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The manipulation of weed behaviour for control purposes

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Most systems of weed control are based upon the concept that only that proportion of the population which appears as seedlings or as vegetative sprouts in any one year needs to be controlled. This is inefficient, for those that appear in any one year are often only a small fraction of the total propagules present. Furthermore it may require only one year of unsatisfactory control for the infestation to revert to its original level. Greater efficiency could result from utilizing growth regulating chemicals that will affect the behaviour of the whole population. It is postulated that chemicals for breaking the dormancy of seeds in the soil and chemicals for regulating vegetative regeneration are likely to be the most useful. They could well constitute the next major development in weed control. Other aspects of weed behaviour, which could be manipulated for control purposes, are also considered.

THE PRESENT POSITION

(*a*) *The need for weed control*

The need for weed control requires little justification, but it is not out of place, at the beginning of a consideration of future possibilities in alternative chemical weed control, to emphasize that this need will increase. The world population, which underlies the need, is increasing. It has been estimated that the human population is currently increasing at about 70×10^6 per year, that is about 200000 per day (Wharton, quoted by Wittwer 1977). Because the human population is increasing, so too must crop production. Annual crop losses due to weeds have been estimated at 287.5 Mt, which is about 11.5% of the total world food production (Parker & Fryer 1975). Herbicides are effective as short-term remedies, but weed populations as a whole have proved resilient to them.

(*b*) *The number of weed propagules in the soil*

Roberts & Stokes (1966) calculated the numbers of viable weed seeds in 58 horticultural fields distributed in 23 English counties. They ranged from 16×10^6 to 860×10^6 ha^{-1}, that is 1600 to 86000 m^{-2}. In over half the fields the populations ranged between 50×10^6 and 225×10^6 ha^{-1}. There are also records from a number of farmers' fields. Brenchley & Warington (1930) recorded $84–731 \times 10^6$ ha^{-1} on various plots of the classic Broadbalk experiment at Rothamsted. Milton (1943) recorded $42–267 \times 10^6$ ha^{-1} from fields near Stratford-on-Avon. These figures were determined before the advent of widespread herbicide usage, but more recent figures do not indicate any dramatic changes as a result of herbicides. For example, Roberts (1958) has recorded 566×10^6 ha^{-1} in one field. Determinations of the weed seed content of 32 fields in northwest Oxfordshire have been made at the Weed Research Organization between 1972 and 1977. The totals ranged from 3×10^6 to 555×10^6 viable seeds per hectare. These data do not appear to indicate any general diminution of the weed seeds in the soil.

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Large numbers of vegetative propagules can also occur. In England, Fail (1954) calculated that there were about 320 km of couchgrass (*Agropyron repens*) rhizomes in each hectare of an infestation and, with a bud every 50 mm, they have over 6×10^6 buds (618 $\mathrm{m^{-2}}$). The number of buds on *A. repens* rhizomes has also been calculated by Buchholtz (1962). In a dense stand there were about 430 m $\mathrm{m^{-2}}$ of soil and they bore more than 16000 buds or 161×10^6 $\mathrm{ha^{-1}}$.

Other types of vegetative regeneration can have similarly dense populations. Tubers of yellow nutsedge (*Cyperus esculentus*) recorded in a peat soil in Minnesota, U.S.A., exceeded 9800 $\mathrm{m^{-2}}$ or 98×10^6 $\mathrm{ha^{-1}}$ (Tumbleson & Kommedahl 1961). Each tuber would have several buds, so the number of dormant buds would have been several hundred million.

(*c*) *The proportion of propagules giving rise to new individuals*

With these dense populations of weeds in the soil, how many give rise to new plants each year? Roberts (1966) has reviewed what little information there is available on the number of seedlings arising from a seed population. In general the proportion is small: less than 10% of the total. He also found in a mixed population that when soil is disturbed four times a year the proportion of the total seed population giving rise to seedlings is about 9%, but with less frequent cultivations (twice a year) the proportion was only 6%. These values are considerably smaller than the observed decline in the total number of viable seeds in the soil. These extra losses must have been due to seed death, to predation or failure to reach the surface after germination. In contrast, the annual decline of *Avena fatua* seeds in the soil has been recorded at over 80% (Wilson 1978).

There is a similar situation in vegetative reproduction. Johnson & Buchholtz (1962) have estimated that in undisturbed situations more than 95% of all buds on rhizomes of *Agropyron repens* remain permanently dormant. However, tests have shown that if rhizomes are cut up by cultivation then each fragment, of various lengths from 1 to 15 nodes, will normally develop at least one dominant shoot which will give rise to a new plant (Chancellor 1974). The proportion of buds growing permanently (as opposed to starting into growth and then being inhibited) will depend upon the size of the fragment, which in turn will depend upon the frequency and type of cultivation (Fail 1954). In *Cyperus esculentus*, one tuber planted in the field produced 36 shoots and 332 tubers in 16 weeks and 1900 shoots and 6900 tubers during the first year. The relation between the numbers of shoots and tubers reflects the dormancy that the tubers exhibit (Tumbleson & Kommedahl 1961).

Thus, in general, there are large reserves of propagules, both seeds and vegetative parts, which normally give rise to a relatively small number of plants or shoots during the course of a year.

It is these plants and shoots that are the target of the farmer and the horticulturalist when growing their crops. Weed control can be accomplished in a variety of ways, mechanical, chemical, biological, and what has been called 'physical' weed control measures (Sanwald & Koch 1978), which include u.h.f., laser and heat radiation and electrical treatments. With the exception of soil sterilization by chemicals or steam heating, these various methods frequently serve merely to kill those plants or shoots that have emerged or, in the instance of persistent herbicides, those that will emerge during the chemical's effective period.

As mentioned above, the proportion of the total weed population that will emerge during the course of a season is relatively small, and so weed control systems generally kill only a small part of the weed population. Soil sterilization, although generally effective, is uneconomic in

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farming and is mostly used in horticulture, where it performs a dual role of disease and weed control. However, if the subsequent ingress of weed seeds could be prevented, it would be the ultimate solution to weed problems.

It would seem theoretically possible, with a system of weed control that completely controlled those seedlings or shoots that had emerged above ground, that if the system was continued for a long enough time, weeds could be completely eliminated. Unfortunately, this does not work well in practice, for, although dense infestations of weeds can be reduced by persistence, complete elimination is rarely achieved.

(*d*) *The rate of decline of propagules*

If a farmer does continue applying a weed control treatment that is 100% effective, so that no weed seeds are shed, how long is it before the seed reserves in the soil seed bank are exhausted? A study on this aspect has shown that even under the most favourable conditions of soil disturbance, the rate of decline in the total viable seeds of a mixed population in the soil is on average only about 50% per year (Roberts 1962). Thus, in terms of radioactivity, the seeds have a half-life of 1 year. That is, half of the seeds disappear by death, predation or germination in each 12 months. Therefore if one starts with 100 seeds at the beginning of the year, by December one should have about 50 seeds left and after 2 years about 25 seeds. If continued for 7 years then there should be about only one seed left. The population will then have been reduced to about 1% of its original density, a fact that lends scientific credence to the old saying, 'One year's seeding means seven years' weeding'. One must remember, however, that if one starts with an average population of 100×10^6 ha^{-1}, even after 7 years there will still be 100 seeds per square metre.

Thus as we have seen there are three aspects to the weed problem:

(1) there are large reserves of weed seeds and vegetative fragments in the soil;

(2) only a relatively small proportion of these give rise in any one year to new plants;

(3) the rate of exhaustion of these reserves is slow because of their often extended lifespan combined with various forms of dormancy.

Potential remedies

How then can this problem of weed persistence be solved? Probably the most satisfactory approach would be to find some chemical means of breaking dormancy. For seeds, this has been suggested many times, but equally one should not forget the possibility of preventing the development of dormancy or of inducing dormancy as methods of weed control.

(*a*) *Breaking seed dormancy*

Seed dormancy is broken in Nature by various environmental factors, notably fluctuating temperatures, chilling, light, etc., processes most probably mediated through changes in the levels of endogenous growth regulators. Indeed, the seeds of a large number of species can be stimulated in the laboratory by low concentrations of gibberellic acid. However, the application of gibberellic acid to seeds in the soil would probably be as ineffective as it would be uneconomic.

Chemicals that have long been known to stimulate germination include thiourea and potassium nitrate. Nitrate particularly increases germination in many species, and has been suggested as a means of artificially inducing *Avena fatua* germination so that they may be destroyed before the crop is planted (Sexsmith & Pittman 1963).

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One germination stimulant of considerable importance is ethylene, which is either injected directly into the soil or applied as an ethylene-generating compound such as ethephon (2-chloroethylphosphonic acid). This was tested on *Striga lutea* Lour. (= *S. asiatica*) by Egley & Dale (1970) and found to be very effective. *Striga* is a hemiparasitic plant assigned to the Scrophulariaceae. Hosts of *Striga* species are mostly Gramineae, and *Striga* seed will normally only germinate when it receives a stimulant from the roots of a host plant.

Studies on stimulation of the seeds by other means were undertaken after the discovery in 1956 that *Striga lutea* had inadvertently been introduced into the U.S.A. (Eplee & Langston 1976). It currently infests over 150000 ha of maize crops in North and South Carolina. The danger of it spreading to other areas and other graminaceous crops was immediately realized and a strict quarantine and eradication programme undertaken. When ethylene was first shown to be an effective stimulant of seed germination it was widely used to accelerate the reduction of the numbers of dormant seeds in the soil. Injected into the soil it diffuses more than 1.5 m laterally and to 1 m in depth. In 1974 over 6000 ha were treated (Eplee & Langston 1976).

Further advances in *Striga* control have been through the isolation by Cook *et al.* (1966) of strigol, one of the natural stimulants produced by host roots, the determination of its chemical structure (Cook *et al.* 1972) and finally its synthesis (Heather *et al.* 1974). Strigol is very potent, with one of its two isomers inducing 50% *Striga* germination at a concentration of 10^{-12} M and the other at 10^{-16} M.

This example has been described in some detail to illustrate what can be achieved by using control methods other than herbicides. It also illustrates that the principle of chemical stimulation of seed germination is practicable in the field. *S. lutea* is not the only species whose seeds respond to ethylene and it is rather surprising that more use is not made of it to control other important weed species.

The stimulatory effect of potassium nitrate may be explained by the theory put forward by Roberts (1969). He suggested that some oxidation reaction associated with the pentose phosphate pathway needed to occur before germination could take place, but respiration is a strong competitor for available oxygen because of the affinity of cytochrome oxidase for oxygen. Dormancy breaking is then promoted by the application either of inhibitors of cytochrome oxidase or of an alternative hydrogen acceptor for respiration such as nitrate, nitrite or methylene blue. Potassium nitrate increases the germination of seeds of many species. Another germination stimulant, which is a respiratory inhibitor, is sodium azide. This has been used experimentally in the field to stimulate germination of wild oats (*Avena fatua*) (Fay & Gorecki 1978). They found that disc-incorporated sodium azide at 11.2 kg ha^{-1} increased wild oat emergence from 12% (untreated controls) to approximately 50% of the total wild oat seeds in the soil.

Many other chemicals have been tested for dormancy breaking in seeds, ranging from ethanol and chloroform, effective on a number of grass species (Taylorson 1980), to various fungicides effective on celery (*Apium graveolens*) (Thomas 1973).

These examples illustrate that breaking dormancy in weed seeds lying in the soil is feasible, but as with most remedies it seems unlikely that the ultimate panacea that will stimulate all species will ever be discovered. However, substantial and more rapid diminution of the seed reserves in the soil is now possible, which in association with effective herbicide usage could make weed control systems more efficient. The search for chemical dormancy breakers should be increased, for they could prove to be the next major step forward in weed control.

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(*b*) *Breaking dormancy in rhizome buds*

Dormancy occurs in some rhizomes and is similar in certain respects to the innate dormancy of seeds. For example, *Convallaria majalis* (lily-of-the-valley) has dormancy in its rhizomes that requires up to 3 weeks chilling at 0 °C to break (Wareing 1964). However, such dormancy does not appear to occur in rhizomes of weed species, although dormancy in lateral buds due to the dominance of the rhizome apex is very common. The magnitude of apical dominance varies from species to species. In *Sorghum halepense* and *Agropyron repens* rhizomes it is pronounced, but in *Panicum repens* it is very weak. Those species that have pronounced apical dominance in undisturbed rhizomes will, if cut up by cultivation, redevelop a new dominance system among the lateral shoots on each fragment. This re-establishment of dominance in *Agropyron repens* has been studied in detail (Chancellor 1974).

Because this dominance system is re-established when the rhizome is cut into fragments, it prevents a rapid dissipation of the dormant buds by the farmer and so enables the weed to persist. Consequently a search has been made for chemicals that will prevent the onset of the renewed dominance system. Ethephon, the ethylene-generating chemical, which will break dormancy in many seeds, will also break apical dominance in rhizomes, but only if a green leafy parent shoot is attached. If there is no parent shoot, then dominance appears to be enhanced (Chancellor 1970). However, the lateral buds that are stimulated to grow by ethylene stay as rhizomes and do not become aerial shoots. Furthermore, although dominance is broken within the main rhizome, the buds on these new lateral rhizomes remain dormant, so that unfortunately the weed problem is only aggravated.

A more useful chemical is chlorflurecol-methyl (methyl-2-chloro-9-hydroxyfluorene-9-carboxylate). This prevents the onset of a new dominance system in fragments of rhizome, even when no aerial parent shoot is attached. In addition, it overcomes dominance within the lateral shoots beginning to grow out, so that secondary laterals grow out from them. Chlorfluorecol-methyl also prevents root production and interferes with the perception of gravity by the shoots (Chancellor 1970).

Research at the Weed Research Organization has established that there are at least nine other growth regulatory chemicals that influence both polarity and dominance among shoots arising from rhizome fragments (Chancellor & Leakey 1972).

More recently, it was discovered that gibberellic acid applied to the basal end of rhizome fragments of *Agropyron repens* kept the apex horizontal and maintained dormancy in the lateral buds (Rogan & Smith 1976). This is in agreement with the findings of Kumar & Wareing (1972) and Woolley & Wareing (1972) with the potato (*Solanum andigena*), in which high gibberellin:cytokinin ratios promoted horizontal stolon production from lateral buds while low ratios promoted erect leafy shoots. This could be of importance in control measures, because, rather than allowing rhizomes to be formed and then manipulating the growth pattern of regrowth after cultivation, it would perhaps be more effective to prevent the formation of rhizomes altogether. The aim would be to convert a creeping rhizomatous plant into a static tufted one and make control by conventional means correspondingly easier. This could possibly be accomplished either by reducing the gibberellin content of the parent and transport of gibberellins to the lateral shoots or alternatively by applying synthetic compounds with cytokinin-like activity to alter the balance between the two hormones and prevent horizontal growth.

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(*c*) *Dormancy in tubers, bulbs and turions*

As seen earlier, the number of tubers of *Cyperus esculentus*, and of *C. rotundus* too, can be very large in severe infestations. The data of Tumbleson & Kommedahl (1961) show that the rate of increase can also be very large. They found that a single tuber planted in the field produced 36 shoots and 332 daughter tubers in 16 weeks. Each tuber has a number of sprouts, most of which remain dormant through apical dominance. When the sprouts are disturbed or the dormancy due to the operation of apical dominance is broken, further sprouts will grow out to form new plants. Parker & Dean (1972) tested 38 plant growth regulators on the tubers of *C. rotundus* and found that the cytokinins were very active in promoting sprouting of dormant buds. One active agent was the synthetic cytokinin, 6-benzylamino-9-(tetrahydro-2-pyranyl)-9H-purine (SD 8339). Other compounds such as chlorflurecol-methyl, naptalam and TIBA were less active.

Bulbs of weeds can also present problems and most exhibit dormancy to some extent. Studies with the cultivated onion, *Allium cepa* cv. Elba Globe, have shown that dormancy is due to high inhibitor levels and to low levels of auxin, gibberellins and cytokinins (Abdel-Rahman & Isenberg 1974).

Studies on the bulbs of *Oxalis latifolia* and *O. pes-caprae* by Chawdhry & Sagar (1974) have shown that dormancy is regulated by temperature. Periods of chilling are required followed by higher temperatures to break dormancy. They found, however, that unlike seeds, potassium nitrate, gibberellin and ethephon did not break their dormancy.

Many water plants produce over-wintering vegetative buds called turions. They are formed in the autumn and, after becoming detached, lie on the bottom mud until the water warms up in the following spring when they grow out to form new plants. They exhibit dormancy. Turions are an effective means of perennation and even give some measures of dispersal. They can be an important means of increase for water weeds and are often responsible for recurring infestations. The overwintering buds of *Myriophyllum verticillatum* are dormant when mature and the dormancy can be broken by chilling. Turions of this species vary in their degree of dormancy and dormancy can be broken by cytokinins at a concentration of 10^{-6} M and GA_3 and IAA at 10^{-3} M (Weber & Noodén 1976).

These examples of dormancy in various organs for vegetative propagation appear to be rather similar to dormancy in seeds. The fact that dormancy in many can be broken chemically suggests that here lies a potentially important area for further exploration, for, if we have the ability to regulate dormancy, weed populations could be reduced much more quickly.

One of the main problems of regulating dormancy in seeds and other propagules in the soil lies in the difficulty of getting chemical treatments into them. Ethylene is quite mobile in soil, as mentioned before, but other growth regulators applied as a solution to the soil surface would obviously be less mobile and therefore far less effective. Furthermore, most growth regulators would be very susceptible to breakdown by microorganisms in the soil.

It might therefore be more effective to apply the treatment to the plant before the seed is shed to ensure that it arrives at the target. These treatments might well be termed 'dormancy preventors', for when applied during seed development, or even earlier, many of the seeds are not dormant when shed. For example, Black & Naylor (1959) found that dormancy in wild oat (*Avena fatua*) seeds could be prevented altogether by allowing maturing inflorescences to take GA_3 solution up through their stems. Similarly, Peters *et al.* (1975) applied GA_3 to wild oat

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plants at various stages of growth and found that seed dormancy was affected by applications at or after the seven leaf stage. Herbicides such as chlorfenprop-methyl and benzoylprop-ethyl that kill wild oats were also effective in reducing seed dormancy when applied at sublethal levels during seed development. A similar effect can be obtained in vegetative reproduction. Esashi & Leopold (1969) have shown that dormancy in tubers of *Begonia evansiana* can be prevented by a range of chemicals.

These results suggest that applying regulators to the parent plant might well be effective in preventing dormancy, but it seems that the treatment needs to be applied late in development.

(*d*) *Other potential methods of controlling weeds*

In addition to breaking or preventing dormancy, the possibility of interfering with other aspects of weed reproduction should also be considered. Shedding of seed by arable weeds can be active, e.g. the violent dispersal of the hairy tare (*Vicia hirsuta*) and hairy bitter-cress (*Cardamine hirsuta*), or passive, e.g. that of corn marigold (*Chrysanthemum segetum*) and fumitory (*Fumaria officinalis*). Most weeds shed their seed passively around their roots. When seeds are ripe and abscission is completed they drop off. Almost all weeds achieve a large measure of seed shed before the crop is harvested. This is a most important point, for it ensures that sufficient seed is returned to the soil before the plant is cut down at harvest and burnt or baled into straw with the crop. If a treatment could be discovered that would prevent or merely delay abscission beyond harvest, it would be relatively easy to prevent any return of weed seeds to the soil.

Thimann (1979) considers that the most fundamental advance in agriculture would be the control of plant flowering. He was probably thinking only of crops, where it can already be regulated to some extent in plants such as the pineapple, but it would of course also be of considerable importance in weed control. For, if the time of flowering could be delayed or prevented altogether, populations of many weeds could be very rapidly reduced. Whether a treatment such as this could be used in a growing crop remains to be seen.

Other aspects of plant development and growth could similarly be exploited. These could include the induction of sterility, the prevention of seed development, etc., provided of course that suitable chemicals could be found.

In conclusion, the concept of manipulating crop plants by growth regulators is well established. As yet, however, with few exceptions, the concept has hardly been considered for the control of weeds. It is suggested that the regulation of certain critical aspects of weed behaviour and growth could lead to greatly improved methods of weed control.

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