

## LITERATURE OVERVIEW

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## CHAPTER 1

### LITERATURE OVERVIEW

*“Other seed fell among thorns and the thorns grew up and choked them”*

*Matthew 13:7*

KwaZulu-Natal (KZN) is one of the nine provinces of the Republic of South Africa, characterized by the Great Drakensberg Escarpment to the west and the Indian Ocean to the east. Most of the mean annual rainfall of 845 mm is received during the summer months (October-March) with the mean maximum and minimum temperatures reaching 25.2–30.4°C and -1.4–10.7°C, respectively. An average of 6.1–7.2 hours of sunshine is received in summer (Kars *et al.*, 1999). Growing conditions are more favourable for crop production compared to most of the other provinces. Smaller areas of maize (*Zea mays*), soyabean (*Glycine max*), dry beans (*Phaseolus vulgaris*) and potatoes (*Solanum tuberosum*) are planted in KZN, yet higher yields per hectare are produced compared to provinces with bigger production areas. On average 4.4 tons ha<sup>-1</sup> of maize are produced in KZN (4.6% of the total maize production) compared to the 3.0 tons ha<sup>-1</sup> in the Free State Province which has 38% more land planted to maize (Anonymous 2005).

However, not only is maize the second most important field crop besides sugarcane (*Saccharum officinarum*) in KZN, it also forms part of the agricultural activities that provide 60% of the rural population in the province with food security and a sole or complementary income. Some of the factors that affect agriculture and rural development include poverty, high input costs, uneconomical farm sizes and the quality and quantity of produce (Kars *et al.*, 1999). For instance, for a conservation tillage maize farmer in KZN to make a profit in 2010, more than nine tons of yellow maize per hectare, valued at R1255 ha<sup>-1</sup> (US\$1=R7), had to be produced (Whitehead & Archer 2008). Because weeds are one of the major pests in most cropping systems, it contributes not only to the higher input costs, but to the overall quantity and quality of produce. If weed

interference could be minimized not only could it lead to obtaining higher yields but also contribute to food security.

## 1. WEED MANAGEMENT

There is a close association between weed growth and crop production. Moss (2008) stated that the primary objective of weed management should be to better understand this association in order to improve current weed management and control programmes. Weed control is generally directed at controlling weed seedlings, not only because they are more manageable but weeds become less competitive later in the season. *Amaranthus palmeri* (Palmer amaranth) reduced maize yields between 11 and 91% as amaranth densities increased from 0.5–8 plants m<sup>-1</sup> row (Massinga *et al.*, 2001), while with *Echinochloa crus-galli* (barnyard grass) interference, maize yield loss ranged between 26 and 35% when barnyard grass emerged early. Yield loss due to the latter weed was only 6% when it emerged later in the maize growth season (Bosnic & Swanton 1997).

The development of herbicides during the late 1940s and onwards, provided a simple solution to weed control, resulting in higher crop yields. Currently however, this reliance on chemical control has been critically scrutinized due to the development of herbicide resistance, the negative impact on food and environmental safety, the growth in the organic food production sector (Bastiaans *et al.*, 2008) and shifts in weed populations (Buhler 2002). In addition, the availability and less complicated management of weeds with herbicides in comparison to other methods, gives the impression that weeds can easily be controlled after crop establishment and therefore cultural and tillage methods are in many instances not considered.

Arguments against this simplification of weed management and the reliance on one weed control method have recently been published (Lieberman & Davis 2000; Buhler 2002; Bastiaans *et al.*, 2008). More emphasis should be placed on reducing weed densities, preventing weed reproduction minimizing weed competition and manipulating the crop competitiveness with the weeds. Weed emergence and

density can be reduced through crop rotations, restricting light from reaching the soil surface, the formation of a physical barrier and preventing seed dispersal. Crop competitiveness can be enhanced through modification of the planting date to ensure crop emergence before the weeds, improved cultivars for rapid germination and root development, quicker canopy closure, increased planting populations (Bastiaans *et al.*, 2008) and using allelopathic crop cultivars (Belz 2004; Khanh *et al.*, 2005). Conservation tillage, together with the use of cover crops, are two important factors in adjusting existing weed management systems aimed at reducing weed fitness and improving crop yields.

## 2. CONSERVATION TILLAGE

Although the primary objective of tillage operations is to prepare a crop seedbed and not weed control, tillage influences weed seed germination by reducing the soil surface cover, it changes the soil temperature and moisture patterns, and it alters weed seed distribution in the soil profile (Locke *et al.*, 2002). Land users in South Africa are obliged by law to adhere to the Conservation of Agricultural Resources Act of 1983 to conserve natural resources by, among other things, combating and preventing soil erosion and maintaining the production potential of the soil. Methods such as conservation tillage, suitable conservation works and avoidance of cultivation during periods of high erosion hazard are advised (Russell 1998). Conservation tillage makes use of crop residue left on the soil surface to reduce the impact of raindrops on the soil surface and to reduce the velocity of surface runoff. In KZN, conservation tillage is practised as direct drilling when a blade cuts through the crop residue, opening a furrow into which seed and fertilizer are deposited. It has several advantages over conventional tillage systems as it reduces soil erosion, soil compaction, energy requirements, evaporation and runoff (Russell 1998; Giller *et al.*, 2009).

These advantages came at a cost to weed management as the increased complexity thereof requires a higher level of management. According to Locke *et al.* (2002) careful management with herbicides is required as more post-emergence herbicides could be needed if the weeds were allowed to establish after

crop planting. The introduction of herbicide-resistant genetically modified (GM) crops improved weed control options for conservation agriculture and it could be economically viable if only post-emergence herbicides were used (Reddy 2001). There is, however, a possibility that with the continued use of these GM crops and the limited seed migration into the field, traits such as herbicide resistance could evolve faster than under conventional tillage (Martínez-Ghersa *et al.*, 2000).

Also, weed populations and seed bank dynamics can be altered by conservation tillage. Most of the weed seeds occur in the upper 10 mm of soil and very few below 100 mm (Buhler 1995; Peachy *et al.*, 2004). Small-seeded annual broadleaf and most grass species have the ability to increase prolifically because they germinate and become established when the seeds are at or near the soil surface. Summer annual species that do not require burial for establishment are also well adapted to proliferate (Buhler 1995). Conventional tillage appears to favour *Digitaria sanguinalis* (crab finger-grass), *Sorghum halepense* (Johnson grass) and *Tagetes minuta* (khaki weed), whereas conservation tillage promotes *E. crus-galli* (De La Fuente *et al.*, 1999), *Amaranthus retroflexus* (redroot pigweed), *Setaria viridis* (green foxtail) (Buhler 1992), *Chenopodium album* (common lambsquarters) and *Solanum nigrum* (black nightshade) (Barberi & Mazzoncini 2001). Perennial weed populations tend to increase (Giller *et al.*, 2009) and be more diverse (Locke *et al.*, 2002) under conservation tillage. In KZN, *Cyperus esculentus* (yellow nutsedge), among others, can become a dominant and difficult weed to control in conservation tillage if insufficient weed control is practiced (Fowler 2000).

### **3. CYPERUS ESCULENTUS**

*Cyperus esculentus* is an herbaceous perennial weed which can be identified by an above-ground triangular stem-like fascicle of leaves which later develops into a solid triangular rachis. Thin rhizomes and roots develop from bulbs situated at the base of the fascicle. Rhizomes consist of elongated internodes and nodal cladophylls which differentiate into tubers and shoots (Wills *et al.*, 1980; Stoller

& Sweet 1987). *C. esculentus* spreads mainly through germinating tubers, and not as effectively by sexually produced seeds, which are viable and have longevity, but seedlings lack the vigour for survival in field situations (Stoller & Sweet 1987; Lapham & Drennan 1990).

In most soils, the rhizomes of *C. esculentus* are concentrated in the upper 15 cm of soil, resulting in 80% and more of the tubers occurring in this zone. Very few tubers are found below 20 cm (Friesen & Hamill 1977; Stoller & Sweet 1987). Day length determines the vegetative and reproductive growth of *C. esculentus* periods of 8–12 hours promote tuber formation, and 12–16 hours are conducive for vegetative growth (Friesen & Hamill 1977; Williams 1982). Tubers are formed four to six weeks after seedling emergence (Stoller & Sweet 1987).

During dormancy, storage conditions influence tuber sprouting, as cool moist conditions are more favourable than dry conditions (Friesen & Hamill 1977). Differences in tuber germination and multiple sprouting are not correlated with tuber weights but tuber size does influence seedling vigour (Stoller *et al.*, 1972; Thullen & Keeley 1975). During tuber sprouting, one or more of the buds on the tuber begin to grow. A tuber can have more than one sprout forming, while others stay dormant. The number of sprouts decreases after each germination. More than 60% of the dry weight and nutrients in the tuber are used for the initial sprouting, 6–18% during the second and 2–10% during the third sprouting (Stoller *et al.*, 1972; Thullen & Keeley 1975). Removing sprouts at regular intervals reduces the shoot numbers and tuber longevity, especially when done at four-week intervals (Thullen & Keeley 1975; Stoller & Sweet 1987).

### **3.1 *C. esculentus* interference with crop production**

*Cyperus esculentus* interference with crop production has been demonstrated by various authors. Cotton (*Gossypium hirsutum*) yields decreased linearly with an increase in *C. esculentus* densities. Regression equations revealed an average yield loss of 19 kg ha<sup>-1</sup> for each additional initial tuber m<sup>-1</sup> of crop row (Moffett & McCloskey 1998), and approximately 18 kg ha<sup>-1</sup> for each additional nutsedge

plant m<sup>-2</sup> (Patterson *et al.*, 1980). *C. esculentus* competition with cotton for the entire growth season reduced yields more than if the weed was present for shorter periods of time.

Stoller *et al.* (1979) reported that, although variability was seen from year to year, average maize yield losses were 8% for every 100 shoots m<sup>-2</sup>. Yield reductions were more prominent in years when lower than normal rainfall was received during the growing season. Jooste and van Biljon (1980) found that the second sprouting of *C. esculentus* on the Mphumalanga Highveld in South Africa competed more with maize during the 8–16 week period than in the 0–8 week period. Maize yields were reduced by 11.4% on a Hutton soil (dry soils) and by 23.9% on an Avalon soil form (relatively wet soils). They concluded that it was possible that the first flush of nutsedge may reduce maize yields more than what they reported. Reinhardt and Bezuidenhout (2001) found that maize emergence was retarded in soil where *C. esculentus* grew for 28 days and then removed on the day the maize was sown. Maize was not affected if tubers and maize seeds were planted at the same time.

Cucumber (*Cucumis sativus*) yields were reduced when 15 or more *C. esculentus* plants m<sup>-2</sup> grew with the crop. However, the cucumber plants were able to compete successfully with *C. esculentus* if the crop was seeded at optimum densities, producing an optimum stand (Johnson III & Mullinix Jr 1999). The shoot dry weight of tomatoes (*Lycopersicum esculentum*) were reduced by 34% due to *C. esculentus* competition, with no differences in the interference from below- and above-ground competition (Morales-Payan *et al.*, 2003).

Little and van Staden (2003) reported that *C. esculentus* was the main competitor for water and nutrients with an *Eucalyptus* hybrid clone, *Eucalyptus grandis* x *E. camaldulensis* in Zululand, South Africa, directly after planting, with a subsequent reduction in tree growth. Aqueous extracts of tubers and foliage of immature and mature *C. esculentus* plants inhibited the growth of the essential ectomycorrhiza, *Boletus maxaria* on agar medium isolated from patula pine

(*Pinus patula*) roots (Reinhardt & Bezuidenhout 2001). Their findings proposed that the interference of *C. esculentus* with seedling development of patula pine was indirect, through the primary inhibition of the ectomycorrhizal symbiont *B. maxaria* by allelochemicals released from the weed.

Although Jangaard *et al.* (1971) did not investigate the allelopathic effects of *C. esculentus*, they identified certain phenolic compounds in the tubers that are known for their allelopathic potential. Compounds identified included p-coumaric, ferulic, p-hydroxybenzoic, syringic, vanillic, salicylic, protocatechuic and caffeic acids, with p-coumaric and ferulic acids in higher concentrations. Allelopathic effects were suggested when extracts and dried material of *C. esculentus* and *C. rotundus* (purple nutsedge) reduced the growth of cereals, vegetables and soyabeans (Tames *et al.*, 1973; Meissner *et al.*, 1979; Drost & Doll 1980).

### **3.2 Control measures for *C. esculentus***

Shading reduces the total number of shoots and tubers, dry weight, plant height and leaf area of *C. esculentus* due to its C4 photosynthesis pathway. *C. esculentus* growth was significantly increased when plants were removed from the shade into full sunlight (Patterson 1982). Both Keeley and Thullen (1978) and Santos *et al.* (1997) found that 20–30% shade was detrimental to growth. In contrast, Jordan-Molero and Stoller (1978) reported that 30% shade did not influence the weed's growth. Various crops planted at different plant populations reduced the above-ground growth of *C. esculentus* due to the low intensity of light reaching the weed. Ghafar and Watson (1983) showed that increasing the maize population from 33 300 to 133 300 plants ha<sup>-1</sup> significantly reduced the *C. esculentus* above-ground biomass, tuber number, weight and height at the end of the growing season, with a concomitant significant increase in maize yield. Maize, barley (*Hordeum vulgare*), hemp (*Cannabis sativa*) and stooling rye (*Secale cereale*) reduced the above-ground biomass and density of *C. esculentus* secondary shoots in comparison with when a crop was absent (Lotz *et al.*, 1991).

Crops that create a regime of low light intensity during a long *C. esculentus* growth period suppressed tuber formation more strongly than crops that shadow the weed for a relatively short period of time (Lotz *et al.*, 1991). Various other authors confirmed that shading suppresses tuber formation (Jordan-Molero & Stoller 1978; Keeley & Thullen 1978; Patterson 1982; Li *et al.*, 2001). However, according to Stoller *et al.* (1979), maize planted in 75-cm rows did not provide enough shade to prevent *C. esculentus* from producing tubers. This is supported by Santos *et al.* (1997). Reductions in total leaf area were primarily the result of less leaves produced, as well as them being thinner compared to those in full sunlight (Patterson 1982). Thomas (1969) found that temperature had the greatest effect on *C. esculentus* tuber survival, while the duration of desiccation did not significantly influence tuber survival. A combination of temperature and humidity was more effective in killing tubers than either treatment alone.

Although Stoller and Woolley (1983) and Stoller and Sweet (1987) stated that mulching would not be effective for growth suppression because the leaves of *C. esculentus* have sharp tips that could penetrate hard surfaces, Webster (2005) found that pots covered with 32 µm black-opaque and colourless-clear polyethylene mulches restricted nutsedge growth, as very few shoots emerged through the mulch. The biomass of *C. esculentus* shoots under the mulch was lower compared to the non-mulched treatment, with shoots under the black having a greater biomass than those under the clear mulch. Both mulches reduced tuber production to nearly half of the non-mulched control. Ormeño-Núñez *et al.* (2008) concluded that a dense stooling rye mulch between rows in a vineyard reduced *C. esculentus* growth by 81%.

The limitation of herbicide options for *C. esculentus* control in conservation agriculture and the variability of chemical control (Jooste & van Biljon 1980), creates the opportunity to incorporate the use of cover crops in a weed management system to reduce the weeds' fitness in order to increase crop competitiveness

## 4. COVER CROPS

If the reliance on herbicides for weed management is reduced or eliminated, weed suppression must be approached from a crop cultivation perspective. Interest in the use of cover crops has been motivated primarily to produce crops in a more environmentally sustainable manner. Some of the benefits of cover crops include improving water infiltration, soil structure, reducing soil erosion, releasing nutrients upon decomposition, increasing the soil organic matter and preventing the leaching of N from the previous season (Liebman & Davis 2000). Cover crops can be grown in rotations after the main crop has been harvested or could grow simultaneously during part or all of the main crop season. For the purpose of reducing *C. esculentus* growth in a maize conservation tillage system in KZN, the term cover crop refers to crops planted in autumn after the main crop has been harvested and then killed during the following spring before planting the next main crop into the residues. The cover crop residues remaining on the soil surface could suppress weed growth through environmental and chemical interference.

### 4.1 Weed suppression due to environmental interference

Seed germination is dependent on adequate, but not excessive, supply of water, suitable oxygen:carbon dioxide ratio, and optimum temperatures and light (Monaco *et al.*, 2002). Cover crop residues remaining on the soil surface can physically modify the germination environment by intercepting light and rain and interfering with the heat and water transfer between the soil and atmosphere (Teasdale *et al.*, 2007).

Exposure to light is one of the basic requirements of many weed seeds to germinate. Residues on the soil surface would intercept the incoming radiation promoting dormancy of species with a light requirement. According to Teasdale and Daughtry (1993) light transmission was more obstructed by live hairy vetch (*Vicia villosa*) plants than desiccated hairy vetch material, influencing the suppression of weed growth. Changes in the light spectrum reaching the seed under plant residue could affect the light quality, thereby suppressing germination and growth of photo-dormant species (Teasdale & Mohler 1993). Red

light converts phytochrome to an active form, promoting germination, while far-red light inactivates phytochrome, thus inhibiting germination. Most weed seeds germinate when exposed to the red light portion of sunlight and not in darkness. However, desiccated cover crops have limited influence on the red:far red light ratio due to the absence of chlorophyll (Teasdale & Mohler 1993).

Plant residues on the soil surface lower the soil surface temperature by acting as insulation from the air temperature and intercepting solar radiation thus delaying cooling of the soil surface more than heating (Teasdale & Mohler 2000). Not only could germination be delayed at lower maximum soil temperatures due to the residues but the temperature of the residues itself could suppress germination. Teasdale and Mohler (1993) recorded residue temperatures of 41°C when the air temperature was 37°C. Changes in the soil temperature may enhance mineralization rates, thereby influencing nutrient availability (Facelli & Pickett 1991).

Plant litter on the soil surface may retain some rain water, depending on the litter characteristics (Facelli & Pickett 1991), thereby limiting the amount of water available for germination. During dry periods soil moisture under the residues could be higher creating favourable conditions for germination. However, saturated conditions could reduce germination. *C. album* and *S. viridis* establishment was reduced by soil moistures above field capacity under hairy vetch residues (Teasdale 1993).

The residues on the soil surface may obstruct seedling roots reaching the soil thereby reducing the growth of seeds and sprouts. Seedlings emerging from beneath the residues need to devote more energy penetrating it, leading to higher seedling mortalities. Small seeded species are more sensitive to covering, especially at the cotyledon stage. Once the stored resources of the seed are depleted no energy is available for growth (Baerveldt & Ascard 1999; Liebman & Davis 2000). The degree of weed control provided by the residues is likely to be

influenced by the weed species and growth stage, the thickness of soil cover and the soil type.

## 4.2 Weed suppression due to chemical interference

The allelopathic effects of cover crops on weed growth is the primary means of chemical interference and have been documented (Weston & Duke 2003). Plants interfere directly and indirectly with their neighbours, with a subsequent reduction in growth in any one or both of them as a consequence. Direct effects are attributed to competition and allelopathy, while indirect effects are attributed to changes in the growth environment due to physical effects and the presence of pests and diseases (Hoffman *et al.*, 1996). With competition, growth factors are diminished, while with allelopathy, chemical compounds that are released into the environment affect plant growth (Khanh *et al.*, 2005).

### 4.2.1 Allelopathy research

The root exudation and leaching of allelochemicals from a range of crops employed as cover-, smother-, companion- or intercrops form the basis of a weed management strategy involving allelopathy (Belz 2004; Khanh *et al.*, 2005). However, the discipline of allelopathy has had its share of controversy, in part due to the following limitations: (a) complex research methodology is required for distinguishing between allelopathy and competition (Belz 2004), (b) the widely held assumption that all chemicals extracted from plants would exhibit allelopathic characteristics, and (c) the assumption that the mere presence of allelochemicals in plant tissue presents strong evidence for allelopathy (Inderjit & Callaway 2003).

In the past, to prove that allelopathy was the cause of plant growth inhibition, unrealistic bioassays using leachates or extracts of plant parts in artificial conditions have been used (Foy & Inderjit 2001; Olofsdotter *et al.*, 2002). Bioassays are important in the study and demonstration of allelopathy. Therefore, in order that experiments produce more convincing evidence for the existence and function of allelochemicals they should meet the following criteria: (a) showing allelochemicals being released from the donor plant and arrives in

functional concentrations under natural conditions at the receiver plant, (b) determination of the fate and persistence of allelochemicals in soil, (c) elucidation of the uptake mechanism of the receiver plant and its subsequent response (Blum 1999; Inderjit & Callaway 2003). To discover whether or not these subunits work together, a field study is necessary (Inderjit & Weston 2000; Khanh *et al.*, 2005), but the evaluation of the contribution of each phenomenon to the overall effect in a field situation is difficult and therefore selection of allelopathic cover crop plants under field conditions is not an option (Foy & Inderjit 2001; Olofsdotter *et al.*, 2002). In evaluating the ability of rice to control weed growth, research was focused on bioassays and field work that led to a correlation between growth inhibition and allelochemical release, which formed the basis of a subsequent international breeding programme for developing competitive rice cultivars (Olofsdotter 2001).

#### **4.2.2 Allelochemicals**

All plants synthesize secondary metabolites which are generally considered not important for primary metabolic processes essential for a plant's survival. These metabolites represent a vast number of biologically active compounds, of which some are allelopathic and are referred to as allelochemicals. The allelopathic effect on plants is often the result of a combination of these chemicals released together, as individual compounds are often present in concentrations below their inhibition thresholds (An *et al.*, 1998; Inderjit & Nayyar 2002).

Allelopathic plants do not develop in isolation and environmental conditions influencing plant growth will directly affect allelochemical production and expression. The extent of their phytotoxicity depends on soil characteristics, abiotic and biotic factors, the donor and target plant species and cultivars used (Inderjit & Nayyar 2002).

Adsorption, desorption and degradation of allelochemicals in soil are just as common a phenomena as with herbicides, and therefore, soil texture, organic and

inorganic matter, moisture and micro-organisms as well as allelochemical solubility in water will affect their phytotoxic activity in the soil (Inderjit *et al.*, 2001; Kobayashi 2004). A recent example of this is the abiotic and biotic variables that degraded the allelochemical parthenin released from the alien invader plant *Parthenium hysterophorus* (Parthenium), causing it to have short but variable half-lives in soil, depending on temperature, moisture and microbial activity (Belz *et al.*, 2009). Soil micro-organisms can use allelochemicals as a food source and if allelochemicals are released, the micro-organism population can increase in response. Plant growth inhibition can be the result not only of the allelochemicals present but also because the micro-organisms can transform these compounds to new chemicals of lower or higher bioactivity. In addition, microbes can immobilize nutrients, with subsequent reduction in plant growth (Schmidt & Ley 1999).

The abiotic factors water and nutrient content, temperature and applied herbicides have a significant influence on the availability of allelochemicals. In a review by Tang *et al.* (1995) various examples were given in which stress factors caused an elevation in allelochemicals. Gershenson (1984) came to the conclusion that the accumulation of secondary metabolites under stress conditions must be an adaptive response to conditions under which the function of these compounds becomes important. Einhellig (1987) showed how certain herbicides synergize or supplement the activity of allelochemicals, which can have implications for conservation tillage as it is dependent on herbicide use. The fate of allelochemicals under stress cannot be generalized. The availability of growth resources for donor and target plants can be influenced by the presence of allelochemicals. Donor plants may be less influenced due to their adaptation to the stress, while target plants could lack this ability. Damage is therefore caused by abiotic stress or allelochemicals, or by both (Inderjit & Nayyar 2002).

Choosing the cover crop species and cultivar would also have an impact on the allelopathic effect produced on weed species (Weston & Duke 2003). Differences in their ability to suppress weed growth were reported for, among others, stooling

rye and its different cultivars (Pérez & Ormeño-Núñez 1993; Burgos *et al.*, 1999), wheat (*Triticum aestivum*) (Tollenaar *et al.*, 1993) and clover (*Trifolium* sp) (Creamer *et al.*, 1996).

Reports on the influence of allelochemicals on plants most frequently identified effects which are readily observed in the field or under controlled conditions. Delayed or inhibited germination and the stimulation or inhibition of root and shoot growth are often reported (Rizvi *et al.*, 1992). The major difficulty is to separate secondary effects from primary causes. An important question that always remains is whether or not the inhibitor reaches the active site in the plant in sufficient concentration to specifically influence that reaction, and if other processes may also be affected.

The mode of action of a chemical can broadly be divided into a direct and an indirect action (Rizvi *et al.*, 1992). Effects through the alteration of soil properties, nutritional status and an altered population or activity of micro-organisms and nematodes represent the indirect action. Direct action involves the biochemical/physiological effects of allelochemicals on various important processes of plant growth and metabolism. Some of the processes influenced by allelochemicals are:

- reduction in mineral uptake;
- inhibition of cytology and ultrastructure;
- inactivation of phytohormones and upsetting their balance, and
- inhibition of photosynthesis, respiration and protein synthesis (Rice 1984; Putnam 1985).

Under natural conditions the action of allelochemicals seems to revolve around a fine-tuned regulatory process in which many such compounds may act together on one or more of the above processes (Rizvi *et al.*, 1992).

## 4.3 Cover crops used

### 4.3.1 Cereals: stooling rye and oats

Stooling rye is an annual cereal crop with a fibrous root system and hollow stems that can reach heights of 80–180 cm, depending on the cultivar. As a green plant it is utilized as a green manure and animal fodder, especially during the winter, while the grain is used for flour and alcohol production. In the cooler regions of KZN it is planted as animal fodder in autumn and used from May to September. Oats is a tufted winter-growing annual and in South Africa, oats are mainly produced as a winter grazing or green feed and produce the highest amount of forage per unit area. Planting commence in March and April with the main growth from March to October (Dickinson *et al.*, 1990).

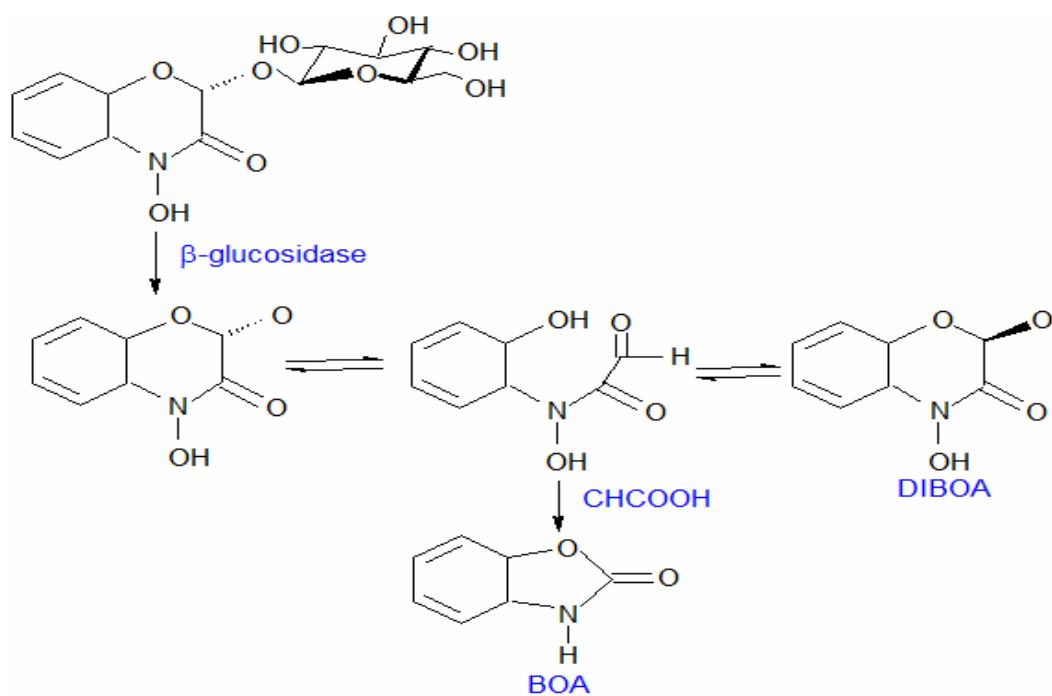
Stooling rye is preferred as a cover crop due to its potential to produce abundant biomass that suppress weed emergence and growth (Koger *et al.*, 2002). In the absence of herbicides, grass control by a stooling rye cover crop increased by 46–61% above the no-cover or conservation tillage system (Yenish *et al.*, 1996), while the biomass of *C. album*, *Polygonum aviculare* (prostrate knotweed) and *Fallopia convolvulus* (climbing knotweed) were reduced by the stooling rye cultivar 'Forrajero-Baer' (Pérez & Ormeño-Núñez 1993).

Oats reduced the number of individuals of *Picris echioides* (bristly ox-tongue) by 94% (de Bertoldi *et al.*, 2009). Weed density was reduced by oats and grazing vetch (*Vicia dasycarpa*) with 90 and 80% respectively while reduction by lupins (*Lupinus angustifolius*) were less successful at only 23% compared to the control plots (Murungu *et al.*, 2010). In trials done by Seavers and Wright (1999) oats were more suppressive than barley and wheat. They concluded that the suppressive effect was not only due to the canopy that was formed as the oats had the slowest canopy development of the test species but retained their weed growth reduction throughout the growing season. This was confirmed by Fourie *et al.* (2006) who reported effective long-term control of summer weeds with oats, rye and black oats (*Avena strigosa*).

The influence of residues on crop growth and weed suppression varies with the time of cover desiccation, resulting in partial suppression of specific weed species. In tomatoes, stooling rye provided 4–8 weeks control after planting, depending on the season and time of desiccation (Smeda & Weller 1996). Soyabean yields were significantly higher when planted into stooling rye residues that were killed two weeks before planting compared to treatments that were planted a day after the stooling rye was killed (Liebl *et al.*, 1992). This was confirmed by Rimbault *et al.* (1990) who found that crop growth was retarded if planted into stooling rye immediately after the stooling rye was killed. The effect was increased when used in a no-till system compared to a conventional tillage system. According to Yenish *et al.* (1995), the residual effect of killed stooling rye does not persist beyond 170 days.

The reduction in weed growth is further influenced by cultivar choice although differences of opinion exist about the attributes of different cultivars. Walters *et al.* (2005) found that the cultivars ‘Elbon’ and ‘Matice’ provided better weed suppression due to their higher yields and soil coverage, while Tollenaar *et al.* (1993) found that ‘Kodiak’ and ‘Gordon’ reduced maize yields the most, despite their low yields and therefore low biomass. They attributed it to the higher below-ground biomass. In addition, higher benzoxazolinone content were found in ‘Bonal’ and ‘Aroostok’, although they did not have the highest yields (Burgos *et al.*, 1999). The cultivar ‘Wheeler’ reduced maize heights and yields when the maize was planted immediately after the stooling rye was killed (Rimbault *et al.*, 1990) The benzoxazolinone content of ‘Bates’ increased between 30 and 60 days after planting and decreased thereafter (Burgos *et al.*, 1999). The differences in weed suppression could be attributed to the decomposition products of stooling rye tissue of different ages. According to Wójcik-Wojtkowiak *et al.* (1990), tilling plants gave the highest level of inhibition, but crop residues did not exhibit toxicity. The level of toxicity was found to be dependent on decomposition time and increase as tissue degraded, reaching a maximum after 3-4 weeks of degradation before decreasing.

Favonoids and saponins have been identified in oats (de Bertoldi *et al.*, 2009), while one of the allelochemical groups responsible for the allelopathic expression of stooling rye is collectively called benzoxazolinones or benzoxazinones (Belz 2004). The production of BOA (benzoxazolin-2(3H)-one) involves two precursors, a benzoxazinoid acetal glucoside and its aglucone (Figure 1). The acetal glucosides DIBOA-Glc are transformed to aglucone DIBOA (2,4-dihydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one which, in turn, forms BOA (Sicker *et al.*, 2004). Weed control in the field could be attributed to the formation of AZOB (azoperoxide) which would increase the phytotoxicity.



**FIGURE 1** Chemical formation of BOA from DIBOA (Sicker *et al.*, 2004)

Glucosides are regarded as non-toxic in juvenile plants and are stored in the vacuole until needed. Aglucones are released when plants are attacked by insects or fungi, when residues are being decomposed, and through root exudation (Yenish *et al.*, 1995; Burgos *et al.*, 1999). DIBOA is chemically unstable in solutions and during decomposition and is therefore converted to BOA. According to Burgos and Talbert (2000), BOA is not solely responsible for the phytotoxic reactions in plants.

Low concentrations of allelochemicals are rapidly broken down by microbes in the soil and are adsorbed onto the soil colloids (Kobayashi 2004). The continuous release of allelochemicals from the donor plants into the rhizosphere will compensate for these loss factors. It must be borne in mind that an effect on the receptor plant would only be noticed if the plant is susceptible to the allelochemicals in such a way that it would cause damage or result in the death of the plant. Chiapusio *et al.* (2004) and Belz *et al.* (2007) confirmed that the effect of allelochemicals is dependent on the concentration. Typically, at the higher concentrations the growth inhibiting effects are most severe, whereas growth stimulation is possible at the lowest concentrations of a particular compound. BOA is also more concentrated in certain plant parts than in others. Rice *et al.* (2005) confirmed work done by Tang *et al.* (1975) that more BOA occurs in stooling rye shoots than in the roots.

According to Chase and Nair (1991), it is very difficult to determine the concentrations of compounds at a specific point in time in nature. These compounds can function on their own or in combination with others. Benzoxazolinones should be resistant to microbial transformation to have any allelopathic effect (Yenish *et al.*, 1995). The allelopathic activity in the field should be high due to exudation by roots and decomposition of material. Microbes convert BOA into AZOB (2,2'-oxo-1,1'-azobenzene), which has a higher toxicity than DIBOA and BOA (Nair *et al.*, 1990; Chase & Nair 1991). Rice *et al.* (2005) identified DIBOA and BOA in shoot tissue of stooling rye while DIMBOA glucose ((2R)-2-beta-D-glucopyranosyloxy-4-hydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one) and MBOA (2,4-hydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one) were more prevalent in root tissue. Lettuce (*Lactuca sativa*) was more affected by crude extracts of the shoot tissue than the root tissue.

In a study conducted by Burgos and Talbert (2000) results showed that small-seeded seeds are more sensitive to benzoxazolinones than large-seeded species. However, there was variation between the reactions of small seeds. Therefore, seed size alone apparently does not account for the variability in allelopathic

expression. The root and stem elongation of cucumber was more effected by DIBOA than BOA in a petri dish bioassay (Burgos *et al.*, 2004).

#### **4.3.2 Annual ryegrass**

Annual ryegrass (*Lolium multiflorum*) is an annual pasture species which provides additional fodder to animals. Cultivars are divided into two categories, Italian and Westerworld cultivars. Italian ryegrass cultivars need vernalisation in order to become reproductive and can be sown in autumn or spring. If planting occurs in spring a longer grazing period is obtained. Westerworld types are sown in autumn and will become reproductive as soon as the day length increases and they then flower in spring. The two types of cultivars are further divided into diploids and tetraploids, with diploids having narrow, shorter leaves, but being more hardy and with greater density than the tetraploids (Dickinson *et al.*, 1990).

Decomposition of annual ryegrass residues is slow and residues remain on the soil surface for longer (Reddy 2001). Despite this, weed growth suppression is variable, as *Brachiaria ramosa* (browntop millet) suppression declined over time, but *C. esculentus* growth remained constant. In comparison with other cover crops tested, annual ryegrass suppressed weed growth the most (Burgos & Talbert 1996; Reddy 2001).

Interference from annual ryegrass is ascribed to the finer root system of annual ryegrass enlarging the root area, allowing more nutrients and water to be extracted (Liebl & Worsham 1987; Stone *et al.*, 1998). In addition, nitrogen mineralization can be exploited better because of a more effective root system (Kramberger *et al.*, 2008). Data are lacking regarding the allelopathic potential and identity of putative allelochemicals in annual ryegrass even though circumstantial evidence exists that the species is allelopathic (Smith & Martin 1994). Various allelochemicals have been identified in other Poaceae species (Sánchez-Moreiras *et al.*, 2004).

Despite the potential for weed suppression and other advantages a cover crop offers, annual ryegrass residues reportedly has a negative influence on the growth of wheat (Appleby *et al.*, 1976), southern pea (*Vigna unguiculata*) (Burgos & Talbert 1996) and soyabean (Reddy 2001) growth as yields were reduced when planted into the residues. However, (Russo *et al.*, 2006) stated that environmental conditions, more than the presence of annual ryegrass residues, reduced pumpkin (*Cucurbita* spp) yields.

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