Agriculture
Canada

Research Branch
Direction générale de la recherche

Technical Bulletin 1988-7E

Dormoat physiology

Canada

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JUDITH FRÉGEAU
Plant Research Centre
Ottawa, Ontario

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Research Branch
Agriculture Canada
1988

Copies of this publication are available from
Director
Plant Research Centre
Research Branch, Agriculture Canada
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Ottawa, Ontario
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Produced by Research Program Service

Cat. No.: A54-8/1988-7E
ISBN: 0-662-16141-6

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Summary

The publication covers research on some physiological aspects of seed dormancy in dormoats, hybrids between Avena sativa L. and A. fatua L. It is intended as a reference document on the information gained so far with the several approaches taken to investigate the emergence problem of this experimental crop. The research was initiated to gain insight into the dormancy behavior of the seeds for 2 purposes: 1) to develop a management protocol to ensure good uniform emergence in the spring following fall planting and 2) to develop a screening test to assess the dormoat potential of lines in the breeding program. The results show that the seed behavior in the field is as sporadic and unpredictable as that of the wild oat parent. Artificially inducing secondary dormancy to modify the spring behavior was not successful in improving emergence over the non-treated seeds even though high levels of laboratory dormancy were induced in some lines. The publication concludes that the concept of a universal management protocol for the dormoat lines now available in the breeding program should probably be abandoned. The field responses of the seeds were shown to be complex and multilevelled and to be able to manipulate these responses to achieve predictability calls for long-termed, innovative, interdisciplinary approaches. One of the main shortcomings of dormoats seems to be a lack of winter hardiness in the dormant seeds. A very high percentage of seeds are lost over the winter as the seeds cannot survive temperature and moisture stresses encountered throughout the season. On the short-term, the problem of finding a dormoat line that could be successful as a commercial crop may still be explored through breeding with new strategies, as the routes already chosen have not yielded a candidate.

Résumé

Le présent bulletin s'intéresse à certains aspects physiologiques de la dormance des graines de dormoat, une avoine dormante obtenue par croisement entre Avena sativa L. et A. fatua L.. La publication traite de l'information obtenue grâce aux différentes approches prises pour l'étude du problème de levée printanière chez cette semence expérimentale. Les objectifs du programme de recherche étaient doubles: 1) le développement d'un protocole de régie favorisant une levée printanière uniforme lors d'une semis automnal et 2) le développement d'un test de tamisage pour l'évaluation des lignées du programme de sélection. Malgré des différences au niveau des types et/ou des taux de dormance, les comportements de germination au champs des semences de plusieurs lignées dormoat demeurent sporadiques et imprévisibles, semblables à ceux de la folle-avoine. Malgré le succès en laboratoire de l'induction d'un taux élevé de dormance secondaire, la levée printanière en champs de la plupart des semences ainsi traitées n'a connu aucune amélioration. A la lumière des résultats obtenus, le concept d'un protocole de régie universel pour les lignées dormantes de l'actuel programme de sélection devrait probablement être rejeté. Une des faiblesses importantes de ces lignées semble être un manque de tolérance aux stress hivernaux, telles les fluctuations majeures de températures et d'humidité pouvant se rencontrer dans le sol au cours de la saison, et pouvant entrainer une perte élevée des semences dormantes. Les comportements en champs des dormoats sont multiples et complexes tant et si bien que la compréhension et la manipulation de ces réponses, afin d'en prédire les résultats, demandent des efforts de recherche innovateurs, interdisciplinaires et de longue durée. A court terme, l'obtention d'une lignée dormoat ayant un potentiel commercial est susceptible d'être encore explorée en utilisant de nouvelles stratégies de sélection puisque jusqu'à maintenant celles choisies n'y sont pas encore parvenues.

DORMOAT RESEARCH: PHYSIOLOGY

INTRODUCTION

Literature review

Dormoats - The problem of reduced yield potential in oats led the oat breeder at the Plant Research Centre (Burrows, 1964) to attempt to breed a different type of crop whereby the producer would sow dormant spring-type seed in the fall and have that dormant seed overwinter as a seed but germinate in early spring to take advantage of early spring rains and cool temperatures. This class of oats was termed "dormoats" and it is intended to be grown in climates with severe winters and short growing seasons. To breed a commercial oat with seed dormancy, dormoats have been synthesized from crosses between Avena sativa L. and A. fatua L. (wild oat). Some of the seed dormancy characteristics of the wild oat have been combined with the desirable agronomic characteristics of spring-type oats. Dormoat seed and dormoat plants have been selected to resemble the cultivars of commercial importance and the seed has been selected so that it will not shatter like the seed of wild oats. The dormoat breeding program is large and diversified and the agronomic performance of the best dormoat strains is close to conventional spring cultivars when non-dormant seed of dormoats is sown as a spring crop. When the breeding project began, it was hoped that strains of dormoat could be isolated whose seed would act in unison and would be completely dormant in fall, would hold the dormancy overwinter and would break dormancy and grow luxuriously in spring time.

Although, some advances have been made towards this objective, the main concern in the development of the dormoat crop has been to increase percentage emergence in spring of autumn-sown seeds. Mechanisms influencing winter survival and spring emergence are related to the dormancy of the seeds. Physiological studies aimed at understanding the nature of dormancy of dormoat seeds were carried initially by Andrews and Burrows (1972) with lines selected from the breeding program of the time. Different levels of dormancy and different patterns of afterripening were observed under laboratory conditions of storage and germination tests. In their first paper, looking at the various germination behaviors in the laboratory, and spring-emergence in the field, the authors concluded that secondary dormancy induction was probably occurring in some seeds since conditions in the field in the autumn should have favored their germination. They made the observation that a long primary dormancy was not a pre-requisite for higher spring emergence since lines having it were no better than some having short primary dormancy. They also observed that a secondary dormancy was induced in the laboratory when seeds with primary dormancy were imbibed on water at 20°C and failed to germinate.

The authors pursued their studies trying to artificially induce secondary dormancy treating partially after-ripened seeds by soaking in water and incubating them in an enclosed humid atmosphere for two weeks, (Andrews and Burrows 1974). The treatment caused some damage to the embryos but emergence the following spring was improved. Of the amount sown in the fall, 5% to 30% more seeds emerged in the spring because of the treatment. Under

laboratory conditions, dormancy was more pronounced at 20°C than 7°C and on moist paper in petri dishes than in potted soil. This early work showed that some dormoats could be manipulated into a secondary dormancy more successfully than others and this led to an improved spring emergence when sown in the fall. However, the amount and reliability of the emergence still needed improvement.

Wild Oat - For the past 30 years, Naylor, Simpson and various colleagues from the University of Saskatchewan, have studied dormancy in wild oat, trying to explain its mechanism and the biological basis for persistence in this species. Since wild oat was the source of the dormancy genes in dormoat, it is very relevant to review the findings of this group. They began their work with the assumptions that the worldwide success of this species as a weed depends on genetic heterogeneity within populations and the capacity for rapid and sensitive response to the environment. They were able to show that differences in germination behaviour within wild oat populations have a genetic basis. Breeding experiments showed that parental lines differ in at least three genes controlling rate of after-ripening. A whole spectrum of lines ranging from those with long-term dormancy (D) to those characterized by the absence of dormancy (ND) were generated for more in-depth studies. In 1983, Naylor and his co-workers subjected some lines from the D and ND groups to a field experiment with and without summer-fallow to monitor which group emerged the following year. A relatively large proportion of ND seeds shed in the autumn, germinated prior to or during the following spring while D seeds produced in the same crop, tended to escape elimination by remaining dormant through the subsequent growing season. There were, however, some lines, classified either as D or ND, which did not follow this behaviour. One factor of their field and laboratory studies was to confirm that the expression of genes conferring seed dormancy in the Gramineae is sensitive to several environmental factors. Temperature experienced by the maternal plant during seed development and by seeds following maturation has an effect on the expression of dormancy genes. The imposition of water stress on maternal plants during seed development also affect the level of dormancy achieved. Light inhibits germination in ND seeds and this inhibition is intensity-dependent: the higher the light intensity, the greater the inhibition. This germination inhibition is also accentuated by higher incubation temperatures. Thus, wild oat dormancy has a plasticity attached to its phenotypic expression.

Naylor pointed out that **it is difficult to distinguish contrasting phenotypic classes through conventional breeding experiments** because the only trait that can be used is their rates of germination under standard conditions. In some cases germination can extend over many weeks in a sample of F_1 seeds, which are presumably genetically identical. This trait is also highly sensitive to various environmental factors only some of which are known and controlled under laboratory conditions probably obscuring phenotypic differences. Furthermore, as stated by Simpson 1978, **analysis, by experimental techniques, of the full nature of a seed-environment system that exhibits dormancy is very difficult. Seeds cannot be considered in the absence of environment and the dynamic nature of the changes that occur during the arbitrary time frame chosen to measure rate of change must also be kept in**

mind. Results from Naylor's field experiment indicated that factors other than duration of dormancy, as measured in the laboratory, also contribute in determining relative fitness under field conditions. The total effect of genetic and environmental factors on the three stages of the life cycle of A. fatua plants, i.e. vegetative growth, seed maturation, and the incubation period following seed maturation, may provide flexible strategies for their survival. However, in spite of numerous studies on factors that influence the degree of dormancy of seeds, there is still no general agreement about the nature of the control mechanism involved.

In view of this plastic response in the expression of wild oat dormancy genes with environmental factors, the problem of synchronicity (or reliable and uniform spring emergence) of the dormoat crop is not surprising.

Objectives of the program

In 1982, when physiological studies on dormoats were re-established at Agriculture Canada, the general objectives of the program were to study the physiological and biochemical processes controlling seed dormancy in dormoats and to work on environmental and biological factors needed for the induction of a secondary dormancy in dormoats. In the context of supporting the dormoat breeding program, the immediate priorities were narrowed to the development of an effective seed management protocol to obtain uniform spring emergence of the dormoat crop and to try to develop test(s) to facilitate screening of potential dormoat lines.

Approach

According to Burrows (1986), three main physiological processes had to be satisfied before dormoat seeds could emerge in springtime:

- completion of primary dormancy is a pre-requisite to spring germination (= after-ripening);
- after-ripened seeds need to be induced into a state of secondary dormancy so they fail to germinate in the fall;
- and secondary dormancy must be released by winter to permit germination in springtime.

The seed management step required for dormoats would be introduced to complete the after-ripening period and induce the secondary dormancy step prior to planting in fall.

Secondary dormancy develops in seeds after shedding or harvest, when germination is prevented by unfavourable environmental conditions. The term secondary dormancy is used to describe that particular state of seed which renders it ungerminable in an environment which previously supported its germination. In general, secondary dormancy is seen to follow inhibition of germination, although no single environmental factor can be held responsible for the inhibition. Temperature, absence of light or oxygen, presence of volatile or allelopathic inhibitors, and moisture conditions may all contribute to inhibition of germination and, thereby, enable induction of secondary dormancy. Among these, temperature is an important rate-determining factor (Karssen 1981). Sawhney and Naylor (1980), were able to show evidence for the induction of a secondary dormancy in wild oat by high incubation temperature (T°) of the seeds. The wild oat strains used had a short primary dormancy, so the induction of this thermodormancy occurred in after-ripened seeds. The germination behavior of these wild oat strains resembles the behaviour observed with many of the superior dormoat strains (Burrows 1986).

Preliminary studies on the effect of high T°-high moisture incubation (40°C) of dormoat seeds were done by the oat breeder (Burrows, unpublished results) with some strains. The experiments were done on freshly harvested material which was probably in a state of partial or complete primary dormancy. In one experiment a large portion of material was killed but a few strains did not germinate when brought to room T°. These strains showed some germination when the seeds were allowed to dry and two to three months of room T° storage had taken place. Thus, there was evidence that a kind of thermodormancy might have been induced in these strains but it was also possible that the seeds were completely dormant to begin with. In a second experiment, the heat treatment survival of a large number of dormoat strains was looked at and some of these demonstrated good germination after at least a month of treatment. The winter survival of the material from either the first or the second experiments was not verified in the field.

Considering these preliminary results, it was decided that the immediate emphasis in the new physiology program would be on the determinations of the conditions needed to achieve a good thermodormancy induction of the seeds. Germination evaluation in the laboratory and field emergence in the spring would be conducted. The major constraint of the program at the beginning was the availability of the seeds, i.e. maximum amount of each line was approximately 200 g, which restricted the type and number of possibilities that could be investigated.

EXPERIMENTAL DESIGNS AND RESULTS

Research

Secondary dormancy induction by high temperature and high moisture - In view of the breeder's attempts at secondary dormancy induction with high temperature-high moisture treatment, preliminary experiments in the winter of 1982 were designed to gain information on temperature and moisture conditions required to achieve induction. The original experiments were done in a disaffected growth cabinet. The cabinet provided an insulated room where large numbers of seeds could be treated with the temperature and moisture environment maintained reasonably well. The temperature used was 40°C with the seeds in an imbibed state and kept moist throughout the treatment by using humidifiers and direct watering 3 times daily. Temperature was achieved and maintained by the use of a portable household heater. Flexibility in terms of changing temperature or moisture level was not possible in this room. We decided to investigate the effect of lower temperatures, i.e. 25°C, 30°C, and 35°C, in petri dishes, in growth cabinets and with year-old seeds, (the only ones available then). Germination occurred at the three temperatures. 35°C favored accelerated degradation of the endosperm reserves. This liquified endosperm was more prone to fungal and bacterial invasion which led to some seed death within a few days. At 40°C, in petri dishes, no germination occurred but there was a significant loss of viability with increasing time of exposure; dormoat lines were variable in their capacity to withstand the treatment up to a week. Differences were noticed between the lines in how

fast breakdown of the seed reserves would take place. However, the most significant difference was between dormoat and cultivated oat; within 3 days, the endosperm of oat was liquified whereas dormoats were still at a hard dough stage (Fig. 1). This high moisture-high temperature treatment is usually referred to in the literature as an "aging" condition; thus, it is not surprising to observe a loss in viability after a week of exposure.

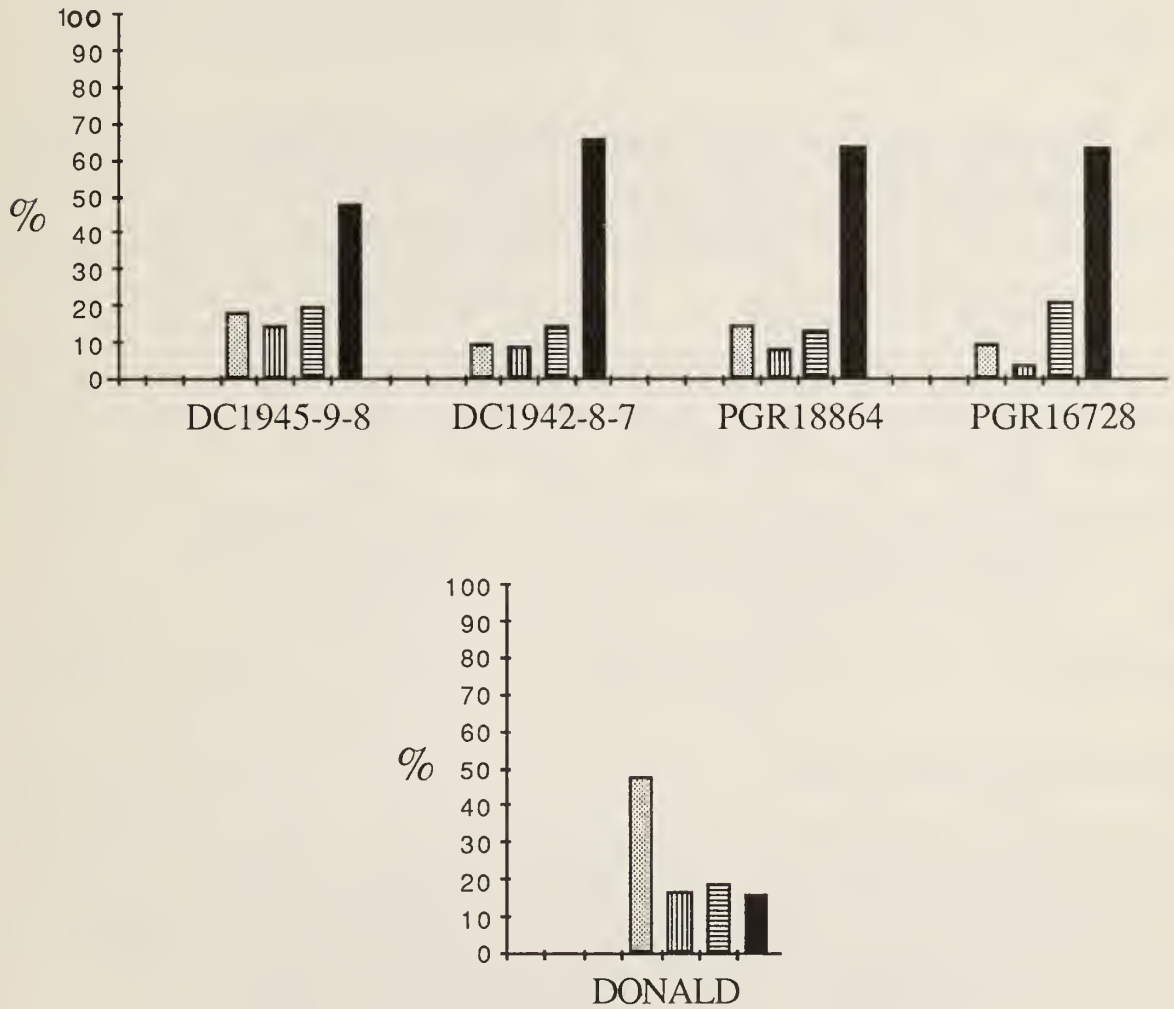


Fig. 1. Percentage distribution of endosperm degradation after 3 days at 40°C in petri dishes ▨ sick (dead), ▥ liquid, ▤ soft dough, ■ hard dough. (5 replicates, 50 seeds) (SE = ± 3%).

There were no readings on the decrease in viability with the breeder's original experiment, survival was fairly good even after a 1 month exposure. We decided to re-use the original set-up in the disaffected growth cabinet and assess viability under these conditions. Temperature was maintained at 40°C but, contrary to a controlled cabinet situation, the moisture environment was fluctuating: from 98% R.H. when the seeds were watered, down to approximately 80% R.H. between these daily waterings and even further down (65% R.H.) overnight. The overnight period was approximately 15 hours during which time the seed coats dried completely and the caryopsis itself started losing water. Viability under these conditions was improved significantly as shown in Table 1.

Table 1. Percentage viability* of year-old dormoat lines placed for different lengths of exposure to 40°C in two moisture environments. (Mean of 5 replicates of 50 seeds, S.E. = ±5%).

Lines	Continuous 100% R.H.		Intermittent 100% R.H.		
	4 days	7 days	4 days	7 days	14 days
PGR16728	33	0	73	62	42
PGR18864	60	0	100	62	25
PGR8658	20	0	77	68	13
PGR18863	33	0	100	89	28
Donald	0	0	58	34	0

* Tetrazolium Test (Anon. 1976)

Thus, fluctuating moisture levels, in conjunction with 40°C, were more favorable in preventing germination and maintaining viability; these conditions were chosen as the secondary dormancy induction treatment for the fall '82 field experiment. One week exposure time was chosen as it seems to give a good difference between cultivated oats and dormoats with still over 60% viability in these latter. Thirty dormoat lines were treated approximately 8 weeks after harvest and were planted in the field at the end of October '82 for spring emergence readings. The same lines were also monitored in the laboratory for germination studies.

The original seeds had displayed no dormancy when germinated in soil at 20°C but some residual dormancy when incubated in petri dishes at 20°C. Assessment of the lines after the treatment, under these same conditions, indicated that there was induction of a secondary dormancy. This dormancy was more pronounced when the seeds were incubated in petri plates as compared to soil and there was also variations amongst the strains for the level of induced secondary dormant seeds, as shown in Table 2.

Table 2. Distribution of the dormancy response of 30 dormoat lines treated for 1 week at 40°C and intermittent high R.H.*

% Dormant**	Media	
	Soil	Petri Dish
0	1	5
1-20	15	4
21-40	9 (wild oat)	8
41-60	4	7
61-80	1	4 (wild oat)
81-100	-	2

* No dormancy with 4 oat cultivars subjected to the same treatment.
** Germination test performed without drying the seeds at the end of the treatment; in soil and in petri dish at 20°C.

Three lines were studied further because they survived very well the treatment and also displayed good secondary dormancy induction. Table 3 gives the results when treated seeds were tested for viability with the tetrazolium test and their germination response to incubation with gibberellic acid, (GA).

Table 3. Percentage viability and percentage germination with gibberellic acid (100 ppm) for 3 dormoat lines after secondary dormancy induction (mean of 3 replicates of 50 seeds, SE ± 4%).

Lines	Viability %	+GA Germination %
PGR18870	97	64
PGR18871	96	64
PGR18874	47	80

PGR18870 and PGR18871 had over 60% of their seeds fully germinable. PGR18874 had approximately 50% of its seeds showing the red embryo typical of the tetrazolium test but it responded very well to GA incubation; the low tetrazolium response may be an indication that the part of the respiratory pathway reacting with tetrazolium salts was altered by the heat treatment. Results in Table 4 show the effect of the induction treatment on these lines and their differential response depending on the incubation media used.

Table 4. Percentage dormancy before and after the induction treatment. Germination at 20°C for 3 weeks. (Mean of 3 replicates of 50 seeds, SE ± 5%).

Lines	Control		Treatment	
	Soil %	Petri %	Soil %	Petri %
PGR18870	0	9	20	75
PGR18871	5	33	80	85
PGR18874	11	28	60	85

Emergence in the spring was not very good in terms of numbers, i.e. less than 3% of the amount sown emerged; this germination occurred with treated seeds in only 6 lines out of 30 amongst which were the three dormoats studied in the laboratory.

Secondary dormancy of these three dormoats was assessed in the lab after 16 weeks of room temperature storage. Fig. 2 illustrates the extent of after-ripening achieved when tested at 20°C with two incubation media.

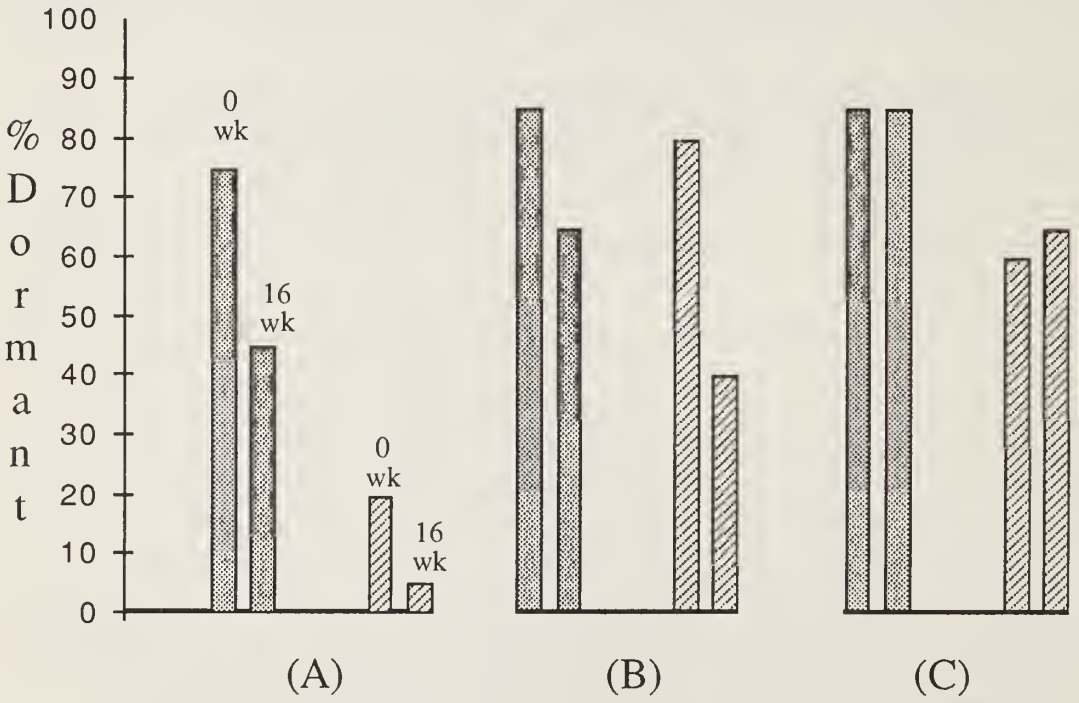


Fig. 2. Disappearance of secondary dormancy expressed in petri dish or in soil after 16 weeks of room temperature storage; ▨ petri dish, ▨ soil. A: PGR18870, B: PGR18871, C: PGR18874. (Mean of 3 replicates of 50 seeds, SE = ± 10%).

After 16 weeks of dry storage, PGR18874 had not lost the induced secondary dormancy whereas both PGR18870 and PGR18871 displayed less dormant seeds. The two dormoats differed in the extent of their response to incubation in soil after the treatment.

A portion of secondary dormant seeds was stored dried at -20°C immediately after the end of the treatment period. These seeds were used to study expression of dormancy in soil in relation to 1) the presence of the hulls and 2) the exposure of the secondary dormant seeds to a period of desiccation.

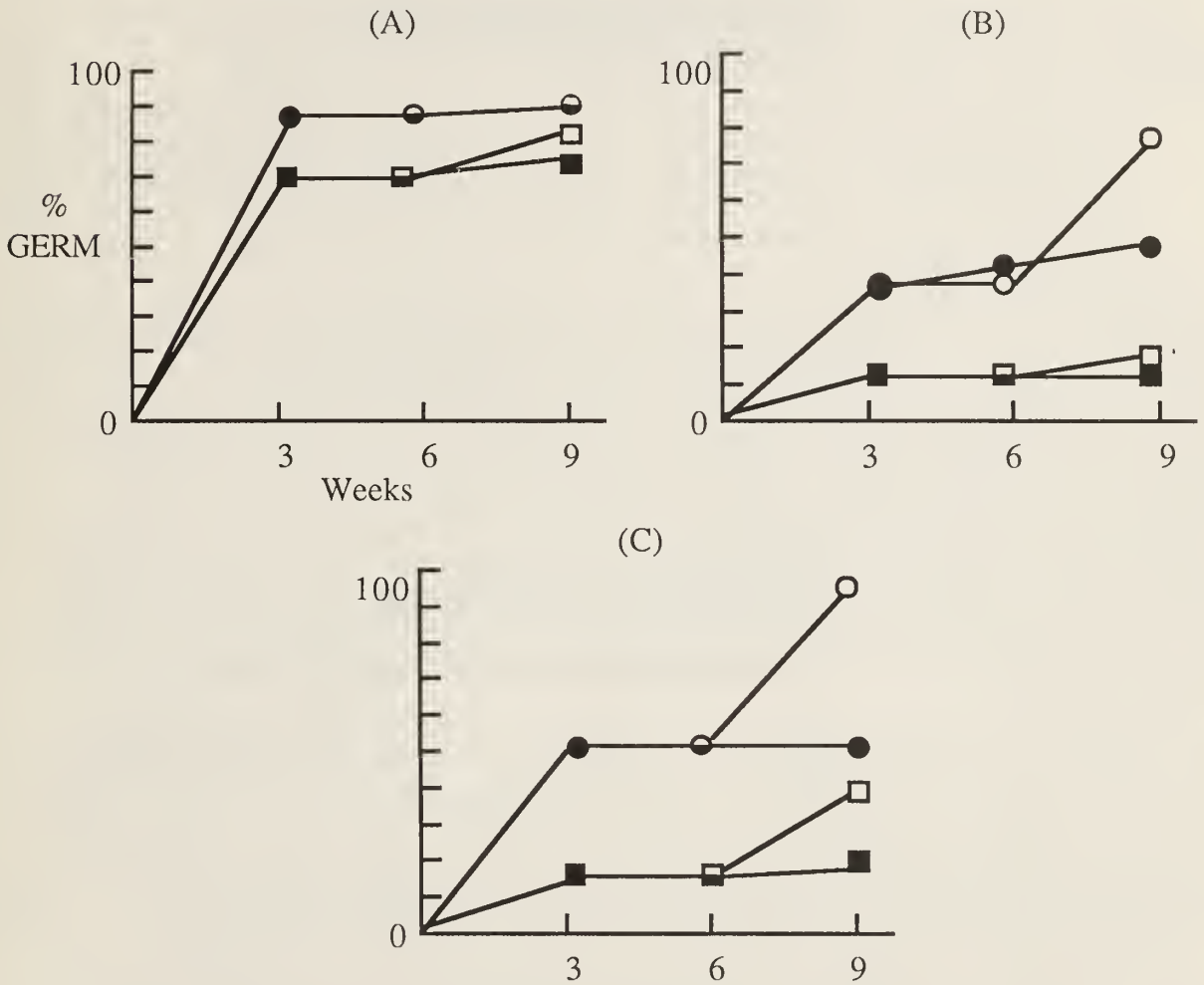


Fig. 3. Effect of removing hulls and a 3-week desiccation period on emergence from secondary dormancy as expressed in soil. ■ hulls, ● no-hulls, □,○ desiccated. A: PGR18870, B: PGR18871, C: PGR18874. (Mean of 3 replicates of 30 seeds, SE = ±5%).

Fig. 3 illustrates the response, as percentage germination, for PGR18870, PGR18871 and PGR18874. In the 3 lines, removal of the hulls promoted germination of part of the dormant seeds. A further 6 weeks did not favor more emergence for the pots kept watered with either hulled or dehulled seeds. A desiccation period of 3 weeks after the initial germination period pushed emergence higher in each dormoat but their response differed depending on the absence or presence of hulls. PGR18870 displayed more seedlings in the pots with hulled seeds whereas PGR18871 responded to desiccation only if the hulls were removed. Desiccation was effective in increasing germination in both hulled and dehulled seeds of PGR18874.

Effect of after-ripening on secondary dormancy induction - Throughout the years, the oat breeder (Burrows, unpublished results) made a few observations while breeding improved dormoats:

- Selection for good spring emergence also brought selection for high fall emergence; consequently, there was a gradual shifting in the breeding program to populations requiring shorter after-ripening periods, and
- There was always better emergence when seeds were planted right after harvest.

Knowing that after-ripening is slower for seeds left under field conditions, ie. in the ground, one way of explaining these two observations is illustrated in fig. 4 for hypothetical short and long after-ripening dormoats. The full curve describes the disappearance of dormancy for seeds kept in dry room temperature storage and the dotted curve, the disappearance of dormancy as it might happen when the seeds are planted in the field at different times after harvest. Fall germination would increase with later plantings since more seeds become fully germinable with time in dry storage. The shaded area represents the seeds which have the potential to germinate in the spring since they have satisfied their after-ripening requirement and are prevented from germinating by the arrival of the winter season. Thus, timing of the field planting seems to be important for survival and emergence the following spring.

In his 1978 review, Simpson also pointed to the fact that survival of dormant seeds in soil depends critically on the preservation of endosperm reserves until the onset of germination; endosperm hydrolysis in dormant seeds would cause swelling, bursting and rotting. Naylor's group found that in wild oat D lines, there was coadaptation of seed dormancy with rigorous dependence of endosperm hydrolysis on GA produced by the germinating embryo while ND lines showed variability in the degree of autonomy of their endosperm.

Combining these dormoats observations and the wild oat results with the fact that induction of secondary dormancy improved spring emergence in late plantings of some dormoat strains, possible mechanisms were put forward to explain how survival and emergence of fall planted dormoats may be achieved:

- The better spring emergence observed because the seeds are planted at harvest time may be due to the fact that endosperm stability is maintained in the ground, (because after-ripening has not been satisfied), while the mechanism for secondary dormancy gets induced.

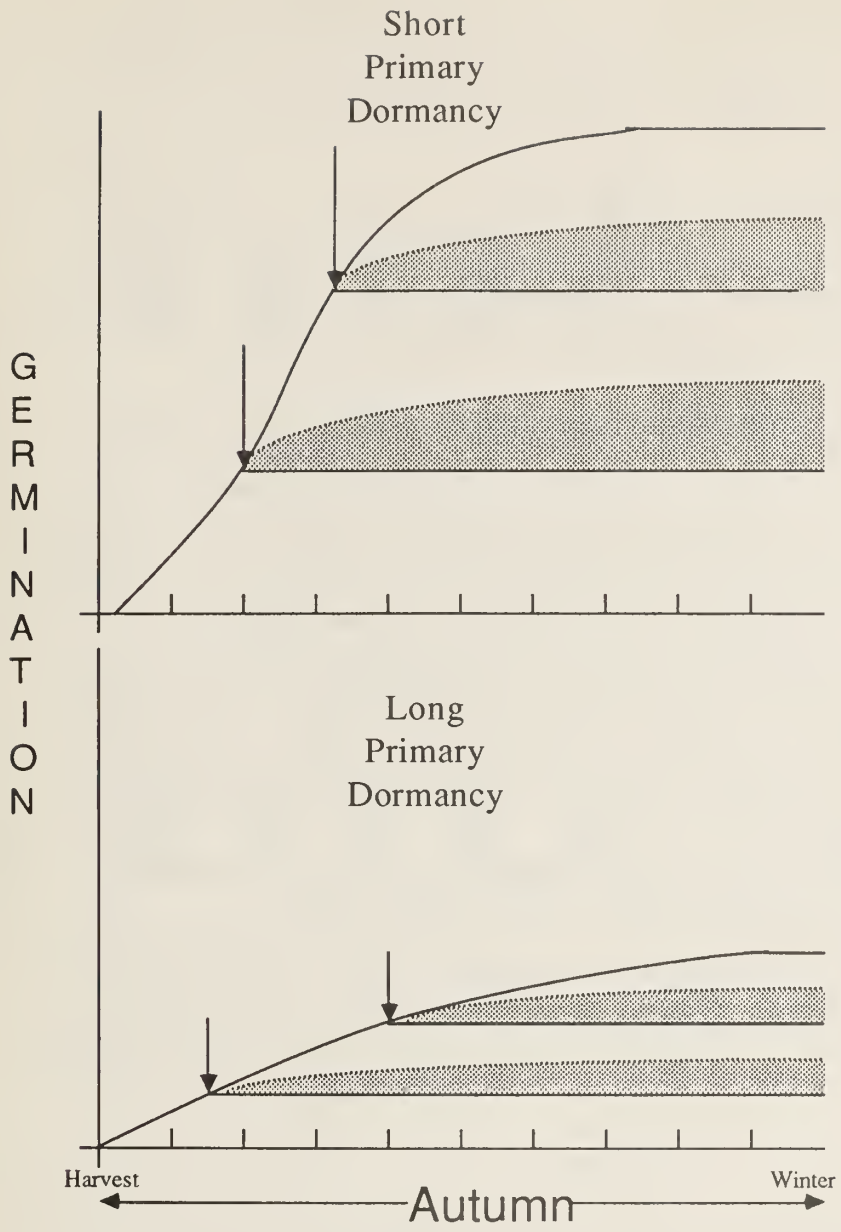


Fig. 4. Hypothetical after-ripening in dry storage — and following field planting at different times ... for two types of primary dormancy.

- Dormoats with short after-ripening have control over endosperm hydrolysis while in primary dormancy but the gene(s) for rigorous control of endosperm hydrolysis when dormancy is over may or may not be present. Thus, if absent, as soon as the embryo is after-ripened, the endosperm is autonomous and water is enough to trigger hydrolysis.
- If endosperm stability must be kept there may be two routes for achieving good artificially induced secondary dormancy in dormoats:
  - with after-ripened seeds: there is a need to have lines where the embryo maintains control of endosperm hydrolysis.
  - with not after-ripened seeds: genes for rigorous control may not be required and just potential for induction into secondary dormancy has to be present.

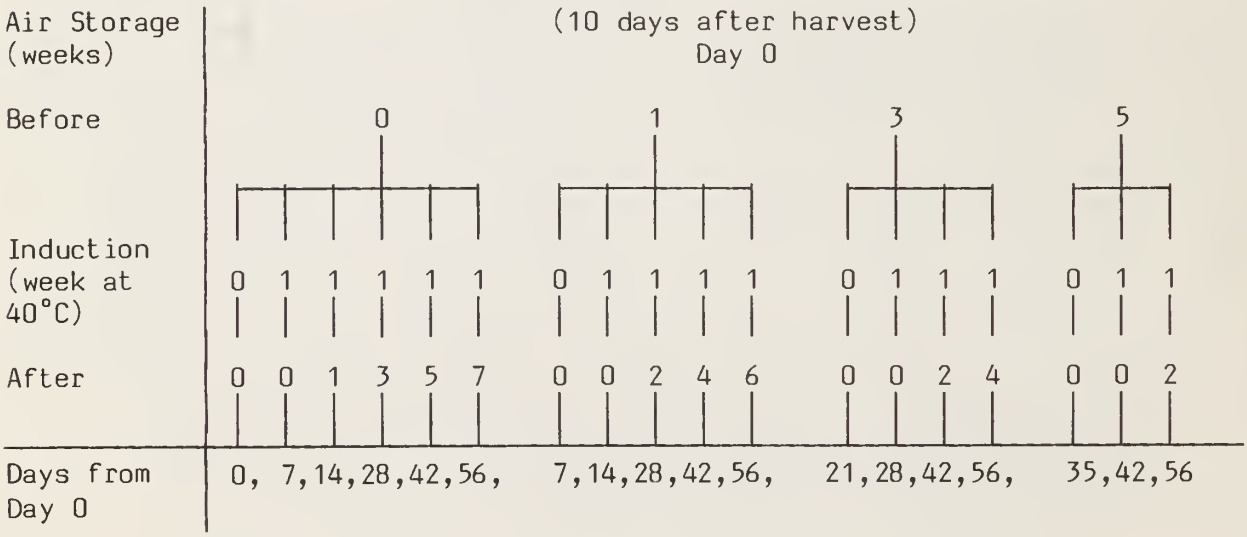
The objective of the Fall 1983 experiment was to explore the effect on spring emergence of variations in the timing of the induction treatment as well as in the planting in the field in relation to the after-ripening status. Primary seeds of three dormoats and one oat cultivar were used.

PGR18867 - a dormoat with 40% survival and emergence after 1 week in 40°C but no secondary dormancy induction; may have genes for embryo control over endosperm since survival was substantial but the timing of the induction may have been wrong in 1982.

PGR18874 - showed 75% dormancy induction in laboratory with less than 5% spring emergence in the field but still the best out of 30 lines tested in Fall 1982 late planting. Timing of planting may have been wrong in 1982; an earlier induction may allow more time for after-ripening in the field and thus better spring emergence.

PGR18860 - never heat treated but enough seeds available to include an additional storage condition ie. freezer storage.

The diagram outlined below describes the 18 different combinations of induction period and storage before and after induction that were tested in replicates, at 3 different sites. This experiment was a major undertaking both in terms of field work, since it meant several field trips for planting, and in the laboratory with 18 treatments for 4 lines replicated 3 times.



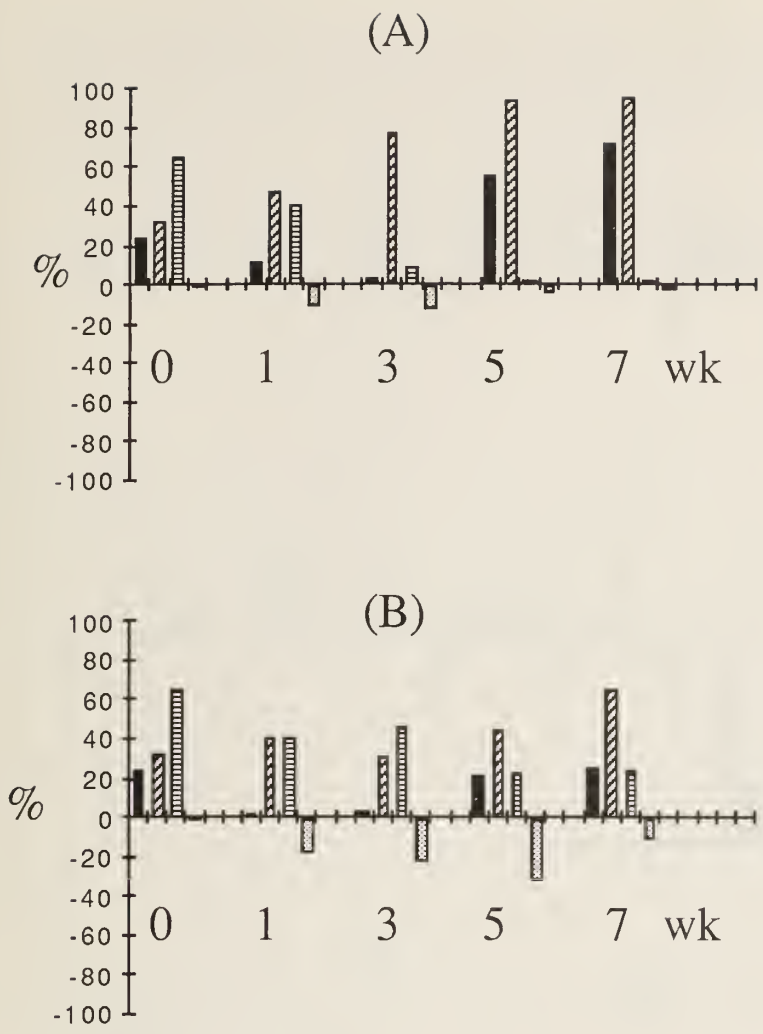


Fig. 5. Histogram of percentage germinating (■ petri dish or ▨ potted soil), sick (▩ potted soil) or dormant (▤ potted soil) untreated seeds of PGR18860 with increasing weeks of afterripening. A: Air-stored seeds, B: Freezer-stored seeds, (50 seeds, 3 replicates).

Fig. 5 and 6 are histograms of the status of the control seeds illustrating the disappearance with time of primary dormancy in the 3 dormoats. The bar colored black on the histogram represents petri dish germination, the other three bars illustrate the results from tests done in potted soil.

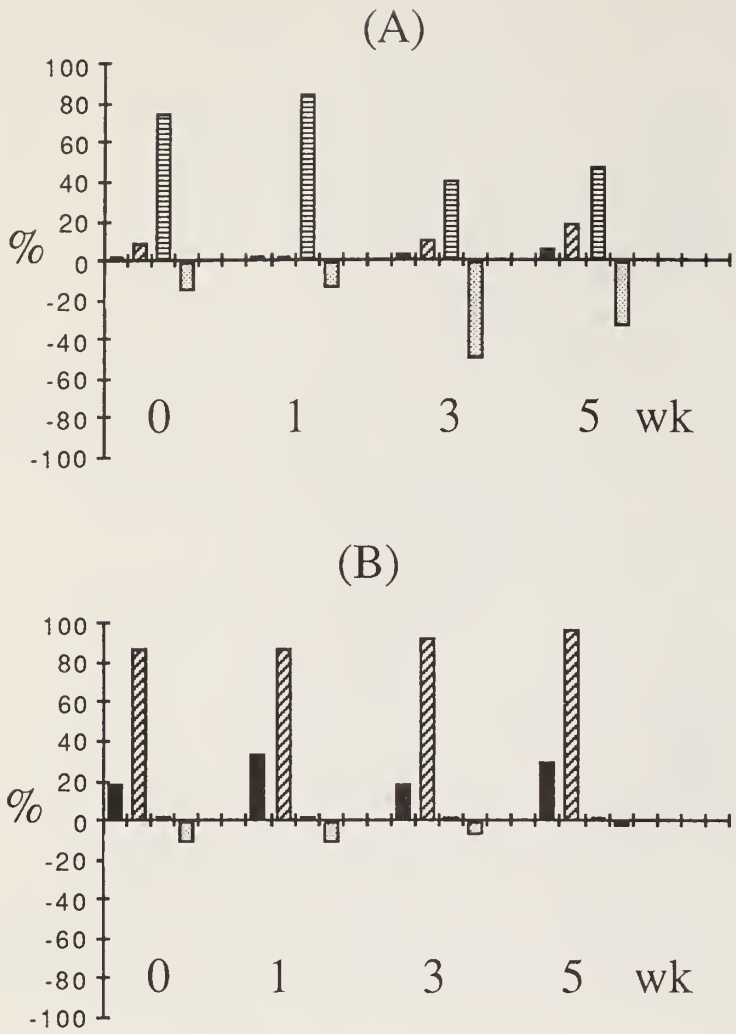


Fig. 6. Histogram of percentage germinating (■ petri dish or ▨ potted soil), sick (▩ potted soil) or dormant (▤ potted soil) untreated seeds with increasing weeks of room temperature afterripening. A: PGR18874 and B: PGR18867.

Germination was again higher in potted soil than in petri dish. Line PGR18867 did not show any dormancy in soil at harvest time; line PGR18860 displayed approximately 70% dormant seeds and by week 5 none of it remained. Line PGR18874 was very dormant at harvest time (approximately 85%) and over 40% remained in primary dormancy by week 5. Looking at the pattern of awakening in PGR18874 we see that the seeds are slowly coming out of dormancy around week 3 with germination in soil and in petri dish being noticed. By week 3, there is also a big increase in the percentage of sick seeds (50%)

indicating that as after-ripening progresses, there may be a transition period where endosperm degradation can proceed while the embryo is not yet ready to germinate; in week 5, more embryos are germinating and losses due to disease are decreasing. Losses for lines PGR18860 or PGR18867 were minimal, (within expectation).

Storage in the freezer prevented only partially the after-ripening of line PGR18860 since by week 7, there was a reversal of germinating vs dormant seeds when the germination profile of freezer storage is compared to the one obtained at harvest time (0 week), (Fig. 5B).

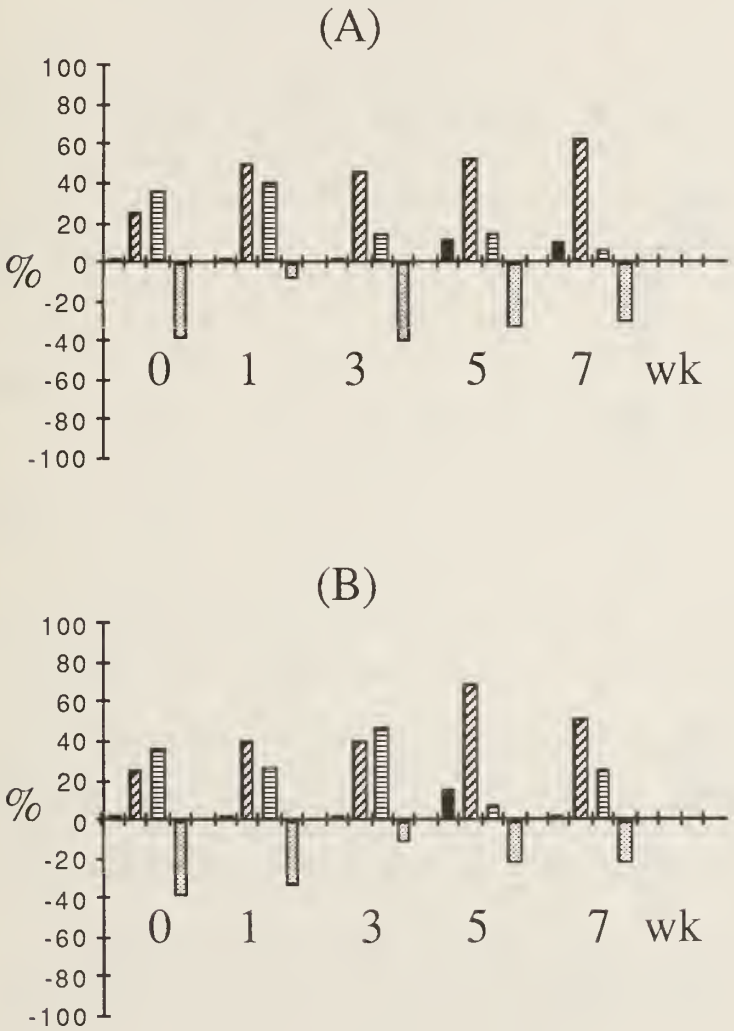


Fig. 7. Histogram of percentage germinating (■ petri dish or ▨ potted soil), sick (▩ potted soil) or dormant (▤ potted soil) treated seeds of PGR18860 with increasing weeks of afterripening. A: Air-stored seeds, B: freezer-stored seeds, (50 seeds, 3 replicates).

As illustrated in Figs. 7 and 8, a one-week treatment did not increase the dormancy level of the three dormoats. For both PGR18874 and PGR18867 (Fig. 8) dormancy was decreased and the treatment increased the percentage of sick seeds. Line PGR18860 (Fig. 7) showed less diseased seeds than the other two. There is a slight indication that the dormancy status for this line may have been changed, especially in weeks 5 and 7, when the results in petri dish are looked at. The behavior profile from the freezer-stored material was not changed much by the treatment and the dormancy status was not improved (Fig. 7B).

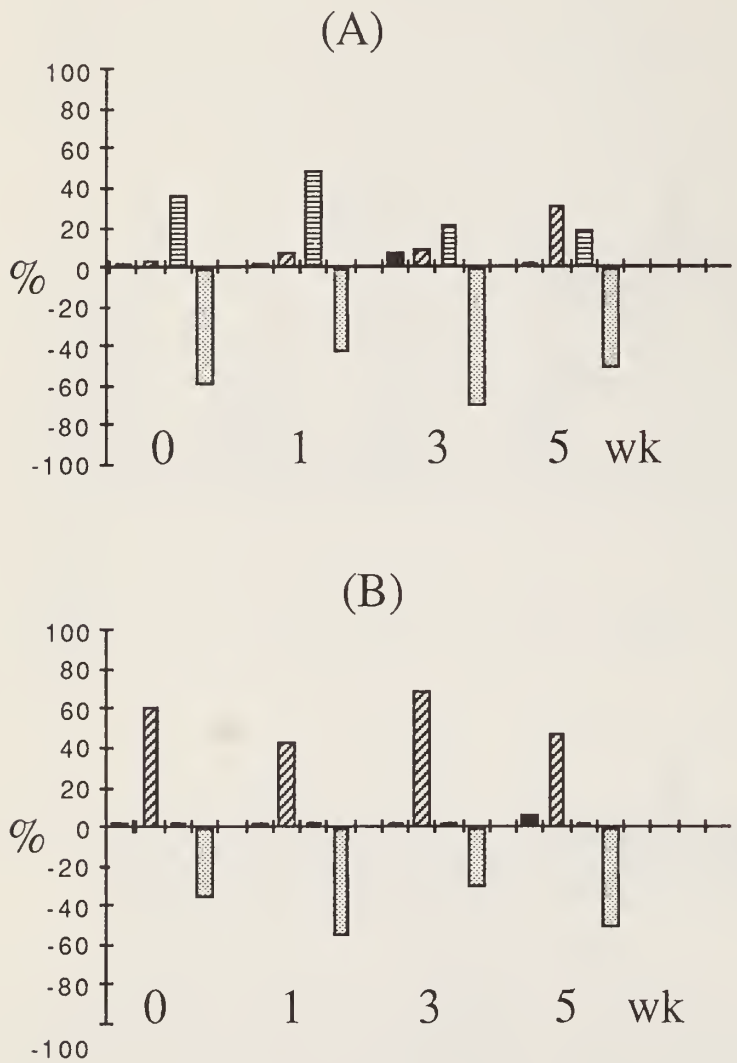


Fig. 8. Histogram of percentage germinating (■ petri dish or ▨ potted soil), sick (▩ potted soil) or dormant (▤ potted soil) treated seeds with increasing weeks of room temperature afterripening. A: PGR18874 and B: PGR18867.

Results of the proportion of seeds either dormant, germinating or sick after 3 weeks in potted soil at 20°C for some of the different length of storage conditions tested are presented in Tables 5 to 7.

Table 5. Responses of seeds of PGR18860 following weeks of storage applied either before or after a 1-week high temperature treatment. Results recorded after 3 weeks in potted soil.*

Status of Seed (%)	WEEKS OF STORAGE									
	0		1		3		5		7	
	No Treatment	Treatment	Before	After	Before	After	Before	After	Before	After
Germinated	33	25	50 **40**	49	46 **41**	81	53 **70**	89	63 **52**	61
Dormant	66	36	41 **27**	34	14 **47**	7	14 **8**	3	6 **26**	1
Sick	2	39	9 **33**	17	40 **12**	12	33 **22**	8	31 **22**	38

* Bold print = results from freezer - stored seeds.

Sick seeds are basically seeds where the endosperm has degraded and become infected by microorganisms without embryo germination occurring. The increase germination as time after heat-treatment progresses, reflects the awakening of the seeds that were in primary dormancy when the treatment was given; the response parallels the one obtained with the time related control group (Fig. 5 and 6) and is not due to the heat treatment.

From a previous experiment, we knew that line PGR18874 could respond to the treatment but it did not do so in '83. The other experiment was done on seeds without residual primary dormancy showing in either petri dish or potted soil. Depth of primary dormancy or length of time required for completion of after-ripening will vary from year to year depending on the environmental conditions during grain development. Unfortunately, two factors prevented extending the experiment: the amount of seeds available and the accessibility of the field for planting in late fall. Nevertheless, the importance of the timing of the induction is reinforced by the fact that a "sensitivity" window was noticed in the degradation of the endosperm in control seeds still in after-ripening (Fig. 6A).

Table 6. Responses of seeds of PGR18874 following weeks of storage applied either before or after a 1-week high temperature treatment. Results after 3 weeks in potted soil.

Status of Seed (%)	WEEKS OF STORAGE							
	0		1		3		5	
	No Treatment	Treatment	Before	After	Before	After	Before	After
Germinated	9	3	8	8	9	25	31	28
Dormant	75	37	49	36	21	7	18	4
Sick	16	60	43	56	70	68	51	68

Table 7. Responses of seeds of PGR18867 following weeks of storage applied either before or after a 1-week high temperature treatment. Results after 3 weeks in potted soil.

Status of Seed (%)	WEEKS OF STORAGE							
	0		1		3		5	
	No Treatment	Treatment	Before	After	Before	After	Before	After
Germinated	87	61	44	56	69	70	48	59
Dormant	1	1	1	0	0	0	0	0
Sick	12	36	55	44	31	30	52	41

Line PGR18867 behaved in a manner similar to a previous heat treatment experiment (Fall 1982), where it did not respond to the heat treatment but could withstand it. Differences in the timing of the induction did not change its response; its high germination even after 1 week of heat stress probably points to the presence of some form of embryo control over endosperm hydrolysis without the ability to respond to the secondary dormancy induction treatment used here.

The field results could almost be anticipated both for control and treated seeds. Neither PGR18874 or PGR18867 emerged in the field in springtime; PGR18874 probably because of its slow type of after-ripening and the high losses due to the treatment, and PGR18867 probably because of its lack of dormancy which allowed germination at planting time, in the Fall. Seedlings emergence was noticed for PGR18860 with untreated material coming from freezer storage, where part of the primary dormancy was kept. The

dormancy noticed in the lab for the late treated material, between incubation in soil and in petri dish, did not help in improving spring emergence for PGR18860. Some of the control field plots of PGR18874 were dug out in late spring to check on the status of the buried seeds; seeds were retrieved without any hulls left on them after their stay in the field but in good shape, without sign of germination, thus, still in dormancy.

Eventhough the field results were not encouraging, some useful observations were made:

- Lines able to respond to the induction treatment are required.
- Timing of induction is probably important.
- The induced dormancy should not be as "strong" as the one observed in PGR18874 primary dormancy but more, (in terms of after-ripening),

Effect of lengths of induction treatment on secondary dormancy

The previous experiment dealt with only one duration of treatment on the basis that efficiency of dormancy induction may be in the timing of exposure to the treatment. The next experiment was designed to look at the effect of different lengths of the high temperature-high moisture treatment on induction into secondary dormancy at different stages of after-ripening. It was impossible to do this experiment with the lines used in the previous one because there was not enough seeds left of any of them to allow it. Thus, three dormoats were chosen from the 1983 physiology program increases:

PGR18859: had never been used before in induction studies.

PGR18876: had previously been heat selected in Dr. Burrows preliminary experiment (1981); increased in 1982 and found to have a long after-ripening.

PGR18870: showed high survival after 1 week of high temperature-high moisture treatment but no sign of induction under laboratory evaluation; its response in the field, in spring, was fair.

The responses of Donald and Elgin (two commercial oat cultivars) were also monitored. Primary seeds were used at 4, 8 and 12 weeks after harvest. Treatment was in a cabinet at 40°C, with the moisture conditions previously described for 2, 4, 7, 10 and 14 days after which the seeds were taken out, split into 3 subsamples (each replicated 3 times) and processed by being either:

- planted directly in potted soil at 20°C.
- germinated in petri dish with 300 µM GA, at 7°C, to check sensitivity to the hormone.
- subjected to the tetrazolium test to check for seed viability.

As expected, viability for Donald and Elgin decreased as length of exposure increased. Both PGR18859 and PGR18870 were able to survive the high temperature-high moisture treatment showing, after 14 days of exposure, 65% and 80% germination respectively. For the 12-weeks after-ripening period, no dormancy induction occurred for these 2 dormoats.

Secondary dormancy was induced in line PGR18876 at approximately the same levels regardless of the after-ripening status. Fig. 9 illustrates the dormancy levels obtained in the 12-week after-ripened seeds with increased time of exposure to high temperature-high moisture conditions.

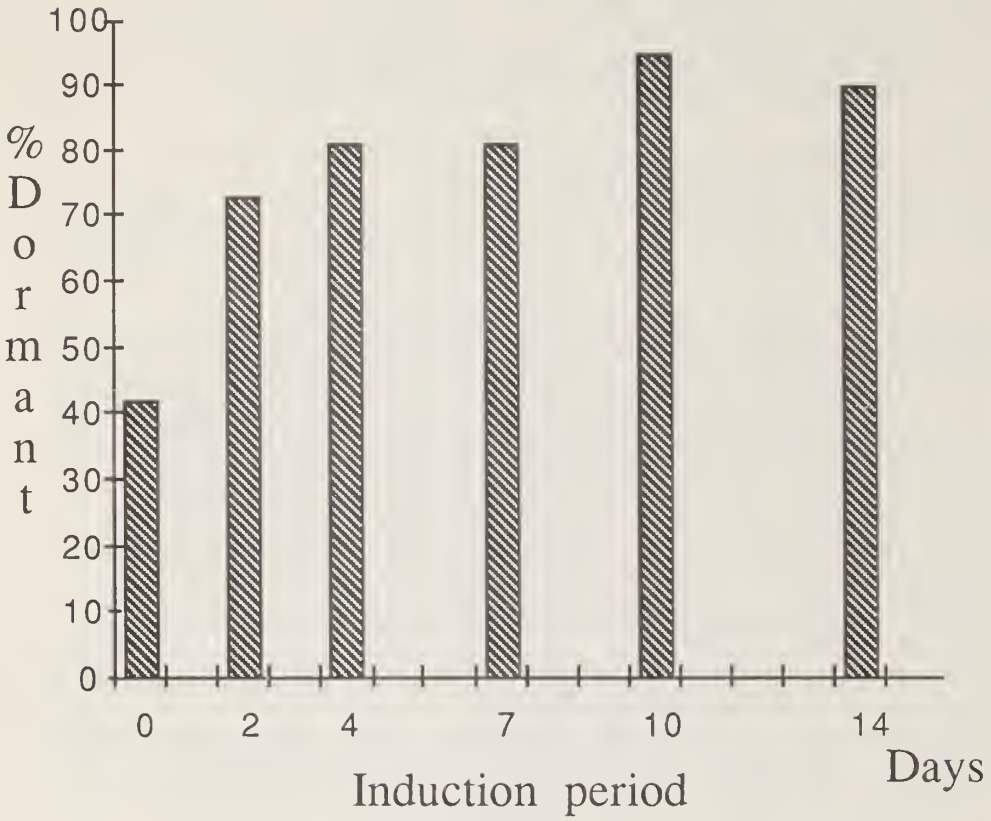


Fig. 9. Soil dormancy of line PGR18876 following various periods of exposure to the high T° - high moisture treatment. (3 replicates, 50 seeds).

42% of the seeds were still in primary dormancy after 12-weeks of after-ripening. Secondary dormancy was induced within 2 days; the dormancy level being pushed up 30%. A 14-day exposure brought the percentage further up,(17% approximately). Fig. 10 illustrates the response of these 12 weeks after-ripened seeds to 300 μM gibberellic acid. Approximately 35% of the treated seeds did not respond to GA by the 4th day of induction and this remained constant until the end of the treatment (14 days).

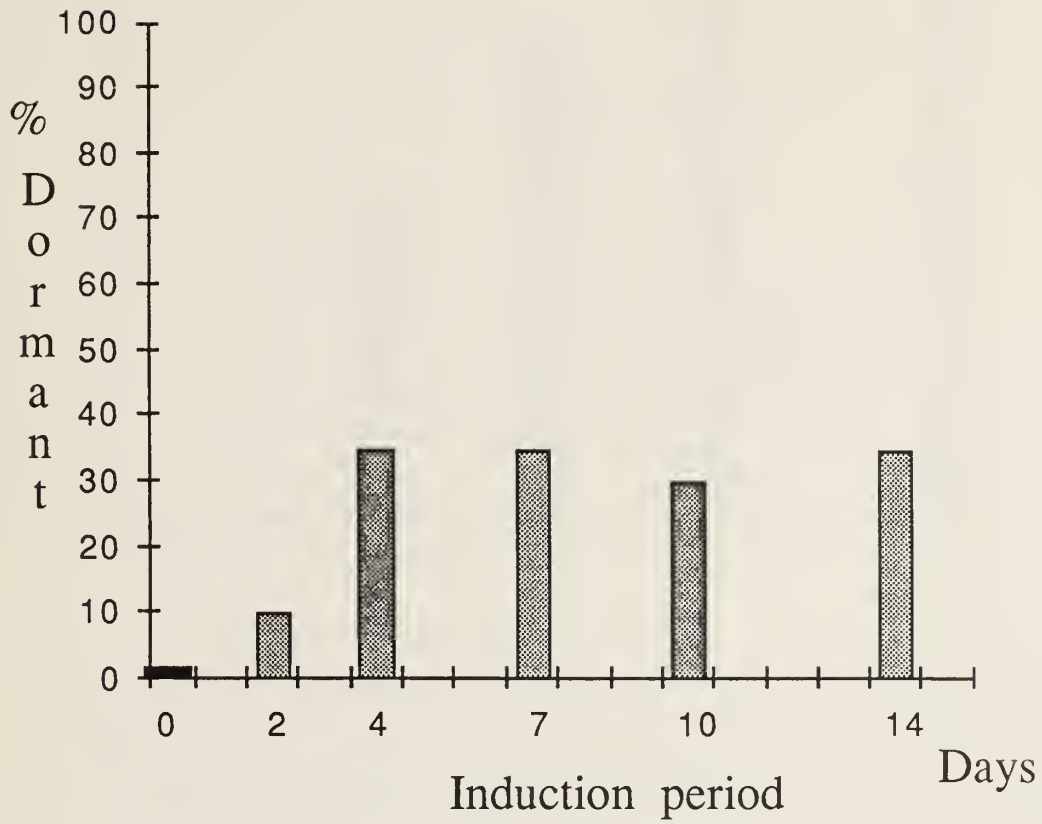
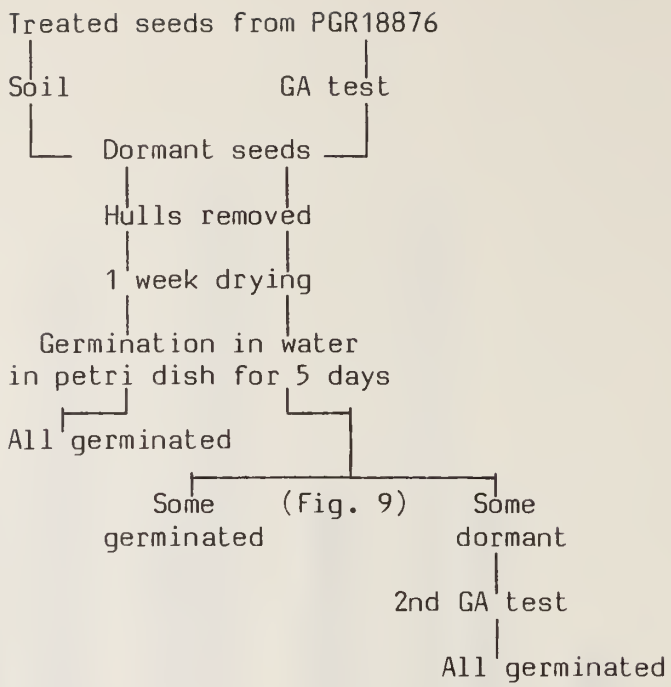


Fig. 10. Percent dormant seeds following exposure of secondary dormant seeds of PGR18876 to 300 μM GA^3. (3 replicates, 50 seeds).

The dormant seeds from both tests (potted soil and petri dish with GA),were dehulled (to check if they were still viable) and left to dry for 1 week. The seeds were re-subjected to germinating conditions as outlined in the following diagram:



The drying period was enough to remove dormancy in the material that came from potted soil but it was only partially successful on the dormant seeds that were GA-insensitive after the treatment. As duration of the induction period increased, the seeds seemed to have gone into "deeper" stages of dormancy. There was a gradual increase in the percentage of seeds remaining dormant: half of the GA-insensitive seeds for the 4 day-induction to all of the GA-insensitive seeds for the 14 day-induction, as illustrated in Fig. 11. These seeds were still viable and responded to GA this second time. The petri dish environment either superimposed another requirement for germination, i.e. modified the induced secondary dormancy, or it allowed for the expression of this particular aspect of the dormancy.

The effect of the presence or absence of hulls on the response of line PGR18876 to dormancy induction conditions was investigated with seeds left to after-ripen at room temperature for 5 months and with seeds stored in the freezer after 8 weeks of afterripening. The seeds were treated for 2 days at 40°C and constant 100% R.H. Different responses to the treatment were noticed depending on the storage conditions, (Table 8). In the fully after-ripened seeds, secondary dormancy was only expressed in petri dishes and hulls were required to induce the dormancy but not for its expression. In the partially after-ripened seeds, 45% were still in primary dormancy and part of this dormancy was dependent on the presence of the hulls. The high temperature-high moisture treatment applied to hulled seeds increased only slightly the level of dormancy already present; it did however make expression of the dormancy completely independent of the presence of the hulls. The same treatment applied to dehulled seeds doubled the percentage of dormancy as compared to the dehulled control. With or without treatment, partially after-ripened seeds did not allow different dormancy responses between a potted soil or petri dish environment.

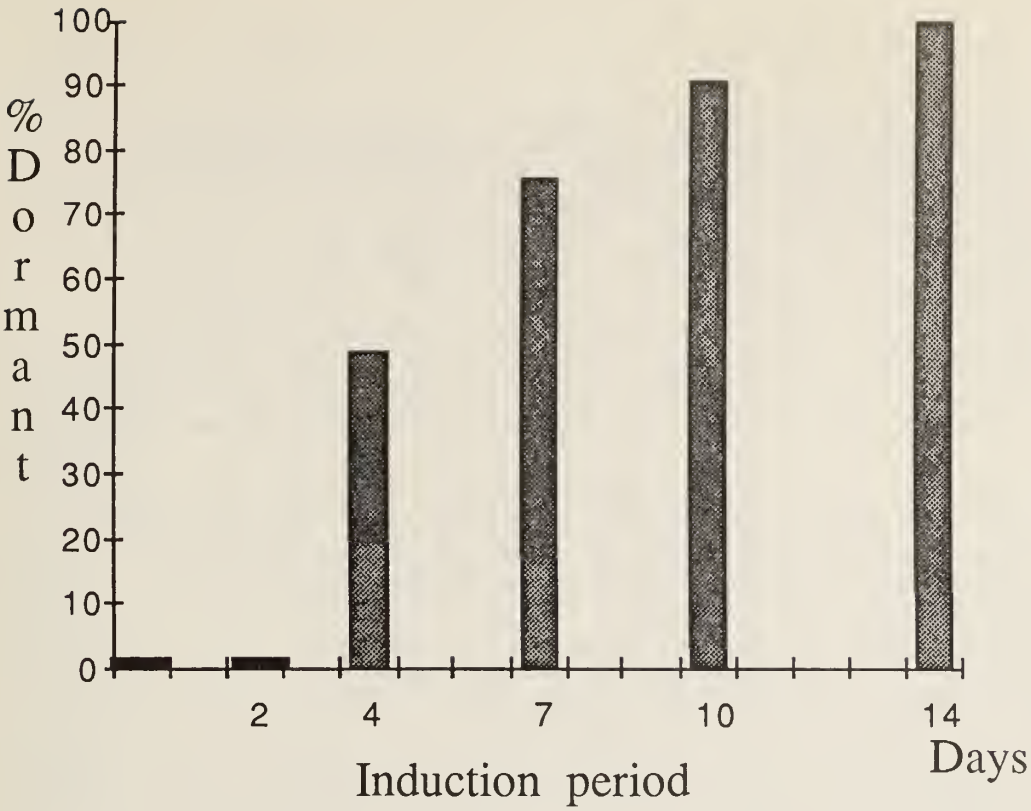


Fig. 11. Percentage of GA-insensitive seeds not responding in germination test following a 1-week desiccation period.

Table 8. Effect of presence or absence of hulls on the percentage of dormant seeds of line PGR18876 after 2 days at 40°C and constant 100% R.H. (3 reps of 50 seeds/each)*

	Fully After-ripened Seeds		Partially After-ripened Seeds	
	Soil (%)	Petri (%)	Soil (%)	Petri (%)
Control				
+ Hulls	0	0	45±6	43±5
- Hulls	0	0	19±2	14±4
Treatment				
+ Hulls	0	23±5	59±9	55±7
- Hulls				
before	0	4±2	38±4	37±8
after	0	21±1	51±9	68±4

* germination test: 3 weeks at 20°C

Response of dormoats to various treatments for secondary dormancy induction and better spring emergence - Knowledge gained from the field results of the two previous fall experiments were taken into account in designing this experiment both in terms of types of treatment and lines to be treated. Secondary dormancy induction by incubation under N_2, was also explored based on a report (Symons et al., 1986) of its effect on wild oat populations. Imbibition for a few days, under a nitrogen atmosphere gave evidence of a modification of the germination behavior at lower temperatures when tried with a partially afterripened dormoat line. This response was interesting in terms of fall planting and the nitrogen treatment was further examined also.

Seeds from 16 dormoats and 3 oat cultivars were treated and planted in late October. For each one, the materials used were seeds from the 1984 harvest, stored prior to planting either at room temperature or in the freezer, and seeds from room temperature storage treated for secondary dormancy induction following 3 protocols:

- High temperature (40°C)-high moisture for one week.
- Nitrogen gas - high moisture - 30°C for 2 days.
- Coumarin coating at 5×10^{-3} M applied as an acetone solution under vacuum (Burrows, unpublished method).

Again, the experiment involved monitoring spring emergence in the field as well as germination behavior in the laboratory under different temperatures and media. An average of 850 seeds, replicated twice, were treated and planted for each treatment. Coumarin did not improve spring emergence in the field or provide any difference in the laboratory tests as compared to the room temperature control. The nitrogen treatment was also ineffective in terms of improving field emergence and was even detrimental to the health of most seeds except for line PGR18874 whose seeds survived the treatment very well but were not induced into a secondary dormancy.

The room temperature stored seeds (Table 9) displayed very little dormancy in potted soil; dormancy was expressed in petri dish with some lines showing temperature differentials. In terms of spring emergence however, results were very poor except for lines PGR18865 and PGR18862 with approximately 5% emergence of the planted seeds.

Storing the seeds in the freezer and planting late was beneficial to spring emergence of almost all dormoat lines (Table 10). Best performances were observed for PGR18865 and PGR18862 followed by PGR18873 and PGR18869,eventhough in terms of percentage, the results were relatively low ranging from 12 to 3%. In the laboratory tests, these lines showed little dormancy in potted soil but expressed a T° dependent dormancy in petri dish. High levels of dormancy in both potted soil and petri dish were not favorable to spring emergence as observed with lines PGR18870, PGR18871, PGR18874, PGR18876 and PGR8658.

Table 9. Percentage dormancy in laboratory tests* and field emergence** for room-stored seeds.

Lines	% Dormant				Field Spring Emergence (No. of seedlings)
	Soil		Petri		
	13°	20°	13°	20°	
PGR18866	0	0	0	0	0
PGR18868	0	0	0	0	3
PGR18870	0	0	15	13	5
PGR18871	0	0	25	37	3
PGR18874	3	8	48	25	1
PGR18876	5	6	30	52	8
PGR8658	12	12	23	53	11
PGR16727	0	6	0	3	1
PGR18869	0	0	0	0	4
PGR18872	0	0	20	10	5
PGR18873	0	0	10	25	8
PGR18875	8	12	20	17	1
PGR16728	0	0	0	0	1
PGR18865	0	0	17	7	41 ± 10
PGR18861	0	0	12	18	3
PGR18862	15	5	38	28	67 ± 15
Elgin	0	0	0	0	0
Donald	0	0	0	0	0
Lamar	0	0	0	0	0

* 100 seeds, replicated 2x, SD = ±4%
** 850 seeds, replicated 2x

Table 10. Percentage dormancy in laboratory tests* and field emergence** for freezer stored seeds.

Lines	% Dormant				Field Spring Emergence (No. of seedlings)
	Soil		Petri		
	13°	20°	13°	20°	
PGR18866	5	13	20	30	4
PGR18868	7	3	22	43	14
PGR18870	18	22	42	62	14
PGR18871	53	60	47	57	10
PGR18874	37	55	60	90	4
PGR18876	22	67	58	87	14
PGR8658	35	53	63	70	16
PGR16727	2	12	15	42	14
PGR18869	5	0	32	23	25 ± 10
PGR18872	7	0	33	55	10
PGR18873	12	17	23	63	32 ± 12
PGR18875	0	23	13	45	3
PGR16728	0	0	0	10	9
PGR18865	5	2	43	57	104 ± 23
PGR18861	17	17	28	45	4
PGR18862	22	25	52	72	61 ± 15
Elgin	2	3	0	0	0
Donald	2	2	0	0	0
Lamar	2	3	0	0	0

* 100 seeds, replicated 2x, SD = ±4%
** 850 seeds, replicated 2x

Treating room temperature stored seeds with high temperature-high moisture caused a lot of seed damage but did improve spring emergence in a few lines (Table 11).

- in lines PGR18865 and PGR18862 with approximately 20% and 10% spring emergence respectively when corrections are made for losses due to treatment, and
- in lines PGR18875 and PGR16727 which showed low (4-7%) but better emergence when compared to the performance of their untreated seeds.

Table 11. Percentage sick and dormancy in laboratory tests* and field emergence** for heat-treated seeds.

Lines	% Sick	% Dormant				Spring Field Emergence (No. of seedlings)
		Soil		Petri		
		13°	20°	13°	20°	
PGR18866	50	5	2	37	42	3
PGR18868	55	0	0	8	8	6
PGR18870	37	5	21	42	45	10
PGR18871	40	28	37	42	40	6
PGR18874	35	58	60	57	67	7
PGR18876	38	45	34	25	40	7
PGR8658	47	42	29	43	37	11
PGR16727	60	0	0	3	20	23
PGR18869	62	0	0	13	15	8
PGR18872	47	0	0	45	38	12
PGR18873	42	15	46	35	35	3
PGR18875	30	7	30	43	43	21
PGR16728	62	0	0	2	22	6
PGR18865	23	17	32	47	57	126 ± 26
PGR18861	48	0	17	18	22	12
PGR18862	25	0	15	43	63	100 ± 18
Elgin	97	0	0	0	0	0
Donald	97	0	0	0	0	0
Lamar	45	0	0	0	0	0

* 100 seeds, replicated 2x, SD = ±7%
** 850 seeds, replicated 2x

The status of the seeds that did not emerge in the spring, was not verified. Results in the laboratory indicated however, that secondary dormancy had been induced in all dormoats; each line responding to a different degree. Again, high levels of secondary dormancy in both potted soil and petri dish did not guarantee higher field emergence in the spring. The lines with the best performance (PGR18865 and PGR18862) were also the best survivors of the treatment.

In summary 3 points can be made:

- Laboratory results did not help in predicting field emergence.
- Late planting of either freezer-stored seeds or high temperature-high moisture treated seeds provided better emergence than a late planting of seeds stored at room temperature only.
- More lines responded to the first procedure (i.e. freezer-storage) but for lines that were responsive to both, the heat treatment gave higher levels of emergence.

Winter survival and spring emergence of dormoats without artificial secondary dormancy induction - While pursuing the improvement of spring emergence via the secondary dormancy induction route (described above), it was realized that more information was needed on the fate of dormoats after they are planted in the field in the fall since spring germination was so low in both previous field experiments. An attempt at retrieving seeds from the ground was done in late spring 1983 but it was impossible to account for all of the seeds since there was no means of insuring a complete recovery of either the dead, germinated or dormant ones. Thus, this next experiment was designed with this objective and to allow further studies on the retrieved dormant seeds. An early planting was chosen to reproduce the breeder's observation that best emergence was always achieved with planting immediately after harvest. Part of these results have been submitted for publication (Frégeau and Burrows 1988a).

Four oat strains were chosen for this study. A. sativa cv. Donald is a commercial spring oat and it served as the nondormant control. Dormoat lines PGR8658, 16727 and 16728 were selected from the breeding program at the Plant Research Centre. These lines had survived several cycles of selection for seed dormancy and winter survival under natural field conditions. From qualitative observations over several years, lines PGR8658 and PGR16727 had low autumn germination and low spring emergence, whereas, line PGR16728 had high autumn germination but the remaining ungerminated seeds germinated well in spring.

Freshly harvested seeds (1984) were used after they had been cleaned at ambient temperatures.

Seed quantities were weighed to give approximately 500 seeds of each line, which were then mixed with 200 cm^3 of soil collected from the planting site and packed into a fiberglass mesh bag (28 cm x 9 cm). In early September 1984, bags were placed in a trench in the field at a depth similar to normal sowing (8cm). The trench was refilled with soil using a specially constructed tractor attachment designed to insure proper distribution of soil around and over the bags. Four groups of replicated bags were sown in a randomized block design for each line. Three groups were used for retrievals at 3 different times after sowing and 1 group was to remain in the ground for visual counts of field emergence in the fall and in the spring. After 12, 20 and 29 weeks, (December 1984, February 1985, and May 1985 respectively), bags of each line were recovered from unfrozen or frozen soil retaining enough soil around the bag to prevent light from reaching the ungerminated seeds. These bags were placed in a growth chamber for 5 days at 4°C day/2°C night to allow gradual thawing of the soil. Working under a green light made up of a 25 w. bulb wrapped in two layers of green cinemoid film (Andrews et al., 1972), primary seeds only were retrieved and used for germination tests without surface sterilization.

Germination tests in petri plates consisted of three replicates of 50 seeds each, placed on two Eaton-Dikeman no. 613 filter papers and wetted with 4 mls of test solution, in 9 cm disposable petri plates. Plates were sealed with parafilm, enclosed in foil paper and placed in temperature controlled cabinets, at 7° or 20° ± 0.5°C. Distilled water was used throughout for aqueous test solution as well as for preparing gibberellic acid (GA_3) at 300 µM. All germination tests were terminated after 21 days and interim recordings of germination were made under a green safelight.

Three replicates of 50 seeds were also planted at a depth of about 3 cm in 12.5 x 12.5 cm fibre pots containing a mixture of sterilized potting soil with peat moss. Pots were placed in a cabinet at 7°C or 20°C ± 0.5°C. Emergence counts were taken weekly for a period of 21 days.

Dormancy was expressed in the 3 dormoats but not in the spring oat Donald. All Donald seeds germinated at 7°C and 20°C in soil. Generally, incubating dormoat seeds at 7°C led to greater germination than at 20°C. This dormancy was completely overcome by GA_3. The 3 dormoats differed in their level of dormancy; PGR8658 showed the lowest percentage of germination in all treatments while PGR16728 displayed the least dormancy and PGR16727 an intermediate level (Table 12).

Table 12. Percentage germination of spring oat and dormoat seeds under controlled environment in soil at 7°C and at 20°C and with 300 µM GA_3 in Petri plates (Mean ± S.E.)

Lines PGR No.	Soil 7°C	Soil 20°C	Petri Plates (GA_3) 20°C
Donald	97 ± 3	100 ± 0	100 ± 0
8658	53 ± 6	26 ± 7	99 ± 2
16727	97 ± 3	66 ± 5	100 ± 0
16728	95 ± 3	84 ± 2	100 ± 0

The percentage germination of the 3 dormoats increased with length of dry storage. The strains differed, however, in their rate of after-ripening. PGR8658 showed a slow increase to 90% germination over 16 weeks of storage while PGR16728 reached approximately 100% germination by 8 weeks and PGR16727 reached approximately 90% after only 2 weeks (Fig. 12). The emergence values in autumn (October 1984) and in spring (May 1985), of Donald and the three dormoat strains, are presented in Table 13. Donald emerged completely within the first month of burial. Approximately 78% of the seeds of PGR16728 also germinated while, for PGR16727 and PGR8658, 15 to 20% of the planted seeds emerged. For the 3 dormoats, most of the remaining seeds were found to be dormant but viable upon retrieval from the buried fiberglass bags in autumn and also in spring. Emergence in spring was low, but similar for the 3 lines when the data are expressed as a percentage of total seed sown. However, when the numbers are expressed as a percentage of the number of dormant seeds, PGR16728 displayed a much greater spring emergence, i.e. 47% as compared to approximately 10% for the other 2 dormoats.

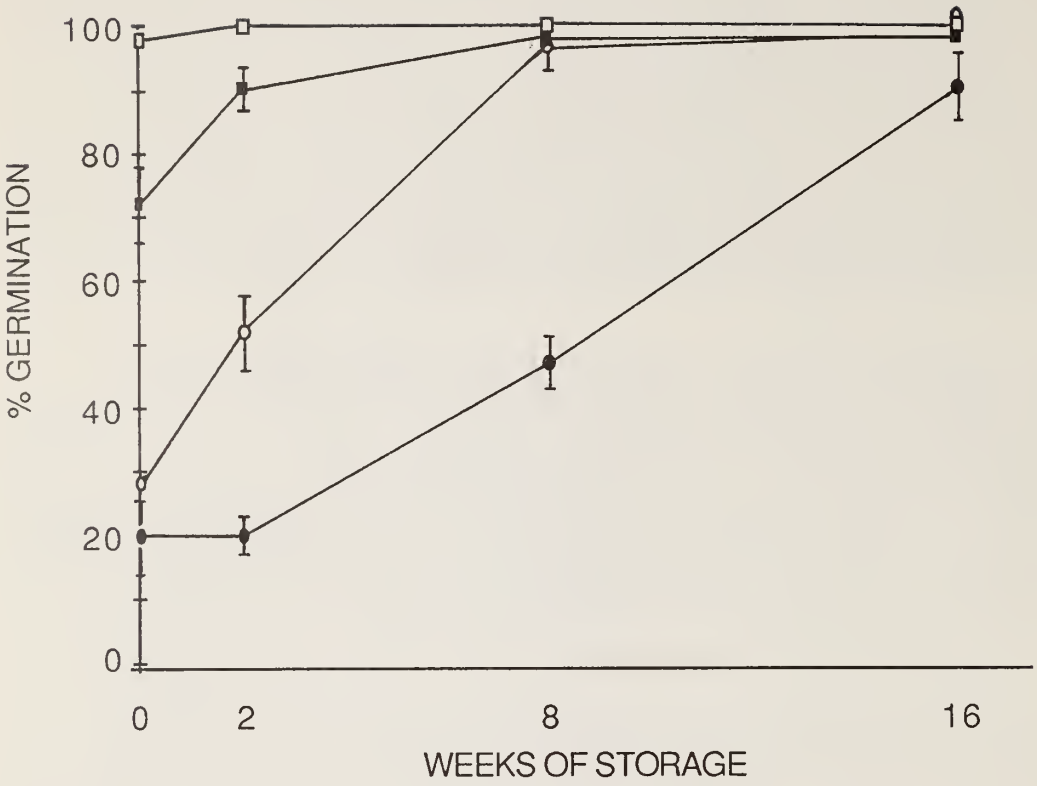


Fig 12. Germination in Petri plates at 20°C following increasing time of dry storage at room temperature: □ , Donald; ○ , PGR16727; ■ , PGR16728; ●, PGR8658.

The dormant seeds retrieved from the field were subjected to a germination test in potted soil in a controlled environment. The test was only possible for lines PGR8658 and PGR16727 since not enough dormant seeds of PGR16728 could be retrieved from each bag. In late autumn, approximately 15% of field dormant PGR8658 seeds, germinated under laboratory conditions (Fig. 13). This percentage rose to 20% in February and no further change was observed in May. A slight stimulation of germination was evident at 20°C as compared to 7°C. In contrast, 20°C markedly stimulated germination of PGR16727 which was the opposite response to the one obtained before burial in autumn. Approximately 7% of the field dormant seeds germinated in the laboratory at 20°C by late autumn and unlike PGR8658, this percentage increased steadily throughout the winter to reach 62% by May. Germination at 7°C did not follow the same increase and remained at approximately 20%. GA_3 completely overcame the dormancy of both lines at each retrieval (data not shown).

Table 13. Field emergence in autumn (October 1984), status of the retrieved seeds and emergence in spring (May 1985).

	Autumn				Spring		
Lines	Sown	Emerged		Dormant	Emerged		
PGR No.	Mean[a] ± s.e.	Mean ± s.e.	%	Mean ± s.e.	Mean ± s.e.	% of Sown	% of Dormant
Donald	441 ± 22	425 ± 20	96	-	-	-	-
8658	444 ± 21	94 ± 9	21	336 ± 15	27 ± 9	6	8
16727	547 ± 18	80 ± 16	15	445 ± 16	43 ± 20	8	10
16728	484 ± 36	377 ± 22	78	96 ± 14	45 ± 16	9	47

a = mean of 5 replicates.

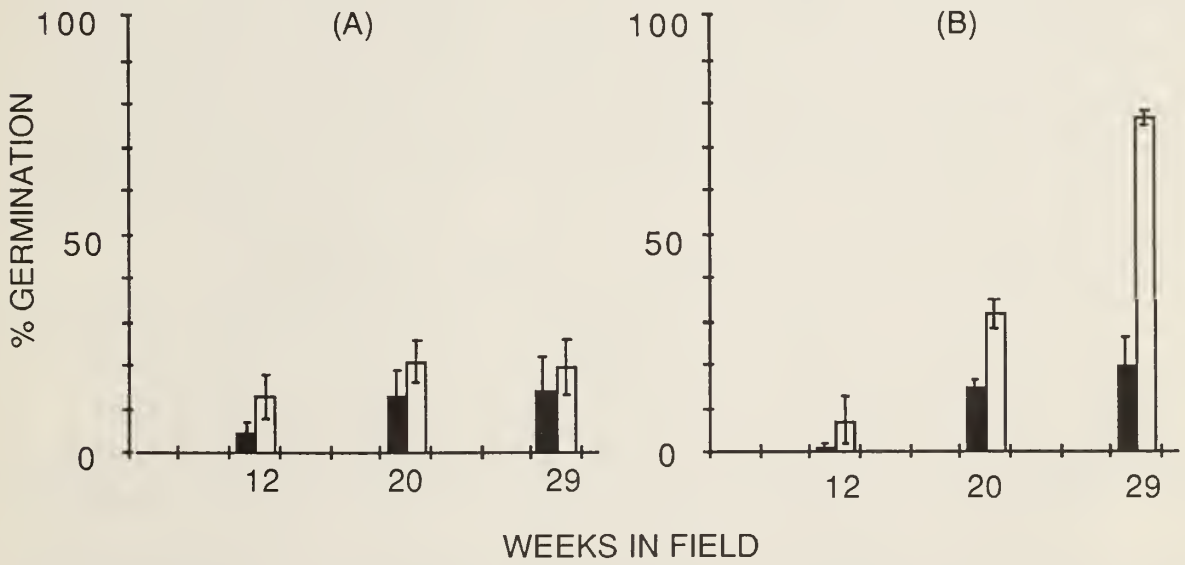


Fig. 13. Laboratory germination of retrieved seeds from PGR8658 (A) and PGR16727 (B) in soil at 7°C ■ and 20°C □ throughout the seasons I = ± S.E.

Soil surface temperatures in late summer at the time of planting were 20°C or higher and it was anticipated from the germinations under controlled environment, that PGR8658 would display a low germination and PGR16728 a high one after burial in the field. Fall emergence was as expected for these two dormoats; the proportion of seeds that germinated was equivalent to the portion of the population identified previously in the laboratory as nondormant. Seeds that failed to emerge in September 1984 were dormant but not dead since GA could stimulate their germination at each retrieval time. The complete emergence of Donald was as predicted. Laboratory germination did not predict the behavior of PGR16727 in the field; emergence was much lower than expected, dropping to only 15% germination when 66% of the seed population had been classified as nondormant in the laboratory. Apparently approximately 50% of PGR16727 seeds reentered the dormant state with burial in the field. It is known that unfavorable germination conditions prior to the natural germination of the seed can render dormant again, seeds without dormancy or can intensify the dormancy of partially (or relatively) dormant seeds (Bewley and Black, 1982). The environmental factor(s) triggering this response in PGR16727 are unknown at this time but it is possible that a light requirement developed after burial as it happens for several weed species (Bewley and Black, 1982).

By late autumn, only a small percentage of the dormant population of PGR8658 and PGR16727 were able to germinate when retrieved and given conditions previously favorable in laboratory tests. Perhaps this is because field observations of wild oats have demonstrated that the period of after-ripening is prolonged under field conditions compared to dry storage in the laboratory, (Simpson, 1978). PGR8658 had a long after-ripening in dry storage, compared to the other strains, and a large portion of the population was innately dormant so the low percentage germination of the retrieved seeds in late fall was not surprising. As expected, the freezing temperatures of winter prevented the after-ripening of the remaining dormant seeds since the germination of PGR8658 retrieved in early spring was more or less the same as in late autumn. The situation was different for PGR16727 since the dormancy status changed throughout the autumn and winter. The seeds gradually switched from being completely dormant to a type of dormancy expressed at low temperature in contrast to the promotive germination effects of low temperature observed before burial. This dormancy reached by most of PGR16727 seeds was not, however, favorable to emergence in early spring since prevailing cool temperatures were inhibitory to germination. These results are similar to the observations of Karssen (1980/81) on buried weed seeds where dormancy changed substantially during the seasons. Increases and decreases in dormancy during burial in soil are often part of annual cycles (Karssen, 1980/81) and this is recognized as being of great survival value for a weed.

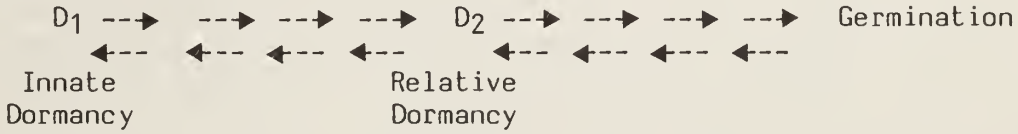
The dormancy patterns observed in the dormoats fit this survival strategy. The results clearly demonstrated that the germination behavior of dormoats is basically still that of a weed without the seed shattering characteristics.

Field and laboratory responses of dormoats to low or high temperature - high moisture treatment.

It became obvious that ways of describing and understanding these field and laboratory observations were required to try to formulate a model that may allow some predictions in terms of emergence and/or survival. Buried weed seeds have been shown to go through dormancy - non-dormancy cycles. Maintenance of dormancy and timing of germination are important phases that help adapt weeds to their environment and the annual dormancy cycle is an important component of predictive models of weed pest management. Baskin and Baskin, in their 1985 paper on weed dormancy, viewed the weed dormancy cycle as a continuum or gradient of changes in germination responses. Three types of germination behavior are described in the literature (Vegis 1964). These will be gradually expressed with time as the seeds pass through in either direction:

The seeds start by being
innately dormant (where they will not germinate under any set of normal environmental conditions),
to a state of
relative dormancy, (during which they germinate only under a limited range of environmental conditions),
to finally being
non dormant (where the seeds will germinate over the widest range of conditions possible for the species).

Relative dormancy is a dynamic physiological condition where germination is regulated by the changing physiological requirements of the seeds in relation to changes in the environment. Along the same line, but more biochemical, Khan and Zeng (1985) indicated that seeds probably have two dynamic energy-coupled processes: germination and dormancy induction. Depending upon whether one or both processes are blocked, an engagement of germination or dormancy induction or prevention of both processes may occur. Graphically it can be represented as



Laboratory assessment of dormancy, in terms of environmental requirements, allows only for some relative differences to be established because of the limited situations that can be tested. It is apparent from the field and laboratory behavior of the lines that dormoats have both "quantitative" and "qualitative" differences in terms of dormancy mechanisms,(similar laboratory assessment but very different field results). The extent of the qualitative differences will be difficult to assess in the laboratory and the relative dormancy status of a line will probably never be fully described.

These definitions of dormancy were applied in analysis of previous results to help formulate a new experimental design. Retrieved seeds gave physiological support for a dormancy continuum in buried dormoats as gradual shifts in the germination requirements of the seeds were observed.

Unfortunately, the changing requirements are not always met by the outdoor environment and prevention of germination will favor the dormancy induction route. The imbibed seeds will gradually be induced into a secondary dormancy as it probably happened to seeds of PGR16727 in 1984 when early spring conditions did not match their higher T° requirements for germination.

Nevertheless, the model illustrated on the previous page is pointing at the **seeds in relative dormancy** as one of the **pivoting factors for emergence.** This model also opened the possible option of manipulating the dormancy status of a population in either direction depending on the extent of afterripening and planting time in the field:

- innately dormant becoming relatively dormant
- almost germinable reverting to a status with relative dormancy

This next experiment was designed to try these approaches; the goal of the experiment was to manipulate the dormancy status of various dormoat lines to maximise the number of seeds in a relative dormancy that will, hopefully, have the germination "route" favored by spring conditions. The experiment was extensive in terms of treatments and lines. Selection of the lines for the experiment was based on their past laboratory and field behavior and what it could mean in terms of the model just described. With the insight gained from 1984, previous treatments were slightly modified (within the limits of available equipment) to approximate possible outdoor environmental conditions. A major constraint of the experiment was the time factor, dormancy being a transient trait. Furthermore, it was impossible to foresee the extent of the response of a line since it will likely vary from year to year according to the conditions prevailing during grain development. Five dormoats were selected from the breeding program. PGR8658 had a large portion of the seed population in deep dormancy at harvest and with fall planting it showed low autumn and low spring field emergence; PGR16728 had a large portion of its seed population able to germinate at harvest which led to high autumn germination but germination of the remaining seeds in spring was substantial. PGR18865, demonstrated the best spring emergence of over 200 lines in a preliminary screening test for secondary dormancy induction by high temperature treatment. PGR16727 had a large portion of seeds responding by natural secondary dormancy which brought variable survival and emergence levels. Finally, PGR18873 demonstrated the best spring emergence from a late planting of freezer-stored seeds. Part of these results have been submitted for publication (Frégeau and Burrows 1988b).

Freshly harvested seeds (1985) were cleaned and then sieved to separate the primary seeds which were used in this experiment.

Seed quantities were weighed to give approximately 400 seeds and each lot packaged into a fiberglass mesh bag (28 cm x 9 cm). For each line, groups of replicated bags were subjected to different treatments before randomized planting in the field and germination assessment in the laboratory. There were two field control groups: an early control planted in the field 3 weeks after harvest and a late one planted 7 weeks after harvest. Four groups were used for the induction of secondary dormancy by temperature treatments. A cold treatment was applied to two groups three weeks after harvest; using tempered distilled water, the seeds were imbibed and kept moist, in the dark, at 4 ± 1°C for 3 weeks between 2 sheets of Whatman No. 1 chromatography paper. The cold-treated seeds were then brought to room temperature; one

group was planted right away and the other was dried for 2 days in an air stream with planting in the field done 5 days later, which was 7 weeks after harvest. The remaining groups were treated either 3 weeks (early) or 6 weeks (late) after harvest; using tempered distilled water, seeds were imbibed and kept moist at 30 ± 1°C for 1 week between 2 sheets of Whatman No. 1 chromatography paper. These heat-treated seeds were brought to room temperature, dried in an air stream for 2 days and were planted the following day or approximately 7 weeks after harvest. Two other groups of seeds, requiring no temperature treatments, were also tested: seeds processed as the early control but with their hulls removed by hand and seeds processed as the late control with, however, the storage done at -20°C from harvest time.

Germination and potted soil emergence tests were performed in the laboratory as previously. For the field experiment, three main blocks were planted; one block for December retrievals, one for May retrievals and one to remain in the ground to obtain visual counts of field emergence in the spring. Planting was done as previously. On retrieval days, bags were dug out and the state of the enclosed seeds was assessed; the lemma and palea of any sound seed were peeled to evaluate the appearance of the caryopsis itself. A tetrazolium test, (Anon., 1976), was performed on randomized selected samples of sound caryopsis to confirm viability.

The original intent of using cold-treatment on dormoats was the possibility that cold imbibition might help in breaking the deep dormancy of certain lines, including PGR8658. The milder conditions for the heat treatment were chosen with the idea that temperatures, in the 30°C range, could be a triggering environmental factor encountered by germinable seeds planted in the field in late August; this situation may favor the dormancy route and induce a deeper state of dormancy in the seed. If this occurred in lines such as PGR16728, this would result in a greater number of dormant seeds, perhaps leading to a greater number of seeds remaining dormant in the field. Emergence of line PGR16728 may be improved by this treatment. Results from the laboratory tests done on the untreated and treated seeds are presented in tables 14 to 18. All lines treated were planted in the field and monitored simultaneously in the laboratory. At the end of the laboratory tests, it was obvious that the extent of the response in terms of secondary dormancy was quite variable. This, plus the almost unmanageable workload in terms of retrievals, led to the decision to restrict seed retrievals in late fall and spring to 3 lines x 4 treatments: PGR8658, PGR16728, PGR18865 and early and late controls, cold treatment-dry and heat late. Spring emergence was recorded for all lines and treatments and in retrospect, the choice just outlined for retrievals proved to be a good one.

In the laboratory assessments, seeds germinating in Petri dishes at 20°C were classified as having reached the germinable state whereas seeds not germinating in soil at 7°C were considered innately dormant. The difference between the germination results of these two tests was assumed as representing the seeds in relative dormancy. Results from PGR18873 (Table 14) and PGR16727 (Table 15) are given to show their laboratory behavior and will not be discussed as spring emergence was almost nil.

Table 14. Percentage germination of PGR18873 in potted soil and petri plates at 20°C and 7°C before field planting, Each result represents the mean ± S.E. of 3 replicates of 50 seeds.

Treatment	Soil		Petri	
	7°	20°	7°	20°
Early Control	72 ± 4	46 ± 2	48 ± 16	24 ± 6
Peeled Control	96 ± 4	88 ± 4	62 ± 16	56 ± 6
Late Control	78 ± 8	80 ± 6	68 ± 6	58 ± 6
Freezer Storage	66 ± 6	54 ± 2	46 ± 6	28 ± 10
Cold - wet	46 ± 12	30 ± 8	32 ± 4	34 ± 14

Table 15. Percentage germination of PGR16727 in potted soil and petri plates at 20°C and 7°C before field planting, Each result represents the mean ± S.E. of 3 replicates of 50 seeds.

Treatment	Soil		Petri	
	7°	20°	7°	20°
Early Control	86 ± 18	78 ± 6	78 ± 10	54 ± 8
Peeled Control	96 ± 2	96 ± 2	98 ± 2	80 ± 4
Late Control	94 ± 2	96 ± 2	92 ± 4	92 ± 6
Freezer Storage	88 ± 4	98 ± 6	84 ± 2	42 ± 8
Cold				
- wet	88 ± 6	84 ± 18	84 ± 8	84 ± 14
- dry	74 ± 8	76 ± 14	60 ± 8	28 ± 4
Heat				
- early	88 ± 6	90 ± 6	70 ± 18	50 ± 32
- late	38 ± 12	52 ± 2	10 ± 6	2 ± 2

Untreated seeds (controls) from the other three dormoats responded differently to the temperatures or media used to test their germination potential. For the early control seeds from PGR8658, approximately 35% were completely dormant and 30% were germinable (Table 16). The remainder of the seeds were in relative dormancy linked mainly to temperature, i.e. more seeds were dormant at 20°C than at 7°C. Removal of the hulls changed the behavior in soil but not in petri dish. With time in storage, (late control) this temperature related dormancy disappeared and a small part of the population displayed a relative dormancy linked to the media.

Table 16. Percentage germination of PGR8658 in potted soil and petri plates at 20°C and 7°C before field planting. Each result represents the mean ± S.E. of 3 replicates of 50 seeds.

Treatment	Soil		Petri	
	7°	20°	7°	20°
Early Control	66 ± 7	27 ± 6	53 ± 7	31 ± 6
Peeled Control	98 ± 2	82 ± 6	58 ± 2	48 ± 16
Late Control	79 ± 3	82 ± 3	67 ± 10	70 ± 4
Freezer Storage	64 ± 14	44 ± 10	46 ± 12	32 ± 10
Cold				
- Wet	24 ± 12	28 ± 10	40 ± 12	28 ± 6
- Dry	33 ± 3	22 ± 3	25 ± 7	15 ± 3
Heat				
- Early	46 ± 2	32 ± 10	12 ± 2	4 ± 2
- Late	23 ± 4	23 ± 3	2 ± 3	1 ± 2

For PGR18865 (Table 17), approximately 20% of the untreated seeds were completely dormant and roughly 40% were germinable. The remainder of the population displayed a relative dormancy expressed not in soil but in the petri dish environment and without any temperature effect. Disappearance of this dormancy was slower since late control seeds were responding as the early control ones. Removal of hulls favored more germination but maintained the media effect.

Table 17. Percentage germination of PGR18865 in potted soil and Petri plates at 20°C and 7°C before field planting. Each result represents the mean ± S.E. of 3 replicates of 50 seeds.

Treatment	Soil		Petri	
	7°	20°	7°	20°
Early Control	77 ± 3	77 ± 7	33 ± 5	41 ± 1
Peeled Control	95 ± 3	96 ± 3	64 ± 6	57 ± 12
Late Control	82 ± 10	84 ± 10	42 ± 4	54 ± 6
Freezer Storage	62 ± 6	68 ± 6	34 ± 2	34 ± 4
Cold				
- wet	33 ± 6	37 ± 11	14 ± 3	13 ± 1
- dry	37 ± 3	66 ± 4	8 ± 3	6 ± 3
Heat				
- early	26 ± 10	30 ± 4	8 ± 6	2 ± 2
- late	18 ± 4	20 ± 8	4 ± 2	4 ± 6

PGR16728 (Table 18) had no dormancy left when tested in soil, 3 weeks after harvest; in Petri dish, a small portion of the population was slightly dormant i.e. a relative dormancy. Seeds of PGR16728 late control were completely germinable.

Table 18. Percentage germination of PGR16728 in potted soil and Petri plates at 20°C and 7°C before field planting. Each result represents the mean ± S.E. of 3 replicates of 50 seeds.

Treatment	Soil		Petri	
	7°	20°	7°	20°
Early Control	97 ± 1	98 ± 2	91 ± 3	81 ± 8
Peeled Control	88 ± 4	98 ± 2	98 ± 2	94 ± 4
Late Control	99 ± 1	99 ± 1	98 ± 2	99 ± 1
Freezer Storage	94 ± 6	98 ± 2	94 ± 4	84 ± 2
Cold				
- Wet	82 ± 10	86 ± 8	80 ± 6	74 ± 4
- Dry	70 ± 3	85 ± 7	57 ± 13	29 ± 4
Heat				
- Early	78 ± 10	88 ± 8	22 ± 16	2 ± 2
- Late	59 ± 11	73 ± 8	11 ± 9	3 ± 3

Both heat and cold treatments increased the level of dormancy in the three dormoat lines. Following these treatments, some differences were also noted in the type of relative dormancy displayed by the seeds. For germination in potted soil, seeds of the early control were basically as the cold-treated seeds were prior to their treatment whereas the late control seeds were similar to the heat treated seeds prior to their treatment.

Cold treatment only slightly modified the 20°C responses of PGR8658 seeds (Table 16); but increased dormancy was noticeable at 7°C, whether in soil or in petri dish. Cold treatment pushed the completely germinable seeds of PGR16728 (Table 18) into being more sensitive to environmental conditions. Following the treatment, germination became linked to both the type of media and the temperature used. Contrary to the usual behavior, there was slightly more dormant seeds in soil at 7°C rather than at 20°C; in petri dishes, dormancy was more pronounced at 20°C. The responses of PGR18865 (Table 17) were again linked primarily to the media. Approximately 30% of the previously completely germinable seeds reverted to a new dormancy status; the seeds were dormant in petri dish regardless of temperature but the behavior in soil became linked to temperature. The relative dormancy in soil was only expressed at 7°C, cold treatment did not significantly modify the germination behavior when seeds were tested in soil at 20°C.

Heat treated seeds of PGR8658 (Table 16) showed a relative dormancy linked to the media instead of the temperature and a large portion of the population reverted to being completely dormant. Heat treatment also favored petri dish dormancy of a large portion of seeds of PGR16728 (Table 18). On the other hand, the treatment did not modify the media-linked relative dormancy of PGR18865 (Table 17) except that less seeds displayed it as more of them became completely dormant.

Seeds from PGR8658, PGR16728 and PGR18865 were retrieved from the field in early December to assess dormancy status of their seed populations as they entered winter, (Table 19). Neither cold or heat treatments improved the dormancy levels already present in the seed populations. The number of ungerminated seeds found in cold-treated samples was similar to that observed in the early control while the level of dormancy in late control and heat treatment were also similar. Thus, even though laboratory assessment indicated more dormancy in treated seeds than in controls, it was not reflected in the field-planted population sampled in late autumn.

Although the level of dormancy might not have been increased by the treatments, it was possible that the type of dormancy (i.e. quality) had been modified and allowed better winter survival and spring emergence. The status of the field population was assessed in early spring and results from these spring retrievals are presented in Tables 20 to 22. Two points are striking for controls and treatments following winter exposure: the high levels of dead seeds and the high degree of variability between replicates within a treatment.

Table 19. Percentage of the sown seed population in dormancy in the field at the end of the fall season (December 1985). Each result represents the mean ± S.E. of 3 replicates.

Treatment	PGR8658 %	PGR16728 %	PGR18865 %
Early Control	70±1	20±8	65±1
Late Control	33±4	12±1	72±4
Cold	71±2	18±4	71±4
Heat	34±7	22±5	72±5

Table 20. Spring status of the part of the seed population of PGR8658 that was dormant in December 1985. Seeds were retrieved from the ground in May 1986. Results are expressed in percentage of the total number of fall dormant seeds. Each result represents the mean ± S.E. of 3 field replicates.

Treatment	Dead %	Dormant %	Germ. %
Early Control	70±19	28±19	3±1
Late Control	68±22	31±22	1±1
Cold	75±7	23±7	2±1
Heat	70±12	29±13	1±1

Most of the seeds of PGR8658 did not survive winter and this observation was consistant with previous results. Surviving seeds were dormant and the treatments did not favor spring emergence.

Table 21. Spring status of the part of the seed population of PGR18865 that was dormant in December 1985. Seeds were retrieved from the ground in May 1986. Results are expressed in percentage of the total number of fall dormant seeds. Each result represents the mean ± S.E. of 3 field replicates.

Treatment	Dead %	Dormant %	Germ. %
Early Control	61±18	15±6	25±12
Late Control	84±5	8±2	8±4
Cold	79±7	7±3	14±4
Heat	61±8	13±8	26±8

Even though the two controls of line PGR18865 were comparable in terms of laboratory behavior and number of dormant seeds entering winter, the late control suffered greater damage by the end of winter. "Cold treatment dry" proved successful in inducing a high level of relative secondary dormancy in the laboratory but in the field, it was not more successful than the late control. "Late heat treatment" was effective in modifying the response of PGR18865. Prior to treatment, seeds were in a comparable after-ripening status to the ones from the late control and heat treatment reverted their behavior to one similar to the early control. In the field, "late heat treatment" allowed for an increase in survival as well as in emergence but it did not improve the performance of PGR18865 in relation to an early planting of untreated seeds.

Table 22. Spring status of the part of the seed population of PGR16728 that was dormant in December 1985. Seeds were retrieved from the ground in May 1986. Results are expressed in percentage of the total number of fall dormant seeds. Each result represents the mean ± S.E. of 3 field replicates.

Treatment	Dead %	Dormant %	Germ. %
Early Control	34±14	7±7	58±6
Late Control	92±5	6±4	2±2
Cold	61±5	3±2	35±7
Heat	67±9	11±3	22±7

Regardless of treatment, only about 20% or less of PGR16728 seed remained dormant in the field in December (Table 22). Most of these dormant seeds did not survive winter except for the early control where both survival and emergence were relatively successful. The transient aspects of dormancy and of the seed's capacity to respond is emphasized when results from early and late controls of PGR16728 are compared. There was only 4 weeks difference between these two controls and within this afterripening period, there was a loss in the capacity of the seeds to be induced into a dormancy allowing for survival. Cold treatment prevented part of the afterripening from occurring as performance was better than the late control but not as good as the early control, while heat treatment lowered the number of dead seeds as compared to the late control but it was not as efficient in doing so as the early control.

Spring emergence was also calculated as a percent of total seed sown, (Table 23), and the best performance for these 3 dormoats was again the early control planted in September.

Table 23. Spring emergence expressed as percentage of total amount sown in fall. Each result represents the mean ± S.E. of 3 field replicates.

Treatment	PGR8658 %	PGR16728 %	DC1358-7 %
Early Control	2±1	17±7	16±8
Late Control	1±1	1±1	5±3
Cold	1±1	7±3	10±3
Heat	1±1	5±3	18±5

In summary:

A large proportion of the fall dormant seeds did not survive winter and there were large variations in spring between replicates of either the controls or the treatments. Thus: **survival of dormoat seeds through winter is not only dependent upon the maintenance of the seeds in an ungerminated state but also on the ability of the imbibed dormant seeds to resist overwintering stresses like freezing, excess moisture, etc.**

Effects of treatments:

- Laboratory: Seeds from each dormoat showed secondary dormancy induction after both cold and heat treatment.
- Field:
  i) The treatments did not really improve the percentage of the population entering winter as dormant seeds.
  ii) The treatments improved survival and emergence over the late control for both PGR16728 and PGR18865.
  iii) Best for all dormoats was still the early control (September planting).

Responses of PGR18865 to cold treatment - The original intent of using cold treatment on dormoats was that it might reduce innate dormancy in lines that had a high level of seeds at that stage in the dormancy continuum. Results did not follow expectations since more dormancy was found at the end of the treatment. Even though the first intent was not met, the treatment did increase the level of relative dormancy in line PGR18865. Since a form of secondary relative dormancy seemed to be one of the routes for manipulating spring emergence, it was decided to further study the behavior of PGR18865 with cold treatment and the effect of drying the seeds. The objectives of the experiment were to repeat the previous laboratory results and explore the drying effect in relation to the temperature at which the drying was done, i.e. room temperature or 5°C. The primary seeds used here had been put at -20°C, 3 weeks after harvest and left there for 6 months before being taken out for the experiment. They were in storage at the same after-ripening stage reached by the group of seeds treated in the fall. Hand dehulled seeds were included in the design to study a possible interaction by the hulls on dormancy induction. Cold treatment lasted 3 weeks and drying was done with an air current for one day at room temperature (T°) and 2 days at 5°C. Laboratory germination was done as before with the addition of a germination test with $NaNO_3$ as a possible promoter. Results are presented in Table 24; results from the previous cold treatment experiment are also included for comparison. Germination of untreated seeds, left in room T° storage for the same 3 weeks, was also recorded. Untreated seeds showed again a media related dormancy with however, a slight temperature effect in petri dish not detected in September. Removing the hulls slightly increased germination; but maintained the media differential and the temperature effect in petri dish.

Cold treatment modified germination behavior; more seeds were found dormant after the treatment. However, the profile of germination was not as previously. In "cold-wet", the media related dormancy was still present but a temperature differential was also expressed in soil. Drying the seeds at room T°, did not favour, as in September, a T° related dormancy expressed in soil; instead, germination in soil was increased to a similar level at both temperatures but the media differential was maintained. Seeds were also more responsive to $NaNO_3$ stimulation following drying. Hulls were not required for dormancy induction by cold treatment and drying just increased the number of germinating seeds. On the other hand, drying the seeds at a low T° modified only slightly the germination behavior from what was found with "cold-wet": more seeds germinated in soil at 20°C and there was a slightly higher response to $NaNO_3$ stimulation.

Thus, even though the untreated seeds had very similar laboratory behavior before and after 6 month-freezer storage, their responses to cold treatments were not similar especially in terms of relative dormancy. The complexity of these various patterns of germination makes it difficult to interpret the results. Storage in the freezer brought about changes that made the seeds respond differently. This points at the **sensitivity of these seeds in their capacity to modify their behavior in response to a change in the environment.** Keeping in mind that seeds in relative dormancy require certain environmental stimulus at their optimum for germination, it is easy to understand that interactions between environmental factors will occur and will be reflected in the seeds' responses; a good example being the various expression of dormancy displayed by PGR18865. Thus, in trying to get a clearer idea of the results in terms of the dormancy continuum concept, an illustrated qualitative interpretation of the behavior of PGR18865 was elaborated (Fig. 14).

Table 24. Percentage germination of PGR18865 with or without a 3 week-cold treatment, followed by no drying period or a drying period at either room T° or 5°C. Each measure is the mean ± SE of 3 replicates of 50 seeds.

Date	Seeds	Treatments	Soil		Petri			
			7°	20°	7°	20°	GA_3 (300 µM)	$NaNO_3$ (100mM)
September 1985	Hulled	Early Control	77 ± 3	77 ± 7	33 ± 5	41 ± 1	100	-*
		Cold - wet	33 ± 6	37 ± 11	14 ± 3	13 ± 1	88 ± 3	-
		Cold - dry Room T°	37 ± 3	66 ± 4	8 ± 3	6 ± 3	85 ± 7	-
	Dehulled	Early Control	95 ± 3	96 ± 3	64 ± 6	57 ± 12		
March 1986	Hulled	Control	81 ± 1	83 ± 5	26 ± 3	44 ± 5	100	81 ± 5
		Control - 3 weeks	83 ± 3	90 ± 3	41 ± 4	71 ± 4	-	-
		Cold - wet	46 ± 9	18 ± 6	4 ± 3	7 ± 1	74 ± 10	20 ± 2
		Cold - dry Room T°	64 ± 8	59 ± 8	8 ± 3	35 ± 5	83 ± 6	70 ± 6
		Cold - dry 5°C	39 ± 10	32 ± 4	8 + 3	5 ± 1	85 ± 7	39 ± 3
	Dehulled	Control	98 ± 2	92 ± 7	35 ± 3	62 ± 5	-	-
		Control - 3 weeks	-	-	57 ± 5	73 ± 2	-	-
		Cold - wet	30 ± 7	32 ± 8	13 ± 6	10 ± 4	100	27 ± 9
		Cold - dry Room T°	66 ± 12	56 ± 7	35 ± 5	36 ± 7	100	77 ± 2

* - = not done

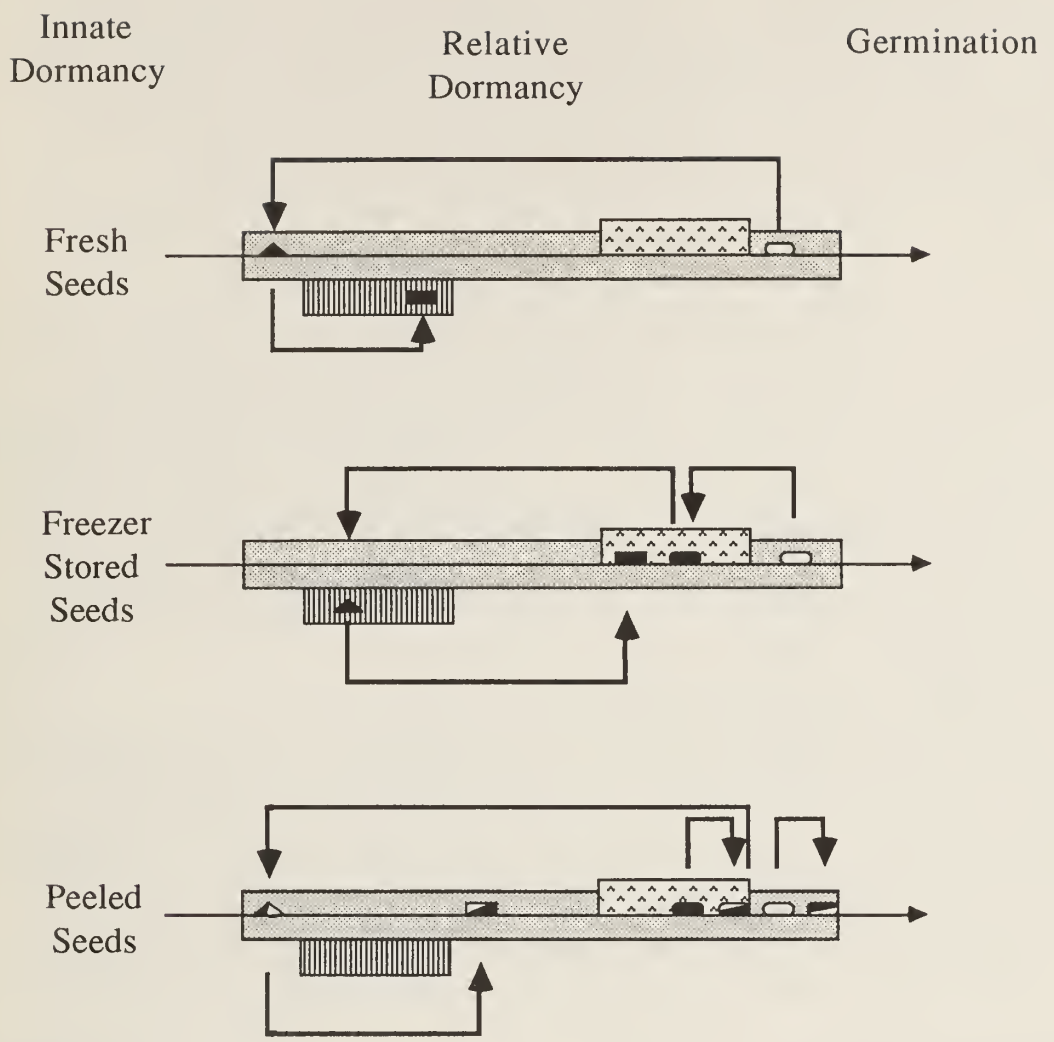


Fig. 14. Qualitative description of dormancy status of line PGR18865 at harvest time, following freezer-storage and with hulls removed. ▭ : relative dormancy (RD) linked to the media, ▭ : RD linked to T° with a media-RD, ▭ : RD linked to T° when conditions for media RD are optimum for germination, ▬ : seed after freezer, ⬭ : seed at harvest, ▲ : seed after cold treatment-wet, ▬ : seed after cold treatment-dry, ⬭ : seed peeled in September, ⬭ : seed peeled after freezer.

This representation is more than likely oversimplified since very limited conditions were tested. Nevertheless, Fig. 14 shows that the response of the seed will be dictated by its position in the continuum at the time it perceives the environmental stimulus. All the environmental conditions have to be in the optimum range required by the line before germination can occur. At certain times in the continuum there may be one environmental stimuli dominant over the others i.e. the seeds will respond to other stimulus only if the environmental interactions in terms of the dominant one are perceived as optimum for germination. Furthermore, there may be different "windows" of responses, the dominant behavior interacting simultaneously with some (horizontal axis) or separately with others (vertical axis). As illustrated for PGR18865 a relative dormancy linked to the Petri dish environment seems to be the prevalent behavior as it was always expressed in the partially afterripened seed population. In relation to temperature, two different dormancy behaviors were shown in PGR18865 depending on the afterripening status or in response to a treatment. One type of dormancy occurred only in Petri dish, in response to temperature, and along with the relative dormancy already present because of the media itself. The other type of response linked to temperature was expressed only in soil (not in Petri dish), at a stage in the dormancy continuum where it seems temperature will influence dormancy only if the environment, in terms of moisture, is perceived as optimum for germination. Thus emergence in the field is bound to vary from year to year and even for a given year, within the field, since the seeds' response is dependent on:

- the primary dormancy status at planting time,
- the environmental conditions throughout the seasons and
- the microenvironment surrounding the seeds.

It may be that lines displaying levels of natural dormancy preventing them from germinating in the fall and in the spring (whatever proportion of innate and relative primary dormancy), are responsive to several environmental stimulus in the manner just observed, oversimplified, for PGR18865. Lines, like PGR16728, with very low levels of natural dormancy may not have this same complex response to the environment which could explain their easy spring emergence but at the same time their low dormancy to start with, (high fall germination). This is yet another aspect of the dilemma we are facing with dormoats.

Screening of Breeding Program

Screening the breeding program to assist in selection of the lines with the best potential to be manipulated for spring emergence was also part of the mandate of the physiology program. Since studies on the management protocol were exploring temperature as the triggering factor, it was decided to use, as a selection criteria, the response of the breeding lines to various temperature treatments in relation to both the responses of lines on which physiological studies were carried out and of regular oat cultivars.

Winter 1983 - Four hundred dormoat entries from the 1982 Ottawa Observational test were evaluated for their survival after a 1 week exposure to high temperature (40°C) high moisture treatment. The seeds were treated in January 1983 when afterripening was completed. Ten grams of seeds were treated and 100 seeds taken out and planted in soil, in a greenhouse. Germination was recorded after 3 weeks; the status of the ungerminated seeds was not checked. Table 25 gives a summary of the report given to the breeder with the suggestion that the best lines within families with high emergence should be kept.

Winter 1984 - Screening as it was done in 1983 was not practical space- and time-wise for a larger number of lines. Along the 1983 rationale, a testing protocol in petri dish was developed to evaluate the resistance of dormoat lines to a heat stress under high moisture conditions. The protocol was used as a selecting procedure for lines that **may have a potential** for

Table 25. Screening of dormoat entries in 1982 Ottawa Observational Test

Identity (Family)	Common parent	No. of Lines treated	% Germination $\bar{X}$ ± SD
82-DO-1	OA 228	21	36 ± 22
82-DO-1	DO 28	9	50 ± 12
82-DO-1	Rodney	35	16 ± 11
82-DO-2	Hammon	36	23 ± 12
82-DO-2	OA 338-2	42	28 ± 21
82-DO-3	OA 375-1	22	26 ± 12
82-DO-3	OA 404-5	33	31 ± 19
82-DO-4	OA 400-15	26	28 ± 18
82-DO-4	OA 405-5	20	30 ± 14
82-DO-5	OA 414-3	49	23 ± 8
82-DO-5	OA 424-1	46	15 ± 15
82-DO-6	OA 406-1	25	61 ± 20
82-DO-6	OA 407-4	43	47 ± 21
Elgin			7
Woodstock			21
Sentinel			10
Donald			15
Hinoat			43
Lamar			36
Terra			9
Shaw			13
Oxford			14

secondary dormancy induction. Seeds were put in a germinator at 40°C, in 15 cm petri dishes with 2 filter papers and 8 ml of water for 3 days. They were then taken out and put at 20°C for 7 days, at the end of which numbers of germinated, sick and dormant seeds were recorded. 1300 dormoat lines were evaluated following this method and results were given to the breeder.

The treatment for secondary dormancy induction (40°C, 1 week) was also applied to 200 lines, (some hulless), to select the responsive types and enough seeds for spring planting increases of the best performing ones were treated and given to the breeder.

Winter 1986 - A testing protocol was required for screening early generation dormoats (F_2s) after the afterripening has been completed. Germination rates at 20°C and 30°C were used with 100 seeds placed embryo up in 15 cm petri dishes, 2 filter papers and 8 ml of water. For naked dormoats, germination was recorded at 12 hours and 24 hours and seeds were considered germinated when the radicle had emerged from the seed coat. Hulled seeds were monitored at 24 hours, 36 hours and 48 hours and were considered germinated when the radicle had emerged from the hulls. 134 lines were tested and results given to the breeder with the suggestions of keeping the lines showing the slowest rate of germination since there is a chance that their response is due to the presence of dormancy genes.

DISCUSSION

When the physiology program on dormoats was re-established in 1982, it was decided that working on a management protocol for dormancy was the best approach to try to make the crop a commercial success. After 4 years of field experiments combined with laboratory studies, we have not achieved the development of an effective seed management protocol to allow good uniform spring emergence of dormoats. Progress has been made however, in the realisation that the problem is complex and multileveled.

Wild oat research has given indications on the extreme plasticity of the dormancy trait since environmental factors can influence expression at all stages of development, even the vegetative mother-plant. In terms of period of afterripening, differences are also noticed with varying the wild oat genotypes but also within the same plant i.e. seeds in the upper part of a panicle (early maturing) require less afterripening than lower ones and secondary seeds are more dormant than primary seeds.

Each dormoat experiment was performed to pursue evidence(s) gathered from the previous one. Field and laboratory results demonstrated how difficult the problem is and brought into perspective the logistic involved in studying it. We are able to manipulate the crop in the laboratory and the lines selected for studies have behaviors that are very interesting for their physiological implications. Laboratory germination behavior is not however, sufficient to help build a predictive model of field emergence because it still does not encompass enough of the complexity of the seed-environment system. In these laboratory studies, we only explored responses to specific variations in the water environment and/or the temperature. In terms of the temperature factor, it is possible that a method of analysis based on experiments at constant temperature may be inappropriate for assessing the course of germination in the field where erratic fluctuations of temperature are superimposed on

systematic diurnal cycles. An example of the enormous complexity of looking at all the facets of the effect of only one environmental factor on the germination responses of seeds was given by Totterdell and Roberts (1980) where they identified **nine attributes of a diurnal temperature cycle which could be important controlling factors.** These were: the number of cycles, the amplitude of temperature fluctuation, the values of the upper and the lower temperatures, the time spent at the upper and the lower temperatures, the rates of warming and cooling and the timing of the cycles with respect to the start of imbibition.

The sequence of these various events may also play an important role in the dormancy breaking mechanism and we did observe "windows" of sensitivity in the responses of some dormoats. Furthermore when seed is sown in soil, fundamental changes in the physiological status of the imbibed seed will probably take place. The fact that several environmental factors can interact with the buried dormoat seeds, either separately or cumulatively to favor germination or dormancy, will most likely modify the behavior of the seeds whether it has been artificially imposed or not.

Two particularly striking points evolved from the field experiments. For both controls and treatments for all lines tested, a high proportion of seed was dead by spring, and the degree of variability between replicates was high. We have not investigated the mechanism by which the loss of viability could occur in dormoats. Obviously, survival of dormoat seeds through winter is not only dependent upon the maintenance of the seeds in an ungerminated state but also on the ability of the imbibed dormant seeds to resist overwintering stresses such as freezing, excess moisture, etc. Jackson et al. (1981) made the observation that part of the variability in the degree to which dormoats emerged could probably be attributed to moisture accumulation in the field over the winter or in early spring. On the subject of traits that could contribute to viability of wild oat seeds in soil, Naylor (1983) suggested that the preservation of endosperm reserve materials until the onset of germination was probably critically important. Endosperm hydrolysis in dormoat seeds would cause swelling, bursting and rotting. Even though we did not attempt to measure the presence of hydrolytic enzymes in the fully imbibed fall dormant seeds, the appearance of the endosperm at the December retrievals, after 7 weeks in the ground, was normal with no evidence of liquefaction of reserve materials. Whether the control over reserve degradation was lost during the winter or the loss in viability was due to the lack of winter resistance in the embryo itself is not known.

CONCLUSION

We did not expect from each line the same level of performance for each treatment and the observed responses varied among the lines and treatments. The lines we studied have behaviors partly expressing what we were striving for, for example: line PGR18865 or line PGR16728 have relatively good spring emergence which needed to be improved. We were not successful in achieving improvements in spring emergence over that of an early planting for the many dormoat lines used throughout these several experiments. It is possible that the methods used to modify the dormancy patterns, or the timing of the treatments, were not appropriate for either the lines we selected or the type of dormancy inherent in these lines.

At the beginning of the project, the feeling was that a "universal" management protocol may be found for dormoats, with different degrees of responses depending on the lines. After almost 5 years of experimenting with the crop, analysing the array of responses of several lines to simple treatments, it seems that this "universal" concept should be reconsidered. The dormancy traits present in dormoats are still expressed with the basic features of the wild oat parent. Looking at the problem with a weed ecologist's terminology, we are trying to manipulate the multileveled **"adaptative strategy"** of the seeds where it is probably the most complex i.e. the secondary dormancy responses or, in ecology terms, the **"consequential strategy"** of the seeds. Dormancies falling in this category develop in response to the environment surrounding the seeds and are greatly responsible for the capacity of a weed to adapt to almost any environment. On the other hand, the primary dormancies represent the part labelled as **"predictive strategy"**, working to prevent germination immediately after the seeds have fallen on the ground. Working at the primary dormancy level is already very complex and difficult, as witnessed by the years of research that have and are still going into understanding primary dormancy in wild oat. With secondary dormancies, we have to consider the seed-environment system where several factors interplay and are responsible for inducing the adaptative responses of the seeds. As written by Chadoeuf-Hannel (1985):

> "Une meilleure compréhension de ces phénomènes ne sera possible que dans la mesure où les études physiologiques et biochimiques de la dormance ou de la germination intègreront l'environnement des semences, c'est-à-dire le sol."

This is not easy as such and if we also want to be able to manipulate the responses to achieve predictability, it calls for long-termed, innovative, interdisciplinary approaches.

It is possible that the problem of finding a successful line on a somewhat shorter-term may still be explored through breeding with, however, new strategies as the routes already chosen have not yielded a candidate. The array of dormancy behavior shown by dormoats indicates that amongst the strains available with or without treatments, there is probably enough variability in terms of levels of fall dormant seeds to ensure that some lines have an adequate amount of ungerminated seeds in the ground before winter, for the purpose of a commercial crop. The shortcoming of these dormoat lines seem to be in the area of cold resistance of the seeds since damage by winter played an important role in survival as shown by the large mortality in both treated and untreated seeds at the end of winter. Cold resistance as such, has not been emphasized in the dormoat breeding program and this particular trait may not have been present in the wild oat parent as the need of a weed is survival of the species, not of all seeds. The results from the dormoat field experiments confirmed the superiority of the spring emergence mechanism (whatever it is) of PGR16728 in the few seeds that are still dormant in the fall. Amongst the lines used in the experiments described here, PGR16728 is the only line having in its parentage a winter oat from which cold resistance traits may have been transferred and thus re-enforcing the idea that dormoats in general may be lacking in this area.

Since there doesn't seem to be sufficient seed winter resistance in the breeding material, crossing programs with winter oats have been initiated to introduce in dormoats, traits that may contribute to better seed winter resistance and hopefully also contribute to an eventual commercial success of a line.

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