Allelopathy and self-defence in plants

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Summary

Some of the physical and chemical attributes of plants which act in their defence are briefly reviewed. Data on allelopathic activity, as demonstrated by several Australian weed species, are discussed and allelopathy is placed in the more general context of defences based on phytochemicals.

Introduction

The term 'resistance' is currently used in several contexts which appertain to plant protection. Weed scientists, for example, are concerned at the increasing numbers of weed populations which are developing resistance to herbicides, particularly the triazines. Ali and Souza Machado (1981) report that 13 species are showing resistance to triazines in more than 25 locations in North America. Amongst these species are some of the world's worst weeds (Holm *et al.*, 1977), including amaranths (*Amaranthus* spp.) (Ahrens *et al.*, 1979), fat hen (*Chenopodium album* L.) (Warwick and Black, 1980) and winter grass (*Poa annua* L.) (Darmency and Gasquez, 1981). So widespread is the phenomenon that Hensley (1981) discussed a method for the identification of triazine resistant and susceptible biotypes of several significant weed species.

Burdon and Marshall (1981) addressed a different aspect of resistance in weeds, namely, resistance to agents of biological control. Resistance remains relatively high in populations of weeds where reproduction is predominantly by sexual means. Where apomixis occurs or where reproduction is primarily vegetative, resistance to biological control agents is likely to be less than in the former case.

A third aspect of resistance is of longer standing. Breeding for resistance (or tolerance), particularly to disease, in agricultural plants is an accepted objective. Dalmacio (1979) reviewed sources of resistance and other factors which affect the success of breeding in disease-resistance programmes. Natural populations, including those of important pasture species such as white clover (*Trifolium repens* L.) (Burdon, 1980), offer much wider variation in disease resistance than is found in highly selected strains of such species. However, the basis and costs of disease resistance in plants remain imperfectly understood.

Harlan (1976) stated that 'If, for example, the defence strategy calls for the production of an array of fungitoxic or fungistatic compounds or enzymes that detoxify pathotoxins, it would seem likely that such productions would compete with other metabolic processes and would require continuous selection for maintenance.'

From the foregoing it is apparent that, where genetic variability is great, the potential for the development of different forms of resistance in plants is enhanced. Defensive strategies are a component of resistance and are clearly identified by Harlan with phytochemicals. The potential for genetic manipulation of phytochemicals to the defensive advantage of crop and pasture plants has, however, been largely ignored, in part because neither the costs to which Harlan alludes nor the potential benefits to the plants have been adequately evaluated.

Self-defence adaptations of plants

That self-defence in plants has remained relatively uninvestigated is surprising. The plant, whilst enjoying the advantages of autotrophy, is immobile and cannot escape the attentions of pests, predators or competitors. Animals, including man, enjoy the advantages of mobility yet still employ many defensive stratagems, including the use of chemicals. It might, therefore, be expected that the immobile plant, with a paucity of alternative stratagems, would depend heavily upon chemicals for self-defence against many organisms.

The means by which plants defend themselves physically are well understood and generally accepted. For example, the cuticle, together with epicuticular wax, may act as a barrier to attack by other organisms (Cutter, 1976). The epidermis frequently carries trichomes which complement the defensive function. The simple trichome may irritate a predator or render a plant less palatable. The stinging trichome delivers a repellent chemical, and the glandular trichome appears to act as a repository for chemicals which act as defensive agents. The insect-repellent properties of chemicals contained in the trichomes of tobacco (*Nicotiana tabacum* L.) (Thurston *et al.*, 1966) is a well-known example.

So far as is known, all plants have the potential to produce chemicals which may perform defensive functions (Whittaker, 1970) but the potential of crop plants to do so may be somewhat less than that of other species. Waller and Nowacki (1978) commented that 'Only the 0.1% of angiosperm plants that have become cultivated for human food are, to a certain degree, free from poisons, thanks mostly to plant breeding efforts; their wild ancestors were often not so innocent.'

In the context of allelopathy, which may be defined as biochemical interactions between plants, Lovett and Levitt (1981) discussed evidence which tended to confirm that the allelopathic potential of many crop species may have been reduced, relative to that of weed members of the same family, as a result of the concentration of plant breeding effort on other objectives. For example, whilst Rice (1974) discussed evidence for allelopathic activities of several species of weed-type sunflower, Lovett *et al.* (1982) reported that such activity appears to occur only at a very low incidence in Australian cultivated sunflowers. This finding accorded with that of Massantini *et al.* (1977) that only two of 141 soybean lines tested evinced allelopathic activity. Allelochemicals may act on organisms other than plants so that the general self-defence capability of many crops may have been significantly reduced by selection, either conscious or unconscious.

The chemicals involved in self-defence are of the group termed 'secondary compounds', that is, compounds which are produced as off-shoots of primary metabolic pathways (Levin, 1976). They are, chemically, very diverse (Schildknecht, 1981). Of the wide range of secondary compounds produced some, for example the phenolics, are cosmopolitan, whilst others are associated with particular families of plants, for example, the glucosinolates with the Brassicaceae (Kjaer, 1976). It should be noted that, although the nature and precise role of these chemicals are as yet imperfectly defined, they are normal constituents of the plants which produce them.

Levin (1976) pointed out that the production of secondary compounds places an energy demand upon the plant. This suggests that the production of the chemicals is purposeful and the fact that plants have frequently evolved specialized means of storing the chemicals, for example, trichomes, again suggests an important role for the chemicals contained therein.

Examples of allelopathy

Although discussed for more than 150 years (Rice, 1974), allelopathy remains contentious. In part this is the result of methods, including maceration, grinding and extraction with solvents, which have been employed to obtain chemicals from plants. Current workers tend to minimize damage to the plants concerned, attempting to simulate events which occur in the field. In addition, some proponents of allelopathy have often failed to recognize that allelopathic phenomena comprise a part only of the interactions between climate, soil, plants and sometimes other organisms. Occasionally allelopathy may be the dominant and readily recognizable element in interference between plant species; more often it will be subtle and may be difficult to discern.

Allelopathy between weeds and crop or pasture species has frequently been recorded but, as noted, allelopathy in crop plants is relatively uncommon. There are a number of reports of allelopathic manifestations by important pasture grasses, which often affect legumes adversely. Amongst these Naqvi and Muller (1975) found that Italian ryegrass (*Lolium multiflorum* Lam.) had water soluble toxins in the above ground parts and roots. Several other pasture plants, including clovers (*Trifolium* spp.) were differentially affected by the toxins produced. Moreira and Rosa (1976) are amongst a number of workers who have investigated allelopathic effects in rhizomatous grasses, in their case couch (*Cynodon dactylon* (L.) Pers.) and torpedo grass (*Panicum repens* L.). The difficulties of accurately defining the significance of allelopathic phenomena are compounded where the chemicals are produced underground.

Even trees may be adversely affected by the allelochemicals of grasses. For example, tall fescue (*Festuca arundinacea* Schreb.) and giant fox-tail (*Setaria faberi* Herrm.) have negative effects on, respectively, seedlings of liquidamber (*Liquidambar* spp.) and loblolly pine (*Pinus taeda* L.) (Gilmore, 1977, 1980). Conversely, trees may affect the growth of associated pasture species, as shown by Al-Mousawi and Al-Naib (1975) and Trenbath and Fox (1976) working with species of *Eucalyptus*. Buffel grass (*Cenchrus ciliaris* L.) (Akhtar *et al.*, 1977) and limpograss (*Hemarthia altissima* (Poir.) Stapf & Hubb.) (Young *et al.*, 1979) are among tropical grasses with which allelopathy has been associated; in the latter example the legume greenleaf desmodium (*Desmodium intortum* (Miller) Fawc. & Rendle) was inhibited.

Weeds of pastures have also commanded some attention. Allelopathy resulting from chemicals produced by wireweed (*Polygonum aviculare* L.) has been implicated in reduced germination of barrel medic (*Medicago truncatula* Gaertn.) in South Australia by Kloot and Boyce (1982). Like Muller (1966) they concluded that interference with cell division during early growth was the probable primary mode of action of the allelochemicals concerned.

In experiments by the author with Kempton's weed (*Stevia eupatoria* (Spreng) Willd.) allelopathy was observed to contribute to interference by this species with white clover. The weed bears profuse trichomes and is strongly aromatic. When air-dried material was placed in a closed system through which air was continuously circulated, sufficient chemicals were released to decrease significantly the radicle length of white clover seeds germinating in the system but physically separated from the weed material. Where similar weed material was sandwiched between moist filter papers upon which white clover seeds were germinated in petri dishes strongly inhibitory effects were observed (Table 1).

These examples tend to confirm that, in the pasture situation, legumes are susceptible to allelochemicals, whether produced by grasses or by weeds.

Combinations of defensive activities have been documented in other contexts, for example, Schildknecht (1981) reported that gympie (*Dendrocnide moroides* (Wedd.) Chew) not only has the stinging trichome typical of the nettle family (Urticaceae) but, when its leaves are picked, emits sufficient chemical to cause keen irritation to the mucous membranes of the nose and eyes.

Weeds of the genus *Camelina*, members of the Brassicaceae, were reported to use chemical weapons against the crop plant flax (*Linum usitatissimum* L.) by Grümmer and Beyer (1960). For the weed to affect crop production it was necessary for rain to fall in the field at a particular time of year, implying that stage of growth was important to chemical production by the weed and/or to the susceptibility of the crop to these chemicals. In our work (Lovett and Sagar, 1978; Lovett and Duffield, 1981) we have shown that a potent allelochemical is produced by the action of bacteria which live on the leaves of false flax (*Camelina sativa*) and break down a complex chemical exuded by those leaves into simpler

Table 1 Effects of leachates of *Stevia eupatoria* plant parts on germination and early growth of white clover (means of five replicates)

Hours from sowing	Germination (x/25) 24	48	72	Radicle length (mm) 72
control	6.80 a	16.00 a	17.00 a	15.2 a
leaves	0 b	0.20 b	1.20 b	3.5 b
stems	1.00 b	2.40 c	4.20 c	8.1 c
flowers	0.60 b	2.60 c	4.00 c	6.0 bc

Treatment means which are identified by the same letter are not significantly different at the 5% level, Studentized Range Test.

Table 2 Moisture content of soil after five days incubation in the presence of differing concentrations of benzylamine (means of ten replicates). After Lovett (1982)

concentration of benzylamine (mg L^{-1})	0	10	100	1000	10000
moisture content (mg water per g soil)	18.5 a	19.9 ab	21.0 b	20.6 b	25.0 c

Treatment means which are identified by the same letter are not significantly different at the 5% level, Studentized Range Test.

components. One of these, benzylamine, appears to be able, in small concentrations, to disrupt the functioning of cell membranes. Such disruption, whilst probably not lethal, may affect the efficiency of the affected plant to a marked degree.

In further work we have produced evidence (Lovett, 1982) that benzylamine may significantly modify soil structure, possibly through the creation of hydrophobic, or water-repellent, conditions. Such conditions affect infiltration of water into soil and germination may be impaired (Bond, 1972). Data presented in Table 2 indicate increasing moisture content of soil with increasing concentration of benzylamine, a consequence of a progressive breakdown of surface soil structure and inhibition of water loss. Thus this particular secondary compound or allelochemical, may act directly upon the plant or indirectly through an effect upon the soil in which it is growing.

The production of volatile secondary compounds by aromatic shrubs has been investigated in some plant communities. Muller (1966) reported that terpenes produced by *Salvia leucophylla* Greene and other aromatic shrubs in chaparral communities in southern California severely inhibited the growth of herbaceous species in their vicinity. The aromatic compounds may act directly upon such plants or may be adsorbed from the atmosphere upon dry soil particles and retained for several months in an active state (Muller, 1966). It was concluded that the terpenes probably produced their effects through interference with cell division.

In parts of eastern Australia, mintweed (*S. reflexa*) is a significant weed. Washings of mintweed foliage inhibit the germination and early growth of wheat (Table 3), the activity of the chemicals concerned being modified by soil type (Lovett and Lynch, 1979). The chemicals are probably similar to those discussed by Muller (1966) and appear to be stored in trichomes upon the leaves of mintweed (Lovett and Speak, 1979). Aromatics released by mintweed can also affect wheat seedlings germinating in a closed system such as that described for experiments with *Stevia eupatoria*.

As more is learned of the nature of chemicals involved in various defensive functions, it is becoming apparent that a chemical investigated in the context of allelopathy may also play a defensive role against organisms other than plants. For example, Selander *et al.* (1974) discussed experiments in which the concentration of volatile substances such as α-pinene determined whether some species of insect were attracted or repelled by pine trees. This chemical is one of the terpenes present in *Salvia leucophylla* (Muller, 1966) and tentatively identified in *S. reflexa* by Lovett and Levitt (1981). The concentration effect appears to be similar to one which we have defined for some allelochemicals (Figure 1) and which can be extended to many different types of biological response to given chemicals.

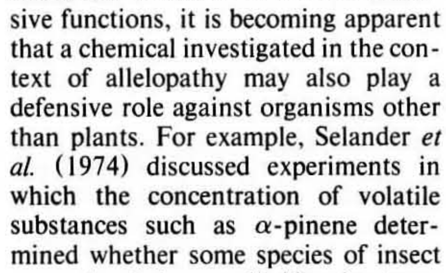

Figure 1 Biological response curve to increasing concentrations of natural chemicals

Table 3 Effect of leaf washings of mintweed on germination and early growth of wheat in soil (means of four replicates). After Lovett and Levitt (1981)

		Days after sowing					
		5	6	7	8	9	10
emergence (%)	sterile water (control)	42.5	70.0	77.5	80.0	82.5	87.5
	mintweed washings	20.0	32.5	45.0	47.5	50.0	50.0
	P	<0.05	<0.01	<0.01	<0.01	<0.05	<0.01
height of coleoptile (mm)	sterile water (control)	20.8	29.5	54.8	81.8	102.0	111.7
	mintweed washings	9.5	18.7	35.1	66.3	86.0	108.1
	P	<0.01	<0.001	<0.05	N.S.	N.S.	N.S.

The compound α-pinene may also act in defence against vertebrates. Sheehy and Winward (1981), working in Oregon, found that seven taxa of sagebrush (*Artemisia* spp.) differed in palatability to mule deer and domestic sheep. *Artemisia* spp. are high in monoterpenoids and Welch and McArthur (1981) cited data which showed that the concentration of α-pinene and an unidentified monoterpene accounted for 90% of the variation in mule deer utilization of various sagebrush taxa. In studies carried out in Utah, Welch and McArthur (1981) determined that the monoterpenoid content of *A. tridentata* Nutt., one of the species studied by Sheehy and Winward (1981), was itself variable, suggesting that a good potential exists for selection for palatability of rangeland species to animals, or for the self-defence of such species.

Dimensions of self-defence in plants

Through links such as those between a chemical occurring in North American shrubs, an Australian weed and Finnish pine trees, and which have similar effects on very different organisms, an understanding of the role of secondary chemical compounds in the self-defence of plants is beginning to emerge. In the context of weed science, it is intriguing that some of the primary effects of allelochemicals on plants bear similarities to those which are currently under investigation in the herbicide industry, for example, interference with cell division, nucleic acid metabolism and protein synthesis (Moreland, 1980). Naturally-occurring secondary chemical compounds promoting such effects are frequently selective and active at small dose rates. There are few, if any, reports of these compounds having long-term detrimental effects upon the environment. All of these characteristics are desired in the new generations of herbicides and other pesticides.

Conclusion

The significance of genetic variation in relation to several aspects of 'resistance' was noted in the introduction to this paper. Available data suggest that the genetic control of phytochemicals in plants is relatively simple but that, as indicated by Waller and Nowacki (1978), selection which has taken place in crop species has tended to diminish the phytochemical content. The defensive potential inherent in these compounds has similarly been reduced.

Given the apparent value of defensive chemicals to weeds, the potential for reversing the established trend and augmenting other modes of genetically controlled resistance through selection for such compounds in useful agricultural plants merits further investigation.

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