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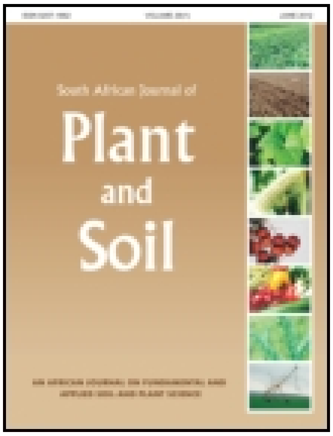

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Influence of glyphosate, other herbicides and genetically modified herbicide-resistant crops on soil microbiota: a review

Karen Wolmarans[a] & Wijnand J Swart[a]
[a] Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa

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Review Paper

Influence of glyphosate, other herbicides and genetically modified herbicide-resistant crops on soil microbiota: a review

Karen Wolmarans and Wijnand J Swart*

Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa
** Corresponding author, e-mail: swartwj@ufs.ac.za*

The use of herbicides and genetically modified crops that are herbicide tolerant (HT) is said to adversely affect soil microbial biodiversity, thus negatively influencing the soil ecosystem. Concern has also been raised regarding the potential increase in crop disease incidence and severity caused by the increased cultivation of HT crops and, specifically, the use of glyphosate-resistant (GR) crops. According to reports, the practice could lead to a decrease in soil fertility and plant nutrition, leading to weakened crops that are more susceptible to pathogen attack. Current literature on how glyphosate, other herbicides and HT crops influence soil microbiota is reviewed. Emphasis is placed on negative and positive effects of herbicides *per se* on soil microbiota. Specific reference is made to the effect of glyphosate and GR crops, either positive or negative, on soil micro-organisms and plant nutrition.

Keywords: genetic modification, glyphosate, herbicides, microbial ecology, resistance

Introduction

The soil ecosystem is extremely complex, containing many thousands of different species of bacteria, protozoa and fungi, as well as micro- and macrofauna (Young and Crawford 2004; Turbé et al. 2010). The spatially and temporally variable soil environment provides many key ecosystem services (Young and Crawford 2004; Turbé et al. 2010) and the maintenance of soil quality is therefore critical for ensuring the sustainability of food production and its positive effect on the environment (Bastida et al. 2008).

Soil is a dynamic system in which physical, chemical and biological components interact (Bastida et al. 2009). Within this system, micro-organisms perform an important task in the decomposition and transformation of organic soil materials, which is crucial for the functioning of the carbon, nitrogen and phosphorus cycles (Bastida et al. 2009). Soil provides a complex medium for many positive and negative interactions with crop plants in the agro-ecosystem, thus affecting the productivity and sustainability of the cropping system above- and belowground (Young and Crawford 2004; Turbé et al. 2010).

A major environmental concern is any negative side effects of pesticides on non-target soil organisms (Carlisle and Trevors 1988). Unfortunately, it is often difficult to measure and predict the impacts of agrochemicals, such as herbicides, on natural communities (Marrs and Frost 1997). Another important factor to keep in mind, when assessing possible impacts of pesticides on the ecosystem, is the fact that pesticides differ from each other with regard to their environmental behaviour and toxicological profile. Differences include chemical structure, different dose–response relationships, the type of organisms sensitive to toxic effects and the nature of toxic effects caused by the pesticide (van Eerd et al. 2003; Kleter et al. 2008).

Since soil micro-organisms play critically important roles in soil ecosystem processes, it is important to examine the impact of herbicides, as well as genetically modified (GM) crops, on the dynamics of micro-organisms in the rhizosphere (Dunfield and Germida 2004). Any impact that GM plants or herbicides may have on the rhizosphere and associated microbes could, in turn, have positive or negative effects on plant health and the soil ecosystem. Transgenic or GM plants possess novel genes that can impart beneficial characteristics such as herbicide tolerance. The potential for interaction between transgenic plants and the soil microbial community is not well understood. Consequently, acknowledgement that these interactions could affect the soil ecosystem has initiated numerous studies. Novel proteins have, for example, been shown to be released from transgenic plants into the soil ecosystem, eventually influencing the biodiversity of microbial communities by selectively stimulating the growth of organisms that can utilise them as nutrients (Araujo et al. 2003; Dunfield and Germida 2004; Andersen et al. 2007; Marais et al. 2011; Partoazar et al. 2011; Zobiole et al. 2012).

Changes in soil microbial communities associated with growing transgenic crops are less drastic and transient in comparison with agricultural practices such as crop rotation, tillage, herbicide usage and irrigation (Dunfield and Germida 2004). Yet, minor alterations in the diversity of the microbial community, such as the removal or appearance of specific functional groups of bacteria such as plant-growth-promoting rhizobacteria, phytopathogenic organisms or key organisms responsible for nutrient cycling processes, can affect ecosystem functioning. The impact of GM crops on the dynamics of rhizosphere microbial populations therefore requires further study (Dunfield and Germida 2004).

Much controversy surrounds the use of glyphosate in agro-ecosystems for weed control. Some researchers believe that the use of glyphosate and glyphosate-resistant (GR) crops hold no threat for agricultural sustainability or soil and environmental quality (Araujo et al. 2003; Cerdeira and Duke 2006; Kleter et al. 2008; Marais et al. 2011; Lane et al. 2012), whereas others choose to believe the opposite (Sanogo et al. 2000; Neumann et al. 2006; Johal and Huber 2009; Kremer and Means 2009; Zobiole et al. 2011, 2012; Druille et al. 2013). Interest in microbial functionality has grown in recent years as researchers seek to understand the relationship between microbial communities and their surrounding environment (Bastida et al. 2009). One approach toward studying the impact of GM plants on soil micro-organisms is to study the structure and functioning of the whole community, rather than to focus on a specific group of micro-organisms (Dunfield and Germida 2004).

This review will focus on (1) the effects, both inhibitory and stimulatory, of herbicides *per se* on soil microbiota in general, with specific reference to glyphosate, and (2) the effect, either positive or negative, that herbicide-resistant crops have on soil micro-organisms and plant nutrition.

The effect of herbicides on soil microbiota

Agrochemical manufacturers constantly pursue the development of agrochemicals that are (1) effective against target organisms, (2) not persistent in the environment and (3) and have low toxicities to non-target organisms (Carlisle and Trevors 1988). However, the regular use of certain agrochemicals in conventional crop management has caused serious environmental and health problems, including loss of biodiversity and certain human disorders (Liu et al. 1999; Ghorbani et al. 2008; Thongprakaisang et al. 2013). Regardless, herbicides are widely used in modern agriculture to control weedy plant species (Liu et al. 1997). To achieve high crop productivity, protection of crops against competition from weeds and attack by pathogens and herbivorous insects is required (Oerke and Dehne 2004). The heavy utilisation of herbicides and their persistence and transfer into trophic food webs can, however, cause major environmental contamination (Imfeld and Vuillemier 2012). Similarly, concern regarding their effect on non-target organisms has grown considerably (Nyström et al. 1999; Cedergreen and Streibig 2005; Sebiomo et al. 2011; Druille et al. 2013).

Serious questions are being raised about the potentially harmful effects of herbicides on consumers and the ecosystem (Zaltauskaite and Brazaityte 2011). There is increasing concern that herbicides not only affect target organisms but also non-target organisms such as microbial communities present in the soil environment (Haney et al. 2002; Partoazar et al. 2011; Sebiomo et al. 2011). These non-target effects may impact on many important soil functions such as organic matter degradation and the nitrogen cycle (Sebiomo et al. 2011; Zaltauskaite and Brazaityte 2011). Ignoring the potential non-target detrimental side effects of any agricultural chemical may therefore have dire consequences for food security, such as rendering soils infertile, crops non-productive and plants less nutritious (Altman and Campbell 1977).

The soil ecosystem can be altered by herbicides through direct and indirect effects on various components of the soil microflora, including saprophytes, plant pathogens, pathogen antagonists or mycorrhizae (Lévesque and Rahe 1992, Ghorbani et al. 2008, Sanyal and Shrestha 2008), which can result in increased or decreased disease incidence. Phytotoxicity and disease enhancement are two of the most commonly reported problems of herbicide use on crops. It is generally accepted that herbicide-induced weakening of a plant can predispose the plant to infection by facultative pathogens (Lévesque and Rahe 1992).

Negative herbicidal effects

The usage of herbicides may have indirect impacts on the whole ecosystem. These indirect impacts may be relatively severe because herbicide effects on target as well as non-target organisms may disrupt community structure and ecosystem function (Zaltauskaite and Brazaityte 2011). Certain herbicides, when applied to soil in large amounts, accumulate, leading to herbicide residues that can be ingested by invertebrates, absorbed by plants or broken-down by microbes into various breakdown products (Subhani et al. 2000; Krutz et al. 2010; Duke et al. 2012). There is often a significant response of soil microbial activity to herbicide treatment, either directly to the herbicide or to the breakdown products of the herbicide. Adaptation of microbial communities to herbicides and associated chemical residues, seen as an increase in microbial activity, can occur over weeks of continuous treatment (Sebiomo et al. 2011).

The introduction of GR crops has greatly increased the volume and scope of glyphosate usage (Cerdeira and Duke 2006) and much is still to be learnt about the fate of glyphosate in soils. A number of counteracting biotic and abiotic factors could be important for determining its degradation rate through the soil profile. Factors such as soil pH, clay content, soil organic carbon (SOC) and soil depth are very important in terms of herbicide degradation and sorption and associated microbial activity (Borggaard and Gimsing 2008). Sorption, which may reflect bioavailability (Jensen et al. 2004), is closely linked to SOC and declines with soil depth. Microbial degradation rates of herbicides are usually assumed to decrease down the soil profile and the amount of herbicides leaching through soil reflects the interaction of degradation and sorption processes in both topsoil and subsoil (Fomsgaard 1995). Most soil microorganisms are present in the top 5 cm of soil where SOC is usually highest (Wolf and Wagner 2005). Sorption, degradation and leaching of glyphosate therefore can be very different from soil to soil, although it has been shown that sorption is more controlled by soil pH and clay content than SOC (Gimsing et al. 2004; Farenhorst et al. 2009).

There is conflicting literature on the effects of glyphosate on mineral nutrition, nitrogen fixation and plant disease on GR crops. Glyphosate is said to reduce shoot concentrations of mineral nutrients in GR soybeans (Zobiole et al. 2010b), and affect photosynthesis, nutrient accumulation and rhizobial nodulation (Zobiole et al. 2012). The extensive use of glyphosate has intensified deficiencies of numerous essential micronutrients and certain macronutrients (Kremer and Means 2009; Tesfamariam et al. 2009). Glyphosate in soil reportedly stimulates oxidative soil microbes that reduce nutrient availability by decreasing their solubility for plant uptake (Kremer and Means 2009). An increase in the proportion of bacteria that oxidise manganese and a decrease in the pseudomonad component that antagonise fungal pathogens have been reported in the rhizosphere of GR soybean and maize (Kremer and Means 2009). Several enzymes function with manganese in the shikimate pathway and are responsible for plant responses to stress and defence against pathogens. Inhibition of the enzymes in the shikimate pathway of a plant renders it highly susceptible to various species of soil-borne pathogens in genera such as *Fusarium*, *Pythium*, *Phytophthora* and *Rhizoctonia* (Lévesque and Rahe 1992; Larson et al. 2006; Johal and Huber 2009; Kremer and Means 2009). In sharp contrast to these reports, Duke et al. (2012) state that most of the literature indicates that mineral nutrition and crop disease in GR crops are not affected by either the GR trait or by the application of glyphosate.

Microbial biomass

Herbicides have been shown to affect microbial biomass in soil. For instance, the use of uracils (HRAC Group $C_1^{(5)}$) and specifically the active ingredient bromacil, reduces microbial biomass significantly, an effect that can last up to 11 months after application (Sanders et al. 1996). A significant reduction in microbial biomass consequently can delay the breakdown of this active ingredient. Furthermore, severe stress on soil microflora caused by bromacil may interfere with the ability of microbes to degrade the herbicide after only two applications with possible consequences for maximum allowed residues in the crop at harvest (Sanders et al. 1996). Similarly, the application of imazethapyr to a silty loam and a loamy soil leads to a shift in the soil community structure as seen in a reduction of soil microbial biomass carbon (Zhang et al. 2010).

Fungi

Plant–herbicide–pathogen interactions can have negative repercussions that should not be ignored (Altman and Campbell 1977). For example, when the roots of plants that have been treated with herbicides die, they become colonised by facultative parasites such as *Pythium* spp., *Rhizoctonia solani* and *Fusarium* spp. as a result of the exudation of sugars and other carbon sources from the dead roots. *Rhizoctonia* root disease of wheat increased when a mixture of paraquat and diquat was applied close to the sowing date (Roger et al. 1994). The problem was due to a lack of competing organisms and was overcome by allowing a greater time between application and sowing date (Roger et al. 1994), in order to allow for competition by soil micro-organisms. It has been observed that the application of glyphosate or paraquat in bean fields also results in an increase of *Pythium* spp. in the soil (Descalzo et al. 1998).

Glyphosate blocks the synthesis of phenylalanine-derived phenols via the inhibition of the enzyme 5-enolpyruvyl shikimic acid-3-phosphate synthase, thereby inhibiting the production of phenolics, including lignin precursors and some classes of phytoalexins involved in resistance of plants to disease (Lévesque and Rahe 1992). Glyphosate also stimulates soil-borne pathogens and other soil microbes to reduce nutrient availability and efficiency and increases drought stress in plants (Johal and Huber 2009; Zobiole et al. 2012). Glyphosate is reportedly a potent microbiocide and because its high degree of sorption to clay minerals increases with decreasing soil pH, it can reduce beneficial organisms involved in the suppression of soil-borne diseases (Lévesque and Rahe 1992; Kremer and Means 2009; Zobiole et al. 2011; Druille et al. 2013).

Glyphosate application increased *Pythium* populations in soil with a high humus content after foliar application to bean seedlings, probably because the root residues of the dying plants caused a temporary elevation in populations of the pathogen, which consequently increased the damping-off potential of the soil (Descalzo et al. 1998). Glyphosate also increased *Fusarium solani* f. sp. *glycines* in the rhizosphere of GR soybean (Sanogo et al. 2000) and disease caused by *R. solani* and *Fusarium oxysporum* f. sp. *betae* in GR sugar beet (Larson et al. 2006). However, Njiti et al. (2003) showed that glyphosate and GR soybean did not increase *Fusarium solani* f. sp. *glycines* significantly. The contradictory effect in GR soybean was presumably due to genotype differences.

Glyphosate has been found to increase root disease of wheat (caused by various *Pythium* spp.) in a minimum tillage situation when it was used to kill weeds close to the date of sowing (Pittaway 1995). The increase was attributed to the pathogens increasing their inoculum potential on the weed residues prior to sowing (Pittaway 1995). This probably occurs because of the predisposition of weeds to *Pythium* infection (Lévesque and Rahe 1992), availability of glyphosate as a nutrient source and a temporary reduction in populations of competing micro-organisms (Partoazar et al. 2011).

Bacteria

Herbicides have been shown to have negative impacts on soil bacterial populations. For example, although no decrease in bacterial numbers in soil treated with atrazine was observed, untreated soil showed an eight-fold increase in bacterial numbers (Cole 1976). Although repeated application of atrazine did not affect the abundance of bacteria producing hydrolytic enzymes, a transient inhibition of bacterial growth was observed during the first week of application (Cole 1976). The mere observation that bacterial numbers did not increase nor decrease with atrazine application does not suggest that this herbicide has no effect on the bacterial populations. In fact, the increase in bacterial numbers in untreated soil suggests that the atrazine does in fact negatively affect bacterial populations by an eight-fold factor.

Soil bacterial populations have also been shown to be much lower, during the first week after herbicide application, in soils treated with atrazine, atrazine and metolachlor, and paraquat and glyphosate, respectively (Sebiomo et al. 2011), while paraquat has also been shown to temporarily stress and inhibit bacterial populations (Kopytko et al.

2002). Glyphosate also has been observed to cause a decrease in pseudomonad populations, which antagonise fungal pathogens in soil (Kremer and Means 2009). It has also been observed that alachlor and paraquat are toxic to bacteria (Sahid et al. 1992).

There are also contradictory studies with respect to glyphosate effects on micro-organisms. The application of glyphosate to unsterile soil is reported to decrease bacterial populations (Mekwatanakarn and Sivasithamparam 1987), and in other instances increase populations (Partoazar et al. 2011). Populations of actinomycetes increased after application of glyphosate, whereas bacteria showed a slight reduction (Araujo et al. 2003). In contrast, no increase of actinomycete or bacteria populations was observed after glyphosate or diquat/paraquat mixture applications (Carlisle and Trevors 1988). In contrast, there are reports that the application of glyphosate and a mixture of diquat and paraquat, respectively, to unsterile soil had no effect on actinomycete numbers (Mekwatanakarn and Sivasithamparam 1987).

Other micro-organisms

Certain herbicides have been shown to be toxic to some soil fauna. For instance, paraquat has been shown to be toxic to non-target organisms, such as Collembola (Curry 1970). Similarly, Zaltauskaite and Brazaityte (2011) observed that the application of sulfonylurea herbicides caused 50–100% mortality of the aquatic micro-invertebrate *Daphnia magna* due to runoff into drainage sites and rivers. Atrazine application to soil may also affect certain Collembola species, such as *Entomobrya musatica* (Al-Assiuty and Khalil 1996). Effects include direct toxicity and negative effects on reproduction and the fecundity of the animals that could adversely affect abundance and development of the organism (Al-Assiuty and Khalil 1996). In contrast, Sabatini et al (1998) observed no direct effect of the herbicide triasulfuron, at the recommended field rate, on the Collembola species *Onychiurus pseudogranulosus*. However, atrazine may be taken up through the body surface, even when applied at the recommended field rate, and lead to a direct lethal effect (Sabatini et al. 1998). Atrazine and monuron have been shown to decrease the number of wireworms (*Agriotes* spp.) and springtails (Collembola suborder Arthropleona) in grassland soils (Fox 1964). Atrazine also has been shown to reduce earthworm populations in grassland soils (Fox 1964) and glyphosate has been shown to be toxic to earthworms Neumann et al. 2006).

Any impact herbicides may have on soil fauna may adversely affect plant health due to a decrease in mineral and oxygen availability as a result of less channelling in soil. A further effect is less predation of potential plant pathogenic organisms by other soil fauna (Brown et al. 2001). Whatever effect herbicides have on soil fauna, it can result in a shift in the soil faunal community that will have a positive or negative impact on ecosystem functions.

Positive herbicidal effects

Degradation by soil micro-organisms is probably the most important and common pathway responsible for the breakdown of herbicides that can have positive effects on soil microbes (Subhani et al. 2000). Some herbicides are degraded by means of co-metabolism, which follows first-order kinetics and the organisms responsible show no capacity to increase following degradation of the compound (Aislabie and Lloyd-Jones 1995). Other herbicides are degraded by growth-linked metabolism, in which organisms responsible for biodegradation have adapted to use the herbicide as an energy and nutrient source, resulting in cell proliferation and an increase in degradation rate over time (Aislabie and Lloyd-Jones 1995).

Most herbicides used at normal field rates are generally considered to have no major or long-term effect on gross soil microbial activities (Subhani et al. 2000; Zabaloy et al. 2008). However, Crouzet et al (2010) also stated that mesotrione, at doses far exceeding the recommended field rates, has an impact on non-target soil organisms. Some reports indicate that herbicide application to soil may lead to the proliferation of general or specific organisms that can utilise a particular chemical in the herbicide for nutrition (Audus 1951; Brazil et al. 1995; Paulin et al. 2011). This observation can be substantiated by the fact that certain herbicides, especially hormone-based types, can disappear from the soil due to microbial decomposition (Chandra et al. 1960).

The synergistic interaction of the microbial community in the rhizosphere may also facilitate degradation of recalcitrant compounds (Costa et al. 2000). For instance, atrazine concentration decreases in the rhizosphere compared to non-vegetated areas (Costa et al. 2000). The degradation of atrazine is higher in a rhizosphere-dominated system, where the half-life is 7 d, compared with non-vegetated soil where the half-life is greater than 45 d (Costa et al. 2000). Similarly, mesotrione, a selective herbicide used for maize crops, applied at the recommended field rate is quickly dissipated from a chernozem soil type and has no consistent impact on soil microbial communities (Crouzet et al. 2010), suggesting that it is degraded by soil micro-organisms.

The degradation of glyphosate in most soils is slow or non-existent, since it is not ‘biodegradable’ and degradation is primarily by microbial co-metabolism, because microorganisms are not able to use glyphosate as a carbon source and because the degradation of glyphosate has been correlated with the general microbial activity of the soil (Borggaard and Gimsing 2008). Araujo et al. (2003) however, claimed that glyphosate is indeed biodegraded by soil micro-organisms and that this phenomenon has a positive effect on soil microbial activity in both the long and short term. Soil microbial activity increases with the application of glyphosate. This could be due to the utilisation of glyphosate as a potential carbon or nutrient source (Partoazar et al. 2011; Duke et al. 2012). In addition, glyphosate may also serve as a more utilisable phosphorus source to soil microbes rather than a carbon source (Partoazar et al. 2011). An increase in microbial activity due to glyphosate application may be beneficial or detrimental toward soil quality. Beneficial effects include increased plant growth and production due to greater availability of nutrients, resulting from mineralisation of glyphosate mediated by soil micro-organisms. On the other hand, increased microbial activity and high microbial populations may also sequester plant nutrients in microbial biomass, decrease crop growth and yields, and increase susceptibility to pests and disease (Yamada and Xe 2000; Wolf and Wagner 2005).

Microbial biomass

The amount of herbicide available to soil micro-organisms depends on various factors, including available nutrients, pH, temperature and moisture, although these factors differ in importance depending on the herbicide involved (Weber et al. 1993). For instance, the application of bentazon at the recommended field rate to soil does not significantly affect the microbial community, even in the absence of microbial degradation (Allievi et al. 1996). The addition of atrazine to a semi-arid soil with low organic matter content, resulting in increased microbial activity, can be explained by adaptation of the resident microbial community to the xenobiotic product (Moreno et al. 2007).

Fungi

Fungal species react differently to herbicides, even within the same genus. For instance, three different basidiomycete species were reported to have different levels of degradation on the herbicides chlortoluron, isoproturon and diuron. *Ceriporiopsis subvermispora* degraded chlortuloron 18%, isoproturon 60% and diuron 18%; *Coniophora puteana* 13%, 69% and 38%, respectively; and *Phlebia radiata* 33%, 25% and 82%, respectively (Khadrani et al. 1999). Claims have been made that repeated application of atrazine does not affect the number of viable fungi in any way (Cole 1976), suggesting that herbicides can elicit different reactions by different fungi. Certain fungal species are benefitted by herbicide addition, whereas others are inhibited (Mekwatanakarn and Sivasithamparam 1987; Lévesque and Rahe 1992; Fernandez et al. 2009). This could lead to the false perception of increased total microbial activity, whereas in fact only a specific population of organisms, which are able to utilise the specific herbicide, are benefited through natural selection (Araujo et al. 2003). For instance, herbicides may reduce the severity of plant diseases by stimulating certain microbial antagonists that can suppress soil pathogens (Katan and Eshel 1973).

In contrast to the negative effect of increasing disease incidence (Descalzo et al. 1998), glyphosate exhibits a positive effect against some fungi, which provide disease control benefits (Anderson and Kolmer 2005; Feng et al. 2008). It has been shown to have both preventive as well as curative activity against *Puccinia striiformis* f. sp. *tritici* and *Puccinia triticina* in GR wheat (Anderson and Kolmer 2005; Feng et al. 2008). Glyphosate also reportedly reduces the incidence of Asian soybean rust, *Phakospora pachyrhizi* in GR soybeans (Feng et al. 2008).

Microbial activity can be stimulated by the presence of glyphosate (Busse et al. 2001; Haney et al. 2002; Partoazar et al. 2011; Duke et al. 2012). Some studies report increased fungal populations following treatment with a mixture of diquat and paraquat (Mekwatanakarn and Sivasithamparam 1987) and glyphosate (Carlisle and Trevors 1988; Lévesque and Rahe 1992; Araujo et al. 2003; Fernandez et al. 2009). Lévesque and Rahe (1992) presented evidence that herbicides can potentially increase or decrease the incidence of plant disease by having a direct effect on various components of the soil microflora, such as plant pathogens, antagonists or mycorrhizae. Fernandez et al. (2009) reported that previous glyphosate use was consistently positively associated with higher Fusarium head blight (FHB) levels caused by the most important FHB pathogens, *Fusarium avenaceum* (teleomorph *Gibberella avenacea* Cook), *Fusarium graminearum* (teleomorph *G. zeae*) as well as other fungi, suggesting that the herbicide might cause changes in fungal communities. Krzyśko-Lupicka and Orlik (1997) observed that glyphosate added to a sandy clay soil, with a history of repeated glyphosate treatment, appeared to select for specific fungal species that were able to use it as a nutrient source. Such shifts in fungal communities might be due to the fact that certain fungi are able to use glyphosate as a nutrient and energy source (Araujo et al. 2003).

Bacteria

The degradation of atrazine in soils is a result of the activity of bacteria that are able to use the compound as a source of carbon or nitrogen (Mandelbaum et al. 1993). Increase in soil microbial respiration observed after atrazine addition thus could be due its utilisation as a substrate for micro-organisms such as *Pseudomonas* spp. (Mandelbaum et al. 1993). The stimulation of bacterial populations in soil by atrazine (Ros et al. 2006) as well as the stimulation of aerobic heterotrophic bacterial populations by glyphosate, 2,4-D-dichlorophenoxyacetic acid (2,4-D) and metsulfuron (Zabaloy et al. 2008) has also been documented. Kremer and Means (2009) reported that glyphosate increases the proportion of bacteria able to oxidise manganese. The heterotrophic bacterial population in a soil with a long history of glyphosate application increases significantly after glyphosate application. This could be due to the bacterial population using the herbicide as a nutrient source (Partoazar et al. 2011). Busse et al. (2000) also observed an increase in total and viable bacteria after glyphosate application, with *Pseudomonas*, *Arthrobacter*, *Xanthomonas* and *Bacillius* spp. increasing in population dominance.

The effect of genetically modified herbicide-resistant crops on soil microbiota

The interaction of GM crops with soil biota is complex, requiring both specific and broad-spectrum assessments (Birch et al. 2007). The soil biotic structure is affected by most of the common variables in agricultural practices, including crop species, water stress, fertilisation, soil tillage, herbicide regimes, pH, SOC, clay content and depth. Thus it is not surprising that GM crops also affect the soil ecosystem (Birch et al. 2007).

In 2005, almost 90% of the 100 million ha of transgenic crops grown annually worldwide were GR or had GR genes stacked with *Bacillus thuringiensis* (BT*)* toxin-based insect-resistant genes, raising concern about GM crop-associated changes in crops and management practices (Birch et al. 2007). Furthermore, the increasing use of GR crops has also increased concerns regarding the potential environmental impact of repeated applications of glyphosate (Haney et al. 2002). Repeated applications of glyphosate are the norm in GM crops. Thus, indirectly, GM crops with over-application of the product over time might have an increased effect on micrororganisms, compared with limited applications in non-GM crops. While no significant negative environmental effects have been documented in areas where these GR crops are grown, claims have been made that GR crops may significantly alter rhizosphere communities (Hart et al. 2009; Zobiole et al. 2011, 2012).

Pline-Srnic (2005) expressed concern among growers about GR crops that include perceptions of increased sensitivity to diseases and environmental stress. Enhanced root colonisation of GR crops by microbes could lead to the development of root disease, competition with roots for nutrients, or selection and enrichment in soils of specific micro-organisms that are either detrimental or beneficial for crop growth (Kremer et al. 2005). Genetically modified crops can have direct negative effects through the toxicity of an expressed GM trait on key non-target species or broader functional groups of micro-organisms (Johal and Huber 2009; Zobiole et al. 2011). There also can be indirect impacts via trophic interactions at multiple levels, and the soil ecosystem can be affected by unintended changes in the metabolism of the GM plant. Furthermore, pathogenic fungi may build up in soil and become a potential problem for subsequent crops, especially GR crops, cultivated in the same field (Kremer et al. 2005; Kremer and Means 2009; Johal and Huber 2009). Knowledge of the impact of transgenic crop residues on soil microbial ecology is therefore essential for understanding the long-term agronomic and environmental effects of GM crops. It can assist in developing appropriate management practices for minimising potential negative impacts of herbicides (Fang et al. 2007).

Impacts on rhizosphere micro-organisms

The potential impact of GM plants on the dynamics of the rhizosphere and root-interior microbial community can be either positive or negative in terms of plant health and ecosystem sustainability. Even only minor alterations in the diversity of microbial communities could affect soil health and ecosystem function (Dunfield and Germida 2004). Based on field evaluations of micro-fauna and micro-organisms, Griffiths et al. (2007) concluded that there are no negative soil ecological consequences for soil biota associated with the use of BT- or herbicide-tolerant (HT) maize in place of conventional cultivars. Other land management options, such as tillage, crop species and a sound pest management regime, have a more significant effect on the biology of soil than GM maize (Griffiths et al. 2007). Yet, certain reports do claim that GR cropping systems change the soil environment by introducing novel compounds and glyphosate into the soil environment (Kremer et al. 2005; Johal and Huber 2009; Zobiole et al. 2011, 2012). Soil microbial communities, in particular rhizosphere microbes, may therefore be particularly sensitive to the effects of transgenic crops because of their close proximity (Dunfield and Germida 2004).

Negative impacts of glyphosate-resistant crops on plant nutrition

The use of HT crops and herbicides, such as glyphosate, in agricultural production systems significantly changes nutrient availability and plant efficiency for a number of essential plant nutrients (Neumann et al. 2006). Increased disease incidence, yield loss and a reduction in crop quality may be the consequence of micronutrient deficiencies. Glyphosate reduces shoot concentrations of mineral nutrients in GR soybeans. Irrespective of glyphosate applications, concentrations of shoot macro- and micronutrients were found to be lower in the near-isogenic GR cultivars compared with their respective non-GR parental lines (Zobiole et al. 2010c). Glyphosate may cause some of these changes either through direct toxicity or indirectly through changes in populations of soil organisms that are important for nutrient access, availability or plant uptake (Neumann et al. 2006).

Unfortunately, very little research has examined the direct and indirect effects of transgenic crops and their management on microbial-mediated nutrient transformation in soil. Despite widespread public concern, no conclusive research has been presented yet that current transgenic crops are causing significant stimulation or suppression of soil nutrient transformation in field environments (Motavalli et al. 2004). Micronutrients play an essential role in plant protection by acting as regulators, activators and inhibitors of plant defence mechanisms that provide resistance to stress and disease (Gordon 2007; Cakmak et al. 2009). The chelation of micronutrients by glyphosate renders them unavailable to plants, which may lead to a compromise in plant defences and an increase in pathogenesis. An increase in the severity of many abiotic as well as infectious diseases of GR as well as non-GR crops also has been observed.

The micronutrient manganese acts as a cofactor that activates 35 different enzymes (Gordon 2007). Some enzymes activated by manganese lead to the biosynthesis of aromatic amino acids such as tyrosine and secondary products such as lignin and flavonoids, which stimulate root nodulation in legumes. In manganese-deficient plants, a lower concentration of lignin and flavonoids leads to a decrease in disease resistance (Gordon 2007). Studies have found that GR soybeans had a manganese deficiency in contrast to conventional soybeans. Evidence also suggests that glyphosate may interfere with manganese metabolism and also adversely affect soil microbial populations responsible for the reduction of manganese to a form available to plants (Gordon 2007). Untreated micronutrient deficiencies can also lead to yield losses, reduced crop quality and increased disease incidence (Huber and Haneklaus 2007). The addition of the herbicide-resistant gene and subsequent repeated applications of glyphosate thus may be a major contributor to nutrient deficiencies in soil.

Early applications of glyphosate have been shown to delay nitrogen fixation and decrease biomass as well as the accumulation of nitrogen in different GR soybean cultivars (King et al. 2001; Zobiole et al. 2010d, 2012). An evaluation of different cultivar maturity groups on different soil types also revealed a significant decrease in macro- and micronutrients in leaf tissue, symbiotic N_2 fixation, photosynthesis and seed composition in GR soybean (Zobiole et al. 2010a, 2010b, 2010c, 2010d, 2010e, 2012). Calcium, magnesium, zinc, manganese and copper were the most commonly reduced mineral nutrients (Zobiole et al. 2010c). Most of the nutrients that were reduced by the GR gene were further reduced when glyphosate was applied (Zobiole et al. 2010c, 2012). Glyphosate may also interfere with uptake and translocation of calcium, magnesium, iron and manganese, by crops, possibly by binding and thus immobilising the nutrients (Cakmak et al. 2009).

Conclusions

A great deal of uncertainty remains regarding the use of herbicides and HT transgenic crops and the possible harmful effects these practices may, or may not, have on soil microbiota and soil fertility (Sahid et al. 1992). Interactions in the soil environment between xenobiotics and soil biota should be viewed as a dynamic process, involving many complex mechanisms (Meharg 1996). By not acknowledging these interactions when investigating the environmental behaviour of herbicides, gross misperceptions of their ecological implications will be fostered (Meharg 1996).

The advent of genetic engineering presents opportunities for novel methods of plant protection against pests with decreased reliance on potentially dangerous chemicals used to control pests and diseases. Generally, few negative impacts are observed with GR crops in comparison to conventional crops. Favourable environmental effects of the glyphosate-containing herbicide regimes on GR crops appear feasible, provided appropriate measures for maintaining biodiversity and prevention of volunteers and gene flow are applied (Kleter et al. 2008). However, literature on the topic is sparse and far more research to investigate the effect that GR crops may or may not have on ecosystem functioning is considered a high priority.

It is clear that the type of herbicide plays a major role with regard to how soil microbes react to it in the soil environment. Sublethal doses of herbicides may either protect or predispose crops to disease (Lévesque and Rahe 1992). Herbicides can directly alter the nature of soil ecosystems through promotion or suppression of activities of plant pathogens or beneficial micro-organisms. Indirect effects include fungal colonisation of roots rapidly following application of certain herbicides; non-specialised facultative pathogens can increase their inoculum potential on weeds, or volunteers treated with herbicide, and subsequently cause crop disease. Soil-borne fungi can act as synergists in the herbicidal action of glyphosate, possibly because glyphosate blocks the production of phenolics involved in disease resistance of plants to these pathogens (Lévesque and Rahe 1992).

The literature reviewed clearly shows that many factors contribute to how free-living soil microbes, rhizosphere microbes and plant pathogens will react to herbicide application, as well as the introduction of transgenic plants into the soil ecosystem. Soil type plays a role with regard to how soil organisms react, because microbial biomass varies significantly between soils depending on soil depth, pH, clay content and SOC (Krzyśko-Lupicka and Orlik 1997; Descalzo et al. 1998; Crouzet et al. 2010; Duke et al. 2012). Furthermore, the mineralisation and microbial degradation of certain herbicides is controlled by active carbon present in the soil (Willems et al. 1996).

Glyphosate application may increase soil microbial activity, which may be either beneficial or detrimental toward plant growth, and soil quality (Partoazar et al. 2011). It should also be kept in mind that increased microbial activity could be perceived as a positive effect. It could be ascribed to an increase in certain groups of microbes that are able to utilise the xenobiotic compound, thus still leading to a shift in the community structure that could in turn lead to negative side effects on crops (Macur et al. 2007).

This review has demonstrated that much controversy exists around the usage of GR crops, glyphosate and herbicides *per se* in terms of the potential negative or positive effects their utilisation may have on mineral nutrition and non-target microbiota that influence crop growth, health and productivity. Maximal utilisation of cultural and management practices that increase the availability of nutrients to negate possible deleterious effects of herbicides and HT crops therefore should be incorporated into crop production programs to facilitate optimal production efficiency and sustainable disease control.

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