Brassica cover cropping for weed management: A review

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Abstract

Cover crops offer many benefits for farmers seeking to reduce their reliance on external inputs. These include maintaining and improving soil quality, preventing erosion and, in some cases, allelopathic weed control. Allelopathic potential has been well documented for cover crops such as cereal rye (*Secale cereale* L.), hairy vetch (*Vicia villosa* Roth) and red clover (*Trifolium pratense* L.). Much less is known about other potentially allelopathic cover crops, including certain brassicaceous species that are normally grown for their oilseeds, including canola and rapeseed (both *Brassica napus* L.) and mustards (e.g., *Sinapis alba* L., white and yellow mustard). Because of their potential contribution to pest management, there is increased interest in growing brassicas, both as cover crops and as seed crops harvested for oil production. In this review, we first discuss unique attributes of brassicas that make them promising options for pest management, as well as generally beneficial cover crops. Next, we review the literature from controlled settings on the effects of brassicas, brassica extracts and isolated compounds contained therein on seed germination, seedling emergence and establishment, and seedling growth—effects that, combined or taken alone, could contribute to reducing the density and vigor of weed communities in the field. Field studies examining the detrimental effects of brassicas in rotation with other crops, as well as examining the effects of brassica cover crops on weed dynamics in subsequent crops, also are reviewed. Finally, we review some important agronomic considerations about the use of brassica cover crops.

Key words: brassicas, cover crop residues, green manure, allelopathy

Introduction

One of the hallmarks of sustainable agriculture systems is the use of multiple tactics to address short- and long-term goals concerning pest and soil management. In this context, single tactics that provide multiple benefits are of vital importance. The practice of cover cropping is such a tactic, providing many services to agroecosystems, including improved soil quality, increased nutrient cycling and pest management[1]. Given the prominence of weeds as a production-related problem for organic and diversified vegetable growers[2], cover crops are often chosen and managed for weed control.

The weed suppressive effects of winter rye (*Secale cereale* L.), hairy vetch (*Vicia villosa* L.) and red clover (*Trifolium pratense* L.) cover crops have been well documented[3–8]. Other cover crops, including certain brassica species, have been examined for weed control on a more limited basis. However, there is good reason to consider brassicas as a cover cropping option when weed management is a priority. Members of the *Brassicaceae* family contain glucosinolates—sulfur-containing molecules that are hydrolyzed to form compounds toxic to a variety of soil-borne organisms, including weeds[9]. Laboratory and greenhouse studies suggest that the hydrolysis products of glucosinolates, as well as brassica residues and extracts containing these compounds, are toxic to weeds[10–16], insect pests[17,18] and pathogens[19–21]. In addition, a limited number of field studies have confirmed the ability of brassicas in rotations to suppress weeds[22–24], nematodes[25] and fungal pathogens[26].

These pest-management possibilities, in addition to general benefits of cover cropping, make members of the *Brassicaceae* promising cover crops for use in agronomic and horticultural systems. Several recent reviews have addressed glucosinolate chemistry and the potential use of brassicas for the management of insect pests and plant pathogens[9,27–29]. Here we review the literature, with a focus on the use of brassica cover crops for weed control in agricultural and horticultural production systems.

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Brassica Cover Crops: Unique Characteristics

Members of the *Brassicaceae*, including yellow and white mustards (e.g., *Sinapis alba* L.), canola (*Brassica napus* L.) and rapeseed (also *B. napus* L.), are being used increasingly as cover crops in temperate regions of North America. These species are typically grown for their seeds, which are harvested for oil production, as with canola and rapeseed, or used for condiment production, as with mustard. However, each of these species can also be grown as a short-season cover crop or, if climate allows, as an overwintering cover crop.

Rapid growth and nutrient capture

Both spring- and fall-planted brassica cover crops can rapidly produce biomass. Winter varieties of rapeseed and canola can provide more than 80% ground cover during the winter[30], an important consideration for erosion control. Fall-planted rapeseed cover crops in eastern Washington and southern Idaho yielded 3000–8000 kg dry biomass ha^{-1} by the time they were incorporated the following spring[22,23,30]. In Maine, spring-planted yellow mustard produced 3000–4500 kg dry biomass ha^{-1} 1.5 months after planting (Haramoto, unpublished data). On the other hand, Krishnan et al.[24] reported much lower biomass production (500–1400 kg dry biomass ha^{-1}) in Nebraska for mustards and rapeseed.

Brassicas are also capable of capturing excess nitrate remaining after crop harvest, preventing nitrogen (N) loss from leaching, with overwintering cover crops being more efficient than those that are frost-killed[31–33]. Overwintering rapeseed, forage turnip (*Brassica napus* L.), canola and white mustard were equal to winter wheat (*Triticum aestivum* L.), winter barley (*Hordeum vulgare* L.), winter rye and Italian ryegrass (*Lolium multiflorum* Lam.) in their capture of excess N in the fall[32,33]. The N scavenging in these studies was related to biomass production. Canola and forage turnip cover crops sown in August and incorporated at the end of October were similar to barley in their capacity to capture excess N following sweet corn (*Zea mays* L.) harvest[31]. White mustard planted after sweet corn harvest was able to capture more N than a sudangrass (*Sorghum bicolor* L.) cover crop[33]. As mustards are frost-sensitive, the fate of this captured N then depended on residue management after the cover crop was frost-killed. More N from the mustard biomass was returned to the soil over winter if the residues were incorporated in the fall; whereas spring incorporation of residues led to less N loss. Thus, in addition to providing physical protection, residues left on the soil surface over winter may reduce N leaching. Others have reported N immobilization following incorporation of brassicas[34,35]. Slower release of plant-available N may be beneficial in certain cropping systems as the N is available for the crop instead of weeds that emerge earlier[36]. However, N immobilization may not be desirable for crops with early N demands, making it necessary to consider nutrient management benefits against potential N immobilization.

Biologically active secondary compounds: 'Biofumigants'

All members of the *Brassicaceae* examined to date contain glucosinolates[9]. Glucosinolates consist of a glucose molecule, a sulfur moiety, and a side chain, the composition of which determines their properties. Glucosinolate molecules are not toxic but are enzymatically hydrolyzed to yield a variety of biologically active products, including isothiocyanates, ionic thiocyanates, nitriles, oxazolidinethiones, organic cyanates and epithionitriles[9]. Myrosinase, the enzyme responsible for glucosinolate breakdown, is separated intercellularly from the glucosinolate molecules. Thus, tissue disruption is necessary before biologically active breakdown products are released[9]. In the field, this disruption can be accomplished by mowing, grazing, freezing, tillage or root death.

Mustards, e.g., white and yellow mustards; Indian, brown and Chinese mustards (*Brassica juncea* L.); and black mustard (*Brassica nigra* L.), typically have a high seed glucosinolate content, as evidenced by their biting flavors. In contrast, canola, which has a very low seed glucosinolate content, was derived from cultivars of rapeseed that contained low concentrations of glucosinolates and erucic acid in the seed; these are also referred to as 'double-low' cultivars[37,38]. Canola contains less than 30 µmol of aliphatic glucosinolates g^{-1} of oil, and the oil is less than 2% erucic acid[37]. If the oil contains more of these compounds, it is not classified as canola (Jim Davis, personal communication). Vegetative tissues of canola may contain higher concentrations of these compounds, though typically the glucosinolate content of vegetative tissues is 10% that of the seed (Jim Davis, personal communication). The term 'single-low' refers to rapeseed varieties with a low concentration of erucic acid, below 2% as with canola. Because of early concerns that higher amounts of erucic acid could lead to health problems, low concentrations of this compound determine the suitability of the oil for human consumption, and both canola oil and oil from single-low rapeseed varieties are edible[39,40]. Seed-meal glucosinolate content determines its suitability as a livestock feed supplement, as higher amounts of glucosinolates in feed can lead to goiter in livestock[38–40]. Because of its low glucosinolate content, canola meal can be used for livestock feed. If the glucosinolate content of rapeseed seed meal remains low, it too can be used as a feed supplement.

Profiles of glucosinolate molecules vary between different brassica species[41–43], between individuals of the same species or genotype[30,44,45], and even within different plant tissues of a single individual[46,47]. While different cover crops at particular life stages may be used to manage specific pests[43], complications may arise because the hydrolysis

products of different glucosinolate molecules vary in their toxicity to different organisms[9]. Such targeted pest management may also be complicated by edaphic factors, which can alter the exact profile of hydrolysis products released from glucosinolates. For example, nitrile formation was favored at acidic soil pH, albeit at pH values lower than those typically found in agricultural fields[48,49].

Isothiocyanates and the other glucosinolate derivatives have relatively high vapor pressure and are thoroughly dispersed throughout the surrounding soil, where they may affect soil-borne fungal pathogens, insects and nematodes[50]. Suppression of fungal pathogens by brassica tissues was so promising that one researcher coined the term 'biofumigation', in reference to their effects[20], and the use of incorporated brassica residues has been proposed as an alternative to the use of methyl bromide[51]. Brassica residues inhibit fungal growth and reproduction[20,51,52]; they may also reduce disease pressure in the field[26,53].

The effects of glucosinolates on insect pests have been variable and are complicated by species-specific interactions. Specialist pests may be attracted by glucosinolates and damage from these specialists tends to increase with increasing glucosinolate content of the plant[18,28,29]. Growth rates of generalist insect feeders[17] and feeding by generalist invertebrates and vertebrates[18,54] both declined when the animals were exposed to increasing concentrations of glucosinolates. Incorporation of rapeseed residues before potato (*Solanum tuberosum* L.) cropping reduced Columbia root-knot nematode (*Meloidogyne chitwoodi* Golden et al.) colonization in the zone of residue incorporation for 6 weeks, although nematode damage remained severe enough to cause economic loss[25]. Additions of brassica residues to soil with the root-knot nematode (*Meloidogyne javanica* Treub) reduced the nematode numbers, although the reductions were not correlated with glucosinolate content[55].

Brassica Residues and Allelochemicals: Bioassays in Controlled Environments

Cover crop residues, whether incorporated or left on the soil surface, can affect weed dynamics by reducing or delaying seed germination, reducing establishment and suppressing individual plant growth. Each of these mechanisms can contribute to overall declines in the density and vigor of the weed community[56,57]. Bioassays of isolated glucosinolate hydrolysis products, extracts of brassica residues and brassica residues themselves demonstrate that seed germination, emergence and growth are each adversely affected.

Germination

In purified form, glucosinolate hydrolysis products generally inhibit or delay seed germination. Glucosinolate hydrolysis products likely affect protein synthesis in germinating seeds and emerging seedlings[10]. Allyl isothiocyanate was most effective in suppressing seedling growth

if applied directly within 3 days of germination, suggesting that the effect was due to the relatively large amounts of isothiocyanates absorbed compared to the seedling mass, or that one of the first processes in seed germination was inhibited[10].

Glucosinolate hydrolysis products can inhibit germination of dormant and non-dormant seeds[12,15,58,59]. After exposure to methyl isothiocyanate, ungerminated seeds in one experiment were dissected and found to be dead[12]; however, in another experiment, ungerminated seeds exposed to various isothiocyanates remained viable[59]. Germination of redroot pigweed (*Amaranthus retroflexus* L.) and large crabgrass [*Digitaria sanguinalis* (L.) Scop.] seeds buried in mesh bags in field plots was completely inhibited by 2.7 mM and 5.4 mM methyl isothiocyanate[12]. Various isothiocyanates at 1, 5 and 10 mM inhibited germination of soybean (*Glycine max* L.), corn, wheat, rapeseed, dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers), alfalfa (*Medicago sativa* L.) and cucumber (*Cucumis sativus* L.), with varying toxicities of the isothiocyanates to the plant species[42]. For example, benzyl isothiocyanate inhibited germination of dandelion and alfalfa seeds at lower concentrations than the remaining bioassay species. Applications of other isothiocyanates to a number of different species produced similar results (Table 1). Typically, a reduction in seed germination rates was positively correlated with the concentration added, but with a high degree of variability, even in these highly controlled experimental conditions.

Isothiocyanates may also delay germination, causing an increase in the time to 50% germination from 2.7 to 8.5 days for large crabgrass exposed to 1 mM methyl isothiocyanate[12]. Higher concentrations of methyl isothiocyanate (2.7 and 5.4 mM) applied to field soil suppressed emergence of weeds for up to 7 weeks, while lower concentrations suppressed emergence for shorter periods of time.

In addition to the effects of isolated isothiocyanates noted above, volatile and water-soluble brassica extracts also may inhibit or delay germination. In Petri dish assays, volatile compounds released from black and brown mustard caused 89% and 100% inhibition of lettuce (*Lactuca sativa* L.) seed germination, respectively[13]. Volatiles from these residues, along with those from rapeseed, white mustard and kale (*Brassica oleracea* L.) residues caused an 8–19% inhibition of barnyard grass [*Echinochloa crus-galli* (L.) Beauv.] germination, but had no effect on wheat. Water-soluble extracts from various rapeseed and mustard cultivars failed to inhibit the germination of wheat seeds[11], although similar extracts from rapeseed leaves and stems inhibited and delayed germination of lettuce seeds in another study[60]. Extracts of wild radish (*Raphanus raphanistrum* L.) residues inhibited germination of pitted morning glory (*Ipomoea lacunosa* L.), sicklepod (*Senna obtusifolia* L.), prickly sida (*Sida spinosa* L.) and yellow nutsedge (*Cyperus esculentus* L.)[61]. Volatile and water-soluble extracts from rapeseed meal also inhibited the germination of lettuce seeds[62].

Table 1. Effects of different isothiocyanates on seed germination. The lower value in the concentration range represents either the lowest concentration tested or the maximum concentration at which no effect was noted; the maximum value is the maximum concentration tested.

Isothiocyanate	Concentration range (mM)	Species tested[1]	Effect on germination	Reference
Allyl	0.1–0.3	Wheat	3–13% decrease	15
Methyl	0–100	Wheat	No effect to 88% decrease	57
Methyl	0.1–4	Large crabgrass	No effect to 97% decrease	12
Methyl	0.1–4	Dormant large crabgrass	Increase to 95% decrease	12
Methyl	1–10	Scentless mayweed	23–100% decrease	57
Methyl	1–10	Smooth pigweed, barnyard grass, spiny sowthistle	No effect to complete inhibition	57
Methyl	1–10	Blackgrass	No effect to 80% decrease	57
Benzyl	0.2–0.6	Velvetleaf	No effect to complete inhibition	56
Benzyl	0.2–1	Corn	No effect at any concentration	56
Benzyl	0.2–1	Soybean	No effect to 58% decrease	56
Benzyl, butyl, phenyl, methyl, ethyl	0.1–0.3	Wheat	No effect at any concentration	15
2-phenethyl	0.1–0.3	Wheat	8–38% decrease	15

[1] Species tested included: wheat (*Triticum aestivum* L.), large crabgrass [*Digitaria sanguinalis* (L.) Scop.], scentless mayweed (*Matricaria inodora* L.), smooth pigweed (*Amaranthus hybridus* L.), barnyard grass [*Echinochloa crus-galli* (L.) Beauv], spiny sowthistle [*Sonchus asper* (L.) Hill], blackgrass (*Alopecurus myosuroides* Huds.), velvetleaf (*Abutilon theophrasti* Medic.), corn (*Zea mays* L.), and soybean (*Glycine max* L.).

Establishment

Mixed with soil, brassica residues can reduce seedling emergence, a combination of effects on the processes of germination and early seedling growth. Rapeseed residues decreased the number of hairy nightshade (*Solanum sarrachoides* Sendtner), longspine sandbur [*Cenchrus longispinus* (Hack.) Fern.] and hemp sesbania [*Sesbania exaltata* (Raf.) Rybd. Ex A.W. Hill] seedlings that emerged in greenhouse pots[22,42], although velvetleaf (*Abutilon theophrasti* Medicus) emergence was not affected[24]. Similarly, white and brown mustard residues decreased the emergence of kochia [*Kochia scoparia* (L.) Schrad.], shepherd's purse [*Capsella bursa-pastoris* (L.) Medicus.], green foxtail [*Setaria viridis* (L.) Beauv.], redroot pigweed, hemp sesbania and velvetleaf[23,24,42]. Turnip-rape (*Brassica napus* L.) residue decreased the emergence of spiny sowthistle (*Sonchus asper* L.) by over 50%, but actually increased the emergence of smooth pigweed (*Amaranthus hybridus* L.)[59]. Common chickweed [*Stellaria media* (L.) Vill.] emergence was decreased as the amount of rapeseed residue added to pots was increased[23], indicating that incorporating more residue would lead to improved weed control.

Some of the observed between-species variation in brassica residue effects on germination and/or establishment may be due to differences in seed size. Smaller seeds are, in general, more susceptible to residue-mediated stresses, including allelopathy[59,63–65]. Petersen et al.[59], for example, noted that the same concentration of methyl isothiocyanate caused a 79% decrease in germination for spiny sowthistle and only a 5% decrease for wheat, an effect attributed to differences in seed size (0.2 g thousand^{-1}

spiny sowthistle seeds compared to 45.3 g thousand^{-1} wheat seeds). However, germination of smooth pigweed and spiny sowthistle, which have similar seed mass (0.5 and 0.2 g thousand^{-1} seeds, respectively), was similarly affected by isolated isothiocyanates, but was affected very differently by turnip-rape residues, as noted above. As this example suggests, efforts to establish a threshold seed size at which inhibition of germination is likely to occur has thus far been unsuccessful[64,66]. Factors other than seed size, including seed morphology[67,68] and biochemical composition[63–64], may also determine a seed's ability to withstand these stresses.

Growth of established seedlings

In laboratory assays, isothiocyanates also inhibit growth of established seedlings. Benzyl isothiocyanate, for example, at 0.4 mM, completely suppressed seedling growth and prevented secondary root formation of velvetleaf; half this concentration caused root rot in developing seedlings, while their shoots remained unaffected[58]. Wheat root length, on the other hand, was only slightly reduced by this compound[15]. Similar concentrations of other isothiocyanates, including 2-phenethyl-, allyl- and methyl-isothiocyanate, caused reductions in coleoptile and root elongation of wheat seedlings[15].

Water-soluble extracts from canola root, stem and leaf tissues suppressed the growth of wheat, barley and corn seedlings, even after only one day of incubation[16]. Extracts of canola leaves were the most phytotoxic to the seedlings, causing decreased coleoptile and radicle elongation compared to the control[16]. Similarly, water-soluble extracts from dead black mustard stalks and leaves were effective

in decreasing radicle growth of rigid ryegrass (*Bromus rigidus* Roth.)[69]. Volatile allyl isothiocyanate produced from macerated black mustard tissues also reduced the growth of rigid ryegrass, but tended not to persist in the environment[69]. Extracts of wild radish residues reduced cotton (*Gossypium hirsutum* L.) radicle length by 75%; pitted morning glory radicle length was inhibited by 63%[61].

Seedlings grown in soil with incorporated rapeseed or mustard residues are affected in ways comparable to those exposed to residue extracts. Several similar experiments have demonstrated that kochia, shepherd's purse, green foxtail, hairy nightshade, redroot pigweed and velvetleaf seedling biomass was decreased when grown with mustard or rapeseed residues (0.04–0.05 g residue g^{-1} soil) compared to those grown without[22–24]. For example, when compared to potato residue, rapeseed residue decreased hairy nightshade and longspine sandbur biomass by 82 and 83%, respectively after 3 weeks[22]. Likewise, fresh white mustard residue reduced hairy nightshade and green foxtail seedling biomass by 83% and 70%, respectively, compared to seedlings grown without brassica residues[22]. Despite these generally comparable results, other studies suggest that mustard residues may be more effective in suppressing seedling growth than rapeseed, especially the growth of smaller-seeded species such as kochia and shepherd's purse[23]. Unexpectedly, the growth of wheat seedlings was actually increased by similar amounts of mustard and rapeseed residues when compared to soil alone, a result that is potentially attributable to the larger seedling size of wheat[42].

Effects of Brassica Rotation Crops on Weeds

Despite the generally promising laboratory, greenhouse and field results discussed above, the issue of whether brassica cover crops are allelopathic and can consistently provide weed control remains contentious. Differentiation between multiple 'residue-mediated' effects of cover crop residues, whether incorporated or left on the soil surface, and clear allelopathic mechanisms is difficult[70]. These residue-mediated effects may result from physical, biological or chemical changes to the soil environment, each of which may impact weeds[65]. Physical effects may result from changes to soil temperature or light penetration to the soil surface, each of which may impact weed seed germination[6]. These effects may be particularly pronounced when cover crop residues remain on the soil surface. An example of biological residue-mediated effects includes cover crop residues providing a habitat for seed predators or decay agents[57]. In addition to allelopathy, chemical residue-mediated effects may include nutrient sequestration or release, particularly that of nitrogen in the case of leguminous cover crops[36]. Regardless of the exact mechanism, in several natural and manipulated ecosystems, brassicas

have had a negative impact on surrounding plants, or following crops. For example, historically, dyer's woad (*Isatis tinctoria* L.) cultivation was restricted because of harmful effects on following crops[71]; others noted that reduced grass and clover yields were common on fields that previously grew brassicas[72]. Yield loss in flax (*Linum usitatissimum* L.) was greater in crops containing brassicaceous weeds than in flax infested by other types of weeds[73]. Annual grasslands in southern California contain monospecific stands of black mustard that yearly perpetuate themselves[69]. Studies of this system revealed that neither soil nor edaphic factors were responsible for the exclusion of grasses from these areas; likewise, preferential animal grazing and competition were ruled out. However, water-soluble compounds leached from the dead mustard residues during the rainy season inhibited the germination of rigid ryegrass and reduced its growth, supporting the conclusion that allelochemicals leached from the brassica tissues were responsible for excluding the grasses and maintaining the monospecific black mustard stands[69].

Early in the culture of rapeseed as an oilseed crop, growers reported negative effects of rapeseed residues on subsequent cereal crops[74]. Heavy rapeseed-residue-containing stubble and plant debris, as would be left in a combine windrow, decreased the dry biomass and height of wheat, barley and oats (*Avena sativa* L.) compared to a light rapeseed residue composed of stubble only[74]. Density of the cereals was similar in the two residue treatments, indicating that the abundant residues were stunting the growth of established plants[74]. Interestingly, severity of root rot in the cereals was lower following the heavy residue, consistent with reports that brassica residues may help manage fungal pathogens[74].

Rapeseed windrows also contained viable seed, lost through the combining process, that could germinate as volunteer plants. Simulating this, Vera et al.[67] found that incorporated rapeseed and mustard seedlings reduced the establishment, delayed the development and reduced the seed yield of the subsequent crops. Oilseeds, including rapeseed and flax, were more sensitive than the cereals tested, including barley and wheat; oat growth was not affected at all[67]. Both mustard and rapeseed seedlings caused similar decreases in growth, despite presumable differences in glucosinolate content, which was not measured[67].

In other examples, nitrogen immobilization has been suggested as the cause of reduced plant growth following brassicas[68,75]. Growth of alfalfa, a legume, was not affected by the incorporation of wheat or rapeseed residues, while barley and bromegrass (*Bromus inermis* Leyss) showed signs of nitrogen deficiency[75]. However, Bell and Muller[69] found no differences in soil nitrogen content between areas dominated by black mustard and areas dominated by annual grasses. Similarly, addition of nitrogen to wheat grown after different brassica species and cultivars did not change the effects of the residues on wheat growth or yield[11].

Effects of Brassica Cover Crops on Weeds

Rotation effects of brassicas have led to investigations on their use as cover crops, grown without harvesting of the seed, for weed control. In south-central Washington, where fall-planted rapeseed will typically overwinter, the effects of rapeseed residue on weeds in a subsequent potato crop was compared to sudangrass residue and a fallow treatment[22]. Fall-planted rapeseed residues were incorporated in the spring, while sudangrass residues were incorporated the previous fall after they were frost-killed; potatoes were then planted into these residues. In the subsequent potato crops, mid-season weed density following rapeseed was decreased by 73–85% relative to weed density following fallow and sudangrass, respectively, in the 2 years of the study; however, these mid-season weed densities were extremely low ($<1 \, m^{-2}$). At the end of the season, weed biomass was decreased by 50–97% by rapeseed compared to fallow and sudangrass, respectively. Potato yield was greater following rapeseed than following fallow in both years, indicating that the potato plants were not harmed by the residues.

The effects of fall-planted brassicas on weeds in green pea (*Pisum sativum* L.) were also examined in northwestern Washington[23]. In this study, brassicas included rapeseed and white mustard; rapeseed successfully overwintered in both years, while white mustard was winter-killed in 1 year. Weed density at 30 days after planting was lower following rapeseed and white mustard than following wheat, although weed biomass at pea harvest was similar following all cover crops. Rapeseed residue also consistently decreased pea density and pea yield, effects that were not observed following white mustard. Other field studies including green pea reported a reduction in establishment following both rapeseed[76] and white mustard[26].

Spring-planted mustards can be incorporated into rotations before a cash crop, or planted in succession in fallowed fields. Krishnan et al.[24], at two sites in eastern Nebraska, planted soybean into residues of spring-planted rapeseed, two varieties of white mustard, and brown mustard. Weed biomass, measured at 4 and 6 weeks after soybean emergence, was lower following these cover crops at one location, but not at another. The weed control from these brassica residues was not agronomically sufficient, however, as both locations suffered yield loss following all cover crops if herbicides were not applied. Soybean yields were similar for all cover crops and a fallow treatment, suggesting that the brassica residues did not harm the soybean plants.

Field studies testing the effects of spring-planted brassica residues on weed and crop emergence and growth were recently conducted in central Maine[66]. Sixteen bioassay species, including both crops and weeds, were planted into fallow plots and plots that grew and received incorporated residues of three brassica cover crops—rapeseed, canola and yellow mustard—and three non-brassica cover crops—buckwheat (*Fagopyrum esculentum* Moench.), oats and
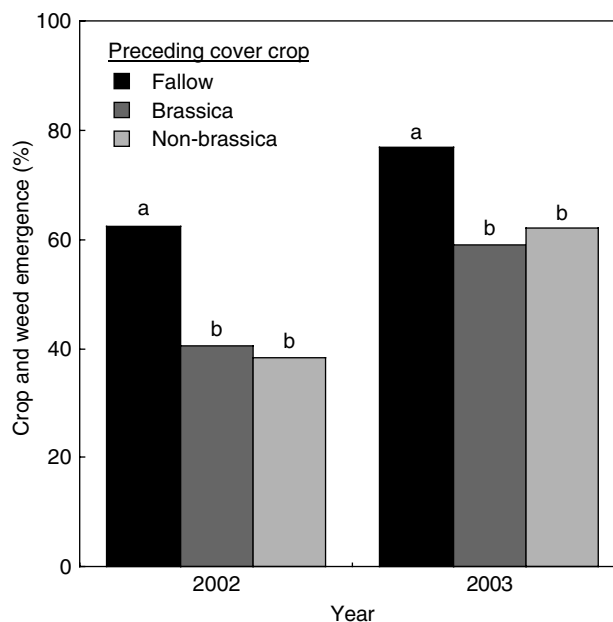

Figure 1. Effect of incorporated cover crop residues on mean emergence of 11 crop and weed species in 2002 and 15 in 2003. Based on analysis of variance of results, data were averaged over the crop and weed species. Single degree of freedom contrasts ($\alpha = 0.05$) compared emergence following no cover crop (fallow, $n = 44$ in 2002 and $n = 60$ in 2003), to emergence following incorporation of brassica (yellow mustard, spring canola and winter rapeseed; $n = 131$ in 2002 and $n = 176$ in 2003) and non-brassica (buckwheat, oat and crimson clover; $n = 131$ in 2002 and $n = 177$ in 2003) cover crops[66]. Within each year, means with the same lower-case letter were not significantly different ($P > 0.05$).

crimson clover (*Trifolium incarnatum* L.). Averaged over bioassay species, all cover crop residues decreased seedling emergence compared to fallow but, unexpectedly, there were no differences in emergence detected following the brassica cover crops and non-brassica cover crops which lacked glucosinolates, even for species with smaller seeds (Fig. 1). In another experiment, green bean (*Phaseolus vulgaris* L.), redroot pigweed and a mixture of the two species were planted into fallow plots and plots that grew and received incorporated residues of canola and yellow mustard. Although the biomass values of both green bean and redroot pigweed were often lower following the brassica cover crops, and lowest following the high-glucosinolate mustard, differences were not significant (Fig. 2). Competition reduced green bean and redroot pigweed height and biomass, but interspecific interference was unaffected by the incorporated brassica residues. Similarly, marketable green bean yield was lower in plots containing redroot pigweed than in plots with green bean grown alone, but incorporated brassica residues did not mediate the competitive effect. These results suggest that the observed weed suppression by brassica cover crops in the field[22–24], when compared to soil without residues, is likely related to their effects on establishment but not on
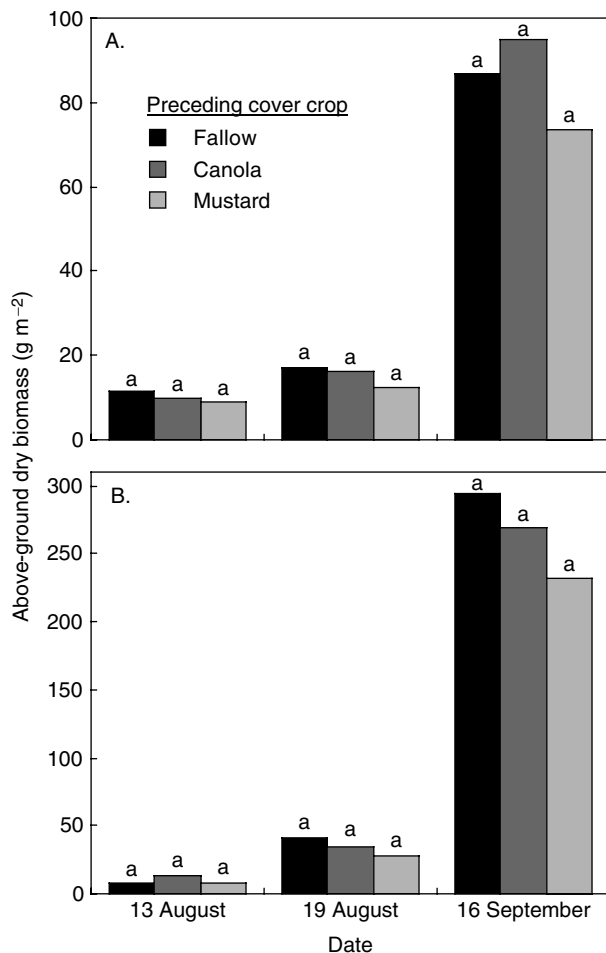
Figure 2. Effect of incorporated low-glucosinolate (canola) and high-glucosinolate (mustard) brassica cover crop residues on above-ground dry biomass of green bean (A) and redroot pigweed (B) subsequently grown in a mixture at fixed densities in 2002; results were similar in 2003. Within each harvest date, means with the same lower-case letter were not significantly different ($P > 0.05$)[66].

the growth of established individuals. The similar effects of the brassica and non-brassica residues on establishment contradict results from several other field studies, which suggest that the impacts of brassicas on weed suppression are greater than those provided by other cover crops[22,23]. These discrepancies highlight the variable nature of residue-mediated effects and emphasize the need to consider the complex relationships among management, species (cover crops, weeds and crops) and edaphic conditions.

Management Strategies and Considerations

Effects of environment and growth stage on glucosinolate production

Some brassicas, including canola, are selected to have low concentrations of glucosinolates in their seeds, and generally have lower concentrations in the vegetative tissue as well[46,77,78]. However, environmental and soil characteristics, as well as management practices, may produce plants with higher and more variable levels of glucosinolates[45,46,79]. A comparison of single-low and double-low rapeseed cultivars found that stems of one double-low cultivar contained a glucosinolate concentration similar to that of the single-low cultivar—over twice the concentration found in the other double-low cultivars[46].

Fertilization with nitrogen and phosphorus increases brassica biomass production and may also increase glucosinolate production[79]. Phosphorus fertilization (60 kg P_2O_5 ha^{-1}) and high levels of nitrogen (132 kg N ha^{-1}) increased the glucosinolate content of a variety of forage brassicas by an average of 26%; the same amount of nitrogen at lower phosphorus levels did not affect glucosinolate production[79]. Both fertilization and drought conditions before or after flowering can lead to large increases in the concentration of glucosinolates in rapeseed seed[78].

Plant growth stage also affects glucosinolate content. Glucosinolate concentrations of brassica tissues usually decrease as the seeds germinate and seedlings grow[77]. However, plant biomass increases rapidly during this time, leading to a maximal glucosinolate *content* (the product of concentration and biomass) in the whole plant before flowering[43,46]. Not until glucosinolate concentrations were expressed on a per plant basis, rather than per unit biomass, was it realized that glucosinolates were being diluted by increasing biomass[71,80].

Growers seeking to use brassica cover crops for weed suppression would be most interested in the glucosinolate content per unit area. Maximal glucosinolate content for the entire plant typically occurs at maturity[46,77], but the plants are generally incorporated prior to this stage, to avoid potential problems with subsequent volunteer seedlings. Glucosinolate content of the vegetative tissues is maximal prior to flowering[43,46], although overall plant biomass at this stage is still relatively low. Thus, growers face a trade-off—incorporate smaller amounts of biomass with the highest glucosinolate content, or wait until flowering has progressed to incorporate more biomass with less glucosinolates. The particular goals of the farmer would aid in making this decision.

Types of effective glucosinolates

Different brassicas have different glucosinolate profiles[30,41–43], which may contribute to the conflicting results of some studies, as different glucosinolate hydrolysis products may have different effects on seed germination and seedling growth (Table 1). In addition, not all brassicas release isothiocyanates; the predominate volatiles released from leaves of certain turnip and rapeseed varieties were the fatty acid derivatives, *cis*-3-hexen-1-ol and *cis*-3-hexen-1-yl acetate[42]. Other studies have identified *trans*-β-ocimene as the dominant volatile in certain Indian mustards, and verbenone as the dominant volatile in black

mustard[81]. Effects of these secondary compounds on seedling germination and growth are largely unknown[81].

Both volatile and water-soluble compounds have been implicated in suppressing seed germination[60], although hydrolyzing brassica tissues is sufficient to remove volatile compounds. Water-soluble compounds from hydrolyzed leaf and stem tissue of rapeseed completely inhibited the germination of lettuce seeds, while water-soluble root extracts from the same hydrolyzed tissues caused only a delay in germination[60]. Only volatiles from intact tissues affected germination, causing a delay, as well as a reduction in lettuce seed germination[60]. Under field conditions, volatiles from brassica residues are extremely short-lived (see below) and water-soluble compounds leached from the residues would likely have the largest impact on germinating seeds.

Limited soil life of glucosinolate hydrolysis products

Glucosinolate hydrolysis products tend to be very ephemeral and do not persist in the soil environment[50,59,69]. After incorporation of brassica residues, release of isothiocyanates is rapid, with concentrations dropping to less than half of the maximum by 72 h[50]. When isothiocyanates are applied directly, as opposed to being applied in glucosinolate form or in residues, the disappearance is even more rapid. For example, the half-life of 2-phenylethyl isothiocyanate applied to soil was approximately 1 h; it was completely undetectable after 91 h[82]. Morra and Kirkegaard[50] measured isothiocynates in soil 24 h after the incorporation of Indian mustard or rapeseed residues. The Indian mustard plots averaged 1.2 nmol isothiocyanate g^{-1} soil, while plots with incorporated rapeseed residue averaged 0.8 nmol isothiocyanate g^{-1} soil, concentrations similar to those found by Gardiner et al.[83] following incorporation of rapeseed residues. However, it is notable that these concentrations are more than an order of magnitude less than those found to inhibit seed germination (Table 1) and seedling growth in laboratory settings[12,15,58,59].

The low concentrations of isothiocyanates found in the soil following incorporation of brassica residues are partially due to the low release efficiency of biologically active breakdown products from glucosinolates. For example, soil concentration of isothiocyanates represented only 0.1–1.0% of the glucosinolate pool following incorporation of Indian mustard and rapeseed residues[50,84]. Other studies have shown similarly low conversion rates of glucosinolates to isothiocyanates and other hydrolysis products[83,85,86]. These studies suggest that the limiting factor in determining isothiocyanate evolution into soil is not the glucosinolate content of the plant, but release efficiency of the hydrolysis products. Practices that further disrupt plant tissue at, or before, incorporation may increase the release of isothiocyanates. Morra and Kirkegaard[50] found that freezing residues caused more cellular disruption and led to a greater release efficiency of isothiocyanates; frozen leaf discs of Indian mustard released 39 nmol isothiocyanates g^{-1} soil in a moderately dry soil. Release of isothiocyanates from these frozen leaf discs was greater in waterlogged soils, with a concentration of 75 nmol isothiocyanates g^{-1} soil. However, release of isothiocyanates does not ensure bioavailability. Glucosinolate hydrolysis products released from macerated tissue may react with organic matter in the tissue itself and may not be released into the environment[87]. Soil characteristics, particularly organic matter and clay content, also affect both the types of compounds released upon glucosinolate hydrolysis, but also, perhaps more importantly, on the adsorption of these compounds to soil particles[87].

Release of glucosinolate hydrolysis products may occur rapidly following incorporation of residues; alternatively, they may be slowly exuded from roots of living plants or leached from dropped leaves on the soil surface. Dyer's woad released indolyl glucosinolate compounds from its roots[71]; canola released 2-phenylethyl isothiocyanate into its rhizosphere[82]. Soil sampled from pots containing a low-glucosinolate rapeseed cultivar contained 24 ng allyl isothiocyanate g^{-1} soil, while soil in pots containing wild-type rapeseed contained 60 ng allyl isothiocyanate g^{-1} soil[70]. Because the soil was sampled without incorporated plant residues, isothiocyanate was presumably released from the growing roots. The slow and steady release of isothiocyanates may keep soil concentrations at levels effective for suppressing pathogens and reducing seed germination.

Effects on beneficial organisms

Nitrifying bacteria, rhizobacteria and mycorrhizae are often desirable in agricultural soils, especially those in systems with reduced external inputs. Plant secondary compounds that harm fungal pathogens and reduce seed germination might also be expected to harm the organisms that are beneficial, and often essential, to healthy agricultural soils. Daily applications of low concentrations (<4 nM) of 2-phenylethyl isothiocyanate were sufficient to change the active portion of the soil microbial community composed of bacteria and eukaryotes[82]. These results indicate that brassica residues could affect critical microbial processes, including nitrification, nitrogen fixation and mycorrhizal symbioses.

Nitrogen mineralization from brassica residues is slower than predicted by their C:N ratio, suggesting that glucosinolate hydrolysis products inhibit the actions of soil microbes involved in nitrogen cycling[34]. Populations of both ammonium-oxidizing and nitrite-oxidizing bacteria were adversely affected by applications of isothiocyanates, with soil- and isothiocyanate-specific effects on growth rate and population levels[88]. Nitrification capacity was reduced by 35–65% following 10 µg applications of different isothiocyanates to 1 g of soil[88], while addition of 0.5 µg of 2-propenyl isothiocyanate g^{-1} dry soil was sufficient to completely inhibit nitrification[89]. This latter concentration is similar to those that inhibited seed germination and seedling growth (Table 1), but still higher than that found in

the soil following residue incorporation[50]. Isothiocyanates also acted synergistically with volatile sulfur compounds (including dimethyl sulfide) to cause greater inhibition of nitrification[88].

Compounds harmful to microbes may also affect beneficial rhizobacteria (*Rhizobium* spp.) that form root nodules on legumes, assimilating atmospheric nitrogen in the well-known symbiotic association. For example, nodulation of green peas following incorporated white mustard residue was reduced compared to those following fallow[26]. As soil nitrogen concentrations were not reported, these observational differences cannot be attributed solely to the presence of white mustard residues. However, Scott and Knudsen[76] found that green peas grown in soil with incorporated rapeseed residues had similar numbers of nodules to those grown in soil with no residues, and that carbon utilization was similar between rhizobacteria from these two groups. Rhizobacteria isolated from green pea plants grown in soil with rapeseed residues were similar to those isolated from soil without residue[76]. Adverse affects on pea growth, including reduced germination, poor root development and shorter plants, were noted in both of these experiments, as well as by other researchers[90].

Mycorrhizae are very important for healthy plant growth in agroecosystems, although plants in the *Brassicaceae* do not form mycorrhizal associations[91]. Despite the potent anti-fungal properties of glucosinolate hydrolysis products, there does not seem to be a consistent effect of brassicas on mycorrhizal spore germination, or the mycorrhizal infection of nearby plants. Compared to those near tomato (*Lycopersicon esculentum* Mill.) and tobacco (*Nicotiana tabacum* L.) roots, vesicular arbuscular mycorrhizal (VAM) hyphae near brassica roots had fewer germ tube branches and fewer hyphal tufts, suggesting that they may be harmed by compounds leaching from brassica roots[92]. Onions (*Allium cepa* L.) grown in the same pot as swede (*Brassica napus* L.) had a smaller percentage of root length infected by mycorrhizae[93]. This evidence conflicts with other studies that have demonstrated that mycorrhizal plants grown with brassicas are not affected[94]. In addition, there is typically no effect on mycorrhizal infection by brassicas in rotation with mycorrhizal plants[92,94–97]. While isothiocyanates are capable of killing certain species of VAM fungi, other VAM species may have the capacity to detoxify glucosinolates, as these fungi differ widely in their response to anti-fungal compounds[92]. Other non-brassicaceous plants that release glucosinolates from their roots, including papaya (*Carica papaya* L.) and nasturtium cress (*Tropaeolum* spp.), do form mycorrhizal associations, suggesting that the glucosinolates themselves are not toxic to all mycorrhizae and that other mechanisms prevent brassicas from forming this association[91].

Conclusions

Brassica cover crops have been suggested as a possible solution to many pest problems in agricultural and horticultural systems. Considerable evidence of the negative effects of brassica residues on seed germination and growth supports the idea that brassica cover crops can be used as 'biofumigants'. Suppression of weed density and weed biomass in field experiments further bolsters this idea. However, mechanisms behind this observed effect on weed communities in different crops remain unknown, as our recent field studies in Maine failed to find support for hypotheses that brassica residues would: (1) provide additional suppression of seedling recruitment beyond that provided by other non-brassicaceous cover crops; and (2) reduce the growth of established plants. Clearly, many factors influence the pest-management potential of brassicas, and earlier suggestions that brassica cover-cropping systems may be 'tailor-made' to specific pest problems may prove to be both overly optimistic and too difficult to be practical to growers. Brassica cover crops do have a place in low-input farming systems as substitutes for other, more conventional cover crops. Their ability to suppress soil-borne disease pathogens may prove extremely beneficial. Although their effects on beneficial mycorrhizae, rhizobia and free-living nitrogen-fixing bacteria must be considered, evidence suggests that brassica residues will not cause significant harm to these beneficial biota. As with most tactics utilized in low-input farming systems, multiple benefits may result from their use, but it remains important to use multiple tactics for a strong program of weed management.

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