

Utilization of Allelopathy for Weed Management in Agroecosystems

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ABSTRACT

Biorational alternatives are gaining increased attention for weed control because of concerns related to pesticide usage and dwindling numbers of labeled products, particularly for minor-use crops. Allelopathy offers potential for biorational weed control through the production and release of allelochemicals from leaves, flowers, seeds, stems, and roots of living or decomposing plant materials. Under appropriate conditions, allelochemicals may be released in quantities suppressive to developing weed seedlings. Allelochemicals often exhibit selectivity, similar to synthetic herbicides. Two main approaches have been investigated for allelopathic weed suppression. One is use of living rotational crops or mulches that interfere with the growth of surrounding weeds [e.g., tall red fescue, *Festuca arundinacea* Schreb.; creeping red fescue, *F. rubra* L. subsp. *commutata*; asparagus, *Asparagus officinalis* L. var. *atilis*]; sorghum, *Sorghum bicolor* (L.) Moench; alfalfa, *Medicago sativa* L.; black mustard, *Brassica nigra* (L.) Koch; and oat, *Avena sativa* L.]. Attempts to select germplasm with enhanced suppressive ability have been limited. The second is use of cover crop residues or living mulches to suppress weed growth for variable lengths of time (e.g., winter rye, *Secale cereale* L.; winter wheat, *Triticum aestivum* L.; and sorghum). Cover crop residues may selectively provide weed suppression through their physical presence on the soil surface and by release of allelochemicals or microbially altered allelochemicals. The ability to understand the physiological basis for allelopathy in a crop plant may allow the weed scientist or ecologist to work closely with molecular biologists or traditional plant breeders to selectively enhance the traits responsible for weed suppression.

THE TERM ALLELOPATHY, first introduced by Molisch (1937), refers to biochemical interactions among plants, including those mediated by microorganisms. This broad definition of allelopathy is appropriate because considerable research has indicated the involvement of microorganisms and lower plants in production of phytotoxins (Putnam, 1986). Allelopathy is an important mechanism of plant interference mediated by the addition of plant-produced phytotoxins to the plant environment. Chemicals with allelopathic potential are present in virtually all plants and in most tissues, including leaves, stems, flowers, roots, seeds, and buds. Under appropriate conditions, these chemicals may be released into the environment, generally the rhizosphere, in sufficient quantities to affect neighboring plants. The other main mechanism of plant interference is a subtractive process and is caused by competition for required resources such as light, nutrients, water, and CO₂ (Putnam, 1986). These interference mechanisms are difficult, if not impossible, to separate in the field, but both have been well documented in studies performed under controlled conditions.

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During the past 30 yr, the potential impacts of allelopathy on agriculture have been described and discussed (Putnam, 1985; Putnam and Duke, 1978; Putnam and Weston, 1986; Rice, 1984; Shilling et al., 1985). Much research has centered on the detrimental effects of living plants or their residues upon growth of higher plants and crop yields. Replanting problems, autotoxicity, toxicity of mulch stubble, problems with crop rotations, and direct interference by certain plants or weeds have been attributed to allelochemicals.

Putnam and Duke (1974) first explored the possibility of utilizing allelopathic crops to dominate or inhibit weed growth in agricultural sites. Initially, they considered incorporation of allelopathic characteristics into crop germplasm, which could lead to the development of weed-suppressive cultivars. Later, other approaches were described, including the use of allelopathic rotational crops, intercrops, or cover crops for effective weed suppression (Putnam and Duke, 1978).

The diversity of allelochemicals produced by plants is vast, and chemicals range in structure from simple hydrocarbons to complex polycyclic aromatics. Almost every class of secondary metabolites has been implicated in allelopathic interactions (Putnam, 1988). In certain cases, primary metabolites or major intermediates are also involved (Rice, 1984). Much time and effort has been spent on identifying novel secondary products isolated from higher plants in attempts to develop pharmaceuticals and products with medicinal value. Many of these novel compounds may also exhibit herbicidal activity and, consequently, interest exists in utilizing natural products for synthetic herbicidal templates (Duke, 1986).

ROTATIONAL CROPS TO REDUCE WEED GROWTH

The use or manipulation of rotational crops that provide weed suppression can be an effective cultural means to provide weed control with minimal application of pesticides. Small grain and vegetable producers have used rotational crops or smother crops for centuries to eliminate specific weeds or reduce weed populations as a whole. Smother crops such as rye (*Secale cereale* L.), wheat (*Triticum aestivum* L.), buckwheat (*Fagopyrum esculentum* Moench), black mustard [*Brassica nigra* (L.) Koch], or sorghum-sudangrass hybrids [*Sorghum bicolor* (L.) Moench × *S. sudanense* (Piper) Stapf] can be very effective in weed population reduction (Table 1). Many of these crops become quickly established (Putnam, 1990) and compete for resources used by weeds. Overland (1966) suggests that many of them suppress weeds through a combination of competition and allelochemicals produced by the living or decomposing crop.

Abbreviations: PSII, photosystem II.

Table 1. Common cover or smother crops utilized for weed interference, with their identified allelochemicals.

Common name	Scientific name	Allelochemicals	References
black mustard	<i>Brassica nigra</i> (L.) Koch	allyl isothiocyanate, other water-soluble inhibitors	Bell and Muller, 1973; Muller, 1969
buckwheat	<i>Fagopyrum esculentum</i> Moench	fatty acids	Tsuzuki et al., 1987
clover (red, white); sweetclover	<i>Trifolium</i> spp.; <i>Melilotus</i> spp.	isoflavonoids, phenolics	Rice, 1984
oat	<i>Avena sativa</i> L.	phenolic acids, scopoletin	Rice, 1984; Guenzi and McCalla, 1966
rye	<i>Secale cereale</i>	phenolic acids, benzoxazinones	Barnes and Putnam, 1987; Mwaja et al. 1995; Nair et al., 1990; Shilling et al., 1985
wheat	<i>Triticum aestivum</i> L.	phenolic acids, simple acids	Shilling et al., 1985; Guenzi and McCalla, 1966
sorghum, sudangrass	<i>Sorghum</i> spp.	phenolic acids, dhurrin, sorgoleone, <i>p</i> -hydroxy benzaldehyde, <i>p</i> -hydroxy benzoic acid	Einhellig et al., 1993; Forney and Foy, 1985; Netzley and Butler, 1986; Nicollier et al., 1983; Nimal et al., 1983; Weston et al., 1989

Buckwheat

Buckwheat is known to have potent weed suppressive properties and, hence, is often cited as a smother crop that reduces weed interference over time, in a cumulative manner (Rice, 1984). For example, buckwheat suppressed the total biomass accumulation and leaf area of lambsquarters (*Chenopodium album* L.) and also decreased the uptake of N, P, and K (Dzyubenko and Petrenko, 1971; Rice, 1984). Their findings indicate that competition for resources may play an important role in long-term weed suppression. In contrast, cover crops such as oat (*Avena sativa* L.) also had a marked effect on growth reduction of lambsquarters, but did not decrease subsequent nutrient uptake in seedlings as did buckwheat. They concluded that oat exhibits a strong allelopathic effect in addition to the competitive role in growth inhibition. Even the reduced uptake of nutrients in lambsquarters growing with buckwheat may have a chemical source. One mechanism of allelochemical action is interference with nutrient uptake (Einhellig, 1995).

Black Mustard

Black mustard sometimes invades the grasslands of coastal California and forms pure stands over time (Muller, 1969). Interestingly, grass seeds were observed to germinate and emerge in great density in grassy areas surrounding mustard establishments, but not in areas immediately adjacent to the mustard stand, even with optimal water supplies and high densities of grass seeds. Mustard seeds, however, germinated well within the mustard stand. In later studies, Bell and Muller (1973) found soil factors such as pH, temperature, nutrients, and moisture were not different between grass and mustard-infested areas. Foraging studies showed the majority of grass seeds were not affected by animal predators. Light measurements and the use of artificial shading also indicated that light was not a factor in the observed patterning. The researchers concluded that an allelopathic mechanism was involved.

Bell and Muller (1973) found large quantities of allyl isothiocyanate were produced when mustard vegetation was crushed or macerated. The extracted compound also adsorbed onto soil, and the resulting treated soil was inhibitory to the germination of grass seeds. Inhibition dissipated in the laboratory after a period of 9 wk. Volatile compounds did not appear responsible for the

patterning of grass observed; however, water-soluble compounds leached from dead stems and leaves of mustard were very inhibitory to grass germination. Field experiments showed that treatments containing soil immediately surrounding mustard plants plus mustard stalks had significantly fewer grass seedlings than those treatments without mustard establishment or where mustard residues were removed. Bell and Muller (1973) concluded that the pure stands of *B. nigra* observed in California resulted from the suppressive activity of leached toxins created by the action of rainwater upon dead stems and leaves of the previous crop of mustard.

Fields of *Brassica* species, including black mustard, are often under cultivation in the northeastern USA, Europe, and western Canada. I have seen pure stands of mustard in Michigan in which few, if any, weeds were found between plants or rows and in which no herbicides were applied. Northern growers have also mentioned the weed suppressive properties of the *Brassica* spp., particularly the mustards. In California, Jimenez-Osornio and Gliessman (1987) found yields of broccoli (*Brassica oleracea* L. var. *italica* Plenck) were increased by up to 50% when wild mustard (*B. campestris* L.) was included in the cropping system by interplanting. Yield increases may have been associated with increased diversity in the cropping system as well as weed suppression.

Sorghums

In the southern USA, growers of horticultural and agronomic row crops often use sorghum-sudangrass hybrids as a green manure, a cover crop, or a smother crop, as do livestock producers. The farm manager at the Horticulture Research Farm, Lexington, KY, has historically planted these hybrids as a green manure crop to prevent soil erosion and to reduce weed infestation during the following year.

Sorghum-sudangrass hybrids and many of the related sorghum species accumulate biomass very rapidly and can attain heights of greater than 2.5 m in less than 6 wk (Forney et al., 1985; Geneve and Weston, 1988). Forney and Foy (1985) used these hybrids as a killed cover crop preceding the no-till establishment of alfalfa (*Medicago sativa* L.) in late summer. Weed populations were significantly reduced (in some cases by eightfold) in alfalfa grown after sorghum-sudangrass hybrid residues in comparison with no residue or foxtail millet

[*Setaria italica* (L.) P. Beauv.] residues. Einhellig and Rasmussen (1989) also noted the strong weed suppressive potential of grain sorghum residues during subsequent establishment of row crops in Nebraska. Density of annual weeds, particularly the broadleaf weeds, was suppressed up to 1 yr following establishment of sorghum as a summer crop in comparison with plots following corn (*Zea mays* L.) or soybean [*Glycine max* (L.) Merr.]. Others have noted the potential of sorghum seeds to interfere with the germination and growth of weed seedlings (Panasiuk et al., 1986). In recent studies, we have observed the reduction in radicle length of green foxtail [*Setaria viridis* (L.) P. Beauv.], velvetleaf (*Abutilon theophrasti* Medikus), and smooth pigweed (*Amaranthus hybridus* L.) in the presence of germinating sorghum seedlings, under conditions where edaphic factors such as light, temperature, nutrients, and water were closely controlled at high levels (Hoffman et al., 1996).

Living plants of sorghum and related species possess a variety of potent inhibitors. Dhurrin, a cyanogenic glycoside causing strong mammalian toxicity, is present in highest concentrations in young sorghum seedlings. When sorghum is injured or stressed, dhurrin is hydrolyzed to HCN, glucose, and *p*-hydroxybenzaldehyde and/or *p*-hydroxybenzoic acid (Nicollier et al., 1983; Weston et al., 1989). Johnsongrass [*Sorghum halepense* (L.) Pers.] is a very serious weed problem in the southern USA and also releases toxins from its rhizomes and herbage. Breakdown products of dhurrin as well as other phenolics contribute to the toxicity of johnsongrass (Abdul-Wahab and Rice, 1967; Nicollier et al., 1983).

More recently, Netzley and Butler (1986) discovered that living sorghum roots exude a long-chain hydroquinone called sorgoleone that exhibits phytotoxicity. In bioassays performed by Einhellig and Souza (1992), sorgoleone was inhibitory to seedling growth of several weeds at extremely low concentrations. Einhellig et al. (1993) also reported that sorgoleone inhibited O₂ evolution in soybean leaf disks and intact chloroplasts in pea (*Pisum sativum* L.) at similar low concentrations.

Most recently, we have performed a series of studies directed towards determining the site or sites of action of sorgoleone causing inhibition of photosynthesis. Sorgoleone proved to be a remarkably potent inhibitor of electron transport in photosystem II in both isolated chloroplasts and PSII membranes (Gonzalez et al., 1997). In these studies, sorgoleone exhibited greater specific activity than DCMU [diuron, *N*'-(3,4-dichlorophenyl)-*N,N*-dimethylurea], one of the most potent photosynthetic inhibitors known. A series of membrane binding studies with selected photosynthetic inhibitors were performed in an attempt to further characterize the binding site and specific mode of action of sorgoleone within the electron transport chain of photosynthesis (Nimbal et al., 1996b). Clear evidence of competitive binding of sorgoleone with atrazine [6-chloro-*N*-ethyl-*N*'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] at the Q_B binding pocket of the D₁ protein was obtained (Gonzalez et al., 1997; Nimbal et al., 1996b). In addition, sorgoleone and DCMU effectively inhibited the decay of variable fluorescence, indicating a blockage of the oxidation of the PSII-reduced

primary electron acceptor by the PSII secondary electron acceptor, Q_B, by displacing Q_B from the D₁ protein (Gonzalez et al., 1997). Further studies have shown that sorgoleone is exuded in large quantities by living root systems of various sorghum accessions and related species and is often produced at levels greater than 1% of the total seedling dry weight (Nimbal et al., 1996a).

ALLELOPATHIC CROP RESIDUES TO REDUCE WEED GROWTH

One common way that allelopathy may be utilized in weed management systems is through the manipulation of allelopathic cover crop residues in annual and perennial cropping systems. Over the past 10 yr, this cultural approach has gained acceptance by producers of corn, soybean, and small and large fruit crops, including grapes (*Vitis* spp.) and vegetables. The suppressed or killed cover crop residues remain on the soil surface, and the succeeding crop can either be transplanted or seeded into the residues using no-tillage equipment. Alternatively, the residues can be incorporated into the soil in the planting area through strip tillage so that conventional equipment can be used or very small-seeded crops could be established. In the case of perennial crops, the cover crop could be established by broadcast seeding in the fall, spring, or summer and then selectively controlled with herbicides later to create a killed residue surrounding an established perennial crop, such as grapes.

The cover crop residue on the soil surface provides many benefits, including conservation of soil and water (Putnam, 1986; Weston, 1990). Also populations of bacteria and pseudomonads were much higher in surface soil from plots containing cover crop residues of rye, wheat, or hairy vetch (*Vicia villosa* Roth) than in plots with no residue (Zablotowicz et al., 1993). The effects of microbial enhancement on cover crop decomposition or release of allelochemicals is unknown, but may contribute to a rapid release of water-soluble inhibitors. The physical presence of the cover crop mulch on the soil surface also has profound effects on weed density and distribution. Reduced tillage studies have shown changes in the species composition of the weed community by modification of the soil environment (Liebman and Janke, 1990; Putnam et al., 1983). Others have shown that density of weed seedlings was inversely correlated with residue densities of the cover crop. Both radiation interception under a wheat straw mulch and soil temperature were reduced with increasing straw density, factors that may contribute to reduced weed infestation levels (Vidal et al., 1994).

Rye

In addition to the significant physical effects a mulch has upon the soil rhizosphere environment and weed populations, several cover crops are known to exhibit strong allelopathic effects that also contribute to weed suppression. Rye produces a dense canopy that competes effectively with weeds for light, moisture, and nutrients. Rye residues reduce weed seed germination and seedling

growth by shading, lowering soil temperatures, moderating diurnal temperature fluctuations, and acting as a physical barrier (Barnes and Putnam, 1987; Vidal et al., 1994). In addition, rye and its residues release allelochemicals that accumulate near the soil surface to further inhibit weed germination and growth. In studies performed by Barnes and Putnam (1983), rye residues were particularly inhibitory to annual broadleaf weeds. The physical presence of the residue itself did not account for the additional suppression observed, when inert mulching materials were compared as controls.

The phytotoxicity of rye and its residues have been attributed to cyclic hydroxamic acids and a complex of simple phenolic acids (Barnes and Putnam, 1987; Shilling et al., 1985). Two benzoxazinones, 2,4-dihydroxy-1,4(2*H*)-benzoxazin-3-one (DIBOA) and its decomposition product, 2(3*H*)-benzoxazolinone (BOA), have been identified in extracts of rye shoots (Barnes and Putnam, 1987). Additional allelochemicals may arise by microbial transformation of compounds from rye residues. Nair et al. (1990) isolated and characterized 2,2'-oxo-1,1'-azobenzene (AZOB), an azoperoxide, produced from rye. This compound was more toxic to seedling growth than BOA or DIBOA.

Rye toxicity is influenced by fertility regime and production environment (Mwaja et al., 1995). The concentrations of BOA and DIBOA were highest in shoot tissues when rye was grown under low or moderate fertility rather than high fertility (Table 2). Ether extracts of dried rye shoots were also less inhibitory when grown under high fertility regimes. Field-grown rye extracts possessed greater inhibitory activity than greenhouse-grown extracts.

Winter Annual Cover Crops

Currently, winter rye is used in many horticultural or agronomic cropping systems. Rye can provide weed suppression for a period of 30 to 75 d, depending on soil and weather conditions (Masiunas et al., 1995; Putnam, 1986). Weed control persists for longer periods when

Table 2. The effects of rye fertility regime upon recovery of ether extracts of rye, DIBOA, and BOA from rye residues (data from Mwaja et al., 1995).

Crop system†	Fertility level‡	Recovery		
		Ether extract	DIBOA	BOA
			mg g ⁻¹	
monoculture of rye	low	2.6	210 ± 8.0§	22 ± 8.5
monoculture of rye	medium	12.1	319 ± 18.5	15 ± 14.0
monoculture of rye	high	5.1	129 ± 5.5	3 ± 2.3
rye + hairy vetch	low	3.9	424 ± 22.3	20 ± 0.9
rye + hairy vetch	medium	6.4	335 ± 3.5	31 ± 25
rye + hairy vetch	high	3.8	139 ± 9.0	3 ± 1.3

† Crop systems included a monoculture of winter rye or a polyculture of winter rye and hairy vetch. Greenhouse-grown rye was harvested after 75 d of growth.

‡ Fertility regimes: low (5 mM NO₃⁻, 0.5 mM P, and 3 mM K), medium (10 mM NO₃⁻, 1 mM P, and 6 mM K), and high (20 mM NO₃⁻, 2 mM P, and 12 mM K) nutrient levels applied in Hoagland's solution. All N was in the form of nitrate. Other nutrients, including S, Ca, Mg, and micronutrients (Fe, Cl, Mn), were added in similar proportions to N, P, and K.

§ Mean ± standard error.

rainfall occurs soon after crop desiccation and dry conditions follow. In recent experiments, we have found rye to be highly weed suppressive for a 4- to 6-wk period in Kentucky. Yields of no-till pumpkins (*Cucurbita pepo* L.) and sweet corn produced in rye residues with one herbicide application in Kentucky were higher than those produced in conventional tillage systems with one herbicide application (Galloway and Weston, 1996). Yields of processing tomato (*Lycopersicon esculentum* Mill.) produced in a rye residue with one herbicide application or hand removal of weeds were similar to or higher than those produced conventionally with herbicides (Masiunas et al., 1995). Yield increases may be related to reduced weed infestations as well as to fertility and moisture differences among treatments.

Winter wheat cover crops are also widely used in agronomic and horticultural cropping systems. Wheat residues suppress weeds due to production of phytotoxins as well as physical mulch effects. Researchers in North Carolina have shown that wheat residues contain phytotoxic phenolics and simple acids (Shilling et al., 1985). Among nine cover crops evaluated, wheat was particularly valuable because it was easy to control chemically, provided reasonable weed suppression, and was least inhibitory to crop seedling establishment (Weston, 1990) (Table 3). Although other killed cover crops such as tall fescue (*Festuca arundinacea* Schreb.), creeping red fescue (*F. rubra* L.), and perennial ryegrass (*Lolium perenne* L.) were exceptionally weed suppressive over an 8-wk period, these cover crops were difficult to control chemically, and seedling crop establishment was significantly reduced even with complete kill of the cover crop, possibly due to phytotoxicity of the residues. In general, large-seeded species that germinated rapidly were most successfully established in no-till cover crop residues compared with small-seeded or slow-germinating species.

Summer Annual Cover Crops

Summer annual cover crops can also be used for weed suppression during late summer and fall of the following

Table 3. Influence of cover crop species on residue accumulation, weed biomass, and succeeding row crop establishment (data from Weston, 1990).

Cover crop	Cover crop biomass†	Weed biomass‡	Row crop density§
		g m ²	no. m ²
Italian ryegrass	134	8.8	12.2b¶
perennial ryegrass	128	11.8	8.2d
creeping red fescue	100	30.6	7.2d
tall fescue	107	37.8	10.2c
white clover	55	—	12.2b
rye	262	94.2	14.4a
wheat	182	92.8	15.7a
barley	225	245.4	14.3a
oat	162	251.2	15.2a
LSD (0.05)	70	42.5	—

† Average final biomass of cover crops obtained 7 mo after seeding at Lexington, KY.

‡ Means presented are for weed biomass (shoot dry weight) collected 60 d following cover crop treatment with 0.6 kg ha⁻¹ glyphosate.

§ Row crop establishment 30 d after direct seeding, averaged over five row crop species.

¶ Means followed by the same letter are not significantly different at the 0.05 probability level.

year. Sorghum or sorghum-sudangrass hybrids can be sown in late summer and allowed to freeze in the fall to minimize the need for chemical control of growth. Sorghum residues have proven useful for weed suppression in orchards and nurseries. Fruit trees and asparagus (*Asparagus officinalis* L.) have shown slight increases in growth and yield after 4 yr of maintenance in a sorghum cover crop residue in comparison with clean cultivation or repeated use of herbicides to maintain bare ground areas (Putnam, 1986). Interestingly, living sorghum (trimmed to minimize competition) and sorghum roots were quite inhibitory to the growth of small woody seedlings, but killed residues were not strongly suppressive of woody species (Geneve and Weston, 1988).

Legume Cover Crops

Legume cover crops are widely used to enhance soil N levels and prevent soil erosion. Limited weed suppression is seen with many of the vetch covers, including hairy vetch, although soil N levels are often improved (Hoffman et al., 1993). Clover (*Trifolium* spp.) and sweetclover (*Melilotus* spp.) cover crops do appear to have some allelopathic potential (Rice, 1984), but are problematic in no-till situations because of difficulty in chemical control of the cover (Weston, 1990). Legumes may be used as living mulches, rather than as killed residues, to aid in weed suppression over time. Clovers and other legume forages are often low growing and, because of dense canopies, can be very competitive with developing weeds. If the legume crop can be maintained in strips away from a transplanted or direct-seeded row crop, successful weed management can be combined with increased N inputs between crop rows.

Mowing, grazing, or herbicide application at low rates are ways to maintain the cover as a living mulch while minimizing its competition with the row crop. Unfortunately, these measures are not always successful. In our recent studies with no-till pumpkins and corn direct-seeded into suppressed ladino (*Trifolium repens* L.) and crimson (*T. incarnatum* L.) clovers, the clover covers resumed strong growth 4 wk after glyphosate application (Galloway and Weston, 1996). The clovers were extremely weed suppressive (reducing up to 90% weed biomass) at planting rates of 7 to 17 kg ha⁻¹, depending on the clover, but reduced corn yields by up to 50% at fall harvest. Vrabel et al. (1980) also found that various clovers reduced sweet corn yields if planted in full covers

between corn rows. Yields were not reduced if strips of legumes were planted between corn rows or if legumes were seeded 5 wk after corn planting.

Environmental Interaction

Crop seedling establishment and growth can be significantly reduced in cover crop residues or when covers are tilled into the soil before planting. This, especially, raises questions regarding the interpretation of data showing inhibition. Establishment or replant problems can occur due to poor seed or transplant placement, lack or excess of soil moisture, nutrient deficiencies, pest problems, or other unknown reasons associated with changes in the microenvironment. It is difficult to determine the reasons why replant problems occur; in some cases, however, allelopathy is suspected. Establishment problems in residues can be limited or widespread. In general, toxicity is minimized when high soil moisture and warm temperatures are maintained during field growth. This may enhance chemical decomposition and microbial activity, especially if the residue is tilled into the soil, resulting in the decomposition of the residues.

What appears as a phytotoxic problem in one season may not be detected in the next. For example, in Kentucky, under dry summer conditions and high temperatures followed by a cool fall, fall-planted broccoli and cabbage (*B. oleracea* L. var. *capitata*) were stunted and slow to mature when following tobacco (*Nicotiana tabacum* L.), whether root residues were tilled into the soil or not (Clements and Weston, 1994). Herbicide carryover and nutrient deficiencies were ruled out as factors associated with reduced crop growth. When the experiment was repeated the following year, stunting was observed but was not as dramatic. During the second year, soil moisture levels for the cole crops were initially higher, and air and soil temperatures were moderate. These more optimal growth conditions also may have minimized allelopathic stress (Einhellig, 1989).

It is now obvious that further studies must be conducted in specific locations with different weed pressures to determine optimal cover crop or intercrop systems to ensure enhanced weed suppression, adequate crop establishment, and limited phytotoxicity. Environmental conditions may certainly play a role in the appearance or disappearance of allelopathic interference over time and may therefore complicate efforts to adapt successful weed management strategies across locations.

Germplasm Selection

Very few attempts have been made to enhance weed suppressive potential of crop plants through conventional or nontraditional breeding programs, even though this is a logical way to integrate biorational approaches to pest control in current production systems (Table 4). Of the work that has been published, cucumber (*Cucumis* spp.), oat, soybean, and sunflower (*Helianthus annuus* L.) germplasm have been evaluated for allelopathic or weed suppressive potential (Putnam, 1986). Differences in allelopathic potential have been observed among accessions and cultivars in these collections. Certain acces-

Table 4. Average weed weights and cucumber vine weights of selected cucumber accessions grown in association with weeds (data from Lockerman and Putnam, 1979).

Accession or cultivar	Cucumber vine wt.		Weed wt. g m ⁻²
	Weeded	Nonweeded	
none	—	—	10.4a†
Pioneer	361a†	234a	4.9b
PI 169391	358a	274b	1.7c
PI 285605	378a	214c	3.6b

† Within columns, means followed by the same letter are not significantly different at the 0.05 probability level.

sions of cucumber actually stimulated plant growth, while several strongly inhibited weed germination and growth (Putnam and Duke, 1974; Lockerman and Putnam, 1979). The growth inhibitors appeared to be water soluble (Lockerman and Putnam, 1981). Screening has also been performed in a perennial ryegrass collection, which indicated that certain accessions have strong weed suppressive activity in orchard floors (Putnam, 1986). Most recently, rye cultivars and accessions are under evaluation by Masiunas et al. (personal communication, 1994) at the University of Illinois in an attempt to study differences in weed suppression.

SUMMARY

Certain cover crops or their residues selectively inhibit particular crop and weed species. This differential sensitivity is observed in field, greenhouse, and laboratory experiments with residues, extracts, and purified allelochemicals. The development of weed management strategies that make use of allelopathic crop plants is receiving increased national and international attention. Biorational pest control strategies are particularly important because environmental preservation is of public concern and the number of effective herbicides and pesticides labeled for many crops is rapidly decreasing.

Allelopathic crops offer potential for development of model herbicides as well as providing a source of germplasm that could be manipulated to enhance weed suppression in an environmentally compatible manner. Until recently, research efforts on sustainable agriculture systems have focused on using cover crop residues for enhanced weed suppression. As we learn more about the mechanisms of allelochemical selectivity, physiological modes of action, and genetic regulation of biosynthesis, we should be able to successfully manipulate our germplasm resources to select for novel secondary products, enhanced production of this chemistry, or regulation of release rate of allelochemicals for improved season-long weed suppression in both living plants and their residues. This area of technology is in its infancy and, although complex, represents a new frontier for scientists interested in integrated weed management strategies.

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