeds. Not only it stimulated germination of intact seeds, but also was effective in preventing the loss of embryo viability due to the prolonged maintenance of

seeds on wet filter paper at high temperatures.

In addition, increase in amylase activity during imbibition was found both in dormant and in partially after-ripened seeds. But accumulation of reducing-sugar could not be seen in dormant seeds. Naylor and Simpson (1962) reported that amylase alone could not hydrolyze raw starch and that only the combination of alpha-amylase and maltase could produce glucose from raw potao starch. In this study, maltase activity was not measured. But the result that reducing-sugar does not accumulate in dormant seeds despite of considerable activity of amylase seems to be explained by a possible role of maltase in the after-ripening. An alternative explanation may be that an unknown mechanism act in dormant seeds, which use reducing-sugar and thus prevents its accumulation. This will be studied in future. In addition, Lau (1962) discussed the importance of delayed germination as an aim in malting barley breeding in connection with beta-amylase activity. In this study, beta-amylase activity was not studied, but will be studied in future together with alpha-amylase activity.

In connection with the after-ripening of *Hordeum spontaneum* seeds, it seems to be of interest to note that Wellington (1956) found the four stages of maturity and after-ripening in wheat seeds, in which the period from the 8th week (harvest ripe stage) to 13th week after anthesis was refered by him as "stage III". He showed that during this stage, the after-ripening occurs even under the moist condition, though it proceed more easily under the dry condition. In *Hordeum spontaneum* seeds, the storage at high temperature acted for the promotion of after-ripening as compared with those at low temperature. Whether the breaking of dormancy at 35°C is attributed to the effect of high temperature itself or to the one of drying at such high temperature will be studied in future, but the present study seems to support the favorable effect of high temperature on after-ripening. At any rate, this will be a simple practical method for shortening the dormancy of *Hordeum spontaneum* seeds.

V. SUMMARY

Seeds of *Hordeum spontaneum* were investigated with a purpose of finding a practical method for breaking dormancy for use in breeding programmes. It was found that embryos are not dormant at harvest ripe, and that their germination are further stimulated by sucrose, gibberellin and their combination. Furthermore, embryo gradually lost its viability during the prolonged imbibition of seed at high temperature.

It was also found that some of the dormancy in *Hordeum spontaneum* seeds can be accounted for by the inhibitory influence of the husk and some of the residual dormancy after dehusking can be attributed to the inhibitory influence of other covering structures. Though the dehusking increases the rate of water absorption slightly, the intact seeds are capable of absorbing sufficient water for

germination. Consequently, the covering structures do not cause dormancy by restricting the entry of water. Similarly, the respiration is increased by dehusking only slightly and the possibility of preventing gaseous exchange by the husk as the causal factor of dormancy is also precluded.

In addition, removal of half of the husk breaks the dormancy of some of the seeds, but the site of the removal can alter the effectiveness of this treatment: removal of a proximal half to embryo is more effective than the one of a distal.

Gibberellin is effective in inducing germination of dormant seeds. The striking effect is obtained by gibberellin-treatment of the dehusked seeds, but the effect is not so great in the halved seeds. Hydrogen peroxide is also effective in stimulating germination.

Prechilling stimulated germination, but the fresh seeds immediately after the harvesting did not respond to prechilling.

In dormant seeds, reducing-sugar did not accumulate within seeds in spite of considerable activity of amylase.

The storage at high temperature is effective in shortening dormancy period. For breaking dormancy of *Hordeum spontaneum* seeds, the seeds are stored at 35–40°C, and the seeds are set to germinated on gibberellin or hydrogen peroxide solution with or without prechilling.

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