CHAPTER 3

Seed Behaviour

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This review of 184 papers from many countries on a wide variety of aspects of seed behaviour is divided into (1) duration of viability, (2) germination and (3) dormancy. Various parts of this section have been covered in a number of previous reviews, notably Stubbs (1956-7), Bachthaler (1957), Thurston (1963b), de Gournay (1964), Barralis (1965) and Fykse (1970).

The main conclusions are that seeds of wild oats can survive in soil up to a maximum of nine years. The rate of depletion is quicker initially under arable than under grassland. Burial appears to aid seed survival, but not to the same extent as in other weeds because wild oats can germinate and emerge from depth. Innate dormancy does not affect the pattern of viability loss. Many fungi are found on the spikelets: several are pathogenic and affect viability. Viability is retained longer in dry storage than in soil. Seeds are killed by one to two months in water or waterlogged soil. At low temperatures seeds can be killed by frost, while at high temperatures seeds can be killed or have dormancy induced or broken. γ-Irradiation can break dormancy or kill seed. Soil type does not greatly affect the duration of seed survival, although peaty soils appear to encourage germination. Seeds do not last longer than two to four months in farm-yard manure, liquid manure or silage, but in compost they can survive longer periods. Only a small proportion of seed survives passage through the digestive system of cattle.

The proportion of seed that is dormant and the time required for seeds to lose dormancy differs considerably between strains of wild oats. Dormancy also varies between seeds in different positions on a single panicle and between the seeds of a single spikelet.

Avena fatua in England and Canada germinates mainly in the spring with a lesser flush in autumn, but in some parts of France and America the autumn flush may be the main one. *A. ludoviciana* in England germinates mainly in the autumn with a lesser flush in spring. The range of temperature over which *A. fatua* can germinate lies between 2° and 35° C. In the field it is between 5° and 13° C. The optimum temperature for *A. fatua* lies between 10° and 24° C and for *A. ludoviciana* between 7° and 13° C. Light can inhibit germination, but various factors influence this effect of light. Cultivation encourages germination through better aeration. Between 10 and 30% of seeds give rise to seedlings. Herbicides applied to the parent plant can affect viability and dormancy as can other chemicals, including fertilisers.

The proportion of seed that is dormant and even the occurrence of dormancy appears to depend upon several factors. After shedding, dormancy

is gradually lost with time, the rate of loss varying greatly. Dormancy can be artifically broken by fertilisers, including nitrates, by gibberellic acid, by removing the hulls, and by pricking. Levels of oxygen and carbon dioxide also affect dormancy, the latter interacting with light. Temperature, both high and low, can break dormancy, but interacts with other factors such as moisture, which by itself can break dormancy by leaching out inhibitors. Secondary dormancy can be induced in wet conditions, especially when the level of oxygen is low, and by certain temperature treatments.

There are several possible mechanisms of dormancy in *A. fatua.* The palea and lemma are said to contain inhibitors and possibly impede gas exchange with, and retard inhibitors leaching from, the caryopsis itself. The caryopsis may also have one or more dormancy systems within itself, which may be controlled by the lack of a germination promoter or the presence of an inhibitor preventing the biosynthesis of a promoter which controls translocation and utilisation of food reserves. It is concluded that the generally stimulatory effect of GA is of great importance and that a search should be made for a cheap substitute that could be used to help control the weed.

There is uncertainty over the exact meaning of some of the terms used in the literature, particularly of those concerned with dormancy and germination. Viability and germination are frequently and incorrectly equated. Viability should be used to mean that a seed is alive, as opposed to non-viable or dead. A viable seed can be either dormant or non-dormant. The term should not be restricted to seeds that will germinate when given suitable conditions, ie non-dormant. The most confusing terms, which are quite frequently used, are 'partially dormant' and 'incompletely after-ripened'. Both terms are ambiguous, for they could mean either that part of the after-ripening period of a batch of seeds had passed, although none as yet had lost its dormancy or, alternatively, that a batch contains some dormant and some non-dormant seeds. It is not always clear which is meant.

There are two widely-used systems of classifying dormancy. In one, if a seed is dormant when shed, it is said to exhibit *primary dormancy.* After this has been lost, and if germination does not occur, a further period of dormancy may be induced in the seed by special conditions. This is called *secondary dormancy.* The other system was proposed by Harper (1957). In this, seed that is shed dormant exhibits *innate dormancy.* If certain environmental conditions prevent germination of non-dormant seed for as long as those conditions last and no longer, then dormancy is *enforced;* but if dormancy persists after the conditions that imposed it have changed then it is *induced.* In wild oats it may be possible to induce secondary dormancy even during the presence of primary dormancy, but there is some doubt as to whether they are separate mechanisms. Secondary dormancy can be induced even though no primary dormancy has occurred. Both systems of classification are used in the text.

Undoubtedly, a greater understanding of the mechanism of seed dormancy in wild oats would have far-reaching effects in many spheres; but for weed control a search should be made for treatments that can either prevent dormancy occurring or can break it once it has occurred. These might be

applied either to the growing plant, the maturing panicles or to seed on or in the soil after it has been shed.

Acknowledgments

The author wishes to thank Miss J. M. Thurston, Dr. A. M. M. Berrie, G. W. Cussans, J. Holroyd and C. Parker for their helpful comments on this Section.

THE DURATION OF WILD OAT SEED VIABILITY

LENGTH OF VIABILITY IN ARABLE SOILS

In arable soils, seeds appear to survive up to an absolute maximum of 9 years. Chepil (1946), in an experiment with planted seeds under Canadian conditions, found that wild oat seeds did not survive beyond 3 years in loam and sandy-loam soils, while in a clay soil a single seedling emerged in the fourth year. In a second experiment one seedling emerged in the fourth year in a sandy loam, but not in the other two soils. In an arable field with a mean population of 663 *A. fatua* plants/m^2, Kurth (1967) found that when seeding was completely prevented the population declined quickly. After 1 year the population was 385 plants/m^2, after 2 years 195/m^2, after 3 years 15/m^2, in the fourth 0.5/m^2 and thereafter no more plants occurred. Banting (1962) reported that, in Canada, 5 years was the minimum period for elimination of seed from heavy clay soils. This confirmed the findings of Thurston (1961) that, under English conditions, *A. ludoviciana* seeds planted in a heavy clay soil survived 2 years 9 months and *A. fatua* 5 years and 1 month. Fykse (1970) in Norway found that wild oat seeds survived 5 years in dry soils and 6-9 years in wet, the longest survivals being in heavy soils. Further work by Banting (1966a) showed that seed could survive up to 7 years. However, in North America, Cates (1917) reported that, in stiff clays in the Red River Valley, *A. fatua* seeds did not survive more than 2 years, but in North Dakota, where soils are sandier and rainfall lighter, they survived 4-6 years. In Utah, Tingey (1961) found that, of seed sown at various depths in arable land, 98% of all seedlings to emerge had emerged within 18 months. In Duvel's buried seed experiment (Goss 1924), *A. fatua* seeds gave 8-18% germination after 1 year's burial, but nil when retested after 2 more years. No further germination occurred up to 21 years. The length of seed survival in arable land therefore lies between 2 and 9 years, with 4-5 years being most frequent. The influence of soil and climatic conditions on seed survival is uncertain as the evidence is conflicting.

LENGTH OF VIABILITY UNDER GRASS

Under grass the conditions are more conducive (initially at least) to seed survival. Baker and Leighty (1957) found that, after 2 years, three times as many seeds had survived under grass as in arable soil, and after 3 years, 15% of those planted were still present under grass and only 3% in arable soil (Baker and Leighty 1958). Fykse (1970) reported that wild oat seed survived

slightly longer under grass than under cereals. It appears in general though, that the maximum length of seed survival is much the same as in arable land. Thurston (1968) found that, under two leys on heavy soils, enough viable seeds remained after 5-6 years to re-infest a subsequent cereal crop. Forbes (1963) (see also *Agriculture* 1961) found that, although there was a marked decline in wild oat seeds after 6 years under grass, 8-9 years were required to eliminate all seed. It appears then that maximum seed longevity is much the same under grass as it is in arable land; but it is probable that the rate of decline is more rapid initially in cultivated land because soil disturbance encourages germination. This is borne out by the report (Banting 1966a) that in Canada loss of viable seed in arable land was rapid in the first and second year, especially near the surface. In Australia, seeds sown in a glasshouse under simulated arable conditions yielded in the first year 90% of all the seedlings to emerge. After 18 months only 2% of the seed remaining was viable (Quail and Carter 1968). In England, *A. fatua* planted in arable conditions germinated mostly in the second spring (Thurston 1961); while, under two leys, the greatest decrease in viable seed (86% and 41%) occurred in the first year after planting (Thurston 1966).

THE EFFECT OF DEPTH OF BURIAL ON SEED SURVIVAL

Although 60-80% of wild oat seedlings emerge from seeds occurring in the top 7.5 cm (3 inches) of the soil, some can come from as deep as 19 cm ($7\frac{1}{2}$ inches) (Holroyd 1964a) or even 23 cm (9 inches) (Thurston 1951a), but the deeper the seed is buried the less the chance of its shoot emerging (Tingey 1961, Fykse 1970) and yet many do germinate at depth (Anghel and Raianu 1960, Fykse 1970). *A. ludoviciana* too has emerged from 20 cm (Barralis 1965). If this is generally true then there can be no conservation of seed from dormancy enforced through deep burial, such as occurs with most other annual weed species. However, Wilson and Cussans (1972) and Wilson (1972) found burial did conserve seed and suggested that the self-burying mechanism might be very important. Hopp (1957) found no conservation effect over a 2-year period; but Banting (1966a) did find that deep burial increased the length of seed survival. In the Duvel buried seed experiment (Goss 1924, Toole and Brown 1946), There was 9% germination of seed (when brought to the surface) after 1 year's burial at 20 cm (8 inches) depth, and 18% of seed from 107 cm (42 inches), though it is doubtful whether this difference is significant. Anghel and Raianu (1960) obtained similar results with seeds buried between 20 and 40 cm deep after 1 and 2 years. On the other hand, Lewis (1958) obtained better germination of seed buried at 13 cm (5 inches) than of seed at 25 or 38 cm (10 or 15 inches) after 1, 2 and 4 years. The evidence on the effect of burial on the length of seed viability is therefore somewhat inconsistent.

THE EFFECT OF DORMANCY UPON SEED SURVIVAL

Enforced dormancy, as defined by Harper (1957), occurring through burial or other environmental conditions, may or may not influence survival; but

innate or induced dormancy (Harper 1957) apparently does not affect the pattern of viability loss (Banting 1966a). Forbes (1963), too, reports that, although seeds were able to survive up to 8-9 years under a ley, there were in fact few dormant seeds after 5 years, for most remaining wild oats could then be induced to germinate by a single spring fallow.

THE EFFECT OF FUNGI AND BACTERIA UPON SEED SURVIVAL

There are several reports in the literature that micro-organisms affect, depress or inhibit the germination and hence survival of wild oat seeds. Voderberg (1965) reported that seeds were damaged by pathogenic fungi and Kurth (1967) thought that the rate of reduction of a wild oat population from 663 plants/m^2 to 0/m^2 over 5 years, when seeding was prevented, was associated with the vulnerability of the seed to micro-organisms. Kiewnick (1961, 1963), in detailed studies of the relationship between micro-organisms and wild oat seed, isolated 52 species of fungi from spikelets of *A. fatua.* Two were Phycomycetes, 5 Ascomycetes and 45 were Fungi Imperfecti. Seven species were found to be pathogenic and plants attacked by *Fusarium culmorum* produced sterile seeds. Rademacher and Kiewnick (1964) showed that *Fusarium* species in the soil and *Chaetomium globosum,* which infests the glumes, inhibited germination of seed, especially in low fertility soils. Up to 15 species of fungi were found per sample of oats (*Avena* sp.) in Italian fields, but their effects if any were not investigated (Rosemberg and Gambogi 1959, Gambogi 1960).

The action of fungi on seeds is influenced both by the season and the conditions. Germination is depressed by the microflora at the peak of its growth in spring and autumn (Kiewnick 1964). Moisture is important here, for seeds kept at 20-22° C and 100% relative humidity for 6 months had their viability decreased by 35% as compared to seeds kept at 60-80% relative humidity (Kiewnick 1963). Fungi are most active in soil at 50% water capacity, but higher water levels induce secondary dormancy in wild oat seeds, which makes them more susceptible to the microflora (Kiewnick 1964) (See also Chapter 10, p. 000 *et seq*).

No evidence is available that fungi affect dormancy (as opposed to viability), although ungerminated seeds have been observed to have 10-50 times as many yeast colonies on them as germinated ones (Kommedahl *et al* 1958).

Bacteria have not been investigated, but there is evidence which suggests that wild oat hulls (palea and lemma) contain a bacterial inhibitor (Naylor and Christie 1957).

THE DURATION OF VIABILITY IN DRY STORAGE

In general, seed viability is retained longer in dry storage than in the soil and dormancy too is more prolonged. Over a period of 2 years, wild oat seed was found to retain its viability better under dry conditions than it did in the soil (Hopp 1957). Seeds stored in a granary (Lewis 1958) showed 62%

germination after 2 years, although it was down to 8% in the fourth year. In contrast, Bachthaler (1957) reported a rapid loss of seed viability after 2 years in dry storage. The loss of dormancy in dry storage was found by Kurth (1965 and 1967) to be only 5% after 6 months, 10% after 12 months, 25% after 24 months, 54% after 36 months, 76% after 48 months and 79% after 52 months. The observations of Thurston (1961) were very similar in that *A. fatua* seeds after 4 years of dry storage yielded 72% germination with 28% dormancy; but *A. ludoviciana* had apparently a shorter period of dormancy, for 86% germinated with none remaining dormant. Subsequently (after 8 years), the first seeds on spikelets of *A. ludoviciana* were tested alone and gave 98% germination with 1% dormant. Fifty-year old seeds, possibly of *A. fatua,* stored in unsealed glass jars at room temperature were dead when tested, but one of two samples that were 25 years old gave 4% germination (Simon 1958). One batch of *A. sativa* germinated after 125 years.

SEED SURVIVAL IN WATER OR WATER-LOGGED SOILS

Bruns (1965) found that no wild oat seeds germinated after being submerged for 6, 18 or 42 months in a fresh-water canal at Washington, USA. Rademacher and Kiewnick (1964) showed that seeds were dead by 49 days after submersion, and survival was reduced to only 36 days if air trapped in the glumes was removed. Similarly wild oat seeds were found not to survive 2 months in water-logged soils (Lewis 1961).

SEED SURVIVAL AT EXTREMES OF TEMPERATURE AND UNDER γ-IRRADIATION

In wintry conditions seeds have been damaged by frost (Voderberg 1965), or killed when they were on the soil surface (Thurston 1962b, Fykse 1970), or when buried at 3 cm depth outside in a Russian winter for 66 days (−19.6° to −29° C) (Topornina 1958).

At the other end of the temperature scale, dormancy has been induced in *A. ludoviciana* by keeping seed for 7 weeks at 27° C, and seed killed when kept at 32° C for 2 months: at 27° C, 50% of *A. fatua* seed died and 90% of the rest became dormant (Thurston 1963b). At higher temperatures for shorter periods, Metz (1970) found that it took 90 minutes at a minimum of 120° C to kill mature caryopses, while after 110° C for 10 minutes the seeds gave 96% germination. Yet Hopkins (1936) found that 15 minutes at 105° C was sufficient to kill all seed. After 15 minutes at 100° C there was 7% germination, while at 90° C and below for the same time there was no reduction of viability. Seeds of *A. fatua* and *A. ludoviciana* in sacks have been passed through a sack drier and, although temperatures reached 81-135° C and 105° C was maintained or exceeded for 4-7½ minutes on the sides and faces of the sacks, a maximum of only 40% of the seeds were killed (Williams and Thurston 1964). A flame gun generating 1100-1200° C killed seeds of *Avena* spp. in about ¼ second (Vyalykh 1971). At sub-lethal temperatures, as

in stubble or straw burning in the field (Thurston 1964b; Whybrew 1964) dormancy was broken by the heat.

Tests to investigate the possibility of killing seed in soil by γ-irradiation showed that all non-dormant seed was killed by 20-50 kR, while lower doses (2-4 kR) merely stimulated germination (Süss and Bachthaler 1968). They concluded it would be economic only for small quantities of soil.

THE EFFECT OF SOIL TYPE UPON SEED SURVIVAL

Hopp (1957) found that there was no clear difference between soils in seed survival over a 2-year period. Fykse (1970) found that germination was best in the first year in a humic soil as opposed to a loamy-sand and a sandy-loam; but that seed perished more quickly in the humic soil. Swedan (1970) also found germination to be quicker in a peat soil than in sand or in a loam during a 6-month period. On the other hand Bachthaler (1957) found germination to be as good in alkaline peat as in heavy alluvial soils and that pH and soil structure were only of indirect importance. Watkins (1971) reported that soil pH had no effect on germination of *A. ludoviciana*. Fykse (1970) confirmed the finding of Lewis (1958) that seeds survived longer in mineral soil than in peat. These reports, which are consistent in that peat usually appears to favour speedy germination, indicate perhaps that aeration or some other factor in peat encourages early germination and so rapid exhaustion of seeds. Cates (1917) reported that seeds in stiff clays did not survive beyond 2 years, but in lighter soils they survived for 4-6 years.

THE EFFECT OF MANURE, COMPOST AND SILAGE UPON SEED SURVIVAL

Caryopses survived long periods when composted (Wiberg 1959); but only 7 weeks in farmyard manure (Metz 1970). A small proportion of wild oat seeds remained viable for 12-13 weeks in a manure heap (Kirk and Courtney 1972). When seeds were buried in various places in a manure heap, it was found (Courtney 1973a) that those at the base of the heap, where temperatures were lower, survived longest. He also found that when seeds were scattered on bedding in a bullock pen some survived for at least 3 months. Romashkevich (1960) found that seeds of *A. fatua* did not survive 21 days in fermenting dung.

Hopp (1957) found, in a 2-year test, that seed longevity in soil was unaffected by applications of dung, green manure or fertilisers while Thurston (1964b) found that farmyard manure applied to soil stimulated seeds to germinate though not so many as did an inorganic NPK fertiliser (Rademacher and Kiewnick 1964).

Rieder (1966) tested six batches of seed collected in three separate years in liquid manure. Five batches did not survive 20 days, but the sixth was still giving 53% germination after 40 days. This was confirmed in general by Metz (1970) who found 21 days to be the limit of seed survival in liquid manure. Courtney (1973a) also found that *A. fatua* seeds were killed by six weeks in

pig slurry, but a few survived in a fairly dry beef cattle slurry. After two months in silage made from sugar beet tops or waste, no seeds germinated (Denmark 1960), while Metz (1970) found seeds did not survive longer than 14 days in silage.

THE EFFECTS OF ANIMAL DIGESTION ON SEEDS

Atkeson *et al* (1934) fed wild oat seeds (74% viability) to cattle and, of those retrieved after 47 hours digestion, only 10% were viable. Of 2000 seeds of *A. ludoviciana* fed to a calf, only 10 passed through undamaged and germinated (Thurston 1963b) and yet Metz (1970) reported that seeds of *A. fatua* fed to cattle were mostly passed through undigested. Kirk and Courtney (1972) found that up to 12% of *A. fatua* seeds were viable after passing through bullocks. The effects of other animals are unknown.

THE GERMINATION OF WILD OAT SEED

VARIATIONS IN GERMINATION BEHAVIOUR

The main species of wild oat (*Avena fatua* L.) has been divided into subspecies and/or varieties and tested for differences in seed behaviour (Sexsmith 1959a,b,c, Rijkslandbouwhogeschool 1961a, etc). In Belgium (Rijkslandbouwhogeschool 1961a) dormancy in *A. fatua* ssp. *septentrionalis* var. *valdepilosa* was found to be very much lower than in other varieties (89% germinated as compared to a mean of 15% for other varieties). A similar result was reported by Thurston (1963b). In Norway, Fykse (1970) found little or no difference between varieties in respect of total seed viability, their temperature requirements for germination, their response to chemicals and the effects of storage upon them; but they differed considerably in the duration of their after-ripening period and consequently in the time of achieving maturity. The last character was inconsistent even for samples of a single variety obtained from a single field. In Canada and elsewhere (Johnson 1935a, Lute 1938, Toole and Coffman 1940, Baker and Leighty 1957, Bachthaler 1957, Sexsmith 1959a,b,c, 1967, 1969 and Marshall and Jain 1970) marked differences between various collections of wild oat seed have been reported.

According to Coffman and Stanton (1938), freshly harvested seeds of cultivars of *A. sativa* showed all degrees of prompt, slow and delayed germination, while seeds of *A. byzantina*, *A. fatua* and *A. sterilis* var. *ludoviciana* (= *A. ludoviciana*) were all slow or delayed. A single variety of *A. nuda* germinated promptly. After storage for 7-10 weeks, only two cultivars of *A. sativa* and *A. sterilis* var. *ludoviciana* still showed slow or delayed germination. They found dormancy was not particularly associated with time of maturity, growth habit, cold resistance or moisture content.

The duration of dormancy varies, not only between different types of wild oats, but also between seeds in different positions on the same panicle (Johnson 1935a, Thurston 1963b) and, too, between the primary and

secondary florets of a single spikelet (Thurston 1969). The primary florets required a shorter period of after-ripening than the secondary ones (Johnson 1935a, Rijkslandbouwhogeschool 1960). Guillemenet (1971a) found this was especially true of *A. ludoviciana.* These features have also been found in *A. sativa* (Schwendiman and Shands 1943). Studies (Thurston 1964a) on *A. fatua* have shown the importance of the latitude of the place of origin in determining the time of flowering, the numbers of seeds produced and the percentage of seeds that were dormant.

Soil type appears to have no influence upon seed vitality; but seeds produced by plants grown on a fen soil appeared to have less dormancy than those grown on other soils (Odgaard 1972). However, the plants on fen soil were slower growing and later maturing: this result might therefore have been due simply to seed immaturity (see Thurston 1963b).

These variations should be borne in mind when considering the following data on germination and dormancy.

PERIODICITY OF GERMINATION

Avena fatua germinates mainly in the spring and to a lesser extent in autumn, although this pattern is influenced to some extent by the varieties present (as mentioned above) and by the conditions (Malzew 1930, Fykse 1970). Further details of the germination periodicity are given by Chepil (1946) and by Thurston (1961, 1963b). Chepil reported that, under Canadian conditions, *A. fatua* germinates between mid-April and the end of October, with the spring peak between mid-April and the end of May, and the later peak in July. The spring peak is possibly slightly earlier in England (Thurston 1961), because of climatic differences. Tingey (1961), in America, has, however, reported that *A. fatua* tends to emerge more often in autumn than in spring. This might indicate that under his conditions there was less, or shorter, dormancy and/or a better opportunity for autumn germination. Alternatively, the plant was *A. fatua* ssp. *septentrionalis,* which has a similar germination pattern to *A. ludoviciana* (Thurston: personal communication).

A. ludoviciana, the winter wild oat, germinates mainly in the autumn with a lesser peak in spring, at least in the first year (Thurston 1961). Thus *A. fatua* in England germinates mainly in March-April and *A. ludoviciana* in October-March (Thurston 1963b).

Guillemenet (1971a) in central France tested freshly-shed seeds of *A. fatua* and *A. ludoviciana* by planting them in soil in October. After six weeks most of the lower seeds of *A. ludoviciana* spikelets had germinated and he concluded they had no dormancy; but, of the upper seeds, only 26% had germinated and, even at the end of the following March, only a further 31% had done so. He concluded that the dormancy of some seeds had been broken by the winter's cold, but the residue would have to wait until the next autumn to germinate with the new crop of lower seeds. *A. fatua* (mixed lower and upper seeds) showed 63% germination after six weeks and a further 14% by the end of March. They were intermediate in emergence between upper and lower seeds of *A. ludoviciana* (perhaps because they were mixed). This

report of mainly autumn germination by *A. fatua* supports that of Tingey (1961).

THE INFLUENCE OF TEMPERATURE ON GERMINATION

In laboratory or glasshouse experiments, the range of temperatures within which *A. fatua* germinated varied between 2° and 35°C (Koch 1968), 4° and 30°C (Kurth 1967), 4° and 20°C (Anghel and Rainu 1960), 6° and 24°C (Dubetz *et al* 1962) and at least between 10°C and 21°C, but not at 4°C (Friesen and Shebeski 1961). Quail and Carter (1968) found that both *A. fatua* and *A. ludoviciana* germinated in a glasshouse only when the mean weekly minimum was below 20°C and the mean weekly maximum below 28°C. The optimum temperature for *A. fatua,* which presumably includes least dormancy and the most rapid germination, was reported as being 10°C (Thurston 1963b), 15°C (Koch 1968), 18-20°C (Kiseleva 1956) and 24°C (Dubetz *et al* 1962), although Friesen and Shebeski (1961) stated that germination at 10°C was slow and after 28 days had only reached 75% of that obtained at higher temperatures. The optimum temperature for germination of *A. ludoviciana* has been reported as 10°C (Quail and Carter 1969) and as 7-13°C (Thurston 1963b). *A. sterilis* at 10°C took nine days before starting to germinate, at 7°C 15 days and at 4°C 21 days. Similarly, increasing periods of time were required to reach full germination, which varied from 45-58% (Ellern and Tadmor 1966).

In the field in Germany, Kühnel (1965) found that germination of *A. fatua* occurred 10-14 days after the soil temperature first exceeded 5°C, while, in Russia, Zverev (1966) found germination occurred when the soil temperature reached 10-13°C and practically ceased again when it reached 20-22°C. More recent work in England (Chancellor and Peters 1972) showed that germination was initiated when the soil temperature reached 6-7°C.

Germination of both *A. fatua* and *A. ludoviciana* were relatively good at 10°C, but at 5° and 18°C they showed contrasting behaviour. At 5°C the germination of *A. fatua* was poor while that of *A. ludoviciana* was good; but at 18°C the positions were reversed. The poor germination of *A. ludoviciana* at 18°C may be due to a single recessive gene and the poor germination of *A. fatua* at 5°C to three further recessive loci (Whittington *et al* 1970). However, they caution that the germination behaviour may be equally well attributed to environmental factors during grain development; such factors are known to have marked effects on germination.

THE EFFECTS OF LIGHT ON DORMANT AND NON–DORMANT SEEDS

Earlier workers on the behaviour of wild oat seed suggested that light had no effect upon seed germination (Zade 1912, Atwood 1914); but, unlike many other weeds (Wesson and Wareing 1969), light is now known to be inhibitory to the germination of wild oat seed. However, Johnson (1935a) found that light, although inhibitory to the germination of fully ripe seed, stimulated germination slightly during the early stages of after-ripening. Cumming

(1957) found that light decreased the germination of 'partially dormant' seed, but not of non-dormant seed and Black and Naylor (1957) that both tungsten and fluorescent light proved inhibitory.

Various factors influence the effect of light. Seeds in their pales have been reported to be most responsive to light (Hart and Berrie 1966). Thurston (1963b), however, has suggested that light is unlikely to penetrate the hulls, particularly as in Britain they are frequently dark-brown in colour; nonetheless long-days of 16 hours did have an inhibitory effect upon both *A. fatua* and *A. ludoviciana* (Thurston 1964a). It has also been reported (Quail and Carter 1969) that, in continuous light, *A. ludoviciana* seeds after-ripened more rapidly than in the dark, despite light being inhibitory to germination. This, they suggested, indicates that after-ripening and germination are two separate processes. Lack of carbon dioxide increased the degree of inhibition by light, but increasing the level of CO_2 to 3% (by volume) offset inhibition completely (Hart and Berrie 1966). Further increase to 20% inhibited germination again, both in light and dark. Water also influenced the effects of light. It was found that, with small amounts of water, the seed was inhibited, but with excessive amounts germination was promoted as compared to seed kept in the dark (Hsiao and Simpson 1971). Furthermore blue, red and far-red light all inhibited germination with small amounts of water, but with large amounts there was no difference between them and darkness. Cumming and Hay (1958) found that white, blue and infra-red radiation inhibited 'partially dormant' seeds, but not non-dormant ones, nor ones in which dormancy had been broken. However, they found that red light had no effect.

These findings throw doubt on whether seed burial is useful to the plant. Cumming and Hay (1958) observed that in natural conditions only 10% of partially-dormant seeds on the surface germinated, while seed buried at one inch, or left on the surface in the dark, germinated 55-65%. To bury fresh seeds and so encourage their germination should help therefore to reduce populations. Indeed, Cumming (1957) found that autumn cultivations did encourage this and so helped to reduce infestations, although Kollár (1968) reported that more seeds germinate on the surface than when shallowly buried. However, even if seed is not buried, Banting (1962) found that the light inhibition system does not greatly prolong seed survival; so it is probably better not to bury the seed, because burial is possibly more likely to lead to survival on other grounds (Wilson and Cussans 1972). Covering the ground with straw in autumn has been found to have little effect on germination of *A fatua* in the following year (McCurdy 1960a).

THE EFFECTS OF TILLAGE ON GERMINATION

Cultivation appears generally to increase germination provided it is carried out during a period when germination occurs naturally. Banting (1966a), for example, found that cultivation in mid-July had little effect on germination and hence on persistence. In two experiments, Bibbey (1935) found that 5-6 times more seedlings emerged on cultivated than on uncultivated soil, and

concluded that soil aeration might be an important factor. This was confirmed by work with harrows by Müllverstedt (1963b). On the other hand Thurston (1961) did not find cultivations stimulatory to germination, which she found was determined more by properties of the seeds themselves than by cultivations or weather. Whybrew (1964) found that stubble cultivations over eight years caused more seeds to germinate in autumn, but this did not prevent an increase in wild oat populations in spring barley sown at the normal time. In six experiments over two years, early autumn (as compared with late autumn) cultivations resulted in a two to three-fold increase of seedlings in the following spring, possibly because burial helps retain viability better (Wilson and Cussans 1972). Fykse (1970) found that the effects of a fallow prior to sowing spring cereals depended upon the variety of wild oats present. In general, harrowing delayed germination which, with early cereals, was useful.

THE VIABILITY OF IMMATURE SEEDS

Unripe seeds of both *A. fatua* and *A. ludoviciana* were found by Thurston (1963b) to be viable and non-dormant. Kurth (1965) found *A. fatua* seeds were not viable at the milk stage, but were viable at the waxy stage and were dormant when ripe. However, the speed of onset of viability and dormancy were affected by the conditions during formation (Thurston 1963b) just as the percentage of seed that became dormant was influenced by the temperature during their development (Sexsmith 1969). Quail and Carter (1969) reported that 60% of primary seeds of *A. ludoviciana*, that were viable, were dormant by one week after anthesis and Thurston (1953a, 1963b) showed that, in *A. ludoviciana*, 80% of the first seeds and 100% of second seeds might be dormant by 25 days after anthesis. However, dormancy, when it does occur in immature seeds, was found to be more prolonged than in more mature seeds collected 21 days later (Barralis 1965). The time of onset of viability and dormancy in maturing caryopses of *A. fatua* was investigated in Canada by Andrews and Simpson (1969). They found that seeds of a non-dormant strain germinated as early as 10 days after fertilisation, but those of a dormant strain did not germinate at all during development.

THE PROPORTION OF SEEDS PRODUCING SEEDLINGS

As this can only be accurately investigated by sowing seeds, the relevance of the results to natural populations is inevitably open to question; but it is of interest that all three reports in the literature give somewhat similar figures. Thurston (1961) recorded that, in an experiment with 3000 seeds sown per plot with various cultural treatments over seven years, 20% of the seed yielded seedlings. In another experiment Tingey (1961) found all seedlings that emerged from sown seed had done so by the third year and that they formed 10% of the original seed. Finally, in a greenhouse experiment, Quail and Carter (1968) found that 30% of seed sown gave rise to seedlings. Whether or not these results relate to natural germination is unknown.

THE EFFECTS ON SEED GERMINATION OF SPRAYS APPLIED TO THE PARENT PLANT

2,4-D, MCPA and 2,4,5-T applied at 1.1, 2.8 and 5.6 kg/ha all decreased seed numbers slightly with increasing dose (Aamisepp 1959). 1.1 and 2.8 kg/ha had no effect upon germination; but at 5.6 kg/ha they increased germination to varying degrees. Dalapon was tested at 0.56, 2.24 and 6.7 kg/ha at six stages of growth (Anderson and Helgeson 1958). 0.56 kg/ha had no effect upon germination or survival of the seedlings; 2.24 kg/ha delayed emergence by one week, which many later outgrew, while 6.7 kg/ha not only delayed emergence by a week, but also affected the seedlings, so that only 2.7-8.3% of them survived 5-6 weeks. Dalapon at 4.48-17.9 kg/ha applied at the boot stage did not prevent viable seeds being formed, but most of the seeds from treated plants failed to develop beyond the coleoptile stage (Anderson and Helgeson 1955b). A 5% solution of sodium cacodylate and 10 and 15% solutions of dalapon applied to inflorescences of *A. fatua* at the milk stage prevented formation of viable seeds except by secondary untreated inflorescences (May 1972). Maleic hydrazide has proved perhaps the most interesting and potentially useful chemical for control. Application of 0.49-0.56 kg/ha when the seed was at the milky stage reduced germination from between 53-58% down to 0-7% (Banting 1960). At 0.28, 0.56 and 1.12 kg/ha it has reduced total viability to 65%, 3% and 2% respectively (Hay 1955). Similar results were obtained with doses between 0.56 and 2.24 kg/ha applied at the milk or dough stage by Anderson and Helgeson (1955a), Brown (1955a), Ebell and Corns (1955), Friesen and Walker (1955) and Molberg and Leggett (1955a). Knowles (1953) successfully prevented seed set in one season by spraying emerged panicles with maleic hydrazide. Thurston (1963b), however, reported that maleic hydrazide was unsuitable because it caused damage to barley at concentrations giving less than 50% sterility in wild oats. Sulphuric acid used for pea desiccation killed two-thirds of wild oat seeds in emerged panicles and had no effect upon the dormancy of survivors; but, in a second field, no seeds were killed and 40% lost their dormancy (Thurston 1968). A 10% solution of glyphosate applied to inflorescences of *A. fatua* at the soft and hard cheese stages prevented formation of seed capable of producing healthy plants (May 1972).

THE EFFECTS OF CHEMICALS ON SEEDS

The effects of gibberellic acid and nitrates are discussed in relation to the breaking of dormancy (pp. 00-00). A number of tests have been carried out to see whether different chemicals at various doses either kill seed or stimulate germination by breaking dormancy. One of the earliest investigators, Johnson (1935a), found that ether and sodium thiocyanate had little effect, but chlorhydrin and dichlorethylene were definitely injurious to wild oat seed. In later tests, Peterson (1956) found that calcium cyanamide increased germination, but Wiberg (1959) found that it shortened the life span of wild oat seeds when applied in compost. Potassium sulphate, like potassium nitrate, stimulated germination (Sinyagin and Teper 1967), while

thiourea was found to have no effect (Swedan 1970). Fykse (1970) tested a wide range of chemicals containing nitrogen. The effects depended on dose as well as chemical and ranged from injurious to stimulatory. For seeds stored outside, potassium nitrate proved the most stimulating. Hoffman (1961) subjected seeds to hydrogen and ethylene at 703 kg/cm^2 for 15 minutes and then released the pressure suddenly. This raised germination from 4% to 78% and 62%, respectively.

Tests with herbicides have proved interesting. Friesen and Henne (1962) exposed intact or dehulled seeds to di-allate vapour for up to six days. Germination progressively decreased with increasing exposure and seedlings of survivors were abnormal. These effects were not reduced by storage of seed for up to 13 weeks after treatment and they concluded that the treatment could affect dormant seed. Hierholzer (1965) sprayed seeds on the soil surface with paraquat at 0.56, 1.12 and 2.24 kg/ha. Although the seeds germinated, they soon stopped growth and by 27 days all were dead. Seeds on the surface, or 2-2.5 cm deep, when sprayed with 5.6 kg/ha propham failed to emerge. Yet Rydrych and Sealey (1964) found that the susceptibility of seeds to propham varied with the strain. Sprayed with 5-6 kg/ha 2,4-D, MCPA and 3,4-D, there were 20-30% fewer seedlings, while 2,4,5-T at the same dose hardly affected emergence (Shebeski and Burrows 1954).

Osvald (1950) suggested that a root-exudate from rye inhibited seed germination in the field, but this was not confirmed by tests in England (Thurston 1962c).

DORMANCY IN WILD OAT SEED

THE OCCURRENCE OF DORMANCY

The occurrence of dormancy has already been discussed in connection with variations in germination behaviour (p. 00). Dormancy in *A. fatua* is innate (Andrews and Simpson 1969), develops during ripening (Thurston 1963b, Kurth 1965) or even later (Bibbey 1948). *A. ludoviciana* seeds have developed dormancy while maturing (Quail and Carter 1969).

The percentage of seed becoming dormant was influenced by the temperature during development (Sexsmith 1969). In England, 50% of the seeds of *A. ludoviciana* were dormant at harvest and with the exception of a single variety, 95% of the seeds of *A. fatua* were dormant (Thurston 1963b). A gradual loss of dormancy with time, the rate of loss being greatly influenced by the strain of wild oats and by the environmental conditions, has been recorded by Andrews (1967), Andrews and Simpson (1969) and Fykse (1970). Hybrids with cultivated oats (*A. fatua* x *A. sativa*) showed delayed germination (dormancy) to be an inherited recessive character, which was loosely linked with the *fatua*-type of seed articulation (Garber and Quisenberry 1923, Johnson 1935b). *A. barbata* Brot. seeds were found under American conditions to be completely dormant for 3-4 months after collection (Laude 1956).

In general, all diploid and tetraploid species or varieties of the genus *Avena* have a long dormant period with the exception of *A. abyssinica* and *A. strigosa,* which have none. In hexaploids the dormant period varies greatly, *A. fatua* having the longest (Nishiyama and Inamori 1966). In *A. fatua* L., 2n = 42; in *A. ludoviciana* Dur, 2n = 42; in *A. strigosa* Shreb. 2n = 14 (Clapham, Tutin and Warburg 1962).

THE BREAKING OF DORMANCY

Dormancy in the seed can be broken by various means, most of which break dormancy in other weed species. Potassium nitrate virtually overcame dormancy (Johnson 1935a) or reduced it (Hay and Cumming 1959), especially if followed by 10-14 days at 4.4-7.2°C (Baker and Leighty 1958). Dormant *A. sativa* has also responded (Schwendiman and Shands 1943). Bachthaler (1957) found that a fertiliser containing N, P and K had no effect at all. However, Sexsmith and Pittman (1963), Rademacher and Kiewnick (1964), Watkins (1966, 1970), Sinyagin and Teper (1967) and Fykse (1970) all found various fertilisers containing N stimulated germination of *A. fatua.* Watkins (1971) found that germination of *A. ludoviciana* also increased with increasing rate of fertiliser.

There are several reports that the presence of the hull (palea and lemma) enforced dormancy and that its removal allowed germination (Zade 1909, Ivanovskaya 1943, Bachthaler 1957, Baker and Leighty 1958, Hay and Cumming 1959, Anghel and Raianu 1960, Kurth 1965, Barralis 1965). Removing the hull lessened dormancy in *A. sativa* too (Shwendiman and Shands 1943). That the hull induces dormancy was proved by Naylor and Christie (1957), who tested ground-up hulls on dehulled caryopses under nitrogen treatment and found that dormancy was increased by 46%. However, dormancy can be induced even in the absence of hulls (Hay 1962) while germination can occur in the presence of a hull (Thurston: personal communication) so more than one type of dormancy can occur.

Pricking the seed or cutting off its distal end has been widely recommended as a method of breaking dormancy (Zade 1909, Johnson 1935a, Naylor and Christie 1957, Hay and Cumming 1959, Rijkslandbouwhogeschool 1960, Thurston 1963b).

Gibberellic acid has proved active in breaking dormancy of seeds. Hay and Cumming (1959), Simpson (1965) and others reported it to be effective. The effective concentration has been given as 50 ppm (Green and Helgeson 1957a, Helgeson and Green 1957a) and 500 ppm (Koch 1968, Swedan 1970), while 500-1000 ppm has been reported as effective only on some batches (Corns 1960). Thurston (1962a) reported that 25 ppm overcame dormancy in *A. ludoviciana,* but had no effect on *A. fatua.* There is some evidence too that there is a greater effect with increasing age of the seed (Green and Helgeson 1957); but Cobb and Jones (1962) reported that GA accelerated germination during the first 6-7 months only and after 12 months had no effect at all. Barralis (1965) reported that the presence of palea and lemma reduced the effect of GA. The important influence of GA on dormancy was demonstrated

by Black and Naylor (1959) who prevented seed dormancy by allowing maturing inflorescences to take it up. On the other hand excised embryos are very sensitive and have been used to bioassay GA. Concentrations lower than 10^{-3} ppm have been detected (Naylor and Simpson 1961b). Helgeson and Green (1958) showed that extracts from wild oat seedlings were effective in breaking seed dormancy. Hybrid seed (*A. sativa* x *A. fatua*) was also stimulated by GA (Andrews and Burrows 1972).

Levels of oxygen and carbon dioxide are of importance in germination and dormancy. Atwood (1914) thought that delay in germination was mainly due to restricted oxygen supply to the embryo, possibly by the seed coat (which is the pericarp and testa fused). Johnson (1935a) found that air enriched with oxygen increased germination although pure oxygen had little effect. Baker and Leighty (1958) also found that increasing the oxygen content increased germination slightly, although one batch of seed did not respond. Johnson believed that after-ripening might consist of changes in the seed coat, which allowed increased permeability to oxygen. Müllverstedt (1961, 1963a) found that *A. fatua* required 6-8% of oxygen to start germinating and 12% to achieve 75% germination in soil. Hay and Cumming (1959) and Cobb and Jones (1962) found hydrogen peroxide stimulated germination. The effect of carbon dioxide varied with the level present (Hart and Berrie 1966). A lack of carbon dioxide increased the inhibition of germination by light; but 3% CO_2 allowed germination in light, while 20% inhibited germination again, both in light and dark and at all levels of oxygen.

Hoffman (1961) found that, if seeds giving 4% germination were subjected to 703 kg/cm^2 for 15 minutes in hydrogen or ethylene followed by a sudden release of pressure, then germination was increased to 78 and 62% respectively. Süss and Bachthaler (1968) reported that γ-irradiation at doses of 2-4 kR stimulated germination of *A. fatua.*

THE EFFECTS OF TEMPERATURE ON DORMANCY

The evidence on the effect of temperature levels or changes upon dormancy is somewhat conflicting, possibly because seed batches differ in their requirements and because there appear to be interactions with other factors such as moisture and age of the seed. Low temperatures would be expected to break dormancy and several reports confirm this, but whether the operative factor is the level to which the temperature descends or the extent of the fluctuation itself is often uncertain. Kurth (1965), for example, found that temporary reductions of temperature increased germination. Chilling of *A. fatua* seed was found essential to break dormancy in some instances (Zade 1909, Bornemann 1910) and of *A. ludoviciana,* too (Barralis 1965). Freezing was also effective (Johnson 1935a) and even -10°C for 7 days increased germination from 28% to 44% (Rijkslandbouwhogeschool 1960), but for longer periods this low temperature might well kill the seeds (Topornina 1958, Thurston 1962b, Fykse 1970).

At higher temperatures there are several reports of dormancy breaking. Seed kept at 6-9°C lost dormancy, from 72.5% at 18 days to 43.5% after 66 days (Topornina 1958), though whether this was solely a consequence of the temperature is unknown. Seeds (*Avena* sp.) with or without hulls given 17 days at 20-30°C before planting produced more seedlings than those planted direct into soil (Ivanovskaya 1943). *A. fatua* keeps viability longest and loses most dormancy at 10°C (Thurston 1963b) and dry storage at 16°C for five months has reduced dormancy to 50%, although storage at 4°, 7° or 21°C had less effect (Thurston 1963a). Banting (1966b) reported warm dry conditions as conducive to dormancy breaking: it took three years to after-ripen seed stored at 18°C and 40°C alternately; but at < 18°C some seed was still dormant after five years. The presence or absence of the hulls (palea and lemma) is reported by Fykse (1970) to influence the effect of temperature: seeds enclosed by their hulls germinated better at 20°C, while those without hulls germinated better at 10°C. *A. ludoviciana* is reported as after-ripening more rapidly with increasing temperatures up to 30°C, with the optimum levels lying between 25-30°C (Quail and Carter 1969).

Temperature is also important in the development of primary dormancy. Sexsmith (1969) grew two varieties of *A fatua* in a greenhouse at different temperatures and found that 31 to 100% more dormant seeds were produced by plants grown at 15.6°C in moist soil than by plants grown at 26.7°C in drier soil. The difference was affected by the age of the seed and the variety grown.

Having lost the primary dormancy, seed can still have secondary dormancy induced in it under certain conditions. Indicative of the conflicting nature of the data is the report by Kiseleva (1956) that the temperatures (0-5°C and 25-30°C) most likely to break primary dormancy are equally able to induce secondary dormancy, especially in freshly-collected seeds. This is confirmed by another report that dormancy can be induced in *A. ludoviciana* by keeping seeds at 27°C for seven weeks (Thurston 1963b). However, in *A. fatua* seeds kept at 27°C for seven weeks, half the seeds died and, of those surviving, 90% were dormant. The interaction of moisture with temperature was recorded by Bachthaler (1957), who stated that dormancy can be induced in imbibed seeds by fluctuating temperatures, but the degree of imbibition is important. Conversely, in dry seeds, fluctuating temperatures increased germination. In addition, he records that cold, wet, soil conditions will also induce secondary dormancy. Once seed is dormant it has been found that low temperatures and dry storage will prolong the dormancy (Johnson 1935a). At higher but sub-lethal temperatures, such as occur when stubble or straw is burnt in the field, dormancy can be broken by the heat (Thurston 1964b, Whybrew 1964). Seedling emergence in the following year was found to be greater on burnt than on unburnt areas (Viel 1963). Seeds collected from burnt-over stubble gave 9% germination as compared to 3% from unburnt areas (Brown 1953). Stubble burning was found to be equal to N fertiliser in stimulating germination of *A. ludoviciana* (Watkins 1970); but there was no need to do both, as burning after adding fertiliser did not increase seedling emergence. It could be that burning acts in part by making more nitrogen available.

THE EFFECTS OF MOISTURE ON DORMANCY

Moisture has several effects, both direct and indirect, on seed dormancy. Without water, seeds cannot germinate; with excess water, secondary dormancy can be induced, especially when the level of oxygen is low (Hay and Cumming 1957, Lewis 1961, Kiewnick 1964, Banting 1966b, Andrews and Burrows 1974). An excess of moisture with fluctuating temperatures has also led to secondary dormancy (Bachthaler 1957). Prolonged excess of moisture leads eventually to death and autolysis of the seed (Lewis 1961, Kiewnick 1964, Banting 1966b). In between absolute drought and excessive moisture, fluctuations between wet and dry are reported by many to stimulate germination (Zade 1909, Munerati and Zapparoli 1912, Wehsarg 1927, 1954, Bachthaler 1957, Banting 1966b). Black (1959) suggested that water can also affect dormancy by leaching out inhibitors. Atwood (1914) stated that after-ripening was independent of the water content of the seed and that dormancy in several *Avena* spp. was found to be largely independent of moisture content, although those with a higher moisture content did not germinate so rapidly (Coffman and Stanton 1938). Yet Quail and Carter (1969) found that, with increasing temperatures up to 30° C and with increasing relative humidities between 16 and 100%, seed of *A. ludoviciana* after-ripened more rapidly. Hsaio and Simpson (1971) also found that the water content of the caryopsis interacted with several other factors to affect dormancy.

Kiewnick (1964) studied the influence of moisture on seeds and the microflora. He found fungi were most active at a soil water capacity of 50%, but a higher level than this induced secondary dormancy in the seed, which increased susceptibility to the microflora. He found that the optimum soil moisture level for germination of wild oat seed was between 14.6 and 17%. In contrast, Koch (1968) found the greatest number of seedlings emerged when the soil moisture was between 70 and 90% of the total water capacity.

Tests carried out by Sexsmith (1967, 1969) showed that external conditions during growth and maturation of wild oat seeds modified the genetic expression of dormancy. Plants grown in 15.6° C in moist soil (75% available moisture) produced 31-100% more dormant seeds than plants grown at 26.7° C in drier soil (25% available moisture).

THE INDUCTION OF SECONDARY DORMANCY

Primary dormancy can be lost under natural conditions after a variable period of time, or seed may not have it at all. While in the non-dormant and as yet ungerminated state, a seed can acquire secondary dormancy naturally (Banting 1966a) or it can be artifically induced by soaking in boiled water (Hay 1955, Hay and Cumming 1959). The presence of palea and lemma can prevent its induction, possibly because air is trapped around the caryopsis (Barralis 1965). Wet conditions with a lack of oxygen appear to be the main causes of secondary dormancy (Black 1959, Hay 1962, Voderberg 1965, Hart and Berrie 1968) although certain temperatures can also influence it, for more secondary dormancy was induced at 25° C than at 7° C (Hay 1962) and

at 24°C than at 18°C (Kommedahl 1958). It can be induced by fluctuating temperatures under moist conditions (Bachthaler 1957), by high temperatures (25-30°C) (Kiseleva 1956, Thurston 1963b) and by low ones too (0°-5°C) (Kiseleva 1956). Johnson (1935a) found that placing 'incompletely after-ripened' seeds under germinative conditions also induced secondary dormancy. Soaking seeds in coumarin increased the amount of dormancy induced, but MH, IAA, 2,4-D and a number of metabolic inhibitors did not (Hay 1960). When seeds of Dormoats (*A. sativa* x *A. fatua*) with primary dormancy failed to germinate, a secondary dormancy was induced, which could be broken by 2-3 weeks at −10°C; but not by 4 months at +2°C (Canada 1972).

THE MECHANISM OF DORMANCY

Dormancy, or delayed germination as it has been called, is an inherited characteristic in wild oat, which behaves as a recessive in *A. fatua* x *A. sativa* crosses (Garber and Quisenberry 1923, Johnson 1935b). The basic mechanism involved in seed dormancy, although intensively studied, still remains largely unknown.

Dormancy was thought originally to be due to a restriction in the oxygen supply to the seed, probably through impermeability of its coat. The process of after-ripening or loss of dormancy was considered to involve changes in seed coat tissue, which increased its permeability (Atwood 1914, Johnson 1935a). Later investigations showed this to be incorrect (Naylor and Christie 1957, Simmonds and Simpson 1971).

The hull (lemma and palea) which surrounds the seed has been implicated in dormancy and may certainly regulate germination to some extent. Naylor and Christie (1957) found that the rate of germination was depressed by the presence of the hull. Ground-up hulls too when tested on dehulled caryopses increased dormancy from 16 to 62%. Furthermore, Black and Naylor (1957) found that a water extract of hulls inhibited lettuce germination. Anghel and Rainu (1960) showed that the percentage germination of *A. fatua* and *A. ludoviciana* could be increased if the lemma and palea were opened or divided and further increased if removed altogether. Chromatographed aqueous extracts of the hull showed two inhibitory regions (in equal amounts to caryopsis extracts) (Black 1959). He suggested that the hulls had a three-fold action (i) by the inhibitors they contained, (ii) by impeding gas exchange and (iii) by retarding leaching of inhibitors from the caryopsis itself.

Whatever the importance of the hull, the caryopsis itself is obviously the site of the main germination regulation system and the presence of a definite embryo dormancy in wild oats has been demonstrated by Simpson (1965). The importance of GA as a dormancy regulator has been frequently reported (see p. 79-80). Helgeson and Green (1957a) showed that 50 ppm of GA increased wild oat germination from under 13% to over 70% and realising the potential use of it suggested autumn applications in the field to break dormancy in freshly shed seed. In 1959 Black and Naylor made the important discovery that by allowing developing inflorescences of wild oats to take up

GA, dormancy could be prevented. Morgan and Berrie (1970) found that there was a gradient of dormancy in the seeds of individual spikelets of *A. ludoviciana.* The proximal seed was less dormant than the distal, and when a third seed was present it was extremely dormant. They proposed that dormancy in this species depends partly upon the supply of a promotive substance, which is shared among the seeds, and partly upon a process occurring within the caryopsis itself during ripening.

The presence of a GA-like factor was demonstrated by Simpson (1965), who showed that naked dormant embryos required an exogenous source of sugar, amino acids and GA for germination, but non-dormant ones germinated without GA. This factor was not present in freshly-matured dormant seed, but increased with after-ripening over several years before declining gradually. Later work by Andrews (1967) demonstrated three gibberellin-like substances in the caryopsis by extraction and bioassay. One occurred equally in dormant and non-dormant seeds and was associated with caryopsis and embryo growth, while the other two occurred more in non-dormant ones and were associated with germinability of the embryo.

Naylor and Simpson (1961a) suggested that dormancy is controlled by a GA/inhibitor antagonism and that the control of germination during after-ripening was by changes in the level of inhibitor and not of GA. Simpson (1966) further suggested that after-ripening may be the gradual loss of a natural growth retardant that prevents the synthesis of GA in dormant embryos. Hay (1962) suggested that the inhibitor of germination is an electron acceptor and that it blocks the electron transport system at some specific locus where there are no alternative pathways. Furthermore, if the inhibitor is active when in the reduced form and inactive when oxidised this could account for the apparent reversibility of dormancy. Also if the reduced (active) inhibitor is destroyed by oxidases that are activated by wounding, this could explain the stimulatory effect of pricking the seed or cutting off its tip. Andrews (1967) reported that a water-soluble inhibitor occurred in mature dormant embryos, which probably blocked GA synthesis. He suggested that the inhibitor was abscisic acid.

Once GA is produced, its action must lie somewhere along the chain of enzymatic processes that convert the resources of the endosperm to simple sugars for the energy requirements of the embryo during germination (Simpson and Naylor 1962). In 1961b, Naylor and Simpson found that excised embryos of *A. fatua* showed two responses to GA with different concentration optima. The higher dose (c. 50 ppm) was associated with the conversion of starch to sugar and the lower (0.1-1 ppm) with sugar utilisation. In 1962 Simpson and Naylor concluded that part of the stimulatory effect of GA was due to it inducing the synthesis of maltase or activating the pre-formed enzyme. Subsequent work by Chen and Varner (1969), in which labelled maltose was administered to the endosperm of dormant and non-dormant seeds, showed that while non-dormant ones readily converted it to sucrose in the scutellum (cotyledon) and translocated it to the embryo, dormant ones synthesised little sucrose and accumulated maltose and glucose

in the endosperm. They concluded that biosynthesis of sucrose was essential for transport of endosperm reserves to the growing embryo, and that dormant seeds could not synthesise it.

There have been suggestions that dormancy is occasioned by a lack of amylase for starch hydrolysis. Indeed, an amylase inhibitor in *A. sativa* cv. Victory, which could be leached out in running water to give increased germination, was reported by Elliott and Leopold (1953). The possibility that this was also the cause of dormancy in *A. fatua* was considered by Helgeson and Green (1957b). However, leaching for up to 48 hours had no effect upon germination of the seeds. Germination was inhibited in varying degree by extracts of lemmas and paleas and caryopses, and too of leaves, panicles and stems, but not by extracts from whole seeds or glumes (*A. fatua* straw has been shown to contain phytotoxic phenolic compounds that inhibit germination of other plant species in soil (Tinnin and Muller 1971, 1972)).

The question of amylase activity being the key to dormancy was further investigated by Drennan and Berrie (1962). They found in *A. fatua*, *A. ludoviciana* and *A. sativa* that increased amylase activity occurred after germination had started and suggested that the onset of activity in the endosperm was triggered by a stimulus from the growing embryo. Naylor (1966) showed that in excised aleurone tissue the synthesis of α-amylase could be started by giving GA or a mixture of amino acids and sucrose. In *A. fatua* enzyme synthesis in aleurone tissue was rigorously dependent upon GA from the embryo, a feature which he concluded would contribute to its seed longevity, whereas in *A. sativa* the aleurone was much more autonomous in terms of enzyme synthesis, which could account for the relatively short life of its seeds in the soil. This difference and its ecological significance were further considered by Naylor (1969). That amylase activity follows germination and does not start it, has been confirmed by Chen and Chang (1972) and Chen and Park (1973) who further showed that GA at 0.1 μM can stimulate amylase synthesis in dormant *A. fatua* seeds without inducing germination. The concentration of GA required to promote germination was normally greater than 10 μM. Thus rather than being the trigger to germination, amylase activity is itself triggered by GA which is produced during germination.

Hart and Berrie (1968) assayed malic and succinic acid in unimbibed seed of *A. fatua* populations, which had differing levels of dormancy. They concluded from the data that dormancy could be due to restricted activity of succinate dehydrogenase, but Simmonds (1971) presented evidence which suggested that this was unlikely.

Andrews and Simpson (1969) studied the onset of dormancy during maturation, but found unlike previous reports that seeds of a dormant strain did not germinate when immature, even as early as ten days after fertilisation. They showed furthermore that the nature of the endosperm did not influence germination and that dormancy lay within the embryo itself.

Chen and Varner (1970) reported that dormant seeds respire at a measurable rate and can synthesise protein at a rate comparable to that of

non-dormant seeds. Thus dormancy must be due to a specific metabolic block and not to gene repression. Chen (1971) later reported that protein may have been synthesised in dry dormant seeds of *A. fatua.*

Simmonds and Simpson (1971) showed that dormancy is not the result of restricted oxygen uptake, for the rate of oxygen uptake before germination is similar between dormant and non-dormant excised embryos and they showed too that GA can break dormancy without affecting oxygen consumption. They also reported that release from dormancy was associated with a shift in metabolism from the glycolytic pathway to the pentose phosphate pathway (see Roberts 1969). Dormant embryos given GA showed a similar change, which appears an essential preliminary for germination, but how this promotes germination is obscure. It appears therefore that it is the type rather than the rate of oxidative metabolism that is important in dormancy control. Simmonds and Simpson (1972) have presented a model indicating how dormancy control may depend upon Krebs cycle activity and suggest that one aspect of after-ripening may be the development of a mechanism which inhibits it, thus releasing oxygen for the alternative pentose phosphate pathway which is essential for germination.

Relatively little work has been done on the mechanism of secondary (induced) dormancy. Hay (1962) reported that the site of secondary dormancy was in the embryo or endosperm and not in the hull. Black (1959) found that when secondary dormancy is induced under anaerobic conditions there is a marked increase in total inhibitor level in the caryopsis. However, Hay (1962) found inhibitors in both dormant and non-dormant caryopses, which were not responsible for induced dormancy. Andrews and Burrows (1972, 1974) found that Dormoats (*A. sativa* x *A. fatua*) have germination increased by low temperatures (c. 7° C), when in primary dormancy, but not when in secondary dormancy unless 'partial after-ripening' has occurred. This may indicate differing systems of dormancy. Yet Naylor and Christie (1957) found that induced secondary dormancy was similar to primary dormancy both in persistence and in being broken by cutting off part of the seed coat. Hay and Cumming (1959) reported too that seeds in induced dormancy responded like those in primary dormancy to potassium nitrate, hydrogen peroxide, gibberellic acid, hull removal and puncturing of the seed coat. Hart and Berrie (1968) found that secondary dormancy induced by anaerobiosis results in a decrease of malic acid and an increase of succinic acid. Simmonds and Simpson (1972) suggested that the induction of secondary dormancy could be explained either by depletion of adenosine triphosphate, which would encourage Krebs cycle activity and so inactivate the pentose phosphate pathway, thus reimposing dormancy, or alternatively by the production of germination inhibitors. It is possible then that the two types of dormancy are the same.

The mechanism of dormancy is thus incompletely known. It does appear ultimately, however, to rest upon some trigger in the embryo which is set off, possibly by environmental conditions, and generates GA-like factors which in turn initiate growth of the embryo and release food from the endosperm for its growth. From the practical point of view, it would appear that the

prevention or the breaking of seed dormancy is the best aspect of seed behaviour to exploit for control of this weed. A search should therefore be made for suitable treatments which could be applied to the growing plant, to maturing panicles or to seed on the ground after it has been shed. This search has already started at the Weed Research Organisation, although preliminary tests have not been very successful (Chancellor and Parker 1972).

THE LOSS OF DORMANCY WITH INCREASING AGE OF SEED

Seeds, showing 10% germination when collected, kept outside for 0-3 months and then stored in the laboratory, gave 50% germination in December-January (Thurston 1962b). Seed kept indoors at 6-9°C gave 27.5% germination after 18 days and 56.5% after 66 days (Topornina 1958). Voderberg (1965) found that primary dormancy eight months from harvest is generally reduced by 50-65%. Kurth (1965) stored seeds dry and they stayed dormant for 4-5 months. Thereafter they lost dormancy with increasing age until after 4-5 years they gave 80% germination. Anghel and Rainu (1960) obtained 3% germination from three-day old *A. ludoviciana* seed, 67% from two-year old seed and 91% from three-year old seed at 10-20°C alternating temperatures. At a constant 20°C fewer seeds germinated. Seeds buried under a ley were reported (Forbes 1963) to have virtually lost all dormancy after five years. Although the conditions presumably affect the rate of dormancy loss, it appears in general that 50% germination can be obtained from about 2-8 months after the seed is shed and that dormancy is virtually lost after about 4-5 years.