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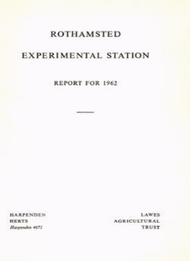

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BIOLOGY AND CONTROL OF WILD OATS

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Wild oats (*Avena fatua* L. and *Avena ludoviciana* Dur.) are serious annual weeds of temperate arable crops, especially cereals. They germinate after the cereals are sown, benefit from the same cultural conditions and shed many seeds before the crop is harvested, infesting the soil with seeds that may remain dormant for several years, producing successive crops of seedlings. Seeds harvested with the crop may block the sieves of the combine-harvester or thresher, and many are not removed but remain to infest the grain.

Wild oats are probably natives of south-west Asia (Malzew, 1930) and are thought to have reached Britain in imported grain. *Avena fatua*, with an abscission-scar and an awn on every floret, was associated with cultivated oats (*Avena sativa*) and other cereals from the Early Iron Age (700–500 B.C.) onwards, sometimes forming a high proportion of the stored grain (Jessen and Helbaek, 1945), and it is now the most abundant weed of cereals in Britain. *A. ludoviciana*, with an abscission-scar on the base of only the first floret of each spikelet, and awns on only the first and second florets, was not recorded in Britain until about the time of the First World War, when it probably arrived in wheat imported from France and in ballast and packing-materials at ports (Thurston, 1954).

Wild oats have long been a problem on Rothamsted farm, especially on Broadbalk, where winter wheat has been grown continuously since 1843, and on Hoosfield, with spring barley yearly since 1852. Whenever possible, wild oats have been controlled on these fields by hand-pulling. Grey (1922) tells of Sir John Lawes and his family and the local schoolchildren helping the farm staff with this work in the evenings. Recently it has been done by volunteers from the laboratory staff.

Broadbalk and Hoosfield became foul with wild oats during the labour shortage of the Second World War, and by 1944 there were almost as many wild oats as crop plants on some plots. Fallowing of one-fifth of Broadbalk each year since 1927, and of the whole of Hoosfield in 1943, failed to control wild oats, and this aroused interest in their biology and especially in seed dormancy.

At that time the only wild oat described in British floras was *A. fatua*, and there was no British work on the biology of wild oats. Publications from France, Germany, Canada, the U.S.A. and Russia (Lagrèze-Fossat, 1856; Zade, 1912; Rabaté, 1913; Clark, 1914; Cates, 1917; Chevalier, 1925; Malzew, 1930; Bibbey, 1935; Toole & Coffman, 1940) showed that wild oats might belong to more than one *Avena* species, that intraspecific variation was considerable and that wild oat seeds could remain dormant in field soil for as much as 5 or 6 years, depending on soil conditions and on the natural dormancy of the seeds. Soil compaction could induce dormancy of buried wild oat seeds. Control by rotation of crops, permitting destruction of seedlings by cultivation, was advocated, but this was inapplicable to experiments on continuous cereal growing. The possibility of spreading wild oats by sowing inadequately cleaned cereal seed was recognised, and also the possibility of transporting wild oat seeds from one field to another by uncleaned machinery, especially threshing-tackle.

Atwood (1914) and Johnson (1935) investigated the causes of dormancy in *A. fatua*, and showed that dormancy could be broken by increasing the amount of oxygen entering the seed, either by cutting or scorching the seed-coat, by soaking in potassium nitrate solution or by increasing the oxygen content of the surrounding atmosphere, and that the position of the developing seed on the panicle affected the onset of dormancy.

Coffman and Stanton (1938) investigated speed of germination in *Avena* species, including *A. fatua* and *A. ludoviciana*, but their seeds cannot have been fully ripe, and ripeness affects dormancy (Zade, 1912). Toole and Coffman (1940) compared germination of *A. fatua* seeds of different appearance and origin at different ages from a range of storage conditions, but their results are difficult to interpret, because they did not distinguish between dormant and dead seeds.

Hopkins (1936) found seeds of *A. fatua* among the most resistant to heat of those he tested, withstanding up to 15 minutes at 115°, which partly explains why Rabaté (1913) found stubble-burning ineffective in controlling wild oats.

Ivanovskaya (1943) found that dormancy of wild oat seeds of an undefined species from Siberia was overcome by removing the seed-coat from above the embryo, or by exposure to frost. Storing dormant seeds in warm air for 8 days also increased germination, 20–30° being more effective than 13–18° (presumably ° C). Seeds whose dormancy had been broken by several months' warm dry storage became dormant again after wetting and drying six times a day for 12 days, but would germinate after subsequent drying in air at 20–30° for 17 days.

Kirk and Pavlychenko (1932) found that wild oat seedlings could be cut so that one or more segments, provided that they included a node, could root and grow new plants. Pavlychenko and Harrington (1934), studying competition between weeds and crops, found that *A. fatua* was one of the most competitive of the 11 weeds investigated, because the shoots and roots were bigger than those of the crops.

Field and glasshouse studies of distribution and germination. Research on wild oats at Rothamsted began in 1944. Plants and seeds from Rothamsted farm were identified by Mr. C. E. Hubbard of Kew Herbarium, whose help throughout the investigation is gratefully acknowledged. The wild oats from Hoosfield spring barley were all *A. fatua*, but of three types, distinguishable by the colour and hairiness of their lemmas. *A. ludoviciana* predominated in the winter wheat on Broadbalk, and all plants were alike. *A. ludoviciana* and the three types of *A. fatua* occurred on other fields at Rothamsted, but Woburn experimental farm had no *A. ludoviciana*.

Field observations and glasshouse experiments on Rothamsted and Woburn seeds (Thurston, 1951b) showed that the reason for the association of one species with spring sowing and the other with autumn sowing was that they differed in season of maximum germination; *A. fatua* germinated mainly in March and April after the last cultivations for spring barley, whereas *A. ludoviciana* germinated between October and March, after winter wheat was sown but was still too small to offer serious competition. Neither species germinated in summer, so seedlings could not be destroyed by cultivating a summer fallow. Both *A. fatua* and *A. ludoviciana* produced seedlings from seeds buried at depths down to 9 in. (23 cm) in clay soil; each inch of overlying soil delayed the emergence of seedlings by about 1 day, but a higher percentage of seeds of *A. ludoviciana* than of *A. fatua* buried at 3–9 in. produced plants, probably because of their greater food reserves. Seeds remaining dormant until the second and third years were not able to penetrate as much overlying soil as those germinating soon after sowing. Dormancy was not induced in seeds sown 9–20 in. deep in pots, presumably because oxygen for germination reached the seeds from below. The maximum survival of buried seeds of *A. fatua* was 3 years in pots, but was longer in the field where the more seeds allowed a smaller percentage of survivors to be detected. *A. ludoviciana* survived only 2 years in pots. The seeds in each spikelet of *A. ludoviciana* germinated in turn, the large first seed first, but the time between germination of successive seeds ranged from a few weeks to a year. Both species tolerated soil acidity down to pH 4·5 or lower. Thus, the Rothamsted wild oats behaved similarly to those previously described from other countries, including *A. fatua* in Western Canada (Chepil, 1946), and some new information on depth of sowing and on dormancy of *A. ludoviciana* was obtained.

Brenchley (1947) summarised what was known about wild oats and appealed for information on successful control-measures. The replies, with comments from the interim results of the Rothamsted experiments (Brenchley & Thurston, 1948), emphasised that there was no universally applicable method for controlling wild oats in cereals. Most relied on late cultivations to destroy seedlings, or early harvesting to prevent seed-shedding, and so decreased crop yields. Two farmers turned hens on to the stubble to eat their wild oat seeds. Others relied on two or more cleaning-crops in succession between cereals in the rotation.

Co-operation between farmers, agricultural advisers and research workers seeking methods of controlling wild oats was continued in 1951 by a wild oat survey in England and Wales. Officers of the National Agricultural Advisory Service and of the National Institute of Agricultural Botany collected samples of wild oat panicles from infested fields visited in the course of their work, and sent the collections with details of soil, cropping, age of infestation and other notes to Rothamsted to be examined and classified by methods worked out in a pilot survey in 1950.* The most important new information was on the extent of infestation by *A. ludoviciana*, which, far from being of academic interest only, was shown to be a major weed of heavy land in Central, Southern and Eastern England, in an area centred on Abingdon, which had one of the earliest records of *A. ludoviciana* on agricultural land in England (Thurston, 1954). Although

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* These results, and all other results quoted without reference to publication, are described in the *Reports of the Rothamsted Experimental Station* for the years 1946–62.

often mixed with *A. fatua*, it was frequently present in sufficient quantity to be a serious problem on its own.

Fortunately, these two were the only wild oat species found. *A. fatua* covered a wider area than *A. ludoviciana*; it occurred on all types of soil wherever wheat and barley were commonly grown. The density of wild oat panicles per acre was directly related to the frequency in the rotation of crops in which wild oats would shed seeds. Deep ploughing often increased the number of panicles per acre in infested fields. Examples were given of spread of wild oats in seed-corn, sacks, machinery and along roads and railways. The 1951 survey dealt only with infested fields, but roadside surveys by the N.A.A.S. (Dadd, 1953) showed that 28–29% of winter cereals and 12–20% of spring cereals in Eastern England were heavily infested with wild oats.

The survey specimens of both species covered a greater range of lemma characters than those from Rothamsted farm, and a few plants appeared to be intermediate in form between wild oats and *A. sativa*. Not all the sorts of wild oats belonged to named varieties, so letters, fA, fB, etc., for *A. fatua* and lA, lB, etc., for *A. ludoviciana* were used to distinguish them. Examples of the different types, from the extremes of their ranges in England, were compared with Rothamsted specimens in a pot experiment, and seeds from these plants grown under identical conditions were tested for dormancy and periodicity of germination (Thurston, 1957).

Most plants bred true for lemma characters. Plants of *A. ludoviciana* were procumbent or prostrate at the maximum-tillering stage, with numerous tillers; only about 50% of the grains were dormant at harvest, and most of the first seeds were non-dormant. Germination was mainly in winter. Plants of all except one type of *A. fatua* were upright in habit with few tillers and averaged 95% dormant seeds at harvest. Some seeds germinated in autumn, but most in spring. The remaining type, fD, resembled *A. ludoviciana* in habit, fewer dormant seeds and winter germination, although it had the spikelet characters of *A. fatua*. According to Malzew (1930), most of the sorts of *A. fatua* belong to ssp. *fatua*, but type fD belongs to ssp. *septentrionalis*. The intermediates between wild and cultivated oats did not breed true for lemma characters and spikelet articulation. The proportion of dormant seeds was small in all F1 plants derived from intermediate types, even when they had wild-type abscission-scars.

Two samples of *A. ludoviciana* type lE collected in the 1951 survey provided mildew-resistant and eelworm-resistant genes useful in breeding cultivated oats (Griffiths *et al.*, 1957).

Neither the Rothamsted observations and experiments (Thurston, 1951b) nor the 1951 Survey (Thurston 1954, 1957) established the maximum survival of wild oat seeds in field soil, but some farmers reported that seeds could survive for at least 70 years in undisturbed soil, germinating when it was cultivated again. The length of survival was studied in four long-term field experiments.

In a field experiment where known numbers of seeds of *A. fatua* and *A. ludoviciana* were sown at two depths, and the plots were cultivated at different times and depths, germination was determined more by the properties of the seeds than by cultivations or weather (Thurston, 1961).

Cultivation did not stimulate germination, in contrast to Bibbey's (1935) results. The maximum survival of *A. fatua*, judged by seedling emergence, was 61 months, and after 7 years very few seeds remained in the soil. This is nearer to the 6 years of Cates (1917) than the 4 years of Chepil (1946). *A. ludoviciana* seedlings appeared for only 33 months, and no seeds remained in the soil 7 years after sowing. *A. fatua* seeds lived slightly longer at 15 cm than at 5 cm depth. Duvel's experiment on buried seeds (Toole & Brown, 1946) also indicated longer survival of deeply buried seeds, but not at such shallow depths as 15 cm. The two species showed their characteristic difference in periodicity of germination, but frozen soil delayed seedling-emergence. More seedlings of *A. fatua* appeared in the second spring than in the first, but 88% of the seedlings of *A. ludoviciana* appeared in the first autumn and winter. The non-dormant first seeds must have accounted for much of this first flush of seedlings. Only about 20% of the seeds sown produced seedlings, although seeds from the same bulk remained viable for more than 8 years when stored dry. With no crop to hide the wild oat seedlings, germination of *A. fatua* was seen continuing until June, but there was no third peak in July, as found in Saskatchewan (Chepil, 1946).

Survival of wild oat seeds has been followed in three fields on clay soils, grassed down in the hope of controlling wild oats. From a field at Yardley Hastings, Northamptonshire, with over 15 million wild oat seeds per acre, soil samples were taken annually by the N.A.A.S. District Officer, and the seeds were washed out and counted at Rothamsted. On a Rothamsted field fresh plots were ploughed in autumn for 5 successive years and the wild oat seedlings were counted. The third field, at Boxworth Experimental Husbandry Farm, Cambridgeshire, had been under ley for 3 years when the first plots were ploughed. At Yardley Hastings and Rothamsted the biggest decreases, 35% and 85% of the viable seeds in the soil, occurred in the first year under ley. Thereafter the numbers decreased slowly, and after 5 years there were still seeds enough to restart the infestation, i.e., over 3,000/acre at Rothamsted and 5 million at Yardley Hastings. At Boxworth the number decreased sharply from 38,000/acre after 3 years to 8,000 after 5 years and none after 9 years (Boxworth, 1961b). The causes of the different death rates of seeds under leys in the different fields are not known. Identification of species of young plants and long-buried seeds was impossible, but seeds of *A. fatua* probably persisted longer than *A. ludoviciana*.

The value of a ley for controlling wild oats is lessened if it becomes reinfested by allowing them to go to seed in the hay, or by introducing fresh seeds in animal fodder (Thurston, 1954). Of 2,000 seeds of *A. ludoviciana* fed to a calf only 10 passed through the animal undamaged and germinated in the dung. No viable wild oat seeds were found in well-rotted dung from the Rothamsted cattleyards, although the animals' feed and bedding probably contained wild oats.

Farmyard manure applied to soil containing wild oat seeds, e.g., in the furrows for planting potatoes, may stimulate germination. When the germination of seeds of *A. fatua* and *A. ludoviciana* sown in pans of well-rotted manure or poor clay soil was compared, approximately 50% more seeds germinated in farmyard manure than in soil in the first year, but in the second year germination in farmyard manure was less than 20% of that in soil. As 72% of all germination occurred in the first year, the total germination in farmyard manure over the 2 years was 83% of that in soil. Germination of both species was quicker in farmyard manure and fewer seedlings were produced than in soil, both effects tending to decrease the reserve of dormant seeds remaining into the second year after sowing. Non-dormant first seeds of *A. ludoviciana* were largely responsible for the many germinating in the first year.

Unwanted straw is often burnt on the field after combine-harvesting cereals. This probably destroys some wild oat seeds (Hopkins, 1936) and breaks the dormancy of others (Atwood, 1914), making them germinate. The seedlings can be destroyed by cultivations before the next crop is sown. Counts after stubble-burning on an infested field showed that there were 10 times as many seedlings of *A. fatua* per unit area where the stubble was burnt as on adjacent unburnt patches, but for every seed germinated on the burnt patches ten remained viable and dormant in the soil. Even after several spring cultivations to destroy seedlings, the next crop was heavily infested with wild oats, agreeing with Rabaté (1913) and Boxworth (1961a) that stubble-burning is not a very successful control for wild oats.

Wild oats from other countries have been compared over 5 years with British specimens. *Avena fatua* appears to be the most widespread species; samples have come from Canada, most European countries, Russia, Iraq, Australia and Pakistan. All except the Canadian samples included type fA, the commonest type in Britain and North-West Europe, with reddish-brown, very hairy lemmas and long callus-hairs, but most samples also included several of the less-common types. Type fF was common in Belgium and Holland, and many Scandinavian specimens were of a type rarely seen in Britain, with grey glabrous or slightly hairy lemmas and short callus-hairs. *Avena ludoviciana* occurred in samples from France, Italy, Greece, Russia, Iraq and Australia. Type lA with brown, very hairy lemmas and long callus-hairs was the commonest, as in Britain, but others occurred. The only Russian sample was type lJ, with yellow, glabrous lemmas, which is uncommon in Britain. Two species not found in Britain were received from Mediterranean countries. Varieties of *Avena sterilis* came from Southern France, Crete, Algeria, Arabia and Israel. These resembled *A. ludoviciana*, which is sometimes classified as a subspecies of *A. sterilis* (Lindenbein & Rademacher, 1960), in spikelet articulation but had larger and more numerous florets. *A. sterilis* var. *maxima* Perez-Lara from Algeria has up to six viable seeds per spikelet, only the first two awned. This variety had the most culms per plant of any wild oat grown in pots at Rothamsted, but they were also the shortest. *A. barbata* Brot., with narrower florets than *A. fatua*, each with an abscission-scar at the base and two long bristle-points at the tip of the very hairy lemma, came from Southern France, Malta, Israel and from regions of similar climate in Australia. The shoots of *A. barbata* lie close to the ground in a rosette until after the panicles begin to emerge, when growth at the lower nodes lifts them erect.

A. fatua and *A. ludoviciana* from other countries resembled the British specimens in habit, but usually flowered earlier than their British counterparts sown on the same day. Time of flowering differed more with the country of origin than between species. Thus, *A. fatua* and *A. ludoviciana* from Russia both took 124 days from sowing to reach 50% panicle emergence, and *A. fatua* and *A. ludoviciana* from Iraq 97 days. Similarly, the interval between sowing and 50% panicle emergence of *A. sterilis* was 93 days from Israel, 119 days from Crete and 134–140 days for France. Averaging all collections of all species in two pot experiments, the mean numbers of days from sowing to 50% panicle emergence were: Israel 93, Iraq 97, Australia 114, Russia 124, Western Europe 129, Britain 135, i.e., it was longer in specimens from higher latitudes. The duration of ear emergence was shortest in *A. fatua* and longest in *A. sterilis*, i.e., it was longer when more panicles were produced.

A pot experiment with *A. fatua* and *A. ludoviciana* from Australia, Iraq and Britain, and *A. sterilis* from Israel sown at 2 month intervals from December to April showed that the number of days from sowing to 50% panicle emergence is determined partly by species and country of origin, and partly by growing conditions. Day-length is probably important, because the Australian wild oats from the first sowing began to flower in early May at 60–70 cm high with four shoots per plant, whereas the third sowing, sown 4 months later, flowered in late May at 30 cm high with only one or two shoots per plant. The Iraq and Israel wild oats were affected in the same way, but less so. The British sorts were the last to flower in all three sowings, although, like the others, they flowered in fewer days from sowing when sown later. The difference between British and foreign *A. fatua* in date of flowering was least at the second sowing and greatest at the third, but the relation of flowering-time of British *A. ludoviciana* to foreign *A. ludoviciana* or *A. sterilis* was scarcely affected by sowing date.

The seeds from the foreign wild oats and their British counterparts grown in pots under the same conditions were very similar in proportion of dormant seeds and periodicity of germination. *A. sterilis* varieties had a similar pattern of germination to *A. ludoviciana*, i.e., the first seeds were nearly non-dormant and the second, third and fourth seeds germinated in turn, the third and fourth seeds germinating mainly in the second and third years from sowing; most seeds germinated in the late autumn and winter. *A. barbata* from Malta, grown in 1958, had 50% germination in the first year; fewer seeds germinated in the second and third years, and a few remained viable but dormant at the end of the third year. Germination was from September to January. *A. barbata* from Crete grown in 1961 also had approximately 50% germination in the first year, but *A. barbata* from France and Australia grown in 1960 had no dormant seeds. The samples of *A. barbata* from different countries should be compared in the same year to see if the differences in dormancy result from growing conditions or from physiological differences.

Laboratory studies of causes of dormancy and methods of breaking it. As the field behaviour of wild oat seeds became known, interest shifted to the causes of dormancy and methods of breaking it. In the last 10 years various aspects have been studied, but some published results are contradictory, and others offer an explanation of dormancy in terms of only one or two of the many factors shown to affect it. Obviously several factors may be involved simultaneously, possibly interacting with each other, and much more work is needed before dormancy in wild oats can be understood completely.

Unripe seeds of *A. fatua* and *A. ludoviciana* are viable but non-dormant. Conditions during ripening affect the speed of onset of viability and dormancy. The topmost seeds of a panicle may be viable before the lowest are free of the enveloping leaf-sheaths. Seeds of *A. ludoviciana* may be fully developed and dormant 15 days after anthesis. Destruction of hand-pulled wild oat plants, even if their panicles are still green, is therefore important. Dormancy develops as the seeds mature, and at 25 days after anthesis 80% of first seeds of *A. ludoviciana* and 100% of second seeds may be dormant. The first seeds of the spikelets soon lose their dormancy in the soil or in dry storage and are ready to germinate in the autumn. This resembles the post-harvest dormancy of cultivated oats (Forward, 1949), and similar factors are probably involved. If the developing first seeds are removed from young spikelets of *A. ludoviciana* the second seeds develop the slight dormancy characteristic of first seeds, instead of their usual prolonged dormancy. Postition in the panicle does not seem to affect dormancy of *A. ludoviciana* as much as Johnson (1935) found for *A. fatua*. Large panicles of *A. ludoviciana* had a larger proportion of viable seeds and a smaller proportion of dormant seeds than small panicles of the same age. When part of the developing panicle was removed dormancy of the remaining seeds of *A. ludoviciana* was decreased. Restriction of food or water supply to the developing seed by competition with other developing seeds or by poor development of the panicle therefore seems to increase dormancy in seeds of *A. ludoviciana*. Removal of part of the panicle of *A. fatua* did not affect the dormancy of the remaining seeds, possibly because 95–100% of the seeds are normally dormant at harvest in England.

In the U.S.A. and Canada *A. fatua* collected at harvest sometimes has a small proportion of dormant seeds (Lute, 1938; Bibbey, 1948). This may be the result of different conditions at ripening, or to collecting them before they are completely ripe. Four samples of Canadian *A. fatua*, grown in pots at Rothamsted and collected by shedding into cellophane bags as the seeds ripened, had the same high proportion of dormant seeds at collection and the same periodicity of germination as British *A. fatua*.

As dormancy of both *A. fatua* and *A. ludoviciana* can be broken by pricking the seed-coat (fused pericarp and testa) surrounding the caryopsis (Atwood, 1914), the development of this coat in the ripening caryopsis should be relevant to the onset of dormancy. Free-hand sections of fresh seeds stained with Nile Blue Sulphate show three chemically distinct layers, one staining blue, one pink, with an unstained layer between them. Microchemical tests show lignin and fatty materials present in the seed-coat. Good sections are difficult to obtain, because the strongly lignified hairs tear the softer tissues of the coat, and no satisfactory series of sections of seed-coats between pollination and seed-shedding has yet been obtained. Ruptures or chemical changes of the seed-coat probably occur during dormancy-breaking by treatment of seeds of *A. fatua* with high pressures (Hoffman, 1961) and by decay in soil or dung.

Opinions differ on the role of the husk or hull, consisting of lemma and palea, in dormancy of wild oats. Johnson (1935) said the hull had no effect on germination of *A. fatua*, and at Rothamsted 100% germination of *A. fatua* and *A. ludoviciana* is obtained by pricking the caryopses through the enveloping hulls, while keeping them moist at suitable temperatures. Moreover, buried seeds may remain dormant for several years after their hulls have rotted. Removal of the hulls by hand may break dormancy of a few seeds, probably by accidentally puncturing the seed coats. However, other workers suggest that hulls may be important in dormancy, but differ in their theories of the mechanism. Hay (1962) found that soaked seeds of *A. fatua* would not germinate unless the hulls were removed completely, or a "window" was cut out above the embryo, and concluded that wet hulls restricted gaseous exchange to the embryo. In contrast, Black (1959) found that loosening the hull or removing the palea and edges of the lemma did not break dormancy, and concluded that gaseous exchange to the caryopsis was not the cause of dormancy of seeds enclosed in wet hulls.

Several workers have extracted germination-inhibitors from intact or ground hulls and assayed them by their effect on germination of intact lettuce seeds or excised embryos of *A. fatua* (Naylor & Christie, 1956; Kommedahl *et al.*, 1958; Black, 1959). Hay (1962) extracted the same kind and amount of inhibitor from dormant and non-dormant seeds, so the inhibitor may not be a cause of dormancy. It may be formed during experimental treatment and not occur in untreated seeds. Further experiments are required to show whether the hulls are important in dormancy under natural conditions, and if so in what way.

If a water-soluble inhibitor causes dormancy, soaking seeds in water might be expected to break dormancy, but soaking increases it (Kommedahl *et al.*, 1958). The temperature and oxygen content of the water and the length of the soaking period are important (Hay & Cumming, 1959; Hay, 1962), but Canadian and Rothamsted results differ on the extent of the effect of oxygenation and on the optimum temperature for inducing dormancy in *A. fatua*. Seeds are being exchanged between Canada and Rothamsted for tests to distinguish between differences in technique and in seed-properties.

The effect of soaking alone, and its dependence on temperature, time and oxygen content must be borne in mind when considering the effect of soaking seeds in dilute solutions. It must also have a bearing on the behaviour of seeds in waterlogged soil. Lewis (1961) found that seeds of *A. fatua* remained dormant below the water-table in pots of sand, loam or peat, while seeds above the water-table germinated, but in loam and peat some seeds died during the second month under water, bringing the proportion surviving nearer to that for 1 month waterlogging in sand.

The temperature to which moist or dry wild oat seeds are exposed after they fall from the plant may affect their dormancy. In two experiments the germination of *A. fatua* seeds after dry storage at controlled temperatures was compared with germination after exposure to changes of temperature and humidity on the surface of the soil for several months, preceded or followed by dry storage at controlled temperatures. In an international experiment on germination of *A. fatua* (Thurston, 1962a) the different conditions experienced by seeds during 3 months on the surface of the soil, followed by dry storage at 20° or room temperature, did not affect viability or dormancy in six out of seven European countries, germination increasing from 10% at collection to 50% after 5 or 6 months in all sets. In Denmark seeds lost viability more quickly out of doors, and those remaining viable retained their dormancy longer. This was probably because the Danish seeds were of a different type from the others. Outdoor temperatures were similar to those in some of the other countries. Dormancy broke more slowly in dry storage at 10° than at 20° in both countries where two temperatures were compared.

As the outdoor treatment of the international experiment ended before the first frost at Rothamsted, and freezing is probably important in breaking dormancy (Ivanovskaya, 1943), another experiment was made with dry storage in incubators at 4°, 7°, 16° and 21° for 5 months from harvest, followed by exposure on the surface of the soil for 1 to 4 months, January to April, or retention in the incubators for 4 months. The minimum temperature on the ground was −3° in April and −7° in the other 3 months. The best dry storage temperature for breaking dormancy was 16°, where 50% of the seeds were ready to germinate in January, after 5 months' storage. The next best treatment was 21°, where only 20% of the seeds lost their dormancy in 9 months. Dormancy-breaking was negligible at 4° and 7°. After 1 month out of doors differences caused by dry storage at different temperatures had disappeared and all sets had 70–75% dormant seeds. After 2 and 3 months out of doors the sets were still alike, but dormancy had decreased to 30%. In April the set previously stored dry at 16° had only 12% dormant seeds, the smallest proportion encountered. In contrast, the other three sets had about 50%, but this was less than the sets stored for the whole 9 months at 21°, 7° or 4°. Evidently the sequence of temperature and humidity changes can affect the dormancy of *A. fatua* seeds.

Dormancy and viability of wild oat seeds, especially *A. ludoviciana*, are affected by temperature during the germination test. The most favourable temperatures for germinating *A. ludoviciana* are between 7° and 13°. All seeds held at 32° died in 2 months, but first seeds of the spikelets held at −1°, 20° and 29° germinated when transferred to 7–13°. Second seeds germinated less readily even at favourable temperatures. Seeds that had lost their natural dormancy in storage became dormant again after keeping them for 7 weeks at 27°; dormancy was not broken by drying and rewetting once at 27°, but the seeds survived this drastic treatment and germinated when transferred to 10°. Exposure to 27° for 1 day or 1 week increased the rate of germination of seeds later kept at 7°, but 1 month at 27° decreased it. The onset of temperature-induced dormancy was sudden. First seeds did not become dormant at 23° and 25°, while they did at 27°. The temperature at which dormancy was induced remained constant at 27° over 3 years for one batch of seeds, but the critical temperature for another batch might be different. In the first experiment, using a different batch of seeds from the main series of experiments, dormancy was induced at 20° and 29°, but the critical temperature was not determined. Dormancy was induced in second seeds at slightly lower temperatures, 25% becoming dormant at 25°. Germination of second seeds at 23° and 25° was increased by previous exposure to 7° for 1 day or 1 week, though not up to that of seeds continuously at 7°.

Seeds of *A. fatua* also retained viability and lost dormancy best at approx. 10°. At 27° about 50% of the seeds died and 90% of the survivors became dormant.

Temperature-induced dormancy is not only important when testing germination, but it may be concerned in the failure of *A. fatua* seeds to germinate in the field in summer even when the soil is moist and disturbed. Conversely, its breaking by prolonged cooling may permit seeds to germinate in winter and spring. However, seeds would rarely reach 27° in British fields even for short periods, and then only when they were at the surface of the soil, or still attached to the panicle.

In comparing the effect on germination of storing seeds in incubators and out of doors, the effect of light was not tested because it seemed unlikely that light would penetrate wild oat husks, especially those with dark pigments, and because germination occurs equally in transparent glass containers in a glasshouse as in opaque ones. However, Cumming and Hay (1958) found that whereas non-dormant *A. fatua* seeds were insensitive to light, partially-dormant seeds (i.e., seeds from a sample comprising some dormant and some non-dormant seeds) were sensitive to quality of light: 60% and 68% germinated in red light and darkness, 8% and 14% in infrared and blue light and 28% in white light. Germination was not affected by intensity or duration of light. Daylight also inhibited germination. Wild oat seeds are occasionally seen germinating on the surface of the soil at Rothamsted, so perhaps light-sensitivity is another difference between British and Canadian *A. fatua*. Dark-brown husks are common in British but rare in Canadian *A. fatua*.

Wild oat seeds have been soaked in solutions of various growth-promoting and inhibiting substances, not necessarily naturally present in wild oat seed. Osvald (1950) reported that a root-exudate of rye inhibited germination of *A. fatua*, but this was not confirmed at Rothamsted (Thurston, 1962b). Helgeson and Green (1957) showed that wild oats (presumably *A. fatua*) germinated about 80% more in petri-dishes with 50 ppm gibberellic acid (GA) than with distilled water. Other workers have sometimes obtained similar results, but most find that soaking in GA is an unreliable method of breaking dormancy, which suggests that the conditions of treatment are important. Naylor and Simpson (1959) showed that the amount of GA required to break dormancy of *A. fatua* depended on the age of the seed, that supplying sucrose increased germination of excised embryos over a range of ages, and that sucrose plus GA was usually more effective than either alone. Leaching newly ripened embryos increased their response to GA alone, but not to GA plus sucrose. Caryopses 2 years old, which no longer responded to GA or sucrose, contained natural gibberellins. Black and Naylor (1959) found that GA taken up by maturing inflorescences prevented the onset of dormancy in developing seeds. Hay (1962) found that the water in which intact seeds of *A. fatua* had been soaked contained an inhibitor of embryo elongation, most of which came from the hulls. The inhibition was best overcome by giving GA plus sucrose, but GA alone or thiourea plus sucrose were also moderately effective.

Soaking in 50 or 25 ppm GA solution for at least 20 hours breaks temperature-induced dormancy of *A. ludoviciana*.

Although GA is useful in the laboratory for breaking dormancy, it is too expensive to use on a field scale, and as it is quickly broken down in soil, it would have to be applied to the young inflorescences, which would require aerial spraying.

According to Hay (personal communication), maleic hydrazide had no effect on dormancy of *A. fatua*. Indole-acetic acid (IAA) and 2,4-D also seemed not to be concerned in dormancy, but seeds of *A. fatua* soaked in 10^{-3} M coumarin solution were completely dormant after 24 hours; they could be made to germinate by puncturing and by GA, so coumarin-induced dormancy resembles natural dormancy.

Placing seeds of *A. fatua* in 0·1% solution of 2,3,6-triphenyltetrazolium chloride stains the embryos of non-dormant seeds, but not of dormant seeds, unless their seed-coats are punctured, when the embryos and the tissues around the puncture stain. When dormant seeds are soaked for 24 hours in tetrazolium solution, and then washed and pricked, only the punctured caryopses stain (Hay, 1962). Various hydrogenases reduce tetrazolium salts to coloured formazans, so pricking must stimulate hydrogenase activity, either directly or indirectly.

Drennan and Berrie (1962) studied the relation of amylase activity to dormancy and germination of *A. fatua* and *A. ludoviciana*. Dry grains and wet dormant grains had very little activity, but non-dormant grains had much during the first few days of conditions permitting germination. Activity, mostly α-amylase but some β-amylase, occurred first in the endosperm, but not until after the embryo had begun to grow, so lack of amylase did not cause dormancy, and GA is unlikely to break dormancy by increasing amylase activity, although the sugar-supply to the embryos is important in dormancy-breaking of young seeds by GA.

Naylor and Christie (1956) found that the respiratory quotient of seeds of *A. fatua* in nitrogen fell as dormancy increased, suggesting that the respiratory substrate changed from carbohydrate to fats during the onset of dormancy. They suggested that a germination-inhibitor might prevent the use of carbohydrate reserves in the endosperm, as shown by Elliott and Leopold (1953) for *A. sativa*, but the findings of Drennan and Berrie (1962) make this unlikely.

Factors affecting the growth of wild oat plants. The morphology and physiology of wild oat plants are important because they govern competition between the crop and wild oats and also the number of wild oat seeds produced. When wild oat plants are grown in pots of soil and compared with cultivated oats, wheat and barley in separate pots, the similarity of weeds and crops is obvious (Thurston, 1951a; 1959). For example, a wild oat plant will take as much nitrogen out of the soil as a crop plant, and will benefit from it in the same ways and to the same extent. Applying nitrogenous fertilisers to an infested field is therefore unlikely to alter the ratio between crop and wild oats.

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Seedlings of *A. fatua* and *A. ludoviciana* are smaller than those of cultivated cereals of the same age in total dry weight, total nitrogen content, leaf area and number of shoots. However, very young wild oat plants have higher net assimilation rates (*E*) than cultivated cereals and soon catch up and pass the crop plants in dry weight, height, etc. The difference in *E* does not persist, and for most of the growing season the *E*s of crops and wild oats are alike. It follows that the crop exerts its greatest competitive effect against wild oats while the weeds are seedlings, and that the crop with the largest leaf area and most shoots earliest in the season will be the most efficient competitor. This has been demonstrated in the field, where the dry weight per unit area of crop in April, when wild oat seedlings appeared, determined its efficiency in restricting growth of *A. fatua* (Thurston, 1962b). In this experiment wheat and rye grew equally well and were equally effective competitors, but barley, which grew poorly on the acid soil, allowed the wild oats, more tolerant of acidity, to flourish. Winter barley was more effective than spring barley in competing against *A. fatua* because it was bigger when the wild oats germinated, and because the spring cultivations for spring barley stimulated germination of *A. fatua*. Even the competitive crops did not kill wild oat seedlings, but checked their growth so much that the wild oats did not tiller and could scarcely be seen in the standing crop. However, even the barley considerably affected the size of the wild oats. These effects, expressed as the mean of 2 years' dry weights of wild oat tops, in g/100 plants in July, growing in the five treatments, were 7 and 8 g in winter wheat and winter rye, 121 g in winter barley, 205 g in spring barley and 699 g in fallow cultivated as for winter cereals.

Wild oat plants produce panicles in succession over a longer period than cultivated cereals (Thurston, 1959). Unless competition from the crop is severe, the tallest project above it, making possible the hand-pulling of isolated plants. But in commercial crops of spring barley at Rothamsted only 50% of the seeds of a plant of *A. fatua* are above the level of the crop, and this limits the control of wild oats by treating the projecting panicles, e.g., by cutting them off above the crop (Thurston, 1962b).

Wild oat seeds, even with their husks and awns, have a smaller 1,000-grain weight than corresponding crops, and *A. fatua* grains weigh less than those of *A. ludoviciana*.

Nitrogen-deficiency symptoms in wild oats were the same as in crops grown in pots (Thurston, 1959). Growth was retarded and leaves turned pale green, then yellow, and began to die. The first symptoms showed later in nitrogen-deficient wild oats than in crops, and the difference between the two levels of nitrogen added as sulphate of ammonia also developed later, presumably because the wild oats were smaller than the crop plants in the early stages.

The nitrogen-status of the soil scarcely affected the 1,000-grain weight and nitrogen content per seed of crops or wild oats. Added nitrogen increased the total seeds per plant of wild oats and of crops, but the number of seeds per inflorescence fluctuated more in wild oats than in crops. Added nitrogen produced more panicles per plant and usually more seeds per panicle, but sometimes the extra panicles were small and numerous.

The response of wild and cultivated oats to manganese was compared in pots (Thurston, 1951a). *A. fatua* showed typical grey-speck lesions in both manganese-deficient soils used, but *A. ludoviciana* developed interveinal chlorosis. In other respects, wild and cultivated oats responded in similar ways to lack of manganese, though the severity of the symptoms differed. Wild oats showed more chlorosis, and their dry weight and manganese content of individual seeds were more affected, but they had less necrosis, flowering was less delayed and numbers of ripe ears at harvest and number of seeds per plant were less affected. Manganese deficiency affected the dry weight of *A. fatua* less than of the cultivated oats, which were less affected than *A. ludoviciana*.

Manganese-deficient wild oat plants had smaller seeds containing less manganese than those of plants receiving adequate manganese, but deficient and normal plants had similar numbers of seeds. Manganese deficiency decreased the proportion of viable and dormant seeds of *A. fatua* and probably also of *A. ludoviciana*. Nitrogen-deficient plants produced fewer seeds than those receiving adequate nitrogen, but they were similar in dry weight and nitrogen content to normal seeds.

Two questions arose from the field experiment on competition between *A. fatua* and cereals. One was the effect of a heavy crop of winter cereal on the number of seeds of *A. fatua* germinating in spring. Because of the patchy distribution of seeds in the soil, the differences between crops in number of wild oat plants per unit area were not significant, but there were indications that, especially in a dry spring, *A. fatua* might remain dormant under thick crops of winter wheat or winter rye and germinate subsequently in spring barley. This requires further investigation. The other question was how far in advance of the wild oats the crop would have to germinate to restrict their growth by competition. This was investigated in pot experiments, where wild oats were grown alone or in competition with crops sown at two rates either at the same time as the wild oats or up to 18 days before them. *A. fatua*, spring barley and spring wheat were sown in spring and *A. ludoviciana*, winter wheat, winter barley and winter rye in autumn. Dormancy of wild oat seeds was broken by pricking the seed-coats with a needle before sowing.

As in the field, the crop with the most tillers early in the season affected growth of wild oats most; in both experiments this was feeding barley. Increasing the number of crop plants per pot decreased seed-production by the wild oat plants; the mean number of seeds per 3 plants of *A. fatua* competing with 0, 3 or 9 crop plants was 748, 181 and 59. Results with *A. ludoviciana* were similar. Seed production of *A. fatua*, competing with crops sown 18 days before it, was only 37%, and of *A. ludoviciana*, competing with crops sown 14 days before it, only 60% of that where crops and wild oats germinated together. Neither viability nor dormancy of the wild oat seeds was significantly affected by treatment. Thus, a difference of a fortnight in sowing-date of the crop probably affects the growth of wild oat plants in it, but early sowing means that fewer wild oat seedlings can be destroyed by cultivation.

There is very little information on the effect of wild oats on the growth of the crop, but each wild oat plant will take enough nutrient from the soil to grow a comparable crop-plant.

The biological basis for the use of herbicides to control wild oats. Research on wild oats at Rothamsted has not included the search for herbicides or the testing of possible chemicals, because such work is done in Britain by the chemical manufacturers and by the Weed Research Organisation. The results of the biological investigations, originally undertaken to provide better control based on traditional crop husbandry methods, however, have found new applications in planning effective chemical control.

The first herbicide proposed to control wild oats was isopropylphenylcarbamate (I.P.C., now called propham). At first it was hoped that applying it as a powder to the panicles at anthesis would prevent wild oats from setting seed, but when *A. ludoviciana* was treated in winter wheat the powder lodged in the upward-pointing wheat flowers, preventing the development of grain, and the pendant wild oat flowers protected by their glumes were almost unaffected. Propham applied to soil before sowing sugar beet or peas is used to control *A. fatua* (Woodford, 1960). TCA (sodium or ammonium trichloroacetate) can be used similarly (Woodford, 1960), but neither TCA nor propham can be used in cereal crops.

Spraying the emerged panicles of wild oats with maleic hydrazide to prevent seed-set was tried in Canada with great success in one year (Knowles, 1953), but seemed unlikely to succeed in England, because here the wild oats ripen before the crop, so the crop would still be at a susceptible stage when the wild oats were sprayed. Small-scale trials confirmed that barley was damaged at concentrations that gave less than 50% seed-sterility in *A. fatua*, and maleic hydrazide was never adopted for wild oat control in England. In Canada it is now used only with crops of flax and some varieties of barley (Canada, 1954).

Two promising chemicals have recently been introduced to control wild oats in cereals. They are barban (4-chloro-2-butynyl-*N* (3-chlorophenyl) carbamate) and diallate (2,3-dichloroallyl diisopropylthiol carbamate). Diallate as "Avadex" worked into the soil before sowing seems effective against *A. fatua* (Moffatt, 1962) and persists long enough to kill most of the spring-germinating seedlings, but it appears slightly more likely than barban to damage the crop. Barban as "Carbyne" is safe with wheat, peas, field beans and sugar beet and with most barley varieties except Proctor and Provost, but it does not always kill the wild oats. When applied to wild oat seedlings it stops them growing for a time, though some may recover later. Best results are obtained by spraying when wild oats are at the 1½- to 2-leaf stage, and are in a vigorous crop, which prevents the wild oats recovering from their initial setback. Obviously, recognition of the wild oat species and knowledge of their periodicity of germination help in determining the best time to apply the chemicals, and a knowledge of the factors involved in competition between wild oats and crop helps to get the maximum control of wild oats with barban. Pfeiffer and Holmes (1961) investigated the effects of seed rate, nitrogenous fertiliser and barban on competition in the field between spring barley and cultivated oats, which they hoped would behave like wild oats. Where their results overlapped those obtained with a natural infestation of *A. fatua* (Thurston, 1962b), agreement was good, so their conclusions are probably applicable to wild oats, i.e., that barban and competition act independently in decreasing growth of oats, their effects being additive, and that applying nitrogen to a mixture of barley and oats stimulates both equally, and therefore does not help to suppress wild oats.

Only spring-germinating *A. fatua* need be considered in spring-sown crops, but in autumn-sown cereals autumn-germinating *A. fatua*, winter-germinating *A. ludoviciana* and spring-germinating *A. fatua* may all be present, and one spraying cannot catch all at the most vulnerable stage of their development. Many autumn-germinating *A. fatua* plants die during the winter, but they can survive in mild winters and favourable situations. Holmes and Pfeiffer (1962) investigated the development of *A. fatua* germinating on different dates in October-sown wheat in three counties in a mild winter and showed that autumn-germinated plants were responsible for 75% of the wild oat spikelets present at harvest. This agrees with the Rothamsted observation that it is the early stages of wild oat development that are most susceptible to crop competition and that the density of the crop when the wild oats first appear that determines the amount of growth they will make subsequently.

Barban can also be used to control *A. ludoviciana* in winter wheat (Holmes & Pfeiffer, 1962), but the crop is more susceptible to damage in early spring than at other times, and many of the wild oats are at their most vulnerable stage in November and December, so winter spraying is desirable provided the soil is not too wet for the sprayer to go on to the field. Using cultivated winter oats instead of wild oats, Holmes and Pfeiffer (1962) showed that the total cereal yield per acre from wheat drilled alone or with oats was approximately the same. Spraying with barban scarcely affected the combined total yield, but the proportion of wheat was greatly increased and its yield more than doubled by spraying with barban in November, which damaged the oats severely without harming the wheat. Control of a heavy infestation of wild oats increased the yield of 9 out of 10 winter wheat varieties by 25–100%, but control of a light to moderate infestation increased yields of five winter wheat varieties by less than 20%. Spraying with barban can evidently control wild oats, and where the infestation would otherwise be heavy can give worthwhile increases in yield.

References

Atwood, W. M. (1914). A physiological study of the germination of *Avena fatua*. *Bot. Gaz.* **57**, 386–410.

Bibbey, R. O. (1935). The influence of environment upon the germination of weed seeds. *Sci. Agric.* **16**, 141–150.

Bibbey, R. O. (1948). Physiological studies of weed seed germination. *Plant Physiol.* **23**, 467–484.

Black, M. (1959). Dormancy studies in seeds of *Avena fatua*. 1. The possible role of germination inhibitors. *Canad. J. Bot.* **37**, 393–402.

Black, M. & Naylor, J. M. (1959). Prevention of the onset of seed dormancy by gibberellic acid. *Nature, Lond.* **184**, 468–469.

Brenchley, W. E. (1947). The control of wild oats. *Agriculture, Lond.* **53**, 436–438.

Brenchley, W. E. & Thurston, J. M. (1948). Suggestions for the control of wild oats. *Agriculture, Lond.* **55**, 12–16.

Boxworth (1961a). Straw burning, stubble cultivations and late sowing for wild oats. *Boxworth Experimental Husbandry Farm. Farm Guide 1961*, 21–22.

Boxworth (1961b). Survival of wild oat seeds. *Agriculture, Lond.* **68**, 390.

Canada (1954). Wild oats can be controlled in barley and flax. *Rep. Dir. exp. Fms Can.* 1953–1954, p. 19.

Cates, H. R. (1917). Methods of controlling or eradicating the wild oat in the hard spring-wheat area. *Fmrs' Bull. U.S. Dep. Agric.* 833.

Chepil, W. S. (1946). Germination of weed seeds. I. Longevity, periodicity of germination and vitality of seeds in cultivated soil. *Sci. Agric.* **26**, 307–346.

Chevalier, A. (1925). Les folles avoines et leur destruction. *Rev. Bot. appl.* **5**, 294–297.

Clark, G. H. (1914). Weeds and weeds seed illustrated and described. *Bull. Dep. Agric. Can.* S-**8**, 16.

Coffman, F. A. & Stanton, T. R. (1938). Variability in germination of freshly-harvested *Avena*. *J. agric. Res.* **57**, 57–72.

Cumming, B. G. & Hay, J. R. (1958). Light and dormancy in wild oats (*Avena fatua* L.). *Nature, Lond.* **182**, 609–610.

Dadd, C. V. (1953). Wild oats. *N.A.A.S. quart. Rev.* **21**, 1–7.

Drennan, D. S. H. & Berrie, A. M. M. (1962). Physiological studies of germination in the genus *Avena*. I. The development of amylase activity. *New Phytol.* **61**, 1–9.

Elliott, B. B. & Leopold, A. C. (1953). An inhibitor of germination and of amylase activity in oat seeds. *Physiol. Plant.* **6**, 65–77.

Forward, B. F. (1949). Studies of germination in oats. *Proc. Ass. off. Seed Anal. N. Amer.* **1949**, 83–84.

Grey, E. (1922). *Rothamsted Experimental Station. Reminiscences, tales and anecdotes 1872–1922.* Harpenden: E. Grey.

Griffiths, D. J., Holden, J. H. W. & Jones, J. M. (1957). Investigations on resistance of oats to stem eelworm, *Ditylenchus dipsaci* Kühn. *Ann. appl. Biol.* **45**, 709–720.

Hay, J. R. (1962). Experiments on the mechanism of induced dormancy in wild oats, *Avena fatua* L. *Canad. J. Bot.* **40**, 191–202.

Hay, J. R. & Cumming, B. G. (1959). A method for inducing dormancy in wild oats (*Avena fatua* L.). *Weeds* **7**, 34–40.

Helgeson, E. A. & Green, J. G. (1957). New weapon against wild oats. *Bi-m. Bull. N. Dak. agric. Exp. Sta.* **455**, 121–122.

Hoffman. O. L. (1961). Breaking wild oat dormancy with gases at high pressure. *Weeds* **9**, 493.

Holmes, H. M. & Pfeiffer, R. K. (1962). Some aspects of the use of barban for wild oat control in winter wheat. *Weed Res.* **2**, 110–121.

Hopkins, C. Y. (1936). Thermal death point of certain weed seeds. *Canad. J. Res.* C–D, **14**, 178–183.

Ivanovskaya, T. L. (1943). The influence of different conditions on the germination of seeds of wild oats. *Proc. Lenin Acad. agric. Sci.* **3**, 28–33. (In Russian.)

Jessen, K. & Helbaek, H. (1945). Cereals in Great Britain and Ireland in prehistoric and early historic times. *Biol. Skr.* **3**, 1–68.

Johnson, L. P. V. (1935). General preliminary studies on the physiology of delayed germination in *Avena fatua*. *Canad. J. Res.* C–D, **13**, 283–300.

Kirk, L. E. & Pavlychenko, T. K. (1932). Vegetative propagation of wild oats, *Avena fatua*, and other economically important species of *Avenae* and *Hordeae*. *Canad. J. Res.* **7**, 204–220.

Knowles, G. (1953). Selective control of wild oats in cereal crops by maleic hydrazide. *Canad. J. agric. Sci.* **33**, 402.

Kommedahl, T., Devay, J. E. & Christensen, C. M. (1958). Factors affecting dormancy and seedling development in wild oats. *Weeds* **6**, 12–18.

Lagrèze-Fossat, A. (1856). De la reproduction de la folle-avoine. *Moniteur des Comices.* (*1856*) 346–348.

Lewis, J. (1961). The influence of water level, soil depth and type on the survival of crop and weed seeds. *Proc. int. Seed Test Ass.* **26**, 68–85.

Lindenbein, W. & Rademacher, B. (1960). *Avena ludoviciana* Dur.—der Winterflughafer. *Saatgut-wirtschaft.* **7**, 191–193.

Lute, A. M. (1938). Germination characteristics of wild oats. *Proc. Ass. off. Seed Anal. N. Amer. 1930–33*, 70–73.

Malzew, A. I. (1930). Wild and Cultivated Oats, section *Euavena* Griseb. *Bull. appl. Bot. Pl.-Breed. Suppl.* **38**.

Moffatt, J. R. (1962). The Farms; Crops, Cereals. *Rep. Rothamst. exp. Sta.* for 1961, p. 191.

Naylor, J. M. & Christie, L. A. (1956). The control of dormancy in wild oats. *Proc. 10th Meet. Nat. Weed Comm. Can.*, (*Western Section*) 56–59.

NAYLOR, J. M. & SIMPSON, G. M. (1961). Dormancy studies in seeds of *Avena fatua*. 2. A gibberellin-sensitive inhibitory mechanism in the embryo. *Canad. J. Bot.* **39**, 281–295.

OSVALD, H. (1950). On antagonism between plants. *Proc. 7th int. bot. Congr.* 167–171.

PALEG, L. G., COOMBE, B. G. & BUTTROSE, M. S. (1962). Physiological effects of gibberellic acid. V. Endosperm responses of barley, wheat and oats. *Plant Physiol.* **37**, 798–803.

PAVLYCHENKO, T. K. & HARRINGTON, J. B. (1934). Competitive efficiency of weeds and cereal crops. *Canad. J. Res.* **10**, 77–94.

PFEIFFER, R. K. & HOLMES, H. M. (1961). A study of the competition between barley and oats as influenced by barley seedrate, nitrogen level and barban treatment. *Weed Res.* **1**, 5–18.

RABATÉ, E. (1913). Les folles avoines. *Progr. agric. vitic.* (*Ed. L'Est-Centre*) **34**, 166–180 (in *Exp. Sta. Rec.* **30**, 531, 1914).

THURSTON, J. M. (1951a). A comparison of the growths of wild and of cultivated oats in manganese-deficient soils. *Ann. appl. Biol.* **38**, 289–302.

THURSTON, J. M. (1951b). Some experiments and field observations on the germination of wild oat (*Avena fatua* and *A. ludoviciana*) seeds in soil and the emergence of seedlings. *Ann. appl. Biol.* **38**, 812–832.

THURSTON, J. M. (1954). A survey of wild oats (*Avena fatua* and *A. ludoviciana*) in England and Wales in 1951. *Ann. appl. Biol.* **41**, 619–636.

THURSTON, J. M. (1957). Morphological and physiological variation in wild oats (*Avena fatua* L. and *A. ludoviciana* Dur.) and in hybrids between wild and cultivated oats. *J. agric. Sci.* **49**, 259–274.

THURSTON, J. M. (1959). A comparative study of the growth of wild oats (*Avena fatua* L. and *A. ludoviciana* Dur.) and of cultivated cereals with varied nitrogen supply. *Ann. appl. Biol.* **47**, 716–739.

THURSTON, J. M. (1960). Dormancy in Weed Seeds. In: *The Biology of Weeds*, ed. J. L. Harper. Oxford: Blackwell, pp. 69–82.

THURSTON, J. M. (1961). The effect of depth of burying and frequency of cultivation on survival and germination of seeds of wild oats (*Avena fatua* L. and *Avena ludoviciana* Dur.). *Weed Res.* **1**, 19–31.

THURSTON, J. M. (1962a). An international experiment on the effect of age and storage conditions on viability and dormancy of *Avena fatua* seeds. *Weed Res.* **2**, 122–129.

THURSTON, J. M. (1962b). The effect of competition from cereal crops on the germination and growth of *Avena fatua* L. in a naturally infested field. *Weed Res.* **2**, 192–207.

TOOLE, E. H. & BROWN, E. (1946). Final result of the Duvel buried seed experiment. *J. agric. Res.* **72**, 201–210.

TOOLE, E. H. and COFFMAN, F. A. (1940). Variations in the dormancy of the seeds of the wild oat, *Avena fatua*. *J. Amer. Soc. Agron.* **32**, 631–638.

WOODFORD, E. K. (edit.) (1960). *Weed Control Handbook*. Oxford: Blackwell Scientific Publications.

ZADE, A. (1912). Der Flughafer (*Avena fatua*). *Arb. dtsch. LandwGes.* **229**, 1–91.

WORK AT ROTHAMSTED ON HONEYBEE SWARMING

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Honeybee colonies reproduce by swarming. The queen of a colony, a proportion of the worker bees and sometimes some drones suddenly leave their nest and fly, forming a well-defined group in the air. Usually the swarm soon clusters on a suitable object, often a branch of a tree. Later it disperses again and flies to find a new home. Sometimes several swarms emerge from a colony over a week or two. Colonies usually begin to rear queens before they swarm. The original queen, if still alive, goes with the first swarm; otherwise swarms contain young unmated queens. Queen rearing in the presence of a laying queen also occurs during "queen supersedure", in which the old queen is replaced without swarming. No reliable method is known for predicting which of these two processes is going to occur.

The use of hives in which the combs are built into movable frames enables colonies to be divided artificially, so that beekeepers no longer need swarms and usually try to prevent swarming, because it weakens the colonies and lessens their honey yield.

The Annual Incidence of Swarming

When beekeepers needed swarming they found that nearly all colonies could be made to swarm by keeping them in small enough hives. Swarming is rarer from hives big enough to accommodate colonies easily when they reach full size, but it does happen. The proportion of colonies that will swarm under these conditions is difficult to discover exactly, because nearly all beekeepers interfere with the colonies they think likely to swarm. On one English honey farm a group of about 300 colonies headed by queens reared the previous summer had the following average percentages of troublesome colonies over 4 years (Simpson, 1957a):

A. Had unsatisfactory queens and were given new ones	5
B. Became queenless before beginning queen rearing and were given new queens	4
C. Began queen rearing, but stopped without swarming	24
D. Began queen rearing and subsequently may have swarmed or might have done so if not given new queens	18
Total	51

The incidence of queen rearing differed greatly from year to year and slightly, but significantly, between different apiary sites. The numbers in groups A and B show that swarming is not the only event that makes colonies require attention during the summer, though some of group B might have swarmed with the first young queens they reared had they been allowed to continue queen rearing instead of being given new laying queens.

Occupied queen cells were removed whenever they were seen, and as it is uncertain how far, if at all, this treatment inhibits swarming, it is impossible to say how many of group C should be included among the swarmers. Certainly not all of them should. Among 58 colonies in Rothamsted apiaries examined weekly without removing queen cells from early May to mid-July 1956, 16 began queen rearing, and although not divided to prevent swarming, did not swarm or change their queens. They destroyed occupied queen cells, often repeatedly, at various stages of maturity; 73 of the young queens reached the larval stage and 39 the pupal stage before they were destroyed. One colony, on which the observations were extended to mid-August, continued queen rearing for 13 weeks and destroyed 29 queen cells at the pupal stage or later. Gary and Morse (1962) showed that colonies sometimes allow young queens to reach maturity and then kill them after, or just before, they emerge from their cells.

Evidently many colonies that begin queen rearing will neither swarm nor replace their queens; the more often and thoroughly apiaries are examined, the more of this abortive queen rearing will be seen and the more the number of colonies likely to swarm will be overestimated.

The Time of Year when Colonies Swarm

Swarming is mainly an early or midsummer event. Jeffree (1951) found that swarming in Wiltshire was commoner before midsummer than after, and English commercial beekeepers do not consider it necessary to look for incipient swarming after mid-July.

Colonies suspend breeding during the winter and their population of adult bees declines. When breeding begins in spring the amount of brood increases for a time along with the number of adult bees available to feed it. Some records of the amounts of worker brood in colonies throughout the summer (Dufour, 1939; Brünnich, 1922; Nolan, 1925) show a maximum in early summer followed by a rapid decline. From this Morland (1930) concluded that swarming results from a seasonal decline in breeding, as would be expected on Gerstung's brood food theory (see below). It now appears that these early brood records were misleading, partly because they were collected in places where the foraging season begins and ends earlier than in England, and partly because their averages were based on the colonies that reared queens as well as on those that did not (Ribbands, 1953). The Rothamsted colonies that did not begin queen rearing in 1956 showed little decline in breeding before the end of July, i.e., well *after* the swarming season and not before it. Breeding declined earlier in the colonies that began queen rearing, but more often than not the queen rearing began while the brood was still increasing. The subsequent decline in breeding may therefore have been a consequence of queen rearing, but could not have caused it (Simpson, 1959).

Fully efficient supersedure (in which the old queen survives until the young one has mated and begun laying) most often occurs in late spring and early autumn. Queen replacement during the summer is usually less efficient, involving swarming, early death of the old queen or repeated destruction of queen cells. In the commercial apiary mentioned above transient queen rearing (group C) was most frequent just after midsummer, so much of it was probably abortive supersedure rather than abortive swarming.

The Causes of Swarming

Because swarming is usually preceded by queen rearing, a cause of swarming has generally been sought in the cause of queen rearing. Queen rearing nearly always begins after a colony is deprived of its queen, when a few of the larvae in worker cells are reared as queens. Huber (1792) showed that it is not sufficient for the worker bees to see, smell or hear their queen to be inhibited from rearing queens, and he supposed that the queen must communicate with the workers by touching their antennae with her own. Butler (1958), however, found that queen rearing, at least by small clusters of bees, could be inhibited by the residue from evaporated ethanol extracts of queens; his own and other work (reviewed by Butler, 1959; Butler, Callow & Johnston, 1961; Pain, 1961) leaves little doubt that a queen's power to inhibit queen rearing depends entirely on inhibitory substances ("pheromones"—Karlson and Lüscher, 1959) produced mainly, perhaps entirely, in her mandibular glands. One of these substances has been identified and synthesised. Butler (1957, 1960) has shown that supersedure is associated with queens that have little power to inhibit queen rearing and yield correspondingly ineffective ethanol extracts. Supersedure has been induced by amputating the reigning queens' front legs (Simpson, 1960a), which presumably interferes with the production or distribution of the inhibitory substances. Simpson (1956) suggested that failure of the reigning queen to prevent queen rearing can also cause swarming, but this has not yet been demonstrated. Several facts support the idea, but others are difficult to reconcile with it.

Small colonies, i.e., those that would require least of the inhibitory substances, rarely swarm when they have adequate hive space. Dividing a large colony into small ones is an effective method of preventing swarming. Queen rearing during the swarming season is more frequent in colonies with old queens than in those with young ones (Simpson, 1957, 1960b). When colonies become too big for their hives many worker bees may hang outside, but before this happens the density of bees inside the hive increases to about three to five times its normal level. The temperature among the bees does not exceed its normal maximum of 34–35° and is possible only because the densely packed bees remain almost motionless (Simpson: unpublished observations). This lack of movement perhaps causes queen rearing by hindering the distribution of the inhibitory substances. Butler (1960) found that queens of swarms from colonies whose owners said they had had ample hive space before swarming gave extracts relatively poor in their ability to inhibit queen rearing, whereas queens from swarms reputed to be caused by crowding gave fully effective extracts.

What is difficult to explain on the queen pheromone deficiency theory of swarming, is the swarming that occurs without queen rearing. The most common example of this is when a colony migrates, or "absconds". This behaviour rarely occurs naturally with European bees, but can be induced by depriving a colony of its hive and combs (Simpson, 1962). Colony migration might be thought a completely different phenomenon from reproductive swarming and one with quite different causes, but a gradation between the two appears when swarming is induced experimentally by putting big colonies into small hives. If the hive is much too small for the colony, so that a large proportion of the bees hang outside, the proportion that goes with the swarm is also large, and often queen rearing does not begin before the swarm emerges. During and after its emergence a swarm seems to behave exactly like an absconding colony.

Even if queen pheromone deficiency can cause both supersedure and swarming, something else must determine which occurs. Some other factor is involved, and this factor could cause both swarming and its associated queen rearing and not merely determine whether swarming or supersedure will result from lack of queen pheromone. Deficiency of hive space clearly is such a factor in the swarming of colonies from small hives, so perhaps the swarming of uncrowded colonies has an analogous explanation.

The factors that decide whether a colony that starts to rear queens will swarm, supersede or indulge in abortive queen rearing may be partly genetic, but the frequency of swarming in the summer and of efficient supersedure in the spring and autumn suggests that there is also a seasonal cycle involved. The growth of colonies to full size changes the proportions of bees of different ages. Gerstung (*c.* 1890) supposed that an increase in the proportion of adult bees to brood, and therefore of food available for larvae, led to the rearing of queens (queen larvae are given more food than worker larvae). Simpson (1957b), however, found that an experimentally induced brood-food surplus did not cause queen rearing or swarming. It is also unlikely that brood-food surplus predisposes to swarming rather than supersedure, as the proportion of adult bees to brood is largest in the autumn supersedure season. As swarming is most frequent at the time of year when most colonies are growing rapidly, it is more likely to be related to a high proportion of young bees to old ones than of adult bees to larvae.

There is some evidence for another kind of seasonal factor. Beekeepers mostly agree that colonies that are big early in the season are more likely to swarm than those that become big later (Holzberlein, 1952), and this cannot be explained on any age balance hypothesis. The decline in swarming after midsummer is often attributed to the prevalence of heavy nectar flows at that time, but nobody seems to have noticed any diminution with heavy nectar flows early in the season. It seems likely that the swarming is at least partially determined by an intrinsic physiological cycle, presumably initiated by emergence of colonies from their winter condition. The existence of some such cycle is also suggested by changes in the state of the fat bodies and salivary glands of worker bees in the course of the summer (Simpson, 1956, 1960c).

The Emergence of a Swarm from its Parent Colony

When a colony swarms some of the worker bees go with the swarm and some stay to continue the parent colony. At one time it was supposed that the bees that swarmed were either the oldest or the youngest, but Rösch

(1930) concluded that a swarm contains bees of all ages in about the same proportions as in the parent colony. At Rothamsted Morland began a more extensive investigation that was completed and published by Butler (1940). This also showed bees of all ages in swarms, but with a bias towards the younger ones. From this it seemed that the bees that stay behind when a colony swarms might be the ones that have flown enough to be familiar with their old position; this would explain why the bees of a swarm usually remain in any new position in which they are hived (Free, 1958), whereas when part of a colony is moved artificially to a new position many bees return to the part left on the old one. This hypothesis was disproved by an experiment (Simpson, 1960e) in which a swarm was found to contain many bees that had previously returned to their old position when moved artificially. Taranov (1947) suggested that the bees that go with a swarm are pre-determined at least several days beforehand. However, putting a colony in a small hive can make it swarm within as little as 24 hours, and colonies have absconded in as little as 4 hours when experimentally removed from their hives and combs. Colonies taken from their hives (one only ½ hour beforehand) have been induced to abscond by holding them close to colonies already absconding. Bees from the absconding colonies landed on the other colonies and started self-propagating disturbances in them that quickly led to absconding (Simpson 1962). Apparently, colonies can quickly become unstable and able to swarm when given the right conditions, so it is unlikely that the bees that go with a swarm are pre-determined. How a colony divides when it swarms is still unexplained.

Huber (1792) noted that an old queen leaving her hive with a swarm appeared to do so unwillingly, but it has been suggested that a swarm that emerges with a virgin queen does so by following her when she goes out to mate. However, Simpson (1960d) saw a virgin queen being driven out of her hive by swarming workers, whereas when the swarm was re-united to the parent colony no disturbance suggestive of swarming was associated with the same queen's later mating flights. When the swarming workers were driving the queen out they did not actually push her; those beside her stopped moving forward in the entrance tunnel whenever she did, with the result that those coming behind ran into them and formed a dense mass through which the queen could not penetrate. Some similar behaviour may explain how a swarm perceives its queen when flying across country (Simpson, 1962). If workers that have lost the smell of their queen because they have got in front of her fall back until they find it again the queen may always be kept in front of the swarm, leaving scent behind her to be perceived by the workers.

REFERENCES

BRÜNNICH, K. (1922). Graphische Darstellung der Legetätigheit einer Bienenkönigin. *Arch. Bienenk.* **4**, 137–147.

BUTLER, C. G. (1940). The ages of bees in a swarm. *Bee World* **21**, 9–10.

BUTLER, C. G. (1957). The process of queen supersedure in colonies of honeybees (*Apis mellifera* Linn.). *Insectes sociaux* **4**, 211–223.

BUTLER, C. G. (1958). The inhibition of queen rearing by feeding queenless worker honeybees (*A. mellifera*) with an extract of "queen substance". *J. Insect Physiol.* **2**, 61–64.

BUTLER, C. G. (1959). Queen substance. *Bee World* **40**, 269–275.

BUTLER, C. G. (1960). The significance of queen substance in swarming and supersedure in honey-bee (*Apis mellifera* L.) colonies. *Proc. R. ent. Soc. Lond. A* **35**, 129–132.

BUTLER, C. G., CALLOW, R. K. & JOHNSTON, N. C. (1961). The isolation and synthesis of queen substance, 9-oxodec-trans-2-enoic acid, a honeybee pheromone. *Proc. roy. Soc. B.* **155**, 417–432.

DUFOUR, L. (1939). Récherches sur la ponte de la reine. *Apiculteur* **83**, 271–280, 293–296, 309–313.

FREE, J. B. (1958). The behaviour of honeybees when their hive is moved to a new site. *Bee World* **39**, 109–115.

GARY, N. E. & MORSE, R. A. (1962). The events following queen cell construction in honeybee (*Apis mellifera* L.) colonies. *J. apic. Res.* **1**, 3–5.

GERSTUNG, F. (*c.* 1890). See: *Der Bien und seine Zucht*, 7th ed. (1926), Berlin: Pfenningstorff, pp. 192–205.

HOLZBERLEIN, J. W. (1952). Swarm prevention—not swarm control. *Amer. Bee-J.* **92**, 195–196.

HUBER, F. (1792). *Nouvelles observations sur les abeilles I.* Geneva: Paschoud.

JEFFREE, E. P. (1951). The swarming period in Wiltshire. *Wiltsh. Beekeep. Gaz.* **74**, 2–3.

KARLSON, P. & LÜSCHER, M. (1959). Pheromone: ein Nomenklaturvorschlag für eine Wirkstoffklasse. *Naturwissenschaften* **46**, 63–64.

MORLAND, D. M. T. (1930). On the causes of swarming in the honey bee (*Apis mellifera* L.): an examination of the brood food theory. *Ann. appl. Biol.* **17**, 137–149.

NOLAN, W. J. (1925). The brood rearing cycle of the honeybee. *Bull. U.S. Dep. Agric.* No. 1349.

PAIN, J. (1961). Sur la phérormone des reines d'abeilles et ses effets physiologiques. *Ann. abeille* **4**, 73–158.

RIBBANDS, C. R. (1953). *The behaviour and social life of honeybees.* London: Bee Research Association.

RÖSCH, G. A. (1930). Untersuchungen über die Arbeitsteilung im Bienenstaat. 2. Die Tätigkeiten der Arbeitsbienen unter experimentell veränderten Bedingungen. *Z. vergl. Physiol.* **12**, 1–71.

SIMPSON, J. (1956). *The behaviour and physiology of the honeybee with particular reference to swarming.* Ph.D. Thesis, University of London.

SIMPSON, J. (1957a). The incidence of swarming among colonies of honey-bees in England. *J. agric. Sci.* **49**, 387–393.

SIMPSON, J. (1957b). Observations on colonies of honey-bees subjected to treatments designed to induce swarming. *Proc. R. ent. Soc. Lond. A* **32**, 185–192.

SIMPSON, J. (1959). Variation in the incidence of swarming among colonies of *Apis mellifera* throughout the summer. *Insectes sociaux* **6**, 85–99.

SIMPSON, J. (1960a). Induction of queen rearing in honeybee colonies by amputation of their queens' front legs. *Bee World* **41**, 286–287.

SIMPSON, J. (1960b). The age of queen honey bees and the tendency of their colonies to swarm. *J. agric. Sci.* **54**, 195.

SIMPSON, J. (1960c). The functions of the salivary glands of *Apis mellifera*. *J. Insect Physiol.* **4**, 107–121.

SIMPSON, J. (1960d). *Problems of swarming behaviour.* London: Central Ass. Beekeep.

SIMPSON, J. (1960e). *Rep. Rothamst. exp. Sta.* for 1959, p. 144.

SIMPSON, J. (1962). *Rep. Rothamst. exp. Sta.* for 1961, p. 157.

TARANOV, G. F. (1947). (The occurrence and development of the swarming instinct in bee colonies.) *Pchelovodstvo* **24**, 44–54.