CHAPTER 1

Literature Review

Introduction

Modern agriculture relies on synthetic chemicals to control weeds as unwanted plants, because they compete with cultivated crops for growth factors (water, light, nutrients and spaces), and harbour pests and plant pathogens (Qasem & Foy, 2001). 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 & Hill, 1989).

Due to increased awareness about the risks involved in the use of synthetic chemicals, much attention is being focused on the alternative methods of weed control. Overuse of synthetic herbicides for weed control over the last five decades has resulted in growing public concern over their impacts upon human health, the environment, and the evolution of herbicide resistant weeds (Vyvyan, 2002). Herbicide resistance in weeds is a rapidly expanding phenomenon resulting in higher costs of production due to the greater weed impact. With current pressures to reduce herbicide usage but maintain cost-effective weed control, the innate ability of crops or cultivars to suppress weed growth has become increasingly important (Efthimiadou *et al.,* 2009).

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). Cultivating a system with allelopathic crops plays an important role in the establishment of sustainable agriculture (Khanh *et al.,* 2005). Wheat (*Triticum aestivum* L.) is known to be allelopathic against crops and weeds (Alsaadawi *et al.,* 1998). Wheat straw reduced weed densities and biomass by an average of 90 % compared with those plots without residues (Putnam and DeFrank, 1983). Narwal *et al.* (1998) reported that wheat straw caused a 16.8 % reduction of broad-leaf weeds but showed no effect on grassy weeds. In fields previously cultivated with wheat, populations of barnyard grass (*Echinochloa crus-galli*) were decreased (Alsaadawi, 2001). Lopes *et al.* (1987) reported that extracts from barnyard grass reduced rice (*Oryza sativa*) radicle and coleoptile growth. Foliage vapours and foliage washings of *Salvia reflexa* adversely affected germination and seedling growth of wheat (Lovett, 1983). Root exudates from wild oat (*Avena fatua*) reduced wheat leaf and root dry mass (Schumacher *et al.,* 1983). Results from Uppar *et al.* (1993) indicated that aqueous extracts of *Commelina benghalensis* inhibited wheat cv Kiran germination by 36.1 %.

In the Western Cape two cropping areas can be defined namely, the Swartland winter rainfall area and the Overberg year-round rainfall area. Wheat is the main crop in both areas and crop rotation systems followed have the aim of sustaining wheat production. The major crop rotation system followed over a four year cycle in the Swartland is wheat-wheat-medic-medic or the less popular system of wheat-canola-wheat-lupine. Because of year-round rainfall in the Overberg region, lucerne which grows actively in summer, is grown for a five to seven year period, followed by wheat-barley-canola-wheat-barley-lupine over a six year period.

In the sections that follow, literature references are clustered according to the chapters for which they are relevant.

Field assessment of crop residues for allelopathic effects on both crops and weeds

Several wild accessions of modem day crops are found to possess allelopathic traits that impart in them resistance against weeds and pests (Hoult & Lovett, 1993). To achieve consistent results in the field from the use of crop residues, it is important to understand the mechanism of allelopathy (Kumar *et al.,* 2009). Field trials investigating crop allelopathy of rice *(Oryza sativa)* 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.

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 in the Western Cape Province, has highlighted the potential exploitation of allelopathy for weed suppressions in cropping systems. 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 Western Cape Province.

Most plants apparently produce secondary metabolites that are phytotoxic to some degree, and in a small number of cases their release into the environment and their capability of causing allelopathic effects towards a number of noxious weeds have been demonstrated. Allelopathy is particularly relevant for weed management strategies applied in minimum and no-till cropping systems (Jones *et al.,* 1999), because weed control in such systems is particularly problematic and basically limited to the use of herbicides. 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). Wheat straw has been found to be an excellent mulch crop in no-till farming due to the presence of triterpenoids and other phenolic acids (Singh *et al.,* 2001).

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 (Batish *et al.,* 2002; Belz, 2004; Khanh *et al.,* 2005; Qasem & Hill, 1989). Chou (1999) found that allelochemicals can be released either through leaching from leaves, decomposition of residues, volatilisation or by root exudation. 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), because phytotoxins are released by intact roots of living crop plants (Weston, 1996). Upon release into crop environment the nature and concentration of allelochemicals may change because of complex environmental conditions and microbial action (Batish *et al.,* 2001). Crop residues can, therefore, be very useful in maintaining the sustainability of agroecosystems, provided they are efficiently managed (Batish *et al.,* 2002). 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).

Apart from allelopathic effects, crop residues can exert an effect on weed germination and establishment through other mechanisms. Release of nutrients from the residues can stimulate weed germination (Teasdale & 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 & 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 & Liebman, 1994; Kumar *et al.,* 2008), mulch effects of a physical nature (Mohler & Teasdale, 1993), stimulation of pathogens or predators of weed seeds (Gallandt *et al.,* 2005), and allelopathy (Weston, 1996).

The availability of soil nitrate had no influence on the degree of phytotoxicity of any stubble type (Purvis, 1990). Soil nutrient status and nitrogen nutrition in particular did not appear to account for the differential effects observed in the field experiments. 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. It is postulated that soil levels of stubble-derived chemicals may be high in one year and low in another, owing to differences in rainfall and temperature between these years (Purvis, 1990). This suggests a far greater likelihood of phytotoxicity if stubble has undergone little weathering or decomposition prior to sowing (Purvis, 1990).

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 growth of the principal weeds in a given area through allelopathic action and thus decrease the need for synthetic herbicides (Wu *et al.,* 1999). Many studies have clearly demonstrated genetic variability of the allelopathic character within crops (Wu *et al.,* 1999), which may be considered as an important genetic reservoir for selection of allelopathic cultivars. As was observed for several genetic traits, allelopathy is interwoven with environmental conditions (Olofsdotter *et al.*, 2002; Weston & Duke, 2003). Thus, in a wide range of environments, the allelopathic potential of a certain cultivar may differ considerably. A clear understanding of such genotype-environmental interactions is required if allelopathy is to become a reliable option for weed management (Belz, 2004).

Greenhouse and laboratory assessment of rotational crops for allelopathic potential that affects both crops and weeds

The allelopathic phenomenon encompasses both detrimental and beneficial interactions between plants through chemicals released by the donor (Xuan & Tsuzuki, 2002). Belz (2004) suggested that crop allelopathy can be exploited for weed management through the release of allelochemicals from intact roots of living plants or decomposition of plant residues and that in annual crops, root exudation of the phytotoxins by the crop is the preferred mechanism.

Kumar *et al.* (2009) suggested that one approach to understanding the allelopathic effects of crop residues is to separate soil effects occurring during the growth of crops from their residue effects. Another approach is to determine which parts of the cover crop—root, shoot, or root plus shoot—has the most suppressive effects on emergence and growth. Nevertheless, Olofsdotter *et al.* (1995) and Wu *et al.* (2000b; 2001) cautioned that an essential need in studying crop allelopathy is simulation of the natural release of allelochemicals so that chemical interference from living donor plants on living receiver plants can be measured.

The complicated nature of interference among plants makes it difficult to separate its components in natural environments (Qasem & Hill, 1989). Therefore, the relative importance of competition and allelopathy as mechanisms of plant interference is generally unknown (Hoffman *et al.*, 1996). 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).

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). Furthermore, white goosefoot residues in the soil have been found to be phytotoxic and to affect the nutrient uptake process in maize and soybean. A better understanding of toxic weed root exudates that inhibit crops will lead to more effective decision making in crop rotation systems (Rice, 1984).

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). Aqueous shoot extracts of buckwheat stimulated Powell amaranth (*Amaranthus powellii* S. Wats.) germination slightly, but inhibited radicle growth (Kumar *et al.,* 2009).

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 & Kalburtji, 2001).

Geographical differentiation and genetic variation of *Lolium* spp in the Western Cape: identification of the hybrid *Lolium multiflorum x perenne* and isolation of the pathogen *Fusarium pseudograminearum*

Widespread repeated use of synthetic herbicides has produced biotypes of annual ryegrass resistant to major herbicide classes (Wu *et al.,* 2003). Mimic weeds such as *Lolium* spp (rye grass) has convergently evolved with cereal crops as a result of unconscious selection by farmers and cannot survive without the agricultural practices to which they have become adapted (Spahillari *et al.,* 1999). Rye grass has been disseminated throughout the world with traditional wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) cultivation and is expected to have complex evolutionary patterns (Holm *et al.,* 1977). Weed species with a high level of genetic diversity, like rye grass, are considered to show significant potential for weed adaptation and decrease the efficacy of weed control.

According to O'Hanlon *et al.* (2000), there is a widespread concern that weed species with higher levels of genetic diversity will exhibit considerable potential for adaptation and, therefore, may be able to reduce the effectiveness of weed control. Weeds have genetic traits that give them remarkable plasticity, allowing them to adapt, regenerate, survive, and thrive in a multitude of ecosystems (Chao *et al.,* 2005). Many agronomic weeds are close relatives of crop plants and studies on the sequencing of a weed genome are likely to provide clues concerning weed phenotypes and their underlying gene networks (Broz & Vivanco, 2009).

A specie's ability to adapt to changing environmental conditions is found in the genetic diversity of its populations. Success in weed populations facing changing agricultural ecosystems often correlates with an abundance of genetic polymorphisms within those populations (Jasieniuk & Maxwell, 2001). Through the process of mutation and selection, however, weeds evolve resistance to herbicides when they are used repeatedly (Tranel & Trucco, 2009). Rigid ryegrass (*L. rigidum*) (Monaghan, 1980) was regarded by Tranel and Trucco (2009) to be the most important weed in terms of it having evolved resistance to multiple herbicides.

Perennial ryegrass (*L. perenne* L.) (Charmet & Balfourier, 1994) is native to most of Europe and parts of the Mediterranean and Middle East areas, whereas rigid rye grass is distributed all around the Mediterranean. The genus *Lolium* consists of two groups of species, which are outbreeding and inbreeding, respectively (Senda *et al*., 2005). The genetic diversity of outbreeding rye grass has been studied in relation to the characterisation of genetic resources of Italian ryegrass (*L. multiflorum* Lam.) (Charmet & Balfourier, 1994) and perennial ryegrass. Analysis of the frequency and distribution of genetic variation in natural populations of perennial ryegrass has supported the view that its centre of origin is the Fertile Crescent (Middle East) and that its distribution expanded following a clinical geographical pattern (Senda *et al*., 2005). Balfourier *et al*. (2000) reported that despite the weak genetic differentiation, significant patterns of geographical variation with respect to diversity indices and allele frequencies have been observed in perennial rye grass. In contrast, no spatial organisation of diversity has been detected in rigid rye grass (Balfourier *et al*., 2000).

Allelopathic root exudates of the weed *Lolium multiflorum x perenne* and crops influence plant growth and changes in the soil microbial community

Several studies have shown that some crop cultivars are allelopathic and that their inhibitory effects on weeds can cause significant suppression of the latter plants' growth under field conditions (Olofsdotter *et al.,* 1999; Wu *et al.,* 1999).

Alsaadawi *et al.* (2005) concluded that sorghum cultivars differ in allelopathic potential and that the exploitation of cultivars with higher allelopathic capacity would be of value for weed control, particularly in no-tillage cropping systems. Several rice cultivars identified in the individual screenings of weeds of rice were successful in substantial root growth inhibition of more than one weed type (Seal *et al.,* 2005). Belz (2007) discussed breeding efforts in wheat *(Triticum aestivum)* and barley *(Hordeum vulgare)* which showed that early vigour and allelopathy against perennial ryegrass were significantly related to field weed suppression, whereby the relative importance proved to be cultivar and crop specific.

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). Because the rhizosphere is the densely populated area of the soil where plant roots must compete with invading root systems of neighbouring plants and with soil-borne micro-organisms for space, water and mineral nutrients, interactions within the rhizosphere are based on complex exchanges involving a multitude of biotic and abiotic factors. However, below-ground biological interactions that are driven by root exudates are probably more complex than above-ground interactions (Lin *et al.,* 2007).

Micro-organisms have a profound effect on the allelopathic activity by altering and/or transforming the amount of allelochemicals, particularly the phenolic acids in the soil, depending upon the available carbon source and other environmental factors (Singh *et al.,* 2001). The microbes may metabolise the released phenolic acids by addition or deletion of side groups, polymerisation, production of other organic molecules and/or incorporation of carbon from other phenolic acids into microbial biomass (Blum, 1996). Furthermore, in the soil the preferential utilisation of carbon sources may also affect the plant-microbe soil system and the allelopathic phenomenon (Singh *et al.,* 2001).

The term allelopathy has been broadened, according to Kazinczi *et al.* (2005), to include not only plant-to-plant, but also plant-to-micro-organism interactions. Most of the natural products involved with allelopathy are compounds of secondary metabolism that are synthesised by plants and micro-organisms (Pacheco & Pohlan, 2007). 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. Such products, termed allelopathic compounds, have been shown to play a role in allelopathy, defined here as inhibitory effects of secondary metabolites against either competitors or predators (Leflaive & Ten-Hage, 2007). Belz *et al.* (2009) reported on the degradation of parthenin, an allelopathic compound in the invasive species *Parthenium hysterophorus* L., which is most likely governed by physico-chemical processes combined with microbial activity. Ehrenfeld (2006) reported that allelochemicals are widespread in invasive species and can affect soil microbial communities and microbially-mediated ecosystem processes.

Micro-organisms have a profound effect on allelopathic activity by altering and/or transforming the amount of allelochemicals (Singh *et al.,* 2001). On the other hand, allelochemicals may influence the growth of micro-organisms positively or negatively thereby indirectly interfering with the availability of nutrients, particularly nitrogen and phosphorus, in the soil (Wardle & Nilsson, 1997). Furthermore, microbial communities provide useful data for studying impacts of environmental events. Micro-organisms are present in virtually all environments and are typically the first organisms to react to chemical and physical changes in the environment. Allelopathy can be better understood in terms of soil microbial ecology when the roles of soil micro-organisms in chemically-mediated interactions between plants are evaluated (Inderjit, 2005).