

Research Findings

The Effects of Nitrogen Form on Interactions with Potassium

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Abstract

Nitrogen and potassium are major nutrients in crop fertilization. The monovalent cation K^+ is the ionic form of K in soil and is taken up as such by plants. For N there are several ionic and non-ionic forms in soil but plant uptake by non-legumes is usually restricted to the two main monovalent ionic forms: NH_4^+ , a cation and NO_3^- , an anion. The source of N available to plants and N transformations within the soil, influence K reactions in soil, K absorption by roots, short and long-distance transport within the plant, as well as K demand by crops. NH_4^+ and K^+ share similar valence and size properties, and consequently compete for the same exchangeable and non-exchangeable sites of soil particles. The form of N fertilizer can thus affect K availability in both the short and long-term. In the short-term, K concentration in the soil solution may increase following NH_4^+ fertilization, whereas long-term NH_4^+ fertilization has been reported to deplete exchangeable and non-exchangeable K in soil. The available N form affects K adsorption to root surfaces and plant membranes. Transport of K^+ through plant membranes is affected both by NH_4^+ and NO_3^- by direct competition between K^+ and NH_4^+ for transporters, as well as by indirect effects of electrical balance following NH_4^+ assimilation. K^+ transport to plant shoots decreases with an increasing NH_4^+/NO_3^- ratio in the root zone; the long distance transport of NO_3^- in plants is related to K^+ recycling within the plant. The effects of K^+ on fruit quality have been shown to be dependent on the N source.

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Table 1. Comparison of different properties of nitrogen and potassium in soil and plant.

Property	Nitrogen	Potassium
Soil-composition	A component of organic matter, anion and cation forms, solid, dissolved and gases forms	Inorganic cation or component of soil minerals
Soil-reactions	Complex chemical reactions in soil, involving microorganisms	Simple chemical reactions in soils
Plant-uptake mechanism	Taken up in two main ionic forms: NH_4^+ and NO_3^-	Taken up only as K^+
Plant-physiological role	A major component of proteins, nucleic acid and numerous other organic compounds	An osmotic-regulator

Consequently, the interactions of K^+ with N forms have practical implications for fertilization of crops.

Introduction

Nitrogen and potassium are major crop nutrients and fertilizer components. Römheld and Kirkby (2010) recently reviewing the subject of K in agriculture considered topics including soil K availability, K uptake by plants, as well as physiological and practical aspects of plant K status. General interactions between N and K in crop fertilization have been described by Milford and Johnston (2007). The main focus of this work was to draw attention to the requirement for adequate K supply to crops in order to optimize yield response to N fertilization. Potassium status of the soil was shown to exert a considerable influence on crop uptake and response to N, as a consequence of the physiological role of K in plants. Recently, the K nutrition of crops under varied regimes of nitrogen supply was reviewed by Zhang *et al.* (2010). The present mini-review focuses on the effect of N form on crop response to K in agriculture. The paper specifically discusses the interactions of NH_4^+ and NO_3^- with K^+ in the entire soil-plant system. It includes the following areas of interest: the influence of N source and the effects of N transformations within the soil on soil K reactions; K absorption by roots; short and long-distance transport of K in plants; and whole plant response to K supply and K demand.

Ammonium and potassium interactions in soil

The main broad differences between K and N properties in relation to their chemical reactions in soil, uptake by plants and their roles in plant physiology are presented in Table 1. The exclusive monovalent ionic form of K in the soil contrasts to the several ionic and non-ionic forms of N which are present. This means that potassium is taken up by plants as K^+ whereas nitrogen can be absorbed as NH_4^+ , a cation and as NO_3^- , an anion. Nitrogen is a major constituent of organic molecules in plants which include amino-acids, proteins and nucleic acids. On the other hand, K remains exclusively as an inorganic cation, with one of its major physiological roles as an osmotic-regulator in plant tissues. This difference between plant N and K raises the question of possible interactions or competition between these two nutrients. NH_4^+ and K^+ are both univalent cations and have a similar ionic radius (2.8Å^0). Consequently, they compete for the same exchangeable and non-exchangeable sites of soil particles. The form of N fertilizer can thus affect K availability both in the short- and long-term.

Potassium availability to plants in soil is governed by the transfer between four main pools in the soil: structural, fixed (non-exchangeable), exchangeable and soluble (Römheld and Kirkby, 2010). The soluble and exchangeable phases

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exist in all soils, the latter providing negative charge sites on clay mineral surfaces and organic matter. The fixed or non-exchangeable phase exists only in micaceous type clays (2:1 layers like illite, vermiculite and other clays from this group) (Römheld and Kirkby, 2010; Zhang *et al.*, 2010). In soils, equilibrium exists between these different pools and the relationship between them is presented in Fig. 1. The size of the soil solution pool is very small, about 5 percent of total crop demand at any given time (McLean and Watson, 1985), and 0.1-0.2 percent of the total soil K. However, it plays a crucial role in the K cycle as can be seen in Fig. 1. It is the only pool that is available for plants and it is in equilibrium with exchangeable K (1-2% of the total soil K) and fixed K (1-10% of the total soil K). These pools are the main contributors to K supply to plants because of the very rapid rate of exchange of soluble ions with exchangeable ions, occurring in less than seconds (Eick *et al.*, 1990; Bar-Tal *et al.*, 1995; Sparks, 2003). When K^+ is removed from the solution by plant uptake or leaching, the soil solution is rapidly replenished by K^+ from exchangeable sites, whereas the fixed clay replenishes the exchangeable sites slowly by a diffusion controlled process. The main K pool in soil (90-98%) is the structural K in minerals like micas and feldspars, but the release of this form to the soil solution during the process of weathering is very slow. Microbial biomass provides an additional K pool in soil which contains from 2.1-25.4 $\mu\text{g K g}^{-1}$ soil or 0.1 percent of the $\text{NH}_4^+\text{NO}_3^-$ extracted K (Khan *et al.*, 2009). This pool and the role of micro-organisms is not crucial for the K cycle, as it is in the N cycle, because the main form of K in living tissues is the ion K^+ which is readily transferred to the soil solution.

Soil K status influences K uptake by plant roots. The amount of K in the soil depends on soil type, production level, retention or removal of crop residues and the input of K as fertilizer or as a

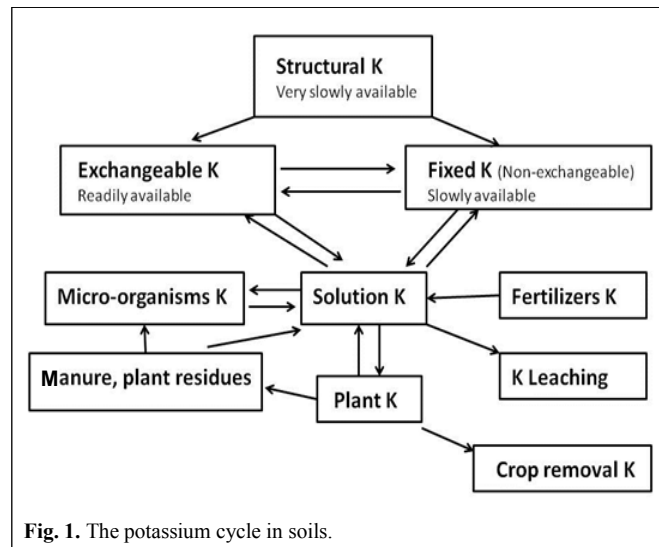


Fig. 1. The potassium cycle in soils.

component of irrigation water. Imbalance in fertilizer application, especially N fertilizers with no K, is very common. This leads to a deficiency in K due to the continuous removal of K during crop uptake that alters the amount and status of remaining K (Römheld and Kirkby, 2010). Release and fixation rates of K in soil are highly dependent on soil K balance, confirming that these are reversible processes that depend on plant uptake and fertilizer inputs (Bar-Tal *et al.*, 1991; Simonsson *et al.*, 2007). In a greenhouse experiment, where corn was grown in pots (3 kg soil) for one season, the control treatment (nil K input) resulted in the release of 2.6 and 1.1 mmol kg^{-1} from loess and sandy loam soils, respectively (Bar-Tal *et al.*, 1991). In the same experiment, application of 30 mmol K per pot resulted in fixation of 1.33 and 1.20 mmol kg^{-1} to a loess and a sandy loam soil, respectively. These changes in non-exchangeable K are quite considerable when compared to the initial levels of 7.6 and 1.9 mmol kg^{-1} in the loess and the sandy loam soils, respectively. This may be explained by the use of small volume pots which enhanced the rate of changes in the soil. Under field conditions, however, the same processes would be expected to induce these changes at a much slower rate; taking several years to

obtain similar results. Crop uptake of K under a negative soil K balance due to imbalanced NPK fertilization in the field is mainly met through K released from non-exchangeable sources (Römheld and Kirkby, 2010; Lal *et al.*, 2007). On the other hand, a considerable increase in fixed K is observed in permanent plot experiments in high K input treatments (Benbi and Biswas, 1999) and in pot experiments (Bar-Tal *et al.*, 1991).

The NH_4^+ ion is also present in soil solution and in exchangeable and fixed soil pools. There is also equilibrium between these forms as was described for K. The main chemical difference between K^+ and NH_4^+ is that the latter can also be oxidized to nitrite and NO_3^- , mainly through microbial activity. Only the fixed phase NH_4^+ is relatively protected from the oxidation process and can be retained in the clay interlayers for long periods. The similar properties of the K^+ and NH_4^+ ions leads to strong interactions between them in the soil. Both ions are held by the same non-exchangeable sites in the interlayers and edges of interlayers of the 2:1 clay minerals. Consequently, a simple competition where application of one ion should displace the other and increase its fraction in soil solution is to be expected. However, the reality is more complex and application of NH_4^+

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or K^+ to soil may lead to increases as well as decreases in the non-exchangeable pool of the counter ion. Some examples and the possible explanations are presented below.

Simultaneous injection of anhydrous ammonia (AA) and a KCl solution in a silty clay loam soil decreased K^+ fixation, whereas the concentrations of the exchangeable and soluble K^+ increased (Stehouwer and Johnson, 1991). The decrease in K^+ fixation was attributed to preferential NH_4^+ fixation blocking K^+ fixation and the increased exchangeable K^+ explained by a decrease in K^+ fixation (Fig. 2) and to pH-induced increases in cation-exchange capacity (primarily in the organic fraction) (Stehouwer and Johnson, 1991). Liu *et al.* (1997) reported that in field experiments, the soil fixation capacities for both NH_4^+ and K were significantly reduced by sustained high rates of K fertilization, but not by N fertilization. Kenan *et al.* (1999) also found that the fixation of NH_4^+ was reduced by K addition before NH_4^+ was added, and that the reduction was proportional to the amount of K previously fixed. Enhanced K^+ fixation with increasing K application rates and reduction with increasing NH_4^+ application rates was reported by Chen and MacKenzie (1992) and Du *et al.* (2007). The sequence of NH_4^+ and K^+ application may influence K fixation. Chen *et al.* (2007) reported that NH_4^+ at high rates of application before K fertilization to rice plants resulted in poor growth and reduced K uptake compared to NH_4^+ application after K fertilization. However, when NO_3^- was used as the N source, plant growth was not affected by the order in which N and K were applied. The explanation for the negative effect of the early NH_4^+ application on K availability was that the NH_4^+ blocked the non-exchangeable sites, thus reducing the capacity of the soil to store K to meet the continuous consumption by the plants. Evangelou and Lumbanraja (2002) reported that the surface of vermiculite clay exhibits

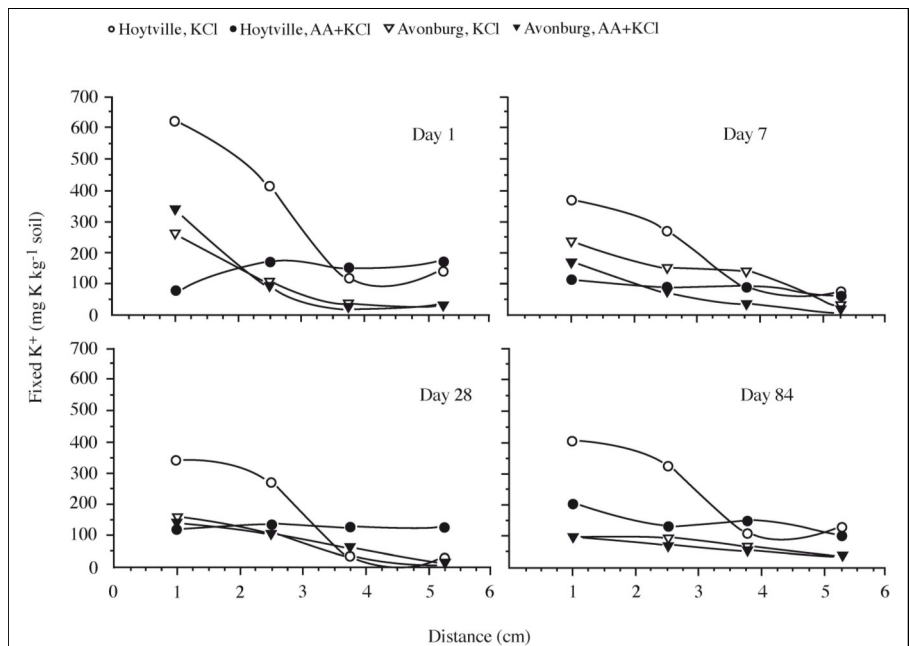


Fig. 2. Distribution of fixed K^+ fertilizer over time and distance from the injection point in Hoytville and Avonburg soils following injection of KCl or anhydrous ammonia (AA) + KCl.

Adapted from (and redrawn): Stehouwer and Johnson, 1991; Soil Science Society American Journal 55:1374.

high specificity for K^+ at low-K fractional loads which cause the clay interlayer to collapse and thus a large proportion of interlayer NH_4^+ most likely becomes fixed. The available exchange sites appear to have relatively lower affinity for NH_4^+ . Therefore, the data indicates that availability of applied NH_4^+ in vermiculitic soils would depend on the presence or absence of applied K^+ .

Clay minerals of the smectite type have a unique structure that enables a high exchangeable cation capacity in the interlayers. The size of the hydrated exchangeable cation affects the interlayer distance. Changes in the composition of the exchangeable cations affect the interlayer distance or swelling of the clay. However, the high affinity of K^+ and NH_4^+ ions to exchangeable sites leads to their gradual fixation, a process which results in transformation of smectite to illite. The transformation from smectite to illite is a pedological or geological process that takes thousands of years to complete. When one considers transformations on a

geological scale, the effect of temperature on this transformation was found to be critical, starting at 50 to 60°C. In the past few decades, new observations have indicated that the transformation of smectite to illite occurs also under ambient air temperature conditions with the relatively short time scales associated with soil cultivation. Such fast transformation has been shown in laboratory conditions under cycles of wetting and drying (Eberl *et al.*, 1986 and 1993). Sandler and Harlavan (2006) suggested that high K concentrations may lead to this transformation without wetting and drying cycles. In vitro experiments of K^+ and NH_4^+ fixation under wetting and drying cycles were conducted and the illitization of the original smectite by both ions was similar (Miklos and Ciel, 1993). The formation of illite from smectite in experimental field plots (Versailles) fertilized by inorganic K fertilizer and manure have been reported by Pernes-Debuyser *et al.* (2003). Additional laboratory experiments showed that the

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changes over one growing season were measureable (Barré *et al.*, 2007a, 2007b and 2008). The opposite process of fast release of interlayer K and decomposition of illite clay due to agricultural activity has also been reported. The most extreme cases were observed in a rice field where wetting and drying cycles are common and the potassium is easily leached, leading to measureable changes over a relatively short time of 30 years (Li *et al.*, 2003). Continuous maize cropping over several decades resulted in decomposition of soil illite, whereas no change was obtained under a corn-oat-hay rotation with the same fertilization treatment (Velde and Peck, 2002).

Numerous published data indicate that K^+ and NH_4^+ are attracted by the same exchange sites with similar affinity. A slight preference for K^+ over NH_4^+ has been demonstrated in laboratory exchange isotherms (Fig. 3, Chung and Zasoski, 1994). They also reported that similar exchange isotherms were obtained in the bulk solution and rhizosphere, independent of the solution pH and ionic strength. Consequently, the concentration of NH_4^+ in the soil solution has a strong and direct impact on the distribution of K^+ between the soil solution and the exchange complex

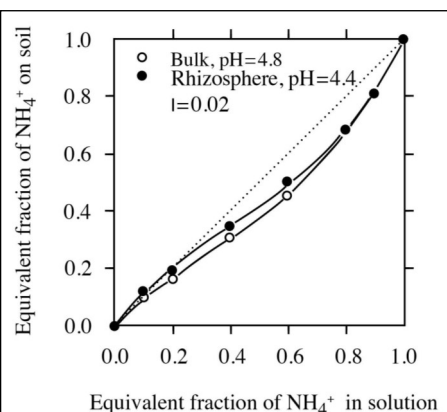


Fig. 3. Exchange isotherm for NH_4^+ -K exchange in bulk soil of peach seedling at solution ionic strength of 0.02. The dotted line is non-preference line.

Adapted from (and redrawn): Chung and Zasoski, 1994; Soil Science Society American Journal 58:1368-1375.

and vice versa. The situation becomes more complex when the soil contains additional cations. In a laboratory study, Evangelou and Lumbanraja (2002) investigated the exchange of K^+ - NH_4^+ - Ca^{2+} on vermiculite and hydroxy-aluminium vermiculite. They found that in the case of vermiculite, binary exchange data alone may not be able to predict ternary exchange data. However, in the case of hydroxy-aluminium interlayered vermiculite, binary data may be able to predict ternary data as long as the third cation's distribution between exchange and solution phases remains constant across the isotherm. Liu *et al.* (1997) found that K^+ application enhanced NH_4^+ fixation but reduced the amount of exchangeable NH_4^+ on the clay surface. Wang *et al.* (2010) reported that the application of the fertilizer ammonium sulfate to different soil types from China in incubation experiments significantly altered the distribution between pools of native K and added K in the soils. Addition of ammonium sulfate significantly increased water-soluble K^+ and decreased exchangeable K^+ in almost all the soils except the paddy soil that contained considerable amounts of 2:1 type clay minerals with K^+ added. Added ammonium sulfate also reduced the formation of fixed K^+ in the soils with K^+ added and suppressed the release of fixed K^+ in the three studied soils without K^+ added.

The nitrogen source may significantly affect rhizosphere pH (Nye, 1981; Marschner, 1995; Marschner and Römheld, 1996; Bar-Yosef, 1999; Bloom *et al.*, 2003). The common N fertilizer sources in soil systems are urea, NH_4^+ and NO_3^- . Urea is the cheapest N source (per N unit) and is the most concentrated N fertilizer (46%); it is highly soluble, moves easily in irrigation water and is therefore widely used in agriculture. The hydrolysis process of urea yields the derivative NH_4^+ ions - and thus urea is a source of the NH_4^+ form for plant nutrition. Rapid adsorption on the surface sites of the

solid phases, and nitrification reactions diminish the NH_4^+ content in soils and media, and hence, rhizosphere NH_4^+ concentrations are commonly low even under irrigation with a high NH_4^+ -/ NO_3^- -N ratio.

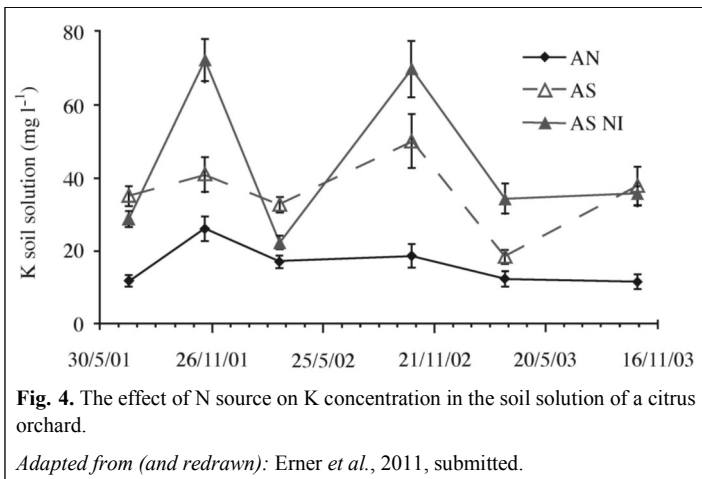
In the field, the transformation of NH_4^+ to NO_3^- is usually a rapid process, between days to weeks, depending on temperature, soil moisture and pH. Therefore, in most fertilizer application methods the form of N should not have a strong impact on K distribution between the exchangeable and solution phases. However, when continuous fertigation is used it is expected that the N source will effect K concentration in the solution in the wetted soil, and several studies have validated this assumption. For example, during the irrigation season, K^+ concentration in the soil solution of a citrus orchard increased when N was applied as ammonium sulfate, as opposed to ammonium nitrate (Fig. 4, Erner *et al.*, 2011, submitted). The application of a nitrification inhibitor enhanced the effect of the ammonium sulfate on soil solution K^+ concentration, indicating that the effect of the fertilizer on K concentration was via the NH_4^+ - K^+ exchange process.

Another mechanism by which the N source influences K availability and leaching is unique to calcareous soils common in arid and semi-arid regions. In carbonate-bearing soil, the acid produced by nitrification of NH_4^+ gives rise to an increase in the concentrations of Ca^{2+} and Mg^{2+} in the soil solution, which can exchange with K^+ , leading to higher K^+ solution (unpublished data of the author, Kolahchi and Jalali, 2007).

Potassium and nitrogen interactions in plants

Nitrogen is a unique nutrient that can be absorbed either as the cation NH_4^+ or the anion NO_3^- (Marschner, 1995). This characteristic of nitrogen influences plant nutrition in general and the uptake

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of other elements that are taken up as ions as well as numerous physiological processes in plants (Marschner, 1995; Forde and Clarkson, 1999; Mengel and Kirkby, 2001; Epstein and Bloom, 2005). The cation-anion balance in plant tissues is maintained by diffusible and non-diffusible organic and inorganic ions, and has been found to be notably affected by the sources of N nutrition (Marschner, 1995; Mengel and Kirkby, 2001; Epstein and Bloom, 2005). It has been widely reported that NH_4^+ nutrition depressed the uptake of cations, especially in leaves and petioles, and that NO_3^- nutrition depressed that of anions (Kirkby and Mengel, 1967).

The nitrogen source has a strong impact on soil rhizosphere and the rhizosphere pH *via* three mechanisms (Marschner, 1995; Marschner and Römheld, 1996; Bar-Yosef, 1999): (i) displacement of H^+/OH^- adsorbed on the solid phase; (ii) nitrification/denitrification reactions; and (iii) release or uptake of H^+ by roots in response to NH_4^+ or NO_3^- uptake, respectively. Mechanisms (i) and (ii) are not associated with any plant activity, and affect the whole volume of the fertigated substrate, whereas mechanism (iii) is directly related to the uptake of nutritional elements, and may be very effective in changing the pH because it affects a limited volume in the immediate vicinity of the roots (Moorby *et al.*, 1984; Gahoonia and Nielsen,

1992; Gahoonia *et al.*, 1992; Marschner and Römheld, 1996; Taylor and Bloom, 1998; Bloom *et al.*, 2003). The extent of the pH changes caused by the three mechanisms described above depends on soil properties, plant activity, and all the environmental factors that affect nitrification rate.

Transport through membranes and long-distance transport in plant

The selective transport of nutrients through plant membranes is mainly regulated by transporters (Hirsch *et al.*, 1998). Two distinct membrane transport systems for K uptake by plants have been described: high and low affinity transport systems (HATS and LATS); (Maathuis, 2007; Maathuis and Sanders, 1997; Nieves-Cordones *et al.*, 2007). At low external K^+ concentrations (<1 mM), HATS are dominant; while at higher external K^+ concentrations (>1 mM) LATS become dominant, mostly via ion channels (Maathuis and Sanders, 1997; Hirsch *et al.*, 1998). Over the past two decades, the complex system of K^+ transporters and the genes encoding them have been identified (Szczzerba *et al.*, 2009).

NH_4^+ inhibits HATS which operate primarily at low external K^+ concentrations (<1 mM), while LATS,

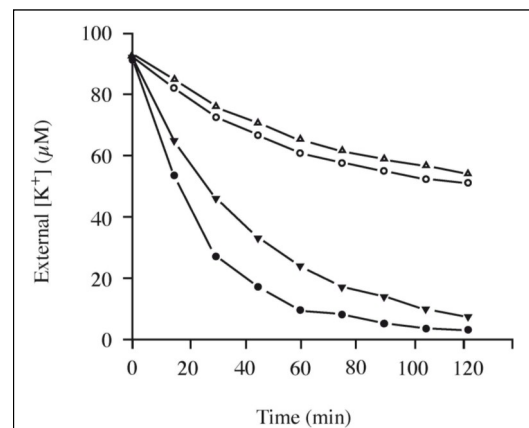


Fig. 5. Effects of NH_4^+ on high affinity K^+ uptake in plants grown with or without NH_4^+ in the absence or in the presence of NaCl.

Adapted from (and redrawn): Nieves-Cordones et al., 2007; Plant Science 172:273-280.

After K^+ starvation for seven days, K^+ depletion experiments were performed in the absence of NH_4^+ (closed symbols) or in the presence of 1 mM NH_4^+ (open symbols). One group of plants received the NaCl treatment (50 mM final NaCl concentration) (triangles) and the other remained in the NaCl free solution (circles).

which dominates at higher K^+ external concentrations, are relatively NH_4^+ insensitive (Hirsch *et al.*, 1998; Nieves-Cordones *et al.*, 2007 and others) (Fig. 5). On the other hand, NO_3^- -grown plants regulate cytosolic K^+ concentrations at high K^+ external concentration better than NH_4^+ -grown plants by potassium efflux through LATS (Szczzerba *et al.*, 2006).

NO_3^- is a univalent anion that can serve as a counter ion to K^+ (Abdolzadeh *et al.*, 2008; Guo *et al.*, 2007; Jarvis *et al.*, 1990; Lu *et al.*, 2005; Mathuis, 2007; Pettersson, 1984) and *vice versa*. Ivasshikina and Feyziev (1998) reported that the rate of NO_3^- uptake by maize seedlings was faster when K^+ served as the accompanying counter ion, rather than the other main cations, Ca^{2+} , Mg^{2+} and Na^+ (Fig. 6). It was found that growing sugarcane seedlings in a K^+ depleted nutrient solution for a 3 1/2-month period reduced the roots' capacity to absorb NO_3^- (Subasinghe, 2006). On the other hand, growing sugarcane seedling in an N depleted nutrient solution reduced the initial K^+

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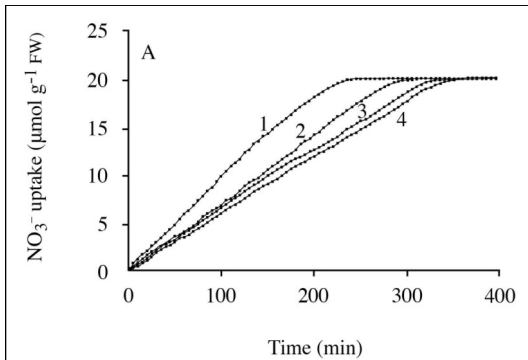


Fig. 6. The time course of NO_3^- uptake by maize seedlings from solutions, containing $\text{Ca}^{2+} \text{K}^+$ (1); $\text{Ca}^{2+} \text{Mg}^{2+}$ (2); $\text{Ca}^{2+} \text{Na}^+$ (3); Ca^{2+} (4) as accompanying cations.

Adapted from (and redrawn): Ivashikina & Feyziev, 1998; Plant Science 131:25-34.

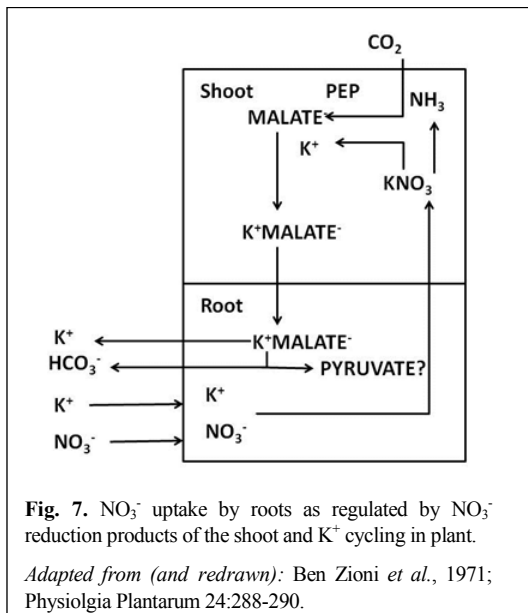


Fig. 7. NO_3^- uptake by roots as regulated by NO_3^- reduction products of the shoot and K^+ cycling in plant.

Adapted from (and redrawn): Ben Zioni *et al.*, 1971; Physiologia Plantarum 24:288-290.

uptake rates and decreased the affinity of roots for K^+ .

The potassium ion is easily mobilized in the whole plant because it is not assimilated in organic compounds. Like other cations, it is transported from the root system upward to the canopy via the xylem, but it also has the property of high phloem mobility and, as a result, a high degree of re-translocation via the phloem (Marschner, 1995). K uptake and re-translocation play an important role in NO_3^- transport from roots to shoots as a counter ion and assimilate loading in the phloem (Maathuis, 2007). A conceptual model of K circulation

and NO_3^- uptake was suggested by Ben Zioni *et al.* (1971). According to this model, NO_3^- is absorbed by roots and transported via the xylem to the shoots with K^+ as the counter ion. In the shoot, NO_3^- is reduced and assimilated into organic compounds, whereas K^+ is transported downward to the roots with malate via the phloem (Fig. 7). Then the root takes up more NO_3^- and exudes HCO_3^- to maintain electro-neutrality or takes up more K^+ , according to the external and internal K concentrations and the N form. The rate of uptake and partitioning of K in plants can be modified depending on the N forms

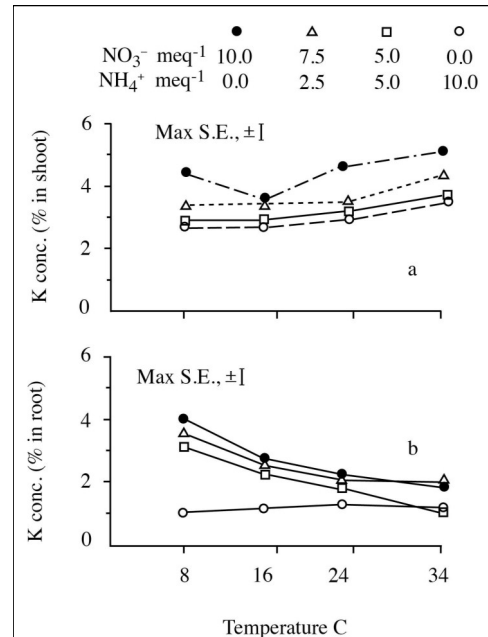


Fig. 8. Nutrient solution temperature and percentage $\text{NO}_3^-/\text{NH}_4^+$ effect on percent K in the tomato plants. a. shoot; b. root.

Adapted from (and redrawn): Ganmore-Neumann and Kafkafi, 1980; Agronomy Journal 72:762-766.

supplied. NH_4^+ -N as the sole N source caused a decrease in potassium uptake relative to the NO_3^- -N supply in tobacco (Lu *et al.*, 2005) and (Ganmore-Neumann and Kafkafi, 1980) tomato plants. In tobacco plants, using NH_4^+ as the sole N source resulted in more K translocated to leaves than NO_3^- in terms of the amounts of xylem-transported K (Lu *et al.*, 2005). In contrast, Ganmore-Neumann and Kafkafi (1980) reported that increasing the $\text{NO}_3^-/\text{NH}_4^+$ ratio in the solution resulted in higher K concentrations both in roots and leaves of tomato plants (Fig. 8), in agreement with other reports that roots treated with high levels of NO_3^- absorbed and translocated more K^+ (^{86}Rb) than seedlings treated with low levels of NO_3^- (Pettersson, 1984; Zsoldos *et al.*, 1990). Ganmore-Neumann and Kafkafi (1980) showed that temperature elevation from 8 to 34°C resulted in a gradual decrease and increase of K content in roots and shoots, respectively, due to enhanced transport from increased temperatures (Fig. 8). Engels and Kirkby (2001)

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reported that cycling and recycling of K^+ increased with increasing shoot growth rate, which is in accordance with the suggested model by Ben Zioni *et al.* (1971). Cytosolic K^+ concentrations vary between 40 and 200 mM, depending on K^+ supply and nitrogen form (NO_3^- or NH_4^+) demonstrating the strong impact of N form on potassium dynamics in plants (Szczerba *et al.*, 2006).

Effects on whole plant, crop yield and quality

The nitrogen form is an important factor for plant development and yield. Increasing the N- NH_4^+ :N- NO_3^- ratio in the N fertilizer reduced the uptake of K^+ and other mineral cations, but increased the uptake of mineral anions by tomato (Kirkby and Mengel, 1967; Ganmore-Neumann and Kafkafi, 1980) and other crops as has been reported in numerous publications. Bar-Tal *et al.* (2001b) demonstrated that the uptake of Ca^{+2} and K^+ increased quadratically as the N- NO_3^- :N- NH_4^+ ratio increased, throughout the studied range of 0.25 to 4.0 (Fig. 9).

K^+ depletion of the nutrient solution enhances the absorption of NH_4^+ -N, but in contrast suppresses the absorption, translocation, and assimilation of NO_3^- -N, while simultaneously lowering leaf nitrate reductase activity (NRA). This behavior suggests that plants require an adequate supply of K for absorbing NO_3^- -N and maintaining high levels of NRA as compared with the assimilation of NH_4^+ -N (Ali *et al.*, 1991). K^+ activates plant enzymes functioning in NH_4^+ assimilation and transport of amino acids (Hagin *et al.*, 1990). Therefore, an adequate supply of K^+ enhances NH_4^+ utilization and thus improves yield when both N forms are applied together. Potassium has been shown to strongly stimulate carboxylic acid accumulation in fruits (Erner *et al.*, 1993). This is because the high rate of K^+ uptake increases the cation-anion balance in the plant tissue and,

in order to maintain electro-neutrality, carboxylates are synthesized (Marschner, 1995). NO_3^- uptake also stimulates carboxylation in plant tissue in order to remove hydroxyls produced in the NO_3^- reduction process and to balance the excess accumulation of cations over anions (Marschner, 1995). Thus, both K^+ and NO_3^- have similar effects on organic acids production in plants leaves and fruits (Serna *et al.*, 1996).

The NH_4^+ : NO_3^- ratio is an important N-management tool, particularly in soil-less culture (Silber and Bar-Tal, 2010) and in soil under fertigation (Bar-Yosef, 1999). For a given N dose and irrigation regime, the N- NO_3^- :N- NH_4^+ ratio affects Ca, Mg, and K uptake (Bar-Tal *et al.*, 2001a, b; Kirkby and Mengel, 1967; Neilsen *et al.*, 1995), and carboxylic acid biosynthesis (Kirkby and Mengel, 1967; Mengel and Kirkby, 2001). However, in a recent experiment investigating the effect of N source on grapefruit, no effect on fruit quality and acid concentration in the fruit was found (Erner *et al.*, 2011, submitted). A possible explanation for this result is: in soil grown plants, two confounding effects of NH_4^+ take part, on the one hand a higher NH_4^+ concentration increases K^+ concentration in the soil solution (Fig. 4) and on the other hand the competition between NH_4^+ and K^+ on root uptake reduced the uptake of K^+ by the trees.

Conclusions

The N form and K application modes have short and long-term effects on potassium availability in soil through exchange and fixation reactions, respectively.

N form effects K^+ absorption by plants through several mechanisms: NH_4^+ and K^+ competition, long distance transport of K^+ - NO_3^- , specific effects of N metabolism on K uptake and vice-versa.

The overall interactions of N form and K^+ application on whole plant response and crop yield are a product of the above described effects.

Proper K^+ application can improve N fertilizing efficiency, increase yield and reduce environmental pollution.

Further studies on the mechanisms of K^+ and NH_4^+ fixation in soil clay minerals are required for better understanding of long-term effects on their availability to plants.

Further studies on the interactions of K^+ , NH_4^+ and NO_3^- at the molecular and whole plant levels are required for improving N and K fertilization.

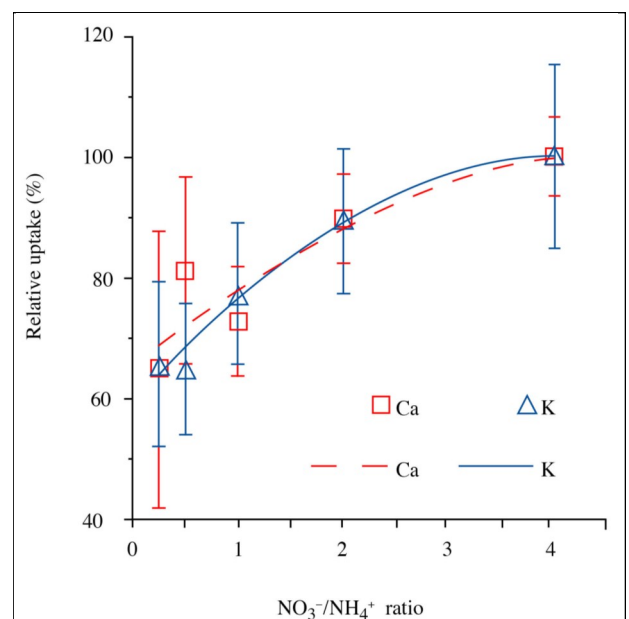


Fig. 9. The Effect of the mineral N form on K and Ca uptake by pepper plant.

Adapted from (and redrawn): Bar-Tal *et al.*, 2001. *HortScience* 36:1252-1259.

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