WEED ECOLOGY

Chairman: Dr. E. Holmes

THE EVOLUTION OF WEEDS IN RELATION TO RESISTANCE TO HERBICIDES

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The experience of research workers in the fields of medicine, bacteriology and applied entomology is that the introduction of a chemical for the control of a parasite or pest is almost inevitably followed by the development of a strain of the organism which is resistant or immune to the action of the chemical. Plant pathologists have also been concerned with this problem, for the breeding of a new variety of crop, resistant to a specific fungal disease, is usually followed by the evolution of a strain of the fungus which is pathogenic to the previously 'resistant' host.

Babers (1953) says of the entomological problems of resistance 'We should remember that in 1947, when farmers and dairy operators first began commenting that DDT was becoming less effective against the housefly, many suggestions without adequate experimentation were made to explain the failures. The use of hard or alkaline water, poor quality or insufficient DDT, too much rain, too much sun, 'other factors' and ignorant operators were all blamed. With a few exceptions the possibility that resistance had developed seems hardly to have been considered.'

This raises the question of how long it will be before those weeds which are at present susceptible to control by herbicides become resistant and again present serious problems. (This problem is briefly discussed by Pfeiffer and Zeller 1953). The question cannot be answered with any degree of precision, but this paper is an attempt to interpret the problem in terms of knowledge obtained in fields where resistance has already appeared and been studied. The problem gains added interest because of its relevance to more general aspects of the evolution of weed species.

In bacteriology and medicine, problems of resistance to drugs have arisen mainly in relation to the use of antibiotics, the 'sulfa-' drugs and other chemicals which possess bactericidal or bacteriostatic properties. Here evidence suggests that at least two mechanisms may operate leading to the development of resistance:

(a) adaptation to withstand the action of a drug followed by inheritance of this type of adaption (Hinshelwood 1949); (inheritance of such an acquired adaption appears to be restricted to micro organisms).

(b) the selection of genetic resistance through the elimination of sensitive forms from a population which contained a very few genetically distinct resistant forms. Before use of the drug these resistant forms may have possessed no advantages over the normal susceptible form, but the removal of competition from the susceptible 'normal' allows the resistant forms to multiply freely. Such resistance may in some cases be due to the ability of the organism to metabolise the drug, e.g. the production of penicillinase by some staphylococci.

In some cases bacteria have not only become adapted or selected to the presence of a drug, but forms have arisen which may require it as an essential nutrient for growth. Bacterial strains have developed under the selective influence of the widespread use of antibiotics and forms are now known which are resistant to penicillin, streptomycin, viomycin, neomycin, chloromycetin, or to the sulfa-drugs. Moreover forms are known which are resistant to several of these anti-biotics or drugs in combination. Bondi et al. (1954) studied 125 strains of staphylococci and found 35 resistant to penicillin alone, 50 resistant to penicillin, streptomycin, chloratetracycline and oxytetracycline and 5 were resistant to these as well as chloramphenicol. It is particularly relevant to the thesis of this paper that such resistant forms of microorganisms have developed in regions in which the toxic substances have been frequently used, e.g. hospital populations of bacteria are characterised by an abundance of resistant forms. There is no evidence that populations of e.g. Staphylococcus aureus have changed where the drugs have not been used. In fact a selected population will normally be less vigorous in competition with unselected forms once the selective factor is removed because selection to a specialised way of life almost inevitably brings with it reduced general efficiency. This is clearly illustrated by Lepper et al. (1953) who demonstrated that in a period of five months during which erythromycin and chloratetracycline were in use there was a rise from 0 to 70% of erythromycin resistant forms in the population, but when penicillin was used and erythromycin discontinued, the percentage of erythromycin resistant forms fell to 28% in the following four months while the proportion of penicillin resistant forms increased.

Florey (1952) states 'the method of dealing with this complication of therapy is obviously to give from the beginning a dose sufficiently large to ensure rapid inhibition and death of the prevailing strains that are present, and to inhibit any less susceptible strains that may emerge'. There can in fact be no selection when there is 100% kill.

Resistance may develop to chemical substances which have a specific action on one metabolic activity of the organism or to more generally toxic substances: for example deliberate selection of protozoa for resistance to mercuric chloride poisoning led to the development of strains tolerant of high concentrations of this chemical (Davenport and Neal 1895). Resistance to damage by X-irradiation has been reported in bacteria (Witkin 1946).

In the fungi the development of resistance is clearly demonstrated in plant pathogens which become resistant to either active or passive host defences. For example, wart disease of potatoes caused by the fungus Synchytrium endobioticum, has been controlled by the breeding of immune varieties of potato. Recently new forms of the fungus have evolved which can attack these 'immune' varieties of potato; such a fungus can be said to have developed resistance to those characteristics of potato varieties which had given previous immunity. There are other and more direct examples of the evolution of fungi to give strains resistant to chemicals, e.g. strains of Aspergillus sp. have arisen which are resistant to the toxic action of copper.

Comparisons made between the reaction of micro-organisms to drugs and that of weeds to herbicides must however be qualified because (a) the breeding system of micro-organisms is peculiar and varied and (b) the conditions of exposure of micro-organisms to drugs may be more continuous and so more effective in selection than exposure of weed populations to herbicides.

The development among insects of strains resistant to insecticides is of great relevance to the consideration of resistance to herbicides in higher plants for in both these cases, diploid, normally sexually reproducing organisms are usually concerned. Also the application of insecticides to insects has essentially the same intermittent nature as the application of herbicides to weeds. Many examples are cited by Babers (1953). Pieris rapae, the small white butterfly, has become resistant to DDT and methoxychlor in parts of Wisconsin and in New South Wales. DDT has failed to control mosquitoes, the louse and the housefly in different areas within 6 years of its intensive use. Perhaps most striking is that in S. Africa the blue livestock tick has become resistant to arsenic dips, BHC, chlordane and toxaphene. Resistance to BHC appeared within 18 months of its first use.

A significant difference between the application of insecticides to insects and the application of herbicides to weeds is that in the former case attempts are often made to eliminate the pest whereas herbicides may in many cases be used only to weaken the weed. Nevertheless selection can operate effectively by modifying the reproductive vigour of an organism as well as through mortality. (Stebbins 1950).

Plant populations are capable of rapid evolution under conditions of active selection. An outstanding instance of this is seen in the work of Sylvén (1937) on the natural selection for resistance of red clover (Trifolium pratense) to the fungus Sclerotinia trifoliorum and the eelworm Tylenchus devastrix. Sylvén showed that when this clover was grown on fields infested by the two organisms, natural selection made a rather susceptible variety more and more resistant towards these two parasites. On areas where these pests were comparatively rare no such selection took place.

Sylvén also showed that heterozygous strains of white clover sampled from the relatively mild climatic conditions of Denmark and Germany and transplanted to the severe climate of S. Sweden became adjusted to this climate in a period of two years by selective elimination of the less hardy individuals. More homozygous material did not respond in this way. Stebbins (1950) and Huxley (1942) give many other examples of the relatively rapid evolution of higher plants in response to some new selective factor in the environment. There exists an outstanding and often quoted example of rapid response to selection among agricultural weeds in the work of Salisbury on Torilis arvensis (spreading hedge parsley) and Aethusa cynapium (fool's parsley) (see Huxley 1942). In these cases dwarf strains or ecotypes of the species characterise stubble fields. The taller strains which may appear are decapitated by harvesting operations before the seed has ripened. In this connection Huxley (1942) says 'it is quite conceivable that good dwarf species may eventually evolve, restricted to the autumnal stubble habitat'.

New strains or species of weed may evolve either by divergence from a pre-existing species under the influence of selection, or by processes following hybridisation which may result in a new species being formed suddenly and without the direct influences of selection.

In some cases, weed populations of a species represent part of a larger population from which a variety, subspecies or even species especially adapted to agricultural land has already been selected. Such a case is Ajuga chamaepitys, rare in Britain but a weed of cultivated land in Central and

Western Europe and parts of N. Africa. This appears to have originated from a polymorphic species Ajuga chia, 'selection having operated to reduce the variability of the stock and to adapt it more closely to the status of a weed of arable land.' (Turrill 1934). A weed believed to have originated by hybridisation followed by chromosome doubling is Galeopsis tetrahit. It is thought that this plant originated by crossing of Galeopsis pubescens and Galeopsis speciosa (both diploid species) and that the sterile hybrid so formed gave rise to the fully fertile polyploid G. tetrahit (Müntzing 1930). This type of evolution is perhaps more likely to occur in weeds than in plants of natural vegetation because the closely related species which are the most likely parents of such hybrids, cohabit much more commonly in cultivated land than in natural communities. This rather remarkable tendency for closely related weed species to cohabit on agricultural land is found in the genera Veronica (the speedwells), Papaver (the poppies), Rumex (the docks) Ranunculus (the buttercups), Senecio (the ragworts and groundsels), Plantago (the plantains) Chenopodium and in many of the grasses and clovers. Such a situation may encourage the formation of hybrids which may become new species in their own right through polyploidy, and it may also allow a flow of genes from one species to a close relative through hybrid swarms (e.g. Senecio jacobaea (ragwort) x S. aquaticus.) Such intragression would increase the effective range of variation (especially polygenic variation) exposed by a species to selective forces. For this reason evolution might be expected to proceed faster in weed species than in inhabitants of natural vegetation. The rate at which a weed could respond to selection by a particular factor introduced into the environment depends on the intensity of selection and the heritable variability of the weed which in turn depends on the nature of its breeding system. It is not possible to predict how these factors will interact in any particular case.

The most effective intensity of selection is that which reduces a population to a small resistant residue which is capable of rapid reproduction. Under these circumstances a large population is maintained on which selection can continue to act and fix the newly selected forms. This implies that selection and subsequent evolution of new strains will be most rapid in organisms which possess a high reproductive capacity. Selection by herbicides should also be rapid where the natural mortality of the organisms is 'density dependent'. This situation arises in organisms of high reproductive capacity, for example the cornfield poppies where there is intense competition between seedlings. Elimination of part of this seedling population, before competition has brought about serious mortality, will allow many to grow to maturity which would otherwise have died naturally. Thus it may be possible for the size of a weed population to remain unchanged but for the population to be changed genetically.

It seems that weed control involving the spraying of early seedling stages is likely to lead to the development of strains of weeds resistant to herbicides by replacing a density dependent mortality with a special selective act. Such spraying may have the effect of killing or suppressing those weeds which compete aggressively with the crop, but may lead to rapid evolution of resistant forms.

The heritable variability of a species is a function of its genetic system, and of the extent of out-breeding. In general, the most rapid evolution will be likely to occur in sexually reproducing organisms with an efficient outbreeding system, (e.g. Papaver spp.) particularly if a certain amount of inbreeding is enforced temporarily. Therefore the rapid evolution of new strains as a result of selection is unlikely to occur in weeds with predominantly vegetative reproduction e.g. Agropyron repens. Moreover plants with a marked tendency to selfing or apomixis may be more conservative than outbreeding species. However even apomictic species may be capable of reacting to a selection when a population contains many different coexisting genotypes which show a differential response to a selective factor (e.g. the work of Sukatschew on Taraxacum, quoted Dobzhansky 1951). Weeds show a great range of types of breeding behaviour and differences may be expected in the ways in which they evolve in response to the regular use of herbicides.

Arable weeds constitute an ecological group selected and maintained in association by their fitness for existence under conditions of crop cultivation. They comprise species which have been selected by the very cultural practises which were originally designed to suppress them. The rotation of crops is practised with the control of weeds as one of its aims, and populations of weeds fluctuate widely in numbers because the environment is constantly changing. It is rare for a weed to be equally adapted to survive autumn and spring cultivations, to persist equally well in leys and arable land, or to compete equally well with roots and with cereals. Because of the alternating cropping practised in crop rotation, weed populations are cyclic, rising to high levels in crops with a life cycle which synchronises with that of the weed but falling to low numbers in the intervening years. Such intense selection as is afforded to weeds by normal crop rotation may reduce the significance of other selective factors e.g. herbicides.

Many of the weedy species of flowering plants have evolved dormancy mechanisms. Seed burial by ploughing and cultivation may enforce dormancy for several years and such a reserve of dormant seed in the soil, germinating and producing crops of weeds in succeeding years, may mask and partly suppress the effects of temporary selection by such selective factors as herbicides. Herbicide treatment may kill all but a few 'resistant' forms in a weed population but in succeeding years the seed of these resistant forms would germinate together with seed of plants unselected by herbicides and remaining from preceding years. Outbreeding between resistant and susceptible strains will tend to mask the resistant characters, while competition between resistant and susceptible strains favours the latter (if the herbicide treatment is not repeated). Weed seeds may often be dispersed with the crop. If seed of resistant plants were spread in this way the factors for resistance might be diluted and lost by outbreeding and competition with the unselected plants in a new habitat. However such seed might alternatively provide a nucleus of resistant forms which could spread under the continued use of herbicides.

Resistance to herbicides might conceivably evolve through modification of the biochemical, morphological or phenological characters of a weed. In some senses biochemical resistance might be considered the only true resistance, morphological and phenological differences might lead to herbicide 'escape' mechanisms. Analogy with the mechanisms of biochemical resistance in insects and in micro-organisms suggests that resistance to herbicides might take the form of (a) modification of a plant's metabolic processes so that an action blocked by the herbicide might be bypassed or (b) a herbicide might itself be metabolised or inactivated by a special enzyme system developed by the resistant organism. In either of these circumstances any resistant population which might arise would remain susceptible to chemically unrelated herbicides. Therefore a rotation of herbicides differing fundamentally in toxic action would minimise the chance of resistant strains becoming established.

Little is known of the role played by morphological differences in determining the susceptibility of different weeds to herbicides. However, differences between a plant's ability to retain and allow penetration of herbicides may sometimes depend on morphological and anatomical features which can undergo modification. Many weed species, e.g. Chenopodium album and Polygonum aviculare are highly variable in morphology and these variations are inherited. Morphologically different varieties of Cirsium arvense have been shown to differ in susceptibility to amino triazole (Anon. 1955). Differences in the angle of inclination of the leaf, type of branching and epidermal characters are likely to have some selective value in so far as they determine the amount of spray retention and penetration. Such differences would not necessarily confer absolute resistance to a particular herbicide, but would be more likely to lower the effect of all types of sprayed chemicals. Changes in weed resistance brought about by the selection of slight morphological changes would probably be slow and likely to be overlooked in the early stages of selection.

Changes in the phenology of weeds are perhaps the most likely changes to follow a continued and systematic programme of herbicide usage. The seeds of many weed species have characteristic dormancy periods which fit them for associated growth with a particular crop. In the genus Camelina autumn and spring germinating sub-species are known and these are associated with different crops and cultivation practices. Papaver rhoeas is normally slow to germinate and only a small proportion of the seeds germinate in the first year but horticulturalists have selected from this species the garden varieties known as 'Shirley' poppies which give almost immediate germination of all the seeds. Where dormancy mechanisms are under this type of genetical control, such operations as the spraying of young weed seedlings are likely to select for strains of the weed which germinate slightly later and avoid the spray damage. A similar problem arises where a weed changes in susceptibility with ageing. Continued spraying at one stage of development could lead to the evolution of phenologically different plants. In this connection it is interesting that Härer (1947) has shown that mutants of Arabidopsis thalliana differ in photo-periodic requirements for flowering. In view of the points raised in the above discussion it would be surprising if active evolution of weeds towards increased resistance had not already started. Blackman (1950) drew attention to the chance of weeds resistant to herbicides arising and Abel (1954) notes that "there is increasing evidence from field experience in that higher doses are now required to control certain weeds, e.g. creeping thistle (Cirsium arvense)". It is of the greatest importance that occasional failures of previously successful measures for weed control should be critically examined - so that - if or when resistance is demonstrated, the pockets of resistance may be isolated and eliminated. Only in this way can the spread of factors for resistance be prevented. It should also be remembered that a farmer or contractor is seldom faced with a weedy field in which there is only one weed; when a herbicide is applied it may kill 100% of the major weed and at the same time have an important selective action on subsidiary but slightly more resistant species.

Bacteriologists with their experience of the problems of resistance to antibiotics have attempted to develop methods of using these substances which at the same time minimise the development of resistance. Some of their findings are relevant to the problems of weed control. The following techniques and methods may prove important as ways of delaying the evolution of resistance to herbicides (modified from recommendations listed by Bryson and Szybalski (1955) in relation to microbiological resistance)

(1) Multiple herbicide treatment would be based on the assumption that plants resistant to one chemical may be eliminated by another. The spontaneous occurrence of multiple-resistant mutants is very rare and so a combination of two independently acting herbicides should, in theory, greatly hinder the development of resistant strains. Whenever possible simultaneous treatment with two toxic substances is preferable to their use in sequence.

(2) Choice of a herbicide to which resistance might develop by a single step is less desirable than a herbicide with complex action to which resistance can only develop in a stepwise manner (e.g. by polygenic inheritance).

(3) A herbicide with rapid action is preferable to one which is slow-acting - particularly if there is a chance that resistant forms in a population, although dying eventually as a result of treatment, may first produce seed.

(4) Synergistic interaction of antibiotics has proved valuable in ensuring 100% kill, and this possibility may exist in the use of herbicides.

(5) Herbicides with mutagenic properties should be avoided, and the mutagenic activity of existing herbicides needs investigation. Phenolic compounds are often mutagenic (D'Amato et al. 1956) and Unrau et al. (1952, 1953 and 1954) have shown that the application of 2,4-D produces meiotic irregularities and chromosome breakage in some crop plants.

The role of the unsprayed part of a weed population must not be overlooked. Populations of weeds in hedgerows, roadsides, headlands and in unsprayed strips of a sprayed field will of course not be selected for resistance, unless spray drift occurs to such an extent that selection occurs in these habitats also. If spray drift occurs onto waste land, it is important that such areas should then be sprayed thoroughly.

However a source of seed of weeds unselected by spraying which may spread into a sprayed field and compete successfully with the resistant remainder from spraying is valuable. Moreover, such a reserve of unselected weeds in the vicinity of a sprayed area provides a buffer, delaying the rapid evolution of resistance, in outbreeding weeds. There is little doubt that the existence of reservoirs of unselected material of weeds, such as exists in buried viable seed and in populations on waste ground is an important partial safeguard against the evolution of herbicide resistant strains.

In a discussion of the evolution of weeds in relation to herbicides the selective effect of herbicides on crops is instructive. Dunham (1953, 1954, and 1955) has shown that varieties of a crop may differ markedly in resistance to herbicides. 'For instance in flax, Redwing has shown no injury from four times the amount of herbicide that reduced yields of Crystal and B5128'. Moreover differences in varietal response of flax to herbicides are genetically controlled. Dunham was unable to demonstrate any change in resistance of a strain after spraying in four consecutive generations - but as flax is generally regarded as predominantly self pollinated, the stocks may have been too homozygous to allow rapid evolution by selection. Detailed study of the nature and inheritance of resistance to herbicides is needed so that further attention may be given to preventing the evolution of resistant strains of weeds.

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Addendum

Since this paper was written it has been reported that Erechtites hieracifolia, which had previously been controlled in sugar cane plantations by applications of 2,4-D has developed strains resistant to this herbicide. Where these strains have appeared, strong doses of contact herbicides are now necessary to kill the weed (Hanson 1956).

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PRELIMINARY STUDIES IN THE COMPARATIVE ECOLOGY OF PAPAVER SPECIES

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The cornfield poppies are important weeds of arable land. Although the application of selective weedkillers has been of great assistance in their eradication it was felt that a better understanding of the life history and general ecology of the poppy might lead to more effective and economical control. Work at Oxford has been designed to compare the biology of five *Papaver* species and in particular to determine what factors influence the relative abundance of these species as weeds.

The five species, *P. rhoeas*, *P. dubium*, *P. argemone*, *P. lecoqii* and *P. hybridum* are closely related and are sometimes found growing together in the same area. The three former species cohabit fairly frequently.

> *P. rhoeas* is a common weed of arable land and waste places throughout Britain, but is rare in the North of Scotland and absent from the Outer Hebrides.
>
> *P. dubium* occurs in similar habitats to *P. rhoeas*, but is less common although it extends further North than *P. rhoeas* and may be locally abundant elsewhere.
>
> *P. argemone* is fairly frequent on light soils in the South of England but becomes rarer in the North. It is found associated with *P. rhoeas* and *P. dubium* as a weed in cereal crops.
>
> *P. lecoqii* is a rare weed usually found on old building sites, road verges, and waste places generally. It is not normally found on arable land and is of no significance as a weed among cereals. The detailed distribution of this species is not known because many workers have confused it with *P. dubium*.
>
> *P. hybridum* occurs as a rare weed of waste places. It appears to be locally frequent in certain parts of Cambridgeshire, but is only found as isolated plants elsewhere.

The species may be listed in order of increasing rarity: *P. rhoeas*, *P. dubium*, *P. argomone*, *P. lecoqii* and *P. hybridum*. They may be split into two groups. The three former species are often found in arable fields as weeds in cereal crops and are frequently sympatric. *P. lecoqii* and *P. hybridum*, on the other hand, are normally absent from such habitats, being confined to road verges, old building sites, quarries and other waste places. The species are usually distinguished on characters of the capsule; a simple key is included at the end of this paper.

In addition to the wild species, the Shirley Poppy (a variety of *P. rhoeas*) was included in some of the experiments, along with a form of *P. hybridum*, of Botanic Garden origin, which differed from the wild type in several morphological characters. This 'variety' is termed *P. hybridum* β for the purposes of this paper although it possibly merits specific rank.

The seed of each species has a definite dormancy period. P. rhoeas, P. dubium and P. argemone exhibit intermittent germination after a period of dormancy lasting several months. P. lecoqii and P. hybridum show a high percentage of germination after a shorter period of dormancy (see graphs). Salisbury (1942) has called this 'spontaneous' germination.

The fact that the two rarer species have shorter periods of dormancy is significant, and could explain their extreme rarity among cereal crops and absence from arable land generally. These species are virtually excluded from such habitats since their early germinating seedlings are destroyed after emergence by late autumn or spring ploughing. Their general rarity may be explained by their very heavy seedling mortality during adverse conditions. Salisbury found that P. hybridum seedlings suffered 48-76% mortality during a moderately severe winter.

Seed of P. rhoeas, P. dubium and P. lecoqii was sown outdoors in boxes during the autumn. In January P. rhoeas and P. dubium had each given less than 5% germination whilst 90% of the P. lecoqii seed had germinated. Severe frost caused 100% mortality of all emerged seedlings. A proportion of the residual seed of P. rhoeas and P. dubium subsequently germinated. Another cause of mortality among newly emerged seedlings was damping off during wet weather. Others were washed out of the soil by heavy rain. These simple observations illustrate the importance of dormancy in the ecological success of a species. A more exact study of the causes of seedling mortality is necessary.

The common species, P. rhoeas, P. dubium and P. argemone, in possessing delayed germination, do not suffer the high seedling mortality exhibited by P. lecoqii and P. hybridum and are consequently better adapted as weeds of arable land. In fact if extreme environmental conditions or agricultural practice eliminate the whole population of seedlings or plants in one year, sufficient dormant seed remains in the soil to reestablish a population the following year. Salisbury (1942) stresses the fact that the delayed germination of a portion of the seed crop is an important insurance against adverse conditions.

P. argemone has a shorter period of dormancy than P. dubium or P. rhoeas. P. rhoeas germinates intermittently, some germination taking place in late spring. In this species there is considerable residual germination which may occur the following season. This is also true to a lesser extent for P. dubium. Brenchley and Warington (1930), working with P. rhoeas, found that 74.80% of the seed germinated during the first year, 16.26% in the second, and 8.94% in the third year after sowing. Dormancy has a high selective value among wild species, this is emphasised by the fact that the Shirley Poppy and P. hybridum β both of 'cultivated' origin, give a high percentage of almost spontaneous germination (see graphs).

Various attempts have been made to break the dormancy of P. rhoeas, P. dubium and P. argemone. Seeds of these species were subject to low temperatures, infra-red irradiation, prolonged washing, and treatment with strong acids and alkali, but no significant increase in germination was observed. Abrasion of the seed coat gave an increase of 15% with P. argemone. Further studies are being made along these lines, as an understanding of the mechanism of dormancy in Papaver species could be of great value in designing cultural practices for their eradication.

Poppy seeds are often ploughed in with the stubble during the autumn and can remain dormant in the soil for considerable periods. Seeds of P. rhoeas are reported by Brenchley and Warington (1930) to be capable of germination after five years burial. Each year spring ploughing brings part of the buried seed population to the surface, where germination will take place under favourable conditions. This enforced dormancy is not to be confused with innate or genetically controlled dormancy previously discussed. The high carbon dioxide/oxygen ratio beneath the surface of the soil is probably the vital factor governing enforced dormancy of buried seeds. Kidd and West (1917) showed that, under natural conditions, dormancy may be enforced by the presence of carbon dioxide around the embryo, respiration being inhibited. Temperature is also of considerable importance. Warington (1936) found that fluctuating temperatures increase the germination of some seeds, this is being investigated for Papaver species. Laboratory experiments have shown that light is not required for germination of poppy seeds, whilst sufficient water for germination is generally present in the soil.

The total number of viable seeds a species can produce is of considerable importance in determining its general abundance. A high reproductive capacity is of particular significance to annual species in which survival depends upon the successful dissemination of viable seed. Salisbury (1942) obtained a measure of reproductive capacity for the four species, P. rhoeas, P. dubium, P. argemone, and P. hybridum, by an examination of their dispersal mechanisms, number of seeds produced per capsule, number of capsules produced per plant, seed viability and germination. Experiments showed that the height at which the capsules are borne was significantly different for each species, this had an effect upon the distance the seed was dispersed. Taller growing species appear to be more efficient in their dispersal. The commoner P. rhoeas and P. dubium have a distinct advantage over the other species in this respect. Average seed output per plant varies with the species: figures quoted are - P. rhoeas 170,000, P. dubium 13,700, P. argemone 2,142, P. hybridum 1,680. Reproduction data obtained in this way may be summarized and the average reproductive capacity for each species calculated.

Reproduction data for British species of Papaver (from Salisbury 1924).

Species	Mean number of capsules per plant	Mean number of seeds per capsule	Mean % germin-ation	Mean repro-ductive capacity
P. argemone	6.81 ± 0.38	313.6 ± 17.7	63	1,347 ± 140
P. hybridum	7.28 ± 0.42	230 ± 14.4	91	1,529 ± 183
P. dubium	6.83 ± 0.34	2,008 ± 126	42	5,757 ± 669
P. rhoeas	12.5 ± 0.6	1,360 ± 125	64	10,928 ± 1,522

It is evident that the two commoner species, P. rhoeas and P. dubium have considerably higher reproductive capacities than the two rarer species, P. argemone and P. hybridum. Reproductive capacity is obviously correlated with distribution. The figures quoted for P. hybridum are slightly higher than those given for the more abundant P. argemone. This, however, is offset by the fact that the seeds of P. hybridum germinate more or less spontaneously and are subject to high mortality whilst those of P. argemone are delayed in their germination.

Success of a particular species may depend upon the time of ripening of its seeds. This is often the case with weeds of arable land. As a rule rapid maturation is advantageous to an annual species.

Flowering data was obtained for P. rhoeas, P. dubium and P. argemone from habitats in which they were sympatric. For this purpose two arable fields were selected and random quadrats layed out in each. The number of flowering heads of each species was noted at regular intervals throughout the flowering season. Results indicate that there is a succession of flowering beginning in early June with P. argemone, followed two to three weeks later by P. dubium, P. rhoeas being the latest species to flower.

The same quadrats were used to determine times of seed ripening. Seed was considered to be ripe on the first signs of capsule dehiscence and dehisced capsules were counted and removed at regular intervals. Times of seed ripening were not significantly different for the three species. P. argemone, therefore, takes longer to ripen its seeds than the other species. P. rhoeas requires the shortest time for maturation. The time required for maturation in P. rhoeas may be important in its success as a weed. Damage to the capsules by birds has been noted in P. argemone, P. dubium has frequently been found with galled capsules, clearly the longer the ripening period the greater is the risk from such hazards.

Although the times of maximum flowering differ there is considerable overlap of the flowering periods of P. rhoeas, P. dubium and P. argemone. P. lecoqii and P. hybridum also flower at the same general time in habitats where they are sympatric with the commoner species. Each species, however, retains its individuality and evidence of hybridization is scanty. P. rhoeas x P. dubium hybrids have been reported on rare occasions. Forms of P. rhoeas possessing adpressed hairs on the stem, a P. dubium characteristic, have been found. Occasional forms of P. dubium with yellow sap, a characteristic of P. lecoqii, are reported, but these two species are morphologically very similar and there has been considerable confusion between them in the past. Many taxonomists have been content to group P. dubium and P. lecoqii together as P. dubium agg.

It was considered of interest to investigate the breeding systems of Papaver species. A number of interspecific crosses were attempted. Plants grown in pots under greenhouse conditions were used. About 20% of the total attempted crosses yielded some seed, whilst in other cases capsules were stimulated to develop normally, but no viable seed was produced. The P. dubium x P. lecoqii cross, and its reciprocal, was successful at almost every attempt. This is significant in view of the close morphological relationship between these two species. Although anthesis takes place at a fairly early stage within the bud, none of the species appears to be self-fertile. Numerous attempts at selfing were made without any seed set being obtained. It is unlikely that seeds are produced apomictically since emasculated flowers failed to produce seed.

The poppies represent a group of closely related species in which the outbreeding mechanism is well developed, which commonly coexist, and which nevertheless remain distinct. Strong genetical barriers obviously exist which prevent the formation of fertile hybrids and keep the species separate. Chromosome numbers are unknown for all the species, but P. argemone appears to differ from P. rhoeas and P. dubium in this respect. Poppies are also of particular interest as a group of species, some members of which are specially adapted as weeds of arable land, whilst others, without these adaptations, are confined in their habitats and less successful as weed species.

Studies of this kind enable us to define more clearly those characters of a plant which enable it to become a weed. A better understanding of the life histories of weed species may lead to more effective control in the future.

The author would like to thank Dr. J. L. Harper, who is supervising the work, for his advice and constructive criticism in the writing of this report.

Acknowledgement

The work is being carried out under a grant given by The Nature Conservancy.

Key to *Papaver* species

1	Capsule smooth	2
	Capsule with stiff hairs or bristles	4
2	Capsule almost globose, about as long as wide	P. RHOEAS
	Capsule obovoid - oblong, at least twice as long as wide	3
3	Capsule narrowed gradually from near the top; latex usually white	P. DUBIUM
	Capsule narrowed suddenly near base; latex turning yellow in air	P. LECOQII
4	Capsule almost globose; bristles spreading numerous	P. HYBRIDUM
	Capsule narrowly obovoid - oblong; bristles few, erect	P. ARGEMONE

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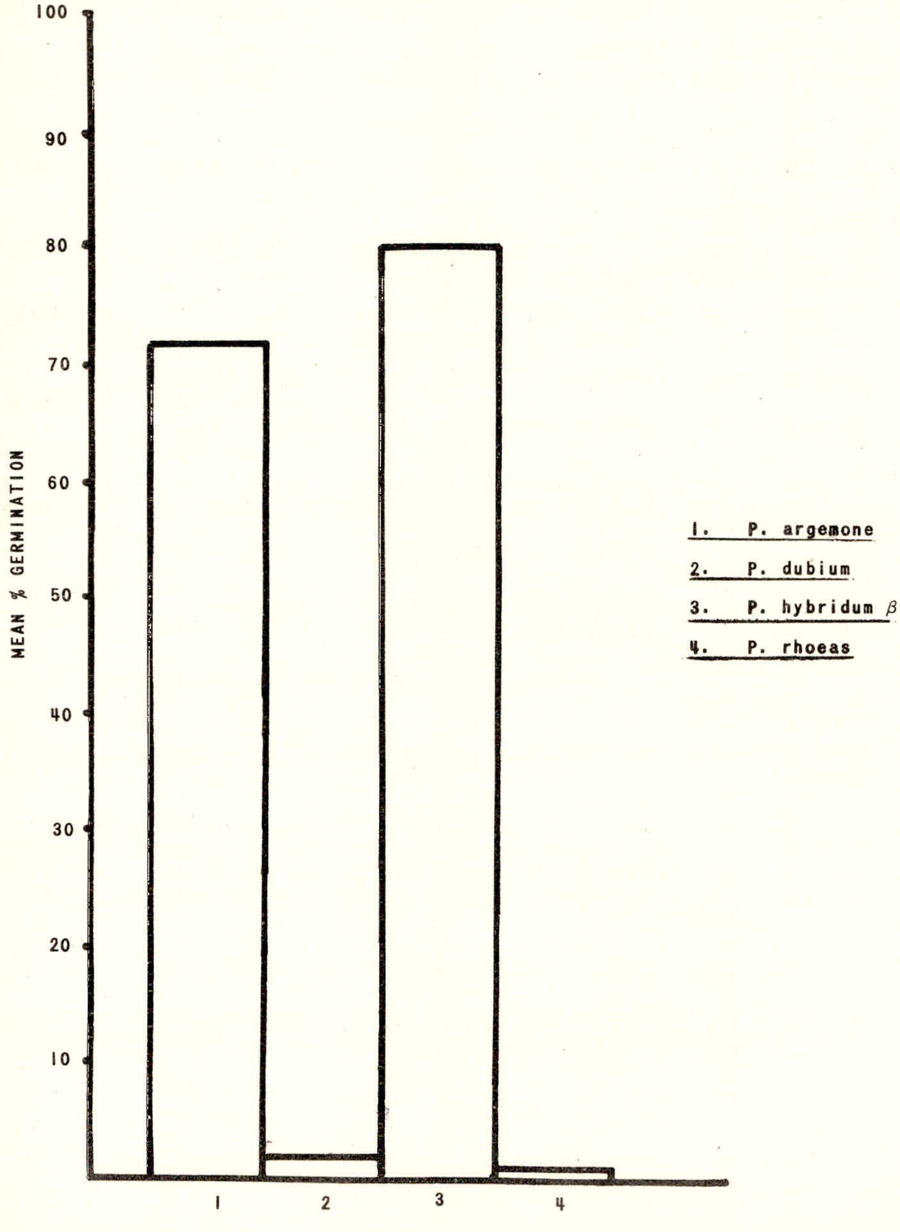
Germination of Papaver species

(1) Seed sown in a range of soils, at 20°C in dark throughout.
Mean % germination after 3 weeks is shown.
Date of sowing 26/4/56.



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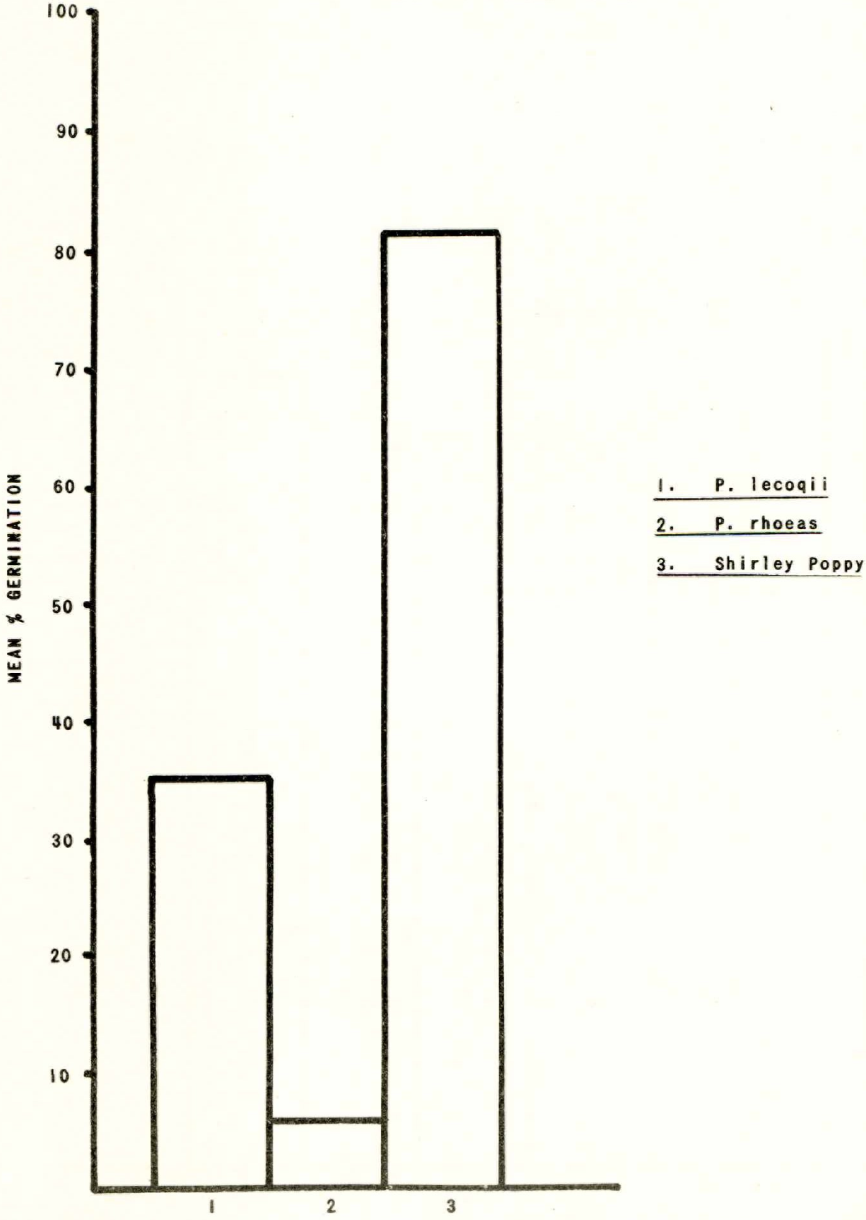
Germination of Papaver species

(2) Seed sown in a range of soils under fluctuating temperature conditions.

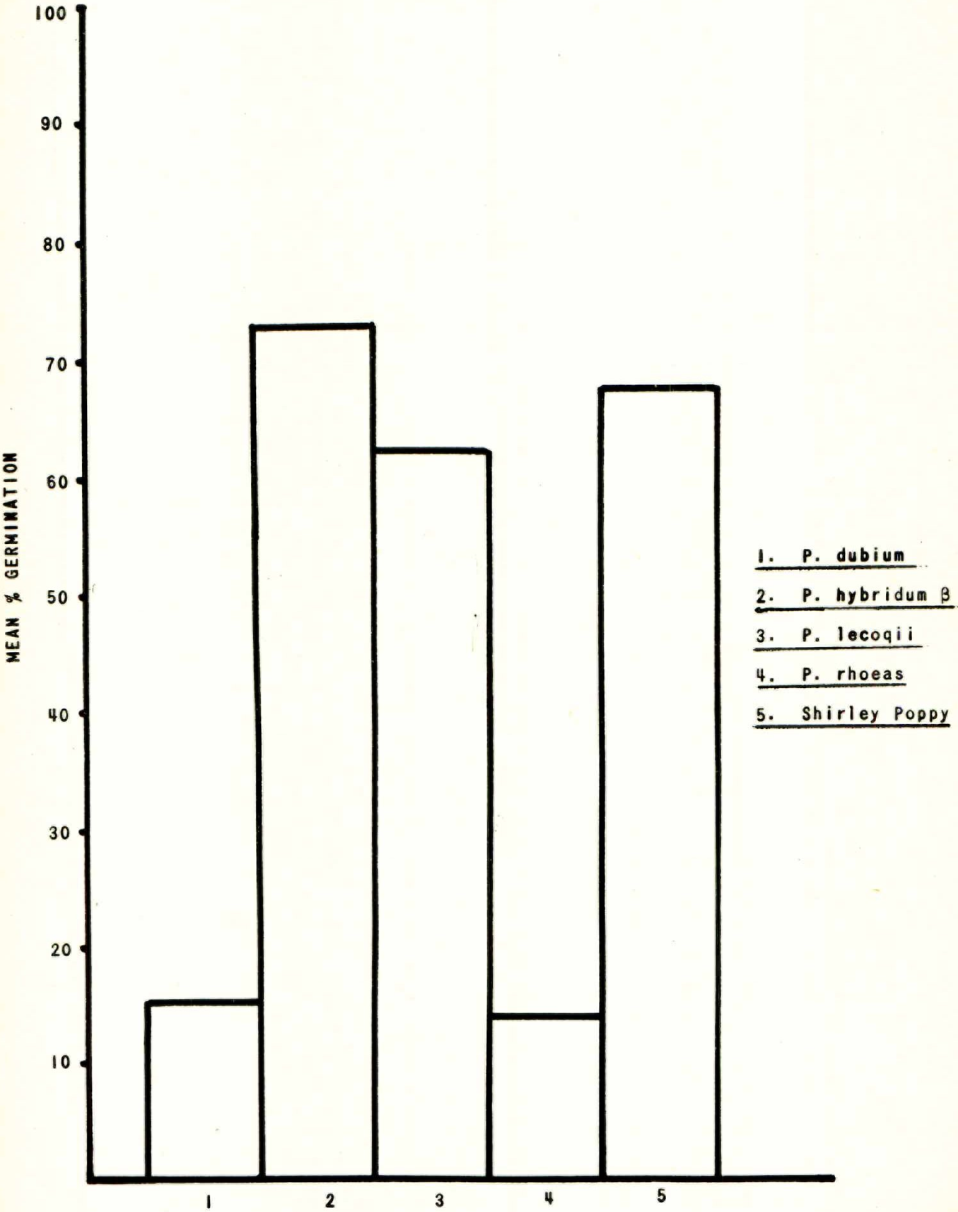
Mean % germination after 14 weeks is shown.
Date of sowing 2/2/56.



Germination of Papaver species

(3) Seed sown in John Innes compost under fluctuating temperature conditions.

Mean % germination after 6 weeks is shown
Date of sowing 14/2/56.



STUDIES ON THE ECOLOGY OF SOME SPECIES OF THE GENUS RUMEX

Patricia Chancellor

A.R.C. Unit of Experimental Agronomy, Oxford

The genus Rumex, which is one of the two main genera of the family Polygonaceae, contains approximately 150 species of which about 23 are found in the British Isles. Of these a number are important weeds, and two, the curled dock (Rumex crispus) and the broad-leaved dock (Rumex obtusifolius) are listed as primary noxious weeds of agricultural land. [Corn Production Acts (Repeal) Act, 1921, and Injurious Weeds Order 1921]. Other closely related weeds are the knotgrasses (Polygonum aviculare agg.), the persicarias (Polygonum persicaria and P. lapathifolium), buckwheat (Fagopyrum esculentum), and the sorrels (Rumex acetosa and R. acetosella).

Five species were selected for study; Rumex obtusifolius and R. crispus because of their importance as agricultural weeds, and three others which, because each appears to have different and characteristic habitat requirement, were included to provide ecological comparisons. R. conglomeratus ('sharp dock') is generally found in damp meadows and on river banks, R. sanguineus ('red-veined dock') in woods and shaded hedgerows, and R. hydrolapathum ('great water dock') in marshy places and shallow water. While R. crispus and R. obtusifolius are ubiquitous, it does seem to be that in general R. crispus occurs more in arable land and established pasture, and R. obtusifolius more in neglected grassland, by roadsides and in waste places, especially where the ground is often disturbed. Both species frequently are found growing together, particularly in grassland. The seed of R. crispus is a common impurity in wheat, oats and barley, as well as in red and white clover (Bates 1948). R. crispus and R. obtusifolius are recorded from all the 112 vice-counties of the British Isles, R. sanguineus from 104, R. conglomeratus from 106 and R. hydrolapathum from 81. The species hybridize fairly freely, the R. crispus x R. obtusifolius hybrid being particularly common. These plants, which are intermediate in vegetative and seed appearance between the parents can often be found on sites bearing mixed populations of the two species. They are generally sterile.

Docks have long been associated with cultivation and disturbed conditions, and this makes the question of how and when the plants were first introduced into Europe generally and Great Britain in particular especially interesting. Fossil and pollen analysis records suggest that the genus became established comparatively late. Godwin (1956) states that pollen occurs characteristically in the late-glacial, and that fossil records are concentrated upon the three periods which generally characterise typical weeds, namely the inter-glacial, full- and late-glacial, and the age of prehistoric cultivation. Although this association of docks with cultivation has not been investigated very thoroughly, it is of interest to note that in Port Meadow, near Oxford, an example of grassland which has been grazed continuously but not cultivated since Domesday Book records, no docks of any kind are present except in disturbed areas near paths and gateways and on the banks of the river. It is well-known that dock infestations frequently start in grassland when the continuity of a sward is broken by trampling etc.

All the docks possess tough, extensive, perennial tap-root systems and all have a high rate of seed production. Salisbury (1942) records Rumex crispus var. trigranulatus (the maritime form of R. crispus) as producing from 25,000 to 40,000 seeds per plant, with an average of 30,000. Of these, germination tests showed a 97-98% viability, giving an average reproductive capacity of 29,000 offspring per plant. Vegetative reproduction may also occur, both by the production of buds from the upper part of the root and by the regeneration of cut segments. It is claimed (Anon. 1950, Healy 1953) that R. obtusifolius will only regenerate from the upper 2.5-3 in. of the root and R. crispus only from the upper 1-1.5 in., but experiments in progress provide evidence that R. crispus will in fact regenerate from 1 cm segments taken at least 5 in. below ground level. The root segments have a remarkable capacity for survival, and this, with their regenerative powers would seem to be the explanation of the rapid reinfestation of fields following cultivation. The ability of plants to regenerate from root fragments confers a great advantage on a weed. Most cultivation practices will cut up and distribute roots as small fragments, and a plant regenerating from such a fragment will normally be provided with abundant food reserves, and will therefore establish more rapidly than a seedling. Observations suggest that natural seed dispersal in docks is particularly inefficient; very large populations of seedlings frequently occur within a small radius of the parent plant, and experimental data presented later in this paper indicates that there is a marked mortality dependent upon density among seedlings.

The penetrating power and the reproductive and regenerative capacity of the roots makes the elimination of docks by mechanical means very difficult. As already stated, splitting the crowns and breaking up the roots by ploughing and discing may ultimately increase rather than decrease the numbers of plants. As yet, no selective chemical treatment will do much more than destroy the top growth of established mature plants although MCPA and 2,4-D will kill R. obtusifolius and R. crispus in the seedling stage, i.e. before a large tap root has been formed. The eradication of docks is therefore a major agricultural problem, and it was partly with this in mind that the present study was undertaken, as detailed study of the biology of the plants may go far towards the discovery of satisfactory methods of control.

Experimental results and discussion

Experiments have been carried out during the season 1955-6 to determine some of the factors influencing the germination and establishment of docks in relation to environmental conditions, particularly soil type and the level of the water table. These experiments are being continued and the following account is to be regarded as an interim report.

Experiment to determine the effect of three water tables and two soil types upon the germination and establishment of five dock species grown alone at two densities and in pairs at one density.

Two types of soil were used, a heavy clay and a medium loam. The soils were placed in 10 in. aluminium pots in which the following water tables were maintained: (a) fully waterlogged (water table at soil surface), (b) semi waterlogged (water table half-way up the pot) and (c) free drainage. The waterlogged and semi waterlogged conditions were obtained by first sealing the bottoms of the pots and then connecting them through a series of polythene siphons to water reservoirs of constant level. The third series of pots were allowed to drain freely from the bottom. Seed was sown at the end of November 1955; each species was sown alone at densities of 50 and 100 seeds per pot, and in combination with each of the other four species at 50 seeds per pot. The experiment involved 120 different combinations of species, density and water table. The pots were completely randomised. In spite of the severe winter when the pots were frozen solid for long periods, a comparatively high proportion of the seeds - up to 50% - germinated. Seedling counts were made at 2-3 weekly intervals following germination, but there was considerable difficulty in distinguishing some of the species at the seedling stage. In September 1956, when many of the plants in the pots had flowered and set seed, seed counts were made and the plants were harvested for dry weight estimations of root and shoot systems.

Preliminary results from this experiment are shown in Figs. 1, 2 and 3. For clarity in Figs. 2 and 3, the two agriculturally less important species, i.e. R. sanguineus and R. hydrolapathum are omitted. The following tentative conclusions may be drawn:

(a) Of the five species, R. crispus, R. conglomeratus and R. sanguineus flowered and set seed during their first season. Under the conditions of the experiment, R. obtusifolius showed no signs of producing flowering shoots, and if this applies in natural habitats it should give R. crispus, which can apparently produce large amounts of seed during the first summer, an advantage over R. obtusifolius in the colonisation of new sites. This may explain the greater abundance of R. crispus in land which is cultivated annually.

(b) Under completely waterlogged conditions only R. crispus produced seed, and under semi waterlogged conditions only R. crispus and R. conglomeratus. R. sanguineus was the least tolerant of water-logging in its ability to flower and set seed.

(c) The relationships between total plant numbers at harvest and the total dry weights of the same plants are complex (cf. Figs. 2 and 3). In general the maximum weight of a species occurs under conditions of free drainage, but the highest plant numbers frequently occur under semi waterlogged conditions. This suggests that the environment which allows optimal seedling establishment is not necessarily that which favours optimal growth.

(d) For single species sowings of R. obtusifolius and R. conglomeratus at all water tables, the total numbers of plants are lower from the higher density of sowing. Similarly with regard to dry weight, in all species except R. sanguineus, at all water tables, total dry weight is lower from the higher density of sowing. This indicates that in these species, seedling mortality increases with increasing seedling density.

The fact that mixed populations of docks (particularly R. obtusifolius and R. crispus) commonly occur, poses special ecological problems. To become established side by side in approximately equal numbers, the plants must have equal or compensating competitive abilities or compete for different requirements. Experimental results and observations indicate that the latter hypothesis is unlikely.

Further results of this and allied experiments will be published later. Although no definite conclusions can be drawn at this stage, it is felt that carefully controlled experiments of this sort may yield information of value in understanding agricultural problems and at the same time contribute to the more fundamental aspects of plant ecology.

The work is being carried out under the supervision of Dr. J. L. Harper, whom the author would like to thank both for the direction of experimental work and in the writing of this report. Thanks are also due to Mrs. J. M. Lee and Miss C. L. Hunt for technical assistance, and particularly to Mr. R. J. Bowerman for setting up and looking after the pot experiments.

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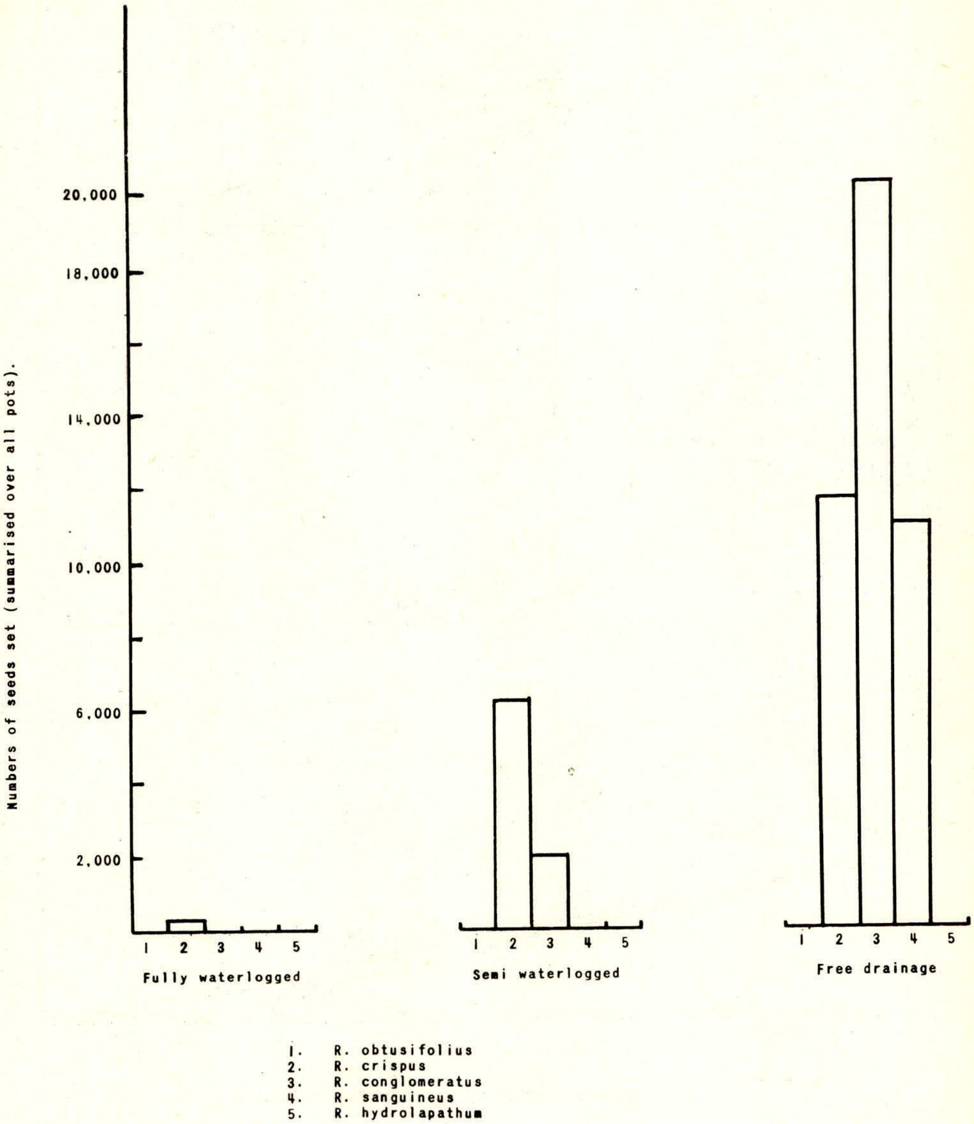
Fig. 1. Overall seed production during first season.



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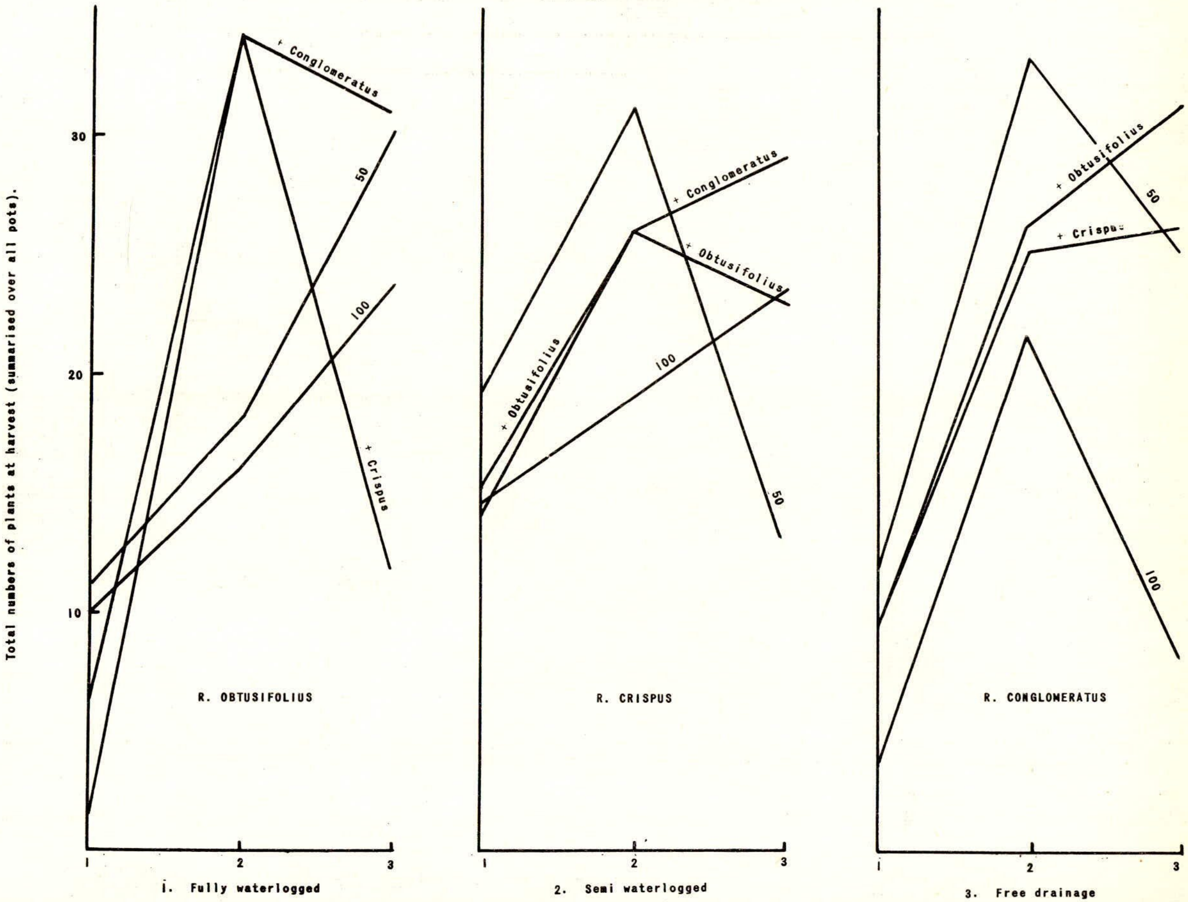
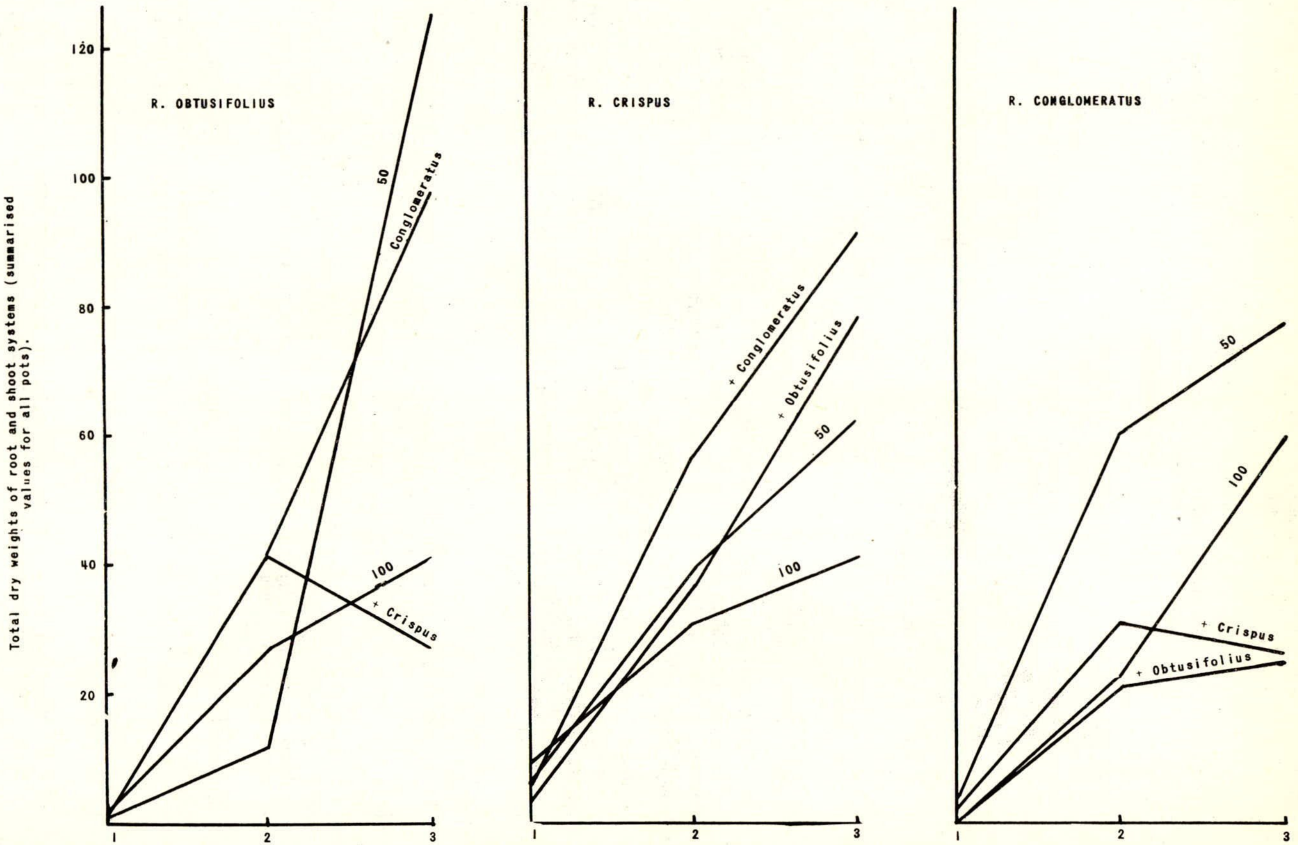
THE EFFECT OF WATER TABLE ON THE ESTABLISHMENT AND GROWTH OF DOCKS

Fig. 2. Counts of total plants at harvest for three species sown alone at 50 and 100 seeds per pot and in the presence of each other at 50 seeds per pot.



THE EFFECT OF WATER TABLE ON THE ESTABLISHMENT AND GROWTH OF DOCKS

Fig. 3. Total dry weights of root and shoot systems at harvest for three species sown alone at 50 and 100 seeds per pot and in the presence of each other at 50 seeds per pot.



1. Fully waterlogged 2. Semi waterlogged 3. Free drainage

DISCUSSION ON THE PREVIOUS THREE PAPERS

Mr. C. V. Dadd

There is a considerable support in the field for the practice of achieving a partial control of weeds which will, for instance in peas, give you your maximum yield response. Is anybody studying the development of resistant strains of weeds from this point of view? It is quite a job in most cases to produce 100% control with low volume spraying. We might find ourselves, if the worst comes to the worst, in a very difficult position without satisfactory alternative herbicides. Is anybody studying this and the extent to which it might become practically important in this country?

Dr. J. L. Harper

Mr. Dadd's point is of the greatest importance. The trend towards reducing applications to sub-lethal levels which are intended to control but not kill the weeds is a policy which provides the ideal conditions for the evolution of resistant strains. I know of no attempts which are being made to study this problem.

Dr. W. E. Ripper

With reference to Dr. Harper's stimulating paper it seems relevant to point out that resistant strains of insects have occurred in those species which have several generations a year, and further in those cases where considerable pressure has been applied. The development of resistance in weeds compared with insects is therefore a slow motion mechanism and it would seem to be likely to occur much later and be of much less importance. In his paper he has drawn many analogies with the development of resistance of microbes which have even more generations a year, therefore as a whole I would think that the economic botanist is far less frightened than his entomological and medical colleagues.

Dr. J. L. Harper

It is certainly true that all the examples I have drawn from fields of medical science and entomology have been concerned with organisms which have several, and in some cases many, generations a year. However, the fact that most flowering plants have only one generation per year (or less) is to a large extent compensated by the very high reproductive capacity of these plants. The rate of evolution will be determined by the rate at which new variations are exposed to selection and the number of generations per year is only one factor contributing to this.

When writing this paper I was tempted to say that the evolution of resistant strains was a problem for 50 or 100 years hence - but it is now clear from the examples of *Erechtites* and of *Cirsium arvense*, that this problem is for now.

Dr. R. K. Pfeiffer

Dr. Harper said that the development of resistant strains of weeds has been proved only quite recently. I wish to draw attention to a quotation in a paper by Linser (1951) according to which such evidence was also obtained in 1949 in Louisiana. Seed obtained from weeds surviving 2,4-D treatment were found to produce plants about twice as resistant to 2,4-D as the previous generation.

Mr. K. Wilson Jones

In the study of resistance of insects to insecticides it has proved necessary in many cases to assess the susceptibility of the insects in a given area to insecticides by laboratory trials before the commencement of the experiments; failing this it is very difficult to come along later and suggest that you have got resistant strains. Does Dr. Harper know of any instances where laboratory tests, or any form of assessment, of the ultimate susceptibility of weeds to herbicides have been made?

Dr. J. L. Harper

Examples of the development of strains of weeds resistant to herbicides are only now beginning to appear and little attempt has been made to search for such strains. I know of no laboratory tests which have yet been carried out as a routine measure in the manner Mr. Wilson Jones suggests. Clearly, if the development of resistant strains becomes a problem, such routine trials become desirable. In this connection a recent paper by Davidson (1) is relevant. He studied the genetics of the resistance shown by strains of the mosquito *Anopheles gambiae* to dieldrin. This resistance was inherited in a simple Medelian fashion. Davidson points out that the normal LD 50 method for comparing the susceptibility of populations to insecticides grossly underestimates the extent of resistance which may develop. In the example quoted the LD 50 of the resistant population was 8 times that for the susceptible population. However, a comparison of the dosage mortality curves showed that the resistant forms were 800 times as resistant as the susceptible populations.

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BIOLOGY, ECOLOGY AND CONTROL OF WILD ONION AND YELLOW RATTLE

Sigurd Håkansson

Royal School of Agriculture, Department of Crop Production, Uppsala, Sweden

Some of the research students at the Department of Crop Production of the Royal School of Agriculture at Uppsala are engaged in weed control research. One of them, Agronom Sigurd Håkansson, is studying some weed problems in the south-east of Sweden. Below follows short summary of his results so far obtained.

Hugo Osvald

Biology, ecology, and control of wild onion

As in certain parts of Great Britain and the United States, so in the south-east of Sweden and on the islands of Öland and Gotland in the Baltic *Allium* species occur as noxious weeds both in cultivated fields and in pastures. Every year in spring and early summer the milk in many districts has an unpleasant odour of onion - particularly on Öland and Gotland - and the grain for milling is often badly infested with bulbils.

In the spring of 1954 an investigation was started in order to find out how to control the different *Allium* species most effectively.

Several *Allium* species have been recorded within the area. As in other countries, however, *Allium vineale* is the most important as a weed. This is true particularly of cultivated fields. In pastures other species such as *A. oleraceum* and *A. scorodoprasum* may sometimes occur abundantly, but *A. vineale* is also here the most common species. The most comprehensive studies have, therefore, been carried out on the behaviour of this species. In many respects these Swedish studies correspond to the admirable study of *Allium vineale* published by Ruth H. Richens in 1947.

In Sweden as in Great Britain the seed setting of *Allium vineale* is rather poor. For this reason the vegetative multiplication, at least with regard to quantity, is the most important one. The following vegetative multiplication organs can be discerned:-

(1) Bulbils among the flowers at the top of the scape.

(2) Offset bulbs which may be subdivided into two types:

(a) major offset bulbs formed in the axil of the innermost leaf of the parent plant, "main bulbs"; and

(b) minor offset bulbs formed in the axil of the outer leaves, "side bulbs".

The main bulbs and the bulbils after a short rest period generally germinate already in the autumn of the year of formation, while the rest period of the side bulbs generally lasts for at least one year. Consequently, the side bulbs enable the species to survive in a field in spite of soil-tilling operations.

Some side bulbs and bulbils may be found germinating in the spring, but generally they germinate in the autumn. The shoots reach a rather varying length before the beginning of the winter. The longest shoot in a population may reach a height of 30-40 cm above soil, while others do not reach the surface. Early in spring the shoots begin to grow again. The plants now reach a stage in which the reserve supply of nutrients is at a minimum, i.e. the supply of the parent plant is exhausted but new bulbs have not yet begun to form. At that stage of development the plants are particularly sensitive to mechanical damage. In the author's experiments the effect of ploughing has been best if done in early spring, but the most highly developed plants can easily be killed by a shallow ploughing in late autumn. Repeated harrowing in the autumn and in the spring also have a good effect.

In cultivated fields scapes with flowers and bulbils are almost exclusively found in winter crops and in leys. In the leys, however, they rarely reach full development because of cutting or grazing. In spring-sown crops there are only few scapes. The explanation is simple. Spring tillage before sowing kills the plants or hampers their growth: in a field with winter crops, on the other hand, the plants may grow without being disturbed by tilling. This leads to the following conclusion. Fields infested with wild onion should be disposed of in such a way that late autumn and, first of all, early spring tillage can be done frequently in the crop rotation. From a study of the frequency of wild onion in fields with different rotational systems it is evident that A. vineale cannot survive for a long time in fields where spring-sown crops occupy a prominent place in the rotation.

In addition, some experiments with chemical control of wild onion have been carried out. In winter cereals spraying in the spring with MCPA compounds, corresponding to 1-1.5 kg/hectare MCPA (acid) generally gives good control, since the growth of scapes and bulbils is hampered quite considerably. The time at which the crop is sprayed is not without importance, but the results so far obtained are not sufficient to permit of any definite conclusions as to the most appropriate time for spraying.

In grasslands spraying in the spring with 2,4-D esters, corresponding to 1-2 kg/hectare 2,4-D (acid) seems to kill most of the wild onion plants. Spraying should be done at least for two consecutive years in order to obtain a lasting and good control.

Biology and control of yellow rattle

In some parts of southern Sweden yellow rattle, Rhinanthus major, occurs as a noxious weed in leys and winter cereals. Yellow rattle is a semi-parasite; where it is frequent, e.g. in a field of rye, the crop will be poor.

Apparently the seeds germinate fairly late in the spring. Therefore, the plants are hardly noticeable until the time of rye earing. Three spraying experiments have been carried out this year, all of them in rye crops.

In Experiment 1, the field was sprayed on May 18, 10-12 days before earing of the rye. At that time about one half of the plants of yellow rattle were at the cotyledon stage and the largest plants were about 5 cm high. Three different formulations of MCPA were employed, namely Agroxon Standard, Agroxon Extra and Phenoxylene Plus, all of them in quantities corresponding to 1140 g/hectare MCPA. The result per 75 sq.m with regard to yellow rattle was as follows:-

	Number of plants	Fresh weight (g)	Average weight (g)
Unsprayed	242	1080	4.46
Agroxon Standard	59	202	3.43
Agroxon Extra	29	123	4.22
Phenoxylene Plus	31	93	3.01

On July 30, all the plants from the plots were collected, counted and weighed: unsprayed plants were generally in post-floral stage and had full-size but still green capsules; sprayed plants were less developed, still flowering plants fairly frequent, and less capsules had been formed.

In Experiment 2 the field was sprayed on May 29 with two different quantities of Agroxon Standard, corresponding to 570 and 1140 g/hectare MCPA (7.5 and 15 litre) and with Agroxon + Sevtox (1140 g MCPA + 680 g dinoseb / 4 litre/hectare). The result calculated per sq.m was:-

	Number of plants			
	May 29 (before spraying)	July 7	Weight of plants (g)	Average weight per plant (g)
Unsprayed	23	24	124	5.1
Agroxon, 7.5 l/ha	28	21	53	2.5
Agroxon 15 l/ha	25	13	21	1.6
Agroxon + Sevtox	20	0	0	-

Consequently, on July 7, about one half of the number of plants had been killed by an application of Agroxon, 15 l/hectare, and the surviving plants were much smaller than those on the untreated plots. Only few of the surviving plants were flowering or could be expected to flower. On plots sprayed with Agroxon + Sevtox all plants of yellow rattle were dead already two days after the treatment.

In order to study the effect of dinoseb formulations separately, some plots of an unsown field heavily infested with yellow rattle were sprayed on June 5 with Agroxon Standard, 15 l/hectare, and Sevtox, 4 and 8 l/hectare. The effect of MCPA was about the same as in Experiment 2. On plots sprayed with Sevtox all yellow rattle plants were dead two days after the treatment.

Consequently, for control of yellow rattle dinoseb is definitely superior to MCPA, since all the yellow rattle plants are killed practically immediately by spraying with a mere 4 l/hectare of Sevtox.

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(1) RICHENS, R. H. (1947) Allium vineale L. (Biological Flora of the British Isles). - J. Ecol., 34, 209-226.

THE ESTABLISHMENT AND GROWTH OF WILD ONION (ALLIUM VINEALE L.) FROM AERIAL BULBILS

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A
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Introduction

The wild onion or crow garlic (Allium vineale L.) is found growing in all vice-counties of England and Wales and in the majority in Scotland and Ireland (Richens, 1947). It appears in open cultivated ground, in grassland and in waste places, especially roadside verges. Many of its habitats are dry and sandy yet it is on heavy land where, once established, it is particularly difficult to eradicate. In such conditions it is a serious weed.

Although flowers are produced, seeds are seldom developed in this country and propagation is almost exclusively vegetative. Three types of vegetative structures are found - aerial bulbils, often carried together with flowers on the same shoot, main or terminal bulbs, and offset bulbs developed from lateral buds in the axils of foliage leaves. (Figure 1).

Suggested control measures centre around cultivation effects (Talbot, 1929; Tinney, 1942). The recommendations of Tinney, for example, take the form of a rotation of 6 years spring cropping, the land being ploughed annually in November. Recently some success has also been claimed for selective herbicides.

The precise reactions of the plant to many farming conditions and operations remain unknown. A series of experiments are therefore being conducted in Cambridge in an attempt to throw light on the establishment, growth and development of the onion under different environmental conditions. This paper deals with two such experiments.

(a) The effects of competition and of variation in soil type and fertility status

Two soil types were used - a sand and a clay. Mechanical analysis showed the former to contain 84.4% of sand particles whilst chemical analysis indicated a slightly acid status, fairly low potash and a medium - high phosphate content. Respective data for the other soil were 51.86% of clay particles, a high lime and potash status, and a low phosphate content.

A compound fertiliser (9% N_2, 9% P_2O_5 and 15% K_2O) was applied to a series of boxes (each measuring 18 x 12 x 7 in.) to produce three levels of fertility. No fertiliser was applied to one-third of the boxes, a further third had 3 cwt per acre added to the top inch of soil prior to sowing, and a top dressing of 1.5 cwt per acre at the end of March 1956. To the remaining boxes, fertiliser was applied at 4 times this rate.

In half the boxes equal numbers of Italian and perennial ryegrass seeds were sown (a total seed rate of 20 lb per acre) between June 8th and 10th 1955 whilst at the same time 50 aerial bulbils were planted just below the soil

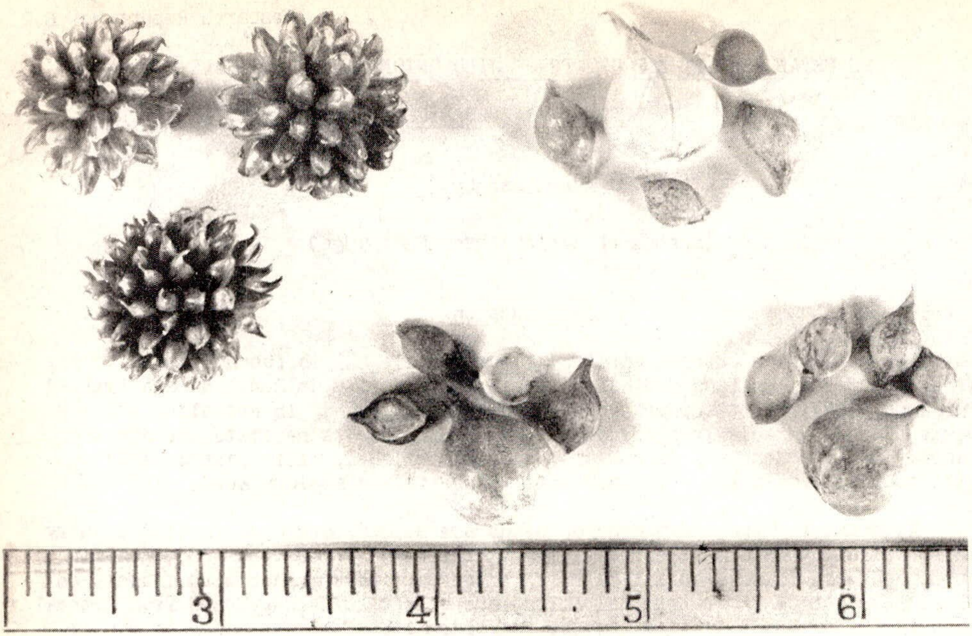


Fig. 1. Aerial bulbil heads, main (or soft-terminal) bulbs with offset bulbs.

surface in all boxes. There were five replicates of each treatment, a total of 60 boxes.

Watering was carried out only when it was considered the soil might dry out. All boxes were periodically weeded but no cutting of the grass was attempted. Counts of onion shoots were made at intervals.

RESULTS

The gross effects of soil type, competition and fertility status on number of onions counted in the boxes throughout the experiment are displayed in Figs. 2 - 4. These data are based on shoot counts, though the final figures taken in early August 1956 are based on bulb counts. It will be observed that the majority of onion shoots died back in early August 1955, and reappeared in late October.

The number of onions growing in competition with ryegrass was probably underestimated in the counts taken during 1956. The shoots are difficult to distinguish from grass and no doubt a few were missed during counting. In addition, competition appeared to shorten the growing season of the onion, and under some adverse conditions the food reserve seems to be withdrawn into the bulb.

When the plants were removed from the boxes their bulbs were weighed and such data, together with final plant counts, are displayed in Table 1.

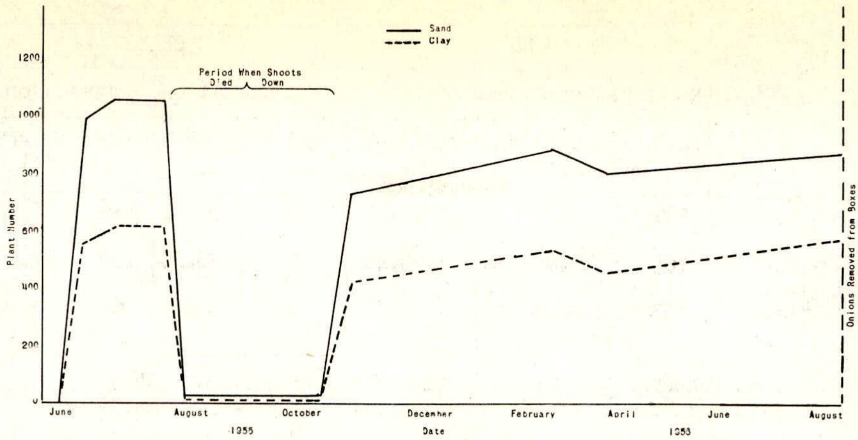


Fig. 2. The Effect of Soil Type on Total Onions Established.

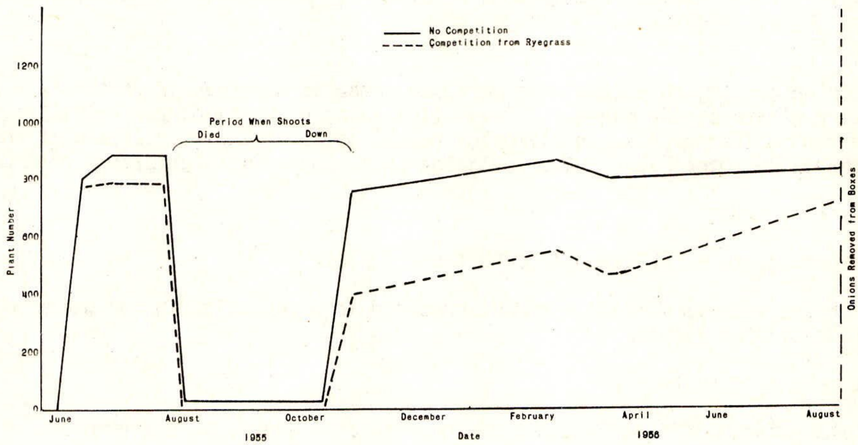


Fig. 3. The Effect of Competition on Total Onions Established.

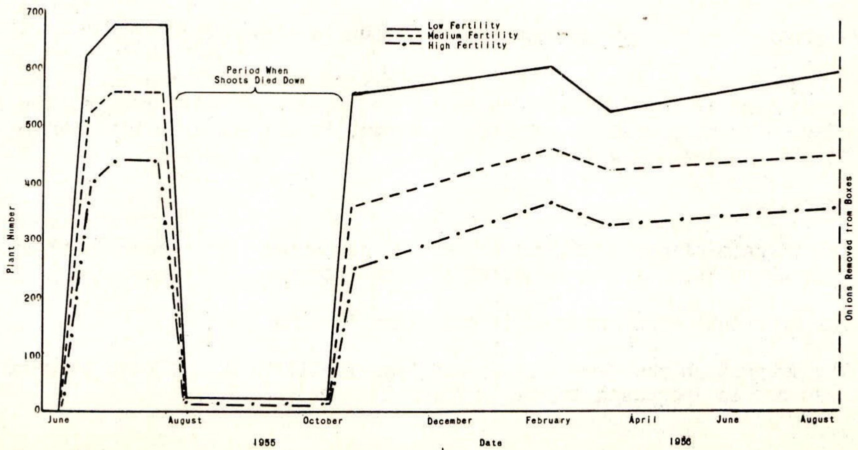


Fig. 4. The Effect of Variation in Fertility Status on Number of Onions.

(47011)

		SAND				CLAY			
		No competition		Competition		No competition		Competition	
		Number	Weight (g)	Number	Weight (g)	Number	Weight (g)	Number	Weight (g)
Fertility Status	Low	209	96.38	190	19.27	128	107.44	130	18.64
	Medium	165	83.79	161	23.40	97	58.89	106	14.07
	High	143	120.86	110	16.39	84	52.49	68	5.73

S.E. Numbers ± 12.0   Sig. diff. (P = 0.05) = 34.3
S.E. Weights ± 10.29   Sig. diff. (P = 0.05) = 29.39

Table 1. Total numbers and weights of onion bulbs removed from different treatments.

Onion number and weight data were subjected to analyses of variance. In addition a correlation was carried out (following corrections for variation in numbers of onions growing in different boxes) to determine the effects of the treatments on onion size. The following is a summary of significant effects.

Number of onions

1. More plants established in sand than in clay.

2. An increase in fertility status resulted in a reduction in the number of established plants.

Total weight of bulbs

1. The greatest effect was that of competition - there was a tremendous reduction in total bulb weight of onions growing with ryegrass compared with that where onions grew alone.

2. A greater weight was produced in sand than in clay.

3. A significant soil x fertility status interaction was detected. Under conditions of low fertility as much total weight of bulbs was prodiced in clay as in sand, yet in conditions of high fertility, much the greater weight was developed in sand.

Size of onions

1. The biggest effect again was the result of competition - much largr onions grew where there was no competition from ryegrass.

2. Larger onions were produced in clay than in sand.

3. The largest onions were grown under high fertility conditions, thegross response to increased nutrients being linear.

4. A significant soil x fertility status interaction was again detected. The effect of increasing fertility resulted in a marked increase in size of bulbs grown in sand but not in those grown in clay.

(b) The results of some possible cultivation effects

Any effects of cultivation on the growth and development of plants appear likely to result from one or a combination of the following:-

1. The stage in the plant's life-history at which cultivations are carried out, when the food reserve contained and its distribution within the plant seem important.

2. The frequency with which cultivations are carried out.

3. The actual effects of cultivations which might bury the plant, damage plant parts or disturb the plant's growth without seriously damaging vital parts,-breaking its root hold, and either leaving it beneath the soil or depositing it on the soil surface. The effects of such disturbances might be influenced by the prevailing growing conditions, especially moisture.

Preliminary experiments were initiated in February 1956 with the object of studying some effects of disturbing the growing onions. Small boxes (14" x 8½" x 2½") were filled with a typically heavy "wild onion" soil to which, following chemical analysis, a complete fertiliser (9% N2, 9% P205 and 15% K20) was added at the rate of 3 cwts. per acre. The boxes were taken into an unheated greenhouse; 28 aerial bulbils were planted in each on February 9th and 10th 1956, and the resulting seedlings were reduced to 20 per box. Three main treatments were considered:-

(a) The roothold of young plants was broken beneath the soil surface (Series A).

(b) Young plants were uprooted, laid on the soil surface and NOT watered (Series B).

(c) Young plants were uprooted, laid on the soil surface and watered (Series C).

The treatments, 4 replicates in each, were imposed at different stages in the growth of the onion, and at different frequencies:-

1st Treatment - mid-March (1)

Treatment	repeated	every	2	weeks	(w)
"	"	"	4	"	(x)
"	"	"	8	"	(y)
"	NOT repeated				(z)

2nd Treatment - end of April (2)

Treatment	repeated	every	2	weeks	(w)
"	"	"	4	"	(x)
"	NOT repeated				(z)

3rd Treatment - mid-June (3)

Treatment repeated every 2 weeks (w)

" NOT repeated (z)

4th Treatment (Control)

Plants allowed to grow undisturbed.

In Series B and C treatments other than the 1st took the form of turning the plant completely over to break any contact with the soil.

A total of 120 boxes was used in the experiment. In deciding on different treatment frequencies use was made of the fact that the plant shoot dies down around mid-July. All onion bulbs were removed from the boxes at this time.

RESULTS

Detailed notes were made every 2 weeks during the course of the experiment on the numbers of plants surviving and their form when subjected to the various treatments.

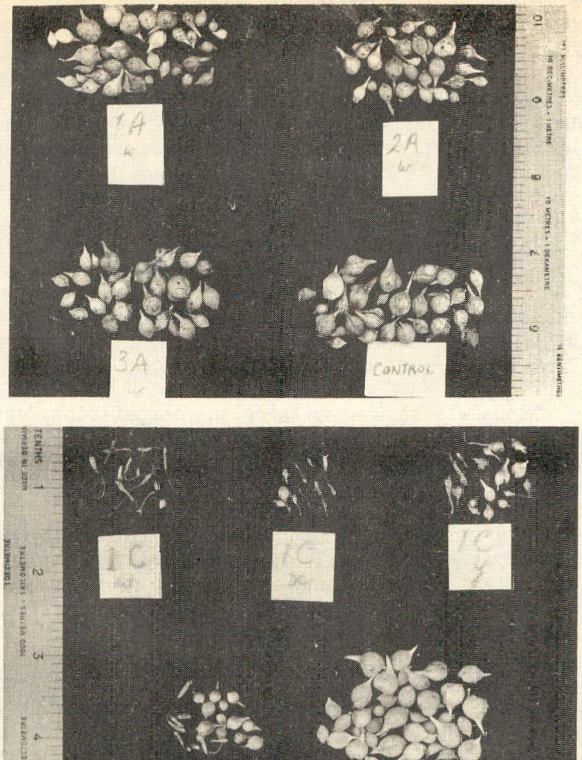
All plants survived the treatments given in Series A. Although the plant's growth was retarded by constant root breakage, in all cases the mid-March treatments produced a stimulating effect on shoot size, and plants left untouched after this initial disturbance actually grew bigger bulbs than did the controls.

Series C treatments had more drastic effects - the stage of growth of the plant when uprooted being an important factor. The effects on plants disturbed in mid-June were slight compared with those pulled up earlier. Plants disturbed once only early in their life made new root and shoot growth. There were many casualties but it is not yet possible accurately to assess the proportion of plants remaining alive at the end of the experiment.

All plants showing signs of life in Series C, together with the bulbs from Series A were weighed, when removed from the boxes - the data are presented in Table 2. Bulbs removed from some typical replicates in Series A and C are displayed in Figs. 5 - 7.

Treatment	Total wt. (g)	Treatment	Total wt. (g)
Control	14.70	Control	14.64
1Aw	10.71	1Cw	0;14
1Ax	17.05	1Cx	0.23
1Ay	12.42	1Cy	0.91
1Az	20.24	1Cz	1.76
2Aw	8.12	2Cw	1.14
2Ax	10.29	2Cx	1.02
2Az	13.32	2Cz	1.69
3Aw	11.20	3Cw	8.11
3Az	16.49	3Cz	12.42
S.E. ± 1.90		S.E. ± 0.85	
Sig.diff. (P = 0.05) = 4.92		Sig.diff. (P = 0.05) = 2.46	

Table 2. Weights of onions removed from different treatments in Series A and C.



"Some effects of different types and frequencies of plant disturbance, for details see text."

In Series B onions pulled up in mid-March retained the colour in their shoots for a considerable time - vestiges of life being observed for some 4-5 weeks. Plants pulled at the end of April transferred all food reserves immediately into a small bulb. After four weeks exposure to greenhouse temperatures, up to 90°F, some 60% of such plants sprouted again when suitable conditions were recreated. This figure fell to zero after 8 weeks exposure. All plants removed in mid-June survived 8 weeks in high temperature conditions.

Discussion

It is clear that soil type, in itself, is not a major factor limiting the growth of the wild onion. Richens (1947) reports the plant growing on all soils save peat whilst data accrued from the reported experiments have shown a greater number of onions established and a higher total bulb weight from sand than from clay. Variation in tilth may account for much of this difference for it is significant that the largest onions were developed on clay.

The growth rate of onions was slow when there was competition, yet only under high fertility conditions did the ryegrass noticeably reduce the number of plants which established. It was in such conditions, especially on clay, that the grass grew thickest.

Increasing the fertility status consistently reduced the number of onions establishing on both soil types - this result is at present inexplicable; as also are the differential effects of fertility status on onion size on the different soil types. Results on onion growth of varying the soil's manurial status and water content merit further investigation.

Breaking the root hold of the young plant, yet allowing it to remain in good growing conditions, would appear to check its increase in size - provided the operation was repeated with sufficient frequency. Such disturbance is not so effective as dragging the young plant out of the ground, a single procedure which if employed in their early growth stages, will kill off a number of plants developing from aerial bulbils. A high mortality rate of such plants can confidently be predicted when the soil is dry; in moist conditions, however, a high proportion are able to survive. The quicker the young plants are dragged from the ground after the aerial bulbils have sprouted, the greater are the chances of killing them. Later in their growth onions are able to transfer food reserves into a bulb which can survive adverse conditions.

Competition from a crop sown after cultivations would certainly reduce the growth rate of the onion and might result in the death of at least a proportion of any young plants previously dragged out on to the soil surface.

Much more data are required on the effects of different types and frequencies of disturbance, and damage, at various stages in the plant's life. Such information would allow of more accurate prediction of particular cultivation effects and might be valuable in showing which were the implements most likely to be effective in wild onion control.

It is a pleasure to record appreciation for his interest and valuable criticism to Professor Sir F. L. Engledow. Thanks are also due to Mr. W. J. Ridgman for his advice on statistical analysis whilst the work would not have been possible in the absence of the technical assistance of Mrs. B. M. Thomas.

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DISCUSSION ON THE PREVIOUS TWO PAPERS

Dr. E. Åberg (Introduction to discussion)

Wild onions appear as weeds on waste lands, on grasslands and in cultivated fields. In England and Wales, as well as in Scotland and Ireland, Allium vineale is found growing in the majority of the vice-counties. Many of its habitats are dry and sandy but it can also be found on heavy soils. Allium spp. appear as weeds along the shores in south-eastern Sweden and on the islands of Öland and Gotland in the Baltic. In the Swedish investigations by Håkansson five species of wild onions have been observed. Of these species Allium vineale is the most common. It is a serious weed both in natural pastures and in cultivated fields. Together with it in the pastures Allium scorodoprasum and Allium oleraceum may be found. Every spring and early summer the milk produced by cows grazing such pastures has an unpleasant odour of onions. Milling of cereals from fields infested with wild onions is often difficult because of the bulbils united with the kernels.

These are the problems. Let us discuss what can be done about them, after we have looked at some data on their biology and ecology. At Cambridge Lazenby has studied the behaviour of Allium vineale grown in sand or clay with various nutrient contents and with or without competition with cultivated plants. In his experiments ryegrass was sown in boxes at the rate of 20 lb/ac. At the same time 50 aerial bulbs were planted just below the soil surface. From the data obtained in his experiments Lazenby concludes that more onions were established in sand than in clay and also that increased fertility of the soil results in a reduction of the number of established plants. The greatest effect Lazenby obtained on the onions, however, was from the competitive effect of ryegrass.

Lazenby also studied the effect of disturbing the young plants by breaking their roothold beneath the soil surface, by uprooting them and leaving them on top of the soil without watering and with watering them. He showed that plants which had their roothold broken but were left beneath the soil all survived. If they were uprooted and left on top of the soil only those which were watered had a chance of surviving.

Lazenby comes to the conclusion that soil type in itself is not an important factor limiting the growth of wild onions. The growth rate of onions was slow when there was competition with ryegrass but it was only under conditions of high soil fertility that the competition from ryegrass resulted in a reduction in the number of onions. From his uprooting experiments he concludes that a high mortality can be expected when the soil is dry but not otherwise. However, he also concludes that the sooner the young plants are dragged from the ground after aerial bulbils have sprouted the greater are the chances of killing them.

Håkansson in his Swedish experiments has studied the biology and ecology of wild onions during the years 1954-56 in fields in areas where wild onions are common. He distinguishes between the following organs of vegetative propagation:

(1) Bulbils among the flowers

(2) Offset bulbs being main bulbs which are formed in the axil of the innermost leaf of the plant, or being side bulbs which are formed in the axil of the outer leaves.

Bulbils and main bulbs after a short rest period generally germinate in the autumn of the year of formation, while the rest period of the side bulbs generally lasts for at least one year. Thus the side bulbs enable the species to survive in a field in spite of tillage.

While some side bulbs and bulbils germinate in the spring most of them germinate in the autumn. Before the winter the longest shoots may reach a height of 30-40 cm above ground, others do not reach soil surface. Early next spring the shoots begin to grow again and some reach a stage where their reserve supply of nutrients is at a minimum, i.e. the supply of the parent plant is used up but new bulbs have not yet been formed. At that stage of development the plants are particularly sensitive to mechanical damage. Ploughing has a very good effect if it is done early in the spring. The most highly developed plants can also be killed by shallow ploughing in the autumn. Repeated harrowing in the autumn and in the spring also has a good effect. Fields infested with wild onions should thus be utilised so that late autumn and early spring tillage can be done frequently in the crop rotation. In natural grasslands increased use of fertilisers in combination with a renovation of pastures may be useful. By such a method the grass competition increases.

Spraying with MCPA 1-1.5 kg a.e./hectare generally gives good control in winter cereals. In grasslands spraying in the spring with 2,4-D, 1-2 kg a.e./hectare has a good effect. 2,4,5-T can also be considered for spraying in grasslands.

Mr. Garrett-Jones

I would maintain that the aerial bulbils are comparatively insignificant in the increase and propagation of _Allium vineale_. From experience of the weed on the Lower Lias formation in the Midlands, I have the impression that under normal agricultural conditions on heavy clay the ground bulbs are by far the more significant. I think the general distribution of the species in the fields in which it occurred rather tended to support this point of view. The density of infestation varied enormously and rather regularly from one part of the field to the other following fairly easily-mapped "contours" through the field. It seems to me to show that it is underground propagation where, of course, the offset plants are in general not distributed over very wide distances from the parent plant, rather than the more widespread distribution by aerial bulbils, which is involved.

Mr. R. S. L. Jeater

I promised Mr. Lazenby that I would try and answer any question on this. I would say that at the moment he has not got enough offsets and main bulbils to do any experiments with these. He is now building up a number of offsets and main bulbs and he will be doing experiments with them during the next year.

Mr. R. J. Chancellor

I should think _Allium vineale_ is a successful weed probably because of the shape and size of the bulbils rather than any sort of degree of spread from its underground parts.

Dr. E. Åberg

For the survival of wild onions in infested fields the side bulbs are probably of greater importance than the bulbils as was stated by Håkansson.

Mr. W. Q. Connold

Many must have read the work of H. Fail on the rotovation of couch and other weed grasses. I am just wondering whether rotovation has any applicability to the wild onion. At first sight it may not seem at all suitable but I would very much like to hear whether anybody is "having a go".