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Gaseous exchanges, growth and foliar anatomy of sugarcane plants grown in potassium (K) deprived nutrient solution

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Abstract

Potassium participates in the plant metabolism and has an important effect on stomata opening, the activation of some enzymes and the mobilization of solutes, with positive effects on photosynthate distribution. Thus, in order to verify the effects of potassium absence on plant gaseous exchanges, growth and leaf anatomy of the sugarcane, an experiment was carried out under greenhouse conditions. The experiment was conducted for 90 days in a greenhouse with nutrient solution, where treatments consisted of the presence (control) and absence of K. The experiment was setup in a completely randomized design with ten repetitions. Gaseous exchanges were evaluated together with plant growth, chloroplast ultrastructure of the diagnostic leaf, chlorophylls content, green color index, total soluble sugars content, starch content, and K accumulation in the plant. Sugarcane plants grown in K-deprived nutrient solutions showed reductions in transpiration (-35%), photosynthesis (-58%), stomatal conductance (-32%), chlorophylls contents *a* (-25%) and *b* (-29%), green color index (-76%), plant height (-22%), tiller diameter (-23%), root density (-53%), K accumulation in the shoots (-76%) and roots (-79%), and dry matter mass of the shoots (-22%) and roots (-23%). The total soluble sugars content (26%) and starch content (28%) in the leaves increased, as well as the intercellular concentration of CO_2 (40%). Sugarcane in the absence of K showed reduced growth due to the influence of this nutrient on gaseous exchanges and alterations in leaf anatomy, suggesting greater focus should be taken on potassium nutrition, mainly in physiological terms, since there are vast agricultural areas with potassium deficiency around the world.

Keywords: dry matter; nutrient; photosynthesis; *Saccharum* spp; sugars; transpiration.
Abbreviations: *A*_net CO_2 assimilation; AST_total soluble sugars; *Ci*_CO_2 intercellular concentration; CW_cell wall; *E*_transpiration; G_granum; GLU_glucose; *gs*_stomatal conductance; K_potassium in the nutrient solution; K^+_potassium ion; ST_starch grain.

Introduction

Potassium deficiency is harmful to vital plant functions, resulting in reduced growth and productivity. K^+ ions alter the cell osmotic potential and turgor pressure, and thus play a significant role in cell extension (Hawkesford et al., 2012). This is a relevant fact since K deficient agricultural soils are common (Römheld and Kirkby, 2010). Potassium fertilizer doses commonly used in agriculture are lower than potassium amounts absorbed by the plants, thus aggravation of potassium nutritional disorders occurs since this element represents up to 6% of the total plant dry matter (Alemán et al., 2011). In literature some studies have reported the effect of potassium on increases in plant growth during the initial sugarcane phase in field conditions (Khosa, 2002; El-Tilib et al., 2004), and there are also reports of less accumulation of this nutrient in shoots and roots of other plant species submitted to potassium deficiency in greenhouse conditions, resulting in reduced growth as a function of physiological alterations (Bednarz and Oosterhuis, 1999; Jordan-Meille and Pellerin, 2008). Potassium is essential for stomata opening because it acts as an osmotic agent in the cell expansion process, playing an important role in CO_2 diffusion and consequently net CO_2 assimilation and transpiration of the plants (Pervez et al., 2004). In this function, it may be replaced by inorganic ions (Very and Sentena, 2003). K^+ also acts by activating enzymes, such as RUBISCO which is important in CO_2 fixation (Weng et al., 2007), plant movements, charge neutralization, transcriptional and post-transcriptional modifications (Maathuis, 2009). In addition, K^+ is very important for the movement of solutes via phloem (Karley and White, 2009) and thus indirectly increases photosynthesis rate. In K^+ deprived plants, carbohydrates start to accumulate in chloroplasts and this leads to a decline of the biochemical phase of photosynthesis (Redy and Zhao, 2005; Karley and White, 2009; Zhao et al., 2001), as well as lower concentrations of chlorophyll a and b, indicating biochemical alterations in the chloroplasts (Jia et al., 2008). The limited production of photosynthates resulting from the impairment of photosynthesis leads to inadequate supply of energy to the sink organs, reducing plant dry matter accumulation and thus plant growth. Potassium deficiency may further result in a hormonal imbalance, decreasing the accumulation of auxins and increasing that of ethylene, resulting in reduced plant growth (Zhi-Yong et al., 2009; Ashley et al., 2006). Studies on potassium absence in sugarcane plants are scarce – two were published at the beginning of the twentieth century (Hartt, 1929; Hartt, 1934) and another at the end of the 1970's (Haag and Accorsi, 1978), focusing on biochemical and symptom evaluations along with growth analysis. More recently, Vale et al. (2011) reported to have found no effect of potassium deficiency on sugarcane plant growth. The effects of potassium deficiency on sugarcane plant physiology and leaf anatomy were not found in the literature, indicating the need for performing studies of this type to gain a better insight of the effects that its absence has on vital processes of the sugarcane plant. Thus, the objective of this work was to verify the effects of potassium absence on gaseous exchanges, growth and leaf anatomy of the sugarcane cultivar RB85 5156.

Results

Potassium accumulation and deficiency symptoms

Potassium deficiency had a significant effect on sugarcane plants ($p \leq 0.05$), resulting in reduced potassium accumulation not only in the shoots but also in the roots. In potassium deficiency the shoots and roots presented reduced potassium accumulation of 76% and 79%, respectively, in comparison with the control treatment (Fig. 1a and 1b). The reduced absorption of potassium by plants in the potassium deprived treatment led to the development of symptoms in the leaf blades and central nervure (reddish brown spots) at the 10th week after bud sprouting, followed by a chlorotic development along the edge of older leaves (Fig. 2a and 2b).

Sugarcane growth

Potassium deficiency resulted in a significant reduction ($p \leq 0.05$) in plant height, tiller diameter, and root density, indicating decreases of 22, 23 and 53%, respectively, in comparison with plants of the control treatment (Fig. 3a, 3b and 3c) and caused a significant reduction ($p \leq 0.05$) in the dry matter content of the plant shoots and roots of 22% and 23%, respectively, in relation to the shoots and roots of plants in the control treatment (Fig. 3d).

Gaseous exchange, chlorophyll and green color index

Potassium deficiency resulted in lower net assimilation of CO_2, transpiration, and stomatal conductance of 58, 35 and 32%, respectively, in relation to the control, indicating a significant reduction ($p \leq 0.05$) in the case of potassium deficiency (Fig. 4a, 4b and 4c). However, the intercellular CO_2 concentration in potassium deficiency was significantly greater ($p \leq 0.05$), by roughly 40%, in comparison with the control treatment (Fig. 4d). In the absence of potassium, concentrations of chlorophylls *a* and *b* and the green color index of the leaves were significantly reduced ($p \leq 0.05$), presenting values lower than those found in the control treatment by approximately 25, 29 and 76%, respectively (Fig. 5a, 5b and 5c). The lower concentrations of chlorophylls *a* and *b* resulted in reduced photosynthesis (net CO_2 assimilation) (Fig. 4a).

Total soluble sugars, starch and leaf anatomy

In potassium deprived sugarcane plants the levels of total soluble sugars (Fig. 6a) and starch (Fig. 6b) were significantly higher ($p \leq 0.05$), by roughly 26 and 28%, respectively, than those found in plants of the control treatment. The chloroplast of sugarcane plants grown under potassium deprivation conditions showed round starch grains scattered in the stroma (Fig. 7b), whereas in the control treatment the chloroplasts showed no starch grain (Fig. 7a).

Discussion

The lower growth and dry matter production shown by sugarcane plants grown under potassium deprivation conditions are a consequence of the low levels of potassium accumulated in the plants (Fig. 1, Fig. 3) since this nutrient plays a vital role in the activation of enzymes, osmotic potential, and carbohydrate translocation in the plant (Leigh and Jones, 1984). The most important effect of potassium deficiency in plants is the fact that they become unable to translocate photosynthates to developing plant organs (Cakmak, 1994; Hawkesford et al., 2012). It is also necessary to consider that since potassium is an osmotic component, it brings about cell turgor which is crucial for cell expansion. According to Rubio et al. (2009), potassium is thought to be related to polar transport and the accumulation of auxins at the cell growth region. Some studies have shown that potassium deprivation promotes a hormonal unbalance and this results in decreased auxin levels, whereas ethylene synthesis increases and the overall effect is that of reduced shoot and root growth (Zhi-Yong et al., 2009; Ashley et al., 2006). In potassium deficient plants the genes controlling ethylene biosynthesis are stimulated to express themselves (Rubio et al., 2009). Furthermore, potassium at deficient levels causes roots to become less dense (Fig. 3c) due to its action in cell membranes as an osmotic component – when under deficiency conditions it reduces cell turgor mainly in phloem tissues and this hampers the transport of photosynthates between source and sink tissues (Krasavina et al., 2005). Although showing lower growth of both shoots and roots, in potassium starved sugarcane plants the proportion between the dry matter content of these two parts was similar to that observed in plants grown in complete nutrient solutions; this was understood as an indication that the absence of potassium does not modify the proportionality with which shoots and roots develop (Fig. 1a and 1b). This reduction in plant growth may be ascribed to alterations in the plant due to the function that potassium plays in the transportation of photosynthates and osmotic components.

The low amount of K^+ accumulated in the shoots and roots of plants growing under potassium deficient conditions is due to this nutrient being the second most absorbed by sugarcane and the K^+ reserve in the stem cuttings was not sufficient for plant demands (Ng, 2002). Some studies have reported effects of potassium omission on plant gaseous exchanges, particularly on stomata conductance and the activity of RUBISCO (Jia et al., 2008; Peng et al., 2006; Weng et al., 2007). The results herein reported show that the reduction in stomata conductance (Fig. 4c) caused reduced CO_2 diffusion and this brought about a dramatic reduction in net CO_2 assimilation (Fig. 4a) and lower transpiration (Fig. 4b). Similar results were reported by Pervez et al. (2004). Under moderate potassium deficiency the stomata are closed, thus protecting the plants from drought stress (Benlloch-González et al., 2012). The reduced photosynthetic efficiency may be ascribed to non-opening of the stomata since potassium plays an important role in maintaining turgor of the guard-cells. Moreover, the absence of potassium may interfere with CO_2 transportation from the mesophyll cells to those of the sheath which reduces photosynthesis in C4 plants since this intercellular transportation is essential for these plants (Huber, 1985). On the other hand, potassium deficiency markedly increased the CO_2 intercellular concentration (Fig. 4d). This may be an indirect effect of the nutrient since stomata aperture is dependent on the accumulation of potassium in the guard-cells. When potassium is absent the stomata are closed, restraining CO_2 which might have origin-

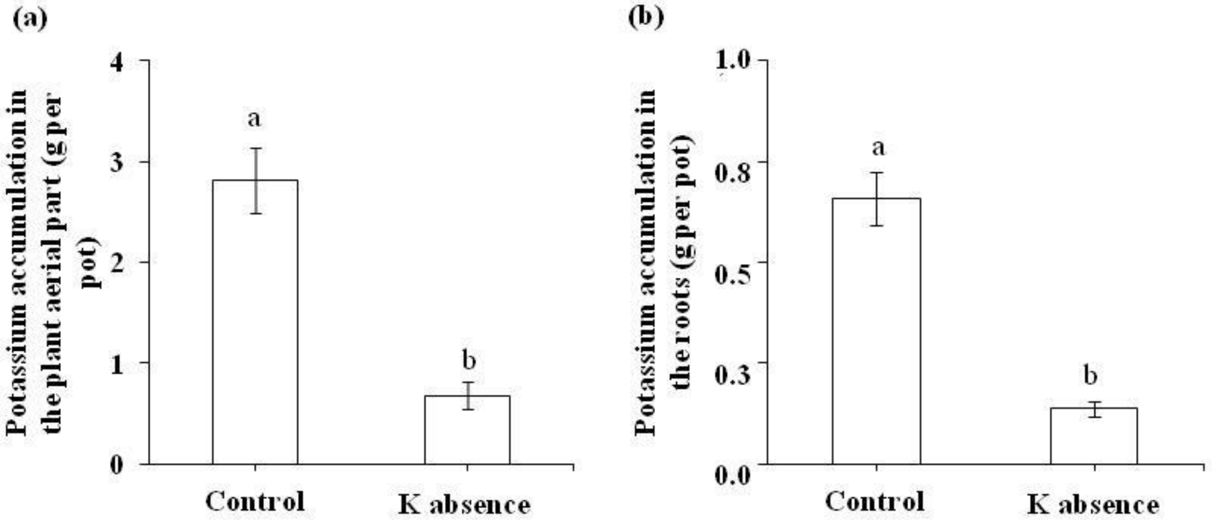

Fig 1. Potassium accumulation in sugarcane plants grown in potassium-deficient conditions: (a) plant shoots, and (b) roots. Means ± sd. n = 10. LSD for potassium accumulation in the plant shoots: 0.23. LSD for potassium accumulation in the roots: 0.05.

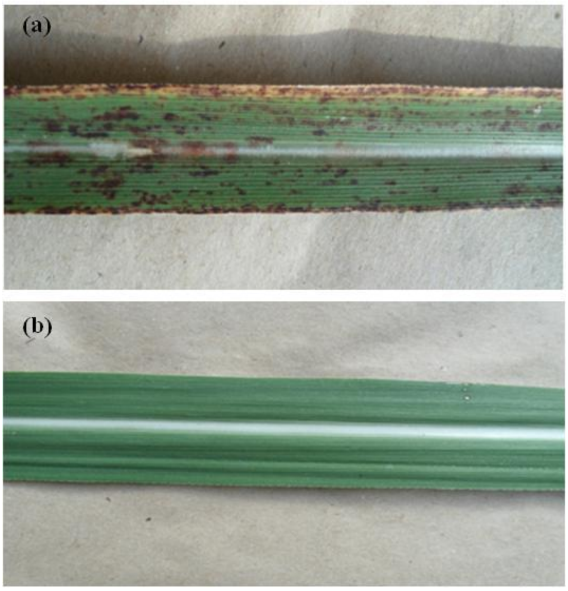

Fig 2. Potassium deficiency symptoms (a) control treatment (b) in (+3) leaves of sugarcane plants. Older leaves showed reddish brown spots on the blade and midrib, and chlorotic borders (a).

ated from the respiration process. PEPcase uses this carbon in the C4 cycle which characterizes the photosynthetic metabolism in sugarcane. However, the photosynthetic process was reduced in comparison with the plants receiving potassium since the intercellular quantity of CO_2, although increased, was not sufficient to increase photosynthesis.

Changes to the activity of several enzymes may be associated with modifications in plant metabolism through negative feedback (Amtmann and Armengaud, 2009), e.g., the accumulation of sugars due to alterations in the source-sink relation or K omission causes reductions in photosynthesis not by means of the stomata mechanism but by inhibition of RUBISCO activity (Karley and White, 2009; Gerardeaux et al., 2010). In addition to stomatal limitations (reduction of stomata conductance) and lower RUBISCO activity, the reduction of photosynthesis is also related to the reduction of chlorophyll pigments, chlorophylls *a* and *b*, and green color index (Fig. 5a, 5b and 5c). Reduction of chlorophylls is actually an indication of biochemical and functional disorders in chloroplasts as a consequence of K omission (Jia et al., 2008). ATP and NADPH consumption in the Calvin cycle is either reduced or null, permitting the generation of free radicals in the photochemical apparatus due to the inexistence of a final oxidized electron acceptor ($NADP^+$), as well as molecules of mono or diphosphate adenosine which result in reactive oxygen species which degrade chloroplast pigments.

The initial symptoms of potassium deficiency were described by Zhao et al. (2001), which included reduced stomata conductance, transpiration and photosynthesis, as well as a higher concentration of intercellular CO_2. These symptoms were confirmed in the present work, nothwithstanding the fact that the present observations were made in plants that were being acclimated to the potassium deprived nutrient solution. In these plants the symptoms of potassium deficiency were observed only in older leaves,

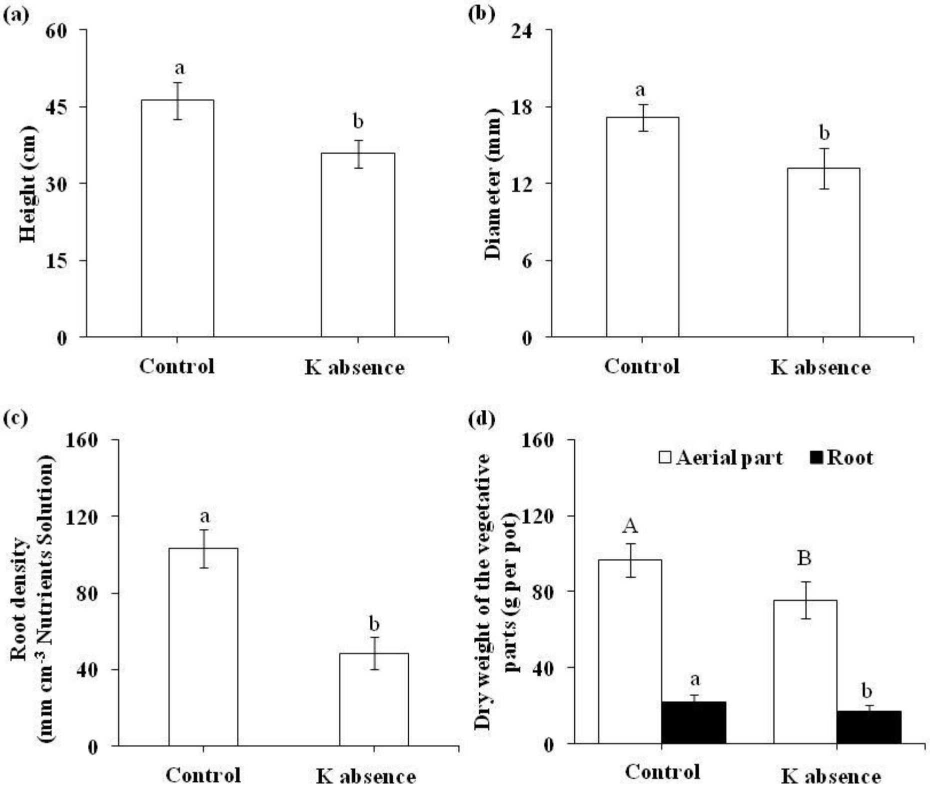

Fig 3. Sugarcane plant growth under conditions of potassium deprivation (a) height, (b) tiller diameter, (c) root density, and (d) plant shoot and root dry matter. Upper case letters compare plant shoot dry matter weight and lower case letters compare root dry matter weight. Means ± sd. n= 10. LSD for height: 3.00. LSD for tiller diameter: 1.26. LSD for root density: 10.78. LSD for plant shoot dry weight: 11.00. LSD for root dry matter weight: 3.01.

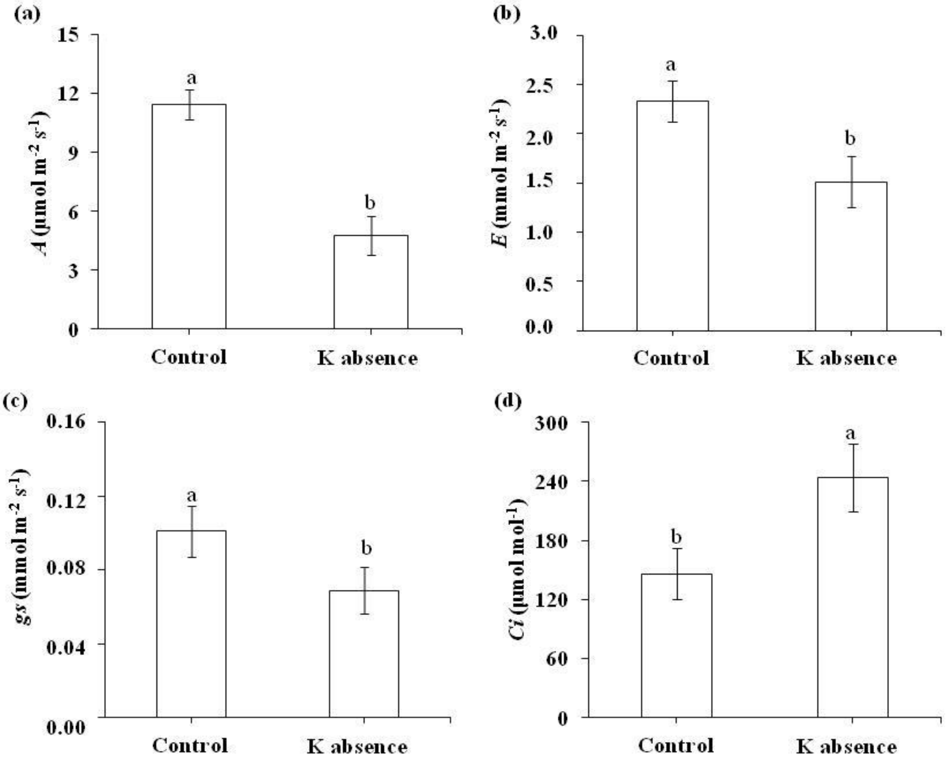

Fig 4. Gaseous exchanges of sugarcane plants under conditions of potassium deprivation (a) net CO_2 assimilation (*A*, µmol m^{-2} s^{-1}), (b) transpiration (*E*, µmol m^{-2} s^{-1}), (c) stomatal conductance (*gs*, mmol m^{-2} s^{-1}) and (d) CO_2 intercellular concentration (*Ci*, µmol m^{-2} s^{-1}). Means ± sd. n = 10. LSD for CO_2 liquid assimilation: 0.92. LSD for transpiration: 0.21. LSD for stomatal conductance: 0.01. LSD for CO_2 intercellular concentration: 28.60.

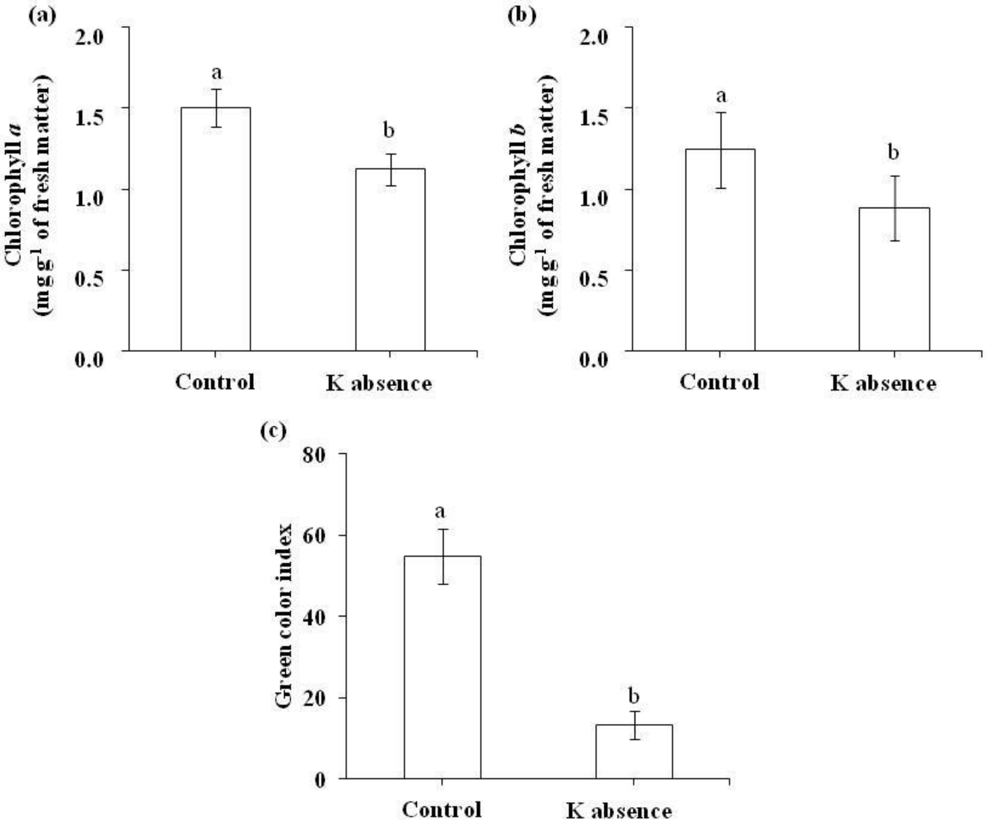

Fig 5. Chlorophylls concentration in sugarcane plants grown under potassium deprivation conditions (a) chlorophyll *a*, (b) chlorophyll *b*, (c) green color index. Means ± sd. n = 10. LSD for chlorophyll *a*: 0.11. LSD for chlorophyll *b*: 0.13. LSD for green color index: 5.05.

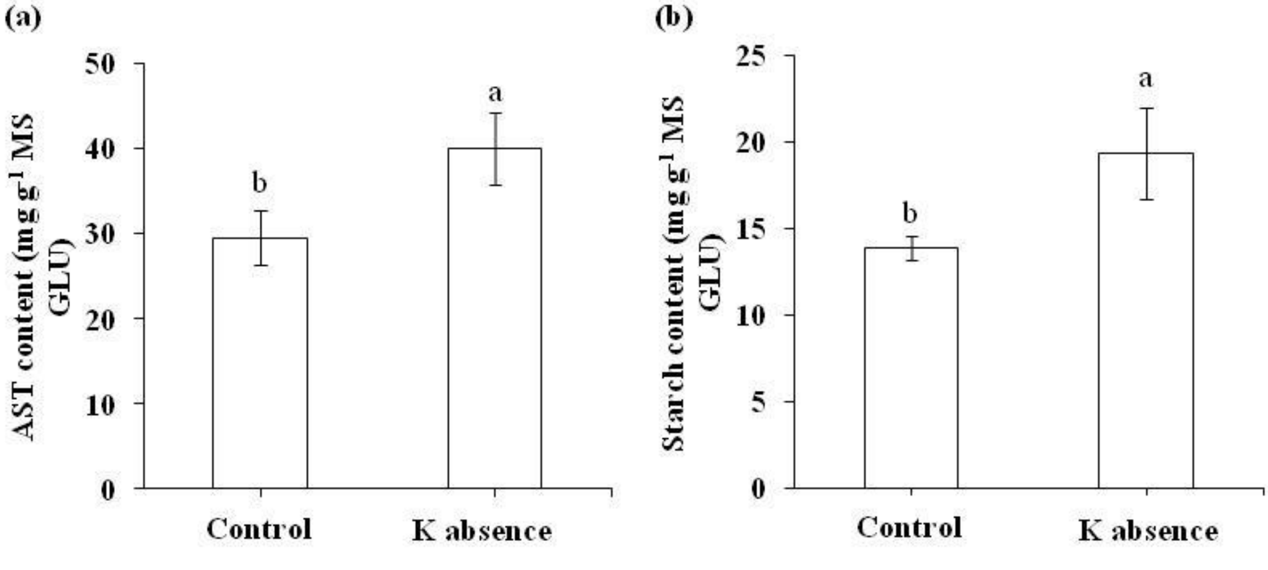

Fig 6. Carbohydrate content in sugarcane plants grown under potassium deprivation conditions, (a) total soluble sugars content (AST), and (b) starch content. Means ± sd. n = 10. LSD for total soluble sugars: 4.18. LSD for starch: 1.82.

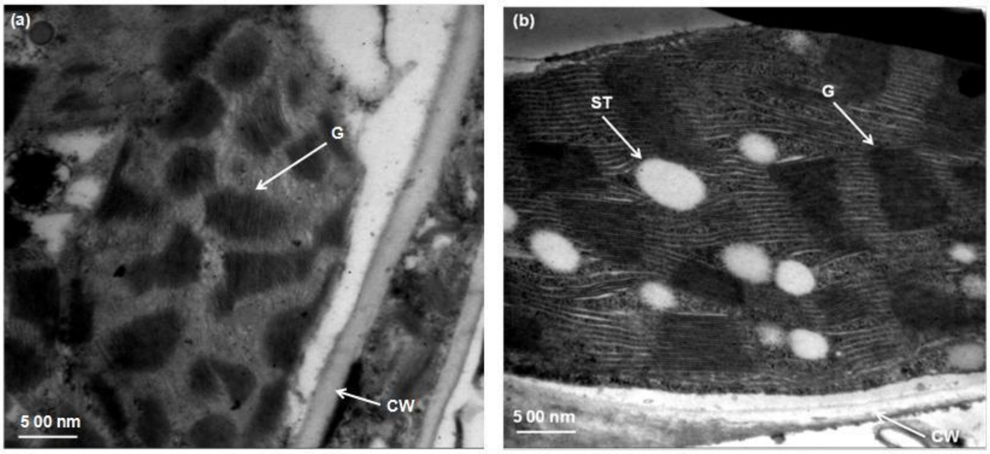

Fig 7. Ultrastructure of chloroplasts in sugarcane leaves, (a) control treatment, and (b) potassium deprived plants. Arrows indicate chloroplast structures ST: starch grain. G: granum. CW: cell wall. In the treatment with potassium deficiency an accumulation of starch grains in the chloroplast was observed, which was not observed in the treatment with potassium.

probably as a consequence of the high mobility presented by potassium in plant tissues. Plants grown in potassium deficient nutrient solutions showed increased levels of total soluble sugars and starch (Fig. 6a and 6b). Higher quantities of starch were found in the chloroplasts of plants grown in nutrient solutions deprived of potassium in comparison with those grown in complete nutrient solutions (Fig. 7a and 7b). This is a peculiar result since the metabolic processes verified during starch conversion are the opposite of those verified during the conversion of soluble sugars, i.e., the synthesis of starch in the chloroplast starting from triose phosphate depends on specific enzymes different from those for the conversion of triose phosphate into sucrose in the cytosol. Since this metabolism is dependent on the amount of orthophosphate, it is possible to assume that potassium omission modifies phosphorus availability or concentration, thus making the conversion of triose phosphate into starch more likely than sucrose. Considering the reduction in photosynthesis it is possible to hypothesize a reduction in soluble organic compounds, amino acids, and an insufficient incorporation of carbon into proteins (Amtmann et al., 2008; Hawkesford et al., 2012). The accumulation of both soluble sugars and starch in plants grown in potassium deficient nutrient solutions may be the result of alterations to the phloem contents, or during the transport of photosynthates. These results are opposed to the negative effects on photosynthesis due to the absence of potassium found in the present work. It is supposed that plants grown under potassium deprivation conditions had reduced photosynthesis as a consequence of an increment in the resistance of the mesophyll tissue and lower stomata conductance. The increase in sugar levels is probably due to inhibiting factors acting on photosynthate flux through the phloem. Zhao et al. (2001) reported to have found that potassium omission in cotton plants causes a reduction in translocation of saccharides, higher accumulation of starch in the chloroplast and reduction of photosynthesis.

Material and Methods

Plant material and experimental site

The experiment was conducted under greenhouse conditions on the UNESP (Paulista State University) campus located at latitude of 21°15’22’’ S, longitude of 48°18’58’’ W and a mean elevation of 575 m above sea level. The sugarcane cultivar used was RB85 5156. During the experiment the greenhouse presented the average day and night temperatures of 30ºC ± 1 and 27ºC ± 1, respectively, average relative humidity of 45%, 12 hour photoperiod and average irradiance of 1800 mmol m^{-2} s^{-1}. Five centimeter long billets with one bud were used. The billets were placed inside 500 mL plastic cups containing washed sand. Fifteen days after emergence, the plants were transplanted to 8 dm^3 propylene pots containing a Hoagland and Arnon (1950) nutrient solution diluted to 50% of the normal concentration and maintained this way for four days. After this period of plant adaptation, the nutrient solution was exchanged for another in which there was no dilution. The plants in this solution made up the control treatment, i.e., the received all nutrients including potassium. In the other treatment potassium was absent but all other nutrients were presented, which were provided using pure reagents. The solutions were continuously aerated and exchanged every week. The pH was adjusted daily using solutions of either HCl 0.1 mol dm^{-3} or NaOH 1 mol dm^{-3} so as to maintain a value of 6.0 ± 0.1.

Experimental design

The experimental units resulting from 2 treatments, with presence (control) and absence of potassium, and 10 replications, totaling 20 units, were distributed in a greenhouse according to a completely random design.

Evaluation of sugarcane growth

At the end of the 90 day experimental period when symptoms of potassium deficiency were observed in the older leaves in the potassium deprivation treatment, the following physiological evaluations of the plant shoots were made: plant height measured from the plant base to the sheath of the first totally expanded leaf with utilization of a graduated ruler and tiller diameter measured at the lower base with the aid of a digital caliper (Starrett 727-2001 ™). The roots were carefully severed from the plant, placed in flasks containing a 20% alcohol solution (v/v) and maintained under refrigeration for determinations of density (mm cm^{-3} nutrient solution) and dry matter (g). Root length was determined by an image analysis system (Delta-T Devices Ltd.). The roots were stained with methylene blue for approximately two minutes and then placed in a tray with water and the root length was determined by image analysis in a scanner

(Hewlett Packard model 5C). The image of each root system was analyzed by a software (Delta-T Scan Root Analysis System) which determined root length (mm) by the Harris and Campbell (1989) method. Root density was calculated by dividing root length by the volume of the nutrient solutions (mm cm^{-3}). After density measurement, the roots were placed in paper bags and placed in a forced ventilation oven to dry at a temperature of 65 °C until a constant weight was reached. The dry weight was determined on an analytical scale (Denver Instruments Company AA-200) with a 1 x 10^{-8} g precision.

Evaluation of Gaseous exchanges, chlorophylls, leaf anatomy, total soluble sugars and starch

The following physiological analyses were performed on leaves displaying potassium deficiency symptoms (leaf +3): net CO_2 assimilation (*A*, μmol m^{-2} s^{-1}), stomatal conductance (*gs*, mmol m^{-2} s^{-1}), transpiration (*E*, μmol m^{-2} s^{-1}), and CO_2 intercellular concentration (*Ci*, μmol m^{-2} s^{-1}). For this purpose the portable photosynthesis analyzer IRGA model Li-6400 Licor (Lincoln, USA) was used. In this period the chlorophyll contents were determined according to the methodology proposed by Arnon (1949) and the green color index with the aid of a CCM200 device (OptiSciences).

In leaves the chloroplast structure was studied by means of transmission microscopy, making use of the leaf blade (an area between 1 and 2 mm^2) collected from the plants. Leaf samples were dehydrated and then fixed using the procedure proposed by Wullschleger and Oosterhuis (1987).

Chemical evaluations utilized leaf samples for the determination of total soluble sugars and starch according to the procedures proposed by Dubois et al. (1956).

Evaluation of potassium accumulation

The plant shoots and the root system were collected and separated, and then washed and dried in a forced ventilation oven at a temperature of 65 °C until reaching a constant weight. After that, potassium content in the plant tissue was determined according to the procedure described by Bataglia et al. (1983). Combining this data with that of plant dry matter, the amounts of accumulated potassium in the plant shoots and root system were calculated.

Statistical analyses

The experimental data were first submitted to analysis of one-way variance (ANOVA) and then the means were compared by the Tukey's test ($p \leq 0.05$).

Conclusion

Sugarcane plants cultivated in the absence of potassium showed reduced growth of both the shoots and root system. In the absence of potassium there was a drastic reduction in transpiration, photosynthesis and chlorophyll contents. On the other hand, there was an increase in total soluble sugars and starch in plant chloroplasts. This study highlighted the effect of potassium deficiency on the physiology and biochemistry of sugarcane, suggesting greater focus on potassium nutrition, especially in terms of plant physiology, since this culture has economic importance and there are vast farmlands with potassium deficiency around the world.

Acknowledgments

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