Introduction

The demand for increased food production is concomitant to the continued growth of the world population. The severity of food shortage is especially serious, in the socalled developing countries, in Africa, Latin America and Asia (Chapin, 1987). In most of these countries, agriculture is faced with major problems of low soil fertility where semiarid, saline and calcareous soils constitute a large proportion of the land. Moreover, soil fertility is further threatened by cultivation practices such as continuous cropping, irrigation problems and soil erosion (Sauerbeck and Helal, 1990). Nevertheless, food demand must be met, consequently, crop cultivation expanded into marginal areas for crop production with regard to nutrient elements and water supply. Low productivity could be overcome to some extent by the use of high-yielding cultivars, however, such cultivars have large nutrient demand which can not be met under the soil conditions described previously. Soil fertility could be improved by adding fertilisers, a choice which is very restricted by the lack of enough capital and fertilisers availability. The low availability of nutrient elements due to fixation, for example, of phosphorous in calcareous soils (Sauerbeck and Helal, 1990) leads to reduced fertiliser efficiency. Unlimited chemical fertiliser use and decreased fertiliser efficiency present serious hazards to the environment through water and air pollution. A promising alternative could be the use of nutrient efficient cultivars. Use of these cultivars could be one of the major components contributing to land use systems, which enable maximum output with minimum input, sustain resources and conserve the environment. Growing nutrient-efficient species or cultivars could mean more efficient soil nutrient and fertiliser use as well as an environmental protecting approach which minimises the use of chemicals, and introduce a strategy of "tailoring the plant to fit the soil" (Rengel, 1999).

Nutrient efficiency

It is now recognised that various species and cultivars within a species vary widely in their ability to thrive in nutrient-deficient environments, indicating that plants differ greatly in their nutrient efficiencies (Jianjun and Gabelman, 1995; Cakmak et al., 1997; Fageria et al., 2001). There is much controversy concerning the concept of nutrient efficiency. However, definitions of nutrient efficiency are based on those emphasising productivity and those emphasising internal nutrient requirement

(Gourley et al., 1994). Considering yield parameters, efficiency with regard to a specific mineral nutrient, is the ability of a species or cultivar to produce a high yield, in a soil limiting in this particular nutrient element for a standard species or cultivar (Buso and Bliss, 1988). Agronomic efficiency is the total harvestable product per unit nutrient applied (Sauerbeck and Helal, 1990; Caradus, 1990). External efficiency or requirement is the nutrient content in the soil necessary to produce a certain portion, for example, 90% of maximum yield (Föhse et al., 1988). Another measurement of nutrient efficiency is the yield response per unit of added nutrient (Blair, 1993). Nutrient efficiency related to utilisation is the dry matter produced per unit nutrient element in the dry matter (Godwin and Blair, 1991). It is equivalent to the reciprocal of the nutrient concentration in the entire plant, often termed as the nutrient efficiency ratio (Gourley et al., 1994). Other workers used nutrient uptake efficiency (Claassen and Jungk, 1982; Buso and Bliss, 1988). Uptake efficiency is defined in terms of total uptake per plant or specific uptake per unit root length (Marschner, 1995). It is related to morphological root characteristics such as root system size and root diameter, which mean an increased root surface per unit of root weight, and root hairs, which allow for efficient nutrient scavenging of a larger soil volume. The second component of the uptake efficiency is the root physiological activity such as differing uptake kinetics, that is maximum uptake (I_{max}), Michaelis Menten kinetics (K_m) and minimum soil solution nutrient concentration (C_{Lmin}), which result in different nutrient uptake rates per unit root and time (Steingrobe and Claassen, 2000). Other mechanisms, which affect the specific uptake efficiency include, chemical mobilisation of nutrients by root exudates, induced pH changes in the rhizosphere and vesicular-arbuscular mycorrhizal (VAM) associations (Marschner, 1995).

Nutrient-efficient species, possess either morphological or physiological characteristics that facilitate higher nutrient uptake and/or better nutrient utilisation, or are able to chemically influence the rhizosphere with a consequent improved nutrient availability (Sattelmacher et al., 1994). Such species are useful in minimising leaching loss of, for example, NO₃, which may be found in the soil in plant available form, and are of paramount importance for taking up such nutrients, which are present in large total amounts in the soil, with relatively small plant available fractions and low concentrations in the soil solution, for example, P, K, Fe, Zn, Cu and Mn (Rengel, 1999).

Potassium fractions in soil

Potassium is one of the most abundant mineral elements and widely distributed constituent of the surface rocks of the earth, making up an estimated 2.6% of the earth's crust by weight, mostly present in minerals classified as feldspars and micas (Black, 1957). Feldspars occur exclusively in sand and silt fractions and to some extent in coarse clay. The micacious biotite and muscovite occur mainly in sand and silt, whereas illite is the main potassium-bearing mineral in the clay fraction of the soil. Except for illite which is of secondary origin, the other mentioned minerals could be of primary or secondary origin (Black, 1957). In feldspars K is imbedded in a crystalline aluminosilicate structure in which the K atom is surrounded and bonded to oxygen atoms. Each K atom is isolated from other K atoms by the bonds in the aluminosilicate part of the crystal structure, extending to completely surround each K atom. Potassium in micas is embedded in a crystalline aluminosilicate structure, but the K atoms lie in planes between molecular aluminosilicate network. Each K atom is surrounded by and bonded to oxygen atoms, however, the aluminosilicate layers are bonded together through the potassium ions by two separate sets of bonds, with each set in the molecular aluminosilicate layer on either side of the K. Potassium is found in soil in different forms with different solubility, depending on whether it is unspecifically electrostaticly bound to the soil colloids or specifically bound in the interlayer of clay minerals (Martin and Sparks, 1985). Hence, potassium is found in the soil liquid phase as exchangeable K, which is un-specifically bound, as fixed K, which is in the interlayer of 3-layer clay minerals specifically bound fraction and matrix-bound K, which is part of the crystals building minerals. The different fractions are also characterised by their extraction method, hence, the fraction which is released by repeated extraction with a 1 M ammonium acetate solution (pH 7), represents the exchangeable K and the remaining fractions represent nonexchangeable K (Scheffer and Schachtschabel, 1998). Depending on the soil type, climate and fertilisation level, adsorbed or readily exchangeable K is only around 100-1000 kg K ha⁻¹. The K concentrations in the soil solution are mostly in the range of 2-20 mg L⁻¹. The different K fractions are in equilibrium as: K in solution \leftrightarrow exchangeable $K \leftrightarrow$ non-exchangeable K, where the equilibrium between the K in solution and exchangeable K is relatively more quickly established than that between exchangeable and non-exchangeable K (Scheffer and Schachtschabel,

1998). Generally soils rich in clay, and depending on their vermiculite and illite content, tend to render water soluble and exchangeable K into a non-exchangeable form, this phenomenon is called "K fixation". It indicates a decrease in the extractability of potassium as a result of interaction of originally soluble or extractable potassium with a soil or mineral (Black, 1957). Three soil characteristics have been found significant with regard to potassium fixation. It increases with: 1) clay content 2) increasing pH (Schachtschabel and Köster, 1960; Kaila, 1965). The third property is the degree of potassium saturation of the cation exchange capacity (CEC), where K fixation is little or non-existent in soils having a potassium saturation exceeding about 4.5%, while those with potassium saturation below about 4% have an increased K fixation (Chaminade, 1936). Potassium fixation is higher in sub-soil as compared to surface soil. In the field K is fixed after an extreme drying of the soil. Potassium fixing is extremely high in clay and loam soils, with expanded 3-layer clay minerals having high charge and low exchangeable K. Such soils are formed from river sediments and are rich in fine clay particles (<0.2 µm). They are formed as a result of the weak transport momentum of the flowing water (Scheffer and Schachtschabel, 1998).

Potassium efficiency

Several researchers reported that plant species differ in their K efficiency (Gardiner and Christensen, 1990; Meyer, 1993; Jianjun and Gabelman, 1995; Trehan and Claassen, 1998; Zhang et al., 1999; Steingrobe and Claassen, 2000; Fageria et al., 2001). Plant species take up considerable amounts of non-exchangeable K, which is the K fraction not extractable by ammonium acetate (Schachtschabel, 1937; Kuchenbuch and Jungk, 1984). However, plant species vary greatly in their ability to acquire non-exchangeable K due to variations in their root morphological and physiological characteristics (Mengel and Steffens, 1985). Therefore, efficient plant species, which are able to make use of the normally not readily available K, could have a significant agronomic importance. Differing K uptake efficiency of plant species was reported for plants grown in nutrient solution (Meyer, 1993; Trehan and Claassen, 1998), and for plants grown in the soil (Fageria et al., 2001), indicating that K uptake depends on plant and soil factors. This is to be expected, since nutrient uptake by plants from the soil results from interactions occurring at the soil-

root interface (Claassen et al., 1986). It is a complex sequence of steps including desorption of ions from the solid phase, movement of nutrients towards the absorbing root, transport of ions through the membranes of the root cells towards the root xylem vessels and transport to the shoot (Claassen and Steingrobe, 1999). As such it is influenced by various soil and plant parameters and their interactions.

Soil and plant parameters related to K uptake from soil

Potassium concentration in the soil solution is often low (Rengel, 1993). As such mass flow, which depends on the water flux and concentration in the soil solution, plays a minor role in K nutrition of plants (Claassen, 1994), and K transport to the roots by diffusion is a quantitatively important process. Hence, soil factors which influence transport play a decisive role in K uptake by plants. The diffusive flux depends on the effective diffusion coefficient (D_e) and the concentration gradient. The effective diffusion coefficient depends on the diffusion coefficient in water (D_L), the buffer power (b), the volumetric water content (Θ) and the tortuosity factor (f). The concentration gradient depends on the difference between the concentration at the root surface (C_{L0}) and the soil solution concentration (C_{Li}) (Claassen and Steingrobe, 1999). Plant factors which influence K uptake include root morphological characteristics such as the root radius (r_0) and root hairs, which increase the root surface area and lead to more efficient K exploitation from a larger soil volume, and the physiological root activity described by the uptake kinetics: I_{max} , K_m and C_{Lmin} (Jungk and Claassen, 1997).

Furthermore chemical mobilisation of nutrients by plant roots, for example, by root exudates or their interactions with micro-organisms may be important for nutrient uptake efficiency (Marschner et al., 1986; Rengel, 1999).

Simulation models for nutrient uptake from soil

Nutrient simulation models are useful to improve our understanding of the processes governing soil supply and plant uptake of mineral nutrients. Two general categories of models are recognised (Rengel, 1993). Empirical models (Yerokun and Christenson, 1990), which describe observed phenomena by statistical means and regressions without trying to explain how they happen. They describe input-output relations not taking into account the underlying processes and as such are often

called "black-box" models (Claassen and Steingrobe, 1999). Empirical models are suitable for practical objectives, since they employ a low number of easily obtainable parameters and the results are sufficient for practical use. The other category includes the mechanistic models (Nye and Marriot, 1969; Claassen and Barber, 1976; Cushman, 1979; Claassen et al., 1986; Claassen, 1994), which try to explain observed phenomena by means of basic biophysical, biochemical and physiological mechanisms, and mathematical description of the underlying processes and as such are more suited for scientific use (Rengel, 1993; Claassen and Steingrobe, 1999). Mechanistic models allow for the understanding of the underlying processes, whereby ideas can be proved, improved or rejected. They enable testing the correctness of our concepts about the interactions between plant and soil with regard to nutrient uptake by comparing modelled and observed results, where a lack of agreement shows areas in which more information and research is needed. Moreover, mechanistic models are valuable means for gaining access to calculating not easily measurable data such as nutrient concentration at the root surface, and for calculating the nutrient uptake from soils as affected by the involved soil and plant factors. By conducting a sensitivity analysis, where only a single input parameter is changed, it is possible to quantify the significance of individual soil and plant factors influencing uptake of a specific nutrient (Claassen et al., 1986; Rengel, 1993; Claassen and Steingrobe, 1999).

To simulate K uptake by the different plant species studied in the scope of this research, the model (NST) of Claassen (1994) which encompasses nutrient uptake by root hairs as well, is used. The model is based on three steps or processes: a) release of nutrients from the solid phase into the soil solution, b) transport of nutrients to roots in the soil liquid phase by mass flow and diffusion (Barber, 1962), c) nutrient uptake into the root which is dependent on the nutrient concentration in the soil solution at the root surface, and can be described by a modified Michaelis-Menten equation derived from enzyme kinetics, and applied by Epstein and Hagen (1952) and modified later by Nielsen (1972).

Chemical K mobilisation

Plant species with increased capacity to render sparingly soluble nutrient forms into plant available ones, or with a higher capacity to transport nutrients across the