1329 Is the impact of K deficiency on cotton (*Gossypium hirsutum*) mainly due to a dysfunction in growth, photosynthesis or water characteristics?

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Abbreviations

DM: dry matter

WUE: water use efficiency

RER: relative expansion rate

Vcmax: maximum velocity of carboxylation

Jmax: electron transport efficiency

Rd: dark respiration

Alpha: quantum efficiency

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Abstract

The effect of potassium nutrition on cotton biomass, leaf area, water characteristics, photosynthesis and gas exchange characteristic, was assessed under glasshouse hydroponic conditions and 4 levels of potassium nutrition. Leaf area, aerial and root biomass were measured. Leaf water potential and osmotic potential were measured and leaf turgor pressure were calculated. Photosynthesis activity was observed. Farquar model parameters were evaluated by A-Ci and A-PAR responses curves. At mild deficicency level, only stomatal conductance, leaf area, dry mater production and partitioning were affected. Maximum assimilation rates and Vcmax decreases only when foliar K decreases to a strong deficiency level. Alpha, Jmax and water characteristics were unaffected whatever the deficiency level was. Foliar sugar accumulation in K deficient leaves may be the key factor affecting nutrition of the growing organs, and photosynthetic capacity of the unfolded and mature leaves.

Introduction

Plant growth modelling under potassium (K) deficiency conditions is hampered by the lack of data on the plant scale. Physiological studies carried out to date on the consequences of

K-deficiency have mostly been focused on single mechanisms in plant organs and cells . K deficiency has various impacts on these mechanisms, but they have not yet been systematically classified. An operational classification of the roles played by K on plant growth was proposed by Leigh and confirmed by Walker , who highlighted the roles of K according to specific cell compartments. Thereafter they suggested that K deficiency could primarily affect the vacuolar cell compartment negatively (physical functions such as turgor maintenance), to the benefit of the cytoplasmic compartment where the metabolite functions would be preserved. This suggested that only turgor maintenance would be reduced when there is just a slight deficiency, leading to reduced cell growth and stomatal conductance, whereas a severe deficiency would lead to additive effects such as disruption of photosynthesis chemistry and carbon allocation . We conducted a K-starvation hydroponic experiment on cotton (*Gossypium hirsutum*) during vegetative growth. Four levels of K nutrition were used to compare the effect of K deficiency on different scales (plant, organ, cell), with the aim of summarizing them in a plant-growth interpretation scheme. We focused especially on growth and development, and on the underlying water and energetic processes associated with the observed disruptions.

Materials and Methods

This experiment was carried out in a greenhouse located at Bordeaux in March and April 2006. After germination, 60 cotton seeds were transplanted into individual 24 l plastic containers containing aerated standard nutrient solution with K present in the form of KCl (0.02, 0.06, 0.3 and 3 mM of K0, K1, K2 and K3, respectively). The pH was adjusted to between 5.5 and 6.5. The solution was renewed weekly.

Thermal time for cotton was calculated as follow: (min+max)/2 -13°C.

Twenty plants were used for continuous non-destructive recording of the plant stage, architecture and leaf area. These plants were those of the last destructive observation. Every 150°C days, five plants per treatment were randomly sampled for additional observations on roots, leaves and stems: biomass and main cations (K, Ca, Mg, Na). Plants components were dried during 48 h at 80 °C. Long term water used efficiency was calculated as the total DM (g) /water transpiration (g) at 494°C days.

RER of leaves at time j was calculated from emergence to the end of expansion as the slope (at time j) of the relationship between logarithm of leaf area (A) and time: $RER_j = [d(\ln A)/dt]_j$. It was calculated by linear regression on the three coupled values of A and t corresponding to times j-1, j and j+1.

At 381 °C days (the second observation date) we obtained the more contrasted leaves K status. Plants were used for other specific measurements such as water and osmotic potentials. Soluble sugars were measured in early-emerged and mature leaves. On the same mature leaves, a gas exchange analyser (LI-6400) was used to determine the response curves of assimilation rate to CO2 and light intensity. Response curves were used to estimate the parameters of the biochemical photosynthesis model developed by Farquhar by non-linear fitting procedures (Systat 10, SPSS Inc, 2000). Maximum assimilation rate was measured at 3000 µmol photons m-2 s-1, 600 ppm CO_2, 65 % Humity Ratio and leaf temperature: 25 °C.

Results

Plant K status

The four treatments led to a broad range of K concentrations in leaves, i.e. 8 to 80 mg g^{-1} (Fig. 1). The values recorded in starved plants were below the critical value for maximum growth : 17 g kg^{-1} for leaf area expansion and 12 g kg^{-1} for canopy photosynthesis. At 381°C days, we obtained the higher K content variability. Parallel to the K starvation, greater Ca and Mg concentrations were observed, but the total amount of cations (K + Ca + Mg + Na) in K starved plants did not fully compensate for the lack of K (187 mM in K0 and 269 mM in K3 at 381 °C days).

Growth and development

At 381°C days, mean DM and leaf area in K0 were 2-fold lower than in K3 (table 1). Biomass distribution in plants was modified by K deficiency as K0 had a greater specific leaf weight, lower stem/shoot and root/shoot ratios. The reduced leaf area was not due to higher senescence or a shorter growth duration but rather to a lower RER just after leaf emergence (< 80°C days). This negative influence of K on RER was particularly marked below 12 mg g^{-1} of K (fig. 2).

Photosynthesis parameters and carbon allocation

The principal results are presented in table 2. The maximum assimilation rate of deficient plants (K0) dropped from 39 to 29 µmol CO_2 m^{-2} s^{-1}. This was probably due to lower stomatal conductance and also to V_{cmax} reduction. K deficiency did not affect J_{max}, alpha or R_d. At mild deficiency (K1), only stomatal conductance was reduced. It was 0.6 mmol $m^{-2}s^{-1}$ while well alimented leaves had 0.7 mmol $m^{-2}s^{-1}$. Stomatal conductance had direct repercussion on assimilation rates as shown in (fig.5). The r^2 between stomatal conductance and assimilation rate is 0.78 for severe deficient plants (K0) while it is from 0.89 to 0.95 for other treatments. That result indicates that, when deficiency becomes severe (K0), assimilation rates is affected by other mechanism than stomatal conductance.

In spite of the reduction in photosynthesis, soluble sugars, especially saccharose and glucose, were over 2-fold more concentrated in K0 than in K3 mature leaves (fig. 3). Consequently, the specific leaf weight was higher (table 1), and carbon was preferentially located in leaves, to the detriment of the roots and stems. Soluble sugars in early initiated leaves (shoot apex) decreased with K deficiency (table 1), which could be linked to a disruption in saccharose transport from source to sink organs.

Water relation characteristics

Unexpectedly, the water potential increased with K deficiency. As osmotical potential was not modified (data not shown) this led to higher turgor pressure, which could be related to the significantly higher cation+soluble sugar contents in K0 than in K3 plants. Nor instant nor long term water use efficiency were significantly modified (table 2).

Discussion – Conclusion

According to the various plant responses, a cluster analysis, determined two threshold values: 1) 16.8 mg K/g DM, below which the first signs of deficiency, appeared on the plant scale; and 2) below 9.6 mg K/g DM, when there was a drastic decrease in the growth parameters (Fig. 5).

This reduced RER rate only occurred during the early stage of leaf growth when the organs were still heterotrophic. This result indicates that leaf area reduction under K deficiency can be attributed to a dysfunction in young leaves development, probably caused by low sugar content of shoot apex (table 1).

Finally, regardless of the K deficiency, saccharose translocation in phloem and stomatal conductance seemed to be the principal mechanisms that were disrupted. Modifications in other variables had minor effects (due to the reduction of photosynthesis) or were the consequence of the accumulation of soluble sugars blocked in the leaves (water characteristics, distribution of biomass and RER reduction).

Plant growth simulations involving K deficiency should thus be built on a carbon-based model and a stomatal opening adjustment. Such simulations do not necessarily include water variables despite the fact that they are known to be closely linked to K.

Table 1: Mean values leaf area, specific leaf weight, hexose in shoot apex and mature leaves, biomass partitioning to the potassium concentration in the nutrient solution 381°C days after planting. Means with the same letters are considered not to differ according to Student test at p = 0.05.

parameter	K0	K1	K2	K3	test F ($p<0.05$)
leaf area (cm^2)	1560 (c)	2400 (b)	3030 (ab)	3210 (a)	**
shoot DM weight (g)	10.8 (c)	16.3 (b)	21.5 (a)	24.0 (a)	**
root/shoot	0.19 (b)	0.26 (a)	0.25 (a)	0.25 (a)	*
stem/shoot	0.35 (c)	0.41 (b)	0.46 (a)	0.47 (a)	**
specific leaf weight ($g\ m^{-2}$)	28.1 (b)	25.1 (a)	25.6 (a)	24.8 (a)	*
hexose content of shoot apex ($mg\ g^{--1}$)	3.3	4.7	12.0	17.9	**NA**[1]

Table 2: Mean values for maximum assimilation rate, average stomatal conductance, photosynthetics parameters and water characteristics to the potassium concentration in the nutrient solution 381°C days after planting. Means with the same letters are considered to not differ according to Student test at p = 0.05.

parameter	K0	K1	K2	K3	test F (p<0.05)
A_{max} (µmol CO^2 m^2s^{-1})	29.6 (b)	34.6 (ab)	35.6 (ab)	39.1 (a)	*
Gs^2 (mmol m^2s^{-1})	0.50 (b)	0.60 (b)	0.70 (a)	0.71 (a)	*
turgor pressure of mature leaves (Mpa)	1.65	1.34	1.10	1.46	**NS**
instant WUE ^{2} (mol CO^2 /mol H_2O)	5.56	5.07	5.29	5.22	**NS**
long term WUE (g MS/g H2O)	5,6	6,2	6,5	6,9	**NS**
V_{cmax} µmol CO^2 m^2s^{-1}	105 (b)	158 (a)	164 (a)	176 (a)	**
J_{max} µEq $gChl^{-1}$ m^2s^{-1}	150	175	210	208	**NS**
alpha mol CO_2/mol photons	0.30	0.26	0.31	0.34	**NS**
R_d µmol CO2 m^2s^{-1}	-6.6	-7.9	-5.7	-11.7	**NS**

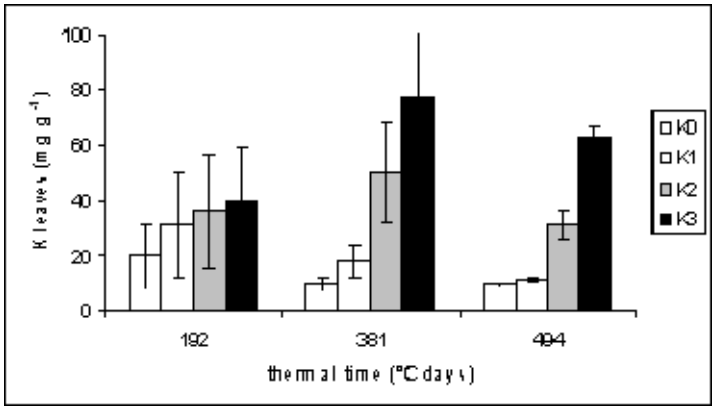

Figure 1: K content in leaves for each K treatment at various times. Vertical bars give the standard deviation.

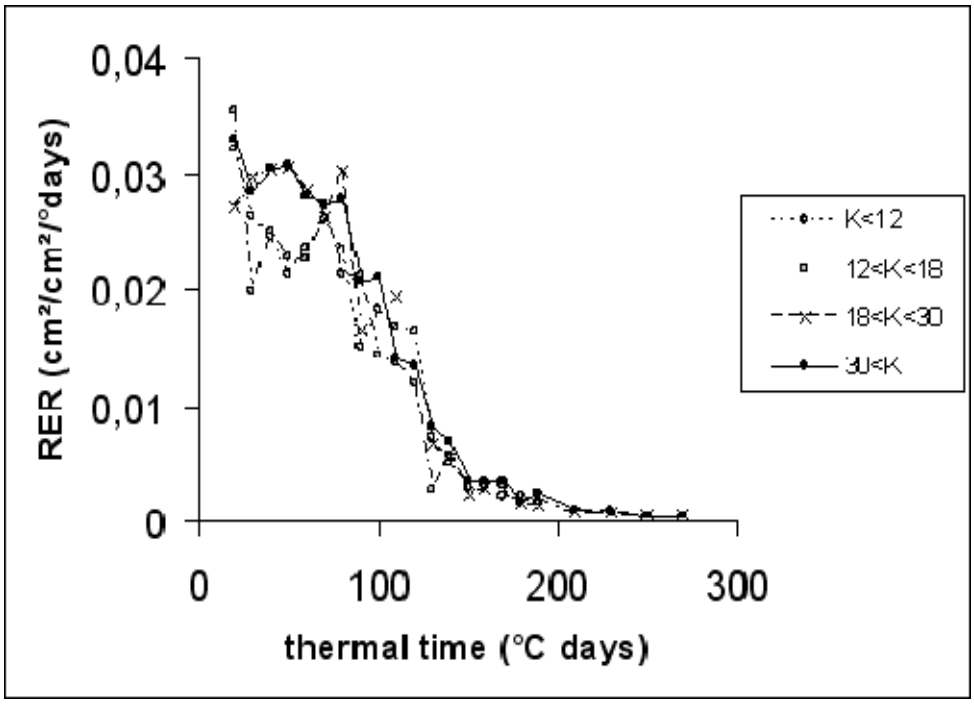

Figure 2: Relative growth rate of leaves area as a function of thermal time and the K interpolated concentration in mainstem leaves. Thermal time from emergence of each organ.

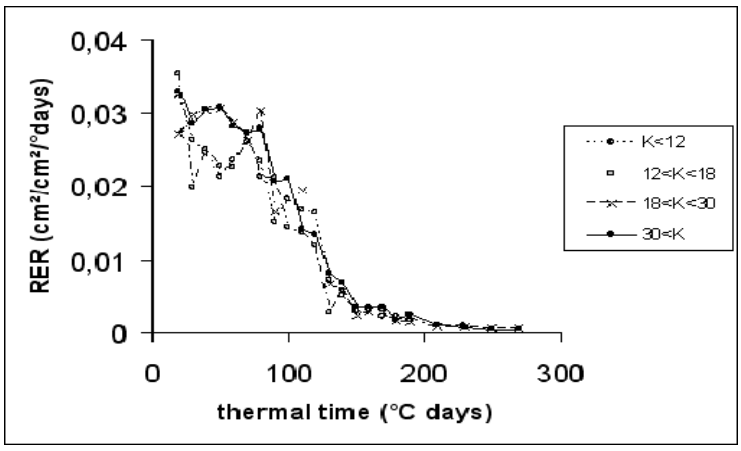

Figure 3: Foliar sugar concentration as a function of K treatments. K0 = 0.02, K1 = 0.07, K2 = 0.3, K4 = 3 mM. Values are the means of the first fully expanded leaf of 5 plants at 381°C days after planting. Vertical bars give the standard deviation. Dark bars: glucose (left Y axis), white bars: fructose (left Y axis), dots: saccharose (right Y axis)

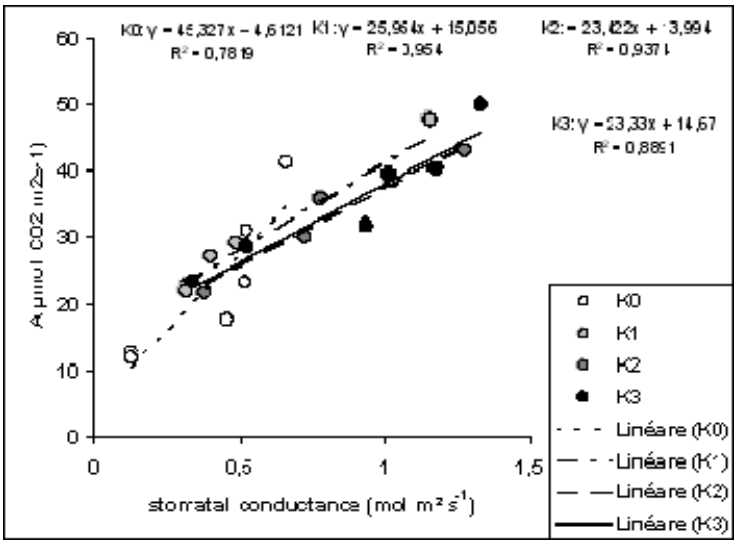

Figure 4: rate of CO2 assimilation (A), as a function of stomatal conductance for 4 levels of potassium in nutrient solution K0 = 0.02, K1 = 0.07, K2 = 0.3, K4 = 3 mM. Measurments were made at 25°C, 75 RH, 400 ppm CO2 and 1500 µmol quantum m-2 s-1 of PAR light intensity.

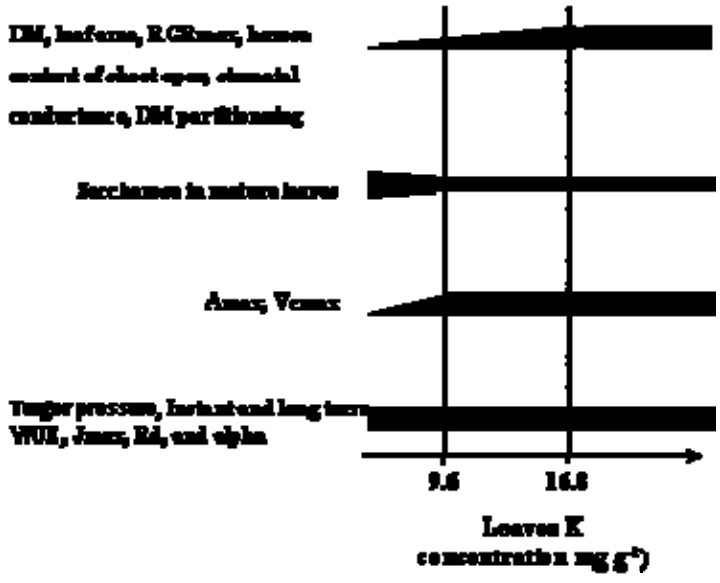

Figure 5: Summary diagram of the cotton response to different levels of K deficiency

1No statistical analysis applicable as shoot apex were regrouped for sugar determination
2at 1500 µmol photons m-2 s-1, 400 ppm CO_2, 65 % Humidity Ratio, Leaf temperature: 25 °C