INTERNATIONAL POTASH INSTITUTE
60 ANNIVERSARY 1952-2012

e-ifc No. 38, September 2014

Scientific Paper

Typical symptoms of potassium deficiency in cotton leaves. Photo by D.M. Oosterhuis.

Potassium and Stress Alleviation: Physiological Functions and Management in Cotton

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Summary

Potassium (K) plays a major role in the basic functions of plant growth and development. In addition, K is also involved in numerous physiological functions related to plant health and tolerance to biotic and abiotic stress. However, deficiencies occur widely resulting in poor growth, lost yield and reduced fiber quality. This review describes the physiological functions of K and the role in stress relief and also provides some agronomic aspects of K requirements, diagnosis of soil and plant K status, and amelioration. The physiological processes described include enzymes and organic compound synthesis regulation, water relations and stomatal regulation, photosynthesis, transport, cell signaling, and plant response to drought stress, cold stress, salt stress, as well as biotic stresses. The agronomic aspects of K fertilization include the K requirements of cotton, K uptake and soil characteristics, genotypic variation in K uptake and use, and characteristics of K deficiency in cotton. In addition, diagnosis and amelioration of K soil and plant status is discussed.

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Introduction

Potassium (K) plays a major role in plant metabolism, growth, development, and yield. Deficiencies of K result in perturbations of numerous physiological functions, including water relations, enzyme activation, charge balance, poor growth, reduced yield, and decreased resistance to stress. Furthermore, K is also involved in numerous physiological functions related to plant health and tolerance to biotic and abiotic stress. For optimal growth and productivity, modern crop production requires a large amount of K, particularly during reproductive development. Potassium is the mineral element, after nitrogen (N), required in the largest amount by plants. The K requirement for optimal plant growth is 2 to 5% of the plant dry weight (Marschner, 1995). However, this requirement is often not met due to adverse soil and plant factors, and deficiencies occur with resulting yield reductions. Furthermore, the concentration of K available to the plant is often influenced by the availability/abundance of other essential elements.

Farmers in the USA and elsewhere are using substantially more commercial fertilizer than 20 years ago and major improvements have been made in how these fertilizers are managed. However, despite soil analyses and subsequent soil applications of fertilizer prior to planting, K deficiencies have occurred sporadically and somewhat unpredictably. This has prompted a renewed focus on K management in cotton with some emphasis on understanding K fertilizer requirements and use by the cotton plant. An efficient fertilizer regime requires an accurate knowledge of the nutrient status of the soil, as well as a reliable tissue analysis during the season to fine tune the fertility status and avoid any unforeseen deficiencies. Fundamental to this is an understanding of the role of the nutrient in plant metabolism, yield formation and in amelioration of stress. This review describes the general agronomic characteristics of K, the physiological functions and mitigation of stress by K, and common methods of deficiency diagnosis and amelioration using cotton as a model crop.

Physiology of potassium

Potassium is an essential macronutrient for plant growth and development that affects many fundamental physiological processes (Clarkson and Hanson, 1980). It is the most abundant cation in plant cells and it can be stored either in the cytoplasm and/or in the vacuole, while the distribution of K concentrations between those compartments determines its function in the plant (Marschner, 1995). Additionally, K is characterized by high mobility not only within short distance transport, such as between individual cells and neighboring tissues, but also within long distance transport, such as through the xylem and phloem. These characteristics convey K as a major nutrient responsible for controlling many physiological and biochemical processes in the plant, such as: enzyme activation, cell osmotic potential regulation, soluble and insoluble molecular anions neutralization, and cell pH stabilization (Marschner, 1995). Potassium plays an integral role in plant-water relations, and is involved in numerous physiological functions where water is involved including transpiration, cell turgor maintenance, stomatal opening and closing, assimilate translocation, enzyme activation, and leaf movements. Lastly, plant photosynthesis, as well as the translocation of carbon (C) and N compounds from production sites into sink organs is greatly dependent on K.

Agronomic aspects of potassium

Importance of potassium in cotton

From an agronomic standpoint, K deficiencies and excesses are financially and environmentally inefficient and have negative yield-impacting consequences. General characteristics of excessive K in cotton (*Gossypium hirsutum* L.) include increased boll rot (Bennett *et al.*, 1965), increased plant height (Bennett *et al.*, 1965; Pettigrew and Meredith, 1997), and delayed maturity (Bennett *et al.*, 1965; Clement-Bailey and Gwathmey, 2007; Gwathmey and Howard, 1998; Gwathmey *et al.*, 2009). Deficiencies of K enhance water deficit stress (Coker *et al.*, 2000), reduce lint percentage (Pettigrew *et al.*, 1996), dry matter production (Gerardeaux *et al.*, 2010; Rosolem *et al.*, 2003; Zhao *et al.*, 2001), plant height (Zhao *et al.*, 2001), leaf area (Gerardeaux *et al.*, 2010; Zhao *et al.*, 2001), internode length (Gerardeaux *et al.*, 2010), seed mass (Pettigrew *et al.*, 1996), boll mass (Pettigrew *et al.*, 1996), N use efficiency (Pettigrew and Meredith, 1997), and lint yield (Gormus, 2002; Pettigrew *et al.*, 1996; Stromberg, 1960). Deficiencies of K also effect crop maturity by stopping reproductive growth prematurely and increasing early season flowering rate (Pettigrew, 2003).

Potassium requirements of cotton

Normal cotton growth and fiber development requires K in quantities second only to N. An average mature cotton crop is estimated to contain between 110-250 kg K ha^{-1} (Hodges, 1992) or about 2 to 5 kg K ha^{-1} day^{-1} (Bassett *et al.*, 1970; Halevy, 1976; Mullins and Burmester, 1991), i.e. about 13 kg K/100 kg lint (Mullins and Burmester, 2009), with 50% of the K in the boll (Rimon, 1989) and 24% in the seed and lint (Mullins and Burmester, 2009). At maturity, the capsule wall of the boll accounts for over 60%, the seed about 27% and the fiber about 10% of all the K accumulated by the boll (Leffler, 1986). Large quantities of K in non-harvested tissues results in only about 20 kg of K required to produce one 218 kg bale of cotton fiber, with about 2.5 to 6 kg being removed mainly by the seeds (Hodges, 1992; Rimon, 1989).

Characteristics of potassium deficiencies in cotton

Cotton is more sensitive to low K availability than most other major field crops, and often shows signs of K deficiency on soils not considered K deficient (Cassman *et al.*, 1989). Visual symptoms of K deficiencies in cotton have traditionally been noted in the lower, more mature leaves and progress from the bottom of the canopy to the top (Dong *et al*., 2004) due to the nutrient's very mobile nature in the plant. The traditional symptoms often begin with interveinal chlorosis of leaves and necrosis of the leaf margins. Leaves become brittle and become bronze in color as the deficiency progresses, and because of these characteristics K deficiencies have been commonly referred to as 'cotton rust' (Maples *et al*., 1988).

Although traditional deficiency symptoms are still occasionally noted, more recent characterization of K deficiencies describe symptoms later in the growing season during boll development in younger leaf deficiencies, and include interveinal leaf chlorosis which turns to a gold-like color as deficiency worsens, causing necrosis of leaf tissues. The occurrence of these K deficiency symptoms was first recognized in California during the early 1960s (Brown *et al*., 1973). These deficiencies manifested themselves during the latter half of the season in a range of soils and cotton cultivars. Visual deficiency symptoms on younger tissues are similar to the traditional symptoms on older leaves, with leaf-edge curl and early defoliation. In contrast to traditional symptoms, however, the deficiencies progress from the top of the canopy to the bottom (Maples *et al*., 1988; Stromberg, 1960).

It is commonly suggested that the two major contributing factors to these shifts in K deficiency characteristics are: (1) an inefficiency of cotton roots to utilize K in the surface exacerbated by genetic shifts to earlier-maturing cultivars which fail to develop as expansive of a root system; and (2) higher yielding, earlier maturing cultivars which require much more K and other nutrients than lower yielding traditional cultivars (Oosterhuis, 1976). Understanding the nature and reasons for late-season cotton K deficiencies should result in reduced frequencies and severities of in-field K deficiencies (Bednarz and Oosterhuis, 1998).

Potassium uptake and soil characteristics

The main mechanisms of plant K uptake from the soil are mass-flow and diffusion (Barber, 1962). Under normal conditions, the vast majority of K uptake occurs through diffusion, as mass-flow may only represent 1-3% of total K uptake (Marschner, 1995; Rosolem *et al*., 2003). Still, the importance of these two mechanisms varies with soil and plant parameters such as root characteristics, plant K requirements, and water flux rates (Baligar, 1985). Cotton uptake of K during the season follows a pattern similar to dry weight accumulation until peak flower, at which time maximum K uptake is reached and begins to decline (Bassett *et al*., 1970; Halevy *et al*., 1987; Schwab *et al*., 2000). This is also the period in which K demand rises dramatically due to the developing boll load as the bolls are the major sinks for this element (Halevy, 1976; Leffler and Tubertini, 1976).

Close up on mild K deficiency in cotton leaf. Photo by D.M. Oosterhuis.

Plants can, in the most basic sense, be considered as nutrient (and more specifically K) wicks. Cotton removes K from the exchangeable sites on soil colloids and organic matter at various soil depths and concentrates the nutrient in above-ground tissues (Brouder and Cassman, 1990). In contrast to crops harvested for their biomass, cotton returns much of the K back to the soil in leaves, stems, and capsule walls (burs). These tissues are either incorporated in the soil's surface or in no-till and conservation tillage systems allowed to decompose on the soil's surface. Due to the negative charge of medium to heavy textured soils and the characteristics of K as a cation, it is not common for K to leach out of these upper soil layers. Many examples of this can be found in the San Joaquin Valley (SJV) in the US. Although this region generally possesses high fertility soils with respect to K (Brown *et al*., 1973) it was one of the first to characterize modern cotton K deficiencies (Stromberg, 1960) due to stratification of K through the profile in the SJV with more K located in the vermiculitic topsoil than subsoil. Depletions of subsoil K have also been noted in America's mid-southern and south-eastern regions (Maples *et al*., 1988).

Mimicking the K stratified characteristics of the SJV, Gulick *et al.* (1989) examined the response of cotton and barley (*Hordeum vulgare* L.) to soil K in layered profiles. Results suggested cotton rooting pattern was very similar to barley in all layers except the topsoil, in which barley had 2.7 times greater root length density than cotton. As a result, cotton K uptake from the topsoil was much lower than barley. Long-term fertility trials conducted in the south-eastern US comparing nutrient uptake of cotton to soybeans (*Glycine max* L.) and maize (*Zea mays* L.) found cotton to be much more sensitive to K deficiencies than the other two crops (Cope, 1981). Research by Brouder and Cassman (1990) in this region examined root growth of two cultivars, one sensitive to K deficiency and a K deficiency tolerant cultivar. The tolerant cultivar was characterized by a larger mean root diameter and increased root extension after peak bloom, at which point most K deficiencies become visually apparent. Furthermore, results from examination of root zone densities suggested neither cultivar utilized nutrients in the topsoil.

Genotypic variation in K uptake and use

It has been suggested that the increasing reports of K deficiencies in modern cultivars may be due to their earlier maturity or increased yields as compared to traditional cultivars (Oosterhuis, 1995). In theory, earlier maturing cultivars will require more K earlier in the growing season than their late-season isolines. Although it seems logical that an earlier maturing cultivar would not have the time to grow as expansive of a root system or store as much K as a later maturing cultivar, experiments testing these theories have shown mixed results.

Scientists began examining differences in K uptake due to maturity (earliness) as early as the mid 1970s. Halevy (1976) found an earlier maturing cultivar to be more sensitive to K deficiencies due to greater K demands by reproductive parts earlier in the growing season and have a relatively smaller root system compared to the later maturing cultivar. The aforementioned characteristics of the earlier cultivar resulted in earlier translocation of K from the leaves to the fruit than in the later maturing cultivar. As a result, the earlier maturing cultivar displayed visual deficiency symptoms earlier than the later maturing cultivar. Clement-Bailey and Gwathmey (2007) reported similar findings. The authors only noted significant increases in yields from additional K for the earlier maturing cultivar (no yield response to additional K was noted in the later maturing cultivar). Results are also in agreement with findings of Tupper *et al.* (1996), who concluded that earlier cultivars required higher levels of soil test K as applications of fertilizer K increased earlier maturing cultivars' yields but failed to greatly impact the yields of later maturing cultivars. Cassman *et al.* (1989) observed differences in K uptake between two cultivars and suggested K uptake from soil was the main factor determining efficiency as partitioning was not different between the two. Furthermore, the author only noticed differences in K efficiency at low K levels; at high K levels differences were not noted. Similar results were noted under controlled growing conditions by López *et al.* (2008). Further uptake research was conducted by Keino *et al.* (1996), who examined the response of K uptake from two cultivars of differing maturities after foliar K was applied. The authors found foliar K doubled the root uptake of K from both the early and late maturing cultivars, although increases in number of squares and shoot tissue and decreases of root length tended to be elevated in the later maturing cultivar.

Still, other research examining cultivars of varying maturity has not shown significant differences in response to K fertility. Pettigrew (1999) and Pettigrew *et al.* (1996) examined the responses of early, mid and late maturing cotton cultivars to varying K fertilizer rates and found genotype to be insignificant. Concern that the previously examined cultivars included genetic differences beyond maturity led the investigator to conduct further research examining the response in two okra and normal leaf-type isogenic pairs (Pettigrew, 2003). This approach was chosen due to the earlier maturity of okra leaf-type cultivars as compared to normal leaf-type cultivars while maintaining more similar genotypic traits than cultivars examined in earlier experiments. Significant responses to K deficiencies were noted, but earlier maturing cultivars did not significantly increase this response. Gwathmey *et al.* (2009) also found no significant differences in K utilization or uptake ratios between cultivars of differing maturity, but suggested differences may be significant under lower K statuses. Although inconsistent, earlier maturing cultivars did have greater K uptake in one out of three years and greater K accumulation in the fruit in two of the three years of the study.

Potassium and relief of stress

Potassium is involved in numerous physiological functions related to plant health and resistance to biotic and abiotic stress, and because of this, K plays an important role in the metabolic and agronomic alleviation of stress.

Drought stress

All plants are subjected to water shortages at some time during their life cycles, resulting in numerous detrimental effects on plant growth. Alleviation of drought stress is therefore a fundamental aspect of crop management. Water-stressed chloroplasts have been observed to suffer increased leakage of K, resulting in further suppression of photosynthesis (Sen Gupta and Berkowitz, 1987). Water-deficit stressed plants, where higher than optimum quantities of K were supplied, were reported to be able to maintain efficient photosynthetic activity (Berkowitz and Whalen, 1985; Pier and Berkowitz, 1987) with higher K concentrations compared to plants where optimal quantities of water was applied (Cakmak and Engels, 1999). This was due to K's ability to maintain CO_2 assimilation rates by regulating stomatal function and balancing cell water relations (Mengel and Kirkby, 2001; Sangakarra *et al.*, 2000). High K levels have also been associated with maintenance of optimum pH values in the chloroplasts' stroma and optimal function of photosynthetic mechanisms (Pier and Berkowitz, 1987).

Cold stress

A positive correlation has been reported between K availability and cold stress tolerance, with lower than optimum K concentrations escalating the negative effects of cold stress (Kafkafi, 1990) while increased K levels enhance plant defense against cold stress, not only promoting production of antioxidative enzymes but also by acting as an osmolyte and lowering the freezing point of sap (Hankerlerler *et al.*, 1997; Kafkafi, 1990; Kant and Kafkafi, 2002).

Salt stress

High sodium (Na) levels in the soil solution significantly reduce K uptake from the plant in the cytoplasm and drives water out of the cell vacuole resulting in decreased cell turgor (Yeo *et al.*, 1991; Zhu *et al.*, 1997). High concentrations of Na cations compete in the soil with K cations, substantially reducing its uptake by the plants (Zhu, 2003). Higher K levels as well as increased capacity of plants to accumulate K have been associated with increased salt-tolerance in a number of crops such as Arabidopsis (Liu and Zhu, 1997; Zhu *et al.*, 1998), wheat (Rascio *et al.*, 2001; Santa-Maria and Epstein, 2001), cucumber (*Cucumis sativus* L.) and pepper (*Piper nigrum* L.) (Kaya *et al.*, 2001) due to K's ability to enhance plants' antioxidative mechanism.

Potassium and biotic stress

High concentrations of K have been reported to alleviate detrimental effects of disease and pest infestations (Bergmann, 1992; Perrenoud, 1990; Prabhu *et al.*, 2007). This has been attributed to the regulation by K of primary metabolic plant functions. High levels of K in the plant promote the synthesis of high molecular weight compounds, such as proteins, starch and cellulose while simultaneously suppressing the formation of soluble sugars, organic acids and amides, compounds indispensable for feeding pathogens and insects (Amtmann *et al.*, 2008; Marschner, 1995). In cotton, K application has been reported to significantly reduce Fusarium wilt and root rot caused by *Fusarium oxysporum* sp. (Prabhu *et al.*, 2007).

Diagnosis and amelioration of plant potassium status

The nutrient demands of current high-yielding varieties are not entirely met by natural soil fertility. The application of fertilizer is therefore required, yet spatial and temporal variability of abiotic and biotic factors results in varying nutrient demands of different fields across seasons. For K, two methods are currently used to determine optimum fertilizer applications.

Soil sampling and analysis

Soil sampling is the traditional method to determine necessary fertilizer applications (Baker *et al.*, 1992). Recommendations for sampling are created by cooperative extension services in each cotton-growing state in the US (in cooperation with the United States Department of Agriculture). Generally, soil sampling should be conducted at the depth of tillage (typically 15 cm) in a zig-zag pattern through uniform areas of each field every three to four years. Mixed soil samples are dried and analyzed for mg K kg^{-1}. Soil testing laboratories typically calibrate their recommendations based upon the type of analysis utilized, type of soil, crop to be grown and estimated yields. Still, deficiencies have been noted under laboratory-determined 'sufficient' levels (Oosterhuis and Weir, 2010). These unanticipated deficiencies may be due to sampling shallow soil depths which cotton may fail to fully exploit (Brouder and Cassman, 1990) or seasonal factors which require a mid-season measurement to accurately determine nutrient demands.

Tissue sampling and analysis

Although the most practical method to detect K deficient areas is through pre-plant soil testing, in-season plant tissue analysis has the potential to also be a valuable tool (Baker *et al.*, 1992). Unfortunately, the characteristics of plant K have complicated the establishment of critical values.

Potassium is generally concentrated in the leaves and stems early in the growth season and is then transferred to the reproductive structures, which become the dominant K sinks, later in the growth season (Bassett *et al.*, 1970; Cassman *et al.*, 1989; Halevy, 1976). These shifts result in a moving target depending upon growth stage. Inability to accurately characterize the sampled plant growth stage and/or failure to accurately describe tissue concentrations at differing locations on the target cotton development curve are major difficulties in tissue sampling programs. Many other genetic and environmental conditions and stresses can also influence K tissue concentrations through shifts in uptake and translocation. Furthermore, cotton takes up K in luxury amounts (Kafkafi, 1990) and this could possibly confuse tissue diagnostic recommendations (Oosterhuis, 1995). All of these properties of K have led to inconsistent and often conflicting reports of critical leaf K values (Reddy and Zhao, 2005).

Contrasting reports on the sensitivities of specific tissues have also been reported. Rosolem and Mikkelsen (1991) suggested that tissue sensitivity to K stress increases in the following order: leaves < bolls < roots < stems. These results suggest that only a severe deficiency would result in decreased leaf K concentrations. In contrast, Bednarz and Oosterhuis (1995) noted the following degrees of sensitivity: bolls < stems < leaves < roots. Still, many reports have suggested petiole sampling is more useful due to its more sensitive nature, noting declines in petiole K concentrations as early as seven days after treatment establishment (Coker *et al.*, 2003).

Amelioration with fertilizer

Although research in SJV stratified soils seemed to suggest that deep-placed K fertilizer would increase K uptake and yields, research from the south-eastern and mid-southern regions of the US often found no consistent yield responses. Mullins *et al.* (1997) examined the response of cotton yield to subsoil and surface applications of K and found no significant difference associated with application method. Further research by Mullins and Burmester (2009) in Alabama - examining subsoil, banded, and broadcast applications of K fertilizer - also noted no significant differences between methods of applications. Adeli and Varco (2002) examined broadcast and banded applications of K in Mississippi and found similar results. The authors only noted consistent yield increases from banded K applications in dry growth seasons. There has been some interest in deep placement of K (Tupper *et al.*, 1988) although yield responses from this method of K placement have been inconsistent (Reeves and Mullins, 1995).

Failure of these banded and subsoil applications to affect yield regardless of soil depth may be best explained by research conducted by Brouder and Cassman (1994). They examined the response of cotton roots and shoots to localized supplies of N, phosphorus (P), and K. Results suggested that although root proliferation and compensatory growth were typically observed after N and P enrichment, neither were observed after K enrichment. Therefore, the quantity and distribution of N through the profile can greatly influence K uptake by influencing root proliferation. This may be one reason why increasing the amount of N fertilizer increases the amount of K uptake (Halevy *et al.*, 1987), but that increasing the amount of K fertilizer does not increase N uptake (Pettigrew and Meredith, 1997).

When soil analysis calls for K, the cotton crop is usually fertilized with a single preplant broadcast application of K fertilizer. Potassium chloride, commonly referred to as muriate of potash, is the most common source of fertilizer K due to its cost and high K composition (IPNI, 2011a). The contained chloride (Cl^-) typically leaches with the application of water and is not considered to negatively affect cotton growth in most humid regions. Still, in arid regions where application of Cl is of concern or where sulfur is needed, potassium sulfate, commonly referred to as sulfate of potash, is another acceptable K source (IPNI, 2011b). Under these conditions research has shown significant cotton yield penalties associated with the use of muriate of potash as compared to sulfate of potash (Pervez *et al.*, 2005). Other sources of K include potassium magnesium sulfate, commonly referred to as Langbeinite, and potassium nitrate, but use of these fertilizers is typically restricted to high value crops and not commonly used in cotton production (IPNI 2011c; IPNI, 2011d).

Mid-season applications are infrequently applied, and foliar applications are only used occasionally to correct K deficiencies during fruiting. Foliar applications of K offer the opportunity of correcting mid-season deficiencies quickly and efficiently, especially late in the season when soil application of K may not be effective. The practice of foliar fertilization has only caught on in cotton production in the last two decades, but there is still considerable speculation about the benefits and correct implementation of this practice. While there are many reports on research involving soil-applied K (e.g. Kerby and Adams, 1985), there are no definitive studies available on the usefulness of foliar-applied K. Earlier research (Oosterhuis, 1976; Oosterhuis *et al.*, 1991) indicated that foliar-applications of K significantly increased seed yield of cotton. There have also been reports of foliar-applications of K improving both lint quality and yield (Oosterhuis *et al.*, 1990; Pettigrew *et al.*, 1996). With the current emphasis on lint quality (Sasser, 1991) and the introduction of high-volume instrumentation classification, the positive effect of K on lint quality may be of paramount importance.

Conclusions

This review has described the major role that K plays in plant physiological processes fundamental to normal growth and yield development of cotton. Potassium deficiency was described and related to functions in the plant. It was shown that K is also involved in numerous physiological functions related to plant health and resistance to biotic and abiotic stress. In addition, the role of K in stress relief was highlighted. Lastly, the agronomic aspects of K requirements, diagnosis of soil and plant K status, and amelioration of K soil and plant status were discussed. However, research has mainly focused on model crops such as arabidopsis or rice and maize with very little or even no information existing on the physiology, biochemistry and most importantly molecular biology of K nutrition in the cotton plant. Identification of the metabolical pathways that may be controlled by K in the cotton plant will improve our understanding of the plant's adaptation to deficiency, aiding farmers to generate more efficient fertilization strategies on marginal soils and additionally provide us with valuable information on targets for future genetic improvement efforts.

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The paper "Potassium and Stress Alleviation: Physiological Functions and Management in Cotton" also appears on the IPI website at:

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