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Effects of Potassium on the Movement of Amino Acids and Sugars into Maize Endosperms

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ABSTRACT: Efforts were made to study effects of potassium (K) on the movement of amino acids and sugars into maize (*Zea mays* L.) kernels and the relationship between grain yield and lodging severity. Developing kernels of maize hybrid B73 x Mol7 were incubated *in vitro* in a reaction mixture containing 50 mM ^{3}H-glutamine, 200 mM ^{14}C-sucrose, and varying amounts of K salts to determine K effects on the transport of these organic nutrients into endosperms. Results indicate that the kinetics of K effect on glutamine and sucrose transports were similar, and the movement of these two organic nutrients into endosperms reached a maximum level when K concentrations increased to 100 mM. The degree of stimulation declined at higher levels of K. There was a positive correlation between grain yield and lodging severity for the four maize hybrids B73 x LH51, FS854, LHE136 x LH82, and A632 x LH39 evaluated. The relationship between dry matter accumulation in kernels and lodging severity of stalk was discussed.

KEY WORDS: Amino acids, grain yield, maize, nutrient unloading, potassium, stalk lodging, sugars, *Zea mays* L.

INTRODUCTION

Potassium (K), unlike phosphorus (P) and nitrogen (N), is not a structural component of plants but plays an important role in regulating biochemical and physiological processes, including assimilate transport (Mengel, 1985; Wolswinkel and Ammerlaan, 1985). Potassium may also affect N utilization (Suelter, 1985), in part, by interacting with N form, ammonium or nitrate, and N amounts to influence dry matter production and yield. Karlen *et al.* (1987) speculated that excessive K accumulation in tissues could result in yield decreases.

Starch and protein are the two major storage components in maize endosperms affecting grain yield and nutritional quality. Sucrose and amino acids provided by the vegetative source are substrates for the synthesis of starch and proteins, respectively, in the developing kernel sink. Thus, the unloading of nutrients from phloem termini into pedicel and the subsequent uptake by the endosperm tissue are important processes that may affect kernel development and dry matter accumulation. However, factors involved in regulating the uptake of nutrients by endosperms in maize are not clear. Although osmotic regulation may be important in

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affecting the movement of amino acids and sugars into maize kernels (Tsai *et al.*, 1980; Tsai, 1983; Tsai *et al.*, 1983; Lee and Tsai, 1985), studies with developing maize kernels incubated *in vitro* with L-[^{3}H]glutamine and D-[^{14}C]glucose indicated that mechanisms of amino acid uptake were different from those of sugars (Lyznik *et al.*, 1989). In contrast to D-glucose uptake, L-glutamine uptake showed substrate-saturable kinetics, and required energy and protein carriers. However, the uptake of D-glucose was not a simple diffusion process either.

Because K has also been shown to affect assimilate transport (Mengel, 1985; Wolswinkel and Ammerlaan, 1985) and plays an essential role in preventing stalk lodging in maize (Arnold *et al.*, 1974), efforts were made to determine whether K may regulate the unloading of nutrients into maize kernels to affect yield and stalk quality.

MATERIALS AND METHODS

Uptake of ^{3}H-glutamine and ^{14}C-sucrose *in vitro*

Developing plants of B73 x Mo17 grown under 268 kg N ha^{-1} were harvested at 20 days post-pollination and brought into the laboratory immediately after collection. Kernels from the center of the cob were removed and the pedicel region was subsequently dissected from them, leaving the basal endosperm transfer cells intact and then assayed according to the procedure described by Lyznik *et al.* (1989). These kernels were pre-incubated in 5 mM sodium phosphate buffer, pH 6.5, for 30 min. Subsequently, four kernels were incubated in 2 ml of a reaction mixture that contained 5 mM sodium phosphate buffer, pH 6.5, 50 mM glutamine (1 μCi, [^{3}H]-glutamine, 44 Ci mmol^{-1}), 200 mM sucrose (2 μCi [^{14}C]-sucrose, 271 mCi mmol^{-1}), and K salts (KCl, K_2SO_4 or K-acetate) at a concentration of 0, 25, 50, 100, or 200 mM. After incubation for four hours at room temperature, the kernels were removed from the reaction mixture, washed with distilled water, and dissected to remove the pericarp and embryo. The endosperm was crushed in a scintillation vial containing 1 ml of 70% ethanol. Subsequently, 100 μl of a mixture of 70% perchloric acid and hydrogen peroxide (1:1, v/v) was added, and the mixture was incubated overnight at room temperature to decolor the solution. After incubation, 10 ml of counting cocktail (Budget-Solve) containing 5% (V/V) protosol (New England Nuclear) was added. About 48 hours later, the radioactivity of ^{14}C and ^{3}H was measured in a liquid scintillation counter (Beckman Model LS 3801) to determine the movement of sucrose and glutamine, respectively, into the endosperm as affected by the various K concentrations. All experiments were repeated twice.

Determination of grain yield and lodging severity

For determinations of grain yield and lodging severity, maize hybrids, B73 x LH51 (which is similar to B73 x Mo17), FS854, LHE136 x LH82, and A632 x LH39 were grown at the Purdue Agronomy Farm in 1990 on a Chalmers silt loam soil (Typic Haplaguall, fine-silty, mixed, mesic). In order to reduce the residual soil N to levels more commonly experienced by growers in the area, maize hybrid B73 x LH51 was grown the previous year without N application. The preplant residual soil N in the top 46 cm, as determined by the

Purdue Soil Testing Lab two weeks before fertilization, was 10 kg ha^{-1} as nitrate and 19 kg ha^{-1} as ammonium. The preplant soil K in the top 46 cm was 290 kg K_2O ha^{-1}.

Anhydrous ammonia (90 kg N ha^{-1}) and KCl (0 or equivalent to 180 kg K_2O ha^{-1}) was knifed in on 76 cm centers in the spring about 2 weeks before planting. Inorganic nutrition treatments were assigned randomly to main plots. Each main plot consisted of 8 rows, 76 cm apart and 23 m long. Subsequently, each main plot was equally divided into two sections 11.5 m long, and each section was planted to two hybrids randomly selected so that each hybrid constituted four adjacent rows in the plot for pollen enrichment. The distance between plants within rows was 22 cm with a plant density of 59,000 plants ha^{-1}. The experimental design was a split-plot with four replications. At maturity, samples were collected from the two center rows of the four rows for each hybrid to determine grain yield. The two outer rows were used as buffer.

Lodging severity (rots and natural lodging combined) was determined by pressure-induced breakage (approximately 2 kg horizontal pressure at a 90 cm height) just before grain harvest and the lodging severity was expressed as % of lodged plants against total.

RESULTS AND DISCUSSION

Effects of potassium on ^{3}H-glutamine and ^{14}C-sucrose uptake

Although the movement of organic nutrients, i.e., sugars and amino acids, into the kernel is, in part, determined by the genetic composition of the kernel (Tsai *et al.*, 1984), other factors such as osmotic potential may also be involved in regulation (Tsai *et al.*, 1980; Tsai, 1983; Lee and Tsai, 1985). The accumulation of soluble amino acids or sugars in the kernel due to a small sink (inability to precipitate) may generate a low osmotic potential to facilitate water movement but reduce solute movement into the kernel. We have shown that zein functions as a primary N sink (Tsai *et al.*, 1980; Tsai, 1983; Tsai *et al.*, 1983) and starch acts as the carbon (C) sink (Lee and Tsai, 1985) to regulate nutrient movements into the kernel. In addition to osmotic regulation, the unloading of organic C and N nutrients into the endosperm appears to be regulated by K. When developing kernels (20 days post-pollination) of B73 x Mo17 were incubated in a solution containing 50 mM ^{3}H-glutamine, 200 mM ^{14}C-sucrose, and various concentrations of K, the uptake of these nutrients was proportional to time of incubation for 8 hours (data not shown), and responded differently to K concentrations (Figs. 1 and 2). The uptake of glutamine and sucrose increased rapidly as the concentration of K increased and reached their maximal levels at about 100 mM. The optimal concentration of K required for stimulating the movement was similar for both glutamine and sucrose. The degree of stimulation declined at higher levels of K. Potassium levels higher than 100 mM decreased net uptake for both nutrients.

The effect of high K concentrations in decreasing the movement appeared to be the result of an allosteric interaction of K rather than effects of anions. As shown in Figs. 1 and 2, three K salts, i.e. KCl, K_2SO_4, and K-acetate showed a similar kinetics in regulating the movement of glutamine and sucrose. However, both sulfate and acetate salts showed a greater stimulation than the chloride salt.

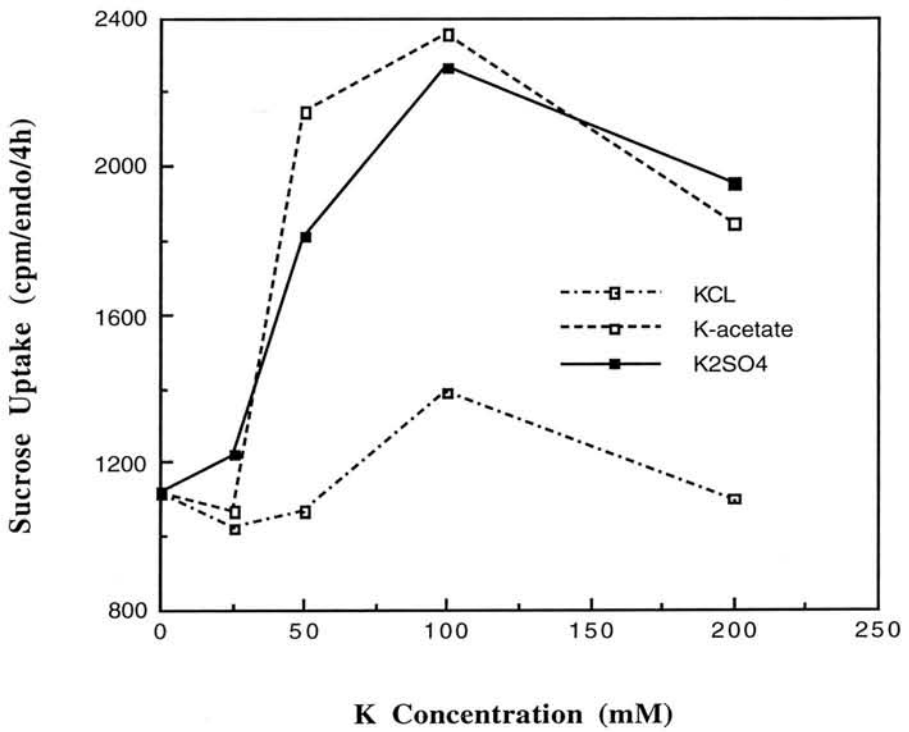

Fig. 1. Effect of K concentrations on the uptake of ^{14}C-sucrose into 20-day-old endosperms of B73 x Mo17.

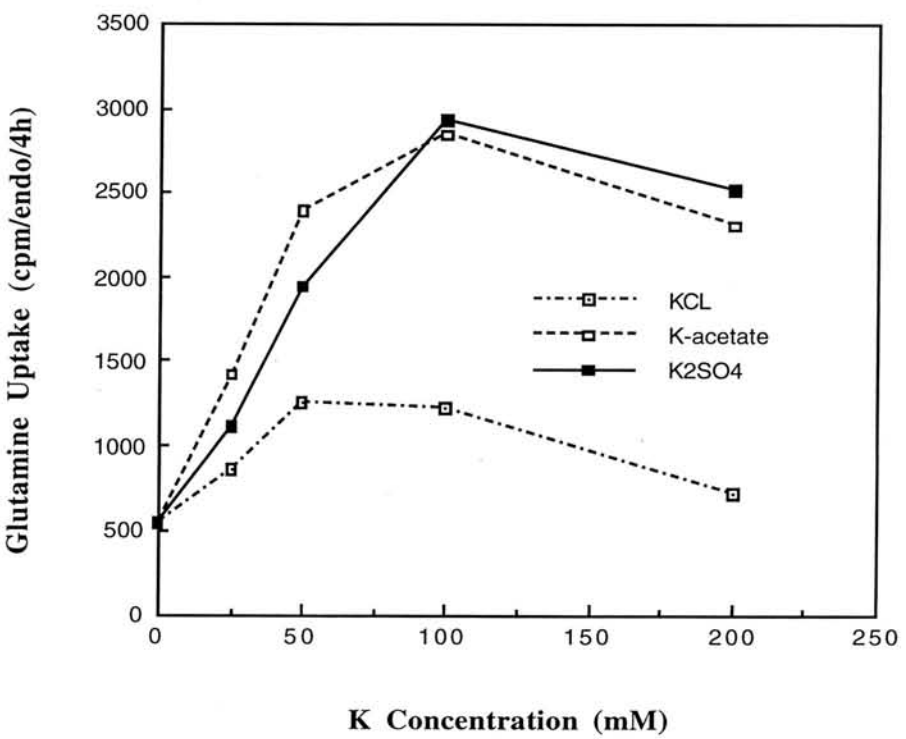

Fig. 2. Effect of K concentrations on the uptake of ^{3}H-glutamine into 20-day-old endosperms of B73 x Mo17.

Effects of supplemental K on grain yield and lodging severity

When grown at 90 kg N ha^{-1}, 180 kg K_2O ha^{-1} of supplemental K suppressed grain yield of B73 x LH51, FS854, and LHE136 x LH82 in comparsion with the controls, with the exception of A632 x LH39 (Table 1). FS854 and LHE136 x LH82 showed a greater severity in lodging than that of A632 x LH39 and B73 x LH51 (Table 1). Although hybrids differed in their severities to lodging, all hybrids evaluated except A632 x LH39 showed improvement in stalk quality at the expense of grain yield when additional K was applied. These observations are consistent with the notion that stalk lodging may be, in part, the result of severe cannibalization of nutrients from the stalk to enhance kernel development and grain yield when grown under N insufficient conditions. Our previous studies have shown that 90 kg N ha^{-1} at the Agronomy Farm was not sufficient for maximum yield (Tsai *et al.*, 1992).

Table 1. Grain yield and lodging severity of maize hybrids grown at 90 kg N ha^{-1} with or without 180 kg K_2O ha^{-1} of supplemental K.

	Grain yield (Mg ha^{-1})		Lodging severity (%)	
Hybrid	0 kg K	180 kg K	0 kg K	180 kg K
B73 x LH51	11.29	10.59*	10	9
FS854	10.72	9.90*	69	55*
LHE136 x LH82	10.91	9.59*	67	56*
A632 x LH39	6.46	7.15	26	31

* Significant difference from 0 kg K control at $p< 0.05$.

Although it is not clear whether all maize hybrids show similar kinetic effects of K on the movement of organic nutrients into endosperms, these kinetics provide an explanation of the critical role of K for high yield production and the relationship of high K conditions to reduced lodging and stalk rot severity. Conceivably, Under high K conditions, less amino acid and sucrose are transported into kernels as compared with the optimum K concentration for grain-fill. This reduced nutrient movement into the kernel should reduce grain yield and reflect less cannibalization of biochemical and structural components in leaf and stalk tissues to maintain better stalk quality, a situation applied to B73 x LH51, FS854, and LHE136 x LH82. Accordingly, A632 x LH39 might require a higher level of K than B73 x LH51, FS854, and LHE136 x LH82 for a maximal level of nutrient movement into kernels.

Our previous studies suggest that when available N from soil or readily available vegetative sources are not sufficient to meet the metabolic and storage requirements of developing kernels, degradation and mobilization of enzymatic and structural components from vegetative tissues could become extensive (Tsai *et al.*, 1986; 1991). The result of this nutrient redistribution from leaves to kernels caused an early termination of photosynthesis and reduced grain yield (Tsai *et al.*, 1991). Extensive mobilizations of nutrients from the stalk to kernels weaken the strength of a stalk and thus predispose the stalk to stalk rot and lodging (Huber *et al.*, 1986). The observation that grain yields and lodging severities were

responding to K treatments for these four hybrids is consistent with the cannibalization hypothesis.

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鉀離子對於氨基酸與醣類運送進入玉米胚乳的影響

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摘　　要

本研究的主要目的在於探討鉀離子對於氨基酸和醣類運送進入玉米種子的影響以及種子產量和植株倒伏的相關性。以發育中的玉米雜交品種 B73xMo17 種子在體外測試不同濃度的鉀離子對於 50mM ^{3}H-glutamine 和 200mM ^{14}C-sucrose 運送的影響。結果發現鉀離子對於氨基酸和醣類運送有相似的調控現像，當鉀離子濃度增加到 100mM 時最能促進有機養份的運送，但是鉀離子濃度增加到 200mM 時反而有抑制的現象。以四個雜交品種 B73xLH51, FS854, LHE136xLH82 及 A632xLH39 進行田間實驗，發現在低氮肥狀態下，鉀肥對於種子的產量和植株倒伏有正相關的影響。本文對於此一正相關性有進一步的討論。

關鍵詞：氨基酸、種子產量、玉米、養分運送、鉀、倒伏、醣類

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