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Review

Manipulating legume/cereal mixtures to optimize the above and below ground interactions in the traditional African cropping systems

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The purpose of mixing legume and cereals in the cropping systems is to optimise the use of spatial, temporal, and physical resources both above- and below ground, by maximising positive interactions (facilitation) and minimising negative ones (competition) among the components. The complex interactions in legume/cereal cropping systems such as those used by traditional farmers have received little research attention. Information from such studies is likely to provide an understanding of plant survival strategies when subjected to stress in mixtures. Current knowledge on how plants in mixtures change their biological and chemical environments and the potential benefits associated with such processes are assessed in this review.

Key words: intercropping, microbial biomass, N_2 fixation, phosphatase activities, pH changes.

INTRODUCTION

Mixed culture (or intercropping) of legumes and cereals is an old practice in tropical agriculture that dates back to ancient civilization. The main objective of intercropping has been to maximise use of resources such as space, light and nutrients (Willey, 1990; Morris and Garrity, 1993; Li et al., 2003b), as well as to improve crop quality and quantity (Nel, 1975; Izaurralde et al., 1990; Mpairwe et al., 2002). Other benefits include water quality control through minimal use of inorganic nitrogen fertilisers that pollute the environment (Crew and Peoples, 2004). The current trend in global agriculture is to search for highly productive, sustainable and environmentally friendly cropping systems (Crew and Peoples, 2004). This has resulted into renewed interest in cropping systems research (Vandermeer, 1989).

When two crops are planted together, interspecific competition or facilitation between plants may occur (Vandermeer, 1989; Zhang et al., 2003). For example, studies have shown that mixtures of cereals and legumes produce higher grain yields than either crop grown alone (Mead and Willey, 1980; Horwith, 1984; Tariah and Wahua, 1985; Ofori and Stern, 1987a; Lawson and Kang, 1990; Watiki et al., 1993; Peter and Runge-Metzger, 1994; Skovgard and Pats, 1999; Rao and Mathuva, 2000; Olufemi et al., 2001; Mpairwe et al., 2002; Dapaah et al., 2003). In such crop mixtures, the yield increases were not only due to improved nitrogen nutrition of the cereal component, but also to other unknown causes (Nel, 1975; Connolly et al., 2001).

Many of the unknown and less researched processes occur in the rhizosphere of mixtures (Connolly et al., 2001; Zhang et al., 2003, 2004). The rhizosphere soil is the narrow zone of soil surrounding the roots where soil, micro-organisms and roots jointly play key roles in the ecosystem. Compared with the bulk soil, the rhizosphere has different biological, physical and chemical soil properties. It is rich in root exudates, and, therefore, play a major role in nutrient mobilisation and microbial activities (Dakora and Phillips, 2002; Dakora, 2003). So far however, little attention has been paid to rhizosphere effects on crops grown in mixtures (Connolly et al., 2001;

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Zhang et al., 2003; 2004), where interaction between different organisms is maximal.

The major management practices employed in mixed cultures to attain good yield includes the enhancement of microclimatic conditions, improved utilisation and recycling of soil nutrients, improved soil quality, provision of favourable habitats for plants and stabilisation of soil, among others (Juma et al., 1997). These conditions are achieved by manipulating management practices such as planting patterns of the mixtures.

Although monoculture systems involving cereals and legumes are well researched many of the complex mixed systems such as those practised by farmers in Africa have received little attention. For example, many planting patterns for legumes and cereals exist in Africa whose belowground interactions have received little research attention and hence their ecology still explored (Connolly et al., 2001).

Intercropping systems are deliberately designed and manipulated to optimise the use of spatial, temporal, and physical resources both above- and belowground, by maximising positive interactions (facilitation) and minimising negative ones (competition) among the components (Willey and Osiru, 1972; Willey, 1979; Mead and Willey, 1980; Horwith, 1985; Ofori and Stern, 1986, 1987a, b; Jose et al., 2000; Silwana and Lucas, 2002). An understanding of the biological and chemical processes and mechanisms involved in the allocation of resources in such systems is essential. The complex interactions in legume/cereal cropping systems such as those used by traditional farmers have received little research attention (Connolly et al., 2001; Zhang et al., 2004) because quantitative rhizosphere studies in the field involving complex mixtures are notoriously difficult and cumbersome. Information from such studies is likely to provide an understanding of plant survival strategies when subjected to stress in mixtures.

INTERACTIONS BETWEEN PLANTS IN MIXTURES

Plant-to-plant interactions can occur in the above- or below-ground plant compartments. Interactions will occur in the growth process, especially when the component species are exploiting growth resources above-and below-ground (Vandermer, 1989; Willey, 1990; Ong et al., 1996) from the same location or at the same time. In crop mixtures, any species utilizing the same combination of resources will be in direct competition. However, based on differences in phenological characteristics of species in mixtures, the interaction among them may lead to an increased capture of a limiting growth resource (Willey and Osiru, 1972; Willey, 1979; Mead and Willey, 1980; Horwith, 1985; Ofori and Stern, 1986, 1987a,b; Silwana and Lucas, 2002) and then accrue greater total yield than the cumulative production of those species if they were grown separately on an equivalent land area (Mead and Willey, 1980; Horwith, 1984; Tariah and Wahua, 1985; Ofori and Stern, 1987a; Lawson and Kang, 1990; Watiki et al., 1993; Peter and Runge-Metzger, 1994; Myaka, 1995; Asafu-Agyei et al., 1997; Skovgard and Pats, 1999; Rao and Mathuva, 2000; Olufemi et al., 2001; Dapaah et al., 2003). Thus, mixed culture systems between cereals and legumes may experience a complex series of inter- and intra-specific interaction (Izaurralde et al., 1990; Giller and Cadisch, 1995; Evans et al., 2001; Li et al., 2003c) guided by modifications and utilisation of light, water, nutrients and enzymes. More studies are needed to quantify such interactions in different legume/cereal mixtures such as those used by farmers in Africa.

Rhizosphere interaction in legume cereal mixtures

Most annual crop mixtures such as those involving cereals and legumes are grown almost at the same period, and develop root systems that explore the same soil zone for resources (Horwith, 1984; Chang and Shibles, 1985a,b; Reddy et al., 1994; Jensen et al., 2003). Under such conditions, below-ground competition for resources such as nutrients is most likely to occur. For example, research has shown that activities in mixed cropping systems involving maize and cowpea occur between the top 30 – 45 cm of soil, and their density decreased with depth (Maurya and Lal, 1981; McIntyre et al., 1997). Because of these interactions, cowpea yields can be reduced significantly relative to that of maize (Watiki et al., 1993). In contrast to some negative effects on yield, root systems in mixtures may provide some of the major favorable effects on soil and plants. These include, amongst others, carbon enrichment through carbon turnover (Ridder et al., 1990; Vanlauwe et al., 1997), release of phenolics, phytosiderophores and carboxylic acids as root exudates by component plants (Dakora and Phillips, 2002; Dakora, 2003). These molecules play a major role in the mineral nutrition of plants. For instance, some studies have shown that, in P-deficient soils, pigeon pea roots use piscidic, malonic, and oxalic acids to solubilise Fe-, Ca- and Al-bound P (Ae et al., 1990). Once mobilised, P and Fe then become available for uptake by the pigeon pea plant as well as by other associated plant species and micro flora in the cropping system.

In aluminum-toxic soils, oxalate released by buckwheat roots forms an Al–oxalate complex that renders the Al non-toxic to plants and mutualistic microbes in the cropping system (Ma et al., 1998). In that way, productivity of the cultural system is enhanced. Whether similar processes take place in legume-cereal mixtures such as those used in Africa, and the extent to which they affect the below ground activities, need to be established. This is due to the fact that, thus far, research efforts on mixed cultures has centered on the intra- and inter-specific competition for light and water, and research reports on competition for nutrients in legumes and cereal mixtures in Africa are limited (Connolly et al., 2001; Zhang et al., 2003, 2004). It is, therefore, of greater importance to explore how the rhizosphere systems of the associated plant species in mixtures interact under different legume-cereal cropping systems.

Rhizospheric pH changes in different management systems in legume/cereal mixtures

Many plants have the ability to modify the pH of their rhizosphere (Hoffland et al., 1989, 1992; Raven et al., 1990; Degenhardt et al., 1998; Muofhe and Dakora, 2000; Dakora and Phillips, 2002) and enhance nutrient availability such as P, K, Ca, and Mg, which are otherwise fixed in unavailable forms (Vandermeer, 1989; Hauggaard-Nielson and Jensen, 2005). For instance, legumes induce several reactions that modify the rhizosphere pH (Jarvis and Robson, 1983; McLay et al., 1997; Tang et al., 1998, 2001) and affect nutrient uptake (Brady, 1990; Vizzatto et al., 1999). For example, Dakora et al. (2000) have shown that due to pH changes in the rhizosphere, *Cyclopia genistoides*, a tea-producing legume indigenous to South Africa, increased nutrient availability in its rhizosphere by 45 – 120% for P, 108 – 161% for K, 120 – 148% for Ca, 127 – 225% for Mg and 117 – 250% for boron (B) compared with bulk non-rhizosphere soil. Hence, legumes may take up higher amounts of base cations, and in the process of balancing internal charge, release H^+ ions into the rhizosphere that results in soil acidification (Jarvis and Robson, 1983; McLay et al., 1997; Tang et al., 1998, 2001; Sas et al., 2001; Dakora and Phillips, 2002; Cheng et al., 2004). Other legumes such as alfalfa, chickpea, lupines, and cowpea can release considerable amounts of organic anions and lower their rhizospere pH (Liptone et al., 1987; Dinkelaker et al., 1989, 1995; Braum and Helmke, 1995; Gilbert et al., 1999; Neumann et al., 1999; Rao et al., 2002; Li et al., 2004b), a condition conducive for the hydrolysis of organic P and hence improving P nutrition for plants and micro organism in the soil. In the same context, white lupine (*Lupinus albus*) exuded organic acids anions and protons that lowered rhizosphere pH and recovered considerable amounts of P from the soil and made them more available to wheat than when it was grown in a monoculture (Horst and Waschkies, 1987; Kamh et al., 1999). Similarly, pigeon pea increased P uptake of the intercropped sorghum by exuding piscidic acid anions that chelated Fe^{3+} and subsequently released P from $FePO_4$ (Ae et al., 1990). In a field experiment, faba bean facilitated P uptake by maize (Zhang et al., 2001; Li et al., 1999, 2003b; Zhang and Li, 2003). In another comparative study, the ability of chickpea to mobilise organic P was shown to be greater than that of maize due to greater exudation of protons and organic acids by chickpea relative to maize (Li et al., 2004a).

Thus, in mixed cultures, plants such as cereals, which do not have strong rhizosphere acidification capacity can benefit directly from nutrients solubilised by legume root exudates. What is, however, not clearly known is the extent of rhizosphere pH changes in mixed cultures involving nodulated legumes and cereals and their influence on other biological and chemical processes in the soil.

N_2 FIXATION IN LEGUMES AND THE ASSOCIATED BENEFITS TO THE CEREAL COMPONENT

Biological nitrogen fixation by grain legume crops has received a lot of attention (Eaglesham et al., 1981; Giller et al., 1991; Izaurralde et al., 1992**;** Giller and Cadisch, 1995; Peoples et al., 2002) because it is a significant N source in agricultural ecosystems (Heichel, 1987; Dakora and Keya, 1997). However, studies on N_2 fixation in complex cereal/legume mixtures are few (Stern, 1993; Peoples et al., 2002). Intercropping usually includes a legume which fixes N_2 that benefits the system, and a cereal component that depends heavily on nitrogen for maximum yield (Ofori and Stern, 1986; Cochran and Schlentner, 1995). Controlled studies have shown a significant direct transfer of fixed-N to the associated non-legume species (Eaglesham et al., 1981; Giller et al., 1991; Frey and Schüepp, 1993; Stern, 1993; Elgersma et al., 2000; Høgh-Jensen and Schjoerring, 2000; Chu et al., 2004). There is evidence that the mineralisation of decomposing legume roots in the soil can increase N availability to the associated crop (Dubach and Russelle, 1994; Schroth et al., 1995; Evans et al., 2001). In mixed cultures, where row arrangements and the distance of the legume from the cereal are far, nitrogen transfer could decrease. Research has shown that competition between cereals and legumes for nitrogen may in turn stimulate N_2 fixation activity in the legumes (Fujita et al., 1990; Hardarson and Atkins, 2003). The cereal component effectively drains the soil of N, forcing the legume to fix more N_2. Therefore it is important to manipulate and establish how the management practice in legume/cereal mixtures may influence N_2 fixation and nutrition in the traditional African cropping systems.

SOIL MICROBIAL BIOMASS IN LEGUME/CEREAL MIXTURES

The microbial biomass is influenced by biological, chemical, and physical properties of the plant-soil system. Generally, soil and plant management practices may have greater influence on the level of soil microbial C (Gupta and Germida, 1988; Dick et al., 1994; Dick, 1997; Alvey et al., 2003). For instance, soil microbial C tend to show the highest values in cropland and grassland soils and the lowest in bare cultivated soils (Brookes et al., 1984; Gupta and Germida, 1988).

Monoculture systems are expected to contain reduced amounts of microbial biomass and activities in comparison to those in mixed cultures (Moore et al., 2000). Studies have indicated that legumes accumulated greater amounts of soil microbial C in the soil than cereals (Walker et al., 2003). This is attributed to lower C:N ratio of legume than that of cereal (Uriyo et al., 1979; Brady, 1990).

Microbial biomass activities could increase after the addition of an energy source. The stimulation of soil microbial biomass activity by organic amendments is higher than that induced by organic fertilisers (Bolton et al., 1985; Goyal et al., 1993; Höflich et al., 2000). Soil organic matter content and soil microbial activities, vital for the nutrient turnover and long term productivity of soil, are enhanced by the balanced application of nutrient and/or organic matter/manure (Bolton et al., 1985; Guan, 1989; Goyal et al., 1993; Höflich et al., 2000; Kanchikerimath and Singh, 2001). Under conditions of adequate nutrient supply such as P, the microbial biomass C will be increased due to improved plant growth and increased turnover of organic matter in the soil (Bolton et al., 1985). Whether the management practices in mixed cultures involving legumes and cereals may favour the stimulation of biological soil activity and, thus, result in a higher turnover of organic substrates in the soil that are utilised by micro-organisms is a good subject to be investigated.

Although there is a lot of information that show the relationship between soil management and soil microbial activity, little is known about these effects under mixed cultures such as those practised by farmers in the tropical / subtropical environments (Dick, 1984; Dick et al., 1988; Deng and Tabatabai, 1996). In this context, the measurement of their activities could provide useful information concerning soil health, and also serve as a good index of biological status in different crop management systems.

PHOSPHATASE ACTIVITY IN LEGUME/CEREAL MIXTURES

Plants have evolved many morphological and enzymatic adaptations to tolerate low phosphate availability. This includes transcription activity of acid phosphatases, which tends to increase under P starvation (Tarafdar and Jungk, 1987; Goldstein, 1992; Duff et al., 1994; del Pozo et al., 1999; Haran et al., 2000; Baldwin et al., 2001; Miller et al., 2001; Li et al., 2002). Phosphatase enzymes in the soil serve several important functions, and are good indicators of soil fertility (Dick and Tabatai, 1992; Eivazi and Tabatabai, 1997; Dick et al., 2000). Under conditions of P deficiency, acid phosphatase secreted from roots is increased (Nakas et al., 1987; Chrost, 1991; Hayes et al., 1999; Li et al., 1997). Gilbert et al. (1999) found that white lupin roots from P-deficient plants had significantly greater acid phosphatase activity in both the root extracts and the root exudates than comparable samples from P-sufficient plants. At different stress levels, these enzymes release phosphate from both cellular (Bariola et al., 1994) and extra cellular (Duff et al., 1994) organic compounds. The transcripts and activity of phosphate transporters are increased to optimise uptake and remobilisation of phosphate in P-deficient plants (Muchhal et al., 1996; Daram et al., 1999; Kai et al., 2002; Karthikeyan et al., 2002; Mudge et al., 2002; Versaw and Harrison, 2002). It is thought that these morphological and enzymatic responses to P starvation are coordinated by both general stress-related and P-specific signalling systems.

The amount of acid phosphatase secreted by plants is genetically controlled, and differs with crop species and varieties (Izaguirre-Mayoral and Carballo, 2002) as well as crop management practices (Patra et al., 1990; Staddon et al., 1998; Wright and Reddy, 2001). Some studies have shown that the amount of enzymes secreted by legumes were 72 % higher than those from cereals (Yadav and Tarafdar, 2001). Li et al. (2004a) found that, chickpea roots were also able to secrete greater amounts of acid phosphatase than maize. The activity of acid phosphatases is expected to be higher in biologically managed systems because of higher quantity of organic C found in those systems. In fact, the activity of acid and alkaline phosphatase was found to correlate with organic matter in various studies (Guan, 1989; Jordan and Kremer, 1994; Aon and Colaneri, 2001).

It is, therefore, anticipated that management practices in mixed cultures that induce P stress in the rhizosphere, may also affect the secretion of these enzymes. To date, there have been few studies examining the influence of cropping system on the phosphatase activity in the rhizosphere of most legumes and cereals grown in Africa. Understanding the dynamics of enzyme activities in these systems is crucial for predicting their interactions as in turn their activities may regulate nutrient uptake and plant growth in the ecosystem.

CONCLUSION

Future research should focus on manipulating the legume /cereal mixtures and establish different survival mechanisms that are used by the plants in stressed environments. Efforts should be geared towards closing the existing gap in rhizosphere research in mixed cultures by correctly outlining the unknown factors that affects plant growth in mixtures. This can lead to increased production through improved plant nutrition, as well as genetic manipulation of different plant species and management practices in the cropping systems.

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