FARRER MEMORIAL ORATION, 1984

W. V. SINGLE

Frost Injury and the Physiology of the Wheat Plant

Frost injury to wheat crops provides yet another of those subjects which William Farrer described in his numerous writings, leaving it for further generations to wonder at the keenness of his observation and the breadth of his understanding.

In a number of articles in the Agricultural Gazette of N.S.W. he provided information concerning some devastating losses to crops, and the climatic conditions causing them, and then analysed the implication for growers and agronomists in terms of planting dates and varieties. The advice is valid today (Farrer 1898, 1905). Rereading these old papers, one cannot but be impressed by his approach to the study of agronomy and his reluctance to make any recommendations without the backing of many years of field experimentation.

It is not surprising that Farrer did not attempt to overcome the problem of frosting by breeding. Much more serious difficulties such as rust and drought beset the industry and, as is well recognised by plant breeders everywhere, each new trait to be selected greatly increases the difficulty of producing a variety. Almost 50 years were to pass before sufficient resources could be mustered to even look at frost in a serious manner, let alone attempt a breeding program.

The Nature of the Problem

It seems paradoxical that the wheat plant, varieties of which are capable of growing in high northern latitudes, should be troubled by cold in Australia. Our wheat is grown mostly in temperate parts of the continent and in fact a great deal more research is going on in the area of heat resistance than that of cold. Nevertheless in 1969 it was estimated that yield losses due to September frosts in N.S.W. and Queensland amounted to 1.36 million tonnes. Damage of this magnitude has not been suffered before or since, but it is an unusual year in which some losses are not recorded, and in 1984 many advisory workers estimated yield reductions in the vicinty of 10% overall.

The root of the problem lies in the nature of our climate and the demands it places on the plant at critical stages of growth. Our summers are too hot and dry for grain production and it is late winter and early spring which provide the combination of temperature and moisture most suitable for this process. Associated with this, however, is the sporadic occurrence of radiation frost, bringing potentially damaging temperatures during the months June to September.

A successful crop must somehow avoid injury from cold in its sensitive stages of development, and yet mature before the heat of summer puts an end to further growth.

A modest research effort has been devoted to wheat frost injury in Australia during the last 30 years, and this tribute to William Farrer provides an appropriate occasion to review some of it. While the virtual restriction of references concerning wheat to Australian sources may also seem appropriate, it is not by choice of the author. The problem is largely confined to wheat growing areas of the southern hemisphere, and only in Australia has a significant amount of research been undertaken.

Crop Development and Freezing Injury

It is well accepted that plants in the vegetative state are in no danger from freezing in the Australian wheat belt and in fact they are normally sown so as to endure the worst of the winter in this phase. Occasionally leaf tips appear to be scorched, but many farmers, probably with justification, regard this as a healthy sign and and like to see the crop "hardened" by a few good frosts.

Here it is that the real difference between our approach and that of research workers overseas becomes obvious. There has been a vast amount of research undertaken in attempts to prevent the death of autumn-sown plants in the northern hemisphere where winter temperatures may be 20° below ours. Even in the dormant stage, seedlings cannot always endure the combination of low temperature, soil movement and disease which characterise this environment, and crops may be wiped out in unusually severe winters. The most common cause of injury appears to be desiccation, brought about by the presence of ice in proximity to shoot

apices which, even if they are able to avoid freezing themselves, are forced to surrender their moisture along the gradient of water potential which exists between ice and unfrozen water at the same temperature (Olien 1981). In wheat grown in areas where the soil does not freeze, as happens here, the growing point remains protected until the elongation of the stem forces the young ear clear of the ground and into the zone of subzero temperatures. By this time the plant has undergone a dramatic change from the purely vegetative to the reproductive state, and a whole new pattern of freezing behaviour is esatablished. In many ways wheat begins to behave as a frost-tender rather than a frost-hardy species, and the techniques employed to research the problem have more in common with those of the horticulturists than the broadacre agronomists. Damage to plants is essentially damage to the reproductive mechanisms, although occasionally stems may be weakened by frost and become unable to support the weight of the grain (Banath and Single, 1976).

One approach to the problem is to delay the onset of the reproductive phase until the danger of frost is diminished to an acceptable level. The obvious method, that of controlling planting date, has shortcomings in the erratic nature of our climate. The wheat plant does, however, offer a number of internal mechanisms which can be manipulated to determine flowering time through breeding.

One of the early attempts to study the factors controlling development in Australian wheats was that of S.L. Macindoe, who was

intrigued by the behaviour of winter wheats such as Winter Minflor, and the possibility of using them to avoid frost. He went some way to unravelling the inheritance of cold requirement in a cross with an early maturing spring selection, a sib of the variety Charter (Macindoe 1948). This work led eventually to the breeding of Winglen and Windebri, but none of the selections produced from this program were early enough in maturity to compete in yield with conventional varieties. It was not until A. T. Pugsley began to quantify the interaction between response to vernalisation and response to photoperiod that an adequate understanding of the mechanisms controlling Australian varieties became available (Pugsley 1966, 1970). With J. R. Syme (1973) and R. H. Martin (1981) he made the way clear for a new generation of winter wheats as typified by Phoenix (Pugsley), King (Syme) and Osprey and Quarrion (Martin). While it cannot be said that an understanding of the underlying physiology of these mechanisms has been much advanced by work in this country, that pertaining to their inheritance certainly has. Such a situation is typical of those traits which can be recognised in a single individual of a breeding population, and are thus easily amenable to genetic analysis.

Of course, long before the genes for vernalisation and photoperiod response had been identified, they were being manipulated in an empirical fashion, particularly by William Farrer himself. His use as parents of early maturing varieties from India and elsewhere changed the face of the wheat industry and in so doing created the very problem to which we are addressed (Farrer 1898).

There is no difficulty whatever in obtaining or breeding cultivars which, on account of their slow development, will escape frost, but the price of this answer to the question is too high.

Numerous studies have shown that severe penalties are incurred if anthesis is unduly delayed (e.g. Doyle and Marcellos 1974, Fischer 1979, Kohn and Storrier 1970, McDonald et al. 1983, Woodruff and Tonks 1983). In fact the average figure derived from a number of studies shows a fall of approximately 15% in yield for each week of delay in anthesis past the optimum date, set by the diminishing risk of frost as mean temperature rises. The reasons for this fall in yield are not fully understood. While moisture is undoubtedly a factor, high temperature per se is also important in shortening the length of the grain filling phase (Marcellos and Single, 1971, Puckeridge 1971; Dawson and Wardlaw 1984) and probably in affecting other facets of starch accumulation.

The study of of frost injury with the ultimate objective of producing cold tolerant cultivars, can thus be seen then as having two major goals. Firstly is the reduction of crop losses due to freak weather patterns such as those experienced in 1969 and 1984. Secondly, of even greater importance is the advancement of the grain filling phase to produce higher and more reliable yields.

Unfortunately it must be stated that progress has been slow. Resistance to freezing is not a character which can be measured on a

single spike, or even a single plant. It can be defined only as an average reaction of a population of plants to a number of stresses which differ in ways not yet clearly understood. For this reason, research has been aimed to a large extent to understanding the nature of frost injury, rather than to seeking an empirical solution.

The work to be described from here onwards was concerned only with stress tolerance or resistance, as opposed to the equally important but quite separate role of frost avoidance in fitting the plant to our unpredictable climate.

From the outset a further division of the problem was recognised in the difference in behaviour of plants before and after the emergence of ears from the leaf sheaths.

The first studies were carried out on plants in the pre-emergence phase. This is of the lesser importance commercially but is easier to study, and made possible the establishment of a number of principles which apply universally.

Frost During Stem Elongation

Early experiments with artificial freezing cabinets provided clear evidence that wheat plants do not freeze spontaneously at those temperatures which are normally injurious in the field, i.e. in the vicinity of $-5°C$. In fact it was necessary to provide sources of ice

nuclei, such as chipped ice or carbon dioxide fog, to induce freezing. In the field it has been noted that hoar frost forms readily at tempertures well above -5°C, so the artificial nuclei went some way to simulating the natural condition (Single 1961, 1964; Marcellos and Single 1976).

However even plants covered with frost in the field did not freeze completely. Although all flag leaves and many lower ones, showed dark streaking due to the presence of internal ice, some or all of the young ears remained supercooled. They were apparently protected from freezing by the enclosing leaf sheaths, and by the nodes of the stems, as often ice could be observed in the lumen of a stem internode, but not in the internode above it, or the ear. Mechanical disruption of the leaf sheath around the ear caused it to freeze and die.

Subsequent experiments in the laboratory showed that ice did indeed spread rapidly along leaves and stems, but was often arrested at the nodes. It also spread readily, but more slowly, in very young ears and in floral organs. See Figure 1.

In leaves, the formation of ice may not be injurious (Marcellos 1977) as it grows in the intercellular spaces and the leaf cells, although suffering some dehydration, can recover. Stems also may not be badly damaged but apical and floral tissues, partly as a result of their lack of intercellular spaces, succumb immediately. Freezing progresses from cell to cell, apparently via the protoplasts, and death results.

From these results arose the general concept that the capacity of reproductive organs to remain supercooled is an essential frost protective mechanism upon which the great bulk of the Australian wheat crop depends.

It can be accepted that as long as crystallisation of water does not occur, no injury is suffered either as a result of supercooling, or of so called temperature shock through sudden chilling (Single and Marcellos 1966).

This view appears to be well founded as far as local observations are concerned, although there have been reports from other countries that wheat may be sensitive to chilling injury or temperature shock. (Suneson 1937, Toda 1965). This could be a cultivar effect and indeed as it has often been observed that the variety Timgalen, and some others carrying the gene Sr36, exhibit a degree of male sterility if the reproductive phase is entered in very cold weather. The worst effect of this appears to be increased outcrossing, without any documented reduction in yield. There has been no record of anthers being frozen preferentially, and given the structure of the wheat flower this would appear most improbable. More likely it is that damage is done to pollen formation at an earlier stage, perhaps meiosis.

Variation in Frost Resistance between Cultivars and Species

Significant differences were found between cultivars and species in their reaction to freezing (Single 1966). In one instance at least this

appears to be under simple genetic control and Fletcher (1976) was able to show that chromosome 5D of the winter wheat Cheyenne strongly influenced tiller survival after stress. Cheyenne was used in crosses with other frost tolerant varieties and appeared to be a useful parent in transmitting resistance to leaf damage (Marcellos 1977).

A general review of the research progress in the early 1970's showed that adequate resistance to freezing in the tillering phases was available along with the techniques to select for it in the field if this was considered necessary on economic grounds. Physiological studies were therefore discontinued in favour of work on the much more important, but more difficult problem of frosting of emerged ears.

Frost in the Heading Stages

With the opening of the flag leaf sheath and extrusion of the spike, a second source of inoculation of ear tissue becomes operative i.e. hoar frost on the surface of glumes and awns. If an ice front succeeds in inoculating these tissues, it has only a short path to traverse before reaching the reproductive organs, and in general it appears that no barriers exist to prevent this happening. In the vast majority of cases which have been examined, identifiable frost damage to awn or glume has never been recorded in the absence of injury to the enclosed ovule or kernel.

The practical result of exposure of the ear tissue is a dramatic

fall in the capacity of the crop to tolerate frost, which is large enough to dictate planting strategies over much of the wheat belt.

Contrary to fairly widespread belief, the process of anthesis is not especially vulnerable. Rather is it a convenient marker of a trough in the plants capacity to withstand frost, which extends from ear emergence to the time when insufficient moisture is present in the grain to freeze.

Ice Nucleation and Spread

Evidence from freezing experiments and observations in the field leads to the belief that in wheat spontaneous internal nucleation of tissue does not normally occur above about $-7^{\circ}C$, the minimum temperature commonly reached in Australian crops. In fact the ability of excised stems and leaves to supercool to between -10° and $-18^{\circ}C$ indicates that internal nucleation sites effective above $-10^{\circ}C$ may be scarce enough to be disregarded in practice (Marcellos and Single, 1979).

Furthermore, the atmosphere appears to be effectively devoid of active nucleators at temperatures in the critical ranges. Therefore it is the plant surface which must provide the active sites for the initiation of freezing.

This comes as no surprise to those familiar with the work of Lindow (1983, 1984) and others in the United States, when extensive studies of

the surface inhabiting bacterium _Pseudomonas_ _syringae_ van Hall and others
are being undertaken. These organisms are capable of initiating freezing
in water at remarkably high temperatures (between -1°C and -2°C) and are
abundant in nature. Ineffective strains have been isolated which are
capable of competing with the nucleating ones and providing a measure of
protection to corn seedlings under field conditions, and in reducing the
number of nucleating bacteria in pear and almond trees. However their
role in the freezing of wheat, and whether they can be manipulated to
advantage in this crop, remains to be seen.

While bacteria are undoubtedly effective in some instances the
abundant formation of ice on newly exposed plant tissues, such as ears
recently emerged from the leaf sheath, suggests either that other sites
are also operative in causing nucleation, or that it will be extremely
difficult to manipulate the process by antibiotics, or antagonistic
organisms.

Whatever the initial cause of nucleation, it obviously occurs
readily even on non-vegetable surfaces such as the roofs and windows of
cars, which would not be expected to support bacteria. Curiously however,
a wheat crop, although bearing such a load of hoar frost that it appears
almost white, may nevertheless be carrying among the ice crystals
abundant free water, which can be shaken out of the ears. This has been
observed at -3.5°C and shows that a considerable proportion of the
epidermal tissues must be free of ice nuclei active at this temperature.

Apparently ice fronts do not spread universally across the surfaces of ears, nor do they enter the tissues with ease. A number of experiments have been carried out in a specially constructed radiation chamber which simulates the cooling process of a natural frost, to determine which are the most likely pathways for ice to follow in its destructive course throughout stressed ears and tillers (Marcellos and Single 1984).

Ears were subjected to direct radiation at $-4°C$, one group of which had their peduncles maintained at $0°C$ to prevent ice from forming in the stems. These were compared with others which achieved the same temperature but were covered and free of moisture, so their only access to freezing was via the flag leaf and peduncle. No consistent differences was observed between treatments which carried a range of temperature between $-3.5°C$ and $-5.2°C$ and injury from zero to 100%. Thus the shielded ears, with only one point of inoculation (the peduncle) were just as badly damaged as those which were liberally covered with ice crystals. However, where ice was present externally, warming the peduncle to prevent ice fronts travelling from the flag leaf was not effective in reducing damage.

These results lead to the conclusion that at least under the conditions of these experiments, only a few points of inoculation were established in each exposed ear, and that freezing progressed via the rachis. Furthermore the rachis, in contrast to its usual behaviour in the pre-emergence stages, offered little resistance to ice propagation.

Evidence from a number of other experiments confirms this. In recording much of this work, the position of each grain on many ears has been noted. Apart from a tendency for more spikelets to be found bearing grain towards the middle of the spike, the general pattern of distribution of injury tends towards a random one, regardless of whether ears are covered with polyethylene bags, or exposed to direct inoculation. (See Figure 2). While at times discrete sections of ears may be sterile, suggesting blocking action within the rachis, this is sometimes overrated in importance due to its spectacular appearance. It is however, the common pattern in ears stressed in the pre-emergence stages, as shown in Figure 1.

Internal Barriers to Ice Formation

While it has been apparent that the nodes of stem, rachis and rachilla are important in determining the distribution of ice, the nature of the tissues involved is far from clear.

There are four possible main pathways by which a crystallisation front may be thought to pass through a node, when the temperature falls far enough to break down its blocking effect.

1) Via the cell walls and middle lamellae. The middle lamellae form the only tissue which may be said to be truly continuous through the nodes and must therefore, in young stems at least, prevent ice formation down to $-7^{\circ}C$ in fully hardened plants. Otherwise shoot apices could

not survive. They are , nevertheless, capable of transmitting water
and therefore porous. It has been shown that as long as pores are
sufficiently small, in the range of 5-10 nm diameter, enclosed water
will not freeze at temperatures of this order (Ashworth and Abeles,
1984).

Cell walls may behave in the same way, but is not possible to
determine from available data whether they are also important in
controlling ice formation.

2) Along the transpiration stream through vessels and tracheids. At the
nodes, vessels are replaced by tracheides which interconnect at the
pits. These have closing membranes formed from the middle lamellae,
which also must have pores small enough to prevent freezing at
moderate temperatures.

3) Through the phloem.

4) From one living cell of the epidermis and sub epidermal layers to
another, via the plasmodesmata.

In the case of young plants it seems that living tissues are
implicated. Short term hardening and dehardening treatments, measured in
days or even hours, markedly affected survival of young ears (Single
1966). It is difficult to imagine how such treatments could modify non-

living tissue in such a way as to increase or decrease pore size of tracheids. With plants, with emerged ears, however, the picture was far less clear. While some significant effects of hardening were observed, these were small and in many experiments undetectable (Single and Marcellos 1974). In this class of material the question must remain open until more refined techniques for the differentiation of frozen or unfrozen water within a wheat node come to hand. Those which are available, such as nuclear magnetic resonance, calorimetry and electrical conductance depend on gross measurements, incapable of focusing on the fine structure of the tissue without disturbing the system.

For the present then, the most we can determine is that internal barriers exist at the nodes and that these are capable of protecting the flowering organs at approximately −4°C from ice fronts which originate at the surfaces of leaves. If the temperature falls much below −4°C, the barriers fail and ice fronts enter the ovules with lethal results, but available data do not define the path or pathways by which this happens.

From the steep nature of the temperature response curve under artificial conditions (Marcellos and Single, 1984) it can be assumed that the internal blocks will be fully effective at any temperature above about −3°C. Any damage occurring at or above this temperature will generally therefore be the result of ice fronts entering the the system directly via the surface of the spike itself, and involving resistance to freezing in a different type of tissue from that involved at nodes.

External Barriers of the Ear to Ice Penetration

Direct inoculation of ear tissue via the surface provides some formidable problems for study.

In the freezing cabinet, when ears were sprayed liberally with water and then inoculated with carbon dioxide fog, the lethal temperature was established at around $-2^{\circ}C$ to $-2.5^{\circ}C$. Yet plants grown under the same conditions survived $-4^{\circ}C$ in the radiation chamber, even though they bore numerous ice crystals.

Similar anomalies have been observed in the field in that ears which survived $-4^{\circ}C$ succumbed to a later frost of -3° to $-3.5^{\circ}C$. The second frost followed a shower of rain, confirming other observations that moisture plays a most important part in promoting injury.

Whether this is by encouraging nucleation, or simply by facilitating the spread of existing ice boundaries, is not known, but it has the rather disturbing implication that the lethal temperature for a crop is far from fixed, and may vary over a range of approximately $2^{\circ}C$.

It also tends to confirm the idea that there are at least two separate resistance mechanisms required by a plant for adequate protection, so selection procedures in any program of breeding cultivars for frost resistance should take these into account.

The nature of surface resistance to ice propagations is a matter only for speculation. Some limited observations with backcrossed lines indicated that neither glaucousness, nor awns, are very important. Experiments in which wax was removed by brushing with detergents must be treated with caution (Single and Marcellos 1974) as this is a drastic treatment which could bring in a number of artifacts.

Lethal Temperatures, Anthesis and Grain Formation

The highest damaging temperature recorded in the Tamworth laboratory was $-1.8°C$ (Single and Marcellos). When applied in association with mechanical removal of wax and detergents, this caused almost complete sterility of ears at flowering. This in only marginally above the freezing point which can be calculated for spikelets from their osmotic potentials when grown under similar conditions; i.e. about $-1.1°C$ (Morgan and King, 1984).

As growth proceeds there appears to be little change in resistance until the grain has reached its full length, as many experiments (unpublished) have shown severe injury resulting from freezing at between $-2°$ and $-2.5°C$.

Once the grain has approximated its maximum length, however a different phenomenon is seen and even $-3°C$ may not prove lethal. Instead the kernels may continue to swell, albeit in a somewhat distorted fashion as shown in figure 3. Instead of containing the normal starchy endosperm,

they are partly filled with clear fluid. On ripening they shrink, but may still be capable of germination. (See Figure 4).

What protects the developing embryo and epidermal layers under these conditions provides an interesting area for speculation, as it would be expected that once the ice front had entered the grain it would destroy all the cells. However, the developing grain does present one great difference from other sensitive parts in that it is an acceptable site for ice crystal formation. The effect of an ice front reaching the mass of fluid in the endosperm would be a strong exotherm, which may protect the embryo and other tissues for long enough for them to lose some water and came to equilibrium with the ice. Only a slight resistance to ice propagation, such as is found in the plasmalemma of many cells would be required for protection under these conditions. As the tissues are vegetative, and part of the developing seed, it is perhaps not surprising that they are capable of surviving what is only a mild degree of moisture stress.

Frost Resistant Cultivars

The behaviour of different cultivars and efforts to improve them by breeding does not properly come within the scope of this review, but can scarcely be ignored in a contribution such as this to the memory of William Farrer.

It is appropriate that the cultivars most tolerant to frost in the heading stages, Kite , Falcon and Eagle were produced by R. H. Martin, a Farrer Medalist. The tolerance of the varieties (albeit not selected deliberately) was recognised in the Tamworth program and techniques developed for selection of the character in breeding populations. This resulted in the selection of Takari by R. J. Fletcher. The character is also present in Sunelg, produced by backcrossing to Kite by the University of Sydney Plant Breeding Institute.

While these varieties may still be severely damaged by frost, they can yield over twice as much as susceptible ones after moderate stress, and point the way to further improvement. Another step of similar magnitude along the road to resistance could have profound effects in permitting earlier flowering and higher yields. Breeding lines are available to make this step, so this next generation of cultivars could make possible a whole new approach to planting strategies, even in frost-liable areas.

Conclusion

In conclusion, may I express my appreciation of assistance and encouragement in this work to a number of people too numerous to mention in toto here; especially however to W. T. Atkinson and S. L. Macindoe for their help in the beginning of my career, to I. A. Watson in whose laboratory the first freezing experiments were undertaken; to A. T. Pugsley, and to H. Marcellos, co-author in many papers cited here, and to

References

Ashworth, E. N. and Abeles, F. B. (1984). Freezing behaviour of water in small pores and the possible role in the freezing of plant tissues. Plant Physiol. 76 : 201-04.

Banath, C. L. and Single, W. V. (1976). Frost injury to wheat stems and grain production. Aust.J.Agric.Res. 27 : 749-53.

Dawson, I. A. and Wardlaw, I. F. (1984). The influence of nutrition on the response of wheat to above-optimal temperature. Aust.J.Agric.Res. 35 : 129-37.

Doyle, A. D. and Marcellos, H. (1974). Time of sowing and wheat yield in northern New South Wales. Aust.J.Exp.Agric.& Anim.Husb. 14 : 93-102.

Farrer, W. (1898). The making and improvement of wheats for Australian conditions. Part 2. Ag.Gaz.N.S.W. 9 : 131-167.

_____ (1900). Notes on the damage done to wheat crops by the late frosts in the spring of 1899. Ag.Gaz.N.S.W. 11 : 675-77.

_____ (1905). Some notes for wheat-growers. 1. Choice of varieties. - 2. Selection of seed. - 3. Treatment of seed for bunt. -4. Manuring. Ag.Gaz.N.S.W. 16 : 462-73.

Fischer, R. A. (1979). Growth and water limitations to dryland wheat yield in Australia: A physiological framework. J.Aust.Inst.Agric.Sci. 45 : 83-100.

Fletcher, R. J. (1976). Physiological and genetic studies of wheat characters associated with frost resistance. Ph.D.thesis, University of Sydney.

Kohn, G. D. and Storrier, R. R. (1970). Time of sowing and wheat production in southern New South Wales. Aust.J.Exp.Agric.& Anim.Husb. 10 : 604-609.

Lindow, S. E. (1983). The role of bacterial ice nucleation in frost injury to plants. Ann.Rev.Phytopathol. 21 : 363-84.

_____ and Connell, J. A. (1984). Reduction of frost injury to almond by control of ice nucleation active bacteria. J.Amer.Soc.Hort.Sci. 109(1) : 48-53.

McDonald, G. K., Sutton, B. G. and Ellison, F. W. (1983). The effect of time of sowing on the grain yield of irrigated wheat in the Namoi Valley, New South Wales. Aust.J.Agric.Res. 34 : 229-40.

Macindoe, S. L. (1948). The nature and inheritance of resistance to stem rust of heat Puccinia graminis tritici possessed by several resistant parents. N.S.W.Dept.of Agric.Sci.Bull. No. 69.

Marcellos, H. (1977). Wheat frost injury - Freezing stress and photosynthesis. Aust.J.Agric.Res. 28 : 557-64.

_____ and Single, W. V. (1971). The influence of cultivar, temperature and photoperiod on post-flowering development of wheat. Aust.J.Agric.Res. 23 : 533-40.

_____ and Single, W. V. (1976). Ice nucleation on wheat. Agric.Meteorol. 16 : 125-9.

_____ and Single, W. V. (1979). Supercooling and heterogeneous nucleation of freezing in tissues of tender plants. Cryobiology. 16 : 74-77.

_____ and Single, W. V. (1984). Frost injury in wheat ears after ear emergence. Aust.J.Plant Physiol. 11 : 7-15.

Martin, R. H. (1981). In Farrer's footsteps: Farrer memorial oration. J.Aust.Inst. 47 : 123-131.

Morgan, J. M. and King, R. W. (1984). Association between loss of leaf turgor, abscisic acid levels and seed set in two wheat culivars. Aust.J.Plant Physiol. 11 : 143-50.

Olien, C. 1R. (1981). Analysis of midwinter freezing stress. pp. 35-59 in Analysis and improvement of plant cold hardiness. C. R. Olien and M. N. Smith eds. C.R.C. Press, Florida.

Puckridge, D. W. (1971). Photosynthesis of wheat under field conditions. III. Seasonal trends in carbon dioxide uptake of crop communities. Aust.J.Agric.Res. 22 : 1-9.

Pugsley, A. T. (1966). The photoperiodic sensitivity of some spring wheats with special reference to the variety Thatcher. Aust.J.Agric.Res. 17 : 591-9.

_____ (1970). A genetic analysis of the spring-winter habit of growth in wheat. Aust.J.Agric.Res. 22 : 21-31.

Single, W. V. (1961). Studies on frost injury to wheat. I. Laboratory freezing tests in relation to the behaviour of varieties in the field. Aust.J.Agric.Res. 12 : 767-82.

Single, W. V. (1964). Studies on frost injury to wheat. II. Ice

formation within the plant. Aust.J.Agric.Res. 15 : 869-75.

_____ (1966). Studies on frost injury to wheat. III. Screening

of varieties for resistance to ear and stem frosting.

Aust.J.Agric.Res. 17 : 601-10.

_____ and Marcellos, H. (1974). Studies of frosast injury to

wheat. IV. Freezing of ears after emergence from the leaf sheath.

Aust.J.Agric.Res. 25 : 679-86.

Syme, J. R. (1973). Quantitative control of flowering tissue in wheat

cultivars by vernalization and photoperiod sensitivities.

Aust.J.Agric.Res. 24 : 657-65.

Woodruff, D. R. and Tonks, J. (1983). Relationship between time of

anthesis and grain yield of wheat genotypes with differing

developmental patterns. Aust.J.Agric.Res. 34 : 1-11.

Figure 1. Ears frosted while enclosed in the flag leaf sheath asnd

subsequently extruded. Note injury to upper peduncles.

Normal ear at right.

Figure 2. Ears showing varying degrees of sterility due to freezing

after emergence.

Figure 3. Unripened grains damaged by freezing to −3°C at the stage

of full elongation, showing, at left, shrinkage and at centre

and right, swelling and distortion of the crease.

Figure 4. Ripened grains from a single ear frozen at −3°C. From the
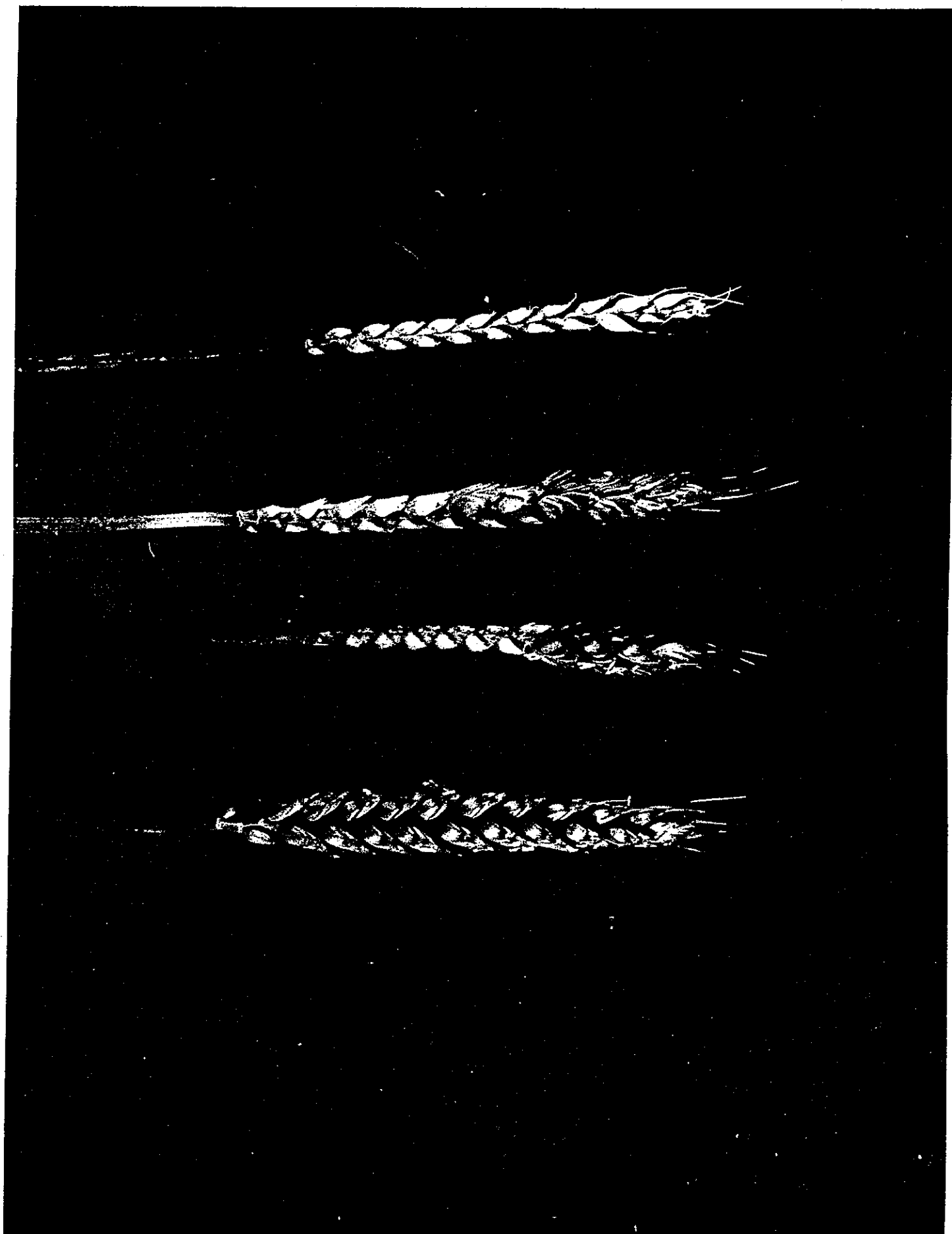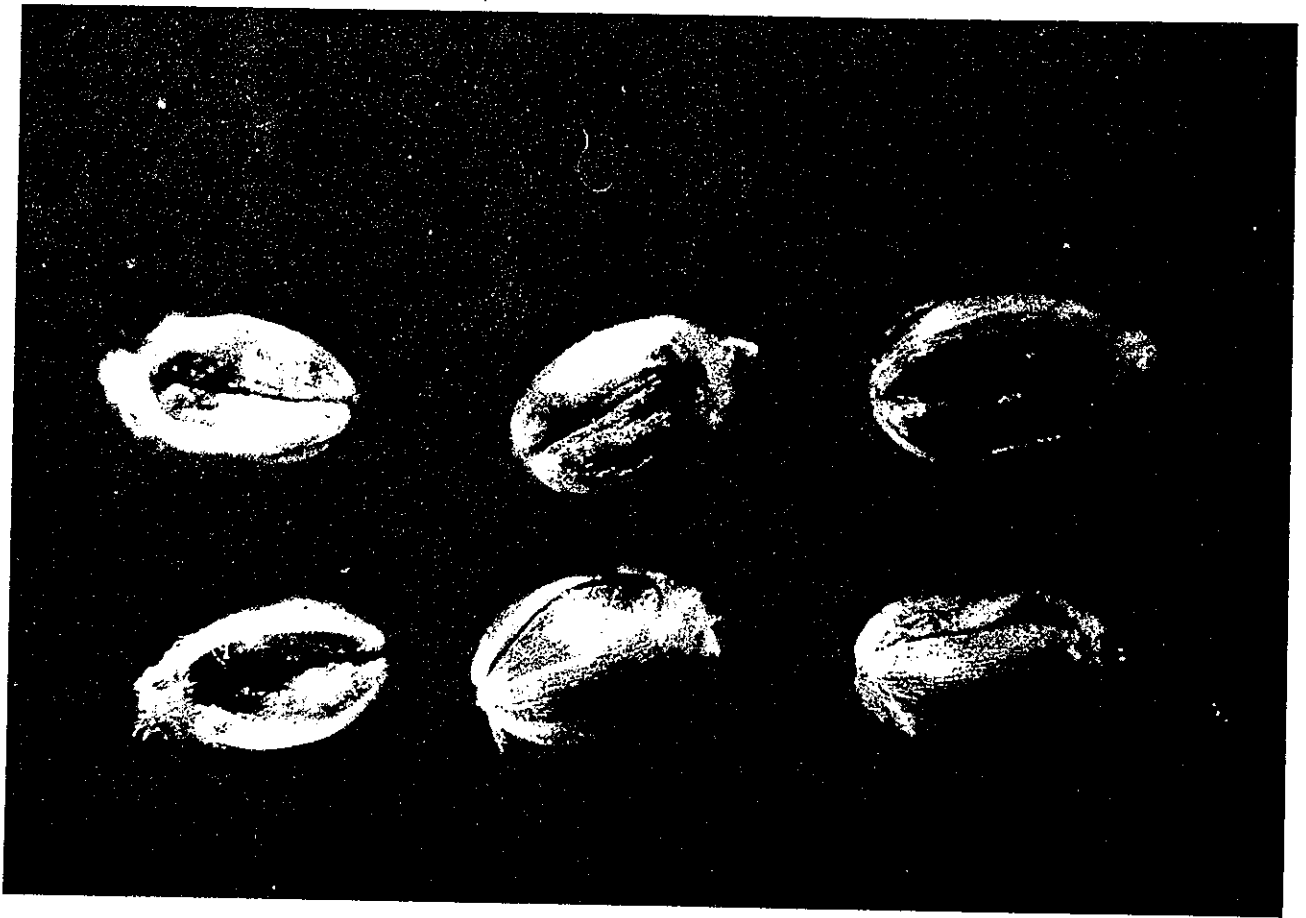
same experiment as those in Figure 3.

Fig 1

Fig 2

Fig 3

Fig4