HGCA

HGCA RESEARCH REVIEW No. 8

SEED DORMANCY AND LONGEVITY IN SELF-SOWN WHEAT AND BARLEY

by

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November
1988

Price: £12.50

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1. Abstract

1.1 Introduction

There is now an urgent need to reduce the serious problem of volunteer cereal plants in order to improve grain sample quality. The failure of shed grain to germinate in time to facilitate removal during the final cultivation is thought to arise from dormancy, a subject which has attracted much research in the past, although little of this has been applied directly to the shed grain of cereals. To avoid confusion, it is necessary to distinguish between the different ways seed dormancy is imposed and it must be recognised that seed in the soil is imbibed and metabolically active. As a living organism, imbibed seed is capable of life-supporting processes, although germination is blocked. Innate dormancy describes the state where seed fails to germinate when conditions are suitable. Induced dormancy is similar to innate but applies where dormancy arises in seed which was once able to germinate. Enforced dormancy indicates seed which is unable to germinate due to inappropriate conditions. Relative dormancy restricts germination to a narrow range of environments.

1.2 Dormancy: the seed and the environment

Innate seed dormancy in cereals arises from the action of a number of mechanisms involving biochemical inhibitors. These originate in the green pericarp and possibly other parts of the seed, and in the tissues of the spikelet, exerting control over the growth processes in the embryo. Most of these inhibitors appear to show varietal differences in terms of degree of production or effect. Cool temperatures during the doughy-ripe stage of grain maturation promote the development of dormancy. Temperature at other

stages of growth appears less important although some evidence suggests that high temperature shortly after ear emergence may cause dormancy. Grains which developed at low temperature may exhibit relative dormancy. Cool temperature retards after-ripening and loss of dormancy and it is therefore likely that this happens more slowly in the field than in the store. However, chilling can also 'trigger' germination. Early growth stages of the grain appear less sensitive to water. It seems that later grain development and the period following harvest ripeness are the most critical phases as far as moisture is concerned since drying may lead to a disruption of the covering tissues of the embryo allowing germination to take place.

The application of fungicides and nitrogen to the growing crop is likely to modify the speed of grain maturation with a possible increase in dormancy at harvest. It is likely that recently harvested grain lying on the soil surface will show enhanced after-ripening compared with grain incorporated into damp soil, germination may also be improved although this is obviously dependent on moisture availability. Lack of oxygen is also thought to affect germination. Growers need to know the state of their crops and soil to enable them to manipulate these where possible. Attention is therefore needed to the possibility of forecasting dormancy in the UK, as practised elsewhere. Moreover, means whereby the problem of shed seed can be estimated are required to permit cultivation and cropping plans to be modified accordingly.

1.3 The longevity of cereal seed

The belief that shed cereal seed will not be a threat to the purity of following crops for more than the immediate season, now seems doubtful although volunteer plants in the next crop may also shed seed and this could be a source of confusion in later years. However, reports of survival for more than twelve months are not infrequent but it certainly appears exceptional for longevity in cereal seed in the soil to last as long as five years. Loss of viability in seed under enforced dormancy in the soil has been attributed to abortive germination at depth and leaking of metabolites, in addition to external influences which will be discussed later. Although it has been thought that germination at a depth too great for emergence may occur, it has to be accepted that enforced dormancy in the soil can last through a full seasonal cycle. There is evidence that cultivation method may affect longevity, mainly from a possible interaction with oxygen levels. Anaerobic conditions, arising from competition with the microflora and the state of the soil, could reduce seed deterioration. Other factors postulated as affecting longevity include: fungicide and nitrogen applications resulting in an increase; herbicides and the presence of microorganisms could reduce longevity and this is likely to be particularly applicable to seeds in a poor state when buried. Seed decay is likely to be greatest under conditions just below those needed for germination. However, many of these suggestions and the actual degree and mechanism of longevity in cereals require confirmation. The relationship of innate and induced dormancy to longevity is unclear.

1.4 Dormancy: the factor of genotype

The problem of dormancy in shed grain is clearly linked to that of pre-harvest sprouting (PHS). One study attributed as much as 64% of the PHS resistance mechanism to dormancy but this is probably an underestimate since the effect of inhibitors in the spikelet tissue was not examined. Very few studies appear to have been carried out on the dormancy of shed grain on, or in the soil. Investigations of stored grain are not fully applicable to grain in the soil since the component of after-ripening is included without the soil moisture effect. On the other hand, studies of PHS resistance are terminated too soon to apply to shed grain and often test the intact ear but not the presence of soil. However, many examinations of dry grain confirm that, under certain conditions, there is a wide range of dormancy, particularly between barley varieties. Dormancy in harvested grain has been investigated by the Official Seed Testing Stations in Cambridge and Edinburgh. The European Brewing Convention also coordinates trials and publishes information on barley. The foremost varietal trend observed in wheat is the frequent association of low dormancy with white grain although overseas breeders have been able to breed white varieties showing a reasonable degree of PHS resistance. The genetics of red grain coat colour, which is associated with high levels of dormancy, are complicated by the fact that several genes are involved in the character which is maternally inherited. The identity of other characteristics related to dormancy and PHS is less certain although seed size, in addition to affecting shedding, is one of the more likely factors. Further work is required to determine the dormancy of varieties when in contact with the soil.

1.5 Genetics and breeding

A reduction in dormancy will usually lead to a lack of protection to pre-harvest sprouting in the ear although means to reduce this could possibly be developed. It is, however, clear that a suitable degree of dormancy in wheat and barley will always be a fine balance and usually a compromise, especially as seed for sowing must also be capable of early germination, so dormancy is likely to be a problem in certain adverse climates. The breeding of suitable varieties is not helped by the complex genetics of dormancy and related characters, particularly in bread wheat, in which there are three genomes, each with dormancy related genes. There are other reasons for a multiplicity of genes, a situation which also affects barley which is a diploid. Breeders are hampered by different forms of inheritance in the progenies of crosses depending on the location of the character within the seed. This arises from the fact that the testa, for example, is maternal tissue, whereas the embryo is, of course, the result of fertilisation. The endosperm, being triploid, carries an extra set of maternal chromosomes. All these structures affect dormancy and it is therefore difficult to assess lines in the course of selection. Seasonal climatic variation is another source of difficulty for the breeder. A number of possible strategies to ameliorate the problem of conflicting requirements have been suggested. For example, it may be feasible to reduce α-amylase in sprouted grain in wheat and triticale by use of the *Rht 3* dwarfing gene although there are certain undesirable effects which may make this unattractive. Another option for wheat is to concentrate on germination inhibitors in those parts of the ear which are normally lost at harvest. It may be possible to modify these and other characters by incorporating genes from the wild relatives of wheat and barley, and advanced genetic transformation is another area that is likely to be explored in this context. Underlying many of these considerations is the highly complex biochemistry of the control of germination which, after much research, is still only partially understood.

1.6 The soil and harvest residues

The major changes in land use and management over the last 25 years have, no doubt, contributed to the apparent increase in cereal volunteers. Amongst these changes, less mouldboard ploughing, straw incorporation and fewer non-cereal breaks figure strongly. Stubble cultivation is likely to alter the after-ripening characteristics of shed grain and it is possible that attempts to create seed beds to encourage germination may actually retard emergence of seed from dormancy following harvest. Choice of main cultivation technique has an important influence on the level in the soil profile in which shed grain is placed and, together with method of straw disposal, will affect other environmental aspects such as proximity of the grain to harvest residues. The environment influences whether the grain ultimately germinates or decays and when the critical stage is reached. Soil type will modify the environment of grain both directly by modifying aeration and indirectly by controlling effectiveness of cultivation. Straw disposal problems may be the largest factor in the volunteer cereal problem. Burning of straw will lead to a considerable loss of grain whereas incorporation may place it in the soil at a point from which the resulting seedlings can emerge in the following crop. The above considerations appear to have been inadequately researched, a deficiency which should be rectified.

1.7 Research requirements

A list of recommendations is included at the end of each of the main chapters of the review. The following examples demonstrate that many aspects of the science and practice of crop production influence dormancy and longevity of seed in the soil:

1. Confirmation of the dormancy mechanism of cereals is necessary to provide a sound base for applied research and the development of means

to manipulate the biology of shed grain. The identity, site of origin, and mode of action of inhibitors should be established. Since genetic and environmental variation has led to dispute regarding the relative importance of the known inhibitors, these investigations should be carried out using grain of different varieties, grown under a wide range of environments.

2. The requirements for the maintenance of life of an imbibed cereal seed under enforced dormancy should be determined and the relationship of innate dormancy to longevity requires investigation.

3. The influence of nitrogen and fungicide applications on the development of dormancy should be examined with particular attention to the speed of natural drying of the grain.

4. After-ripening requirements for shed grain in the field should be measured. Consideration should be given to how post-harvest field management might be directed to meet these needs. What is the effect of burying dormant grain directly after harvest? Is the date of sowing the next crop important?

5. Critical studies of dormancy in recommended varieties of wheat and barley should be carried out in the field using grain which has not been after-ripened but has been subjected to the growing conditions identified as promoting dormancy. It must not be assumed that grain is dormant since this condition is likely to be intermittent. It might be feasible to obtain suitable material grown in an adverse, northerly climate.

6. An improved understanding of the genetics of dormancy and related characters in both wheat and barley would be extremely useful despite the conflicting requirements of PHS resistance and lower dormancy in shed grain. It might be possible to improve PHS resistance by exploiting dormancy promoting features in those parts of the grain which are removed at harvest and less likely to influence the shed grain. Another possibility is that PHS resistance could be derived from

a reduction of water uptake by the ear during later maturation; this might result in PHS protection and less dormancy.

7. The effect of stubble cultivation on the early breaking of dormancy of shed grain should be assessed in different soil types, with and without straw burning.

8. The systems of main cultivation should be investigated to determine how they affect the germination and emergence of shed grain in the next season and the longevity of those seeds which fail to germinate. Particular attention should be given to soil type and the depth in the soil at which grain is placed by each method.

9. The effect of straw disposal techniques on shed grain should be evaluated. The question of possible germination inhibitors in harvest residues should be investigated in the appraisal of procedures for straw disposal.

This review, completed in November 1988 and with 109 pages in the full article, was funded by the HOME-GROWN CEREALS AUTHORITY, Hamlyn House, Highgate Hill, London, N19 5PR, from whom copies may be obtained at a price of £12.50 each (postage and packing included).

2. Glossary of terms and abbreviations

2.1 Terms

Acetic acid

A fatty acid produced during the anaerobic fermentation of organic residues and alcohol. Also termed ethanoic acid.

Addititive inheritance

The cummulative contribution towards a trait of alleles at two or more loci, or, in the absence of dominance, at a single heterozygous locus.

After-ripening

The process of chemical and physiological change involved in the emergence from dormancy.

Aleurone

The outer layer of the endosperm composed of a single cell thickness.

Allele

Shortened form for allelomorph. One of two or more genes at a single locus acting as alternatives in inheritance and having a differing DNA sequence affecting a single product.

Alpha-amylase

An enzyme initiating the breakdown of starch in the cereal endosperm.

Diploid

An individual with two sets of chromosomes (one from each parent).

Dominance

The state of an allele which exhibits full phenotypic expression at a heterozygous locus.

Doughy ripeness

The condition of a grain which is partially desiccated but still soft.

Embryo

The structure within the seed which develops into the seedling at germination. Embryo immaturity describes an organism which will not germinate because of incomplete chemical or physiological development.

Endogenous

A substance or stimulus arising within the organism.

Endosperm

Triploid tissue which surrounds the embryo and for the nourishment of which it contains nutritive reserves, mainly starch with some protein.

Enzyme

A protein which acts as a catalyst for a chemical reaction.

Genetic linkage

The association of genetic traits controlled by different loci situated on the same chromosome.

Genome

The genetic complement of a diploid species. A polyploid will therefore be composed of more than one genome.

Germination inhibitor

An organic compound present in seeds which blocks processes essential to germination. ABA and CT are examples of germination inhibitors.

Germinative capacity

The proportion of seeds which are able to germinate.

Germinative energy

The time taken for seeds to germinate. Dormant seeds have low germinative energy.

Germplasm

The sum total of hereditary material.

Grain coat colour

The colour of the grain arising from pigmentation of the testa with two possible states in wheat: white and red.

Hagberg Falling Number

A test providing an estimation (not a precise measure) of α-amylase activity by measuring the loss of viscosity in a heated flour and water slurry.

Harvest ripeness

The condition of grain capable of being harvested without damage. Dry matter content and firmness are used to test harvest ripeness which is not synonymous with physiological maturity.

Heterosis

Increased production or vigour in a hybrid associated with heterozygosity.

Heterozygosity

The condition of an individual having different alleles at the locus (loci) under consideration.

Hexaploid

Having six haploid sets of chromosomes.

Homoeologous chromosomes

Chromosomes which, although showing similarities, are not fully homologous.

Homologous chromosomes

Chromosomes, derived from separate parents, which will pair during meiosis and contain identical loci.

Homozygosity

The condition of an individual having two identical alleles at the locus (loci) under consideration.

Locus (loci)

The position of a gene on a chromosome.

Maternal inheritance

Inheritance controlled by cytoplasmic genetic factors which are conferred by the female parent.

Naked grained variety

A variety of barley or oats where the lemma and palea are routinely lost at harvest. Also known as 'huskless'.

Open pollinated variety

An inter-pollinating population showing a high degree of genetic equilibrium.

Pericarp

The outer covering of the grain. The pericarp develops from the wall of the ovary and, in the cereals, becomes fused with the testa.

Phenolic compounds

Acidic compounds present in certain spikelet structures and thought to be implicated in dormancy.

Physiological immaturity

The state of a grain requiring after-ripening.

Phytotoxicity

The presence of a substance harmful to the life or development of plants.

Pleiotropy

This indicates that a single gene is responsible for more than one distinct phenotypic effect.

Progeny tests

The evaluation of a genotype by a test of its progeny.

Recessive allele

A gene which is expressed in the phenotype only when the individual is homozygous at the locus concerned.

Scarification

The process whereby abrasive action is applied to the seed coat to break coat-imposed dormancy.

Scutellum

A shield-shaped structure that is part of the cotyledon in some Gramineae and through which nutrients are absorbed from the endosperm into the embryo.

Seed dormancy

Enforced: the seed fails to germinate because the environment is unfavourable.

Innate: the seed will not germinate although all environmental factors are suitable.

Induced: this form of dormancy applies where seed, once able to germinate, is no longer able to do so as a result of climatic conditions.

Relative: the seed will only germinate under a restricted range of conditions.

Seed longevity

The period for which the ungerminated seed remains viable.

Segregation

The separation of alleles at meiosis. At heterozygous loci, this leads to genetic variation amongst the progeny.

Spikelet

A group of florets on the ear (spike) of wheat and barley.

Spikelet structures

Glume: in pairs, they form the outermost bracts of the spikelet.

Lemma: the outer bract of the floret.

Palea: the inner bract of the floret.

Stratification

Applied to a dormancy breaking procedure whereby the seed is subjected to chilling.

Stubble cultivation

Shallow cultivation directly following harvest.

Vernalisation

Low temperature treatment of germinating seeds to enable them to flower in the year of sowing.

Viability

A measure of the proportion of seeds able to germinate (irrespective of the presence of dormancy).

Water sensitivity

The condition whereby excess water prevents germination due to interference with oxygen supply.

Zygote

The cell which results from fertilisation and develops into a new individual.

2.2 Abbreviations

ABA	Abscisic acid
CK	Cytokinins
CHA	Chemical hybridising agent
CMS	Cytoplasmic male sterility
CT	Catechin tannins
DNA	Deoxyribonucleic acid
EBC	European Brewing Convention
GA	Gibberellic acid
HFN	Hagberg falling number
ISTA	International Seed Testing Association
NIAB	National Institute of Agricultural Botany
PHS	Pre-harvest sprouting
PPP	Pentose phosphate pathway

3. Introduction

3.1 The Review

The volunteer cereal problem

There is little doubt that the contamination of grain crops with volunteer cereals now presents a serious problem to the industry. Impurities in grain result in the loss of potential markets or the imposition of price penalties and also restrict cropping plans. However, reliable statistics of the extent of the problem in the field can only be based on the results of the inspection of crops or on an examination of the quality of the grain produced. Although seed crops are scrutinised in these ways, the findings are not typical of cereal crops as a whole and do not provide a valid measurement of volunteers because of costly additional precautions which are often taken in seed production. Despite lack of information, the widespread concern regarding volunteers in grain crops is an indication that the problem is serious.

Cereal producers now face a number of major changes which will almost certainly have a considerable effect on the way the industry of the future operates. Old patterns of supply and demand have been modified by advanced technology and there is reason to believe that genetic manipulation will increase this trend, at least for the immediate future. Agriculture no longer enjoys the status of an industry producing a product in short supply and therefore new levels of efficiency are required to match these developments to enable the grower to compete in a more exacting market. For example, the end user seeks a quality product and this may be confirmed by biochemical tests, if not by eye. Therefore the potential for contamination must be reduced. The public are a further consideration since there is less toleration of straw burning which, although thought to limit volunteers, is seen as an abuse of the environment. Together these forces may mean that the farmer will be forced to achieve higher standards with a more discriminating use of his resources. An examination of the factors controlling the emergence of self-sown wheat and barley is therefore necessary.

The literature

Dormancy is one of the more complex biological questions despite the apparent paradox that it appears very simple and under the direct control of climatic conditions. In reality, however, dormancy and germination are the result of the interaction of highly sophisticated biochemical systems. This is reflected by the literature. Nine years ago, Derera (1980) calculated that during the previous five years, 1000 articles in addition to other publications had been produced dealing with germination. Moreover, taking the four years preceding 1977, Taylorson and Hendricks (1977) computed that 1300 articles had been published. Much material has, of course, followed since these statistics were produced and therefore, with germination as the principal topic, this review presented a formidable task. Whilst an attempt has been made to investigate as much material as possible, it would be unwise to claim completeness. Hopefully, the important references have been considered!

Unfortunately, although much of the extensive literature has a general relevance to this review, the cultivated cereals have not been the subject of as much dormancy orientated research as certain other species. Bradbeer (1988) lists nine species which have attracted the most papers in the scientific literature and it is noteworthy that although *Avena fatua* and *A. ludoviciana* are included, cultivated cereals are not. Certainly, little published work directly relates to the germination potential of soil-borne shed seed of the cultivated cereals. Significant gaps in the understanding of the behaviour of the cereal seed in the soil appear to exist and inhibit the development of means to manipulate agronomic practice against volunteer cereals. For example, growers lack access to information relating to dormancy and longevity of shed grain at the varietal level.

3.2 A classification of seed dormancy

Different meanings have been applied to the term ***dormancy*** in the context of seed. This leads to difficulties in interpreting both new and old literature. Unless the term is defined, it fails to draw a clear distinction between quite separate circumstances. In one instance, for example, the seed is intrinsically unable to germinate without some form of artificial treatment, even when given the normal conditions and nutrients for plant development. This state may arise in two different ways: the seed may never have been able to germinate, or alternatively, it may develop dormancy after a period during which germination was possible, given the correct resources. A further possibility is that the seed, although otherwise able to germinate, is prevented from doing so by some external factor. For the purpose of this review, dormancy will be classed as *innate*, *induced* or *enforced* as defined below on the basis of the work of Harper (1977). It will be noted that whereas innate or induced dormancy may prevent the immediate germination of shed grain, enforced dormancy will be the main handicap facing grain buried in the soil. Others who have published views on the definition of dormancy include: Amen (1968), Villiers (1972).

Innate dormancy

This describes the state where a seed will not germinate even where all the environmental factors favourable for germination are present. For cereals, these include: water, a suitable temperature and oxygen. Dormancy which develops after a period during which germination was possible will be classified as innate where this appears to be under direct genetic control. Innate dormancy has also been termed: *primary, natural, inherent* or *endogenous dormancy.*

Induced domancy

This applies where a seed, once able to germinate, no longer can do so although the conditions for plant development are correct. This term will be applied to dormancy in cereals which arises in once non-dormant seed as a result of climate. It is, however, possible that instances will arise where the distinction between innate and induced dormancy will be unclear. Another term used for this circumstance is *secondary dormancy.*

Enforced dormancy

This arises where a seed fails to germinate because the environment is unfavourable. Cool temperatures and lack of moisture are obvious examples but carbon dioxide concentrations may be implicated according to Major and Roberts (1968b). Seed in a dry store or deep in the soil is under *enforced dormancy*. This type of dormancy has also been referred to as *environmental, exogenous* or *induced dormancy*. The latter, in particular could be a source of confusion with the different form of dormancy described above. It has been logically argued that enforced dormancy is not true dormancy, the seed merely being in a state of quiescence (Bewley and Black 1982).

Relative dormancy

In this state, the seed is only able to germinate under a restricted range of circumstances (Bradbeer 1988). In this respect, it should be noted that many of the above definitions do not relate to sharply defined situations since there will usually be a phase during which seed is emerging from dormancy. This state is also known as *conditional dormancy*.

Distinction should be made between a dormant seed and one that is immature. This question was considered by Gordon *et al* (1979) who aptly remarked that maturity is the result of a "multi-faceted process" where the timing of the different phases will vary between varieties. It is clear that a description of maturity based on moisture content alone falls short of reality since such seed may be physiologically immature. However, grain must often be harvested in this condition to avoid serious shedding and adverse weather. For the purposes of the question of volunteer cereals, it is likely that a grain which is immature but capable of maturation, is as serious a problem as one that is dormant according to any strict meaning of the term. Two further definitions are given below to clarify the question of grain maturity.

Harvest ripeness

This will be taken to indicate grain which is capable of being harvested without damage. The moisture test, together with an assessment of firmness, are frequently used as measures of readiness for harvest. Gordon *et al* (1979) discussed this and pointed out that harvest ripeness is not synonymous with physiological maturity.

After-ripening

This term has been defined as "the process whereby chemical and physiological changes take place while the seeds are emerging from dormancy" (Belderok 1968). Variation in the time taken for this process will be discussed in a later section.

3.3 The natural function of seed dormancy

Without dormancy, nature would allow seeds to germinate at inappropriate periods of the year when conditions for plant development were completely unsuitable. Seed dormancy is an essential component of the survival mechanism of the breeding population in many species. If all seeds germinated in one season, the population would be vulnerable to any disaster. The retention of some seeds provides an insurance, allowing an attempt at regeneration in another year. This is the natural function of each form of dormancy, whether innate, induced or enforced. In the selection and management of cereals for specific levels of dormancy, man seeks to move away from nature.

3.4 Agronomic problems associated with seed dormancy and sprouting

The problem of pre-harvest sprouting (PHS) arises when innate seed dormancy is lacking in cereal crops and this must, of course, be regarded as the principal problem associated with degree of dormancy in cereals. Secondary to this, dormancy presents the opposite problem when shed grain fails to grow before the next sowing, leading to admixture in the next crop. It is therefore clear that dormancy in shed grain is inversely related to the problem of PHS (Black *et al* 1987). An additional difficulty arises from innate or induced dormancy in seed for sowing, produced in certain more northerly climates, making seed conditioning necessary for satisfactory crop establishment.

From the outset of this review an obvious conflict appeared to exist between the requirement for early germination of shed grain and the need for dormancy to preserve grain quality in adverse preharvest conditions. Indeed the latter has formed an important plant breeding objective as will be discussed in a later section. It will therefore be necessary to review some of the alternative measures which could moderate the problem of volunteers without compromising protection to PHS.

Historically, the problems now associated with dormancy were probably less serious. Man has been able to enforce dormancy fairly readily in cereals by placing the seed in dry storage but since he also required the sown seed to germinate freely, there was selection pressure away from genotypes showing innate or induced dormancy. For thousands of years, harvesting did not involve threshing in the field. Whole crop harvesting by labour intensive methods could have resulted in a different level of sprouting compared with modern techniques. There may have been considerable ear loss although the practices of gleaning and the folding of poultry would have reduced volunteer cereals. More importantly in the past, cereals were grown in crop rotation systems which would have reduced volunteers in cereal crops. Handwork was also employed to remove weeds and other unwanted plants although it is doubtful whether our forbears were greatly concerned by cereal plants not true to type. Archaeology has shown that mixtures in stored grain were not uncommon (Beaven 1947). This review therefore has arisen because of the need to maintain and improve the purity of grain.

4. Dormancy: the seed and the environment

4.1 Seed dormancy in cereals

Since most species show a degree of seed dormancy, it is not surprising that a number of highly diverse mechanisms may be found in the plant kingdom. Several comprehensive reviews of seed dormancy as a whole have been published including those of Bewley and Black (1982), Maguire (1975, 1976, 1980 & 1984), Roberts (1972), Nikolaeva (1969) and Barton (1965). Although some authorities have listed as many as ten separate causes of dormancy it is sufficient to cite Maguire (1975) to illustrate the breadth of the subject. Six possible causes of seed dormancy are:

1. Embryo immaturity
2. Impermeability of seed coat
3. Germination inhibitors
4. Physiological immaturity
5. Light sensitivity
6. Mechanical restriction by the seed coat

Further subdivision of the causes of dormancy is possible by a distinction between the embryo and the remainder of the seed. Environmental effects provide another heading under which to classify dormancy systems.

Cereal dormancy involves causes 1 - 4, and these have been the subject of considerable research work and debate for many years, certainly from the early part of this century. Little evidence of light sensitivity in cereals has been found although the available evidence is insufficient to dismiss the possibility that certain soils, particularly those with a high sand content, may allow the entry of light and could therefore modify germination or emergence in light sensitive species, although it must be emphasised that work appears to be needed to demonstrate this possibility in cereals. Mechanical restriction by the seed coat is not known to be a cause of cereal seed dormancy. It is important to appreciate that more than one cause of dormancy may be involved at any one time.

What is it within the seed which blocks germination? Any investigation into the causes and management of innate or induced dormancy in cereals must recognise and seek to understand the biochemical basis of environmental effects. The generally accepted view is that chemical inhibitors acting on the mobilisation of reserves are responsible for much innate dormancy in wheat and barley. These inhibitors are thought to be present in the pericarp, testa and tissues of the spikelet (Corbineau *et al* 1984). Côme and Corbineau (1984) considered that the pericarp and testa were the principal source of inhibitors in wheat whereas the lemma adopted this role in barley. There is, however, evidence that each source is capable of providing inhibition in both species. In wheat, the grain is normally threshed out of the spikelet, although the residues of tissues, such as the lemma, may be retained in the vicinity of the shed grain. Phenolic compounds appear to be involved in this form of dormancy but other compounds produced within the grain are also responsible for inhibition of germination.

Three stages in the germination of cereals have been identified. First, during the later phases of seed growth there is a gradual increase in the number of seeds which have the capacity to germinate. In certain respects, this may be regarded as a continuation of the development of the seed. Secondly, as maturity approaches, germination decreases and dormancy sets in. Thirdly, dormancy is broken by a combination of the passage of time and the effect of certain environmental conditions (Villiers 1972).

Dormancy imposed by seed coat

Many investigators have confirmed that the seed coat is responsible for an inhibitory effect in developing and harvest-ripe grain. Such inhibition of germination can be caused by the inner layer of the green pericarp of wheat, removal of covering layers allowed germination of immature grains to take place (Wellington 1966). During the later stages of maturation, the outer pericarp layer exercises a similar control. More recently in the USA, McCrate *et al* (1982), found an endogenous inhibitor in each of 18 red-grained varieties of wheat tested. As with Wellington's work noted above, removal of the covering layers significantly increased germination response. Experiments of this nature involve difficulties in excluding a possible mechanical effect on the seed coat caused by removal of tissue. However, the weight of evidence strongly supports the existence of biochemical inhibitors in the coat and generally indicates that the quantity of these vary with variety. Many have commented on this aspect, for example, Ringlund (1987) who considered that inhibitors in barley gave rise to dormancy by suppressing enzyme production.

The possibility that the seed coat causes dormancy by inhibiting the passage of oxygen, to the seed appears not to have been supported by experiments carried out under conditions which simulate the field.

Embryo dormancy

The literature on cereal dormancy includes a preponderance of references to the influence of inhibitors produced outside the embryo. Obviously this does not preclude a germination controlling role for this organ. For example, McCrate *et al* (1982) found that wheat embryos differed in their response to germination inhibitors and Gale *et al* (1987) postulated that GA released from the embryo may control certain phases of germination.

Germination inhibitors in the spikelet structures

Hutchinson *et al* (1948) observed that grain still attached to the ear sometimes germinated more slowly than threshed samples which they interpreted as indicative of an inhibitory influence of the ear structures. This finding was confirmed by Wellington (1966) who used aqueous extracts of glumes to inhibit germination with differing results between varieties. The application of ground tissue from the spikelet by McCrate *et al* (1982) was also sufficient to cause dormancy. As with the work of Wellington, the effect varied with the recipient variety. However, McCrate *et al* noted that the effect of glume extract was generally not as great as that produced by inhibitor extracted from wholemeal flour. At harvest maturity, a mean germination for untreated grain of 67% was recorded compared with 41% for the grain treated with extract from the ground tissue. These differences were not so marked after 4 weeks when 9% separated treated and untreated samples. Gibberellic acid counteracted the effect of the inhibitor as far as seed germination was concerned. Further evidence may be obtained from Strand (1980) who also postulated an inhibitory role for "chaff structures" in cereals generally and the white wheats in particular.

Additional support for the presence of inhibitory factors in the spikelet structures may be derived from the naked grain characteristic which is believed to reduce dormancy in certain varieties of barley and oats (Gale 1988). Investigations in Canada (Harvey *et al* 1983) were carried out on barley using a parent with naked grains in a crossing programme with hulled varieties. The resulting naked segregates exhibited low dormancy whereas the hulled segregates included genotypes with high dormancy. This leads to the conclusion that the lemma and palea of barley form at least one of the factors responsible for dormancy. This was supported by removing the hulls from normally hulled lines with a resulting reduction in dormancy. Further work indicated that the loosely attached lemma and palea of naked varieties do, in fact, have germination inhibitors, although they are normally ineffective in this type of variety after harvest since these structures are lost. Other workers, for example, Haferkamp *et al* (1953), have found similar results.

Triticum spelta has a tightly affixed glume and lemma. It is interesting that it is cultivated in areas of Europe which frequently suffer from uncertain harvest weather. The morphology of the spikelet may be beneficial to grain quality in the adverse climate.

4.2 The environment of the developing grain

It is very clear that the environment has a profound effect on the incidence and degree of dormancy in a very wide range of plants (Vegis 1964). It therefore follows that dormancy will vary with season, attempts to manipulate this characteristic must therefore take account of environmental variation. Moreover, since it is neither practicable or desirable to attempt to eliminate dormancy, a greater understanding of environmental effects will assist in reducing the associated problems to a minimum.

Temperature during grain development

Comprehensive studies of the effect of pre-maturity weather conditions on dormancy in wheat were carried out in the Netherlands by Belderok (1961, 1965) and Belderok and Habekotté (1980). Extensive investigations indicated, in agreement with widespread belief, that the level of dormancy in the developing grain was influenced by temperature. The critical growth stage sensitive to temperature was found to be doughy ripeness. The dormant period within a variety declined as the sum of the daily mean temperature increased above 12.5°C.

These findings are supported by work on wheat in the UK by Black *et al* (1987). Additionally, investigations on barley in Norway (Reitan 1987; Ringlund 1987), in Ireland (Curran and McCarthy 1986) and in Japan (Takahashi 1980) have also demonstrated that cool temperatures during ripening, encourage the expression of dormancy after grain maturation. Many earlier investigators also demonstrated that dormancy in wheat and barley was induced by low temperatures.

Since there is no sharp division between dormancy and non-dormancy, the climatic effect may be expressed as relative dormancy which could be described as sensitivity to germination temperature. Rauber (1986) confirmed a greater degree of sensitivity to germination temperature in seeds of barley which had developed at a low temperature.

The effect of heat at other stages of growth was investigated by Belderok (1961) who reached the conclusion that level of temperature did not affect the establishment of dormancy until the doughy ripe stage was reached. Reiner and Loch (1976), however, found evidence in barley of an earlier heat sensitive phase with high temperatures 12-16 days after ear emergence causing longer periods of dormancy (Figure 1). It has not been possible to find further experimental evidence of this reversed heat effect in wheat or barley.

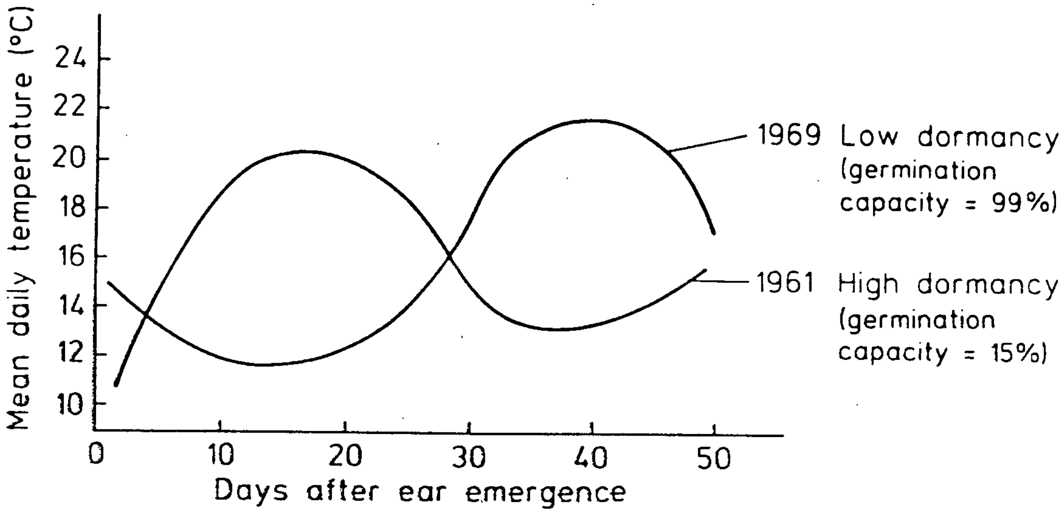

Figure 1. Mean daily temperatures during barley grain development in two separate years with different dormancy levels. Germination tested three weeks after harvest maturity. After Reiner and Loch (1976).

A note of apparent disagreement with the generally accepted view that hot conditions late in grain development reduce dormancy expression was given by Gordon (1980) in Australia. He reported that embryo dormancy was actually reduced after cool ripening periods in certain varieties which exhibited dormancy after warm ripening. This was considered to indicate that the low germinative energy observed in other varieties after cool ripening was due to embryo immaturity, a view which appears not to have been expressed in Northern Europe.

Moisture and the developing grain

Although it is difficult to separate the effects of moisture and temperature, a number of successful investigations have been carried out. Belderok (1961) concluded that the establishment of dormancy was unaffected by degree of water availability *per se* nor relative humidity during the doughy ripe stage affected dormancy. Schrödter and Grahl (1978), however, felt that the influence of relative humidity was of sufficient importance to warrant being taken into account in a PHS and dormancy forecasting scheme. Moreover, Wellington (1966) noting that germination in the immature wheat grain did not occur whilst the inner pericarp remained green, considered that drying of the grain during ripening might lead to a disruption of the covering tissues of the embryo permitting germination to take place. He felt that the degree and rate of drying during ripening could affect dormancy expression in wheat and barley.

Disagreement in findings associated with climate are usually resolved when the factor under dispute is separated from all other factors which inevitably accompany it. Even if moisture fails to affect dormancy under a particular experimental regime, it is possible that concomitant temperature effects will be a source of apparent disagreement.

Differences between varieties in dormancy expression may arise from variation in moisture availability. Varietal differences in the pericarp may have a modifying role and other seed structural variations may also affect water movement and this could contribute to the range of dormancy found in wheat varieties. These points, however, need confirmation.

Mitchell *et al* (1980a) agreed that the drying of the pericarp, which begins a few days after anthesis, forms the principal event preceding germination. It is thought that drying may reduce inhibitory tendencies within the pericarp, a process which starts during the earlier stages of grain development. After the pericarp has begun to dry, the water content of the rest of the grain continues to increase. This is reflected in the overall water content illustrated in Figure 2. The high water content noted here during the early post-anthesis stage of high germinability would not have been typical of a pericarp which had already started to dry. Following this stage, germination declines for a period due to the influence of inhibitors within other tissues.

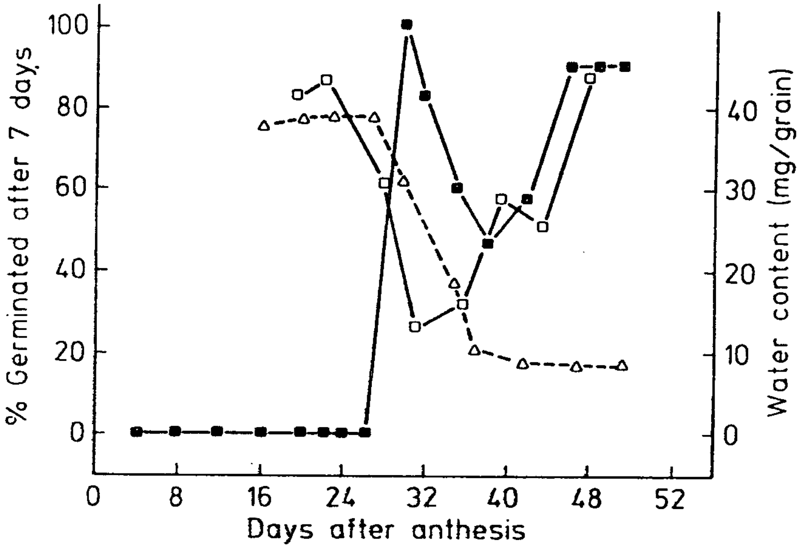

Figure 2. **Germinability of maturing wheat grains (cv. W42). Grains were taken from the ears of field-grown wheat from 4 days after anthesis until near harvest-ripeness and their germinability tested (■ - ■). From 18 days after anthesis grains were collected and dried at room temperature down to 10%- 15% water content (this took up to 7 days) and then tested for germinability (□ - □). Germination tests were done on both types of grain at 20°C for 7 days. The water content during natural drying is also shown (△ - △). After Mitchell *et al* (1980a).**

Chemical applications

Recently there has been interest in the effect of nitrogen and fungicidal treatment on Hagberg Falling Number (HFN) and breadmaking quality. It appears that these treatments could affect the moisture relations of the grain during maturation. It is possible that an increase in moisture during grain development could promote dormancy at harvest ripeness although, as already discussed, it is recognised that there is disagreement regarding the role of water.

High rates of nitrogen application can, of course, cause lodging and the effect of this on PHS will perhaps depend on the growth stage and the dormancy status of the grain at the time. PHS will occur in certain instances but in others, dormancy may accompany lodging if there has been a long cool period. The question of a more direct effect of spring nitrogen on α-amylase and dormancy has not been fully resolved, although there are reports of nitrogen reducing α-amylase activity. Gooding *et al* (1986) and Stevens *et al* (1988), have provided examples of HFN increasing after higher nitrogen treatments, a conclusion which appears to be the predominant view although the reverse has also been found. Variation in dormancy status of the grain tested could be a source of disagreement and interactions with environmental factors must be taken into account. The literature sources do not permit a confident view regarding the direct effect of nitrogen on dormancy.

There is evidence that, in general, plant senescence is delayed by fungicides (Priestley and Bayles 1982). Fungicides, by maintaining the area of green leaf, appear to reduce the speed of drying of the grain during the final phases of development. Morgan *et al* (1986) reported that a reduction in HFN has been associated with fungicide application although the opposite effect has also been observed. Fungicide application reduced HFN in the investigations of Davies *et al* (1986) who noted that this effect was particularly apparent in years which encouraged high α-amylase activity. The hypothesis that the rate of drying of the grain could be modified by fungicide application was discussed by Gooding *et al* (1987). Although more work is clearly required on this subject, investigations have shown that fungicides, in certain circumstances, are associated with an increase in α-amylase activity. It may also therefore be possible to demonstrate an influence on the dormancy of the grain. On the other hand, it is also possible that certain fungicides may have a direct regulatory effect on germination control mechanisms: for example, as noted under section 8.5, fungicides may have a bearing on cytokinin activity.

Pre-harvest sprouting

Section 4.2 has been concerned with the way dormancy status is decided during the development of grain for later expression. Other effects of moisture and temperature have also been investigated by many workers, for example, the work on the germination of grain prior to harvest-ripeness. There will be instances where PHS will occur in this way but since shed grain is normally harvest-ripe, the germinative ability of grain before this stage is considered outside the remit of this review except where the ability to sprout has a direct bearing on the choice of variety.

4.3 Factors affecting the harvest-ripe grain

Grain in the field

In general, it has been found that the dormancy of grain in the field tends to be more prolonged than in stored grain (Belderok and Habekotté 1980). One result is that, as noted by Christian *et al* (1985), shed grain often germinates just before the following crop is sown. Although there may be a number of reasons for grain showing a different level of dormancy in the field compared with the store, the moisture regime is perhaps the most obvious. This was demonstrated in one variety 80 days after anthesis by Belderok (1961). In this instance, the level of germination increased from 35% to 98% where the moisture content of stored grain was halved (to 8%). Wet periods following harvest may therefore encourage retention of dormancy whereas hot, dry post-harvest conditions will not, although timely germination may be prevented by a lack of moisture. Dormancy in Belderok's experiments was also more prolonged after cooler temperatures (8°C compared with 25°C) .

In some respects, Belderok's experiment highlights the difference between grain in the field and that which has been in dry storage, showing that care must be applied when attempting to extrapolate between stored seed and shed grain. Moreover, as was pointed out for barley by Ellis *et al* (1987), the germination characteristics of stored grain are subject to considerable variation largely dependent on dormancy status which, as already noted, is very sensititive to seasonal effects.

Brown *et al* (1948) supports the finding that cool, moist conditions maintain dormancy. They reported instances where the seed of oats and barley retained dormancy for three years when stored at 2°C under "relatively high" humidity. This should not be confused with the chilling effect used to break dormancy in the seed germination test specified by international rules (International Seed Testing Association 1985). Essentially, the test examines seed which has received some after-ripening. In this situation, chilling is used as a 'trigger' rather than to promote seed development. For the purpose of the test, temperature effects are reversed with a cool period being used to break dormancy. Mares (1984) also reported that a regime allowing stratification (variation of temperature) with a cool period, lasting at least two days, is likely to promote a germination response in imbibed grain. Several workers (Black *et al* 1987; Gosling *et al* 1981) have shown that non-after-ripened grain will express relative dormancy at high temperature (20-35°C) whilst a low temperature (5-15°C) tends to break dormancy.

The need for after-ripening

Bewley and Black (1982) cited work which indicated that coat-imposed dormancy in wheat may last 3-7 months in dry storage, depending on variety. The period for barley ranges from 0.5-9 months. The reason seed will germinate before this period has elapsed may be ascribed to the chilling treatment of the germination test or the effect of placing grain in cool soil. As mentioned in the introduction, it is not correct to describe dormancy as an 'all or nothing' situation. The increase in germinative energy is, in fact, normally progressive.

The topic of after-ripening was discussed by Barton (1965a) who noted that it was, in particular, a requirement of many of the grasses. Stokes (1965) considered the factor of temperature and its relationship to after-ripening and Shands *et al* (1967) reviewed the literature regarding the effect of different storage treatments on germination of barley. Although, as already stated, dry storage of grain will not lead to the same results as apply in the soil, certain relevant principles emerge. Barley, for example, is rarely 'physiologically' mature when combine harvested and therefore storage conditions are critical. Warm, moist storage is, of course, detrimental to the retention of viability. Rauber (1986) found that winter barley which had been subjected to low temperatures during seed development required 12 weeks after-ripening in dry storage compared with six weeks for seed which had developed during hot conditions. Clearly, the factors of temperature and moisture are inextricably linked in their effects on germination.

The need for artificial after-ripening does not, of course, normally arise in the UK, although it is necessary in certain more northerly latitudes. The calculation of a dormancy index to assess this was discussed by Strand (1965). In Norway (Arne Wold, personal communication) seed processors routinely after-ripen seed by warm storage at 20°C for a period calculated by using a dormancy index as follows:

$$\mathbf{Index} = \frac{2\,(\,a + b\,)}{3}$$

where a = % fresh ungerminated seeds at 10°C
b = % fresh ungerminated seeds at 20°C

Instances of dormancy in seed affecting crop establishment have also been reported in more temperate climates, for example, for a wheat variety in New Zealand (Young 1985). Although a situation of this nature appears to be exceptional, it provides an indication of the degree of dormancy that *Triticum aestivum* is capable of. However, there is considerable experimental evidence of the need for natural after-ripening of a lesser order across the species. For example, Gosling *et al* (1981) found that wheat grain germinated more quickly at 50 days after anthesis, compared with a period of 40 or fewer days (Figure 3). In this investigation it was found that after 63 days, dormancy was much less evident and it was possible for the grain to germinate without chilling.

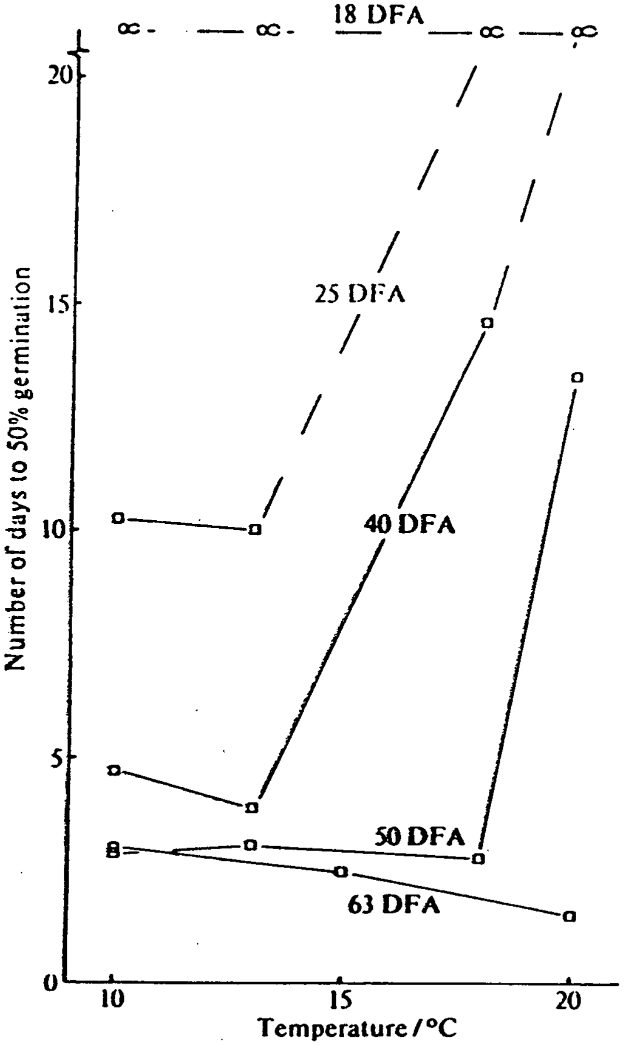

Figure 3. **The effect of temperature on the mean germination period of grains harvested at different ages (DFA = Days From Anthesis). After Gosling *et al* (1981).**

As would be expected, after dormancy has been removed by storage and possibly drying, the speed of germination is increased as temperature of the test rises (Mares 1984). Instances have been reported, however, where immature grain has expressed better germination at high temperature (Strand 1965).

The effect of moisture on after-ripening and germination

The breaking of dormancy, as noted above, is affected by the amount of water present. Wellington (1956a), for example, found that further desiccation of harvest ripe grain was required to break dormancy during after-ripening. This work included a comparison of the germinative energy of grain stored at 10% and 19% moisture (maintained by adjusting relative humidity). The length of this phase ranged from 13-23 weeks after anthesis depending on variety, the weather prior to harvest and position of the grain on the ear (also noted by Hardesty and Elliott 1956). Storage at 10% grain moisture permitted 95% germination whereas 19% grain moisture reduced this to 62%.

The work of Woodbury and Wiebe (1983a & 1983b) suggests differing total moisture requirements for germination depending on the temperature and whether the supply of moisture is continuous. More work would be needed to identify trends although it did appear that any potentially active inhibitors will be most effective if water is plentiful, since this will allow the inhibitor to move around the grain more freely. Dormancy will therefore be more strongly expressed under high levels of moisture. If, however, innate dormancy has been lost, the optimal level of moisture for maximum speed of germination will be greater. However, not all workers are agreed on the role of moisture in dormant grain. Strand (1965) found differences in moisture of little significance in breaking dormancy.

The effect of leaving grains on the soil surface to face exposure to periods of rain interspersed between drying conditions may lead to stimulation of germination. Reasons for this include temperature variation and a possible cracking of the covering layers caused by cycles of wet and dry conditions. This question needs investigation since the answer could affect cultivation policy.

It is customary to partition water uptake by the developing grain into three physiological phases, known collectively as the ***triphasic*** pattern (Bewley and Black 1978; Takahashi 1979). These phases are: imbibition, activation and germination and are illustrated in Figure 4. Those seeds requiring a long activation stage are said to be partially dormant.

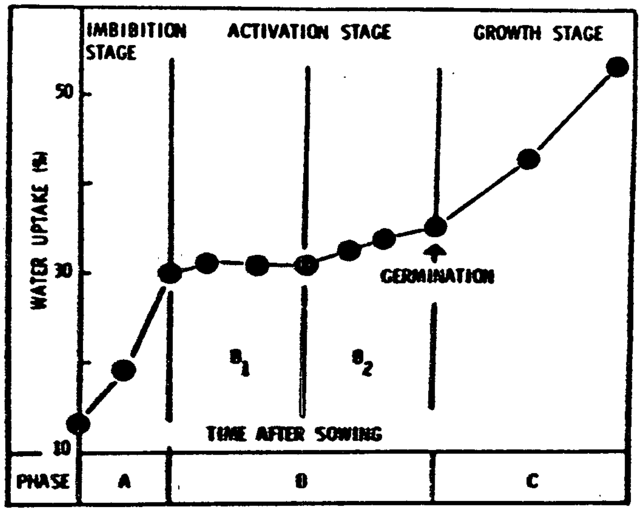

Figure 4. The triphasic pattern of water uptake in germinating cereal seeds. After Takahashi (1980).

The management of shed grain

The foregoing summary of environmental effects indicates that it is necessary to distinguish between grain buried within the soil and grain which lies on the soil surface. Theoretically, ploughing and other forms of cultivation, soon after harvest, are likely to encourage the retention of innate dormancy or the establishment of induced dormancy by placing the grain within a cool, moist environment. Bewley and Black (1982) discussed the role of oxygen in after-ripening and noted that the process in rice and wild oats is accelerated when oxygen levels are raised above normal. It is therefore possible that after-ripening could be retarded if the oxygen supply to buried seeds is reduced in wet soils, although this would be infrequent.

How can shed grain be managed to promote early germination? Clearly, after-ripening must be encouraged and this could occur on the surface of the soil in dry, warm post-harvest conditions. During this period the grain will tend to equilibrate to the moisture content of the surrounding atmosphere and will therefore be affected by relative humidity and the moisture level of the soil surface.

Although the time available for germination would be short, a later stubble cultivation could provide any remaining, after-ripened, grain with a cool, moist environment to 'trigger' germination (Wellington 1966). By contrast, grain placed within the soil shortly after harvest, before after-ripening had occurred, would presumably show delayed breaking of dormancy without any germination until after the following crop had been drilled.

There are, however, two problems which handicap attempts to manipulate shed grain in this way. First, there will be varietal and seasonal differences in the time taken to reach the critical stage at which germination begins. Secondly, it will be necessary to consider the question of straw residues since these are believed to affect seedling growth. As will be described in a later section, incorporation of straw could impair the emergence, not only of volunteer cereals, but also of the succeeding crop. This difficulty is largely removed by the practice of straw burning. It should also be noted that any grains deeply buried by any form of cultivation will be placed under enforced dormancy, a situation discussed elsewhere.

Induced dormancy

The investigations of Belderok and Habekotté (1980), in agreement with Wellington (1966), demonstrated that harvest mature, non-dormant grain can become dormant in a cool, moist environment. During 1977, germinative energy 57 days after harvest maturity typically declined from 90% to 30%. This reduction coincided with unusually low temperature and high relative humidity which was clearly the result of unseasonal weather, also a constant risk in the UK.

4.4 Growth stage, date and environment

The period between anthesis and harvest ripeness may be significant in relation to the development of dormancy. Working with Australian varieties, Gordon *et al* (1979), observed a trend for varieties showing late anthesis to take less time for the final development phase. This may have been due to hotter conditions for these varieties compared with those which reached the same stage of development earlier in the year. Although the climate of the United Kingdom is unreliable, it is possible that relative maturity could affect a variety's exposure to temperature effects and, consequent to this, the expression of dormancy. Differences of this nature would, of course, have no direct genetic origin.

Time of drilling may be relevant to the question of the severity of a volunteer problem in a number of ways. Graham *et al* (1986) reported work which suggests that late sowing increased the competitiveness of volunteer plants. This could well be a result of a greater age gap between volunteers and sown crop with the additional effect of late sowing being less conducive to crop establishment. It is also likely that late attempts to destroy unwanted cereal plants through normal cultivation techniques will be less successful since soil moisture levels will have increased with the advancing season. Obviously total herbicides could be used but this would have economic considerations.

4.5 The feasibility of forecasting degree of dormancy

Forecasting would assist in the management of shed grain by identifying fields at risk in time to influence management plans. Provision of a warning system in the UK could assist in the management of three potential problem areas: malting barley, PHS and shed grain. It might also be feasible for this to be combined with a regional field assessment of the dormancy of shed grain, for which a reliable monitoring system and sampling method would be needed. Forecasts could modify arrangements for straw disposal, cultivation and other aspects of agronomy. In addition, advice relating to the relationship of climate to innate and induced dormancy would be useful. There is also a need for growers to be more accurately informed about the condition of the fields selected for quality production. Allied to this, guidelines for the evaluation of the amount of shed grain by growers are needed to enable field management and use to be more meaningful.

For a number of years, growers in certain countries, including West Germany and the Netherlands have benefitted from regional warnings of dormancy and risk of PHS during the harvest period (Belderok and Habekotté 1980). This information is based on the number of accumulated 'day degrees' during the doughy stage. Belderok (1965, 1968) described a system for warning growers of the likely level of dormancy and tendency to sprout. This forecast was based on the number of temperature degrees exceeding a base level of 12.5°C during the doughy-ripe stage. In West Germany, the likely duration of dormancy in malting barley is also assessed and made known as a service to maltsters. This prediction is based on the number of days with a temperature above 20°C during the second half of grain development.

In Norway (Strand 1983) it was felt that predictions could be based on twice weekly monitoring of dormancy development in the field, a system which could be considered for the UK. Schrödter and Grahl (1978) discussed the relationship of moisture to these predictions. Reiner and Loch (1976) described two temperature sensitive periods in barley, but did not indicate how allowance should be made for the first of these periods in forecasting dormancy. Others who have commented on the forecasting of dormancy and have highlighted some of the problems include: Olsson and Mattsson (1976) and Lallukka (1976).

The need for farmers to be offered, prior to harvest, a prediction of the quality of grain has been identified by Stevens *et al* (1988). It has also been suggested that if seasons with a high risk of sprouting could be predicted, growers could then avoid PHS by harvesting early. Mitchell *et al*

(1980b) discussed this proposal, pointing out in agreement with Reiner and Loch (1976), that observations would need to begin soon after anthesis since some of the predictive methods would otherwise fail. They also believed that considerable work would be required to refine the techniques used in continental Europe since these may be unsuitable for the UK in their present form. However, little further work has since been reported. Irrespective of developments in this area, it is unlikely that this approach would allow varieties with lower resistance to PHS to be adopted.

4.6 Recommendations for research

1. Confirmation of the dormancy mechanism of cereals is necessary to provide a sound base for applied research and the development of means to manipulate the biology of shed grain. The identity, site of origin, and mode of action of inhibitors should be established. Since genetic and environmental variation has led to dispute regarding the relative importance of the known inhibitors, these investigations should be carried out using material of different varieties, grown under a wide range of environments.

2. Consideration should be given to the possibility of using extracts of the spikelet tissues, or formulations of the chemical inhibitors involved, as a spray for the control of PHS without increasing dormancy. Such a route should be environmentally acceptable since 'natural' compounds would be applied. The use of selective sprays to control volunteers has not been considered under the remit of this review. Control by these means would clearly be difficult since, not only is selectivity between species needed, varietal contamination also requires elimination to prevent detrimental effects on grain quality.

3. The influence of the application of nitrogen and fungicide on the development of dormancy should be examined with particular attention to the speed of natural drying of the grain. Since current levels of crop

treatment are a fairly recent innovation, relatively little is known about this aspect.

4. Despite the legacy of research, there are still areas of disagreement regarding the effects of moisture and temperature on the establishment of dormancy. Answers to these questions should be sought to assist growers' understanding of the state of shed grain in their fields.

5. After-ripening requirements for shed grain in the field should be measured. Consideration should be given to how post-harvest field management might be directed to meet these needs. What is the effect of burying dormant grain directly after harvest? Is the date of sowing the next crop important?

6. A feasibility study is needed of the suitability of weather reports as a basis for regional forecasts of conditions likely to cause dormancy. This would enable growers to plan field management and use. Consideration should be given to the possibility of regional assessments of typical levels of dormancy in shed grain.

5. The longevity of cereal seed

5.1 The longevity of buried seed

For centuries, seed longevity has been the subject of mystery, speculation and extravagant claims, many of the latter being based on flimsy, circumstantial evidence. Certain groups of plants do indeed appear to have great seed longevity; this is particularly true of those with impermeable seed coats. It is clear, however, that seed longevity cannot only be explained in terms of the impermeability of the seed coat (Barton 1961). Although extended viability in damp soil is sometimes difficult to understand, in certain species imbibation will actually reduce deterioration of the seed.

Anderson and Baker (1983) reviewed the mechanisms of seed deterioration and concluded that, although certain predisposing environmental factors were identifiable, the underlying biological cause of the loss of viability is unknown. It may be that metabolites are leaked or incorrectly placed as a result of a loss of the integrity of membrane systems, these possibilities are supported by Wilson and McDonald (1986) who reviewed a lipid peroxidation model of seed ageing.

The relationship between dormancy and longevity

Little evidence has been found to suggest that innate or induced dormancy promotes longevity in seeds although Lewis (1961) considered that termination of such dormancy preceded loss of viability in certain non-cereals from amongst those species which express long dormancy. The review of Roberts (1972) failed to demonstrate that such a relationship existed, although more investigational work would be needed to exclude the possibility that soil-borne seed of cereals could retain viability for a longer period if in a state of innate dormancy when buried. This is an important question since, if such a relationship exists, after-ripening prior to burial could reduce longevity.

The physiology of buried seed

Under the typical conditions of Northern Europe, a seed buried too deeply in the soil for germination to occur is usually imbibed but is in a state of enforced dormancy (Roberts 1972): this condition is sometimes described as *quiescence*. Despite this term, the seed is not metabolically inactive even in the absence of growth. As a living organism, it is capable of life-supporting processes including respiration and other metabolic activity. It is also considered that the repair of membranes and cell structures is possible, to a degree, in imbibed seeds (Ross 1984; Villiers 1975), but the biochemical evidence for this is, however, incomplete. For a detailed description of these topics see Bewley and Black (1982).

Timespans

The traditional belief that cereal grain will not retain longevity in the soil for more than a year now appears unlikely (G.W. Cussans, personal communication). It is, however, sometimes difficult to exclude a contribution to a volunteer problem from grain produced and shed from volunteer plants growing in a rape crop, for example. This could be significant when the maturity of volunteers fails to coincide with the intended crop leading to further shedding. Unproven reports suggest a lifespan in the soil for up to five years although longevity of this order will rarely create serious admixture problems.

Clearly the longevity of cultivated cereals should be verified to enable the risks to be assessed. Moreover, since longevity will obviously vary, growers need a reliable method of determining whether the soil in a particular field is likely to contain viable seeds. The provision of guidelines, by which the history of the field may be interpreted, should be considered despite the obvious difficulty of quantifying small environmental effects on the soundness of grain at the start of burial. In view of the possibility that innate dormancy has little influence over longevity, there is a need to identify the soils, cultivation systems and cropping patterns which favour the preservation of viability of soil-borne cultivated cereal seed. This should assist choice and management of fields for quality seed and grain production.

The differences between cereal species

As already mentioned, little substantiated evidence exists for the longevity of cereals in the soil and it is therefore impossible to give a clear picture of differences between crops. Unconfirmed reports suggest that longevity of wheat grain in the soil can extend to five years. Since barley straw is more widely used as bedding, it is often not easy to be certain that contaminating plants have not arisen from farmyard manure. For practical purposes. a three year maximum survival period seems reasonable for barley grain in the soil. Oats, from casual observation, appear to have the greatest longevity of the cultivated cereals with emergence being claimed after five years burial and it is likely that wheat falls between these two.

5.2 Factors affecting longevity

The environment

A single environmental cause for loss of viability of seed in the soil is not evident from the literature. Many of the suggested reasons are probably valid but there is disagreement regarding their relative importance. An improved understanding of the many factors involved is clearly essential if the longevity of shed seed is to be reduced to the minimum by soil management.

Germination is one of the major causes of loss of deeply buried seeds of plant species according to Roberts (1972). This is supported by Lewis (1961) who reported a seed loss of wheat and oats from germination *in situ* after two months' burial in three soil types. Despite this finding, it is clear that many cereal seeds succeed in avoiding germination. There may, however, be a depth in the soil at which enforced dormancy is lost but from which the germinating seedlings are unable to emerge and this may lead to an overall loss of viable seeds from the soil. Whilst recognising the lack of fully confirmed reasons for the phenomenon, the ability of enforced dormancy to prevent the germination of cereal seed through a full seasonal cycle has to be accepted.

As noted by Khan (1977), there is clearly a metabolic block, preventing germination of seed deep in the soil and this is not fully explained by temperature and moisture since, as pointed out by Roberts (1972), these are often suitable for germination despite fairly deep burial. Lewis (1961) felt that soil temperature did not have much direct influence on longevity provided it was stable. The opposite situation of fluctuating soil temperature could act as a 'trigger' for germination. It would therefore be worthwhile to consider a system to optimise cultivation of land containing buried cereal seed in order to promote either deterioration or germination prior to final cultivation. This would have a particular application to cases where seed, shed in the previous season, had retained viability.

Physical seed damage, caused by weather conditions or harvesting, undoubtedly reduces longevity of cereal seed in the soil (Barton 1961). Obviously, deterioration will involve changes to cell and/or tissue structure and may include the degradation of proteins and seed reserves, with implications for seed hormones and enzymes. For a fuller review see Bewley and Black (1982). Tran and Cavanagh (1984) also reviewed the work relating to the difference between the seed stored under dry conditions and that deposited in the soil.

Some have proposed that oxygen or carbon dioxide may play a part in determining seed longevity but Roberts (1972) did not consider these to be significant. According to Villiers (1973), however, there is reason to believe that low concentrations of oxygen could reduce the ageing process by retarding the activity of dormant seeds, a point discussed by Lewis (1961). The question of the influence of oxygen availability on germination will be discussed in section 8.4.

The chemical status of the soil may merit investigation for a number of reasons including the effect of the application of nitrogen on microorganisms. This might be responsible for promoting the growth of organisms with possible differences arising from the form of nitrogen. There is also evidence that nitrogen could stimulate the breaking of dormancy in some species although cereals were not mentioned by Roberts (1972). The action of herbicides could also be considered.

Microorganisms affecting seed in the soil

There are two ways microorganisms can affect seed in the soil. First, deterioration may result from fungal activity leading to decomposition. Secondly, microorganisms could modify the availability of resources, such as oxygen, for the seed which is otherwise ready to germinate.

As might be expected, there is good evidence that soil microorganisms are detrimental to seed longevity. Cherry (1983) indicates that microorganisms can assist in the degrading of seed proteins. Apart from differences in the severity of attack arising from soil type, climate may also be a source of variation. In this respect, the results of an investigation of maize seed by Harper (1955) are interesting. Mortality, largely due to fungal activity was evident and although damage did occur in hot/dry and cold/wet conditions, the greatest losses occurred under conditions of temperature and moisture just below those required for germination. This finding is in line with Barton (1961) and Cherry (1983) who also considered that moisture and warmth would lead to the greatest harm to seed longevity from fungal attack. This point may merit consideration when scheduling cultivation programmes aimed at reducing the viability of soil-borne seed.

Varieties may differ in their response to soil microorganisms as was postulated by Whittington (1973) and Halloin (1983). Seed in the soil stimulates the germination of microbial propagules according to Harman (1983) who also notes that poor quality seed is particularly prone to do this. The seed coat is of special importance in resisting deterioration (Halloin 1983) and this may therefore be one of the reasons for variation in resistance to soil microorganisms.

It is possible that certain microorganisms could be active under anaerobic conditions, further reducing the low germination associated with such a state, a point supported by work at the Letcombe Laboratory (Lynch *et al* 1976; Lynch *et al* 1977; Lynch and Harper 1978). These reports suggest the involvement of saprophytic fungi with an interaction with bacteria: Figure 5 illustrates an apparent association between reduction of germination and competition with microorganisms for soil oxygen.

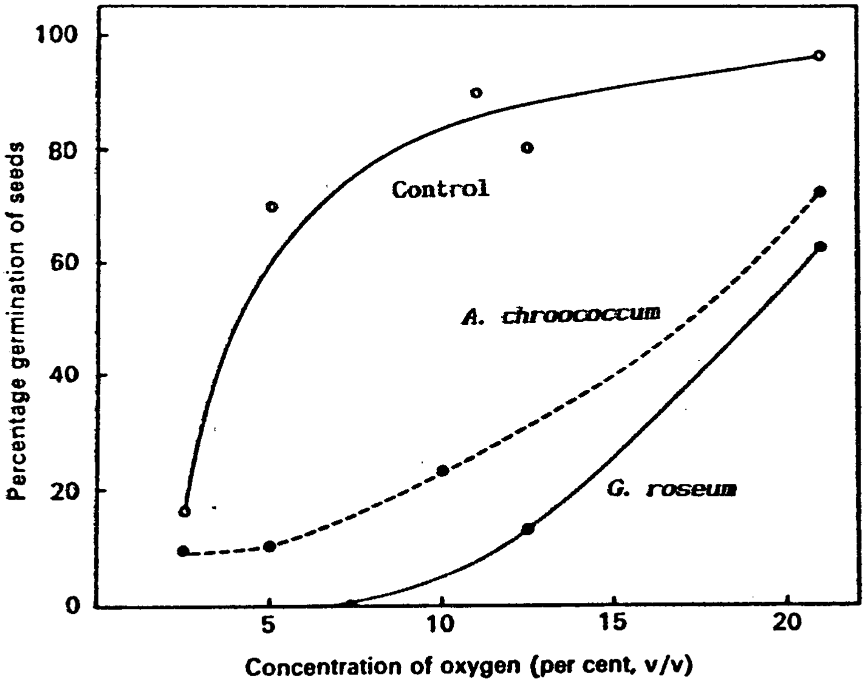

Figure 5. **Effect of a bacterial species (*Azotobacter chroococcum*) and a fungus (*Gliocladium roseum*) on the germination of barley seeds at 20°C in different concentrations of oxygen. After Lynch *et al*** (1977).

5.3 Buried seed experiments

Successful investigations of longevity in the soil at the varietal level in cereals do not appear to have been conducted. By contrast, the longevity of certain plant species such as *Avena fatua* have been the subject of successful investigations and considerable discussion. However, since varieties of wheat and barley vary for many biochemical and morphological grain characters, differences in longevity in soil are likely. In many species of plants, the seed coat is a particularly important defence against seed deterioration since, as already noted, this structure controls nutrient loss and the entry of microorganisms (Halloin 1983).

Kjær (1940) carried out an experiment, designed to last five years, in which seed was buried 25 cm below the soil surface. The seed used for this had been dry stored from harvest until burial which took place during the following May. This work therefore should not be directly related to the question under review since the period of dry storage would result in abnormal degree of after-ripening, making comparison with naturally shed grain difficult. The results for wheat and barley appear inconclusive since no seeds germinated after one year of burial. Lewis (1958) reported the results of the first four years of a 20 year investigation of the longevity of buried crop and weed seeds. Little cereal seed remained viable after four years. Lewis found that hardly any barley germinated after two years whereas a trace of wheat and 3% of oat seed was viable at this stage. The remaining years of this experiment did not yield further information relating to cereals.

In her review of longevity in seeds, Barton (1965b), found little evidence for the survival of cereal seeds in soil irrespective of the depth of burial. The investigations carried out lead to the conclusion that the routine survival of buried cereal seed for several years should not be expected. This does not, however, preclude survival for more than 12 months which is likely to be a cause of cereal volunteers.

5.4 Longevity in dry storage

The cultivated cereals in practice have a shorter viability expectancy than many other species. However, at the extreme, it is believed that barley seed in ***dry storage*** has remained viable for 123 years whereas the longest proven record for wheat is 25 years. The aspect of exceptional longevity is obviously outside the remit of this investigation: those who are interested are directed to the review by Toole (1986).

Reports indicate that wheat and barley are similar in longevity in dry storage. Oats appear to have the greatest longevity and rye the least (MacKay and Tonkin 1967; Lewis 1958). The metabolic status, however, of imbibed seeds will obviously be very different from that of seeds in dry storage.

Genetic variation in the longevity of stored seed has been considered likely. This has been reported for wheat (Thomson 1979). Work with maize and, less convincingly, with peas supports this (Whittington 1973; Ashton 1956). The review of Justice and Bass (1978) gives general support for varietal variation in seed longevity in dry storage. Variations in longevity in the dry state are thought to arise from genetic differences in the testa, whereby some varieties are prone to damage during the harvest process. Work at the Official Seed Testing Station in Cambridge (MacKay and Tonkin 1967; Flood and MacKay 1972), in addition to showing that the field environment of the seed crop affects dry seed longevity, also demonstrated that structural damage, particularly that involving the embryo, is liable to lead to an early loss of viability. As would be expected from these observations, seed with a low initial germination tends to lose viability quickly (Justice and Bass 1978). Differences in longevity also arise from the degree of maturity at harvest, the viability of immature grains has been noted to decline more rapidly. It is likely that some of the above findings relating to dry storage also apply to soil-borne seed.

5.5 Recommendations for research

1. The requirements for the maintenance of life in an imbibed cereal seed under enforced dormancy in the soil should be determined and the relationship of innate dormancy to longevity in seeds also requires investigation.

2. The environmental factors thought to reduce grain longevity should be confirmed. The following topics merit consideration: oxygen level, organic matter, microorganisms, fungicides, nitrogen and herbicides. Additionally, the actual process of loss of longevity should be described to provide an understanding of the effect of attempted manipulation of longevity. Is grain lost by germination at depth? What is the mechanism of decay?

3. Reliable evaluation of the number of years that a significant number of seeds remain viable is needed for each cereal species and the question of varietal differences should be explored. A series of buried seed experiments would provide this information. The seed used should not be after-ripened but should be taken direct from the field. Trials should, of course, be laid down during the period of autumn cultivation.

4. A method for estimating the number of grains placed in the soil following harvest should be devised. The possibility of judgeing the condition and germinative capacity of grain shortly after harvest should be considered since this is known to affect longevity.

6. Dormancy: the factor of genotype

6.1 The relationship between pre-harvest sprouting and dormancy

Clearly a variety having good sprouting resistance will also show dormancy, at least in the short-term. This may well be sufficient to delay germination of shed seed until after completion of final seedbed preparation allowing the seed to germinate in the succeeding crop or subjecting it to a season of enforced dormancy.

The contribution made to PHS by the lack of dormancy in wheat, barley and oats has been estimated by Strand (1980) who concluded that in a wide range of varieties he investigated, 49-64% of variation in sprouting resistance was due to dormancy. This did not include the action of germination inhibitors in the tissues of the spikelet which could, if present, also affect dormancy. Other workers have sought to distinguish between dormancy arising from the embryo and the endosperm. Gordon (1980), acknowledging that dormancy provides protection against PHS, considered that both of these sites of dormancy mechanisms could be manipulated, or protection, in the form of blocks to enzyme activity in the endosperm, might be incorporated into the plant.

Breeders acknowledge that sprouting remains the most difficult component of wheat grain quality to assess (Gale *et al* 1986). The reasons for this are not difficult to identify in view of the limited quantities of material available from a line prior to the F6 generation. The seasonally intermittent occurrence of the problem means that sprouting must be artificially induced. Since small-scale, laboratory germination tests and assays of α-amylase, have proved unreliable (Strand 1980), irrigated field trials are often used. The method employed for the official variety trials for sprouting resistance of wheat in England and Wales is of this type (McVittie and Draper 1982). Other organisations use rain simulating cabinets (Gordon *et al* 1977). Whilst these allow an accurate management of moisture, they do not always reflect the cycles of wet and dry conditions experienced in the field. Variety screening methods were also discussed by Belderok (1968). Pre-harvest sprouting appears to be somewhat less of a problem with barley and therefore comparative varietal data is not obtained for barley from official trials in England & Wales.

Measurement of the tendency to pre-harvest germination examines short-term dormancy of grain in the ear under a prescribed moisture regime. It therefore fails to consider the effect of soil contact on the grain and, in addition, the removal of spikelet tissue, both of which are relevant to shed grain. The assessment of sprouting resistance does, however, examine some aspects of dormancy which are applicable to shed grain but allowance must be made for the differing time scales and environment.

6.2 Comparing the species for dormancy

Wheat and barley

The genetic variation which exists for dormancy in both wheat and barley has enabled man, during the process of domestication and in subsequent variety selection, to decide the level of dormancy he requires (King 1983). It is probable that dormancy has been reduced in both species by the need for a quick turn around between harvest and sowing the next crop. It is also reasonable to conclude that a similar degree of selection pressure has, in general, been applied to each crop. The possible exception to this arises from the use of barley for malting.

The observations of Bewley and Black (1982) suggest that wheat and barley have somewhat similar temporal requirements for after-ripening in dry storage although a trend was noted for a greater inter-genotype range of requirements in barley. It is also of interest that Côme and Corbineau (1984) reported differences between wheat and barley in the site of origin of inhibitors in the coat.

The above theoretical considerations do not permit a confident comparison of the expression of dormancy in the different species. It may well be that factors affecting the relative amount of grain shedding in each species are a more important source of variation in the incidence of volunteer cereals.

It is also obvious that certain types of admixtures are much more conspicuous and harmful than others. For example, immature wheat volunteers in winter barley tend to present harvesting problems. It is also likely that barley volunteers in winter wheat will present a particularly serious sample contamination. Winter cereals appear to be the greatest problem (G.W. Cussans, personal communication). An assessment of major problem areas will help establish the relative risks of volunteers and could assist the formulation of cropping plans and research priorities.

A brief note on dormancy in other cereal species

In general terms, the principles outlined in this review relating to dormancy in wheat and barley are likely to apply to the other cultivated cereal species. It is therefore unlikely that germination of shed grain prior to final cultivation can be relied upon to significantly reduce potential contamination arising from shedding by any of the cereals. However, in certain instances, rye, triticale, durum wheat and the naked varieties of oats are more prone to germination problems than wheat and barley and where this applies, it is likely to reduce longevity even in grains able to germinate after harvest. Naked oats may, as mentioned under section 4.1, have a lower degree of dormancy. Poor germination, however, is likely to be due to embryo damage at harvest (Pickett 1988) and therefore grain that is shed prior to threshing may be unaffected and able to grow before conventional oats. More experience of naked varieties is needed to confirm this point.

Corbineau *et al* (1986) investigated dormancy in cultivated oats and their conclusions indicate broadly similar causes for dormancy in this species as found in barley. Variations between varieties were noted.

Rye is generally considered to possess lower dormancy than red-grained wheats (Strand 1980). As a minor crop in the UK, it is an infrequent, but conspicuous volunteer.

Perhaps of greater concern within the UK is triticale, a crop very much affected by PHS (Derera 1980). Since this crop appears to have a future in the UK and in other parts of Europe, breeders are likely to make an effort to reduce the damage caused by PHS and it is therefore likely that groundkeeper plants of triticale will, at least, become a local problem.

Durum wheats also suffer from a lower resistance to sprouting (Derera 1980). This crop has met with only limited success in the UK but should breeders seek to develop varieties for northern Europe, a greater resistance to PHS with increased dormancy will be a probable aim.

6.3 A survey of dormancy in varieties

Over the years, a number of reports have demonstrated a considerable range in the expression of dormancy between varieties in ***harvested*** seed although little published work appears to be available for current UK varieties. Seed tests for certification purposes carried out at the Official Seed Testing Stations do not allow a full assessment of genotype-environment interactions. This is, however, permitted to a limited extent by the testing of produce from wheat and barley variety trials in England and Wales but this is inadequate as a database for the preparation of guidelines on the dormancy of shed grain. The unpublished data from these trials kindly provided by the OSTS for England and Wales confirms that there is variation between varieties in dormancy after harvest. This work also indicates that varieties which do not show the best resistance to PHS may exhibit dormancy in the harvested seed, a situation partly explained by the early period of high germinative energy illustrated by Figure 2 (page 26).

Wheat

The following scores derived from official trials for resistance to pre-harvest sprouting have been published in the 1988 NIAB *Recommended lists* of wheat (NIAB 1987):

Winter varieties				**Spring varieties**	
Longbow	8	Rendevous	(6)	Alexandria	8
Parade	(8)	Slejpner	6	Axona	8
Brock	7	Brigand	5	Jerico	8
Fenman	7	Brimstone	5	Minaret	8
Hornet	(7)	Galahad	5	Tonic	8
Mercia	6	Avalon	4	Wembley	7
Norman	6				

The highest figure indicates the greatest degree of resistance to sprouting. Figures in brackets denote limited data. Although these results suggest variation for dormancy, a direct relationship with stored or shed grain may not exist. This is apparent, for example, in recently observed instances of dormancy affecting sown seed of the variety Slejpner in the UK (J.H.B. Tonkin and R. Don, personal communications). Although this is an unusual situation in the UK, it is somewhat surprising in view of the intermediate rating for PHS resistance in Slejpner but no doubt reflects a later development of dormancy.

It is also of note that the spring varieties exhibit greater PHS resistance, a difference which has been apparent for a number of years. The reason for this is not clear: possible causes include ear laxness or the presence of an inhibitor in the spikelet structures. However, spring varieties will usually reach anthesis during warmer temperatures than winter wheat and as noted by Reiner and Loch (1976), there may be an early heat sensitive period (see section 4.2). This could promote dormancy establishment in the spring crop. It is also possible that selection pressure has not acted against dormant spring varieties where it clearly presents less of a problem to crop establishment, although there has been a recent tendency to use these varieties as alternative wheats.

Since several mechanisms are involved, there is no reason why a trend towards dormancy should be restricted to spring varieties, vernalisation and cold tolerance have also been associated with dormant genotypes (Gale 1988). The answers to many of the questions relating to dormancy are elusive indicating a complex of factors with some apparent contradictions. Clearly, the selection of dormant varieties could result from other important constraints which restrict breeders to a specific type.

Other investigations supporting the conclusion that wheat varieties vary in expression of dormancy include an examination of an array of North American bread wheats by McCrate *et al* (1982); these showed varation for dormancy and a progressive decline in this characteristic after harvest maturity. Everson and Hart (1961) and Ching and Foote (1961) also reported a range of dormancy in American varieties.

Barley

The OSTS for Scotland has confirmed clear varietal differences in the dormancy of barley (R. Don, personal communication). The varieties, Igri Plaisant, Triumph, Blenheim and Carmargue have been considered to be particularly difficult to test for germination.

An annual survey of dormancy in malting barley varieties is carried out by Dr Bernard Dyer and Partners based in London. Since these results relate to individual crops, grown in different parts of the UK, only two broad conclusions will be drawn. First, varietal differences in dormancy are confirmed by this work. Secondly, dormancy becomes more strongly pronounced in the north of the UK.

The European Brewery Convention publishes details of dormancy in samples of malting barley (EBC 1988). These results represent the testing of produce from variety trials of winter and spring varieties carried out at a large number of trial sites in Europe. The UK contributes two sites: at Cambridge and Warminster. As an assessment of dormancy of stored grain, it is valid to make comparisons between varieties. Moreover, since the tests for germinative energy are carried out after six weeks for winter barley and three weeks for spring barley, there may be a crude relationship to the period during which shed grain is able to germinate in the field prior to final cultivation although it is emphasised that dry grain will respond differently to soil-borne grain. The results for the spring barley trials in the Western European Region indicate that mean germination energy after a five day test ranged from 48-99%, depending on variety, whereas the ultimate mean germination capacity of most varieties tested was in the range 98-99%. For winter barley trials carried out at Cambridge, mean germinative energy after five days ranged from 39-92% with a germinative capacity of 78-92%. Unfortunately, however, many of the results are incompletely reported.

The relevance of dormancy in dry-stored grain to condition of shed grain

The factors controlling dormancy in shed cereal seed are not the same as might be asked about seed in the ear or in dry store. Few studies specifically relate to the dormancy of soil-borne cereal seed. The existing information on the dormancy of varieties, limited as it is, almost without exception relates to seed which has been stored under dry conditions prior to test. Apart from anecdotal information, little is known about the dormancy of shed grain under field moisture conditions or of the effect of the soil and harvest residues on germination of individual varieties. The HGCA coordinated programme of research should therefore examine the innate dormancy of current varieties and the effect of trends in plant breeding.

The source of seed used in the investigation of dormancy

Experiments relating to dormancy require a reliable source of dormant seed. This is particularly important in view of the wide variation of dormancy between seed lots arising from environmental effects during maturation and by the treatment of seed after harvest. It would clearly be desirable to use a sample of known characteristics for a series of tests. Means of preserving dormancy are therefore relevant to this review.

It has been found that dormancy may be preserved by freezing. Amongst those who have investigated this possibility, Mares (1983) described work in Australia with 14 hand-threshed wheat varieties, half being red-grained and half white. The germination characteristics of fresh grain were established after harvest and the grain was frozen at -15°C for up to 9 months at 12% moisture. The results showed that freezing is a suitable method for preserving the germination characteristics of wheat for at least nine months. When the frozen grain was transferred to a constant 12°C, the rate of increase in germinability compared very favourably with the results directly after harvest. It was, however, noted that significant freezing damage occurred when the moisture level of the grain exceeded the critical level.

Other workers apparently use this method (Larsson 1987). Caution should be exercised in procuring grain at the required level of moisture since artificial drying could obviously affect the dormancy of the selected grain.

6.4 Seed coat colour in wheat and dormancy expression

For many years it has been known that red-grained varieties show a greater dormancy than white varieties (Wellington 1956a). Apparently it has been possible to breed white varieties showing relatively high PHS resistance (Gordon 1983), although these varieties do not equal the best red-grained varieties in this respect. Morris and Paulsen (1987), however, indicated success in transferring resistance to PHS between white varieties. Apparently, there is much more variation for this character within the red-grained group of varieties.

Everson and Hart (1961) discussed the question of coat colour and noted a complete or nearly complete lack of dormancy in white wheats they examined apart from one variety with a weak inhibitory system. Derera (1980) summarised the considerable importance of white wheats in world agriculture indicating that research was under way into transferring known sources of resistance to PHS into the white wheat. Should such a programme be successful, it is possible that white varieties could be re-introduced to the UK. Periodic attempts to do this in recent years have met with little success.

The behaviour of white and red wheats during the post-desiccation stage was compared by Wellington and Durham (1961). The lack of dormancy in the white varieties was attributed to weaker covering layers which ruptured more easily, allowing imbibition to take place. It is thought that there is a different origin to dormancy in red wheats, the biochemical basis of which has been discussed by Gordon (1979).

The genetical basis of coat colour has been discussed by Gale (1988). Since coat colour and the associated dormancy is maternally inherited and red is dominant to white, progeny tests will be required to identify the coat colour and certain other aspects of the dormancy response of a breeding line. It appears likely that loci in each of the three genomes control inheritance of red grain colour and these are believed to be addititive for degree of dormancy but not necessarily for visual intensity of pigment (Freed *et al* 1976). Although additivity is difficult to establish, the crossing of isogenic lines could be a means to identify and quantify the effect of different dominant alleles. It should then be possible to manipulate a breeding programme for the desired degree of dormancy.

The question of the physiological basis of the action of these genes has not been resolved. It could be attributed to a pleiotropic effect of the alleles coding for coat colour. It is also possible that separate loci control the two characteristics independently with a tight linkage responsible for the association. However, the evidence for this is weak: there are only a few cases of reasonable dormancy in white wheats whereas one would expect linkage to be broken more frequently and completely.

6.5 Ear morphology and seed condition at shedding

Water relations

Since the maintenance of the dormant condition is affected by moisture level, it is likely that ear morphology may have an influence by modifying water uptake and retention, both associated with PHS. Australian investigations of water uptake by the ear have been reported by King and Richards (1984) and King (1984). The investigations demonstrated that the ears of awned and club wheats, could hold more moisture than varieties not showing these characteristics. Club wheats bear a degree of morphological similarity with the dense-eared varieties as classified by NIAB (1988). In this connection, as mentioned in section 6.3, it is perhaps of significance that spring varieties showing high PHS resistance are typically lax-eared. Further investigation of a possible link between moisture uptake and sprouting should be carried out since a potential source of PHS resistance might be obtained from lax-eared varieties without the direct involvement of dormancy.

In the Australian investigations mentioned above, other features of ear morphology did not appear to significantly influence moisture relations of wheat. However, as pointed out by King (1987), there are wide differences in water uptake between varieties and since these are not fully explained by awns or ear density, further work on ear characters is needed. It appears reasonable that water relations are involved in dormancy and could be affected by a number of ear features such as waxiness. This has been supported by other workers including Strand (1980). Certain factors which are not expressed morphologically are also likely to affect the uptake of moisture. Duffus (1987) has provided a review of the biochemistry involved in this question and has concluded that there is evidence that the water potential of grain is a key factor in the control of PHS.

Seed size

It has been noted that seed size has an effect on germination (Lang 1965). Not only can germination capacity and seedling vigour be reduced in small seeds but speed of germination may also decline. This suggests that the smaller shed grains will tend to show delayed emergence. Although such grains may have a shorter life-span in the soil, they could produce less vigorous plants which may tend to escape final cultivation before the next crop is sown.

In one investigation, a negative association between seed size and α-amylase activity was reported (McCrate *et al* 1981) but this may not conflict with the observation of a decreased germination capacity in small seeds.

It has not been possible to locate work relating to any other aspects of the effect of grain size on the volunteer cereal problem. Refinement of agronomic practice to reduce the incidence of small grains should, however, be investigated. Although seasonal effects on grain size tend to be large, it may be possible to achieve some improvement by careful agronomy. Grain weight is one of the components of yield which has been extensively investigated (Ridgman and Walters 1982; Darwinkel 1978). Interestingly, Ridgman and Walters noted a reduction in grain size in continuously cropped wheat, a system that is also very likely to increase the problem of volunteer cereals by the simple fact that it is continuous.

6.6 Resistance to shattering and shedding

Genetic variation in susceptibility to seed shedding is known to exist and has been an important consideration in the selection of varieties of both wheat and barley.

The 0-9 scores (9 = least shedding) for resistance to shedding in winter wheat varieties published in the 1988 NIAB *Recommended Lists* (NIAB 1987) are as follows:

Winter wheat				**Spring wheat**	
Avalon	8	Apollo	7	Axona	8
Brigand	8	Brock	7	Jerico	8
Brimstone	8	Hornet	7	Alexandria	7
Galahad	8	Norman	7	Minaret	7
Longbow	8	Rendevous	7	Tonic	7
Mercia	8	Slejpner	7	Wembley	6
Parade	8	Fenman	6		

Degree of shedding scores may also have a bearing on maturity at grain loss. The growth stage at which grain is shed may affect degree of longevity. Lewis (1961) noted that immature wheat seed is better able to survive under high water levels than grain which has reached maturity.

In spring barley, ear loss is a recognised problem with differences between varieties. The 0-9 (9 = least ear loss) scores included in the Recommended list are as follows:

Spring barley

Blenheim	7	Klaxon	6
Cameo	7	Natasha	6
Corniche	7	Regatta	6
Digger	7	Triumph	6
Doublet	7	Kym	5
Atem	6		

The above results are included to show that varieties differ in tendency for a natural loss of grain. A distinction should be drawn between grain which passes through the combine and that which is shed direct from the plant. Grain lost from the combine may have different germination characteristics due to smallness and threshing damage and there may also be small maturity differences.

6.7 Recommendations for research

1. Critical studies of dormancy in recommended varieties of wheat and barley should be carried out in the field using grain, which has not been after-ripened but has been subjected to the growing conditions identified as promotive of dormancy. Since a supply of dormant seed should not be assumed, it might be feasible to obtain material grown in a northerly part of the UK with an adverse climate. It would, however, be necessary to commence investigations directly after harvest unless suitable seed was frozen, as described in this chapter.

2. Investigations should be carried out to determine the relationship of grain size to dormancy and late emergence of volunteers. Means of reducing the production of small grains by agronomic practice and improved varieties requires examination. Further refinement of

harvesting equipment and techniques is an obvious route to reduce volunteers.

3. The possible link of a high degree of water uptake with PHS should be confirmed and associated ear characters should be identified to enable breeders to reduce the tendency to sprout without additional dormancy.

7. Genetics and breeding

7.1 Introduction

In the climate of a fast turnover of cereal varieties and even more massive inputs into plant breeding including the improvement of resistance to PHS, research into methods of reducing the volunteer problem must take account of breeding trends. The obvious general link between PHS and dormancy (George 1967; Gordon *et al* 1979; Takahashi 1980) makes it necessary for this review to give an indication of the current policy of breeders aiming to produce new varieties with improved resistance to sprouting.

Two questions, in particular, require answers under this heading. First, is it possible for the plant breeder to develop varieties of wheat and barley which are less likely to present volunteer problems without deleterious effects on other plant characters? Secondly, what direction is breeding taking in these crops - will current objectives lead to the introduction of varieties showing a greater tendency to leave volunteers or a reduction? In order to attempt to predict the outcome in these areas, the genetics of pre-harvest sprouting resistance will be examined.

7.2 Wheat

The need for resistance to PHS

It has been stated "susceptibility to pre-harvest germination in the ear presents breeders in temperate wheat growing areas with the greatest obstacle to producing varieties which consistently yield grain of high bread or noodle-making quality" (Gale *et al* 1986). There is an urgent need to produce a greater proportion of breadmaking grain in the UK. Despite the existence of suitable breadmaking varieties, PHS and associated α-amylase development, which may precede visible germination, often prevents much produce reaching this market. Although millers may vary somewhat in their tolerance of the problem, there is little doubt that the requirement is clearly for minimal levels of this enzyme (Buchanan and Nicholas 1980).

There is also a need for quality for animal feed compounding (Lake 1987). The work of Johnson and Taverner (1987) should, however, be noted in this respect. They found some evidence that sprouting did not adversely affect the feeding quality of wheat grain for poultry and gave a possible improvement for pig feeding. These findings were of a preliminary nature and are probably unlikely to persuade animal feed manufacturers to move away from a preference for a regular supply of sound grain. Moreover, apart from reducing quality, PHS is also likely to result in a substantial reduction in yield, mainly as a result of the removal during threshing of the lighter, sprouted grains. Belderok (1968) felt that a loss in wheat as high as 10% would not be exceptional.

Breeding trends in wheat

For a period of about 40 years, UK breeders have seriously addressed the problem of PHS. Attention to the problem has been encouraged by official trials and the inclusion of resistance data in the Recommended List for winter wheat since 1952. It is noteworthy that although there has been a general overall improvement in resistance to sprouting over this period, it is clear that the problem of PHS is still very much a reality.

The harmful effect of pre-harvest sprouting may be compared with the consequences of the volunteer problem. By comparison with PHS, the volunteer cereal problem, even if shown to be responsive to genetic manipulation, is likely to be given a lower priority by breeders who will seek to redouble efforts to obtain non-sprouting varieties at the expense of greater short-term dormancy as represented in Figure 6. Current plant breeding objectives, if they succeed, are therefore unlikely to contribute to a reduction in groundkeeper cereals and could well result in an increase. Other means of reducing volunteers must therefore be sought. It is believed that the main thrust of this approach should be environmentally orientated.

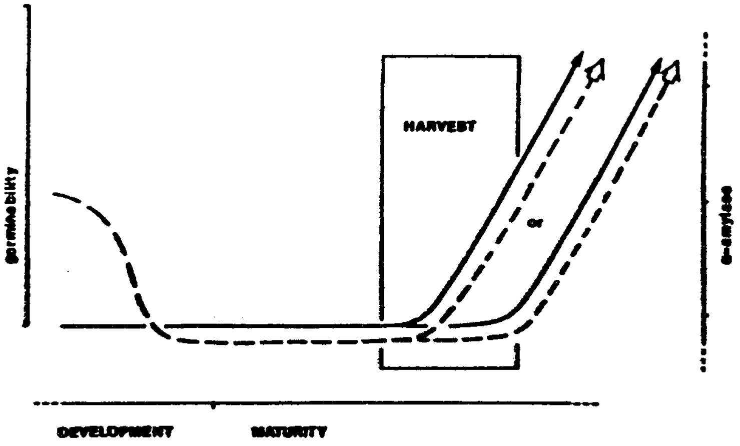

Figure 6. Breeding for extended dormancy germination (solid line) and α-amylase (broken line). After Gale *et al* (1986).

In all cereals, the maximum practicable resistance to PHS is required for the whole of the time the crop is likely to be in the field. Not only is it necessary to prevent germination prior to harvest maturity, protection must also include the period after harvest-ripeness during delayed harvest when conditions may particularly favour germination (Reitan 1987). The interval between the termination of this stage and final cultivation for winter-sown crops may be less than four weeks. The development of a shorter period of sufficiently strong dormancy, even if possible, would therefore compromise resistance to PHS in the uncertain climate of the UK where many weather patterns are possible.

There are, however, certain limits to the degree of dormancy that can be tolerated since it must not interfere with crop establishment. In New Zealand, for example, dormancy has given rise to problems in seed for sowing in a variety of wheat with exceptional PHS resistance (Young 1985). Despite this, it would appear that there is scope to increase dormancy in UK varieties without this drawback.

The genetics of dormancy in wheat

In view of the slow progress in breeding for resistance to PHS in the past, is it correct to forecast the development of varieties having greater dormancy? The following is a summary of the difficulties arising from a limited availability of information of the genetical basis of PHS:

1. Bread wheat is a hexaploid with three sets of homoeologous chromosomes and this complicates inheritance of a number of traits including, in all probability, pre-harvest sprouting. It is considered likely that genes affecting this are present in each component genome.

2. A number of separately inherited plant characters have been found to influence pre-harvest sprouting. Biochemical pathways leading to enzyme production are included here as well as other plant systems affecting seed development.

3. Many of the factors implicated in PHS are certainly highly sensitive to fluctuating environment making genetic analysis and the screening of progenies with small quantities of seed difficult (Gordon *et al* 1977).

4. Non-homozygous plants contain three genetically distinct tissues: the *maternal* plant which includes the glumes and the pericarp of the seed, the *embryo* resulting from fertilisation, and the *endosperm* which is triploid and includes two sets of maternal chromosomes. As a result, it is sometimes difficult to evaluate an effect and to manage it in a breeding programme. An example is seed coat colour for which segregation will not be

> apparent until F2 plants produce seed. On the other hand, the genotype of the aleurone is determined by the zygote and is therefore expressed in the F1.

Since the genetics of PHS are now better understood (Gale 1988), the introduction of more satisfactory varieties in the near future is a possibility. The dormancy of shed grain of wheat is therefore likely to increase.

Possible strategies for breeding wheat varieties having a more suitable expression of dormancy

Gale *et al* (1986) suggested that it may be possible to reduce the α-amylase content of sprouted grain in such a way as to make it more acceptable to the end user. To some extent this has been achieved in lines carrying the *Rht 3* dwarfing gene (Flintham and Gale 1982) which is insensitive to gibberellic acid but seeds of these lines exhibit normal germination. It has also been possible by these means to reduce the development of pre-maturity α-amylase. There are, however, problems associated with this approach. First and foremost, it should be noted that the reduction in height from the *Rht 3* gene has been found to be too severe for inbred wheat varieties.

Attempts to incorporate this gene into wheat varieties of normal height have been unsuccessful since it has not been possible to break what appears to be tight linkage between short straw, low yield and reduction in α-amylase production (Blackman and Payne 1987). Additionally, certain lines carrying *Rht 3* need further sources of sprouting control to provide adequate cover and inclusion of these genes will be a complicating factor. In summary, modification of the varietal production of α-amylase could, in theory, provide a useful further defence against one of the harmful effects associated with sprouting in breadmaking grains. However, even if this were successful, it is unlikely that breeders will be persuaded to reduce dormancy in wheat. α-amylase production is only one of several harmful effects resulting from PHS. Yield is also lost when the lighter, sprouted grains are aspirated out at harvest or during recleaning. There will also be a general decline in quality.

A reduction in the **overall production** of germinative α-amylase by other forms of genetic manipulation is not easy since at least three sets of α-amylase genes are present in wheat (Gale 1988). This approach is distinct from an increase in dormancy which may be regarded as **delaying the *de novo* production** of α-amylase.

Evidence has been found of the existence of genetic variation in the response of wheat embryos to germination inhibitors and for this reason, the measurement of this response was advocated by McCrate *et al* (1982). It appears likely that the question of embryo maturity should be examined since this may be a reason for the failure of harvest-ripe wheat to germinate. However, any modification must not compromise the protection of the grain to PHS. Indeed, Gordon *et al* (1979) suggested selection for embryo immaturity as a useful means of identifying varieties resistant to PHS under cool ripening conditions.

Varietal differences in the presence of germination inhibitors in the spikelet tissues of wheat have been found (Derera *et al* 1977). This source of inhibition may be regarded as separate from that present in the covering layers of the grain. Evidently this type of inhibition is lacking in certain varieties of wheat, a point noted by Derera and Bhatt (1980) who described a breeding strategy for transferring the characteristic to improve PHS resistance. Gale (1988), however, whilst discussing *bract* inhibitors in wheat, indicated that the genetical basis of inhibition is unclear. Despite some lack of information, since it appears possible for breeders to select for the character, consideration should be given to breeding programmes which make use of spikelet inhibitors in wheat for the reduction of PHS without preventing germination of shed grain. It is, however, also possible that inhibitors of this nature could be antagonistic to early germination of shed grain if the spikelet tissues remain associated with the grain on the soil but this could presumably be controlled by suitable management of harvest residues, as discussed in chapter 8.

Hybrid wheat

Since there is still interest in both F1 and F2 hybrid varieties of wheat, it is appropriate to consider the effect that hybrids might have on the volunteer cereal problem. PHS problems have affected both CHA and CMS production of hybrid seed wheat (Doig *et al* 1975; Ellis and Clayton 1975). The cause of this was later thought to be non-genetic in origin (Gale 1988). This review will not analyse the somewhat complex seed production techniques involved but will briefly consider the commercial grain crop produced from hybrid seed. At this stage, any dormancy would be of widespread importance if hybrid varieties of wheat are marketed. The following questions are suggested. What level of dormancy could be tolerated in the F1 or F2? Will the produce of hybrids be uniform for dormancy in the field?

F1 plants will produce grain of a genotype not required for seed unless involved in F2 seed production (for which different conditions will apply) and there will therefore be good reason for maximising dormancy. Indeed, in view of the cost of seed production, it is possible that this will be an objective, at least for the female parent subject to a high risk of PHS during hybrid seed production. Since the F2 grain produced on the F1 plants will be segregating, there will be a need to incorporate as many favourable genes for dormancy as possible in order to reduce unprotected grains to a minimum. Conversely, it is also possible that shed produce of a grain crop sown with F1 seed, will contain a proportion of highly dormant segregants. Broadly, there will be a more pressing need for comprehensive protection against PHS in F2 varieties because the plants and the grain produced will both be segregating.

It is possible that varieties containing the extreme dwarfing gene *Rht* 3 could be used as parents in F1 hybrid varieties without some of the disadvantages associated with inbred production using this gene (Gale *et al* 1988). Used in combination with a normal height parent, a hybrid of acceptable height may be produced. As mentioned earlier, this gene could confer benefits in reducing α-amylase activity in the F1 seed. However, since the F1 seed would certainly be heterozygous for this character, the F2 embryo and endosperm of the grain produced on the F1 plants will only be protected in those segregants containing the dominant allele *Rht 3*.

It is interesting that Gale (1988) reported that heterosis for α-amylase activity had not been noted in the F1.

7.3 Barley

The need for resistance to PHS

Pre-harvest sprouting is also a potential problem in barley. If more than 5% of grains have sprouted the lot will be unsuitable for malting due to potential storage problems and uneven malting (Brookes 1980; Derera 1980). In addition to direct modification of the grain, a number of deleterious effects accompany sprouting including increased microorganism activity (Munck 1987). Since the requirement for low dormancy conflicts with the need for PHS resistance, breeders of malting varieties must seek a compromise which will be a delicate balance of priorities. Malting requires uniform and speedy germination and dormancy is, of course, a hindrance to this particularly in grain exported to the continent where drying is not usually carried out as a means of breaking dormancy (Wood 1986). It is clear, that although dormancy is the principal source of protection against PHS in barley (Reitan 1987), a trend towards a new overall level of greater dormancy in malting varieties will be resisted (Bathgate 1987).

The problem of PHS also affects other users of barley. Ringlund (1987) discussed the detrimental effect of PHS which leads to a lower yield of grain through loss of dry matter. Quality in terms of nutritional value is also generally reduced and, since feed compounders require grain that is sound (Lake 1987), sprouted grain will be difficult to trade in an over-supply situation. As with wheat it is possible, however, that there are instances where PHS will actually increase the protein and fibre digestibility of grain for certain classes of livestock but this is unlikely to outweigh the disadvantages. In fact, Ringlund (1987) suggests that the inhibitors causing dormancy may also contain anti-nutritional factors and there is additionally evidence that sprouted grain could be toxic to pigs in certain instances. Breeders of feed varieties may therefore try to increase dormancy in their selection of varieties. The predominant view therefore appears to be that dormancy "is the most important factor for the control of pre-harvest sprouting" (Ringlund 1987).

The genetics of dormancy in barley

As might be expected for a diploid, the inheritance of dormancy in barley is somewhat less complex than in wheat. However, when Buraas and Skinnes (1984) investigated this aspect they concluded that dormancy was controlled by several recessive genes with no close associations with other agronomic characters. Despite this, the selection of dormant varieties should present fewer problems when compared with wheat. It would therefore appear that breeders may more readily decide the level of dormancy in the barley crop but will need to consider uniform germination for malting.

7.4 Other cereal species

There is little evidence to suggest that the degree of dormancy in varieties of oats which retain their husk at harvest will change significantly. However, as mentioned earlier, germination charactersistics of naked varieties may well differ from the more usual form. Gale (1988) felt that the loss of the spikelet structures could affect dormancy. Frequent damage to the grain at harvest could reduce dormancy as well as longevity although the greater oil content (Valentine 1987) may moderate this somewhat.

Oettler (1987) discussed the breeding of open-pollinated varieties of rye indicating that some improvement in dormancy was possible. However, hybrid varieties, now available in Europe, offer the possibility of greater advances since the inbred parents are open to more direct selection.

Breeding objectives for triticale will certainly include improvement of resistance to the serious problem of PHS which is evident in this crop. A possible route could involve the incorporation of the *Rht 3* dwarfing gene (Chojnacki *et al* 1976). Some of the problems associated with the use of this gene in wheat breeding will, however, also apply to triticale.

7.5 The biochemistry of dormancy

The following summary of the role of biochemical compounds is necessarily brief since it is apparent that a complex interaction of plant hormones is involved in germination (Lenton and Gale 1987; Taylorson and Hendricks 1977). For a description of the chemistry of germination in barley see Enari and Sopanen (1986) and, for cereals as a whole, Duffus (1983).

It should be stated that there is reason to believe that changes in the environment are likely to affect the activity of certain of these compounds differentially. It has been proposed that the hormonal control of germination is a delicate balance between stimulation of germination and inhibition by dormancy (Villiers 1972). For further reviews of cereal chemistry and physiology affecting dormancy see Gale (1988); King (1983); Gordon (1980).

α-amylase

This enzyme reduces starch to sugar. It is present in immature grain but its activity declines to a low level during ripening but reappears when germination begins. It may be found in different parts of the seed including the scutellum, embryo, and the aleurone layer of the endosperm. The actual site of production during germination has been a subject of dispute. Perhaps Cornford *et al* (1987) may be taken as reflecting some of the most recent thought with the recognition that although the aleurone is a major source, a smaller amount of the enzyme is found in the embryo and scutellum. Enzyme activity may, in fact, be demonstrated in the embryo when it is removed from the seed and therefore separated from the influences of inhibitors from other parts of the grain.

The Hagberg Falling Number (HFN) test is used to estimate α-amylase activity in wheat. Although only providing an approximate assessment of enzyme activity (Morgan *et al* 1986), the test is used for the official trials because of extensive commercial use. In addition to differences between varieties in α-amylase activity in ripe grain, more importantly, there is considerable variation within certain varieties from different sites and seasons. PHS normally leads to an increase in the activity of the enzyme (Bingham and Whitmore 1966), although it is apparent that α-amylase production in some varieties may not occur until after sprouting has started (Gordon *et al* 1977), whilst in others, α-amylase activity precedes visible germination. The variation of varieties in α-amylase activity is accompanied by a differing ability to respond to GA (McCrate *et al* 1981a & 1981b). Some of the factors affecting HFN **within** varieties may also be implicated in dormancy of shed grain. However, a comparison of the NIAB Recommended List (NIAB 1987) ratings for PHS resistance with those for HFN indicates that it would not be possible to predict the dormancy of a variety by the test rating.

The wheat variety, Professeur Marchal, is noted as a source of germplasm showing large amounts of α-amylase at harvest ripeness and it has been difficult to select lines having suitable enzyme activity where this variety is a parent (Gale 1988; Bingham and Whitmore 1966). The underlying mechanism of enzyme activity is, however, complex according to Cornford and Black (1985). A problem facing the production of potential breadmaking grain, and of particular relevance to this review, is the fact that a relatively small admixture of a variety showing high α-amylase activity can result in unsuitability for this market (Morgan 1988).

High levels of amylolytic enzyme activity have been associated with a lack of PHS resistance in barley. This was shown by an investigation of Canadian barleys by Harvey *et al* (1983).

Pre-maturity α-amylase

A poor correlation between visible sprouting and α-amylase activity is often noted in wheat. Gale and Lenton (1987), amongst others, have confirmed that α-amylase is produced in certain varieties in cool, wet conditions, prior to harvest-maturity and visible germination. Although this is obviously undesirable to growers and end users, few studies appear to have been carried out and it may well be that pre-maturity enzyme production is implicated in more unsatisfactory results than is generally recognised. Pre-maturity α-amylase is thought to be controlled by one or, at the most, two recessive alleles (Gale 1988). Varieties prone to this problem are also likely to produce high levels of the enzyme during germination. There is evidence that barley may be affected in a similar way (Nicholls 1983). It is clear that a margin of dormancy, sufficient to inactivate these biochemical pathways, is needed in both crops until the grain is harvested. This must allow for difficult seasons and it would therefore appear unrealistic to seek varieties in which the dormancy of shed grain always ends, irrespective of the environment, prior to drilling the succeeding crop.

Abscisic acid (ABA)

Although direct evidence of involvement of ABA in wheat dormancy is lacking, there is an indication that sensitivity to ABA is a feature of varieties showing high dormancy (Gale 1988). High levels of endogenous ABA are associated with the period of dormancy induction (King 1983). It is possible that ABA acts as a promoter of early dormancy until other systems take over as was suggested, albeit without specific reference to cereals, by Taylorson and Hendricks (1977). Bewley and Black (1978) support the suggestion of a dormancy-initiating and maintaining role for ABA. For reviews see Walton (1977), Gale (1988).

Auxins

Radley (1980) reported a possible involvement of auxin hormones which may initially act as inhibitors. Amounts decline towards ripening but at a later stage, when the hormone would promote growth, differences were found, with PHS susceptible varieties showing larger concentrations than those that were resistant.

Catechin tannins (CT)

Catechin tannins have been found to inhibit germination in both wheat and barley (Gale 1988). It is possible that a selection based on simply inherited alleles could play a part in the control of a specific dormancy response.

Cytokinins (CK)

Taylorson and Hendricks (1977) considered that CK has an involvement in terminating the effect of GA inhibition causing seed dormancy in plants in general. Although Bewley and Black (1978) noted that CK may have a role in growth and development, they considered as uncertain the possibility that CK may influence germination since peak CK content occurs a few days after pollination and then declines considerably towards maturity. There is evidence, discussed by Stevens *et al* (1988), to suggest that carbendazim fungicides are involved in CK activity. Thomas (1977) has provided a review of the role of CK.

Gibberellins (GA)

Investigations into the role of gibberellic acid were reported by Paleg (1961) and by Paleg *et al* (1962). They concluded that mobilisation of the endospermal reserves resulted from the secretion of GA produced in the embryo. This GA is transported through the scutellum to the aleurone layer controlling enzyme production and release causing mobilisation of reserves in the endosperm. More recently, Gale *et al* (1987) have discussed the role of GA in the production of pre-germinative α-amylase. The precise role of GA has been discussed by Taylorson and Hendricks (1977) and by Bewley and Black (1978). It appears that towards harvest ripeness, there is a reduction in free GA and an increase in bound, inactive GA. This inactivation may be the reason for the cessation of α-amylase production at harvest-maturity. A release from this state probably occurs at germination.

These hormones are associated with plant growth in a number of ways including the production of pre-maturity α-amylase, the stimulation of germination and cell elongation. A number of alleles exist which, in varying degrees, confer insensitivity to GA and characteristically delay germination and reduce plant height. The semi-dwarf varieties each carry one pair of one of these dominant alleles. Whilst, as already noted, the *Rht 3* dwarfing effect is generally too extreme, the milder forms *Rht 1* and *2* may be affected by other alleles coding for pre-maturity α-amylase. For fuller reviews see Jones and Stoddart (1977), Gale (1988).

Phenolic compounds

These appear to be present in the spikelet structures which enclose the grain. Corbineau *et al* (1986) considered that phenols originating in the spikelet structures of cereals are involved in dormancy. Phenolic compounds may fix oxygen by oxidation (Côme and Tissaoui 1973).

7.6 The potential influence of 'exotic' germplasm

There have been a number of studies of wild wheat species and, to a lesser extent, of species related to barley: one objective is the utilisation of genes to confer added dormancy to the cultivated species. It is highly likely that dormancy exists more commonly in wild than in cultivated species. Of course, transfer is no straightforward task although, in general, the incorporation of alien variation into the cereals has attracted considerable interest. Thomas (1981) has reviewed the breeding techniques.

Mac Key (1987) discussed strategies for the adaptation of dormancy characteristics in this way and noted a number of formidable problems. Despite this, the possible existence of useful genes suggests a long term means of adapting dormancy in the cereals. As with other possible developments, there is little at this stage to suggest that the volunteer problem will benefit. It is perhaps unlikely that the other cultivated *Triticum* spp. will provide germplasm to reduce PHS. This is certainly indicated by investigations including those of Gordon (1983). *Triticum aestivum* showed less α-amylase activity when sprouted than all the other cultivated *Triticum* species apart from the rarely cultivated *T. monococcum*, a conclusion supported by Mares (1987).

It is difficult to assess the possible impact of the extensive current investigations into techniques for genetical manipulation. By using these methods, it might be feasible to adjust proclivity to inappropriate expression of dormancy in a manner which would not increase the PHS problem. For example, PHS could be prevented if sensitivity to light could be incorporated to inhibit germination prior to sowing or burial. Such a system would obviously require a different approach to the cultivation strategies discussed in the next section.

7.7 Recommendations for research

1. An improved understanding of the genetics of dormancy and related characters in both wheat and barley would be extremely useful despite the conflicting requirements of PHS resistance and lower dormancy in shed grain. It might be possible to improve PHS resistance by exploiting dormancy promoting features in those parts of the grain which are removed at harvest and less likely to influence the shed grain. Another possibility is that PHS resistance could be derived from a modification of the water uptake of the ear.

2. The genetics of the characters influencing shedding of grain or complete ears should be studied with the objective of developing breeding strategies for varieties which retain their ears and grain.

8. The soil and harvest residues

8.1 Changes in cultivation practice

During the 25 years, 1960-1985, at least three major changes affected cereal cultivation in the UK and from these much of the cereal volunteer problem arises. First, there were the changes in the distribution of cereals. In fact, the area of cereals increased by around 30%, made possible by reducing grass and non-cereal break crops. There was also a swing from spring cereals to autumn sowing which has also been carried out earlier. All these trends have reduced the opportunities for clearing land of volunteers. A second change may be seen in cultivation practice. Depending on soil type, there has been less use of the mouldboard plough with the introduction of techniques which essentially mix the soil rather than invert it. Thirdly, the additional area of cereal production produces more straw but livestock farming has not increased in line with the cereals. For example, the approximate increase in cattle numbers was only 10% during the 25 year period and consequently, there is a straw surplus with the vexed question of disposal methodology. It may be feasible to manipulate some of these factors, such as cultivation and straw disposal practice in the interests of reducing groundkeeper cereals, subject to a refinement of the available procedures. Overriding economic considerations may prevent the modification of cropping patterns.

8.2 The effect of cultivation method

Cultivations affect shed seed in at least three ways. First, the level in the soil profile in which the seed is placed is largely controlled by the nature of soil cultivations, although it may also be modified by soil type. Depth of seed burial will affect degree of enforced dormancy and longevity of seed. Secondly, timing of cultivations will also influence the physiological condition of the seed and its expression of dormancy and longevity. Thirdly, cultivations will determine the fate of volunteer seedlings when released from innate or enforced dormancy.

Stubble cultivations

Stubble cultivations shortly after harvest have been a traditional practice. An objective was to stimulate emergence of weed seedlings which could be cultivated out before crop drilling. A form of stubble cultivation is now mandatory after straw burning. In chapter 4 it was suggested that stubble cultivations may actually promote the maintenance of dormancy.

Cussans *et al* (1987) reported the results of investigations of stubble cultivation, with and without straw burning. It was found during a count made on 1 October, that cultivation resulted in a 30% increase in the number of plants originating from shed wheat grain. The hypothesis that cultivation extends dormancy is unaffected by this result since burning 'triggers' germination in those seeds which are not killed by heat. However, unburnt stubble-cultivated replicates also showed a similar increase in plant establishment but this may have reflected a low dormancy status in the particular field used. The dormancy of shed grain will be an expression of seasonal and varietal factors. Moreover, the shed grain in the cultivated area would have been protected from the inevitable natural wastage attributable to the foraging activities of birds which may have affected the uncultivated replicates.

It has been recognised that it is advantageous to leave land uncultivated to reduce seeds of certain weed species, in particular wild oats, which due to dormancy will not show a high germination rate after stubble cultivation. There is likely to be a much greater reduction of this species by natural seed loss from the surface than after incorporation (Cussans *et al* 1987). Similarly, natural loss may provide a more reliable means of reducing potential contamination of wheat and barley compared with stubble cultivation. It is worth noting that even those seeds resisting digestion after consumption by predators will have been affected by passage through the intestines. It has been found that enzymes can cause germination or loss of viability in seed having passed through the intestines intact (Tran and Cavanagh 1984). There is also a possibility that the action of the gizzard of birds will either promote germination by scarifying the grain coat or will cause irrevocable damage to the grain.

Stubble cultivation as a control measure against volunteer cereals is subject to a number of handicaps, even in the absence of dormancy. Timely germination of non-dormant, shed grain is dependent on the presence of sufficient soil moisture and this is likely to be a limiting factor in some instances (Cussans and Moss 1988). On the other hand, too much water at final cultivation may impair efficient destruction of volunteer plants. In practice, it is known that volunteer seedlings often germinate immediately prior to the sown crop (Christian *et al* 1985), a result of dormancy and lack of adequate soil moisture following harvest.

The main cultivations

Method of cultivation will have important consequences for cereal volunteers. Basically, there are three possibilities: a) traditional mouldboard ploughing; b) deep tine cultivation; c) direct drilling with little significant cultivation. Although by 1980, a third of autumn-sown cereals were established without ploughing (Graham *et al* 1986), more recently there has been a trend back to the plough as has been shown by surveys. Each of the above soil preparation methods is likely to result in straw (and shed grain) being placed at typically different depths as shown by Figure 7. This may affect dormancy and longevity in shed grain.

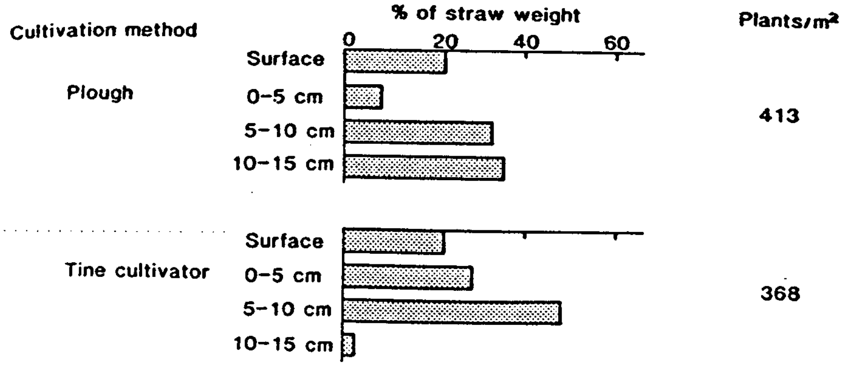

Figure 7. Effect of tillage implement on the distribution of straw in the profile and on plant establishment. After Christian *et al* (1985).

Although problems may arise in the use of the mouldboard plough on heavy clay soils, it is likely to figure in a strategy to control volunteer cereals as it does for blackgrass and sterile brome. Although this is generally considered to be the most effective method of disposing of unburnt straw, some residues will remain on the surface (Christian and Miller 1986) but these will be less than with other systems. The amount of straw remaining on the surface at the various stages between harvest and the estabishment of the following crop may have implications for moisture retention with effects on dormancy and germination of shed grain. It is also likely that ploughing will tend to place shed grain in the lower part of the tilth profile. It has been observed that ploughing often controls volunteers which, on the other hand, are particularly prevalent following straw incorporation (G.W. Cussans, personal communication). This was confirmed by an experiment carried out by Christian *et al* (1988) where a serious infestation of volunteer cereals was reduced by 50% by deeper ploughing, a treatment which could be given further examination.

For ploughing to be effective in burying straw and shed seed well below the surface, good inversion is essential. In this way, it may be possible to concentrate seeds in a deep zone where enforced dormancy will be more effective. By contrast, those seeds near the surface will be affected by fluctuating temperatures and moisture which may 'trigger' germination. Pre-mixing is sometimes advocated as a preliminary to ploughing but such a practice will very likely spread shed grain through the soil profile and increase cereal volunteers. Non-ploughing systems are believed to strongly favour volunteer cereals (Cussans and Moss 1988) and it is interesting to note that they are also thought to lead to a greater yield loss from straw incorporation than ploughing (Davies 1985).

Ploughing will bury a high proportion of seeds to a depth where dormancy will be enforced and at which any germinating seeds will be unable to reach the surface and develop into plants. A study by Budd (1981) on sterile brome, a species lacking in dormancy, lends support to a ploughing strategy for cereals although they have somewhat greater seed longevity. Use could be made of this technique, particularly if means could be developed to predict longevity according to variety or the condition of the shed grain.

The influence of soil disturbance on buried seeds

Cultivation is apparently the best means for reducing the seed content of the soil although this obviously needs to be timed to coincide with conditions which allow growth. This has been shown for certain weed species by Dawkins and Roberts (1967) and Roberts and Feast (1972; 1973) who found that the rate of depletion of the seed bank in the soil was related to the frequency of disturbance. This may not, however, apply to all species as was evident from the work of Courteney (1968). In general, cultivations and other forms of soil disturbance, lead to a depletion of soil-borne viable seeds. Roberts (1981) reviewed this question, and although noting that it is usual for crop species to form only a small proportion of the soil seed bank, a number of his conclusions are pertinent to this investigation. The timing and depth of cultivation relative to buried seed will affect seed loss. Soil type and method of cultivation were also shown to be critical. The application of these principles to the generally short-lived shed seed of cereals should be investigated for the following two reasons. First, is it possible to prevent germination of seed that has been in the soil for twelve months by leaving it undisturbed? Secondly and as an alternative, would it be possible to stimulate germination of such seed by an early cultivation between the harvest and the sowing of the succeeding crop?

Manipulating the soil

Prior to planning cultivation strategy, growers need to know whether a potential volunteer problem exists and therefore a simple means for assessing the quantity of shed grain is needed. A sampling method could be developed to facilitate the counting of shed grains by growers in the field together with guidelines for relating the count to the likely severity of volunteer cereal plants.

Having identified a likely problem, the grower needs to know what action may be taken to encourage early germination or decomposition of shed grain. The biological consequences of the method of straw disposal, preliminary cultivations and of ploughing and other forms of final cultivation should be clearly defined. Methods could be varied from year to year according to risk and the crop to be grown with special arrangements in years of serious shedding or high dormancy and where quality crops are to be grown in the following season. By determining seed longevity, it may be possible to devise a strategy for leaving shed seed ploughed under until viability is lost.

It is possible to derive some support for this proposal from work carried out on wild oats by Thurston (1954) which suggested that deep ploughing may prevent shed seeds emerging in the immediately following season. Whilst this is obviously inappropriate for wild oat control, it may have some merit for volunteer cereals despite the possibility that deep burial may also increase longevity relative to a seed nearer to the surface. However, seed near the surface is more likely to germinate in the current season and therefore the question of longevity is less important in this instance. A rotational system would need a good understanding of the potential contamination level and longevity of shed seed.

8.3 Soil type

Soil type and texture will be likely to affect the germination characteristics of seed (Mayer and Poljakoff-Mayber 1982). This effect principally arises as a result of the modifying influence that these variables have on temperature and moisture.

Soil type and condition will affect the distribution of water and air. This was discussed by Currie (1973) who observed that when moisture is at field capacity, soil crumbs will tend to be saturated whilst the inter-crumb pores will be air-filled, with water draining from the largest first. The soil air content can only be managed by attention to cultivation and clod size. Clearly, there are two aspects to this. First, stubble cultivation, if used, may need modification in adverse conditions although, in the short time available for germination prior to the final cultivation, the effect will be minimal.

Secondly and more important, when shed seeds are ploughed under, it may be possible to modify their enviroment to reduce longevity. If it is confirmed that certain soils restrict germination by limiting oxygen, this could be manipulated by deep cultivation without bringing seed nearer to the surface to allow emergence. It should be stated that germination is likely to depend on the oxygen and moisture status of the soil and the presence of competing soil microorganisms. The content of organic matter will also be of significance as is evident for certain non-cereal species from the investigations of Lewis (1958, 1961) who reported more rapid seed deterioration in an acid peat soil than in loam. Since a very large number of variables are likely to be encountered (Harman 1983), any agronomy guidelines must be related to the basic factors of the gaseous and water relations of the soil. Further aspects of soil moisture relations are discussed by Woodbury and Wiebe (1983) but more work is needed to assess the effect of soil on the shed grain of cereals.

The pH level of the soil also appears to affect germinative energy in barley. Gordon (1973) reported that soils with a high pH (7.5-7.9) gave rise to more germination resistance than a low pH (6.0-6.4). This is in agreement with Roberts (1969) who noted that the removal of both dormancy and water-sensitivity in barley were stimulated by low pH. Nitrate and nitrite were also found to be effective agents for the removal of dormancy, ripe grain may differ from developing grain in response to nitrogen. These points need confirmation for all the cereals and guidelines for relating dormancy to level of soil nitrogen should be devised.

8.4 The levels of oxygen and carbon dioxide

A view has been expressed by Enari and Sopanen (1986) and earlier workers that sub-optimal concentrations of oxygen inhibit germination of seed. The question was discussed by Gordon (1980) who outlined a number of possible mechanisms. Amongst these, he included modification of glucose metabolism, lack of GA synthesis and prevention of ABA breakdown. Gordon also felt that grain coat structure could reduce oxygen availability. Mention has already been made of the possibility that buried seeds in certain soil types could suffer from diminished oxygen assisting enforced dormancy to operate. Wellington (1956b) and Durham and Wellington (1961), however, considered that only severe oxygen tension would limit germination significantly.

Côme and Tissaoui (1973) felt that dormant seeds appeared to require more oxygen for germination than non-dormant seeds, a point also noted in barley by Major and Roberts (1968a, 1968b). Apparently, this is particularly so in cool conditions, with the oxygen requirement increasing as temperature rises. The last mentioned investigators also recorded certain varietal differences in oxygen requirement.

The effects of oxygen and respiratory inhibitors on germinating barley were investigated by Major and Roberts (1968a, 1968b). They reported a complex situation where oxygen provides an early stimulus to germination but later, an inhibition. It was also found that higher than normal levels of carbon dioxide could stimulate germination, particularly where oxygen was in excess. Dormant seeds need to take up more oxygen to germinate than non-dormant but they also give out more carbon dioxide. However, where anaerobic conditions apply, there is no difference between dormant and non-dormant seeds in carbon dioxide output. The question of the possible involvement of the pentose phosphate pathway was considered by Roberts (1973) and Roberts and Smith (1977). Bewley and Black (1982), however, felt that the evidence that dormant seeds were deficient in PPP metabolism was inconclusive but deserved more attention.

It is clear from this brief review of investigational work that the question of the influences of respiratory gases on all types of dormancy is highly complex. It is suggested that the seed in the soil will, at times, be under oxygen deficient, even anaerobic conditions, particularly in some soils and seasons. This could prevent seed germination and therefore consideration should be given to the effect of cultivation on the oxygen status of the soil. The objective of promoting oxygen supply to deeply buried seed may be worth considering since if germination at depth could be stimulated, the resulting seedlings are unlikely to emerge.

Oxygen shortage has been implicated in the condition in barley known as *water sensitivity* (Enari and Sopanen 1986). There is also some evidence that wheat can exhibit this sensitivity (Belderok 1961). Water sensitivity should not be regarded as dormancy, in the strict sense, although it may have a similar effect. Pollock *et al* (1955) found that sensitivity in barley could largely be removed by increasing oxygen to above normal concentrations, but this is of little relevance to field management. It has been thought, on fair evidence, that micro-organisms are involved in water-sensitivity by competing for oxygen.

As might be expected, it is likely that anaerobic conditions will prevent germination in cereals. Lewis (1961) reported that seed of wheat and oats below the water table failed to germinate, an effect similar to water sensitivity. In this state, the seed did not lose viability. This point perhaps suggests the importance of field drainage.

8.5 Straw disposal systems

It has been established that straw burning will reduce the incidence of volunteer wheat plants, wild oats, brome grasses and black-grass (Cussans *et al* 1987). Two main effects were noted:

1. Seeds may be killed by heat.
2. Germination of previously dormant grain may be triggered.

Considering the effects of burning on plant species as a whole, Koller (1972), in addition to the above, identified the following effects:

1. The seed coat may be cracked by heat allowing moisture uptake.
2. The removal of vegetation may encourage germination.

Some very effective burning treatments have been reported, for example, Ellis *et al* (1979) found that a high infestation of cultivated oats was virtually eliminated by burning. An example of the control of blackgrass seedling emergence by burning is illustrated by Figure 8.

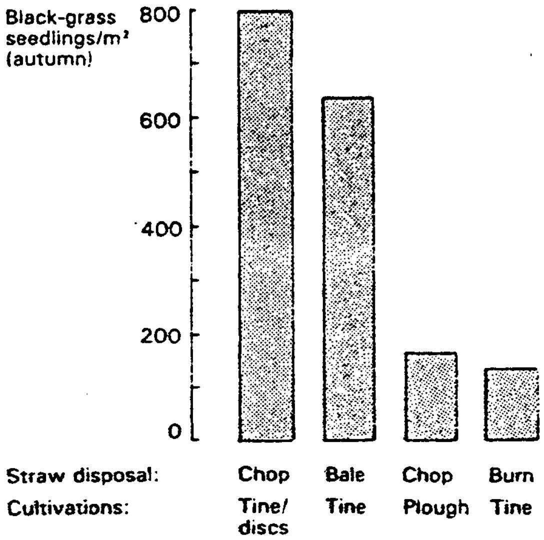

Figure 8. **Effect of combinations of straw disposal and cultivation systems on black-grass in winter wheat. (First year of a long-term trial). After Johnston, Smith and Patterson (1988).**

Studies of volunteer cereal and wild oat infestations show that viable seeds are reduced but not usually eliminated by burning. Degree of destruction depends on effectiveness of the burn and this is often related to the yield of straw. Five times as many volunteer plants were counted on land where only 2.1 t/ha had been burnt, compared with 6.3 t/ha, by Cussans *et al* (1987) who also found that burning reduced viable seeds of wheat by 80%. The germination of seed after burning was thought to be a damage response. The breaking of dormancy in this way may actually increase the number of volunteers in the following crop unless effectively removed; early established volunteers may be the most competitive. Moderate levels of heat generated by fire are known to stimulate seed germination in other plant forms, for example, certain shrubs (Keeley 1977).

A number of possible indirect effects of straw burning have been postulated. In blackgrass, higher germination was found on land carrying burning residues even though the seed was not present at burning. This could indicate an improvement in soil conditions after burning. Alternatively, the effect could arise from the removal of the adverse effects of decaying straw. A further possibility might be the alteration in temperature regimes due to the removal of straw increasing temperature during the day and reducing it at night. It has also been suggested that combustion itself might produce some growth promotive substance. Residues from straw burning may modify and reduce the effectiveness of herbicides, possibly including those applied to control volunteers before drilling the next crop.

The only agronomically satisfactory alternative to burning straw appears to be incorporation (Johnston, Smith and Patterson 1988). The newer equipment for this is designed to mix and bury the straw in a distinct, often shallow, layer in the soil. It would appear that the mouldboard plough is still the only implement to completely bury straw residues.

8.6 The effect of harvest residues remaining in the soil

Obviously, the presence of straw will have a mechanical effect on cultivation and it may, as was noted by Hughes (1979), aggravate the problem of shed cereal grain not germinating prior to the preparation of the next seed bed. The question to be answered is: can straw residues affect the expression of dormancy? Several reports suggest that the presence of straw residues in the soil may give rise to growth regulating substances which can *delay* or completely inhibit germination (Johnston, Smith and Patterson 1988; Ellis 1979; Lynch 1978; Patrick 1971). A retarding effect of straw on germination was reported many years ago by Smith (1948) who noted evidence of an inhibitory factor which varied with planting medium and age of seed.

The effect of straw residues was the subject of a long-term programme of research at the Letcombe Laboratory. A link between poor germination (Figure 9) and the decomposition of straw under anaerobic conditions was established (Lynch *et al* 1976). However, the fate of the non-germinated grains was unclear from this work which was not directly related to the volunteer problem.

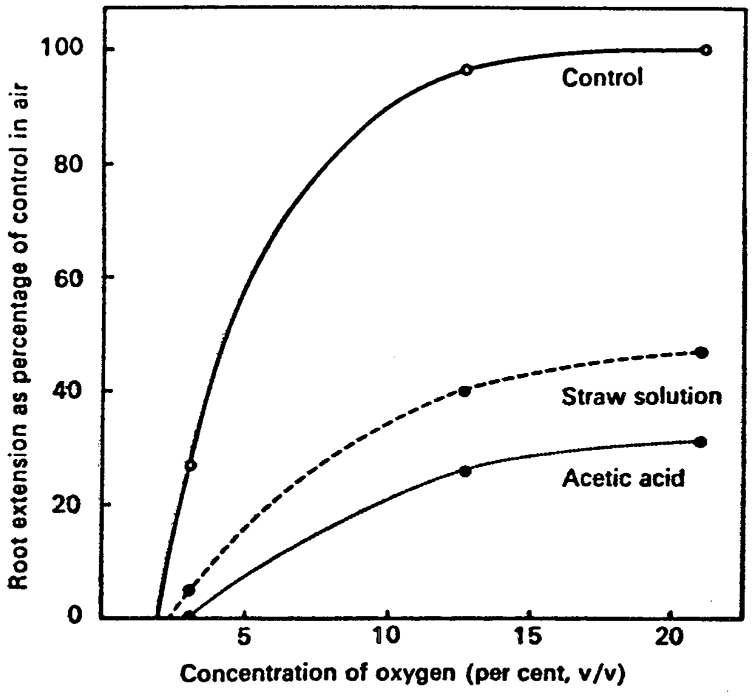

Figure 9. Effect of 15mM-acetic acid and fermented straw solutions on root extension of barley seedlings in atmospheres containing different concentrations of oxygen. The fermented straw solution contained 18mM-acetic acid. After Lynch and Harper (1977).

Acetic acid has been identified as the main product involved in phytotoxicity from straw residues. There is limited evidence of differences between varieties in ability to leave phytotoxic residues but this has not been shown by all investigations. Kimber (1967) found wheat straw inhibited germination in mature grain when measured at 40 hours from the commencement of the test. A reduction by as much as 34% in wheat was noted but rather less was evident in oats. In this work, there were differences arising from the variety used and the degree of decomposition. However, varietal effects were not apparent in an investigation of five varieties, each of wheat and barley, in three soil types by Harper *et al* (1986). They did, however, find evidence that barley may produce a greater degree of toxicity than wheat. This conclusion supports an earlier report (Harper and Lynch 1982) which placed barley and oat straw as similar in this respect. Another report by Harper and Lynch (1981) indicated a fairly rapid decline in acetic acid production. Harper *et al* (1986) found that nitrogen incresed the potential for acetic acid production. The question arises: do those seeds affected by residues, which fail to germinate before final cultivation, remain viable for later emergence?

There are reasons to suspect that the practice of chopping and incorporating straw is likely to encourage seed survival (Cussans *et al* 1987). A further consequence of the introduction of this method of straw disposal is a likely return to ploughing in order to bury the straw residue and leave a straw-free zone for sowing. The alternative is using tines which tend to mix straw in the soil and this may lead to shed grain being lodged in the vicinity of straw. However, the deeper the cultivation, the greater the spread of straw through the soil profile with the effect that the soil-straw mix tends to become diluted with a reduced risk of grain being placed directly next to straw (Christian *et al* 1985). There is evidence, discussed by Christian *et al* (1985) and Oliphant (1982), that seed placed in direct contact with straw exhibits reduced growth. Certainly lower plant populations are associated with the presence of straw but allowance must be made for the confounding factor of slug damage, which is also worse in these conditions.

Whilst the above, necessarily brief, summary does not prove the existence of a link between the phytotoxicity of decaying straw and later emergence of volunteers, it is suggested that there are sufficient indications in the literature to warrant a further investigation. However, this will not be easy as a number of workers have highlighted, for example, Ellis (1979). The laboratory simulation of field conditions will present problems. It is clear that any investigation should include an examination of the effect of variety and soil type. Differences in the latter involving pH and oxygen content in the soil are very likely to be highly relevant.

8.7 Recommendations for research

1. Assess the effect of stubble cultivation, with and without straw burning, on the early breaking of dormancy of shed grain in different soil types.

2. The systems and depths of main cultivation should be investigated to determine how they affect the germination and emergence of shed grain in the next season and the longevity of seeds which fail to germinate. Particular attention should be given to soil type and the depth in the soil at which grain is placed by each method.

3. A strategy should be developed whereby grain may be deeply buried until no longer viable. This would require consideration of a rotation of cultivation methods and an evaluation of their effect on soil aeration.

4. The effect of straw disposal techniques on shed grain should be evaluated. The question of a possible inhibition of germination by residues should be investigated in formulating a procedure to dispose of straw.

5. A measurement should be made of the contribution of natural wastage to the reduction of shed grain in the absence of stubble cultivation.

9. Conclusions

9.1 Concluding comments

Current plant breeding objectives, if they succeed, are unlikely to contribute to a reduction in groundkeeper cereals and could result in an increase. Other means of reducing volunteers must therefore be sought. It is believed that the main thrust of this approach should be environmentally orientated and mainly, but not entirely, non-genetical. Growers need to know varietal differences in dormancy but in the context of the germplasm in use in the UK, it is more likely that volunteers will be controlled by modifying environmental effects. Until more sophisticated genetic transformation techniques are available for cereals, the most effective genetic means to control volunteers may be resistance to shedding in wheat and ear loss in barley rather than attempts to modify plant characters directly related to dormancy, although these should be investigated.

9.2 A strategy for growers

This review has identified a number of potential ways of controlling dormancy and longevity in shed grain. Unfortunately, many of these must currently be regarded as suggestions until confirmed and quantified to enable techniques to be advocated with confidence. Current knowledge, however, permits two recommendations. First, where straw is not removed, it should be burnt although with this recommendation, strong emphasis must be placed on the straw burning code. Secondly, the mouldboard plough should be used where possible. These procedures may be unwelcome but, as this review has attempted to show, other measures to control volunteer cereals are likely to involve compromise and the balancing of opposing factors.

Suitable publications should expound the practical measures available to growers to combat the volunteer problem. Training courses are recommended to assist growers in the understanding of the complex principles involved in the manipulation of dormancy and longevity of shed cereal grain.

10. Acknowledgements

I have greatly appreciated advice from many individuals in several organisations and my thanks are also due to those who have provided unpublished information including: Mr G.W. Cussans of Long Ashton Research Station, Mr R. Don of the Department of Agriculture for Scotland and Dr M.D. Gale of the Institute of Plant Science Research.

Help and encouragement has been given by NIAB colleagues including Dr A.G. Morgan and Mr J.H.B. Tonkin who kindly read the draft of the review and made valuable comments. I am also indebted to Mr A.J. Eade for information, to Mr G.C. Mann and Dr P.S. Wellington (former director) for helpful discussion, to Mr I.E. Wilson for indispensable translations and to the staff of the libraries of the NIAB and Department of Applied Biology of Cambridge University for help with the literature.

Financial support for this review, provided by the **Home-Grown Cereals Authority**, is gratefully acknowledged.

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