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Allelopathic Weed Suppression Through the Use of Cover Crops

Jessica Kelton[1], Andrew J. Price[2] and Jorge Mosjidis[1]
[1]*Auburn University*
[2]*United States Department of Agriculture*
USA

1. Introduction

There has long been observed an inhibitive response by plant species to certain neighboring plants. The Greek philosopher and botanist, Theophrastus, noted this effect from cabbage as early as 300 BC (Willis 1985). Since that time, others have documented similar plant interactions. In 1937, Austrian botanist, Hans Molisch, described this phenomenon as allelopathy, which he determined to be the result of biochemical interactions between plants (Molisch 1937; Putnam and Duke 1978). When first described, allelopathy referred to both deleterious and beneficial interactions between species; since that time, however, allelopathy has been applied to only adverse plant interactions, rather than to both. First described by a Roman scholar during the first century, black walnut (*Juglans nigra* L.) has long served as the common example of allelopathic effects with its ability to inhibit growth of surrounding plants either through decaying leaves or nuts or from the tree itself (Weir et al. 2004). Researchers have continued to examine allelopathy and the mechanism for biochemical inhibition, which was initially scrutinized by many since differentiation between this effect and plant competition remained uncertain (Weir et al. 2004). Subsequent bioassays involving specific chemical compounds extracted from plants have confirmed that certain species do, in fact, produce biochemicals that can inhibit plant germination and growth in the absence of resource competition (Einhellig 1994a).

With confirmation of allelopathy, many investigations have been conducted in order to determine how best to utilize this effect for possible weed control in agricultural settings (Khanh et al. 2005; Olofsdotter 2001; Weston 1996). The ability to inhibit weed growth through the implementation of cover crops into a crop rotation has been a focal point for this research for several reasons. In addition to weed suppression and control through allelopathy, as well as a mulching effect, cover crops provide substantial environmental benefits such as reduced erosion and water runoff (Price et al. 2006; Truman et al. 2003). Moreover, cover crops are readily available and easily adapted to many agricultural situations. Because of these many benefits, including natural weed suppression through allelopathy, the use of cover crops has become a vital component of sustainable agriculture systems, as well as organic production.

Ensuring sufficient food and fiber production for future generations can be hampered by limited options for weed control, particularly in developing countries where yields are reduced by up to 25% by weed competition. Identifying and describing sustainable weed control measures that can be implemented to reduce weed pressure in a number of settings can help safeguard the productivity of agriculture. Therefore, the objectives of this chapter are to describe the fundamentals of allelopathy and how to utilize allelopathic compounds for weed control through cover crop use. The chapter also highlights many of the identified biochemicals, their structures, and the respective cover crops in which they are found. Lastly, we describe the degree of allelopathic potential for a number of cover crops, as determined by laboratory testing.

2. Production and release of allelopathic compounds

Allelochemicals enter the environment from plants in a number of ways, such as plant degradation, volatilization, leaching from plant leaves, and from root exudation (Bertin et al. 2003; Weir et al. 2004). During active plant growth, particularly in early growth stages or during periods of stress, root exudation, either through diffusion, ion channels, or vesicle transport, is the primary method for release of many organic and inorganic compounds into the rhizosphere (Battey and Blackbourn 1993; Uren 2000). These compounds serve a multitude of functions such as improving nutrient uptake, root lubrication, plant growth regulation, microorganism defense, and waste removal (Bertin et al. 2003; Fan et al. 1997; Uren 2000).

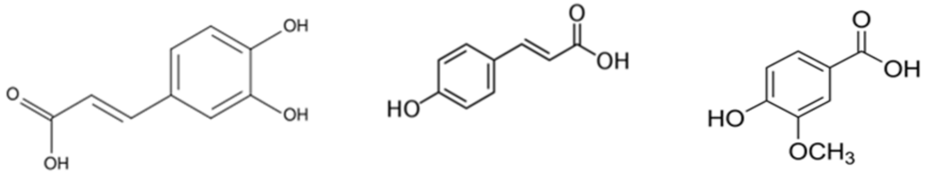
A large proportion of identified allelochemicals are noted to be secondary compounds formed during photosynthetic processes (Einhellig 1994b; Swain 1977). Since many allelopathic chemicals appear to perform no primary metabolic functions, although some compounds such as cinnamic acid and salicylic acid do serve other functions within a plant, it is unclear at this point as to what regulates the release of these compounds (Einhellig 1994a). Many environmental plant stressors have been observed to increase allelochemical release but not necessarily chemical production (Bertin et al. 2003; Inderjit and Weston 2003; Sterling et al. 1987). Plant stressors such as elevated temperature, reduced water availability, and herbivory may cause increased allelochemical release; however, a definitive correlation between environmental factors and allelopathic compounds has yet to be made (Bertin et al. 2003; Pramanik et al. 2000). Continued research directed at isolating and identifying individual root exudates while manipulating environmental stress factors may help to increase our understanding of allelochemical release into the rhizosphere.

3. Allelopathic compounds

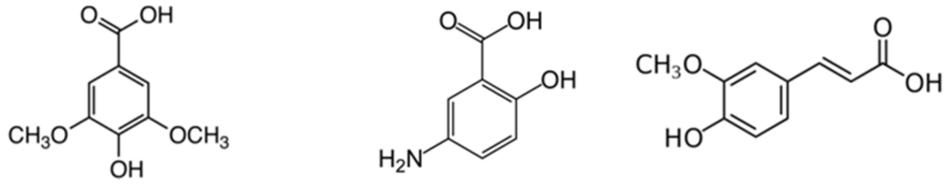
Many allelochemicals have been identified since experiments began to isolate and determine allelopathic potentials of plant compounds. Compounds that have been identified thus far include a variety of chemical classes such as phenolic acids, coumarins, benzoquinones, terpenoids, glucosinolates, and tannins (Chung et al. 2002; Putnam and Duke 1978; Seigler 1996; Swain 1977; Vyvyan 2002). These and other allelochemicals are found in many plant species from woody to herbaceous plants, grasses and broadleaves, weeds and crops. There are many details left to be determined such as regulation and production stimuli and mode of action for inhibition. It is also not readily understood to what extent allelopathic compounds interact with each other and other chemical compounds within the rhizosphere to inhibit surrounding plants. The following sections present several of the structural classes of recognized allelochemicals as well as specific compounds within each group.

3.1 Phenolic acids

Like most allelochemicals, phenolic acids are secondary plant compounds typified by a hydroxylated aromatic ring structure. To date, a number of phenolic acids have been determined to have allelopathic properties and have been measured in extracts from a variety of plant species (Figure 1). Species which have been noted to produce phenolic acids include: rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), mango (*Mangifera indica* L.), and spotted knapweed (*Centaurea stoebe* L.) (Bais et al. 2003; Chung et al. 2002; El-Rokiek et al. 2010; Fitter 2003). Many species, such as rice, contain multiple phenolic compounds along with other allelopathic compounds. In two studies, researchers isolated nine individual phenolic acids from rice hull extracts and 14 different phenolic acids from buffalograss [*Buchloe dactyloides* (Nutt.) Engelm] (Chung et al. 2002; Wu et al. 1998). At this time, however, it is not clear to what degree individual allelochemicals interact to produce plant inhibition. Some reports show a synergistic effect when allelochemicals are in a mixture, while other studies indicate decreased plant inhibition in the presence of a mixture when compared to individual chemical inhibition (Chung et al. 2002; Einhellig 1996).



Caffeic acid
Coumaric acid
Vanillic acid



Syringic acid
p-hydrobenzoic
Ferulic acid

Fig. 1. Phenolic acids identified in many plant species, such as oat (*Avena sativa* L.) and rice (*Oryza sativa* L.), have been found to have allelopathic properties.

Although modes of action for allelopathic chemicals are not readily understood for each identified allelochemical, phenolic acids have been the focus of many studies designed to establish the basis of their allelopathy (Putnam 1985). Early research with phenolic acids indicated that some phenolic acids could function though increasing cell membrane permeability, thus affecting ion transport and metabolism (Glass and Dunlop 1974). More recent studies report disruption of cell division and malformed cellular structures in plants exposed to phenolic acids (Li et al. 2010). Reduced respiration and reduced photosynthetic rates, due to decreased photosynthetic products such as chlorophyll, have also been reported in the presence of phenolic acids (Patterson 1981; Yu et al. 2003). Other studies have cited altered plant enzymatic functions, inhibited protein synthesis, and inactivated plant hormones as inhibitory mechanisms from these allelochemicals (Batish et al. 2008; Li et al. 2010). Each mechanism of plant inhibition can lead to the reduced growth and/or death of an exposed plant; however, it is likely multiple functions within a plant are being affected simultaneously due to the mixture of allelochemicals released from a plant species. Despite the extensive research with phenolic acids, target sites for allelochemical activity within affected plant species remain to be determined for many phenolic compounds.

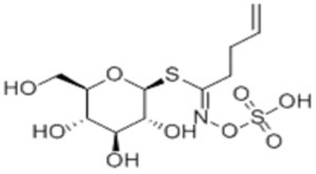
3.2 Glucosinolates

Glucosinolates occur in many plant species, but are widely known to be produced by species within the Brassicaceae family (Figure 2) (Haramoto and Gallandt 2005; Malik et al. 2008; Mithen 2001). Members of this family include: wild radish (*Raphanus raphanistrum* L.), white mustard (*Sinapis alba* L.), turnip (*Brassica campestris* L.), and rapeseed (*Brassica napus* L.). Glucosinolates, secondary metabolites containing sulfur and nitrogen, are enzymatically hydrolyzed by myrosinase in the presence of water to form isothiocynates, the active allelochemicals (Haramoto and Gallandt 2005; Norsworthy and Meehan 2005; Petersen et al. 2001; Price et al. 2005). Previous research examining extracts from glucosinolate-producing plant species have shown inhibition of other species through reduced germination, reduced seedling emergence and reduced size, as well as delayed seed germination (Al-Khatib et al. 1997; Brown and Morra 1996; Malik et al. 2008; Norsworthy et al. 2007; Wolf et al. 1984). Although specific modes of action have not been thoroughly investigated for each compound, it is evident that some plant species are able to tolerate these allelochemicals more readily than other species (Norsworthy and Meehan 2005). Some suggest that seed size variability plays a role in determining inhibitory effects of these allelochemicals; however, this may not be the only determinant for tolerance to these compounds (Haramoto and Gallandt 2005; Westoby et al. 1996). Future research with these allelopathic compounds will likely seek to answer this question, along with identifying the mode of action for plant inhibition, in order to utilize these compounds more effectively in agricultural production.

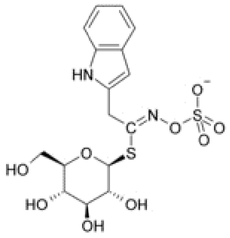
3.3 Coumarins

Coumarin compounds (Figure 3) are found in a range of plant species, particularly from the Apiaceae, Asteraceae and Fabaceae families (Razavi 2011). Coumarins and their derivatives have been identified in plants such as lettuce (*Lactuca sativa* L.), wild oat (*Avena sativa* L.), sweet vernalgrass (*Anthoxanthum odoratum* L.), and a number of other species (Abenavoli et al. 2004; Razavi 2011). Like many other allelochemicals, coumarins have been found to inhibit plant growth by reduced seedling germination and reduced root and shoot growth, likely with interference in photosynthesis, respiration, nutrient uptake and metabolism (Abenavoli et al. 2001; Abenavoli et al. 2004; Razavi et al 2010; Yamamoto 2008).

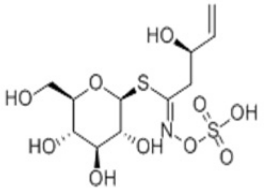
In addition to plant inhibition, biological activity of coumarins includes antibacterial, nematicidal, antifungal, and insecticidal activity; moreover, pharmacological activity of coumarins has been commonly noted in a number of instances with specific compounds functioning to reduce edema and inflammation (Casley-Smith and Casley-Smith 1992; Hoult and Paya 1996; Maddi et al. 1992; Razavi 2011). The broad activity of these compounds has made pharmaceutical use difficult due to the potential for non-target activity. Although allelopathic research has yet to indicate that the broad spectrum activity of coumarins could limit future use of these compounds for weed control, this may require further investigation as research moves forward.



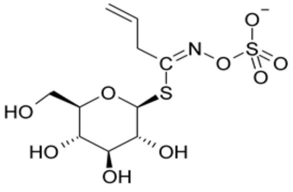
Gluconapin



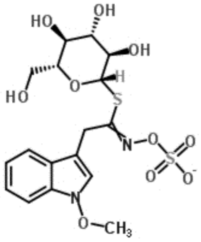
Glucobrassicin



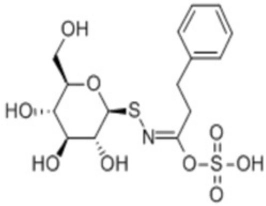
Progoitrin



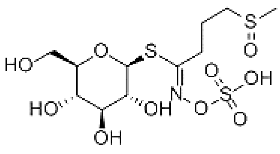
Sinigrin



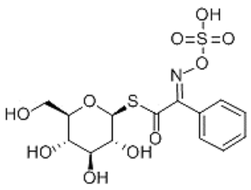
Neoglucobrassicin



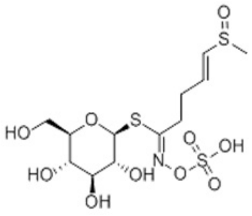
Gluconasturtin



Glucoiberin

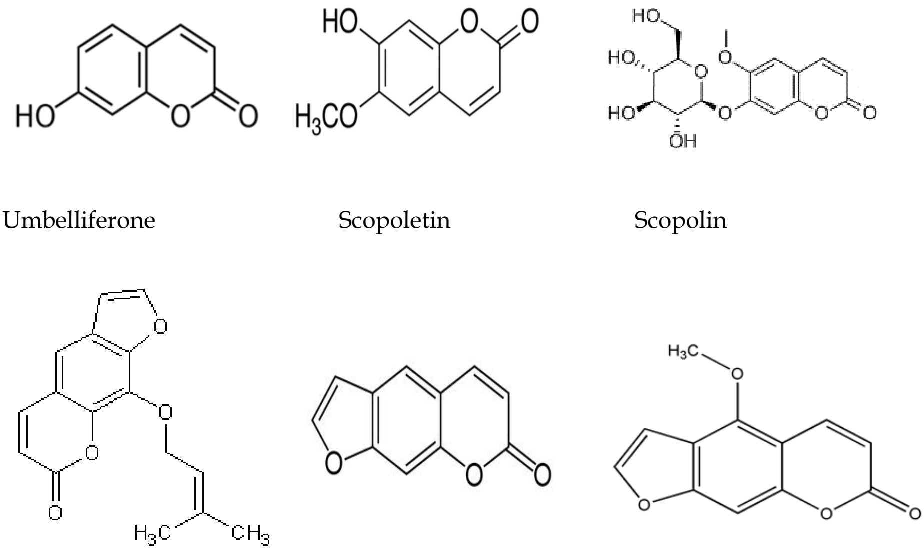


Glucotropaeolin



Glucoraphenin

Fig. 2. Glucosinolates, allelopathic compounds known to be produced by plants in the Brassicaceae family as well as other families, are produced in both the root and shoot regions of plants.



Umbelliferone

Scopoletin

Scopolin

Imperatorin

Psoralen

Bergapten

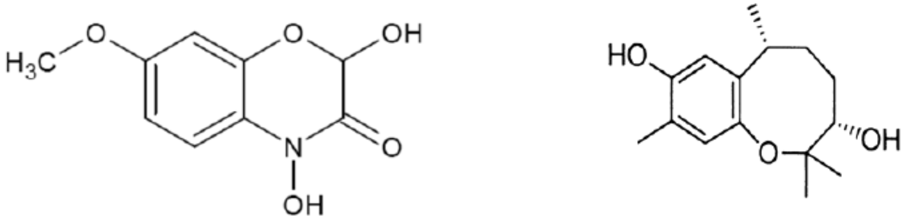
Fig. 3. Coumarins and their subgroups have been identified as allelopathic compounds in several plant families including Apiaceae and Fabaceae.

3.4 Other allelopathic compounds

Many other allelochemicals have been detected in a wide range of species; however, a few compounds have been more widely researched. Classes of allelochemicals under thorough investigation, such as the benzoxazinoids, heliannuols, and benzoquinones, offer potential benefits for weed control in agricultural systems (Figure 4) (Macias et al. 2005; Vyvyan 2002). These classes, described briefly below, represent only a few of the many other compounds that may one day provide substantial weed suppression through allelopathy.

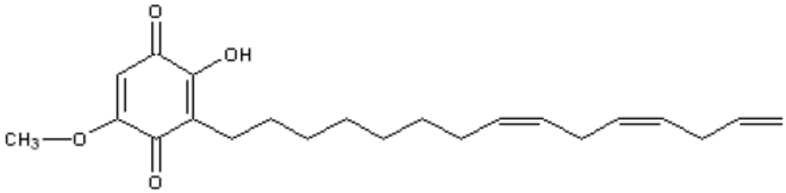
Benzoxazinoid compounds, identified in cereal grains such as wheat and rye, include DIBOA [2,4-dihydroxy-(2*H*)-1,4-benzoxazin-3(4*H*)-one] and DIMBOA [2,3-dihydroxy-7-methoxy-(2*H*)-1,4-benzoxazin-3(4*H*)-one] (Burgos and Talbert 2000; Macias et al. 2005). These compounds are easily degraded into other allelopathic forms, BOA (2-benzoxazolinone) and MBOA (7-methoxy-2-benzoxazolinone), within the soil and can diminish plant germination and growth (Barnes et al. 1987; Burgos and Talbert 2000). In light of the allelopathic properties of BOA and MBOA, it is now recognized that continued research efforts are needed to understand the role of breakdown products of initial allelochemicals in inhibiting plant growth (Macias et al. 2005).

From the sunflower plant (*Helianthus annuus* L.), several compounds have been identified as being allelopathic (Leather 1983; Vyvyan 2002). The heliannuols are classified as phenolic sesquiterpenes and are noted for allelopathic as well as pharmacological activity (Vyvyan 2002). In addition to having been isolated from the sunflower, similarly structured compounds have been detected in animal species as well (Harrison and Crews 1997). Most notable about heliannuolic compounds is their ability to suppress plant growth at relatively low concentrations. Although they have been shown to inhibit growth of many broadleaf weed species, heliannuols appear to have a stimulating effect upon monocotyleden species (Weidenhamer 1996; Vyvyan 2002). This aspect of heliannuol activity may prove difficult when developing weed control applications of these compounds.



DIMBOA

Heliannuol A



Sorgoleone

Fig. 4. Compounds, such as DIMBOA, heliannuol A, and sorgoleone, continue to be studied for their allelopathic properties.

Benzoquinone compounds, primarily sorgoleone, isolated from sorghum [*Sorghum bicolor* (L.) Moench], have also been determined to be highly allelopathic (Netzly et al. 1998). Research with this compound indicates plant growth inhibition is achieved through disruption of photosynthesis as well as reduced chlorophyll development (Einhellig and Souza 1992). Like some other compounds, sorgoleone exhibits selective activity with inhibition of many germinating seedlings but little activity against certain species such as morningglory (*Ipomoea spp.*) (Nimbal et al. 1996). Research conducted with sorghum root exudates compares sorgoleone activity to that of the herbicide, diuron, but has many target sites (Nimbal et al. 1996; Rimando et al. 1998). Thus far, characteristics of sorgoleone show that it is a promising compound for development into a natural herbicide as an alternative to synthetic herbicides.

4. Weed control through allelopathy

Ongoing research into allelopathy seeks to better understand the mechanisms of allelopathy in order to make use of these naturally occurring weed suppressants within agricultural areas. Benefits offered by employing allelopathy as some form of weed control could aid in developing more sustainable agricultural systems for future generations (Einhellig 1994a). Current efforts focus primarily on natural herbicide production and cover crops. Although these concepts are being utilized to some degree, there remains a great deal of research to fully utilize the potential of allelopathy.

The role of naturally derived compounds, or synthetically produced mimics, for use as pesticides has been widely adopted, particularly for insect control. Several plant derived compounds, such as pyrethrum, neem, and nicotine, are important chemicals for insect control in many areas (Isman 2006). Herbicide potentials of isolated plant extracts have been indicated by a number of researchers but to date, few have been marketed. Synthetic compounds, such as cinmethylin, and mesotrione, were developed based upon plant-derived allelochemicals, but release of subsequent plant-based herbicides has lagged (Lee et al. 1997; Macias et al. 2004; Secor 1994; Vyvyan 2002). Slow production and release of herbicides developed in this manner are most likely attributed to limited understanding of the modes of action for many identified allelochemicals. To date, a number of allelochemicals have been isolated and investigated to develop natural herbicides with these compounds. Understanding the mode of action for plant inhibition may aid in the development of new products for the market.

A great deal of research has been devoted to the use of cover crops for weed control. Until recently, however, the allelopathic potential of cover crops has received less attention due, in part, to the lack of knowledge about allelopathy in general. As the functions of allelopathic compounds are beginning to be understood, more focus is being given to the allelochemicals within cover crops. In agricultural settings, cover crops have been in use for a number of years as a ground cover to slow erosion and water runoff as well as to impede germination of weed seed by providing a physical barrier (Kaspar et al. 2001; Price et al. 2008; Sarrantonio and Gallandt 2003). The growing need for sustainable agricultural systems has necessitated increased cover crop research to better utilize these covers for effective weed control. As a result, recent investigations have sought to understand the role of allelopathy for weed suppression within various cover crops (Burgos and Talbert 2000; Khanh et al. 2005; Price et al. 2008; Walters and Young 2008).

5. Allelopathic potential of cover crops

Determining allelopathic potential of exudates of plant species can be difficult and time consuming to complete. Bioassays are generally conducted to identify allelopathic properties of compounds in order to differentiate between allelopathy and mulching effects. Our research has focused on determining the extent of allelopathic effects of available cover crops on weed species as well as crop species. Extract-agar bioassays conducted with radish

(*Raphanus sativus* L.), an indicator species, and cotton (*Gossypium hirsutum* L.) established levels of inhibition for radicle elongation by extracts from cover crops, primarily legumes and cereal grains.

Legume cover crops have the ability to fix atmospheric nitrogen that potentially provides a nitrogen source to the subsequent crop without the need for additional fertilizer applications (Balkcom et al. 2007; Hartwig and Ammon 2002). Legume species such as vetch (*Vicia villosa* Roth), clover (*Trifolium spp.*), black medic (*Medicago lupulina* L.), and winter pea (*Pisum sativum* L.) are typically used as cover crops in agricultural production in the United States (Figure 5) (SARE 2007). Other legume crops beginning to be researched as possible choices for cover crops are sunn hemp (*Crotalaria juncea* L.) and white lupin (*Lupinus albus* L.); however, their availability and use are not as widespread as the previously mentioned legumes. In addition to being a nitrogen source for primary crops, legume covers provide a weed control potential. Due to the rapid degradation of legume residue on the soil surface in comparison to cereal grain residue, weed control through a physical barrier may not last as long into the season as other cover crops.

Fig. 5. Legume cover crops, such as white lupin (in mixture with black oats), provide weed suppression and nitrogen benefits to the subsequent cash crop.

Determining allelopathic effects of legume cover crop extracts concluded that legume covers did inhibit radish and cotton radicle elongation; however, cotton root exhibited less inhibition than that of radish for all included crops (Price et al. 2008) (Figure 6). In our research, hairy vetch had the greatest inhibition while winter pea had the least effect on germinating seedlings. It is important to note that different varieties of cover crops are available for use in agricultural systems and the varieties of one species may differ in level of allelopathy. Although under field conditions, allelopathic performance of these species may fluctuate, it is apparent that these cover crops can provide additional weed control measures over systems that do not include a cover crop.

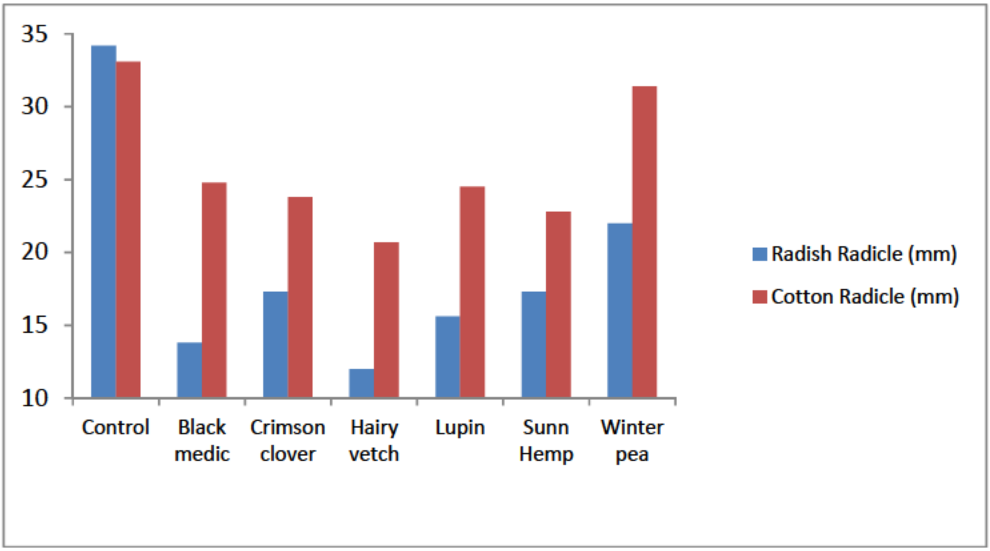


Fig. 6. Legume cover crops affect radicle elongation of different plant species to varying degrees.

Cereal grain crops such as black oat (*Avena strigosa* Schreb), rye, triticale (X *Triticosecale* Wittmack), and wheat, are utilized frequently in conservation systems as cover crops with effective ground cover and weed suppression (Figure 7). Rye is a commonly used cereal cover crop due to its ability to be sown later in the season while maintaining successful growth and its biomass production capability. With increased biomass on the soil surface, weed suppression will be increased as well. Cereal crops will also decay more slowly than more herbaceous plant species and provide some ground cover, and allelochemical release, further into the growing season. Additionally, rye has been noted to be less affected by plant diseases than other cover crops, and aids in reducing insect pests within a system (Wingard 1996).

Like legumes, cereal grain crop exudates in our study were able to significantly inhibit radicle elongation compared to the control (Figure 8). The disparity between radish and cotton radicle inhibition for each cover crop studied suggests that minimized interference with primary crops and increased weed suppression potential could be achieved with the use of cereal grain crops. These allelopathic effects, however, may be amplified or diminished depending on the field environment, plant stress levels, cover crop variety, and a number of other factors involved in determining allelochemical levels. Nevertheless, this research provides a base of allelopathic concentrations and impacts from various cover crops and may be an initial consideration when choosing a cover crop for inclusion in a system.

Fig. 7. Cotton growing in rolled black oat residue. Cereal grain cover crops, like black oat and rye, can be utilized to achieve a large quantity of plant residue on the soil surface.

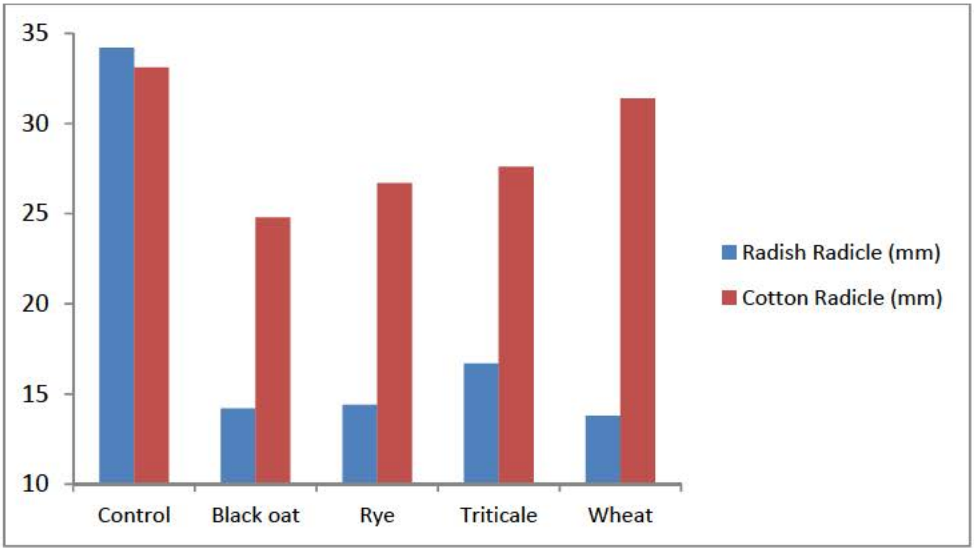


Fig. 8. Radish and cotton radicle elongation is reduced by cereal grain cover crops.

6. Conclusions

The growing demand for sustainable agricultural systems requires that researchers reevaluate current production methods and inputs. To ensure continued productivity and potentially reduce synthetic herbicide requirements, allelopathy has become a focal point for research in the agricultural community. Although, many questions have yet to be resolved, the utilization of allelochemicals for weed suppression remains a promising avenue for reducing herbicide usage. Whether through the development of natural herbicides from isolated allelochemicals or through the application of cover crops with allelopathic properties, allelopathy will most likely be a factor in providing sustainable systems in the future.

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