Allelopathy: a new direction in weed control[†]

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Introduction

Few plant communities could be of greater economic significance to mankind than those formed by crops and weeds. The factors determining the composition of these communities, while of interest to plant ecologists, have attracted less attention from those involved directly in weed control. Weeds tend to be regarded merely as 'plants out of place' for which some means of total eradication will one day be found.

Bunting (1963) in his introduction to 'Crop Production in a Weed-Free Environment' wrote "It is now possible, for many crop situations, to prescribe a chemical treatment which can control weeds completely, and we can foresee a time when such methods will be available for all situations".

Time has proved such hopes raised by the advent of sophisticated herbicides to be false. There has been a change in emphasis from the use of agrochemicals for supposed total weed elimination to the integration of cultural, biological, ecological, mechanical and chemical methods for weed management (Shaw 1982). However, if weed populations are to be maintained below economic threshold levels, a more detailed understanding of the factors controlling weed density and species distribution in the field is required.

Allelopathy

The word allelopathy was devised by the Austrian botanist Hans Molisch (Molisch 1937) and it is perhaps a little unfortunate that this terminology remains in use. The literal translation, 'mutual harm' is misleading, as allelopathic effects are often stimulatory, and the word is frequently mispronounced and/or equated with folklore and mysticism.

Allelopathy is simply the chemical ecology of plants. Other fields of chemical ecology, such as the chemical basis of the interrelationships between plants and insects, or between plants and microorganisms, are readily accepted. The role of plant chemicals in determining the structure of plant communities however, is a neglected area of study.

Many thousands of organic compounds are either actively released or passively leaked from plants. They include both simple and complex organic acids; simple phenols, phenolic and phenylacetic acids, coumarins, quinones, flavonoids and tannins; terpenoids, alkaloids, amino acids, steroids, cyanogenic glycosides and glucosinolates (Moreland *et*

al. 1966, Whittaker and Feeny 1971, Gross 1975, Swain 1977, Rice 1984).

These secondary plant products, or allelochemicals, can be leached from ungerminated seeds, exuded by germinating seeds and the roots of newly emerged seedlings, released actively or passively by exudation, volatilization, leaching, frost damage or the decay of sloughed cells, tissues and organs of established plants, or may enter the soil environment after plant death as the result of the leaching and decomposition of plant remains.

Allelopathic effects are not considered to take precedence over physical factors such as light, minerals, heat and moisture, but to share with them the potential to regulate plant growth (Molisch 1937, Muller and Chou 1972, Rice 1979). Plant chemicals have been shown to play a significant role in the natural patterning of vegetation, plant succession at disturbed sites, nutrient cycling, orchard replant problems and crop-weed interactions. Reviews of the role that allelopathy may play in weed management include those of Altieri and Doll (1978), Gliessman (1983), Putnam (1983), Putnam *et al.* (1983) and Einhellig (1985).

Crop-weed interactions

Many plants, although abundant, are not weeds of crops. Some 30,000 species have been classified as weeds world-wide (Chandler 1985). However, fewer than 250 of these can be regarded as important, of which only about 76 are primary weeds of agriculture, and most surprisingly, the major economic losses to man's food and fibre production are caused by only 18 of these (Holm *et al.* 1977).

There is no doubt that some plants have evolved ecophysiological characteristics which render them more 'weedy' than others (Baker 1974). Perhaps the 'world's worst weeds' (Holm *et al.* 1977) also have the ability to utilize allelopathy to their advantage to a greater extent than previously recognized?

Agrestals (weeds of cultivated land) are often categorized as either colonisers, that is, having characteristics which enable them to invade and dominate, or specialists, that is, having characteristics which enhance their survival in a particular crop (Holzner 1982). Interestingly, research into the chemical ecology of crop-weed interactions has shown that the success of many weed species is due, at least in part, to (i) their ability to utilize allelochemicals to invade, colonize and vigorously compete with crops, and/or (ii) their biochemical as well as morphological adaptation to the crops in which they thrive.

The Colonists

Over 100 species of weed have been shown to release allelochemicals which have a detrimental effect on neighbouring plants. Many familiar names, including *Agropyron repens, Amaranthus retroflexus, Bidens pilosa, Chenopodium album, Cynodon dactylon, Digitaria sanguinalis, Echinochloa crus-galli, Eleusine indica, Polygonum aviculare, Portulaca oleracea, Rumex crispus* and *Sorghum halepense,* appear on the list of 90 allelopathic weeds compiled by Putnam and Weston (1986). Other examples may be found in review articles such as those of Altieri and Doll (1978), Einhellig (1985) and Lovett (1985, 1986) in addition to the numerous research reports on the allelopathic effects of individual species.

The release of inhibitory chemicals into the shared environment greatly enhances the invasive and competitive abilities of some weeds. Four of the five weed species responsible for the greatest economic losses in corn crops in the USA for example, produce allelochemicals capable of reducing crop yield in the absence of other factors (Einhellig 1985). The highest concentrations of allelochemicals are usually released by plants at the germination and seedling stages of development, and chemical dominance can thus be achieved well before plants begin physically competing for water, nutrients or light (Pickering 1917, Dekker and Meggitt 1983). Allelochemicals exuded by weeds have been shown to inhibit crop species by increasing the diffusive resistance of plants and slowing water uptake, by impeding nutrient uptake and/or by inhibiting respiration and photosynthesis (Rice 1984, Balke 1985, Einhellig 1985, 1986).

Allelopathy may also influence the composition of the colonizing weed community and it has been proposed that this is due to differential germination rather than to differential survival (Went 1970). The inhibitory zone of influence created around the seeds of some species at the germination stage can effectively block the germination of other species and lead to the dominance of the weed flora by the former. Species not able to adapt to or modify the resulting distinctive biochemical environment will not be present in the community (Varma 1938, Evenari 1961, Muller 1969, Whittaker 1970).

The Specialists

Holm *et al.* (1977) noted that "the most serious weed species of a principal crop are very often found in every major production area for that crop, regardless of continent". If our principal crop species were changed, would some of our principal weeds fade into insignificance and become innocuous members of the plant kingdom? Several of the specialized weeds associated with *Linum usitatissimum* (flax/linseed) for example, became locally extinct when flax cultivation ceases (Holzner 1982).

Although specialization appears to rely on morphological adaptation and seed mimicry strategies, adaptation to the biochemical niche created by the presence of the host crop may also be involved.

An example: the chemical ecology of wild oats

Weedy *Avena* spp. are plants with colonist and specialist attributes, both of which involve allelopathy. Interference between wild oats and crop species can take place before light, moisture and nutrient availability impose any limitation to plant growth. Crop yield losses, which are often far out of proportion to the amount of the weed present, cannot be attributed solely to competition for physical resources (Muller 1969).

Schumacher *et al.* (1983) demonstrated that coumarin related compounds such as scopoletin and vanillic acid exuded by the roots of *Avena fatua* L. seedlings from the 2-leaf stage of development, significantly inhibited the growth of wheat test plants. The wheat and wild oats were grown in separate containers to exclude physical effects. Water-soluble exudates collected from the root zone of *A. fatua* at the 4-leaf stage reduced the dry weight of wheat roots and shoots by 34 and 26% respectively.

In other studies, Cvetkovic (1980) found that substances produced by germinating *A. fatua* seeds were inhibitory to the early growth of wheat, and Tinnin and Muller (1971, 1972) demonstrated that *A. fatua* utilized allelopathic mechanisms to invade and colonize vast areas of grassland in North America.

Work undertaken by the author with *Avena sterilis* ssp. *ludoviciana* (Durieu) Nyman has shown that wild oat germination and growth are regulated by the biochemical characteristics of soils cropped to wheat, rendering the weed a 'specialist' in this crop (Purvis and Jessop 1985, Purvis 1990a). Experimental evidence indicates that the presence of germinating wheat seeds can stimulate wild oats to emerge at the same time as the crop, whereas emergence into an already established crop is somewhat inhibited. This would appear to be an adaptive strategy to ensure germination at the time most favourable to the proliferation of the species. Field observation in Australia, and overseas data (Pfeiffer *et al.* 1960, Thurston 1962, Cvetkovic 1980) support these findings, although biochemical factors were not considered in the first two named investigations. The data also suggest that wild oat growth and seed production can be biochemically stimulated by the decomposing root and stubble fragments of the previous wheat crop in the second and successive years of continuous wheat monoculture. The biochemicals to which wild oats respond do not have a similar effect on wheat, thus providing a competitive advantage to the weed at the expense of the crop (Purvis 1990a).

Thousands of collective research years and millions of dollars have been expended world-wide on studies involving wild oats, but there has been little, if any, improvement in their control (Fryer 1976, Wilson 1984). Two species are intractable weeds of wheat in Australia; *A. fatua* which predominates in the southern and western areas of the continent (Paterson 1976) and *A. sterilis* (sometimes still referred to as *A. ludoviciana*) which is more prevalent in northern New South Wales and southern Queensland (McNamara 1966, Watkins 1967).

The results of surveys conducted in Australia demonstrate an exponential increase in wild oat numbers with continuous wheat cropping (Wilson *et al.* 1977, Martin and McMillan 1984a,b). Wild oat herbicides can salvage wheat yield in the year of use but do not control wild oats, as seed production is not prevented (Paterson 1977, Wilson 1979a).

Some ecological solutions

The insignificant weeds of agricultural land may simply be plants out of place. The economically important colonists and specialists however, would appear to be plants very much in place, due in part to their ability to utilize allelopathy for niche exploitation.

The Colonists

The aggressive colonizing weeds which produce inhibitory allelochemicals to create their own chemical sphere of influence in a wide range of habitats are more difficult to counteract allelopathically than are the specialist weeds.

Limited success has been achieved through the selection of crop plants with enhanced allelopathic potential which are capable of inhibiting weeds in their vicinity (Putnam and Duke 1974; Fay and Duke 1977; Lockerman and Putnam 1979, 1981; Leather 1983a,b; Banks 1984). However, plant breeding programs are by nature long-term, and problems such as autotoxicity and the need to consider other selection criteria for crop species render this a complicated strategy for weed control. Biotechnology may offer a more rapid method than conventional breeding and selection techniques for the incorporation of natural herbicidal activity into crop cultivars in the future (Einhellig 1985).

More immediate benefit has been derived from the use of thickly sown green cover crops of rye, barley, wheat, oats, sorghum or sudangrass, which are desiccated prior to no-till planting of sunflowers, soybeans, corn, tobacco, pulses or cucurbits. The germination of weed seeds is altered by a combination of physical and biochemical factors. Spectacular results have been obtained with some species, for example, reductions of 99% for *Chenopodium album*, 92% for *Ambrosia artemisiifolia* and 96% for *Amaranthus retroflexus* were recorded in crops of sun-flower and soybeans sown no-till into a desiccated green rye cover crop (Worsham 1984, Shilling *et al.* 1985).

Many of the allelochemicals implicated in the weed suppression have been isolated and their inhibitory potential demonstrated in laboratory tests, although some of the components of the chemical complexes which determine allelopathic activity in field situations have yet to be characterized (Lehle and Putnam 1982, 1983; Liebl and Worsham 1983; Shilling *et al.* 1985).

Allelochemicals released from desiccated cover crops apparently form a zone of inhibition in the surface layers of the soil from which weed seeds normally emerge. The larger seeded crop species are sown below this layer and their germination and growth are either not affected, or are enhanced, by the presence of the surface mulch. Shallow-seeded crops such as carrot, tomato and lettuce vary in their response, tolerating some cover-crop mulches but not others (Putnam and DeFrank 1983, Putnam *et al.* 1983).

Selective effects are observed with most allelopathic phenomena, thus the choice of cover crop also needs to be matched to the weed flora. In a series of experiments in which the principal weed species were *Digitaria sanguinalis*, *Ambrosia artemisiifolia*, *Chenopodium album*, *Polygonum persicaria*, *Setaria viridis* and *Cerastium vulgatum*, Putnam and DeFrank (1979) recorded weed biomass reductions of 90% and 85% in the presence of sorghum and sudangrass mulches respectively, whereas peat moss provided only a marginal reduction and a desiccated cover crop of oats stimulated weed germination and growth.

Benefits of cover cropping additional to weed suppression include protection from erosion, enhanced water penetration and improved organic matter levels (Putnam and DeFrank 1979, 1983). However the method may have limited usefulness in those regions of Australia where clean fallows are necessary for soil water storage.

The Specialists

Specialist weeds which are adapted to the biochemical environment created by a particular crop should be relatively easy to control through an alteration in the biochemical characteristics of the place in which they are growing. One method of achieving this objective would be the rotation of the crop which is promoting the weed with a crop identified as being inhibitory.

The effectiveness of such a strategy for wild oat control was investigated. The significant stimulation of wild oat growth (Fig. 1b) and seed production (Purvis *et al.* 1985) recorded in the presence of wheat stubble highlighted the potential for wild oats to proliferate in wheat cropping situations. Conversely, the significant inhibition of wild oat germination recorded in the presence of sorghum (*Sorghum bicolor* (L.) Moench) stubble in
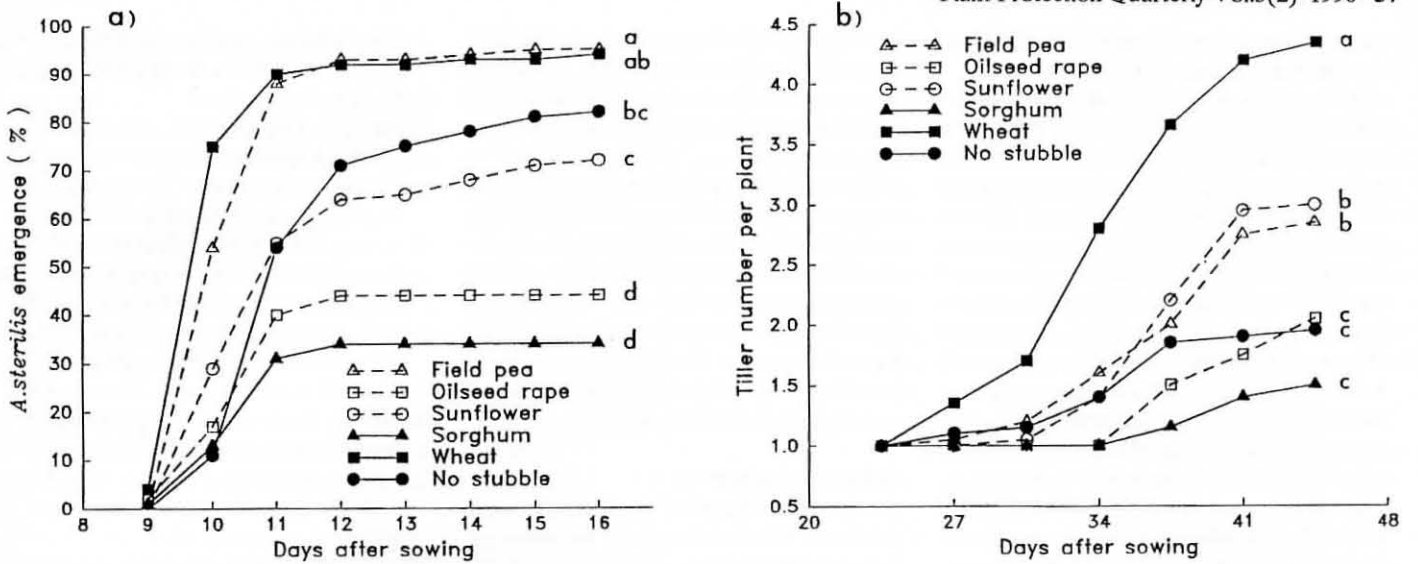
Fig. 1. (a) Emergence and (b): mean tiller number per plant, including the main stem, of *A. sterilis* growing in the presence of milled incorporated stubble (0.5% w/w soil) of five different crop species and a no stubble control. Treatments with common letters at the end-points of the lines are not significantly different at the final measurement (P = 0.05).
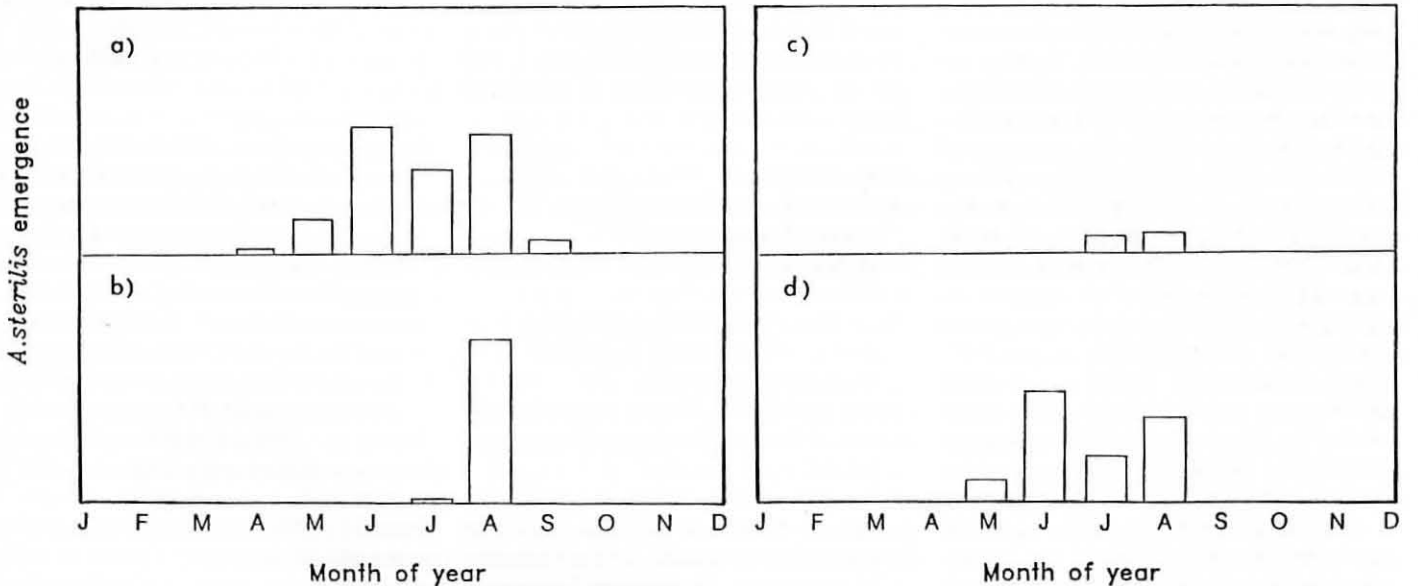

Fig. 2. Emergence pattern of *A. sterilis* following (a) no summer crop, or summer crops of (b); sorghum, (c); mung bean, (d); sunflower.

comparison with the four other stubble types tested (Fig. la) was suggestive of biological antagonism (Purvis 1990b).

Subsequent field tests demonstrated that the presence of a sorghum crop over summer resulted in a dramatically altered germination pattern of wild oats the following winter (Fig. 2b). The pattern was independent of cultivation method (conventional cultivation or zero till) and not affected by the removal of sorghum stubble. It was postulated that the presence of sorghum root exudates altered the dormancy characteristics of the wild oat seeds buried in the soil beneath the crop during the summer phase. These seeds were then not able to respond to the soil temperature and moisture conditions which normally initiate germination.

Wild oat emergence in the winter phase was not suppressed indefinitely by the presence of sorghum in the preceding summer. However, it was significantly delayed and occurred as a discrete peak (Fig. 2b). This

markedly facilitated control of the weed, as no measures additional to the normal presowing operations for the next sorghum crop were required. Conversely, wild oat emergence in soil which had been summer fallowed was more-or-less continuous over the cooler months (Fig. 2a) and it would have been necessary to repeat mechanical or chemical control operations several times during this period to prevent seeding and a greater level of infestation.

Very early sown sorghum may precede the delayed spring emergence peak of wild oats, thus for the method to be completely effective, sorghum should not be sown until spring soil temperatures are too high for wild oats to germinate.

Gross margin analyses showed that wild oats could be effectively controlled without the use of herbicides, and at no cost, in wheat-sorghum rotations in northern NSW and most regions of Queensland (Wilson 1979b). The wheat-sorghum rotation was

more profitable than continuous wheat, in which annual herbicide applications were necessary to maintain wheat yield in the presence of wild oats. The number of sorghum crops in the sequence could be varied from one to three depending on prevailing market prices, and provided farmers did not grow more than two successive wheat crops, they did not normally incur any yield losses due to wild oats (Wilson *et al.* 1977, Wilson 1979b).

The effectiveness of sorghum cropping for wild oat control has been attributed to the maintenance of a clean winter fallow (Philpotts 1975). However, the field-testing of several summer crops has shown that factors other than summer cropping and winter fallowing *per se* are involved. Preliminary findings indicate that the root exudates from different crops exert differential effects on wild oats. The presence of a sunflower *(Helianthus annuus* L.) crop, for example, did not markedly affect wild oat emergence the following winter, while the presence of mung

bean *(Vigna radiata* L.) was more inhibitory to wild oats than was sorghum (Fig. 2).

The success of a strategic crop rotation for wild oat control is dependent on the innate dormancy mechanisms of the wild oat seed being rendered dysfunctional in the presence of inhibitory crop root exudates (Purvis l990b). The resultant alteration in germination pattern from a cool season continuum to a delayed, compressed peak (Fig. 2 b,c) facilitates control in a winter fallow. If a winter crop were to follow-on from the allelopathic summer crop, there should be no early season interference from autumn-germinating wild oats. Additionally, the seed production from those wild oats which subsequently emerge in spring should be significantly reduced by the presence of the established crop, although this has not as yet been examined experimentally.

Herbicides in the 1990s

Legislative restrictions are currently being introduced in some countries to reduce overdependence on agrochemicals. A policy has been implemented in Denmark, for example, to reduce herbicide use by 25% before January 1, 1990 and a further 25% before January 1, 1997 (Haas 1989). Concern relates to contamination of rivers, groundwater supplies, foodstuffs and the foodchain generally, health risks to agricultural workers, injury to non-target neighbouring crops, residual toxicity and the increasingly rapid development of herbicide resistant weeds (Shaw 1982, Auld *et al.* 1987, Dolin *et al.* 1988, McWhorter and Barrentine 1988, Haas 1989). The future of synthetic agrochemicals may also be limited by diminishing reserves of fossil hydrocarbons (Everist 1981).

The ultimate objective of the legislation arising from the Senate Enquiry into Agricultural and Veterinary Chemicals in Australia will be the minimisation of herbicides and their residues in the environment. Much of the vast quantity of herbicides applied annually to our agrosystems provide only a short-term respite from weed competition, with no long-term benefits in terms of reduced weed populations. The need for weed control is not under question, but rather, the methods by which this may be achieved.

Conclusion

The 'world's worst weeds', despite modern technology and the concerted efforts of man, may be so well adapted biochemically to the niches they exploit, that measures taken to control them have only limited effectiveness. The way in which one weed, *A. sterilis* (wild oats), utilizes allelopathy to advantage, and the way in which allelopathy can be employed for its control, have been briefly presented here.

Research into the chemical ecology of plant interactions is complicated by the many biological and environmental factors involved. The results of such research however,

may have practical applications with respect to weed control which are more biologically efficient, cost effective and environmentally safe than some of the methods currently in use.

Practical weed control strategies based on the scientific observation and rigorous field-testing of the *modus operandi* of allelopathic interactions between plants could increase agricultural productivity and sustainability. The implementation of ecologically-based control measures would have the added benefit of a reduction in the input of hazardous chemicals to the environment.

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