

Review article

Changes in plant growth, nutrient dynamics and accumulation of flavonoids and anthocyanins by manipulating the cropping systems involving legumes and cereals- a review

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Abstract

Improved crop production is very important in Africa, especially in such time when food required exceeds food produced. However, improved yield is constrained by a number of biophysical factors including poor planting density, cropping systems and low yielding crop components in mixtures. Manipulation of these factors will not only improve plant growth and grain yield in systems with limited external inputs but will also provide food security and poverty alleviation in small scale farming systems. This review presents the possible influence of these factors on; rhizosphere mineral elements concentration, acid and alkaline phosphatase activities, flavonoids and anthocyanins concentrations, N₂-fixation, photosynthetic activities, leaf chlorophyll contents and their effect on yield improvement in crop components in mixtures.

Keywords: chlorophyll content, phosphatase activities, photosynthesis rate, nutrient concentration, rhizosphere soil.

Abbreviations: LER = Land equivalent ratio, RuBP = Ribulose biphosphate, Rubisco = ribulose-1 - 5-bisphosphate carboxylase/oxygenase.

Introduction

The recent global increases in food and fuel prices have increased the pressure on the agricultural production systems and have caught the attention of many scientists. Previous FAO reports on the state of global food insecurity have shown that about 800 million people in developing countries have insufficient food to eat (FAO, 2000). In sub-Saharan Africa, the food crisis is chronic even though high proportions (70 - 85%) of Africans are active in agriculture (Borlaug, 1991). For example, Africa produced only 5.3% of the world's total cereal crop yield and many reports show that food imports into Africa have increased in the past decade (FAO, 2000; von Braun and Paulino, 1990; World Bank, 1989). According to the World Bank the increase rate of cereal yield in Africa was as low as 0.7% over the years, as opposed to the growth rates of 1.2 - 2.3% in other developing regions of the world (AGRA, 2007). The above mentioned trends are due to low soil fertility, low grain yield, poor N₂ fixing cultivars and cultural practices, severe pests and disease infestations (Boserup, 1981; Cooper et al., 1996; Sanchez et al., 1997). To reverse these trends and increase production of these crops, concerted efforts are needed by various key players. These must be targeted at improving soil fertility; identifying high yielding and N₂ fixing genotypes which are predominantly common in Africa and developing cultural practices which may confer resistance to insect pest and enhance yield stability. This may be achieved by altering plant densities and cropping systems. Cowpea (*Vigna unguiculata* L. Walp.) is among the indigenous African grain legumes grown extensively throughout Africa. It is the most important food legume, fodder and cover crop (Padulosi and

Ng, 1990; Jackai and Adalla, 1997). In addition, to its early maturity potentials, it is versatile in adaptation, drought tolerance, and has a broad range of local genetic diversity. Nutritionally, cowpea grain is rich in protein (20.5 - 31.7%), carbohydrates (56.0 - 65.7%); fat (1.1 - 3.0%), fiber (1.7 - 4.5%) and moisture (6.2 - 8.9%) (Onwuliri and Obu, 2002). The green leaves and young pods of cowpea contain up to 35% protein and are eaten as vegetables. Cowpea also contains other essential nutrients, such as Ca, Fe, nicotinic acid and thiamine (Platt, 1962). Similar to other grain legumes, cowpea has been shown to contain several other important phytochemicals rich in health-related properties (Anderson et al., 1999). Some of the known health promoting phytochemicals in cowpea include phytosterols, saponins, isoflavone, phenolic compounds and antioxidants (Narasinga, 1995; Warrington et al., 2002). Likewise, compounds such as flavonoids, anthroquinones, anthocyanidins and xanthenes commonly present in these legumes, possess remarkable antioxidant activity (Siddhuraju et al., 2002). Diets rich in polyphenolic compounds have been associated with longer life expectancy due to their richness in health-related properties such as anticancer, antiviral, anti-inflammatory activities, effects on capillary fragility and ability to inhibit human platelet aggregation (Stampfer et al., 1993; Deshpande et al., 1996; Hertog and Hollman, 1996). In this regard, increased dietary intake of natural flavonoids and anthocyanins through these legumes may greatly correlate very well with increased health benefits mentioned above. Cowpea has the potential for high grain yields of up to 3,000 kg.ha⁻¹ (Rusoke and Rubaihago, 1994). However, cowpea

grain yields vary widely and are in the average of 200 - 400 kg.ha⁻¹ in Uganda (Sabit et al., 1994), 200 - 300 kg.ha⁻¹ in Nigeria (Alghali, 1992), 400 - 1,000 kg.ha⁻¹ in Cameroon (Langyintuo et al., 2003), 50 - 300 kg.ha⁻¹ in Niger (Sivakumar et al., 1996) and from 1,100 - 1,400 kg.ha⁻¹ in Ghana (Adjei-Nsiah et al., 2008). This implies that farm yields of cowpea ranges between 1.7% and 46.7% of its potential. The observed low yields are attributed to several constraints, including various biological and environmental factors, low levels of symbiotic N₂ fixation, high genotypic variation and poor cultural practices (Onwuliri and Obu, 2002). To increase cowpea production, further work is required on the selection of high yielding genotypes and the assessment of them in different plant densities and cropping systems. Growing cowpea and cereals as intercrops for food production is popular among subsistence farmers in the tropics, sub-tropics, semi arid regions, humid tropics, Mediterranean regions and temperate climates (Francis, 1986). For example it was estimated that 99% of cowpea and 75% of maize (*Zea mays* L.) in Nigeria are grown as mixed culture (Okigho and Greenland, 1976). In Ethiopia, most of the bean production is from mixed culture systems (Seyoum, 1990). Similarly, in Latin America where 60% of maize and 80 - 90% of beans (*Phaseolus vulgaris* L.) are produced by small farmers from mixed culture system (Francis et al., 1976). In Spain, 40% of the cultivated land is used for intercropping (MAPA, 1999). Most of these farmers have adopted this system because they want to maximise space and plant growth resources (Lie et al., 2003b) as well as crop quality and quantity (Mpairwe et al., 2002). However, until recently yields and N₂ fixation from farming practices in Africa has been disappointing and is mainly attributed to poor agronomic practices and low yielding cowpea genotypes used by farmers. Sorghum is the fifth most important small grain cereal crop after wheat, rice, maize and barley (FAO, 2005). It is produced in drier areas of the tropics, often grown in mixture with cowpea in low input cropping systems. In Africa, well managed sorghum crop yields ranged from 1,700 - 4,800 kg.ha⁻¹ (Rohrbach et al., 2005) compared with the currently reported yields of less than 600 kg.ha⁻¹. Growing sorghum in mixture or in succession with cowpea or any other grain legume is one way of improving grain yield. For example sorghum grain yield has been reported to reach 1,620 kg.ha⁻¹ following legume crop compared with 420 kg.ha⁻¹ by continuously growing sorghum (Ncube et al., 2007). Similarly, growing sorghum in mixture with peanuts (*Arachis hypogea* L.) has been shown to be more productive than mono crops combined (Azam-Ali et al., 1990). There is limited information on how different legume plant densities and cropping systems affect sorghum when grown with cowpea genotypes. Plant density defines the number of plants per unit area, which in turn, determines the size of the area available to the individual plant (Wiley, 1979). Plant population is among the major cultural practices that impact on light regimes of the canopy as well as interplant competition, consequently affecting canopy structure and light conversion efficiency (Akunda, 2001). Greater pressure on growth resources has been reported from higher plant densities compared with lower plant densities (Wiley and Osiru, 1972). For instance, in soybean (*Glycine max.* L.), high plant density may influence the extent of the fibrous root system which contributes to enhanced drought tolerance (Pantalone et al., 1999). Similarly, high plant stand may influence foliage arrangement and increased light interception (Fisher and Wilson, 1976). In soybean-sorghum mixed culture, Akunda (2001) reported that varying plant density may be a viable alternative of manipulating the

productivity of crops through their changes in physiological processes. This review seeks to assess the influence of plant density and mixed culture on rhizosphere nutrients, phosphatase activities, flavonoids and anthocyanins concentration, N₂ fixation, photosynthesis and chlorophyll content and yield of cowpea genotypes grown with sorghum.

Some rhizosphere chemical reactions and mineral elements concentration as affected by plant densities, mixed culture practices and different legume genotypes

Several studies have indicated that the rhizosphere pH is greatly influenced by; the relative proportions of cations and anions absorbed by the plant root (Marschner, 1986; Haynes, 1990), the corresponding differences in net excretion of H⁺ and HCO₃⁻ (or OH⁻), excretion of organic and amino acids (Marschner et al., 1987) and release of CO₂ from the roots (Laurent and Eric, 1994). Legumes such as cowpea growing in mixed culture with cereals have the ability to modify soil pH in their rhizosphere (Muofhe and Dakora, 2000; Rao et al., 2002; Li et al., 2004b) through different mechanisms such as response to stress on plant growth in different cropping systems. These mechanisms include net positive excess cations over anions entering the roots of N₂-fixing legumes with characteristic release of protons (Romheld, 1986; Gahoonia et al., 1992). Other mechanisms include changes in redox potential induced by plant roots in the rhizosphere resulting into the release of proton (Ahmad and Nye, 1990), enhanced release of H⁺ as a response to P-deficiency localised behind the root tip as those reported in maize and rape (*Brassica napus* L.) intercrops (Gregory and Hinsinger, 1999) and root excretion of carboxylic acids which are capable of mobilising P by ligand exchange or dissolution and occupation of P-sorption sites (Fox et al., 1990; Gerke, 1995). More recently, Rao et al. (2002) concluded that rhizosphere acidification was light induced and is regulated by photosynthetic activity rather than excess cations uptake in the rhizosphere. These researchers arrived at this conclusion after a NO₃-fed non-symbiotic cowpea plants was put under illumination and significantly raised protons concentration in their rhizosphere similar to the aforementioned mechanisms. As a result of these mechanisms, mineral elements which are otherwise unavailable such as P, K, Ca, and Mg become available for plant nutrition (Vandermeer, 1989; Hauggaard-Nielsen and Jensen, 2005). To date, few studies have reported on the chemistry of the rhizosphere soil, involving complex plant densities, cropping systems and genotypes. A better understanding of such interactions is therefore important.

Phosphatase activities in plant roots and soils as influenced by plant densities, cropping systems and legume genotypes

Phosphatase enzyme activity has been traditionally classified as being acid or alkaline (Vincent et al., 1992). Acid phosphatase enzymes are the principal component of root exudates and occur widely in plant organs (Duff et al., 1994). On the other hand, alkaline phosphatase activity is fungus and bacteria borne mostly found in the soil (Nakas et al., 1987; Tarafdar and Claassen, 1988). Accordingly, these enzymes are involved in the mobilisation of P within the rhizosphere of many cropping systems (Marschner, 1995; Strom, 1997). For example, release of acid phosphatase from roots as root exudates has been implicated as a mechanism to enhance the availability of sparingly soluble mineral elements such as P, Zn, Fe, and Cu (Marschner, 1995; Jones

et al., 1996a). There is evidence that acid phosphatase play major roles in; remobilising internal P from plant organs (Duff et al., 1991; de Pozo et al., 1999; Baldwin et al., 2001), facilitating release of P from organic P-esters by exudation of these enzymes into the rhizosphere (Lefebvre et al., 1990; Miller et al., 2001) and synthesizing glycolate from P-glycolate (Christella and Tolbert, 1978) as well as glycerate from 3-PGA during photorespiration (Randall et al., 1971). The P released is then available for plant nutrition. Such actions could be complex and may benefit the mixed culture systems. Phosphatase activity is greatly affected by soil physical-chemical properties, management practices and cropping systems (Alvarez and Guerrero, 2000; Criquet et al., 2000). Several studies have shown that in different agronomical settings, plants strongly compete with each other for resources (Tilman, 1988; Vandermeer, 1989). In mixed culture systems for instance, optimum intercrop yield advantage is achieved by maximising complementarity while minimising competition between component crops (Willey, 1979; Vandermeer, 1989). The reduction in competition has been suggested to be a primary reason for improved total yields in mixed culture systems (Vandermeer, 1990). Apart from complementary resource use, facilitation has been suggested as a mechanism for obtaining greater total yields in intercrops as opposed to monoculture. Such beneficial interaction could be the result of increased resource availability through root induced changes in the rhizosphere including phosphatase activities (Ae et al., 1990; Vandermeer, 1990). There is evidence that crops that are very good at accessing sparingly available P can have a favourable effect on plants with which they are in mixture with (Horst and Waschki, 1987; Li et al., 2003a). However, plant species and cultivars possess diverse root morphological (Gahoonia et al., 1997) and physiological (Neumann et al., 1999) mechanisms for adapting to low P supply with varying P mobilising processes. Although there is vast literature on acid and alkaline phosphatase activities, effect of different plant densities and cropping systems on these activities (when cowpea and other leguminous genotypes are grown in mixture with cereals such as sorghum) are still inadequate. Availability of such information will provide more understanding of the dynamics of phosphatase activities in mixed cultures and establish their effect on the availability of plant nutrients in such complex systems.

Flavonoids and anthocyanins concentrations as affected by plant densities and cropping systems

Flavonoids and anthocyanins are the major secondary metabolites which occur widely in most plants with a characteristic wide range of colours (Linda, 1999; Dieter, 2006). Physiologically, they are beneficial to the plant itself by acting as effective antioxidants in photosynthetic tissues and screening harmful incident radiation (Hashimoto and Tajima, 1980; Balakumar et al., 1993; Rice-Evans et al., 1997). They also act as protectants of plants from insect pest infestations, diseases and oxidative cell injury (Hedin et al., 1983; Harborne, 1988). On the other hand, the accumulation of these compounds may act as a signal of nutrient limitation in a low plant/soil nutrient environment. For example, flavonoids and anthocyanins accumulation has been related to common nutrient (P, N, K, S, Mn and B) deficiency symptoms in a variety of plants (Murali and Teramura, 1985; Close et al., 2000). These nutritional stresses have been reported to increase flavonoids concentration by regulating availability of substrates expression of enzymes responsible in their synthesis (Yamakawa et al., 1983; Plaxton and

Carswell, 1999). However, some flavonoids induce spore germination and hyphae growth in the establishment of vesicular arbuscular mycorrhizal symbiosis, which is important in P acquisition, uptake and improved soil plant water relationship. Similarly, some studies have shown that flavonoids also act as chemo-attraction in the legume-rhizobium symbiosis at the onset of N₂ fixation process (Caetano et al., 1988; Khan and Bauer, 1988). For example, there is sufficient evidence that some plant flavonoids such as genistein, daidzein and coumestrol function as signals to N₂-fixing microbes leading to interaction with NodD protein of the (*Brady*) *rhizobium* cells, thus, inducing expression of nodulation (*nod*) genes, consequently nodule formation and N₂ fixation (Long, 1989; Recourt et al., 1992; Dakora et al., 1993a; Dakora and Phillips, 1996; Hungria and Stacey, 1997; Phillips, 2000). Furthermore, a group of flavonoids have also been identified as haustoria inducers that promote suicidal germination of *Striga*, a notorious parasitic crop weed in cereals and legumes (Steffens et al., 1982; Ndakidemi and Dakora, 2003). Sorghum has been reported to contain flavonoids such as flavonols, flavonones, flavons and anthocyanins (Haslam, 1998). The most abundant anthocyanins in sorghum grain are 3-deoxyanthocyanidins e.g. apigeninidin and luteolinidin (Awika et al., 2004b) which are particularly abundant in red and black sorghum grain (Dicko et al., 2005a) but rare or absent in other plants (Awika et al., 2004b). In black sorghum for example, apigeninidin and luteolinidin accounted for 50% of the anthocyanins content (Awika et al., 2004a). Apigeninidin and luteolinidin (3-deoxyanthocyanidins) are of interest because they are more stable in organic solvents as well as in acidic solutions than anthocyanidins found in other cereals. Sorghum has been suggested to have a potential advantage as a viable commercial source of anthocyanins reported to have good antioxidant activity (Awika and Rooney, 2004a). It was recently reported that proanthocyanidins such as those found in plants may inhibit the growth of several viruses including human immunodeficiency virus 1 (HIV-1), influenza virus and herpes simplex virus by blocking their entry in the host cells (Hamauzu et al., 2005). Since both cowpea and sorghum are staple food in many of the African countries, growing them in mixed culture may be the main source of natural antioxidants. Flavonoids have also been shown to inhibit seed germination in a variety of legumes and cereal grains and are toxic to seedlings of several species including weeds (Patterson, 1987; Rao, 1990). For example, the flavonoids vitexin and isovitexin which are present in the seed coat of mungbeans are powerful inhibitors of seed germination and seedling growth of other plant species around them (Tang and Zhang, 1986; Khalid et al., 2002). Similarly, triclin and some related flavonoids are considered to be responsible for phytotoxicity exhibited by quack grass residue (Rao, 1990). Therefore, it is suggested that flavonoids may lead to soil sickness and also adversely affect root growth, shoot bleaching, root swelling, inhibition of root hair formation and influences the uptake of mineral elements such phosphate and chloride (Stenlid, 1963; Chang et al., 1969; Rao, 1990). However, the release and accumulation of these phenylpropanoid compounds is dependent on factors such as plant density, cropping systems and genotypes or plant species involved in the cropping systems. It has been reported that flavonoid concentrations vary with cultural practices and varieties (Dykes et al., 2005). For instance, at high plant density many plants occupy the same area and rely on the same resources, thus may become stressed. Similarly, in mixed culture system, more than one crop species grow in a unit area and rely on the same growth factors (Wiley, 1979).

So, high density and mixed culture systems will definitely create competition for the growth factors leading to stress. Similarly, if one of the component crops is competitively stronger for the plant growth factors, stress for such growth factors will then occur (Jensen, 1996). Some studies (Ampong-Nyarko et al., 1994; Hassan et al., 2009; Makoi et al., 2010) have also reported that high plant density and intercropping practices reduced insect pest infestation in cowpea. This was probably due to excessive accumulation of phenolic compounds in plants growing in such systems. Although several studies have shown that stress affects the release of these compounds, further studies are required to assess the effects of flavonoids and anthocyanins compounds in the control of pests (insects, diseases and weeds) in mixed culture systems. Thus, playing important ecological functions such as those involving insecticides, fungicides and herbicides.

Possible influence (s) of different plant densities and cropping systems on N₂ fixation and availability to crops in mixtures

Biological nitrogen fixation (BNF) plays an important role in the N economy of cereal/legume mixed culture. BNF accounted for total N accumulation of between 61 - 77% in cowpea and 58 - 78% in soybean (*Glycine max.* L.) respectively (Ofori et al., 1987; Adjei-Nsiah et al., 2008). Additionally, of the total N accumulated in the component crop such as sorghum, between 11 and 58% was directly transferred through BNF (Fujita and Ofosu-Budu, 1996; Salvagiotti et al., 2008; Peoples et al., 2009). Legume/cereal mixed culture has been reported as potentially advantageous with increased total crop productivity compared with monoculture systems. This has been ascribed to the effective use of water, mineral elements and light in such complex systems (Wiley, 1979; Midmore, 1993; Jensen, 1996). Intercropping system involves simultaneous growing of two or more crops on the same piece of land. Such cultural practices have led to increased size and stability of total grain yield compared with monoculture, especially under small scale and low input farming systems (Ofori and Stern, 1987; Vandermeer, 1989). Amongst others, a reason for mixed culture practices involving legumes and cereal rely on the ability of the legume to fix N₂ which also benefits the associated cereal crop (Heichel, 1987; Dakora and Keya, 1997; Adjei-Nsiah et al., 2008). As a result total grain yields, land use efficiency and efficient utilisation of the limited land resource are increased (Trenbath, 1974; Paperndick, et. al., 1976; Fukai and Trenbath, 1993). A significant direct transfer of fixed N to the associated cereal crop has been observed in controlled studies (Stern, 1993; Elgersma et al., 2000; Chu et al., 2004). Apart from the compelling evidence of increased N availability to the associated crops as a result of mineralisation from the decomposing legume roots (Schroth et al., 1995; Evans et al., 2001), increased total grain yield was also ascribed to less competition and greater complementarity of growth factors between the intercrops (Snaydon and Satorre, 1989; Hauggaard-Nielsen et al., 2001). Legume/cereal mixed culture has been shown to use the available growth resources efficiently compared with their corresponding monoculture (Vandemeer, 1990). However, the efficient use of growth factors in mixed culture systems depends on factors such as plant species, plant morphology, density of component crops, type of management and competitive ability of the component crops (Ofori and Stern, 1987). An improved understanding of how the cropping systems involving different crop components behave with

regard to N fixation will enable proper selection of N fixing leguminous genotypes and the cropping patterns facilitating the process.

Possible influence of altering plant densities, cropping systems and different legume genotypes on photosynthetic activities, leaf chlorophyll contents, δ¹³C and water-use efficiency

Photosynthesis rates and the associated parameters (stomata conductance, intercellular CO₂ concentration and transpiration rate), chlorophyll contents, δ¹³C and water-use efficiency (WUE) are affected by several agronomical factors. It is postulated that changes in plant population in the field, plant arrangements, type of plant species and genotypes involved in such cropping systems would affect photosynthetic parameters (Lima Filho, 2000; Li et al., 2008). Since high plant density is associated with lower grain yield and dry matter due to decreased photosynthesis rate, it is proposed that low plant density will possibly increase such rates (San-oh et al., 2004). For example, increasing plant density has been shown to increase shading in the field, leading to limitation in light intensity, thus, lowering the photosynthesis rate and the associated parameters (Feigenbaum and Mengel, 1979; Hirose et al., 1988; Schieving et al., 1992a). Similarly, the decline in leaf area ratio was related to increased plant density as a result of competition for light (Pons et al., 1989). Several studies have also reported photosynthesis rate variability amongst several crops such as wheat (Evans and Dunstone, 1970; Austin et al., 1982), maize (Heichel and Musgrave, 1969), faba bean (*Vicia faba* L.), pea (*Pisum sativum* L.) (Schulze et al., 1999) and soybean (Buttery et al., 1981) suggesting that the type of component crops involved in cropping systems have an important effect on the gas exchange parameters. For example, variation in C allocated to nodulated legumes and the amount of C respired has been reported to vary with species (Atkins et al., 1978; Herridge and Pate, 1977). Similarly, adaptation to higher C costs during N₂-fixation varies with species. For example, faba bean has greater photosynthetic capacity compared with pea (Schulze et al., 1999). Competition for plant growth factors such as mineral elements under high plant density and mixed culture have led to stress, differences in photosynthesis rates and chlorophyll contents (Akunda, 2001; Ghosh et al., 2006). For example, N and K deficiency due to stress caused by dense population of plants significantly decreased photosynthetic rate and leaf chlorophyll concentration, resulting in increased leaf reflectance (Bednarz et al., 1998; Daughy et al., 2000; Zhao et al., 2001, 2003 & 2005), thus, affecting leaf photosynthetic rate (Muchow and Sinclair, 1994; Zhao et al., 2005). On the other hand, enhancement of plant growth has been closely related to high leaf photosynthesis due to elevated CO₂ concentration, which mostly depends on field plant arrangement and composition such as mixtures. This is because higher CO₂ concentration can suppress RuBP oxygenase activity, decrease photorespiration and increase carbon assimilates for plant growth and development (Lawlor and Mitchell, 2000). Although chlorophyll concentration is an important physiological parameter for indicating plant photosynthesis status, it has been reported that stress related factors may result in increased leaf reflectance due to reduced amount of chlorophyll content. Therefore, affecting its function as an indicator for photosynthesis status in plants (Carter and Knapp, 2001). Plant growth (measured as biomass) is influenced by many factors, including water availability, C accumulation via photosynthesis and the

supply of mineral nutrients. Photosynthetic CO₂ reduction by Rubisco in C3 plants such as cowpea and other legumes is therefore the key process driving growth and agronomic yields in crop species. Theoretically speaking, high ¹³C discrimination (i.e. more negative δ¹³C value) tends to indicate low water-use efficiency, while low ¹³C discrimination (i.e. less negative δ¹³C value) suggests high water-use efficiency (Farquhar and Richards 1984). As a result, the δ¹³C values of crop plant species have been found to correlate with photosynthetic water-use efficiency estimated from gas-exchange studies (Farquhar and Richards 1984). However, very negative δ¹³C values in the leaves of a young legume can also arise from the supply of ¹³C-depleted C to shoots and other organs such as nodules, roots and developing pods by the Rubisco-operated C3 pathway (Yoneyama and Ohtani 1983). But because these organs also fix CO₂ via phosphoenolpyruvate carboxylase (Lawrie and Wheller 1975; Coker and Schubert 1981), this can shift the very negative δ¹³C value of organs to a less negative δ¹³C value. So, it is important to manage agronomic practices by manipulating the cropping systems, plant densities and varieties such that constraints influencing photosynthesis rate and related parameters are minimised. Thus, improving both biological and economical yields of different component crops in mixtures.

Enhanced productivity and grain yield from components in mixed culture systems

Mixed culture advantage (or intercropping productivity) is commonly assessed by land equivalent ratio (LER) (Magino et al., 2004; Dariush et al., 2006). It is defined as the relative land under monoculture that is required to produce the yields achieved under mixed culture (Gocio, 2001). Total land equivalent ratio (LER_t) is obtained by the summation of LER for each crop (i.e. partial LER) in the mixture. When LER_t > 1, mixed culture is advantageous because environmental resources are used more efficiently for plants growth. On the contrary, when LER_t < 1, there is disadvantage because environmental resources are less efficiently used. However, when LER_t = 1 it is considered as there is no effect by growing such crops either as monocrops or intercrops. As shown by Vandermeer (1989), competition and facilitation for growth factors takes place in mixed culture systems. As such, it is possible to obtain the net positive result whereby LER_t > 1, thus indicating that in such mixed cultures, facilitation is contributing more than the competition. In their work on cowpea/sorghum mixed culture with varying number of cowpea rows, Hussain et al. (2000) showed that LER_t > 1 was fairly high in all mixed culture treatments but the highest value of 1.89 was recorded from the sorghum-cowpea 3-rows mixed culture. This indicated that 89% yield advantage was gained due to mixed culture practice attributed to higher facilitation. Likewise, in a wheat (*Triticum aestivum* L.)/chickpea (*Cicer arietinum* L.) mixed culture, LER_t was highest in 4:2 rows, indicating low competition or greater complementary facilitation between the component crops (Zhang and Li, 2003; Li et al., 2004a; Banik et al., 2006). Collectively, the observed mixed culture advantage in these studies were attributed to beneficial complementarities of component crops with regard to mineral elements, light and moisture (Babu et al., 1988). Thus, mixing legumes with cereals could lead to better land use efficiency making it an important component in small scale farming in Africa and other parts of the world. In conclusion, a pre-requisite for a successful legume/cereal intercrops is to obtain adequate plant population density, appropriate cropping system and

highly potential legume genotypes. This will then contribute to the improvement of N₂ fixation, phosphatase activities, flavonoids and anthocyanins and nutrients for plant growth and development.

Acknowledgements

This study was supported by the Cape Peninsula University of Technology through URF project no RP03.

References

- Adjei-Nsiah S, Kuyper TW, Leeuwis C, Abekoe MK, Cobbinah J, Sakyi-Dawson O, Giller KE (2008) Farmer's agronomic and social evaluation of productivity, yield and N₂ fixation in different cowpea varieties and their subsequent residual N effects on a succeeding maize crop. *Nutr Cycl Agroecosyst* 80:199-209
- Ae N, Arihara J, Okada K, Yoshihara T, Johansen C (1990) Phosphorus uptake by pigeon pea and its role in cropping systems of the Indian subcontinent. *Sci* 248:477-480
- AGRA (2007). Alliance for a Green Revolution in Africa: AGRA at work. Retrieved 13th March, 2008 from www.agra-alliance.org/wor
- Ahmad AR and Nye PH (1990) Coupled diffusion and oxidation of ferrous iron in soils. I. Kinetic of oxygenation of ferrous iron in soil suspension. *J Soil Sci* 41:395-409
- Akunda EM (2001) Intercropping and population density effects on yield component, seed quality and photosynthesis of sorghum and soybean. *J Food Technol Africa* 6:96-100
- Alghali AM (1992) Insecticide application schedules to reduce grain yield losses caused by insects of cowpea in Nigeria. *Insect Sci Appl* 13:725-730
- Alvarez S, Guerrero MC (2000) Enzymatic activities associated with decomposition of particulate organic matter in two shallow ponds. *Soil Biol Biochem* 32:1941-1951
- Ampong-Nyarko K, Reddy KV, Nyangor RA, Sexena KN (1994) Reduction of pest attack on sorghum and cowpea by intercropping. *Entomol Exp Appl* 70:179-184.
- Anderson IC, Buxton DR, Hallam A (1999) Performance of annual and perennial crops for biomass production. Department of Agronomy Working paper, Iowa State University, Ames, IA. Atkins CA, Pate JS, Griffiths GJ, White ST (1980) Economy of carbon and nitrogen in nodulated and non-nodulated (NO₃⁻ grown) cowpea (*Vigna unguiculata* L. Walp.). *Plant Physiol* 66:978-983
- Atkins CA, Herridge DF, Pate JS (1978) *The economy of carbon and nitrogen in nitrogen-fixing annual legumes*. Vienna: International Atomic Agency, 211-242.
- Awika JM and Rooney LW (2004) Sorghum phytochemicals and their potential impact on human health. *Phytochem* 65:1199-1221.
- Awika JM, Rooney LW and Waniska RD (2004a) Anthocyanins from black sorghum and their antioxidant properties. *Food Chem* 90:293-301
- Awika JM, Rooney LW and Waniska RD (2004b) Properties of 3-deoxyanthocyanins from sorghum. *J Agric Food Chem* 52:4388-4394
- Azam-Ali SN, Matthews RB, Williams JH, Peacock JM (1990) Light use, water use and performance of individual components of a sorghum/groundnut intercrop. *Exp Agric* 26:413-427
- Babu AM, Lakshmaiah K, Sekhar G (1988) Studies on rainfed sorghum/pulse intercropping system. *J Res APAU* 16:40-42

- Balakumar T, Vincent HB and Paliwal K (1993) On the radiation of UV-B (280-315 nm) with water stress in crop plants. *Physiol Plantar* 87: 217-222
- Baldwin JC, Athikkattuvalasu SK, Raghothama KG (2001) LEPS2, a phosphorus starvation-induced novel acid phosphatase from tomato. *Plant Physiol* 125:728-737
- Banik P, Midya A, Sarkar BK, Ghose SS (2006) Wheat and chickpea intercropping systems in an additive series experiment: Advantages and weed smothering. *Europ J Agron* 24:325-332
- Bednarz CW, Oosterhuis DM, Evans RD (1998) Leaf photosynthesis and carbon isotope discrimination of cotton in response to potassium deficiency. *Environ Exp Bot* 39:131-139
- Borlaug NE (1991) Reaching sub-Saharan Africa's small-scale farmers with improved technology: the Sasakawa-global 2000 experience. *In: Agricultural issues in the 1990s* Garbus I, Pritchard A, Knudsen O (eds.), World Bank, Washington D.C.
- Boserup E (1981) *Population and Technology*. Basil Blackwell, Oxford, UK.
- Buttery BR, Buzzell RI, Findlay WI (1981) Relationships among photosynthetic rate, bean yield and other characters in field-grown cultivars of soybean. *Can J Plant Sci* 61:191-198
- Caetano-Anolles G, Crist-Estes DK, Bauer WD (1988) Chemotaxis of *Rhizobium meliloti* to the plant flavone luteolin requires functional nodulation genes. *J Bacteriol* 170:3164-3169
- Carter GA, Knapp AK (2001) Leaf optical properties in higher plants: Linking spectral characteristics to stress and chlorophyll concentration. *Am J Bot* 88: 677-684.
- Chang C-F, Suzuki A, Kumai S, Tamura S (1969) Chemical studies on 'clover sickness'. Part II. Biological functions of isoflavonoids and their related compounds. *Agric Biol Chem* 33:398-408
- Christeller JT, Tolbert NE (1978) Phosphoglucate phosphatase: purification and properties. *J Biol Chem* 253:1780-1785
- Chu GX, Shen QR, Cao JL (2004) Nitrogen fixation and transfer from peanut to rice cultivated in aerobic soil in an intercropping system and its effect on soil N fertility. *Plant Soil* 263:17-27
- Close DC, Beadle CL, Brown PH, Holz GK (2000) Cold-induced photo inhibition affects establishment of *Eucalyptus nitens* (Deane and Maiden) Maiden and *Eucalyptus globules* Labill. *Trees* 15:32-41.
- Coker GT III, Shubert KR (1981) Carbon dioxide fixation in soybean roots and nodules I. Characterisation and comparison with N₂ fixation and composition of xylem exudates during early nodule development. *Plant Physiol* 67:691-696
- Cooper PJM, Leakey RRB, Rao MR and Reynolds L (1996) Agroforestry and the mitigation of land degradation in the humid and sub-humid tropics of Africa. *Exp Agric* 32: 235-290
- Criquet S, Farnet AM, Tagger S, Le Petit J (2000) Annual variation of phenoloxidase activities in an evergreen oak litter: influence of certain biotic and abiotic factors. *Soil Biol Biochem* 32:1505-1513
- Dakora FD and Keya SO (1997) Contribution of legume nitrogen fixation to sustainable Agriculture in sub-Saharan Africa. *Soil Biol Biochem* 29:809-817
- Dakora FD and Phillips DA (1996) Diverse functions of Isoflavonoids in legumes transcend anti-microbial definitions of phytoalexins. *Physiol Mol Plant Pathol* 49:1-20
- Dakora FD, Joseph CM, Phillips DA (1993) Common bean root exudates contain elevated levels of daidzein and coumestrol in response to *Rhizobium* inoculation. *Mol Plant Microbe Inter* 6:665-668
- Dariush M, Ahad M, Meysam O (2006) Assessing the land equivalent ratio (LER) of two corn (*Zea mays* L.) varieties intercropping at various nitrogen levels in Karaj, Iran. *J Centr Eur Agric* 7:359-364
- Daughy CHT, Walthall CL, Kim MS, de Colstoum EB, McMurtrey III JE (2000) Estimating leaf chlorophyll concentration from leaf and canopy reflectance. *Rem Sensing Environ* 74:229-239
- del Pozo JC, Allona I, Rubio V, Layva A, de la Pena A, Aragoncillo C, Paz-Area J (1999) A type 5 acid phosphatase gene from *Arabidopsis thaliana* is induced by phosphate starvation and by some other types of phosphate mobilizing/oxidative stress conditions. *Plant J* 19:579-589
- Deshpande SS, Deshpande US and Salunkhe DK (1996) Nutritional and health aspects of food antioxidants. p. 361-469. *In: Madhavi DL, Deshpande SS and Salunkhe DK (eds.)*. Food antioxidants. Marcel Dekker, New York.
- Dicko MH, Gruppen H, Traore AS, Van Berkel WJH and Voragen AGJ (2005) Evaluation of the effect of germination on phenolic compounds and antioxidant activities in sorghum varieties. *J Agric Food Chem* 53:2581-2588
- Dieter T (2006) Significance of flavonoids in plant resistance: a review. *Environ Chem Let* 4:147-157
- Duff SM, Plaxton WC (1994) The role of acid phosphatases in plant phosphorus metabolism. *Physiol Plantar* 90:971-800
- Duff SM, Plaxton WC, Lefebvre DD (1991) Phosphate starvation response in plant cells: de novo synthesis and degradation of acid phosphatases. *Proc Nat Acad Sci USA* 88:9538-9542.
- Dykes L, Rooney LW, Waniska RD and Rooney WL (2005) Phenolic compounds and antioxidant activity of sorghum grains of varying genotypes. *J Agric Food Chem* 53:6813-6818
- Elgersma A, Schelplers H, Nassiri M (2000) Interaction between perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) under contrasting nitrogen availability, productivity, seasonal patterns of specie composition, N₂ fixation, N transfer and N recovery. *Plant Soil* 221: 281-299
- Evans J, McNeill AM, Unkovich MJ, Fettel NA, Heenan DP (2001) Net nitrogen balances for cool season grain legume crops and contribution to wheat nitrogen uptake: a review. *Aust J Exp Agric* 41:347-359
- FAO (2000) *FAO Global Information and Early Warning System: Africa Report No. 1*, April 2000
- FAO (2005) *FAOSTAT*. <http://faostat.fao.org/faostat/>
- Farquhar GD, Richards RA (1984) Isotope composition of plant carbon correlates with water use efficiency of wheat genotypes. *Aust J Plant Physiol* 11: 539-552
- Feigenbaum S and Mengel K (1979) The effect of reduced light intensity and sub-optimum potassium supply on N₂ fixation and N turnover in *Rhizobium*-infected Lucerne. *Physiol Plantar* 45:245-249
- Fisher KS, Wilson GL (1976) Studies of grain production in (*Sorghum bicolor* L. Moench.). VII: contribution of plant parts of canopy photosynthesis and grain yield in field situations. *Aust J Agric Res* 27:235-245
- Fox TR and Comerford NB (1990) Low-molecular weight organic acids in selected forest soils in the southern USA. *Soil Sci Soc Am J* 54:1139-1144

- Francis CA (1986) Multiple cropping systems. Macmillan, New York.
- Francis CA, Flor CA, Temple SP (1976) Adapting varieties for intercropping systems in the tropics. *In*: Papandick RI, Sanchez PA, Triplett GB. (Eds.), Multiple Cropping. American Society of Agronomy, Madison, pp. 235-253
- Fujita K, Ofosu-Budu KG (1996) Significance of legumes in Intercropping Systems, Pp. 18-40. *In*: Ito O, Johansen JJ, Adu-Gyamfi K, Katayama JVDK, Kumar Rao and Rego TJ. (eds). Dynamics of Roots and Nitrogen in cropping systems of the Semi arid tropics.
- Fukai S, Trenbath BR (1993) Processes determining intercrop productivity and yields of component crops. *Field Crop Res* 34:247-271
- Gahoonia TS, Care D, Nielsen NE (1997) Root hairs and acquisition of phosphorus by wheat and barley cultivars. *Plant Soil* 191:181-188
- Gahoonia TS, Claassen N and Jungk A (1992) Mobilization of phosphate in different soils by ryegrass supplied with ammonium or nitrate. *Plant Soil* 140:241-248.
- Gerke J (1995) Phosphate, aluminium and iron in the soil solution of three different soils in relation to varying concentrations of citric acid. *Z Pflanzenernaehr Bodenk* 155:339-343
- Ghosh PK, Manna MC, Bandyopadhyay KK, Ajay, Tripathi AK, Wanjari RH, Hati KM, Misra AK, Acharya CL, and Subba Rao A (2006) Interspecific interaction and nutrient use in soybean/sorghum intercropping system. *Agron J* 98:1097-1108
- Gocio M (2001) Intercropping principles and Practises. Agronomy system guide. Fayetteville, AR 72702, Arkansas, USA pp.1-18
- Gregory PJ, Hinsinger P (1999) New approaches to studying chemical and physical changes in the rhizosphere: An overview. *Plant Soil* 211:1-9
- Hamazu Y, Yasui H, Inno T, Kume C and Omanyuda M (2005) Phenolic profile, antioxidant property, and anti-influenza viral activity of Chinese quince (*Pseudocarya sinensis* Schneid.), quince (*Cydonia oblonga* Mill.), and apple (*Malus domestica* Mill.) fruits. *J Agric Food Chem* 53:928-934
- Harborne JB (ed) (1988) The flavonoids. Advances in Research since 1980. Chapman and Hall, London, pp xiii.
- Hashimoto T and Tajima M (1980) Effects of ultraviolet irradiation on growth and pigmentation in seedlings. *Plant Cell Physiol* 21:1559-1571
- Haslam E (1998) Practical polyphenolics: from structure to molecular recognition and physiological action, Cambridge University Press, Cambridge, New York, Melbourne.
- Hassan S (2009) Effect of variety and intercropping on two major cowpea (*Vigna unguiculata* L. Walp) field pests in Mubi, Adamawa State, Nigeria. *J Hort For* 1:14-16
- Hauggaard-Nielsen H, Ambus P, Jensen ES (2001) Temporal and spatial distribution of roots and competition for nitrogen in pea-barley intercrops. A field study employing P-32 technique. *Plant Soil* 236:63-74
- Hauggaard-Nielsen H, Jensen ES (2005) Facilitative root interactions in intercrops. *Plant Soil* 274:237-250
- Haynes RJ (1990) Active ion uptake and maintenance of cation-anion balance: A critical examination of their role in regulating rhizosphere pH. *Plant Soil* 126:247-264
- Hedin PA, Jenkins JN, Collun DH, White WH and Parrott WL (1983) Multiple factors in cotton contributing to resistance to the tobacco budworm, *Heliothis virescens* F. *In*: *Plant resistance to insects*, Hedin PA (ed) American Chemical Society, Washington, DC, 347-367.
- Heichel GH (1987) Legume Nitrogen: Symbiotic fixation and recovery by subsequent crops. *In*: Helsel, Z.R. (eds) Energy in Plant Nutrition and Pest Control. Elsevier Science Publication, Amsterdam pp 63-80
- Heichel GH and Musgrave RB (1969) Varietal differences in net photosynthesis of *Zea mays* L. *Crop Sci* 9:483-486
- Herridge DF, Pate JS (1977) Utilisation of net photosynthate for nitrogen fixation and protein production in an annual legume. *Plant Physiol* 60:759-764
- Hertog MGL and Hollman PCH (1996) Potential health effects of dietary flavonoid quercetin. *Eur J Clinical Nutr* 50:63-64
- Hirose T, Werger MJA, Pons TL, Rhee JWA van (1988) Canopy structure and leaf nitrogen distribution in a stand of *Lysimachia vulgaris* L. as influenced by stand density. *Oecol* 77:145-150
- Horst WJ and Waschkies C (1987) Phosphorous nutrition of spring wheat (*Triticum aestivum* L.) in mixed culture with white lupin (*lupinus-albus* L.). *Pflanzenernaehr Bodenk* 150:1-8
- Hungria M and Stacey G (1997) Molecular signals exchanged between host plants and rhizobia: basic aspects and potential application in agriculture. *Soil Biol Biochem* 29:519-830.
- Hussain I, Jatoi SA, Sayal O, Baloch MS (2000) Green fodder yield and land equivalent ratio of Sorghum – legume association. *Pakistan J Biol Sci* 3:175-176
- Jackai LEN, Adalla CB (1997) Pest management practices in cowpea, a review. Pp. 240-258 *in* Advances in Cowpea Research (Singh BB, Mohan Raj DR, Dashiell KE and Jackai LEN eds.). International Institute of Tropical Agriculture (IITA) and Japan International Research Centre for Agricultural Sciences (JIRCAS), IITA, Ibadan, Nigeria
- Jensen ES (1996) Grain yield, symbiotic N₂-fixation and interspecific competition for inorganic N in pea-barley intercrops. *Plant Soil* 182:25-38
- Jones DL, Prabowo AM, Kochian LV (1996) Kinetics of malate transport and decomposition in acid soils and isolated bacterial populations-the effect of microorganisms on root exudation of malate under Al stress. *Plant Soil* 182:239-247
- Khalid S, Ahmad T and Shad RA (2002) Use of allelopathy in agriculture. *Asian J Plant Sci* 1(3):292-297
- Khan MMA and Bauer WD (1988) Chemotaxis of *Bradyrhizobium japonicum* towards flavones and isoflavones from soybean (abstract No. 760). *Plant Physiol* 86: S-127
- Langyintuo AS, Lowenberg-DeBoer J, Lambert D, Ibro G, Moussa B, Kergna A, Kushwah S, Musa S, and Ntoukam G (2003) Cowpea supply and demand in West and Central Africa. *Field Crop Res* 82:215-231
- Laurent R and Eric M (1994) Factors of acidification of the rhizosphere of mycorrhizal plants: measurement of pCO₂ in the rhizosphere. *Acta Botanica Gall* 144:533-539
- Lawlor DW, Mitchell RAC (2000) Crop ecosystem responses to climatic change: wheat in: Reddy KR, Hodges HF. (Eds). Climate change and Global productivity. CAB International, Wallingford, pp. 57-80
- Lawrie AC, Wheeler CT (1975) Nitrogen fixation in the root nodules of *Vicia faba* L. in relation to the assimilation of carbon. II. The dark fixation of carbon dioxide. *New Phytol* 74:437-445
- Lefebvre DD, Duff SMG, Fife CA, Julien-Inalsingh C, Plaxton WC (1990) Response to phosphate deprivation in *brassica nigra* suspension cells: enhancement of intracellular, cell surface and secreted acid phosphatase

- activities compared to increases in Pi-absorption rate. *Physiologia plantarum* 93:504-511
- Li F, Meng P, Fu D, Wang B (2008) Light distribution, photosynthetic rate and yield in a Paulownia-wheat intercropping system in China. *Agrofor Syst* 74 (2):163-172
- Li L, Tang C, Rengel Z, Zhang FS (2004a) Calcium, magnesium and microelement uptake as affected by phosphorus sources and interspecific root interactions between wheat and chickpea. *Plant Soil* 261:29-37
- Li L, Zhang F, Li X, Christie P, Sun J, Yang S, Tang C (2003a) Interspecific facilitation of nutrient uptake by intercropped maize and faba bean. *Nutr Cycl Agroecosyst* 65:61-71
- Li L, Zhang FS, Li XL, Christie P, Sun JH, Yang SC, Tang C (2003b) Interspecific facilitation of nutrient uptake by intercropped maize and faba bean. *Nutr Cycl Agroecosyst* 68:61-71
- Li SM, Li L, Zhang FS, Tang C. (2004b) Acid phosphatase role in chickpea/maize intercropping. *Ann Bot* 94:297-303
- Lima Filho JMP (2000) Physiological responses of maize and cowpea to intercropping. *Presq agropec bras Brasilia* 35 (5):915-921
- Linda C-S (1999) Environmental significance of anthocyanins in plant stress responses. Invited Review. *Phytochem Photobiol* 70:1-9
- Long SR (1989) Rhizobium legume nodulation: life together in the underground. *Cell* 56:203-214
- Magino HN, Mugisha J, Osiru DSO, Oruko OL (2004) Profitability of sorghum-legume cropping practices among households in Eastern Uganda. *Uganda J Agric Sci* 9:688-692
- Makoi JHJR, Belane AK, Chimphango SBM, Dakora FD (2010). Seed flavonoids and anthocyanins as markers of enhanced plant defence in nodulated cowpea (*Vigna unguiculata* L. Walp). *Field Crops Res* 118:21-27
- MAPA (1999) Anuario de Estadística Agraria. Ministerio de Agricultura, Pesca y Alimentación, Spain.
- Marschner H (1986) Mineral Nutrition of Higher Plants. Academic Press, U.K. 674 pp
- Marschner H (1995) *Mineral nutrition in higher plants, 2nd edn*. Boston, M.A., USA: Academic Press
- Marschner H, Romheld V, Cakmak I (1987) Root induced changes of inherent availability in the rhizosphere. *J Plant Nutr* 10:9-16
- Midmore DJ (1993) Agronomic modification of resource use and intercrop productivity. *Field Crops Res* 34:357-380
- Miller SS, Liu J, Allan DL, Menzhuber CJ, Fedorova M, Vance CP (2001) Molecular control of acid phosphatase secretion into the rhizosphere of proteoid roots from phosphorus-stressed white lupin. *Plant Physiol* 127:594-606
- Mpairwe DR, Sabiiti EN, Ummuna NN, Tegege A, Osuji P (2002) Effect of intercropping cereal crops with forage legumes and source of nutrients on cereal grain yield and fodder dry matter yields. *African Crop Sci J* 10:81-97
- Muchow RC and Sinclair TR (1994) Nitrogen response of leaf photosynthesis and canopy radiation use efficiency in field-grown maize and sorghum. *Crop Sci* 34:721-727
- Muofye ML, Dakora FD (2000) Modification of Rhizosphere pH by the symbiotic legume *Aspalathus linearis* growing in a sandy acidic soil. *Aust J Plant Physiol* 27:1169-1173
- Murali NS, Teramura AH (1985) Effects of ultraviolet-B irradiance on soybean. VI. Influence of phosphorous nutrition on growth and flavonoid content. *Physiologia Plantarum* 63:413-416
- Nakas JP, Gould WD, Klein DA (1987) Origin and expression of phosphatase activity in a semi-arid grassland soil. *Soil Biol Biochem* 19:13-18
- Narasinga RBS (1995) Bioactive phytochemicals in Indian foods. *NFI bulletin* 16.
- Ncube B, Dimes JP, Twomlow S, Mupangwa W, Giller KE (2007) Raising the productivity of smallholder farms under semi-arid conditions by use of small doses of manure and nitrogen: A case of participatory research. *Nutr Cycl Agroecosyst* 77: 53-67.
- Ndakidemi PA and Dakora FD (2003) Legume seed flavonoids and nitrogenous metabolites as signals and protectants in early seedling development. *Funct Plant Biol* 30:729-745
- Neumann G, Massonneau N, Martinoia E, Romheld V (1999) Physiological adaptations to phosphorus deficient during period of root development in white lupin. *Planta* 208:373-382
- Ofori F and Stern WR (1987) Cereal legume intercropping systems. *Adv Agron* 41:41-90
- Ofori F, Pate JS, Stern WR (1987) Evaluation of N₂ fixation and nitrogen economy of a maize/cowpea intercrop system using ¹⁵N dilution methods. *Plant Soil* 102:149-160
- Okigbo BN and Greenland DJ (1976) Intercropping systems in tropical Africa. Pp 63-101 *In: Multiple cropping, Paperndick RI, Sanchez PA, Triplett GB. 1976 (eds). 'Multiple cropping'. American Society of Agronomy, p. 378 special publication No. 27. American Society of Agronomy, Madison, WI*
- Onwuliri VA and Obu JA (2002) Lipids and other constituents of *Vigna unguiculata* and *Phaseolus vulgaris* grown in northern Nigeria. *Food Chem* 78:1-7
- Padulosi S, Ng NQ (1990) Wild *Vigna* species in Africa: their collection and potential utilization. Pp. 58-77. *In Cowpea Genetic Resources (Ng NQ and Monti LM, eds.)*. IITA, Ibadan, Nigeria
- Pantalone VR, Rebetzke GJ, Burton JW, Thomas E. Carter TE Jr, Israel DW (1999) Soybean PI 416937 Root System Contributes to Biomass Accumulation in Reciprocal Grafts *Agron J* 91:840-844
- Paperndick RI, Sanchez PA, Triplett GB (1976) 'Multiple cropping'. American Society of Agronomy, p. 378 (special publication)
- Patterson DT (1987) Effects of allelopathic chemicals on growth and physiological responses of soybean (*Glycine max*). *Weed Sci* 29:53-59
- Peoples MB, Brockwell J, Herridge DJ, Rochester IJ, Alves BJR, Urquiaga S, Boddey RM, Dakora FD, Bhattarai S, Maskey SL, Sampet C, Rerkasem B, Khan DF, Hauggaard-Nielsen H, Jensen ES (2009) The contribution of N₂-fixing crop legumes to the productivity of agricultural systems. A review article. *Symbiosis* 48:1-17
- Philips DA (2000) Biosynthesis and release of rhizobial nodulation gene inducers by legumes. *In Prokaryotic nitrogen fixation: A modal system for the analysis of a biological process (Ed. EW Triplett) pp. 349-364. (Horizon scientific press: Wymondham)*
- Platt BS (1962) "Table of Representative values of food commonly used in tropical countries", *Medical Research Council, Special Rep. Series No. 302*, HMSO, London.
- Plaxton WC, Carswell MC (1999) Metabolic aspects of the phosphate starvation responses in plants: In: Lerner HR, ed. *Plant responses to environmental stress: from phytohormones to genome reorganization*. New York, NY, USA: Marcel-Dekker, 350-372
- Pons TL, Schieving F, Hirose T, Werger MJA (1989) Optimization of leaf nitrogen allocation for canopy

- photosynthesis in *Lysimachia vulgaris* (L.). In: Lambers H, Cambridge ML, Kinings H, Pons TL (eds). Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic, The Hague, pp 175-186
- Randall DD, Tolbert NE, Gremel D (1971) 3-Phosphoglycerate in plants II. Distribution, physiological considerations and comparison with phosphoglycolate phosphatase. *Plant Physiol* 48:480-487
- Rao AS (1990) Root flavonoids. *Bot Rev* 56:1-84
- Rao TP, Yano K, Iijima M, Yamauchi A, Tatsumi J (2002) Regulation of rhizosphere by photosynthetic activity in cowpea (*Vigna unguiculata* L. Walp.) seedlings. *Ann Bot* 89:213-220.
- Recourt K, van Tunen AJ, Mur LA, van Brussel AAN, Lugtenberg BJJ and Kijne JW (1992) Activation of flavonoids biosynthesis in roots of *Vicia sativa* sub-sp. *nigra* by inoculation with *Rhizobium leguminosarum* biovar *viciae*. *Plant Mol Biol* 19:411-420
- Rice-Evans CA, Miller NJ, Paganga G (1997) Antioxidant properties of phenolic compounds. *Tr Plant Sci* 2:152-159
- Rohrbach DD, Mashigaidze AB, Mudhara M (2005) The distribution of relief seed and fertilizer in Zimbabwe. Lesson derived from the 2003/04 season. FAO/ICRISAT Zimbabwe
- Römheld V (1986) pH-Veränderungen in der Rhizosphäre verschiedener Kulturpflanzenarten in Abhängigkeit vom Nährstoffangebot. *Potash Rev* 55:1-8
- Rusoke DG, Rubaihago PR (1994) The influence of some crop protection management practices on yield stability of cowpeas. *African Crop Sci J* 2:143-148
- Sabiti A, Nsubuga ENB, Adipala E, Ngabibeki DS (1994) Socio-economic aspects of cowpea production in Uganda. A rapid rural appraisal. *Uganda J Agric Sci* 2:59-99.
- Salvagiotti F, Cassman KG, Specht JE, Walters DT, Weiss A, Dobermann A (2008) Nitrogen uptake, fixation and response to fertilizer N in soybeans: A review. *Field Crop Res* 108:1-13
- Sanchez PA, Shepherd KD, Soule MJ, Place FM, Buresh RJ, Izac A-MN, Mokwunye AU, Kwasiga FR, Nderitu CG and Woomer PL (1997) Soil fertility replenishment in Africa: an investment in natural resource capital. In: Buresh RJ, Sanchez PA and Calhoun FG (eds) Replenishing Soil Fertility in Africa, pp 1-46. SSSA Special Publication Number 51. Soil Science Society of America, Madison, WI, USA
- San-oh Y, Mano Y, Ookawa T, Hirasawa T (2004) Comparison of dry matter production and associated characteristics between direct-sown and transplanted rice plant in a sub-merged paddy field and relationships to planting patterns. *Field Crop Res* 87: 43-58
- Schieving F, Pons TL, Werger MJA, Hirose T (1992) The vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. *Plant Soil* 14:9-17
- Schroth G, Kolbe D, Balle P, Zech W (1995) Searching for criteria for the selection of efficient tree species for fallow improvement, with special reference to carbon and nitrogen. *Fertilizer Res* 42:297-314
- Schulze S, Keatinge JDH and Wells JG (1999) Productivity and residual effects of legumes in rice-based cropping systems in a warm-temperate environment. I. Legume biomass production and N fixation. *Field Crops Res* 61:23-35
- Seyoum K (1990) Haricot bean production in Kaffa Region: Current status and opportunities for the future. In: Research on Haricot bean in Ethiopia, Proceedings of Bean Research Planning National Workshop, Addis Ababa, Ethiopia, pp. 24-29
- Siddhuraju P, Mohan PS, Becker K (2002) Studies on the antioxidant activity of Indian laburnum (*Cassia fistula* L.): A preliminary assessment of crude extracts from stem bark, leaves, flowers and fruit pulp. *Food Chem* 79:61-67
- Sivakumar MVK, Ntare BR and Roberts JM (1996) Growth, yield and plant water relations of four cowpea (*Vigna unguiculata* [L.] cultivars in the Sahel. *J Agric Sci Camb* 126:183-190
- Snaydon RW, Satorre EH (1989) Bivariate diagrams for plant competition data: modifications and interpretation. *J Applied Ecol* 26:1043-1057
- Stampfer MJ, Henneekens CH, Manson JE, Colditz GA, Rosner B, and Willet WC (1993) Vitamin E consumption and the risk of coronary disease in women. *New England J Med* 328:1444-1449
- Steffens JC, Lynn DG, Kamat VS, Riopel JL (1982) Molecular specificity of haustorial induction in *Agalinis purpurea* (L.) Raf. (Scrophulariaceae). *Ann Bot* 50:1-7
- Stenlid G (1963) The effects of flavonoid compounds on oxidative phosphorylation and on the enzymatic destruction of indoleacetic acid. *Physiologia Plantarum* 16:110-121
- Stern WR (1993) Nitrogen fixation and transfer in intercrop system. *Field Crop Res* 34:335-356
- Strom L (1997) Root exudation of organic acids: importance of nutrient availability and the calcifuge and calcicole behaviour of plants. *Oikos* 80:459-466
- Tang CS and Zhang B (1986) Qualitative and quantitative determination of the allelochemical sphere of germinating mung bean. pp. 229-242. In: Putnum and Tang CS, Eds. The Science of Allelopathy. John Wiley and Sons, New York
- Tarafdar JC, Claassen N (1988) Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatase produced by plant roots and microorganisms. *Biol Fert Soils* 5:308-312
- Tilman D (1988) Plant strategies and the dynamics and function of plant communities. Princeton University press, Princeton, New Jersey, USA. 360p
- Trenbath BR (1974) Biomass productivity of mixtures. *Adv Agron* 26:177-210
- Vandermeer J (1989) The ecology of intercropping. Cambridge University press, Great Britain, Cambridge 237 pp.
- Vandermeer JH (1990) Intercropping. In: Agroecology. Eds. Carrol CR, Vandermeer JH and Rosset PM. Pp. 481-516. McGraw-Hill, New York, USA
- Vincent JB, Crowder MW and Averill BA (1992) Hydrolysis of phosphate monoesters: a biological problem with multiple chemical solutions. *Tr Biochem Sci* 17:105-110
- von Braun J, Paulino L (1990) Food in sub-Saharan Africa: trends, policy changes for the 1990s. *Food Policy* 15:505-517
- Warrington RT, Hale AL, Scheuring DC, Whitaker DW, Blessington T, and Miller Jr. JC (2002) Variability for antioxidant activity in cowpea (*Vigna unguiculata* (L.) Walp) as influenced by genotype and post harvest re-hydration. *HortSci* 37:738
- Wiley RW (1979) Intercropping, its importance and research needs. Part I. Competition and yield advantage. *Field Crop Abstr* 32:1-10
- Wiley RW, Osiru DS (1972) Studies on mixtures of maize and beans (*Phaseolus vulgaris* L.) with particular reference to plant population. *J Agric Sci* 79:517-529

- World Bank (1989) Sub-Saharan Africa: from crises to sustained growth. A long-term perspective study, Washington D.C.
- Yamakawa T, Kato S, Ishida K, Kodama T, Minoda Y (1983) Production of Anthocyanins by *Vitis* Cells in Suspension Culture. *Agric Biol Chem* 47:2185-2191
- Yoneyama T, Ohtani T (1983) Variations of Natural ¹³C Abundances in Leguminous Plants. *Plant Cell Physiol* 24:971-977
- Zhang F, Li L (2003) Using competitive and facilitative interactions in intercropping systems enhances crop productivity and nutrient-use efficiency. *Plant Soil* 248:305-312
- Zhao D, Oosterhuis DM, Bednarz CW (2001) Influence of potassium deficiency on photosynthesis, chlorophyll content, and chloroplast ultrastructure of cotton plants. *Photosynthetica* 39:103-109
- Zhao D, Reddy KR, Kakani VG, Read JJ, Carter GA (2003) Corn (*Zea mays* L.) growth, leaf pigment concentration, photosynthesis and leaf hyperspectral reflectance properties as affected by nitrogen supply. *Plant Soil* 257:205-217
- Zhao D, Reddy KR, Kakani VG, Reddy VR (2005) Nitrogen deficiency effects on plant growth, leaf photosynthesis, and hyperspectral reflectance properties of sorghum. *Eur J Agron* 22:319-403