

Review

Allelopathic weed suppression in agroecosystems: A review of theories and practices

Michael Ignatius Ferreira¹ and Carl Friedrich Reinhardt^{2*}

¹Research and Technology Development Services, Western Cape Department of Agriculture, Private Bag X1, Elsenburg, 7607, South Africa.

²Department of Plant Production and Soil Science, University of Pretoria, Pretoria, South Africa.

Received 27 October, 2015; Accepted 27 January, 2016

Weeds cause great problems to humankind by interfering in food production, health, economic stability, and welfare. The overuse of synthetic herbicides for weed control eventually leads to the evolution of herbicide resistant weeds, which also resulted in growing public concern over their impacts upon human health. The intensification of arable farming has also had a simultaneous impact on the environment. This intensification of the landscape may disrupt natural processes, such as resistance to plant invasion. Therefore, the aim of this review is to address these production constraints by suggesting applications of allelopathy via smother cropping, because this may ease the incidence of herbicide resistance and in the process promote cultivated plant diversity and thereby maintaining healthy agroecosystems. Weed resistance to herbicides presents one of the greatest current economic challenges to agriculture. System-oriented approaches to weed management that make better use of alternative weed management tactics need to be developed. Plant roots exude a wide variety of metabolites, some of which may act as allelochemicals and mediate interactions between plants and other organisms. These metabolites are in essence chemicals from nature which may be exploited for weed management as an alternative weed control option. Smother crops, as well as its mulches, have been shown to release allelochemicals, which were inhibitory to weeds. The principal goal of smother crops is to control weeds by replacing an unmanageable weed population with a manageable smother crop. More data from the grey area where agriculture and ecology overlap will enable the greater use of ecosystem services for crop protection in agricultural production and consequently reduce the incidence of resistance to agricultural chemicals.

Key words: Agroecosystems, allelopathy, cultivated ecosystems, herbicide resistance, smother cropping, mulching.

INTRODUCTION

As pioneering plants, weeds fulfill very important ecological functions, *inter alia* those of colonisation and

stabilisation of bare soil in disturbed areas and thereby setting in motion the ecological process of plant

*Corresponding author. E-mail: mikefe@elsenburg.com. Tel: +27218085279.

succession. However, in agriculture, weeds are of concern because they compete with cultivated crop plants for growth factors (Vyvyan, 2002). Weeds are diverse in their habit and habitats throughout the world. Although they account for not more than 1% of the total plant species on earth, they cause great problems nevertheless to humankind by interfering in food production, health, economic stability, and welfare (Qasem and Foy, 2001). To counteract this, modern agriculture relies on synthetic chemicals to control weeds as unwanted plants, because they compete with cultivated crops for water, light, nutrients, and spaces and harbour pests and plant pathogens (Qasem and Foy, 2001).

Hartwig and Ammon (2002) reported that the discovery of synthetic organic herbicides for weed control in the late 1940s made reduced tillage practices more feasible, because tillage was not the only method of weed control anymore. Agricultural production increased in the 1950s and 1960s, because of increased fertiliser inputs, agricultural chemicals, and fossil fuels, but intensified production is still often associated with environmental pollution (Hartwig and Ammon, 2002). Due to the race for ever greater yields and profits which lead to the overuse of synthetic herbicides for weed control over the last six decades and eventually the evolution of herbicide resistant weeds, pollution was most probably inadvertently caused. This also resulted in growing public concern over their impacts upon human health and the environment (Vyvyan, 2002). Herbicide resistance in weeds threaten cropping system sustainability in many areas around the globe (Harker, 2013) and is a rapidly expanding phenomenon resulting in higher costs of production due to the greater weed impact (Efthimiadou et al., 2009). However, Lichtfouse et al. (2009) argued that while conventional agriculture is driven almost solely by productivity and profit, sustainable agriculture integrates biological, chemical, physical, ecological, economic, and social sciences in a comprehensive way to develop new farming practices that are safe and do not degrade our environment. Also, due to increased awareness about these risks involved in the use of synthetic chemicals, much attention is being focused on the alternative methods of weed control. To this end, Liebman and Davis (2000) and Barberi (2002) suggested that system-oriented approaches to weed management that make better use of alternative weed management tactics need to be developed. According to Khanh et al. (2005) cultivating a system with allelopathic crops plays an important role in the establishment of sustainable agriculture.

Fay and Duke (1977) suggested allelopathy as an alternative to herbicides and an aid for weed control. Allelopathic compounds can be released by live plants or when residues decompose and in general, this results in suppression of weed growth (Liebman and Mohler, 2001). In addition, it was reported by many authors (Belz,

2004; Batish et al., 2002; Khanh et al., 2005; Qasem and Hill, 1989) that when herbicide resistance develops, crop allelopathy can be exploited for weed management by the release of allelochemicals from intact roots of living plants and/or through decomposition of plant residues. According to Weston (1996), strategies to the goal of exploiting the allelopathic phenomenon to manage weeds comprise the use of phytotoxic crop residues or mulches, as well as phytotoxins released by intact roots of growing crop plants. The latter is often denoted by the term crop allelopathy and considered the most promising approach to exploit allelopathy in annual crops (Weston, 1996; Weston and Duke, 2003). Strategies for the implementation of crop residue allelopathy, entails the application of phytotoxic residues or mulches primarily generated by intercropping of allelopathic cover, smother, rotational, or companion crops (Wu et al., 1999). To maintain clarity and for ease of reference, the term 'smother crop' will be used throughout this review for the aforementioned cropping situations, thereby also bringing it in line with FAO (2008) policies.

Not only did herbicide resistance develop due to the overuse of synthetic chemicals, but the intensification of arable farming has also had a simultaneous impact on the other compartments of the environment: soil, water, and air (Médiène et al., 2011), although this was not immediately clear, but was only realised much later. Still, for both farmers and agronomists involved in agricultural production, a key question is how can petrochemical inputs in agroecosystems be decreased to limit their impact on the environment whilst maintaining the productivity and/or profitability of agriculture (Médiène et al., 2011). According to Paine and Harrison (1993), the answer lies in maintaining the productivity of the soil that feeds an ever increasing population which is essential to human needs. Although this provides an answer for the situation below-ground, it does not address above-ground production constraints.

Currently, there is growing evidence on these production constraints which suggest that high levels of synthetic chemical inputs in crop fields and natural habitat fragmentation due to changes in land use are major causes of the rapid decrease of biodiversity in many agricultural landscapes (Médiène et al., 2011). Tscharntke et al. (2005) reported that the main biodiversity losses are due to the transformation from traditional to modern, high-intensity land-use systems in simplified landscapes. This degradation and simplification of agroecosystems caused by the intensification of agricultural practices may affect important ecosystem services via the loss of biodiversity (Tscharntke et al., 2005). Agroecosystems thus have very low levels of biodiversity, and increasing diversity would probably add complementary elements and increase agroecosystem functioning and sustainability (Médiène et al., 2011). The biodiversity function, according to relationships with agricultural activities, describes resistance to biotic (that

is, weed invasions) and abiotic stress (that is, low water infiltration), and the production of cultivated ecosystems (Clergue et al., 2005).

From the discussed literature, it is clear that herbicides not only impacted negatively on weeds with the resultant involvement of herbicide resistance, but also on the environment within which crop production takes place. Therefore, the aim of this review is to address these production constraints by suggesting applications of allelopathy via smother cropping, because this may ease the incidence of herbicide resistance and in the process promote cultivated plant diversity and thereby maintaining healthy agroecosystems.

ALLELOPATHY THEORY

Less than two decades ago allelopathy was regarded as very much a theoretical field of study, but that has changed as continually new data became available and international efforts were coordinated. According to Duke et al. (2000), the natural plant products from higher plants and micro-organisms are biodegradable and eco-friendly, and some of these compounds can be relied upon to enhance crop productivity in a sustainable way. All plants apparently produce secondary metabolites that are phytotoxic to some degree and in a small number of cases their release into the environment and capability of causing allelopathic effects towards a number of noxious weeds have been demonstrated (Belz, 2004). These metabolites are in essence chemicals from nature which may be exploited for weed management, since their environmental toxicology profiles are often safer than synthetic herbicides (Duke et al., 2002). Most of the natural products involved with allelopathy are compounds of secondary metabolism that are synthesised by plants and micro-organisms, because the preferential utilisation of carbon sources in the soil may also affect the plant-microbe soil system and the allelopathic phenomenon (Singh et al., 2001).

Allelopathy is the phenomenon in which a plant produces biochemicals that affect the growth of either itself or other organisms (Liebman and Davis, 2000). Such products termed allelopathic compounds, have been shown to play a role in allelopathy, a term which has been broadened, according to Kazinczi et al. (2005), to include not only plant-to-plant, but also plant-to-micro-organism interactions. The International Allelopathy Society (IAS) has defined allelopathy as follows: 'allelopathy refers to any process involving secondary metabolites produced by plants, micro-organisms, and viruses that influence the growth and development of agricultural and biological systems' (Kruidhof, 2008).

Plant roots exude a wide variety of metabolites including carbohydrates proteins, vitamins, amino acids, and other organic compounds (Kong et al., 2008). Amongst the latter, in particular, those root exudate

components with low molecular weight, may act as allelochemicals and mediate interactions between plants and other organisms in the rhizosphere (Bertin et al., 2003). There is also clear evidence that they can affect crops through the production of toxic chemicals which have a harmful effect on crop growth and development (Qasem and Hill, 1989).

Crops and weeds can release allelochemicals by root exudation, volatilisation, or leaching from plant surfaces or decomposing residues (Belz, 2004). The release of phytotoxins by root exudation attaches the greatest importance in major crops, and the term crop allelopathy chiefly describes the application of allelopathy as a component of the interference of living crop plants with surrounding weeds. Allelopathy is a chemical-mediated process which may be stimulatory or inhibitory (Belz et al., 2005). Some substances, although toxic at higher doses, can be stimulatory or even beneficial at low doses (Duke et al., 2006). Furthermore, the interaction of allelochemicals with soil components upon release from the plant is important in determining whether inhibition of the target plant is likely to occur in the field (Blum, 1996).

Furthermore, allelopathic inhibition is typically the result of the combined action of a group of allelochemicals (Einhellig, 1996). Allelochemicals can be bound to soil organic matter or clay and become inactive (Daldon et al., 1983). These compounds affect soil micro-organisms in ways that significantly alter the ecology of the field where the allelopathic plant and their residues are present (Mamolos and Kalburtji, 2001). The release of phytotoxins by plants has been proposed as an alternative theory for the success of some invasive plants and they have long been suspected of using allelopathic mechanisms to rapidly displace native species (Bais et al., 2003).

HERBICIDE RESISTANCE

The golden era of herbicides was mostly in the period from the 1960s until 1980s when it was regarded as the final nail in the weed coffin, prompting its widespread and large-scale use. Humans have been trying for ages to control weeds effectively and this battle was thought to be won with the discovery of synthetic herbicides, because economically, agricultural efficiency and yields improved drastically. However, the reliance on herbicides did not consider the consequences from its continuous and uncontrolled use, namely the ability of live organisms to adapt to adverse environmental conditions (Gressel, 1991). Weeds contain inherent genetic traits that give them remarkable plasticity, allowing them to adapt, regenerate, survive, and thrive in a multitude of ecosystems (Chao et al. 2005). This resulted in the evolution of weeds with resistance to herbicides which refers to the capacity of a plant to grow and reproduce under the dose of herbicide that is normally lethal to the

species (Yuan et al., 2007). Initially, weeds have evolved slowly in response to ever-changing environments and crop production practices, but now, they are evolving much more quickly due to consistently repeated cropping systems and intense herbicide selection pressures (Korres and Norsworthy, 2015).

Widespread repeated use of synthetic herbicides has produced biotypes of weeds resistant to major herbicide classes (Wu et al., 2003). Weed resistance to herbicides presents one of the greatest current economic challenges to agriculture (Baucom, 2009) with more than 461 biotypes of weed known to be resistant to herbicides (Heap, 2015). The evolution of herbicide resistance further emphasised the need to exploit allelopathy as an alternative weed management option (Gealy et al., 2003). An alternative weed management strategy is integrating smother crops into current cropping systems. The inclusion of a smother crop in a production system has been shown to be an effective method for suppressing weeds and for improving soil chemical, biological and physical properties in various cropping systems (Price and Norsworthy, 2013). In addition, by including these crops, low levels of diversity in agroecosystem will obviously be improved.

AGROECOSYSTEMS

In previous centuries intensified agricultural production was preceded as standard procedure by an uncontrolled and unbridled clearing of land. In fact, large-scale deforestation and eradication of indigenous vegetation was at the order of the day and is in stark contrast with sustainable agriculture in mind. This most probably happened due to ignorance, but rather should have been the controlled and limited clearing of only highly productive land, leaving marginal and riparian zones in undisturbed and pristine condition to provide ecosystem services in a natural way to the benefit of humankind. This was also emphasized by Tscharntke et al. (2005) who suggested that a landscape perspective is needed to understand why agricultural land use has the well-known negative and less known positive effects on biodiversity and related ecosystem services.

According to Médiène et al. (2011) the decline in biodiversity may affect ecosystem functioning and yield, potentially threatening the provision of some services, such as biological pest control and pollination, whilst having a neutral effect on other functional groups. Landscape intensification may disrupt natural processes, such as resistance to plant invasion (Tscharntke et al., 2005). Indeed, evidence of this process is evident in many areas around the world where plant invasions have occurred.

Previous studies have shown that this diversification of cropping systems, modifies biotic and abiotic components and provides important services, such as capturing soil

nutrients and preventing their loss, nitrogen fixation by legumes, increasing soil carbon levels and associated improvements in soil physical and chemical characteristics, increasing biological activity and diversity and suppressing weeds and pests (Hartwig and Ammon 2002). A study by Bullock et al. (2007) also showed that the recreation of diverse fields of conservation value may provide a greater range of life forms and can have a positive impact on agricultural yield, benefitting the farm business. Promoting biodiversity in agroecosystems can increase their sustainability by improving ecosystem functioning, plant productivity increased with plant species richness, and plant diversity can have beneficial effects on pest control by encouraging the natural enemies of crop pests (Gaba et al., 2014).

PRACTICAL APPLICATIONS

Smother cropping

Smother crops and living mulches bring many benefits to crop production. Interest in winter annual smother crops such as winter rye and hairy vetch for ground cover and soil erosion has been increasing in the last 30 years (Hartwig and Ammon, 2002). Kohli et al. (2006) suggested cultural control methods which include crop rotation, use of smother and green manure crops, crop residues, crop genotypes with better competitive and allelopathic ability, manipulation of sowing or planting date, crop density and crop pattern to reduce reliance on particular herbicide groups. Of these cultural methods, the use of smother cropping (FAO, 2008) and mulching should receive more prominence as its application is lagging behind other cultural control methods as it might help to reduce reliance on particular herbicide types (Llewellyn et al., 2007).

The term smother crop refers to a dense and fast growing crop that suppresses or stops the growth of weeds and provides successful long-term weed management which, according to Storkey and Lutman (2008), requires a shift from simply controlling problem weeds with in-crop herbicides to agricultural production systems that are redesigned to manage weeds at all stages of their life cycle. Such systems should restrict weed emergence, reduce weed growth and reproduction, and minimise weed competition with crops.

The principal goal of smother crops is to control weeds by replacing an unmanageable weed population with a manageable smother crop. As weeds and living mulch plants compete for the same resources, weeds can be suppressed by introducing living mulches into cropping systems (Médiène et al., 2011). Smother crops may decrease weed infestations in three ways: (i) preventing weed seed germination and emergence, (ii) decreasing the number of seeds present in the weed seed bank in the soil by limiting seed recruitment, and (iii) increasing

seed predation (Phatak, 1992). Weed suppression by smother crops can be caused by multiple mechanisms, such as competition for space, light, water and nutrients (Dorn et al., 2015). Furthermore, smother crops as well as smother crop mulches, have been shown to release allelochemicals, which were inhibitory to weeds (Singh et al., 2003). One of the earliest reports on this topic was by Fay and Duke (1977) who found that some *Avena* species accessions contained an allelopathic agent that reduced annual weed growth and caused chlorosis, stunting and twisting when planted in close association.

Mulches and plant residues

Upon release into the crop environment, the nature and concentration of allelochemicals may change because of complex environmental conditions and microbial action (Batish et al., 2001). Wheat straw reduced weed densities and biomass by an average of 90% compared with those plots without residues (Putnam and DeFrank, 1983). Crop residues can, therefore, be very useful in maintaining the sustainability of agroecosystems, provided they are efficiently managed (Batish et al., 2002). McCalla and Norstadt (1974) showed that the water soluble substances in wheat residues reduced germination and growth of wheat seedlings. Wheat residues reduced the yield of the subsequent wheat crop. This was attributed to the fact that wheat contains a number of phenolic acids. Furthermore, Sozeri and Ayhan (1998) found in pot experiments, that mixing straw, which was gathered after harvesting, with soil, decreased germination of wheat seeds and increased seedling mortality.

The presence of white goosefoot (*Chenopodium album*) residual material in soil caused growth reduction of wheat, lettuce, lucerne, and various other crop species (Reinhardt et al., 1994). Rye (*Secale cereale* L.) root residues were found to be more suppressive than shoot tissues on growth and emergence of barnyard grass (*Echinochloa crus-galli* L. Beauv.) and growth of sicklepod (*Senna obtusifolia* L. Irwin and Barneby) (Brecke and Shilling 1996; Hoffman et al., 1996).

Apart from allelopathic effects, crop residues can exert an effect on weed germination and establishment through other mechanisms. The release of nutrients from the residues can stimulate weed germination (Teasdale and Pillai, 2005), whereas temporary immobilisation of nutrients from the soil upon decomposition of residues with high C: N ratios can have the opposite effect (Liebman and Mohler, 2001). Most reports dealing with residue-mediated inhibitory effects on receptor plants mention that plant residues decomposing in soil exhibit a progressive decline in phytotoxicity with the most severe inhibition occurring at the early stages (An et al., 2001; Xuan et al., 2005). Weed-suppressive effects of crop residues have been attributed to different mechanisms,

including initial low nitrogen (N) availability following cover crop incorporation (Dyck and Liebman, 1994; Kumar et al., 2008), mulch effects of a physical nature (Mohler and Teasdale, 1993), stimulation of pathogens or predators of weed seeds (Gallandt et al., 2005), and allelopathy (Weston, 1996). Leguminous crops that contain high levels of allelochemicals seem well-suited for residue-mediated weed suppression (Ferreira and Reinhardt, 2010) and can significantly reduce weed seed germination and may hamper seedling growth (Prati and Bossdorf, 2004). Allelopathic effects from crop residue tend to have more pronounced effects on small seeds (Liebman and Davis, 2000).

Satisfactory weed control can be achieved with high mulch depths (> 70 mm) (Marble, 2015). Although the mechanism responsible for weed control is not well understood for all mulch types (Chalker-Scott, 2007), for most weed species, control can be attributed predominantly to light exclusion (Teasdale and Mohler, 2000). Mulches can also act as a physical barrier to weed germination and growth (Marble, 2015). Certain mulch material, like rye (*S. cereale* L.), may also control weeds by leaching allelopathic chemicals (Chalker-Scott, 2007). Germination and growth of small-seeded annuals will suffer from restricted light availability, physical growth barriers and potential allelopathic effects from surface residue (Liebman and Davis, 2000). Surface residues change the chemical environment of the weed seed via allelopathy (Liebman and Davis, 2000). Although it can be effective, using crop residue as allelopathic weed control should be part of a larger weed management plan (Nichols et al., 2015).

Residue management appears to be a key factor in residue-mediated weed suppression (Kruidhof, 2008). Under field conditions, the effective concentration of stubble-derived chemicals at any point in time is greatly influenced by environmental factors (Purvis, 1990). For this reason, high levels of allelochemicals occur only sporadically in soils. However, if they are present at a sensitive physiological stage of plant development, such as seedling emergence, they can exert long-lasting detrimental effects with respect to crop productivity (Purvis, 1990).

Crop allelopathy

According to Belz (2007), crop allelopathy is currently understood as an interaction between a crop and a weed that is taking place in an environment that can significantly influence the whole process. Manipulation of this environment is mediated by several input production factors, and special adaptations might be needed for successful application of crop allelopathy (Belz, 2007). The trend towards conservation tillage, a widening range of crop rotation options and diverse production practices worldwide, has highlighted the potential exploitation of

Table 1. Interaction effects of target plants and allelopathic sunflower cultivars in percentage inhibition (Nikneshan et al., 2011).

Target plant	Sunflower cultivars	Germination inhibition (%)	Seedling mass inhibition (%)
<i>Lolium rigidum</i> Gaudin. (ryegrass)	Alison	44.7±(7.3)	55.6±(6.1)
<i>Lolium rigidum</i> Gaudin. (ryegrass)	Hysun36	10.4±(3.8)	2.9±(1.8)
<i>Lolium rigidum</i> Gaudin. (ryegrass)	Allstar	40.8±(11.1)	52.2±(1.6)
<i>Triticum aestivum</i> L. (wheat)	Alison	-9.6±(2.9)	42.9±(9.0)
<i>Triticum aestivum</i> L. (wheat)	Hysun36	-14.9±(2.6)	12.8±(7.8)
<i>Triticum aestivum</i> L. (wheat)	Allstar	8.2±(0.8)	31.6±(8.0)
<i>Portulaca oleracea</i> L. (common purslane)	Alison	9.1±(0.1)	8.9±(1.6)
<i>Portulaca oleracea</i> L. (common purslane)	Hysun36	5.3±(1.0)	-35.3±(4.2)
<i>Portulaca oleracea</i> L. (common purslane)	Allstar	22.4±(4.5)	-32.4±(3.7)

Standard errors are given in parentheses.

allelopathy for weed suppressions in cropping systems (Jones et al., 1999). Furthermore, the utilisation of allelopathy for weed management is likely to be most beneficial where other options have become limiting due to herbicide resistance and high control costs (Jones et al., 1999). Both the latter factors are serious constraints in the wheat producing areas of the Mediterranean climatic zone of South Africa.

Several wild accessions of modern day crops are found to possess allelopathic traits that impart in them resistance against weeds and pests (Hoult and Lovett, 1993). Field trials investigating crop allelopathy of rice (*Oryza sativa* L.) cultivars showed that crop allelopathy does not kill weeds (Olofsdotter et al., 1999; Olofsdotter, 2001), confirming that crop allelopathy is merely relevant for weed suppression. Available evidence revealed that crop cultivars differ significantly in their abilities to suppress certain weed species and indicates possible development of crop cultivars able to inhibit the growth of the principal weeds in a given area through allelopathic action and thus decrease the need for synthetic herbicides (Wu et al., 1999). The extracts of some sunflower cultivars reduced germination of *Portulaca oleracea* L., suggesting some cultivars may be effective in its control, while others not only had no negative effects but actually stimulated growth (Table 1) (Nikneshan et al., 2011).

Crop allelopathy can be exploited for weed management through the release of allelochemicals from intact roots of living plants and/or through decomposition of plant residues (Batish et al., 2002; Belz, 2004; Khanh et al., 2005; Qasem and Hill, 1989). Crop allelopathy is considered as one of the most promising approaches to impact herbicide use in crops (Duke et al., 2002). Chou (1999) found that allelochemicals can be released either through leaching from leaves, decomposition of residues or by root exudation.

Allelopathic crops when used in rotational sequences are helpful in reducing noxious weeds, improve soil quality and crop yield (Khanh et al., 2005). These crop plants, particularly the legumes, can reduce weed

infestation and increase rice yield by between 20 and 70%, and are suggested for use as natural herbicides (Khanh et al., 2005). Wheat (*Triticum aestivum* L.) is known to be allelopathic against crops and weeds (Alsaadawi et al., 1998). At present, however the evidence is that the nature of crop allelopathy does not allow for a sole reliance on this approach and, thus, planting a certain allelopathic cultivar will be just a component of an integrated weed management system (Wu et al., 1999).

DISCUSSION

As mentioned earlier, high intensity agricultural production resulted in unwanted side effects. Moreover, consequences of this intensive agriculture are now well known with an important increase of atmospheric CO₂ concentrations, water pollution and biodiversity loss. The current challenge is thus to design alternative sustainable cropping systems which maintain food production while reducing externalities (Gaba et al., 2014). Combining optimally integrated weed management tactics (Young, 2012) that discourage weeds with minimal disturbance (no-till, direct seeding), adopting diverse crop rotations and attempting to preclude resource acquisitions by weeds are encouraged (Harker, 2013). Smother cropping, including mulching, crop allelopathy and cultivated ecosystems are innovative additional tactics used. The incidence of growth inhibition of certain weeds and the induction of phytotoxic symptoms by plants and their residues is well documented for many crops, including all major grain crops such as rice, rye, barley, sorghum, and wheat (Belz, 2004). Additionally, the mulch layer of smother crop residues on the soil surface was shown to reduce weed germination, weed emergence (Peachey et al., 2004), and establishment (Teasdale et al., 2008).

Not all smother crops might be equally suitable for each cropping sequence or tillage system. In order to recommend the use of any smother crop for weed

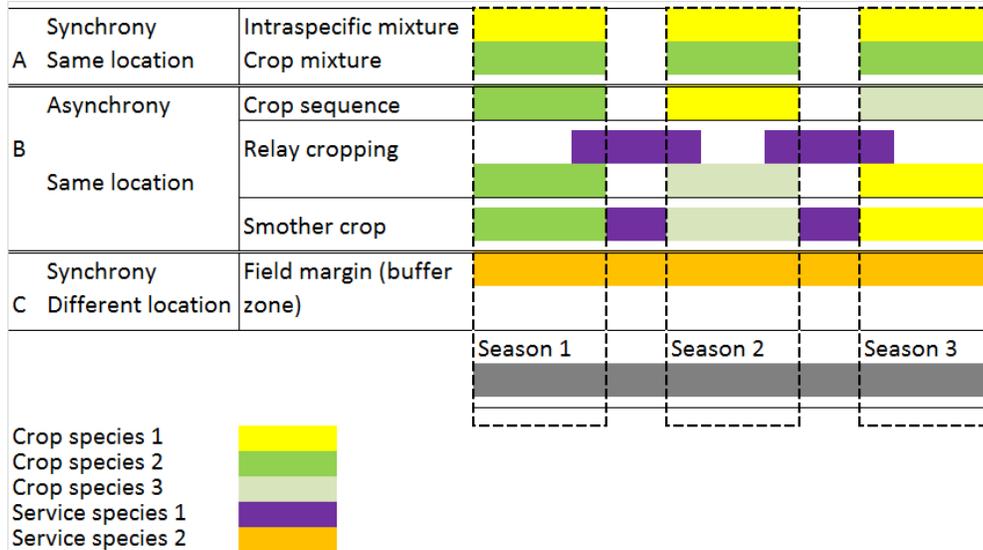


Figure 1. Classification of multiple cropping systems. Coloured boxes show species cultivated for grain production as well as the introduction of service species in some systems. Boxes with dotted lines show cultivation seasons for the different systems (Gaba et al., 2015).

suppression to a farmer, its weed suppressive potential needs to be reliable in a variety of cropping environments (Dorn et al., 2015). The rapid establishment of a dense stand seems a key element for weed suppression by smother crops (Melander et al., 2013). The amount of dry matter production of a smother crop seemed to be more important for weed suppression than cover crop species *per se* (Dorn et al., 2015). In addition, locally adapted smother crops that have rapid establishment and growth, good soil coverage and high dry matter production should be used (Dorn et al., 2015).

Hartwig and Ammon (2002) reported that the introduction of a smother crop increases the diversity of the plants growing on the field. As mentioned before, previous studies have shown that this diversification, by modifying biotic and abiotic components, provides important services, *inter alia* suppressing weeds and pests (Hartwig and Ammon, 2002). These services can improve resource availability and the growth conditions of the crop or decrease the impact of pests, thereby increasing crop productivity (Médiène et al., 2011). In this regard, the benefits of smother cropping are obvious as it will increase biodiversity in many agricultural landscapes, providing some services such as biological pest control and pollination, whilst leaving a neutral effect on other functional groups (Médiène et al., 2011). In addition, Clergue et al. (2005) reported that the biodiversity function also describes resistance to biotic stress and the production of cultivated ecosystems.

Research has also clearly indicated that the effectiveness and consistency of these non-herbicide weed management practices greatly increase when three or more of these practices are simultaneously employed

(Storkey and Lutman, 2008). Once these integrated weed management systems are implemented, herbicides can be used in a more targeted and sustainable manner, preserving their usefulness for decades to come as they are non-renewable resources (Pieterse, 2010).

One of the main ways in which non-crop habitat effects can be used for pest control is through the implementation of buffer zones (hedgerows, beetle banks, adjacent field margins, field boundaries, conservation strips) (Médiène et al., 2011). Earlier, Olson and Wäckers (2007) reported that vegetative buffers in agricultural landscapes can provide a range of important ecological services. This concept of using smother crops as buffer zones in the field was recently confirmed under Mediterranean climatic conditions (Ferreira, unpublished data). Indeed, it is now known that the lack of adequate food in agricultural landscapes is one of the major factors limiting populations of beneficial insects. An added advantage is the growing evidence that complex landscapes are often associated with a greater diversity of natural enemies (Médiène et al., 2011).

Gaba et al. (2015) reviewed examples of multiple cropping systems that aim to use biotic interactions to reduce chemical inputs and provide more ecosystem services than just provisioning (crop production). This concept proposes a classification based on three distinct spatiotemporal arrangements which can be combined and is illustrated in Figure 1 (Gaba et al., 2015).

According to Gaba et al. (2015), the primary aim of multiple cropping systems is to provide provisioning services, while farmers and stakeholders expect these agroecosystems to provide other key ecosystem services. These are mainly regulating services that may

include pest and disease regulation, erosion control, climate regulation and maintenance of soil fertility (Gaba et al., 2015).

This review discussed smother cropping, mulching and crop allelopathy as practical applications in the field. It also emphasised healthy agroecosystems through the application of smother cropping practices. Apart from using it in cropping systems, smother crops can be used to promote cultivated plant diversity in buffer zones and thereby provide beneficial ecosystem services. This will also ease an amount of agricultural chemicals used and consequently reduce the incidence of resistance.

FUTURE RESEARCH NEEDS

Several research needs in the area of allelopathy, smother cropping, and agroecosystems are apparent from this review. These include work on the optimum conditions for the release of allelopathic compounds from living smother crops as well as its mulches. Furthermore, information on all aspects of cultivated ecosystems should be gathered. Also, research on the grey area where agriculture and ecology overlap, will enable the greater use of ecosystem services for crop protection in agricultural production and consequently reduce the incidence of resistance to agricultural chemicals.

Conflict of Interests

The authors have not declared any conflict of interests.

REFERENCES

- Alsaadawi IS, Zwain KHY, Shahata HA (1998). Allelopathic inhibition of growth of rice by wheat residues. *Allelopathy J.* 5:163-169.
- An M, Pratley JJE, Haig TT (2001). Phytotoxicity of *Vulpia* residues: IV. Dynamics of allelochemicals during decomposition of *Vulpia* residues and their corresponding phytotoxicity. *J. Chem. Ecol.* 27:395-409.
- Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003). Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* 301:1377-1380.
- Barberi P (2002). Weed management in organic agriculture: are we addressing the right issues? *Weed Res.* 42:177-193.
- Batish DR, Singh HP, Kohli RK, Kaur S (2001). Crop allelopathy and its role in ecological agriculture. *J. Crop. Prod.* 4:121-161.
- Batish DR, Tung P, Singh HP, Kohli RK (2002). Phytotoxicity of sunflower residues against some summer season crops. *J. Agron. Crop. Sci.* 188:19-24.
- Baucom RS (2009). A herbicide defense trait that is distinct from resistance: The evolutionary ecology and genomics of herbicide tolerance. IN: Stewart CN Jr. (ed.), *Weedy and Invasive Plant Genomics*. Wiley-Blackwell, Iowa, USA.
- Belz RG (2004). Evaluation of allelopathic traits in *Triticum* L. spp. and *Secale cereale* L. PhD Thesis, University of Hohenheim, Stuttgart, Germany.
- Belz RG, Duke SO, Hurlle K (2005). Dose-response – a challenge for allelopathy. *Nonlinearity Biol. Toxicol. Med.* 3:173-211.
- Belz RG, Reinhardt CF, Foxcroft LC, Hurlle K (2007). Residue allelopathy in *Parthenium hysterophorus* L. does parthenin play a leading role? *Crop Prot.* 26:237-245.
- Bertin C, Yang X, Weston LA (2003). The role of root exudates and allelochemicals in the rhizosphere. *Plant Soil* 256:67-83.
- Blum U (1996). Allelopathic interactions involving phenolic acids. *J. Nematol.* 28:259-267.
- Brecke BJ, Shilling DG (1996). Effect of crop species, tillage, and rye (*Secale cereale*) mulch on sicklepod (*Senna obtusifolia*). *Weed Sci.* 44:133-136.
- Bullock JM, Pywell RF, Walker KJ (2007). Long term enhancement of agricultural production by restoration of biodiversity. *J. Appl. Ecol.* 44:6-12.
- Chalker-Scott L (2007). Impact of mulches on landscape plants and the environment—a review. *J. Environ. Hortic.* 25:239-249.
- Chao WS, Horvath DP, Anderson JV, Foley M (2005). Potential model weeds to study genomics, ecology, and physiology in the 21st century. *Weed Sci.* 53:927-937.
- Chou CH (1999). Roles of allelopathy in plant biodiversity and sustainable agriculture. *Crit. Rev. Plant Sci.* 18:609-636.
- Clergue B, Amiaud B, Pervanchon F, Lasserre-Joulin F, Plantureux S (2005). Biodiversity: function and assessment in agricultural areas. A review. *Agron. Sust. Dev.* 25:1-15.
- Daldon BR, Blum U, Weed SB (1983). Allelopathic substances in ecosystems: Effectiveness of sterile soil components in altering recovery of ferulic acid. *J. Chem. Ecol.* 9:1185-1201.
- Dorn B, Jossi W, van der Heijden MGA (2015). Weed suppression by cover crops: comparative on-farm experiments under integrated and organic conservation tillage. *Weed Res.* 55(6):586-597.
- Duke SO, Cedergreen N, Velini ED, Belz RG (2006). Hormesis: is it an important factor in herbicide use and allelopathy? *Outl. Pest. Manage.* 17:29-33.
- Duke SO, Dayan FE, Romagni JG, Rimando AM (2000). Natural products as sources of herbicides: current status and future trends. *Weed Res.* 40:99-111.
- Duke SO, Rimando AM, Bearson SR, Scheffler BE, Ota E, Belz RG (2002). Strategies for the use of natural products for weed management. *J. Pest. Sci.* 27:298-306.
- Dyck E, Liebman M (1994). Soil fertility management as a factor in weed control: the effect of crimson clover residue, synthetic nitrogen fertilizer, and their interaction on emergence and early growth of lambsquarters and sweet corn. *Plant Soil* 167:227-237.
- Efthimiadou AP, Karkanis AC, Bilalis DJ, Efthimiadis P (2009). Review: the phenomenon of crop-weed competition; a problem or a key for sustainable weed management? *J. Food Agric. Environ.* 7:861-868.
- Einhellig FA (1996). Interactions involving allelopathy in cropping systems. *Agron. J.* 88:886-893.
- FAO (Food and Agriculture Organization of the United Nations) (2008). Investing in sustainable agricultural intensification: the role of conservation agriculture. Rome: FAO.
- Fay PK, Duke WB (1977). An assessment of allelopathic potential in *Avena* germplasm. *Weed Sci.* 25:224-228.
- Ferreira MI, Reinhardt CF (2010). Field assessment of crop residues for allelopathic effects on both crops and weeds. *Agron. J.* 102:1593-1600.
- Gaba S, Bretagnolle F, Rigaud T, Philippet L (2014). Managing biotic interactions for ecological intensification of agroecosystems. *Front. Ecol. Evol.* 2:1-9.
- Gaba S, Fried G, Kazakou E, Chauvel B, Navas ML (2014). Agroecological weed control using a functional approach: a review of cropping system diversity. *Agron. Sustain. Dev.* 34:103-119.
- Gaba S, Lescourret F, Boudsocq S, Enjalbert J, Hinsinger P, Journet EP, Navas ML, Wery J, Louarn G, Malézieux E, Pelzer E, Prudent M, Ozier-Lafontaine H (2015). Multiple cropping system as drivers for providing multiple ecosystem services: from concepts to design. *Agron. Sustain. Dev.* 35:607-623.
- Gallandt ER, Molloy T, Lynch RP, Drummond FA (2005). Effect of cover-cropping systems on invertebrate seed predation. *Weed Sci.* 53:69-76.
- Gealy DR, Wailes EJ, Esterninos LE, Chaves RSC (2003). Rice cultivar differences in suppression of barnyardgrass (*Echinochloa crus-galli*) and economics of reduced propanil rates. *Weed Sci.* 51:601-609.
- Gressel J (1991). Why get resistance if it can be prevented or delayed. In: Caselay JC, Cussans GW, Atkin RK (eds.). *Herbicide resistance in weeds and crops*. Oxford: Butterworth-Heinemann. pp. 1-26.
- Harker KN (2013). Slowing weed evolution with integrated weed

- management. *Can. J. Plant Sci.* 93:759-764.
- Hartwig NL, Ammon HU (2002). 50th Anniversary-Invited article: Cover crops and living mulches. *Weed Sci.* 50:688-699.
- Heap I (2015). International survey of herbicide resistant weeds.
- Hoffman ML, Weston LA, Snyder JC, Regnier EE (1996). Allelopathic influence of germinating seeds and seedlings of cover crops on weed species. *Weed Sci.* 44: 579-584.
- Hoult AHC, Lovett JV (1993). Biologically active secondary metabolites of barley. III. A method for identification and quantification of hordenine and gramine in barley by high-performance liquid chromatography. *J. Chem. Ecol.* 19:2245-2254.
- Jones E, Jessop RS, Sindel, BM, Hoult A (1999). Utilising crop residues to control weeds. p. 373-376. IN: Bishop, A. Boersma, M. and Barnes, C.D. (ed.), Proceedings of the 12th Australian Weeds Conference. Tasmanian Weeds Society, Devonport, Australia.
- Kazinczi G, Horváth J, Takács AP (2005). Plant-plant and plant-virus interactions. Lectures and papers presented at the 7th Slovenian Conference on Plant Protection, Zreče, Slovenia, 8-10 March.
- Khanh TD, Chung MI, Xuan TD, Tawata S (2005). The exploitation of crop allelopathy in sustainable agricultural production. *J. Agron. Crop Sci.* 191:172-184.
- Kohli RK, Batish DR, Singh HP (2006). Allelopathic interactions in agroecosystems. IN: Reigosa MJ, Pedrol N, González L (Eds.). *Allelopathy: a physiological process with ecological implications*. Dordrecht: Springer. pp. 465-493.
- Kong CH, Wang P, Zhao H, Xu XH, Zhu YD (2008). Impact of allelochemical exuded from allelopathic rice on soil microbial community. *Soil Biol. Biochem.* 40:1862-1869.
- Korres NE, Norsworthy JK (2015). Influence of a rye cover crop on the critical period for weed control in cotton. *Weed Sci.* 63:346-352.
- Kruidhof HM (2008). Cover crop-based ecological weed management: exploration and optimization. PhD Thesis, Wageningen University, Wageningen, The Netherlands. 156p.
- Kumar V, Brainard DC, Bellinder RR (2008). Suppression of Powell amaranth (*Amaranthus powellii*), shepherd's-purse (*Capsella bursa-pastoris*), and corn chamomile (*Anthemis arvensis*) by buckwheat residues: role of nitrogen and fungal pathogens. *Weed Sci.* 56:271-280.
- Lichtfouse E, Navarrete M, Debaeke P, Souchère V, Alberola C, Ménassieu J (2009). Agronomy for sustainable agriculture: A review. *Agron. Sustain. Dev.* 29:1-6.
- Liebman M, Davis A (2000). Integration of soil, crop and weed management in low-external-input farming systems. *Weed Res.* 40:27-48.
- Liebman M, Mohler CL (2001). Weeds and the soil environment. In: *Ecological Management of Agricultural Weeds*, Liebman M, Mohler CL, Staver CP (Eds.), Cambridge University Press, Cambridge. pp. 210-268.
- Llewellyn RS, Lindner RK, Pannell DJ, Powles SB (2007). Herbicide resistance and the adoption of integrated weed management by Western Australian grain growers. *Agric. Econ.* 36:123-130.
- Mamolos AP, Kalburtji KL (2001). Significance of allelopathy in crop rotation. *J. Crop Prod.* 4:197-218.
- Marble SC (2015). Herbicide and mulch interactions: a review of the literature and the implications for the landscape maintenance industry. *Weed Technol.* 29:341-349.
- McCalla TM, Norstadt FA (1974). Toxicity problems in mulch tillage. p. 29. IN: *Physiology of stressed crops. Volume III. The Stress of Allelochemicals*, 2005. U.S. Gupta (ed.), University of Georgia, Science Publishers, Inc., Enfield (NH), USA.
- Médiène S, Valantin-Morison M, Sarthou JP, de Tourdonnet S, Gosme M, Bertrand M, Roger-Estrade J, Aubertot JN, Rusch A, Motisi N, Pelosi C, Doré T (2011). Agroecosystem management and biotic interactions: A review. *Agron. Sustain. Dev.* J. 31:491-514.
- Melander B, Munier-Jolain N, Charles R (2013). European perspectives on the adoption of non-chemical weed management in reduced-tillage systems for arable crops. *Weed Technol.* 27:231-240.
- Mohler CL, Teasdale JR (1993). Response of weed emergence to rate of *Vicia villosa* Roth and *Secale cereale* L. residue. *Weed Res.* 33:487-499.
- Nichols V, Verhulst N, Cox R, Govaerts B (2015). Weed dynamics and conservation agriculture principles: A Review. *Field Crops Res.* 183:56-68.
- Nikneshan P, Karimmojeni H, Moghanibashi M, Hosseini N (2011). Allelopathic potential of sunflower on weed management in safflower and wheat. *Aust. J. Crop Sci.* 11:1434-1440.
- Olofsdotter M (2001). Getting closer to breeding for competitive ability and the role of allelopathy – an example from rice (*Oryza sativa*). *Weed Technol.* 15:798-806.
- Olofsdotter M, Navarez D, Rebulanan M, Streibig JC (1999). Weed-suppressing rice cultivars – does allelopathy play a role? *Weed Res.* 39:441-454.
- Olson DM, Wäckers FL (2007). Management of field margins to maximize multiple ecological services. *J. Appl. Ecol.* 44:13-21.
- Paine LJ, Harrison H (1993). The historical roots of living mulch and related practices. *HortTechnology* 3:137-142.
- Peachey RE, Williams RD, Mallory-Smith C (2004). Effect of no-till or conventional planting and cover crops residues on weed emergence in vegetable row crop. *Weed Technol.* 18:1023-1030.
- Phatak SC (1992). An integrated sustainable vegetable production system. *HortTechnology* 27:738-741.
- Pieterse PJ (2010). Herbicide resistance in weeds – a threat to effective chemical weed control in South Africa. *S. Afr. J. Plant Soil.* 27:66-73.
- Prati D, Bossdorf O (2004). Allelopathic inhibition of germination by *Alliaria petiolate* (Brassicaceae). *Am. J. Bot.* 91:285-288.
- Price AJ, Norsworthy JK (2013). Cover crops for weed management in southern reduced tillage vegetable cropping systems. *Weed Technol.* 27:212-217.
- Purvis CE (1990). Differential Response of Wheat to Retained Crop Stubbles. I. Effect of Stubble Type and Degree of Decomposition. *Aust. J. Agric. Res.* 41:225-42.
- Putnam AR, DeFrank J (1983). Use of phyto toxic plant residues for selective weed control. *Crop Prot.* 2:173-181.
- Qasem JR, Foy CL (2001). Weed allelopathy, its ecological impacts and future prospect: a review. *J. Crop Prod.* 4:43-120.
- Qasem JR, Hill TA (1989). Possible role of allelopathy in the competition between tomato, *Senecio vulgaris* L. and *Chenopodium album* L. *Weed Res.* 29:349-356.
- Reinhardt CF, Meissner R, Labuschagne N (1994). Allelopathic interaction of *Chenopodium album* L. and certain crop species. *S. Afr. J. Plant Soil* 11:45-49.
- Singh HP, Batish DR, Kohli RK (2001). Allelopathy in agroecosystems: an overview. *J. Crop Prod.* 4:1-41.
- Singh HP, Batish DR, Kohli RK (2003). Allelopathic interactions and allelochemicals: new possibilities for sustainable weed management. *Crit. Rev. Plant Sci.* 22:239-307.
- Sozeri S, Ayhan A (1998). Effect of stubble on wheat seed germination and seedling growth. p. 29. IN: *Physiology of stressed crops. Volume III. The Stress of Allelochemicals 2005*. Gupta US (Ed.), University of Georgia, Science Publishers, Inc., Enfield (NH), USA.
- Storkey F, Lutman P (2008). How can weed management support the development of a more multifunctional agriculture? In: *Proceedings of the Fifth International Weed Science Congress*, 22-27 June 2008. Vancouver, Canada [abstract only]. pp. 215-216.
- Teasdale JR, Abdul-Baki AA, Bong Park Y (2008). Sweet corn production and efficiency of nitrogen use in high cover crop residue. *Agron. Sustain. Dev.* 28:559-565.
- Teasdale JR, Mohler CL (2000). The quantitative relationship between weed emergence and the physical properties of mulches. *Weed Sci.* 48:385-392.
- Teasdale JR, Pillai P (2005). Contribution of ammonium to stimulation of smooth pigweed (*Amaranthus hybridus* L.) germination by extracts of hairy vetch (*Vicia villosa* Roth) residue. *Weed Biol. Manage.* 5:19-25.
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8:857-874.
- Vyvan JR (2002). Allelochemicals as leads for new herbicides and agrochemicals. *Tetrahedron* 58:1631-1646.
- Weston LA (1996). Utilization of allelopathy for weed management in agroeco-systems. *Agron. J.* 88:860-866.
- Weston LA, Duke SO (2003). Weed and crop allelopathy. *Crit. Rev. Plant Sci.* 22:367-389.
- Wu HW, Pratley J, Haig T (2003). Phytotoxic effects of wheat extracts

- on a herbicide-resistant biotype of annual ryegrass (*Lolium rigidum*). J. Agric. Food Chem. 51:4610-4616.
- Wu HW, Pratley J, Lemerle D, Haig T (1999). Crop cultivars with allelopathic capability. Weed Res. 39:171-180.
- Xuan TD, Tawata S, Khanh TD, Chung MI (2005). Decomposition of allelopathic plants in soil. J. Agron. Crop Sci. 191:162-171.
- Young SL (2012). True integrated weed management. Weed Res. 52:107-111.
- Yuan JS, Tranel PJ, Stewart CN Jr (2007). Non-target-site herbicide resistance: A family business. Trends Plant Sci. 12:6-13.