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REGULAR ARTICLE

Effect of carbon assimilation on dry weight production and partitioning during vegetative growth

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Abstract Potassium deficiency is known to deeply impact dry matter yield through a lower photo-assimilates production. The objectives of this study were to find out and classify the principal mechanisms that accounted for the reduction in plant stature. Our approach used the framework of interception-conversion modelling, with focuses on photosynthesis (gas exchange analysis, Farquhar model), plant-water relations (water potential components), and soluble sugars in leaves. Cotton plants were grown during 7 weeks under glasshouse hydroponic conditions and 4 increasing levels of potassium nutrition (K0, K1, K2 and K3). Sugar started to accumulate in mature leaves of K deficient plants at 20 days after emergence (DAE). This was mainly interpreted as the consequence of a low phloem loading for sucrose. At 40 DAE, leaf area and dry weight were reduced in K0 and K1 treatments compared to K2 and K3. Specific leaf weight was much higher in K deficient plants then in non deficient ones. Photosynthesis was reduced but only for severe deficient treatments (K0) and at the last measuring dates (50 DAE). We venture the hypothesis that sugar accumulation may be the key factor affecting nutrition of the growing organs, and photosynthetic capacity of the unfolded and mature leaves.

Keywords Potassium · Cotton · *Gossypium hirsutum* L. · DW partitioning · Specific leaf weight · Photosynthesis · Water potential · Sucrose

Abbreviations

DW	dry weight
DAE	days after emergence
Ψp	pressure potential
Ψs	osmotic potential
Ψ	the water potential
PAR	photosynthetic active radiation
C_i	internal CO_2 pressure
C_a	external CO_2 pressure
PLA	plant leaf area
RUE	radiation use efficiency
J_{max}	electron transport capacity
V_{cmax}	maximum carboxylation rate
α	apparent light efficiency of electron transport

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Rd	dark respiration
SLW	specific leaf weight
Gs	stomatal conductance
$\%DW_L$	% of leaves DW in total DW
R/S	root/shoot

Introduction

Cotton is particularly sensitive to potassium (K) deficiency, much more than other crops (Cassman et al. 1989), with strong impacts on fibre yield and quality (Kerby and Adams 1985; Zhao et al. 2001). An increasing incidence of K deficiency in cotton crops in intensive cropping conditions around the world, such as in USA or Australia, is associated with the introduction of fast fruiting, high yielding cotton cultivars that have a greater demand for K during fructification (Pettigrew 1999; Wright 1999; Camberato and Jones 2005). In the cotton production areas of sub-Saharan Africa, decreases in soil organic matter and low levels of K fertilization have led to an increase in K deficiency (Pieri 1989; Poss et al. 1997).

Plant cells have a high requirement for K for photosynthesis, enzyme activation, protein synthesis, regulation of cell turgor, and ion homeostasis (Marschner 1995). However, K deficiency may not disturb these processes at the same time or K content, since they do not take place in the same parts of the cells (Leigh and Wyn 1984). Some of these processes take place in the cytoplasm (like protein synthesis) and others in the vacuole (like turgor). Compensation phenomena of K-deficiency may also be efficient for some processes like turgor (Leigh and Wyn 1984; Bednarz and Oosterhuis 1998) and inefficient for others like photosynthesis or protein synthesis. From the precedent statements it appears that when K content starts to drop in a plant some physiological dysfunctions may appear immediately while others may appear later.

A reduction in leaf growth has been commonly reported for moderately K-deficient plants of wheat (Rama 1986), soybean (Itoh et al. 1987) and cotton (Xi and Lihua 1989; Pettigrew and Meredith 1997; Reddy et al. 2000; Zhao et al. 2001). The relative decrease in leaf area has been mainly associated with a reduction in the rate of leaf elongation (Jordan-Meille and Pellerin 2004). The physiological cause of this reduction, however, is still subject of controversy. Some authors attribute leaf area reduction to limited cell expansion caused by a decrease in the osmotic regulation of the plant water status by K (Leigh and Wyn 1984; Mengel and Kirkby 2001; Benlloch-Gonzàles et al. 2008). Others highlight the role of K in phloem transport of sugars from source leaves to sink organs (roots, fruits and apical buds) (Huber 1985; Cakmak et al. 1994a), which may reduce leaf growth potential without affecting photosynthesis at the source (Mengel and Viro 1974a).

During acute deficiency whereby the concentration of K in plant leaves is less than 20 mg g^{-1} of DW or 25 mM (Leigh and Wyn 1984; Bednarz and Oosterhuis 1999; Reddy et al. 2000), DW production is drastically reduced and exceeds what we could expect from a reduction in sunlight interception caused by a smaller leaf area. DW reduction may be the consequence of a reduction in photosynthesis per leaf unit area (Bednarz and Oosterhuis 1999; Zhao et al. 2001; Jordan-Meille and Pellerin 2008; Pettigrew 2008). Three major causes of a reduction of photosynthesis under K deficiency have been implicated: (i) reduced stomatal and mesophyll conductance (Terry and Ulrich 1973; Longstreth and Nobel 1980; Pervez et al. 2004): (ii) a negative feedback on CO_2 assimilation rates induced by the accumulation of soluble sugars (Bednarz et al. 1998; Roitsch 1999) which can impact negatively on the activity of the enzyme Rubisco (Farquhar et al. 1980); (iii) impaired counterbalancing by K^+ of H^+ accumulation during electron transport across the thylakoid membrane (Mengel 1984; Tester and Blatt 1989; Weng et al. 2007). The photosynthetic model proposed by Farquhar and Sharkey (1982) is appropriate to quantify among these three mechanisms which ones are affected by K-deficiency.

It is yet unclear whether photosynthate translocation or insufficient osmotic pressure is the key mechanism affecting plant physiology (photosynthesis, leaf area expansion, DW partitioning) under moderate and acute K deficiency. Recently, different hexoses and sucrose have been recognised as important signal molecules in source-sink regulation (Roitsch and Gonzales 2004). This strengthens "sucrose impaired translocation" as the main dysfunction under K deficiency and lead to the suggestion it is necessary to re-examine the source−sink relationship of the plant under the influence of the stress. Characterizing sugar accumulates in leaves (Huber 1984) and plant water status (Mengel and Arneke 1982) will be useful in

determining the physiological mechanisms underlying K deficiency.

The objectives of this study is to investigate changes in carbon assimilation associated with different levels of K deficiency such as stomatal conductance, photosynthesis or biochemistry and to relate them to associated impacts at plant scale such as radiation use efficiency (Sinclair and Muchow 1999), DW production and resource partitioning.

Materials and methods

Plants

The H 279-1 cotton (*Gossypium hirsutum* L.) cultivar was pre-germinated and transplanted in hydroponic pots 2 days after emergence on March 9th 2006 in a glasshouse at the INRA Domaine de la Grande Ferrade (44° 50′ N, 0° 34′ W, Bordeaux, France). Seedlings were thinned to one per pot. Overall, there were sixty 24 l randomly arranged polyvinyl chloride (PVC) pots. The nutrient solutions were changed weekly and the pH corrected to a value of 6.5. The growth chamber was programmed at 25°C/20°C (day/night) and 65% relative humidity. Plants were grown under natural light conditions. Pots were filled with deionized water and the nutrient solution composed of 14 mM NO_3^-, 2 mM NH_4^+, 4 mM Ca^{2+}, 2 mM PO_4^{3-}, 2 mM SO_4^{2-}, 2 mM Mg^{2+}, 1 mM Fe^{3+}, 48 µM H_3BO_3, 7.3 µM Cl^-, 3.7 µM Mn^{2+}, 0.77 µM Zn^{2+}, 0.32 µM Cu^{2+} and 0.12 µM MoO_3.

Four K levels in nutrient solution were tested: a control (K3) with 3 mM of K, and three levels of K deficiency, i.e. K2, K1 and K0 with 0.3, 0.07 and 0.02 mM of KCl, respectively. According to a previous experiment these levels led to a wide range of leaf K contents. The experimental design was randomized with each experimental treatment repeated 5 times. Plants were harvested at 20, 40 and 50 DAE. Plant DW components were dried during 48 h at 80°C.

Measurements

Air temperature and humidity were measured using two sensors (HMP35C Sensor Vaisala, Helsinki, Finland) positioned on top of a 1.5 m high pole located in the centre of the experimental design. Light intensity was monitored using four PAR sensors (SP1110 pyranometers). Data was collected using a data logger (21X, Campbell Scientific, UK) every 5 min and averaged on an hourly basis.

Water relation measurements

The leaf water potential was measured with the "Scholander-bomb" (Scholander et al. 1965). Osmolarity was determined in leaf disk samples by freezing point depression (Roebling osmometer, LH Roebling, Berlin, Germany). Ψp was calculated from values obtained for Ψs and Ψ according to the following equation (Hsiao 1973): $\Psi = \Psi s = \Psi p$.

Photosynthetic rates

Carbon assimilation was measured on the first fully expanded leaves 20, 40 and 50 DAE. At these ages, plants were in the vegetative exponential growth phase. Gas exchange measurements were conducted with a LICOR 6400 (LI-6400; **LICOR** Inc., NE, USA) with the air temperature and relative humidity inside the leaf chamber controlled at 25°C and 60 %, respectively. The photosynthetic rate response to leaf internal partial pressure of CO_2 (Ci) was obtained by decreasing the ambient CO_2 (Ca) concentration from 400, 200, 100 and 50 ppm. Incident PAR level was maintained at a high level of 3,000 µmol PAR $m^{-2}s^{-1}$ to have non limiting light condition. The light response curves were obtained at 400 ppm of CO_2 and by decreasing incident light intensities. Range of light intensity was 2,000, 1,250, 800, 400, 200, 100 and 0 at the first date (20 DAE) and 3,000 µmol, 1,500 µmol, 800 µmol, 400 µmol 200 µmol, 100 µmol and 0 µmol PAR $m^{-2}s^{-1}$ at latest dates (40 and 50 DAE). Maximum light intensity was modified between 20 DAE and the other dates when we realized that cotton had not reached saturation at 2,000 µmol PAR $m^{-2}s^{-1}$. Photosynthesis was measured around 5 min after each change in C_a or PAR when a steady state was reached. C_i/C_a, the relative CO_2 partial pressure between external and internal stomatal chambers was calculated at the three dates for 400 ppm of ambient CO_2 and 3,000 µmol PAR $m^{-2}s^{-1}$.

Daily gas exchange survey

At 50 DAE, the leaves' gas exchange under "natural" conditions was measured every 2 h

throughout a day using a LICOR 6400. According to the natural light conditions, light intensities were settled at 300 µmol, 600 µmol, 1,500 µmol, 800 µmol and 300 µmol PAR $m^{-2}s^{-1}$ respectively at 10 h, 12 h, 14 h, 16 h and 18 h. Even though these values are low, they reflect greenhouse light conditions and certainly some shading by the structure.

Cations analysis

K, Ca, Mg and Na content were determined from plant material in the following way: dried material was milled to pass a 1 mm sieve. It was then ashed at 550°C. The ashes were then digested in a 1*M* nitric acid which was boiled off. The residue was taken up in hot 0.5*M* nitric acid and the volume cooled down. The cations were determined by atomic emission or absorption.

Sugar analysis

Soluble sugars (glucose, fructose and sucrose) from leaf disks and root apices were extracted in boiling 80% ethanol for 15 min. The extraction was repeated a second time in ethanol and a third time with water (Moing et al. 1992). All extracts were evaporated to dryness and frozen until analysis. Soluble sugar concentrations were then measured by the microtitre plate-adapted enzymatic according to Kunst et al. (1984). All samples and standards were determined as the mean value of two replicates assay wells. End-point determination for the three soluble sugars was based on the reduction of NAD to NADH (Jones et al. 1977). First step was glucose determination by phosphorylation of glucose to G6P and NAD and to 6PGlcU and NADH as the final step of the reaction sequence. The last sequence was quantified by spectrophotometric method. The second step was fructose determination by enzymatic transformation of fructose to glucose and the previously described conversion of G6P. As fructose assay is accomplished in the same well as glucose assay, they are temporally separated, and fructose is determined by substraction of glucose prior to isomerisation from total glucose at the end of the assay. Sucrose determination was based on the cleavage of sucrose into glucose and fructose by sucrose phosphorylase. Fructose was then converted into glucose, as previously described and total glucose was measured by the spectrophotometric method on a Microplate reader (ELx 800 uv, BIO-TEK Instruments, Winooski, USA). Sucrose was determined by substraction of glucose and fructose prior to sucrose phosphorylation from the total glucose at the end of the assay.

Calculating

- PLA was calculated as follows: the sum of individual leaf sizes.
- Intercepted PAR was calculated as follows: 0.48* total radiation* PLA. Since there was little self-shading as our experiment involved only plants in the early vegetative stage, light interception was linearly related to PLA. Value of 0.48 is the ratio of PAR to total radiation (Tao et al. 2005)
- RUE was calculated as follows: total dry biomass divided by the cumulated intercepted PAR between emergence and the last sampling date.

Modelling photosynthesis

Photosynthesis can be biochemically limited by one of two basic mechanisms: the Rubisco activity and the rate of RuBP regeneration which can be determined by looking at J_{max} (Lawlor 2002). To determine which of these mechanisms were affected by K deficiency, we used the model of Farquhar et al. (1980), based on the use of A-Ci and A-PAR response curves. Response curves were used to estimate parameters of the biochemical photosynthesis model developed by Farquhar et al. (1980) by non-linear fitting procedures (Systat 10, SPSS Inc 2000). V_{cmax}, α, Rd and J_{max} were calculated according to Von Caemmerer and Farquhar (1981). Under light saturated conditions and Ci below 200 ppm, we assumed that assimilation was limited by RubisCO functioning, and at low light intensity (<800 µmol $m^{-2}s^{-1}$), we assumed RubP regeneration became limiting. S (the concentration of photophosphorylation site) , Kc (the turnover number of carboxylase site) and Ko (the turnover number of oxygenase site) temperature dependency were calculated according to Leuning (1990, 2002). V_{cmax}, J_{max}, α and Rd did not have the same number of observations as J_{max}, and α were obtained by model regression with light response curves, V_{cmax} with CO_2 response curves and Rd from both.

Plant growth modelling

To discuss the relative effects of photosynthesis and carbon allocation, a growth model was built using carbon budget formalism. This approach is commonly used for crop modelling (Cotons®, EPIC, CERES) (Tardieu et al. 1999). It uses the specific leaf weight to calculate leaf area production of plant net photosynthesis:

$$\Delta\text{leaf area}/\Delta t = \text{net photosynthesis}*p/\text{SLW}$$

where p is the proportion of carbon allocated to leaves the same day. Values of p and SLW were calculated daily from the three measurement dates and decayed to negative asymptotes. One relationship was calculated for every treatment.

The complete model was built on the basis of following factors:

- Starting leaf area was the leaf area measured on the third day of the experiment and starting dry weight was the average dry seed weight.
- Light interception: It was assumed that all leaves intercept light without any leaf shading and at the same efficiency. Daily photosynthesis was thus certainly overestimated, but we considered that as our experiment lasted 50 DAE, most leaves were fully efficient and there would be little auto-shading.
- Photosynthesis was calculated hourly. Night respiration value was considered equal to observed dark respiration value. To identify the plant net assimilation rates, we used the mean response for each treatment (mean of five leaves) of assimilation to varying light intensity. These response curves where established at 20, 40 and 50 DAE.
- We supposed that, on a weight basis, cotton plants had only vegetative organs. The relative carbon content of dry weight was measured for each treatment. Simulated dry weight production was calculated as follows:

[simulated net carbon assimilation/observed relative carbon content].

In parallel, we ran one simplified model that didn't take the SLW and the DW partitioning to leaves changes among K treatments into account (default data remained unchanged between treatments, equal to those of K3 treatment). The model adaptability was evaluated by R^2 and a between simulated and observed data. R^2 is the coefficient of determination of the regression formula for the model, where a is the slope of the linear regression curve between observed and predicted values. We ran the models and compared to observed data.

Data analysis

An analysis of variance (ANOVA) was carried out according to the general linear model of the Statistical Analysis System (SAS Institute, Cary, NC, USA). Data means were tested using the Student-Newman-Keuls test, and significant differences were based on a 0.05 probability value.

Results

Leaf K and other major cation contents

The foliar K concentrations significantly differed between treatments from the first to the last measurement date (Table 1). The leaf K contents declined in the K0 and K1 treatments while K2 and K3 had more stable leaf K contents. At 20 DAE, the K0 leaf K content was 18 mg g^{-1} of DW, which was significantly lower than in the other treatments. Then it fell to 10 and 8 mg g^{-1} at 40 DAE and 50 DAE respectively. Obvious visible symptoms (interveinal chlorosis) of leaf K deficiency on K0 treatments appeared at around 40 DAE. From the second measurement date to the end of the experiment, the leaf K contents differed highly significantly between treatments. As expected, foliar potassium levels were very high in the K2 and K3 treatments, even at the last measurement date (23 mg g^{-1} and 42 mg g^{-1}). K deficiency did not affect the total foliar nitrogen concentration (data not shown). Ca, Mg and Na concentrations were significantly higher in K deprived plants. Therefore, the calculated sum of cations in tissue water (K + Ca + Mg + Na), calculated on basis of the assumption that all of these cations were in a soluble form, was significantly lower in K deprived plants (Table 1). This suggests that the higher uptake of other cations (Ca, Mg, Na) by K deprived plants does not potentially offset the lack of molarity due to the lower K content.

Table 1 Variations in K content in leaf DW (mg g^{-1}), total cation molarity (mM) and soluble sugars content in leaf DW (mg g^{-1}) at the three measurement dates, according to the potassium concentration in the nutrient solution. Means with the same letters are considered to be not different at p=0.05

Parameter	K0	K1	K2	K3	Student test
Foliar K at 20 DAE	18 (c)	31 (b)	33 (ab)	36 (a)	**
Foliar K at 40 DAE	10 (d)	18 (c)	33 (b)	43 (a)	***
Foliar K at 50 DAE	8 (d)	11 (c)	23 (b)	42 (a)	***
Total foliar cations (mM) at 50 DAE	187 (a)	198 (b)	222 (b)	269 (c)	**
Hexose at 20 DAE	12	8	7	6	*
Hexose at 40 DAE	48 (a)	22 (b)	21 (b)	17 (b)	***
Hexose at 50 DAE	45 (a)	24 (b)	8 (c)	5 (c)	***
Sucrose at 20 DAE	52	43	37	44	**NS**
Sucrose at 40 DAE	141 (a)	61 (b)	59 (b)	76 (b)	***
Sucrose at 50 DAE	152 (a)	73 (b)	54 (b)	52 (b)	***

Levels not connected by the same letter in the same lines are significantly different according to the Student's t test.. NS: p>0.05, *: 0.01 < p<0.05, **: 0.001 < p<0.01; ***: p<0.001

Effects of K-deficiency on the main growth parameters: DW, C allocation, SLW, leaf area and RUE

At 50 DAE, plant development, estimated as the number of nodes on the main stem, was not different between treatments (Table 2). The DW values were 51.8 g, 59.8 g and 64.8 g per plant for the K1, K2 and K3 treatments, respectively. In contrast, average weight from K0 treatment was 22.7 g per plant, i.e. less than half the biomass produced in the other treatments. Detrimental effects started to be significant at 40 DAE.

Table 2 Mean values for leaf area, mainstem node number, total DM, proportion of leaves in DM, root/shoot ratio, SLW, Ci/Ca, total water content and RUE according to the potassium concentration in the nutrient solution

Parameter	K0	K1	K2	K3	Student test
Leaf area (cm^2) at 20 DAE	220	194	249	226	**NS**
Leaf area (cm^2) at 40 DAE	1,561 (a)	2402 (b)	3,031 (c)	3,211 (c)	**
Leaf area (cm^2) at 50 DAE	2,304 (a)	4825 (b)	5,656 (bc)	6,055 (c)	**
Mainstem node number at 50 DAE	9.67	10.67	10.25	10.33	**NS**
Total DW (g $plant^{-1}$) at 20 DAE	1.15	0.81	1.27	1.23	**NS**
Total DW (g $plant^{-1}$) at 40 DAE	13.03 (a)	20.59 (b)	27.21 (c)	30.51 (c)	***
Total DW (g $plant^{-1}$) at 50 DAE	22.7 (a)	51.8 (b)	59.8 (b)	64.8 (b)	***
Leaves in DW (%) at 20 DAE	60.9 (a)	60.83 (a)	59.23 (a)	54.94 (b)	*
Leaves in DW (%) at 40 DAE	54.1 (a)	46.9 (b)	43.1 (c)	41.7 (c)	***
Leaves in DW (%) at 50 DAE	54.9 (a)	43.5 (b)	40.7 (c)	38.5 (c)	***
Root/shoot at 20 DAE	0.17	0.14	0.15	0.19	**NS**
Root/shoot at 40 DAE	0.19 (a)	0.26 (b)	0.25 (b)	0.25 (b)	*
Root/shoot at 50 DAE	0.17 (a)	0.23 (b)	0.22 (b)	0.22 (b)	*
SLW (mg cm^{-2}) at 20 DAE	3.20	2.65	3.01	2.99	**NS**
SLW (mg cm^{-2}) at 40 DAE	4.52 (a)	4.02 (b)	3.78 (b)	3.98 (b)	*
SLW (mg cm^{-2}) at 50 DAE	5.39 (a)	4.66 (b)	4.28 (c)	4.14 (c)	*
Ci/Ca at 20 DAE	0.71	0.80	0.76	0.76	**NS**
Ci/Ca at 40 DAE	0.67	0.71	0.73	0.75	**NS**
Ci/Ca at 50 DAE	0.82	0.74	0.56	0.67	**NS**
RUE in g DW MJ^{-1} PAR at 50 DAE	1.97 (a)	2.65 (b)	2.69 (b)	2.74 (b)	**

Levels not connected by the same letter in the same lines are significantly different according to the Student's t test.. NS: p>0.05, *: 0.01 < p<0.05, **: 0.001 < p<0.01; ***: p<0.001

In addition, dry weight allocation was modified for the highest K deficiency treatments. The R/S ratio for the K0 treatment remained at a constant value of 0.17±0.02, whereas it increased with time up to 0.25±0.01 for treatments K1 to K3. This was mainly due to the higher contribution of leaves in the total DW (Table 2). In addition to this modification, K0 treatment plants had significantly higher SLW values from the second measurement date and the differences between treatments increased with time (Table 2): SLW ranged from 5.39 mg cm^{-2} to 4.14 mg cm^{-2} for K0 and K3, respectively, at the end of the experiment. As a result of the reduced DW and increased SLW induced by the K deficiency, leaf areas were significantly different between treatments at the last sampling date, increasing with greater K availability. Finally, RUE was significantly lower for the K0 treatment plants (1.97 g DW MJ^{-1}), compared to the three other treatments, with mean values ranging from 2.65 to 2.74 g DW MJ^{-1}.

Effect of K-deficiency on leaf and apex soluble sugar content

The sucrose concentration of matures leaves accounted for most of the soluble sugar in each treatment. In the K0 treatment plants the sucrose concentration was significantly higher at 40 and 50 DAE, i.e. even surpassing 15% of the leaf DW at the last sampling date. This content at the latest date is very high compared with the leaf DW content of the K1, K2 and K3 treatment which ranked from 52 to 73 mg g^{-1} of the leaf DW (Table 1). Note that the sucrose concentration drastically increased (Fig. 1) when the K concentration dropped below 15 mg g^{-1} (100 mM) at 40 and 50 DAE. The same trend was noted for hexose concentration, which was also significantly higher in the leaves of the K0 treatment plants at all dates. Unlike mature leaves, the shoot and root apexes of the K0 treatment plants had lower hexose content than all the other treatments (relative content less than 50%; data not shown). In order to have sufficient material for sugar analysis, we had to combine the apices from the 5 plants in each treatment. Thus the results cannot be statistically supported due to the lack of replications.

Effects of potassium on plant-water relations

For treatments K1 to K3, the plant water content measured at the whole plant scale decreased linearly during the experiment from 92 to 88%. The water content of the K0 treatment plants followed the same trend, although the values were significantly 1% lower (data not shown). However, when only leaves are taken into account, difference between treatments is no longer existent (data not shown). Measurements obtained on the first fully expanded leaves showed that K deficiency had slight but positive effects on turgor, as deduced from the water and osmotic potential measurements (Fig. 2). For instance, the water potential ranged from −0.6 to −1.4 MPa and lowest values were shown by leaves with a higher K content. The osmotic potential ranged from −1.8 to −0.9 MPa. The maximum value of −0.9 MPa was obtained with a leaf K content of 15 to 30 mg g^{-1}, whereas leaves with higher and lower K contents had osmotic potentials ranging from −1 to −1.8 MPa respectively.

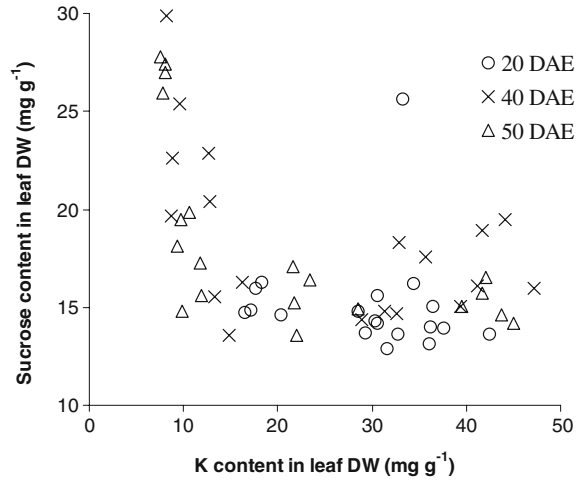

Fig. 1 Relationship between sucrose and potassium concentrations in the first expanded leaves at 20, 40 and 50 DAE

Photosynthetic activity

Analysis of light and CO_2 response curves

K deficiency did not affect CO_2 assimilation at early stages (20 DAE). The PAR and CO_2 response curves were not significantly different (Figs. 3a and 4a). The maximum assimilation rate at high light intensity was approximately 20 µmol CO_2 $m^{-2}s^{-1}$ for all treatments. In contrast, CO_2 assimilation differed among treatments for the light response curves at 50 DAE and CO2 response curves at 40 and 50 DAE. K0 had

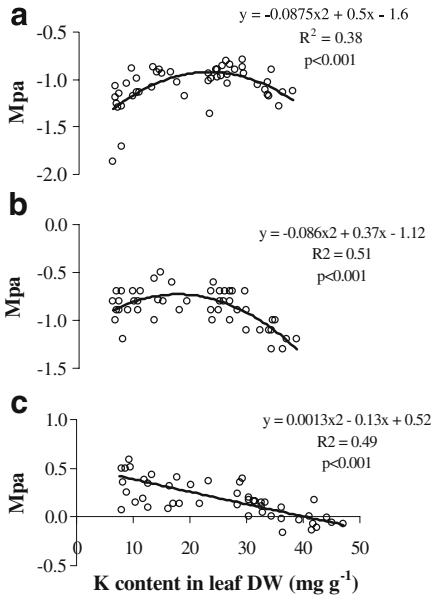

Fig. 2 Leaf osmotic **a**, water **b** and turgor **c** pressures as a function of leaf K content. Data, quadratic regression model, regression coefficient and sign. test. Measurements were performed at 20, 40 and 50 DAE

lower assimilation rates (Figs. 3b c, 4b). Maximum assimilation rates were not achieved even with a light intensity of 3,000 µmol photons $m^{-2}s^{-1}$.

Net assimilation was affected by the K treatments at low CO_2 concentration. The initial slope of the assimilation rate as a function of the internal CO_2 concentration was different for K0 as compared to the other treatments (Fig. 4), which could be related to the significant regression coefficient obtained between V_{cmax} and the leaf K content (Fig. 5). Dark respiration was not affected. K0 treatments had decreased in photosynthesis rate by 15 to 30% at compared to control. The light saturated maximum rate of electron transport (J_{max}) and quantum efficiency (α) were not significantly affected by the K leaf status.

Stomatal conductance

Figure 6 shows the average Gs response throughout the measurement day at 50 DAE. The curves only showed an effect of the K treatment on Gs for the K0 treatment. Nevertheless, those results should be taken with caution as stomatal behaviour may be subject to photosynthesis feedback (Yu et al. 2001). The relative Gs values (Gs K0/Gs K3) rose from 0.28 at the beginning of the day (10:00) up to nearly 1 at the last sampling hour (18:00), whereas the radiation intensity was the same for those two periods (300 µmol./$m^{-2}s^{-1}$). In addition to the Gs measurement, we calculated the C_i/C_a but the values didn't differ statistically among K- treatments.

DW production simulation

A simple model of dry weight production was built at the plant scale using input variables such as leaf dry

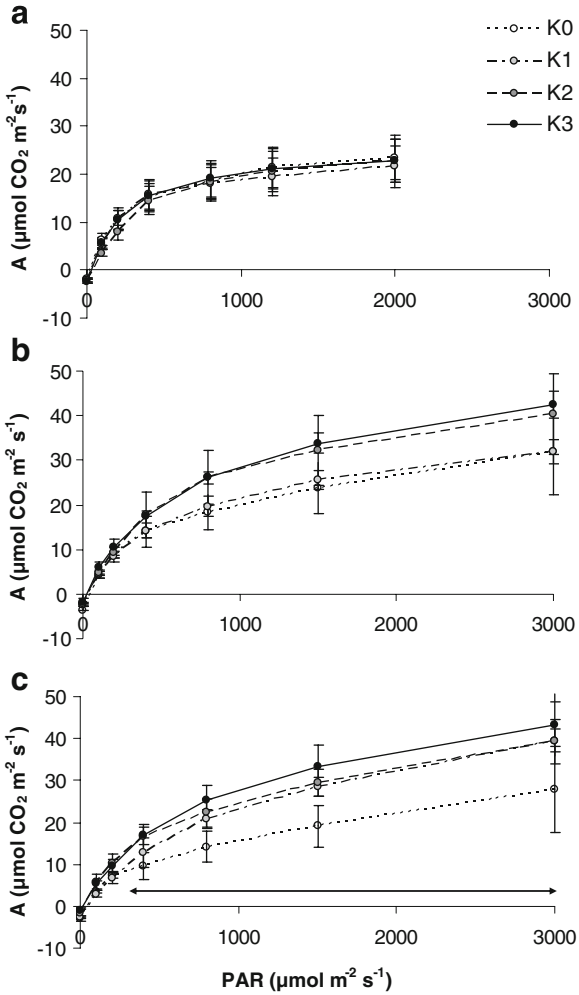

Fig. 3 Response curve of net assimilation to light intensity for four potassium levels, measured at 20 DAE **a**, 40 DAE **b** and 50 DAE **b**. Each value is the mean for five plants. Vertical bars represent +/− standard deviation. The horizontal bar indicates that the difference in assimilation between treatments is significant at $P<0.05$. Measurements were obtained at air T= 25°C, RH=60 % and air CO_2=400 µmol mol^{-1}

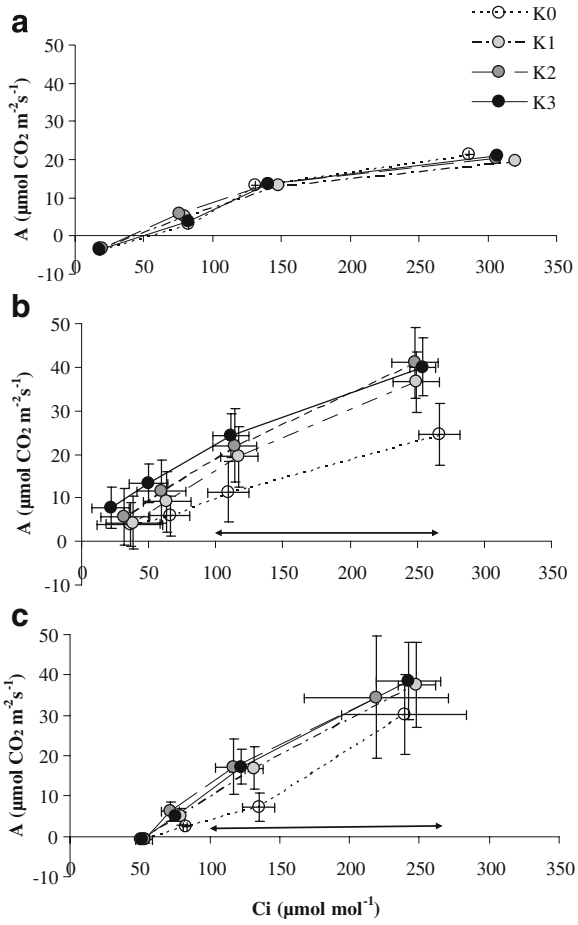

Fig. 4 Average response curve of net assimilation to internal CO_2 concentration (Ci) for four potassium levels, measured at 20 DAE **a**, 40 **b** and 50 DAE **c**. Each value is the means for four plants. Vertical and horizontal bars around each point represent +/− the standard deviation. The horizontal bar indicates that the difference the assimilation between treatments is significant at $P<0.05$ Measurements were obtained at air T= 25°C, RH=60% and PAR=3,000 µmol photons $m^{-2}s^{-1}$

weight ratio, SLW and net photosynthesis response to light (response curves 3a, b and c). As leaf K content was not stable throughout the experiment, especially for K0 and K1 treatments, we attributed different response curves to plants according to their daily interpolated leaf K content. We extrapolated the date at which the plants from K1 and K0 treatments changed status. Concerning plants from K1 treatment, the simulation of assimilation rates started with a "K2 light response curve" until their foliar K fell under 18 mg g^{-1} after which the "K1 light response curve" was applied. We started the simulation of assimilation rates of plants from K0 treatment with a "K1 light response curve" followed by a "K0 light response curve" used when the foliar K dropped under 10 mg g^{-1}. Figure 8 shows comparison between simulated and observed DW for each individual plant. The simulations with complete model gave a fairly good estimation of observed DW as the regression slope (a) was 0.91 and the R^2 was 0.69. Simulation of plant DW accumulation without K effect on partitioning gave a bad estimation: R^2 was only 0.50 (*P* not significant).

Discussion

Characterisation of K deficiency

The experiments were designed to analyze the effects of K starvation on the growth of cotton plants under hydroponic conditions, and on some associated physiological processes related to carbon and water status. A wide range of plant K contents were obtained in the experiment ranging from 8 to 42 mg g^{-1} of leaf DW at the end of the experiment. These values are in the usual range of values recorded in such experiments on cotton plants (Brouder and Cassman 1994; Bednarz and Oosterhuis 1998). K concentrations in K0 treatment dropped down to values considered critical for growth (Leigh and Wyn 1984; Bednarz and Oosterhuis 1999; Reddy and Zhao 2005). On the contrary, the K2 and K3 treatments could both be considered a priori as non-limiting throughout the experiment. K1 was assumed to be non-deficient from the beginning to 40 DAE and slightly deficient afterwards.

K did not affect the plant water status

In our hydroponic conditions, plants did not suffer from a lack of water supply. K-starved plants in their natural environment have lower water content than non starved plants (Leigh and Wyn 1984) but in the present experiment, leaf water content was not different among treatments. On one hand, the low osmotic potential measured (Fig. 2a) for the non-limiting treatment (K3) can be attributed to plant K excess consumption (Table 1), given the well-known role of K with respect to osmotic regulation (Mengel and Arneke 1982; Barraclough and Leigh 1993; Caroll et al. 1994). The calculated contribution of K

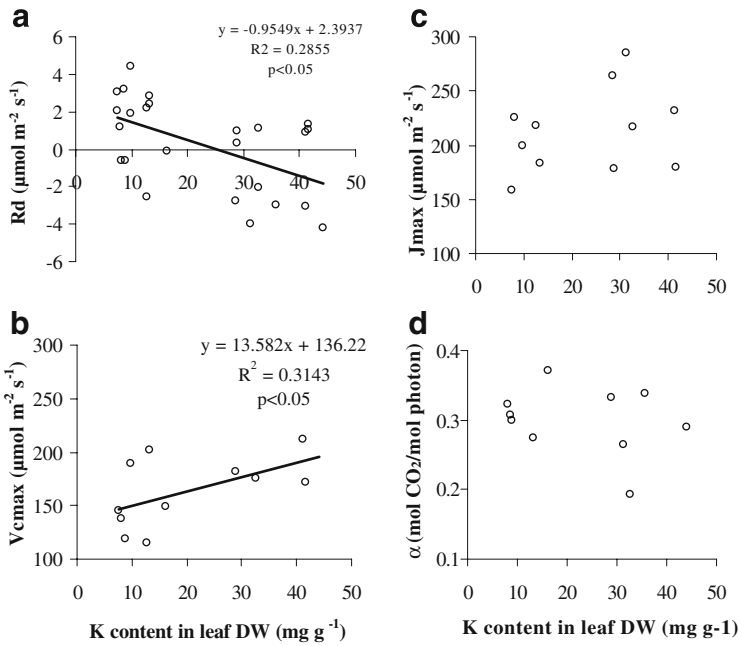

Fig. 5 Dark respiration **a**, Vcmax **b**, Jmax **c** and α **d** as a function of K content in leaf DW. Linear regression equations and R^2 when $P<0.05$ at 40 and 50 DAE

to the osmotic potential (Fig. 7) was based on the assumption that the osmotic potential could be mainly explained by the sum of cations (expressed towards tissue water), and the soluble sugar content. Hence, for high K concentrations, the K contribution to the total osmolarity was predominant, and even probably underestimated because some of the Ca and Mg found in plant tissues may not be in soluble state. On the other hand, low K content leaves also had a low osmotic potential, due to the high leaf sugar content (Fig. 1) and the relative increase in compensation cations other than K, which is a common trend noted under K deficiency (Pujos and Morard 1997; Henning

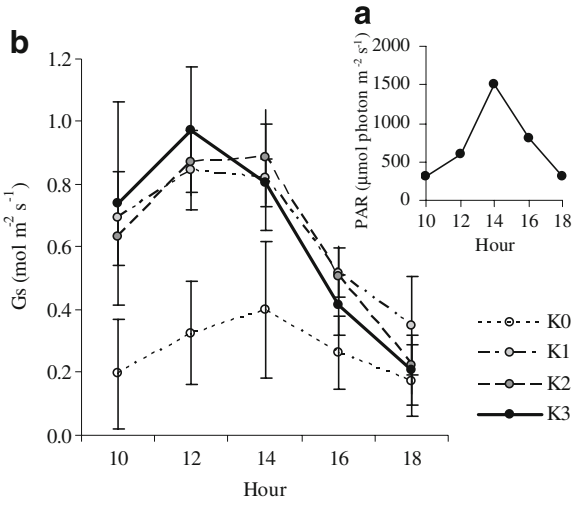

Fig. 6 Variations in PAR **a** and g_s **b** within a day for 4 potassium treatments taken at 50 DAE. Values are means of 5 plants. Vertical bars represent +/− standard deviation. Measurements were obtained at natural radiation. Leaf temperature was maintained to 25°C and RH to 60%, CO2 R=400 µmol mol^{-1}

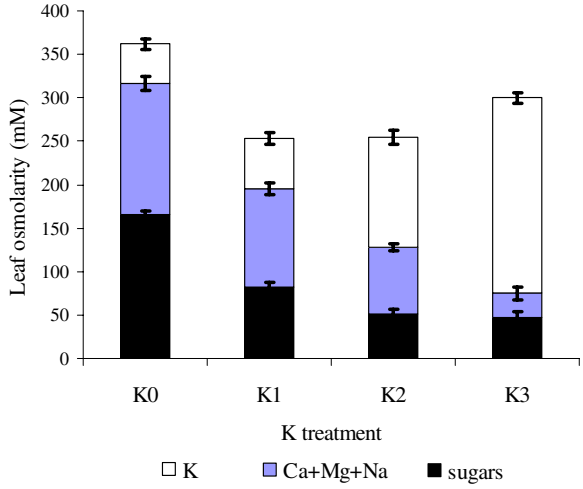

Fig. 7 K, other inorganic cation (Ca + Mg + Na) and sugar osmolarity for 4 K treatments at 50 DAE. Values are means for the first fully expanded leaf of 5 plants. Vertical bars represent +/− standard deviation

2003). According to our calculation, sugar accumulation in K0 deficient leaves accounted for around 50% of the osmolarity, compared to 30% in K1 leaves and less than 20% in K2 and K3 leaves. This highlights the role of sugar compensation in K deficient leaves (Scherer and Schubert 1982; Huber 1984; Pettigrew 1999), and especially for sucrose (Talbott and Zeiger 1998; Pretorius et al. 1999).

Review of the effects of the K-deficiency on DW allocation and sugar accumulation

K deficiency significantly decreased leaf area and dry weight accumulation (Table 2), which were both reduced by 60% between treatments K3 and K0 at the end of the experiment. Root biomass was much more affected than aerial biomass. This observation is closely in line with several authors on diverse plants (Ericsson 1995, Egilla et al. 2001, El Dessougi et al. 2002), and particularly on cotton plants (Zhao et al. 2001). Moreover, SLW, R/S and $\%DW_L$ were significantly different among K treatments (Table 2). This last variable was the only one among all growth variables observed in the experiment that differed significantly among treatments as soon as 20 DAE.

Our hypothesis is that these morphological patterns are accounted for by sugar accumulation in mature leaves. K deficiency led to a spectacular accumulation of soluble sugars especially for sucrose (Fig. 1), as already reported in a wide range of plants (Scherer and Schubert 1982; Huber 1984; Itoh et al. 1987; Cakmak et al. 1994a; Zhao et al. 2001), including cotton (Bednarz and Oosterhuis 1999; Pettigrew 1999). Many convergent results consolidate this assumption:

- Soluble sugars accumulation, especially hexose, is precocious. It occurs significantly as soon as 20 DAE (Table 1), simultaneously to the modified $\%DW_L$, and before the other growth variable become significantly different (leaf area, SLW, R/S).
- Sugar accumulation in mature leaves seems to be closely related to the SLW, whose increase for treatments K0 and K1 is explained for more than 15% by their accumulation. This relationship between carbon export ratio and SLW has already been underlined by Reddy et al. (1989). Pettigrew (1999) found the same trend although the sugar contribution to the SLW increase was significantly smaller (5%).
- Parallel to the accumulation in mature leaves, low sugar concentrations were measured in roots and leaf apexes, which could account for the lower R/S ratio and lower leaf area, even at mild K-deficiency (Table 2).

Overall, the present study provides evidence that K starvation globally decreases the translocation of photosynthetic products in plants by acting directly on the phloem loading and/or transport into cells in sinks as already reported by other authors (Conti and Geiger 1982; Cakmak et al. 1994b; Marschner et al. 1996; Pettigrew 1999). Phloem loading dysfunction under K-deficiency has been confirmed by labelled CO_2 studies (Mengel and Viro 1974b). This dysfunction in sucrose transport might also be advanced to explain the photosynthesis disturbance.

Effect of K-deficiency on carbon assimilation

The ability of plants to transform light into dry weigh was decreased, as shown by the lower RUE calculated on the most starving plants (K0, Table 2). Under our conditions, RUE values ranged from 1.97 to 2.74 g DW MJ^{-1} PAR (for treatment K0 and K3 respectively). These values are 30 to 40 % above those reported by Rosenthal and Gerik (1991) and Sadras and Wilson (1997) in irrigated field trials, where they obtained RUE values ranging from 1.3 to 1.9 g DW MJ^{-1}. This difference is not surprising as we calculated RUE on the total biomass basis while RUE on field studies was calculated on aerial biomass basis. Moreover, even irrigated and well fertilized conditions are not as optimal as hydroponic conditions. It should be emphasized that the decrease in RUE due to K starvation was corroborated by instantaneous photosynthesis measurements which showed differences between treatments from 40 DAE. However, they can not be directly compared, as RUE is a time-integrative parameter.

Photosynthesis was reduced (Figs. 3 and 4) for the most K-starved plants, from the second measurement date until the end of the experiment. The decrease in photosynthesis might be partly explained by the lower reactivity of stomata towards environmental conditions (Fig. 6). However, it should be underlined that stomatal dysfunction is in contradiction to the absence

of detrimental effects of the K-deficiency on leaf water potentials (Fig. 2), and especially to the high level of sucrose in leaves (Fig. 7), whose role as a primary guard cell osmoregulator is well-known (Talbott Zeiger 1998). Non stomatal reduction of photosynthesis was also demonstrated in Fig. 4. Once more, sugar accumulation may account more or less directly to this dysfunction, with two possible underlying mechanisms: (i) a negative metabolic feedback exerted by sugar accumulation (Goldschmidt and Huber 1992; Rook and Bevan 2003; Koch 2004), which affects the maximum carboxylation velocity (V_{cmax}, Fig. 5) prior to any other photosynthetic parameter (Farquhar et al. 1980), and (ii) a detrimental effect exerted by the leaves' thickness (through higher specific leaf weight) on mesophyl diffusion conductance (Terry and Ulrich 1973). However they are not exclusive and the unchanged C_i/C_a tends to favour the hypothesis that both carbon assimilation and carbon input by stomatal aperture are responsible of the decline of the photosynthesis (Ehleringer and Cerling 1995).

Biomass production modelling

Now, to what extent was the growth potential affected by lower photosynthesis? We ran a simple model of dry weight production at the plant scale using the simulated leaf area, net photosynthesis response to light (response curves 3a, b and c), $\%DW_{L,}$ C content in DW and SLW as input variables. The best estimation of DW production by the complete model compared to the estimation by the model with only photosynthesis effect (Fig. 8) led to conclude that the photosynthesis modification may not be sufficient to take into account the observed changes in total DW of cotton plants under K deficiency. Therefore, there must be a growing constraint, whose effect is additive to the least photosynthesis. We may conclude, like Triboulot and Pritchard (1997) that cell-wall extensibility may be the cause of this decrease but we also establish the hypothesis that there might be a morphogenetic signal to developing organs (Black et al. 1995) (Waclawovsky et al. 2006).

K overall effects on cotton morphology and physiology

K deficient cotton plants are characterized by a marked reduction in assimilates production and translocation. Not only do the plants have smaller leaf area, but also the leaves are less efficient photosynthetically. Moreover, the source leaves appear to keep much of the assimilates and not translocate them to the reproductive sinks, i.e. young leaves, stems, reproductive sinks and roots. As a result, the concentration of plant nutrient and soluble sugars in leaves contributed to the increased SLW. Our results highlight the role of potassium as a counter-ion for phloem transport rather than its roles on plant-water relation. The present study carried additional information about the sequence of response to K deficiency, the physiological processes involved, and their relative importance. Under our experimental conditions, the first difference between treatments concerned the accumulation of DW in mature leaves, as soon as 20 DAE, before a decrease in leaf area or in photosynthesis were noticeable. Sugar accumulation offset the osmotic potential loss by K depletion so that plant water status was not particularly unfavourable for K deficient plants. Later on, and for K concentrations in leaves below 10 mg g^{-1}, the sugar accumulation reached such levels that photosynthesis and carbon partitioning were deeply modified. The decrease in photosynthesis coincided with reduction in stomatal conductance, but stomatal conductance may not be the only mechanism limiting carbon fixation in K deficient leaves. Additional effects of a negative feedback of the sugar accumulation on carboxylation were also demonstrated.

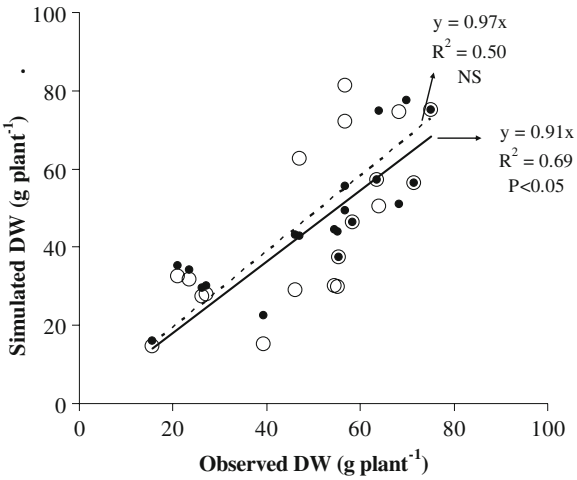

Fig. 8 Observed and simulated DW of cotton plants. Full circles (●) represent data from complete model and empty circles (○) data from model with only photosynthesis effect

In our hydroponic conditions, smaller root growth resulting from the K starvation did not impact on the nutrient uptake. However, it can be easily understood that in natural conditions, this would emphasize the effects of the deficiency, thus leading to more detrimental effects at the plant scale, with negative effects on yield potential and fibre quality.

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References

Barraclough PB, Leigh RA (1993) Grass yield in relation to potassium supply and the concentration of cations in tissue water. J Agric Sci 121:283–287

Bednarz CW, Oosterhuis DM (1998) Development of a protocol to study the effects of potassium deficiency in cotton under controlled environmental conditions. J Plant Nutr 21:329–339. doi:10.1080/01904169809365407

Bednarz CW, Oosterhuis DM (1999) Physiological changes associated with potassium deficiency in cotton. J Plant Nutr 22:303–313. doi:10.1080/01904169909365628

Bednarz CW, Oosterhuis DM, Evans RD (1998) Leaf photosynthesis and carbon isotope discrimination of cotton in response to potassium deficiency. Environ Exp Bot 39:131–139. doi:10.1016/S0098-8472(97)00039-7

Benlloch-Gonzàles M, Arquero O, Fournier JM, Barranco D, Benlloch M (2008) K^+ starvation inhibits water-stress-induced stomatal closure. J Plant Physiol 165:623–630. doi:10.1016/j.jplph.2007.05.010

Black CC, Loboda T, Chen JQ, Sung SJS (1995) Can sucrose cleavage enzymes serve as markers for sink strenght and is sucrose a signal molecule during plant sink development. American Society of Plant physiologists, 49–64

Brouder SM, Cassman KG (1994) Evaluation of a mechanistic model of potassium uptake by cotton in vermiculitic soil. Soil Science society american proceedings 58:1174–1183

Cakmak I, Hengeler C, Marschner H (1994a) Changes in phloem export of sucrose in leaves in response to phosphorus, potassium and magnesium deficiency in bean plants. J Exp Bot 45:1251–1257. doi:10.1093/jxb/45.9.1251

Cakmak I, Hengeler C, Marschner H (1994b) Partitioning of shoot and root dry matter and carbohydrates in bean plants suffering from phosphorus, potassium and magnesium deficiency. J Exp Bot 45:1245–1250. doi:10.1093/jxb/45.9.1245

Camberato JJ, Jones MA (2005) Differences in potassium requirement and response by older and modern cotton varieties. Better crops 89:18–20

Caroll MJ, Slaughter LH, Krouse JM (1994) Turgor potential and osmotic constituents of Kentucky bluegrass leaves supplied with four levels of potassium. Agron J 86:1079–1083

Cassman KG, Kerby TA, Roberts BA, Bryant DC, Brouder SM (1989) Differential response of two cotton cultivars to fertilizer and soil potassium. Agron J 81:870–876

Conti TR, Geiger DR (1982) Potassium nutrition and translocation in sugar beet. Plant Physiol 70:168–172. doi:10.1104/pp.70.1.168

Egilla JN, Davies FTJ, Drew CJ, Drew MC (2001) Effect of potassium on drought resistance of Hibiscus rosa-sinensis cv. Leprechaun: Plant growth, leaf macro- and micronutrient content and root longevity. Plant Soil 229:214–224

Ehleringer JR, Cerling TE (1995) Atmospheric CO2 and the ratio of intercellular to ambient CO2 concentrations in plants. Tree Physiol 15:105–111

El Dessougi H, Claassen N, Steingrobe B (2002) Potassium efficiency mechanisms of wheat, barley, and sugar beet grown on a K fixing soil under controlled conditions. J Plant Nutr Soil Sci 165:732–737

Ericsson T (1995) Growth and shoot: root ratio of seedlings in relation to nutrient availability. Plant Soil 168-169:205–214

Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. Annu Rev Plant Physiol 33:317–345. doi:10.1146/annurev.pp.33.060182.001533

Farquhar GD, Von Caemerer S, Berry JA (1980) A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. Planta 149:78–90. doi:10.1007/BF00386231

Goldschmidt EE, Huber SC (1992) Regulation of photosynthesis by end-product accumulation in leaves of plants storing starch, sucrose, and hexose sugars. Plant Physiol 99:1443–1448. doi:10.1104/pp.99.4.1443

Henning HJ (2003) The effect of potassium deficiency on growth and N2-fixation in Trifolium repens. Physiol Plant 119:440–449. doi:10.1034/j.1399-3054.2003.00189.x

Hsiao TC (1973) Plant responses to water stress. Annu Rev Plant Physiol 24:519–570. doi:10.1146/annurev.pp.24.060173.002511

Huber SC (1984) Biochemical Basis for Effects of K-Deficiency on Assimilate Export Rate and Accumulation of Soluble Sugars in Soybean Leaves. Plant Physiol 76:424–430. doi:10.1104/pp.76.2.424

Huber SC (1985) Role of potassium in photosynthesis and respiration. In: Munson RD (ed) Potassium Agriculture. American Society of Agronomiy, Madison, WI, pp 339–369

Itoh K, Nakamura Y, Kawata H, Yamada T, Ohta E, Sakata M (1987) Effect of osmotic stress on turgor pressure in mung bean root cells. Plant Cell Physiol 28:987–994

Jones MGK, Outlaw WH Jr, Lowry OH (1977) Enzymic Assay of 10–7 to 10–14 Moles of Sucrose in Plant Tissues. Plant Physiol 60:379–383. doi:10.1104/pp.60.3.379

Jordan-Meille L, Pellerin S (2004) Leaf area establishment of a maize (*Zea mays* L.) field crop under potassium deficiency. Plant Soil 265:75–92. doi:10.1007/s11104-005-0695-z

Jordan-Meille L, Pellerin S (2008) Shoot and root growth of hydroponic maize (Zea mays L.) as influenced by K deficiency. Plant Soil 304:157–168. doi:10.1007/s11104-007-9534-8

Kerby TA, Adams F (1985) Potassium Nutrition of Cotton. In: Munson RD (ed) Potassium. Agric. American Society of Agronomy, Madison

Koch KE (2004) Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development. Curr Opin Plant Biol 7:235–246. doi:10.1016/j.pbi.2004.03.014

Kunst A, Draeger B, Ziegenhorn J (1984) UV-methods with hexokinase and glucose-6-phosphate dehydrogenase. Weinheim, Deerfield Beach, Florida

Lawlor DW (2002) Limitation to photosynthesis in water-stressed leaves: stomata vs. metabolism and the role of ATP. Ann Bot (Lond) 89:871–885. doi:10.1093/aob/mcf110

Leigh RA, Wyn JRG (1984) A hypothesis relating critical potassium concentrations for growth to the distribution and functions of this ion in the plant cell. New Phytol 97:1–13. doi:10.1111/j.1469-8137.1984.tb04103.x

Leuning R (1990) Modelling stomatal behaviour and photosynthesis of Eucalyptus grandis. Funct Plant Biol 17:159–175. doi:10.1071/PP9900159

Leuning R (2002) Temperature dependence of two parameters in a photosynthesis model. Plant Cell Environ 25:1205–1210. doi:10.1046/j.1365-3040.2002.00898.x

Longstreth DJ, Nobel DJ (1980) Nutrient influences on leaf photosynthesis. Effects of nitrogen, phosphorus, and potassium for *Gossypium hirsutum* L. Plant Physiol 65:541–543. doi:10.1104/pp.65.3.541

Marschner H (1995) Mineral Nutrition of Higher Plants. Academic press, London

Marschner H, Kirkby E, Cakmak I (1996) Effect of mineral nutritional status on shoot-root partitioning of photo-assimilates and cycling of mineral nutrients. J Exp Bot 47:1255–1263

Mengel K (1984) Le potassium en physiologie végétale. Acad. Agri, de France, pp 1365–1376

Mengel K, Arneke WW (1982) Effect of potassium on the water potential, the pressure potential, the osmotic potential and cell elongation in leaves of Phaseolus vulgaris. Physiol Plant 54:402–408. doi:10.1111/j.1399-3054.1982.tb00699.x

Mengel K, Kirkby EA (2001) Principles of plant nutrition. Kluwer academy publishers

Mengel K, Viro M (1974a) Effect of potassium supply on the transport of photosynthates to the fruits of tomatoes. Physiol Plant 30:295–300. doi:10.1111/j.1399-3054.1974.tb03660.x

Mengel K, Viro M (1974b) Effect of Potassium Supply on the Transport of Photosynthates to the Fruits of Tomatoes (Lycopersicon esculentum). Physiol Plant 30:295–300. doi:10.1111/j.1399-3054.1974.tb03660.x

Moing A, Escobar-Gutierrez A, Gaudillère JP (1992) Carbon Fluxes in Mature Peach Leaves. Plant Physiol 106:591–600

Pervez H, Ashraf M, Makhdum MI (2004) Influence of potassium nutrition on gas exchange characteristics and water relations in cotton (*Gossypium hirsutum* L.). Photosynthetica 42:251–255. doi:10.1023/B:PHOT.0000040597.62743.5b

Pettigrew T (2008) Potassium influences on yield and quality production for maize, wheat, soybean and cotton. Physiol Plant 133:670–681. doi:10.1111/j.1399-3054.2008.01073.x

Pettigrew WT (1999) Potassium deficiency increases specific leaf weights and leaf glucose levels in field-grown cotton. Agron J 91:962–968

Pettigrew WT, Meredith WR (1997) Dry matter production, nutrient uptake, and growth of cotton as affected by potassium fertilization. J Plant Nutr 20:531–548. doi:10.1080/01904169709365272

Pieri C (1989) Fertilité des savannes: Bilan de trente ans de recherche et de développement agricole au sud du Sahara. CIRAD/IRAT, Paris

Poss R, Fardeau JC, Saragoni H (1997) Sustainable agriculture in the tropics: the case of potassium under maize cropping in Togo. Nutr Cycl Agroecosyst 46:205–213

Pretorius JC, Nieuwoudt DT, Eksteen D (1999) Sucrose synthesis and translocation in Zea mays L. during early growth, when subjected to N and K deficiency. S Afr J Plant Soil 16:173–179

Pujos A, Morard P (1997) Effects of potassium deficiency on tomato growth and mineral nutrition at the early production stage. Plant Soil 189:189–196. doi:10.1023/A:1004263304657

Rama R (1986) Potassium requirement for growth and its related processes determined by plant analysis in wheat. Plant Soil 96:125–131. doi:10.1007/BF02375001

Reddy KR, Zhao D (2005) Interactive effects of elevated CO_2 and potassium deficiency on the photosynthesis, growth, and biomass partitionning of cotton. Field Crops Res 94:201–213. doi:10.1016/j.fcr.2005.01.004

Reddy RK, Hodges HF, Varco J (2000) Potassium nutrition of cotton. In: Hearn RA (ed) Bulletin 1094. Office of Agricultural Communications, Mississipi State University Division of Agriculture, Mississipi State, pp 1–10

Reddy VR, Acock B, Baker D, Acock M (1989) Seasonnal leaf area-leaf weight relationships in the cotton canopy. Agron J 81:1–4

Roitsch T (1999) Source-sink regulation by sugar and stress. Curr Opin Plant Biol 2:198–206. doi:10.1016/S1369-5266(99)80036-3

Roitsch T, Gonzales M (2004) Function and regulation of plant invertases: sweet sensations. Trends Plant Sci 9:606–613. doi:10.1016/j.tplants.2004.10.009

Rook F, Bevan MW (2003) Genetic approaches to understanding sugar-response pathways. J Exp Bot 54:495–501. doi:10.1093/jxb/erg054

Rosenthal WD, Gerik TJ (1991) Radiation use efficiency among cotton cultivars. Agron J 83:655–658

Sadras VO, Wilson LJ (1997) Growth analysis of cotton crops infested with spider mites: I. Light interception and radiation-use efficiency. Crop Sci 37:481–491

Scherer H, Schubert WS (1982) Effect of potassium nutrition on growth rate, carbohydrate content and water retention in young wheat plants. Z Pflanz Bodenk 145:237–245. doi:10.1002/jpln.19821450304

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. Negative hydrostatic pressure can be measured in plants. Science 148:339–346. doi:10.1126/science.148.3668.339

Sinclair TR, Muchow RC (1999) Radiation use efficiency. Adv Agron 65:215–265. doi:10.1016/S0065-2113(08)60914-1

Talbott LD, Zeiger E (1998) The role of sucrose in guard cell osmoregulation. J Exp Bot 49:329–337. doi:10.1093/jexbot/49.suppl_1.329

Tao F, Yokozawa M, Zhang Z, Xu Y, Hayashi Y (2005) Remote sensing of crop production in China by production efficiency models: models comparisons, estimates and uncertainties. Ecol Modell 183:385–396. doi:10.1016/j.ecolmodel.2004.08.023

Tardieu F, Granier C, Muller B (1999) Modelling leaf expansion in a fluctuating environment: are changes in specific leaf area a consequence of changes in expansion rate? New Phytol 143:33–43. doi:10.1046/j.1469-8137.1999.00433.x

Terry N, Ulrich A (1973) Effects of potassium deficiency on the photosynthesis and respiration leaves of sugar beet. Plant Physiol 51:783–786. doi:10.1104/pp. 51.4.783

Tester M, Blatt MR (1989) Direct measurement of K + channels in thylakoid membranes by incorporation of vesicles into planar lipid bilayers. Plant Physiol 91:249–252. doi:10.1104/pp.91.1.249

Triboulot MB, Pritchard J (1997) Effects of potassium deficiency on cell water relations and elongation of tap and lateral roots of maritime pine seedlings. New Phytol 135:269–272. doi:10.1046/j.1469-8137.1997.00647.x

Von Caemmerer S, Farquhar GD (1981) Some relathionships between the biochemistry of photosynthesis and gas exchange of leaves. Planta 153:433–451

Waclawovsky AJ, Loureiro ME, Rd Freitas, Cd Rocha, Cano MA, Fontes EP (2006) Evidence for the sucrose-binding protein role in carbohydrate metabolism and transport at early developmental stage. Physiol Plant 128:391–404. doi:10.1111/j.1399-3054.2006.00751.x

Weng X, Zheng C, Xu H, Sun J (2007) Characteristics of photosynthesis and functions of the water-water cycle in rice (Oryza sativa) leaves in response to potassium deficiency. Physiol Plant 131:614–621. doi:10.1111/j.1399-3054.2007.00978.x

Wright PR (1999) Premature senescence of cotton (*Gossypium hirsutum* L.)- Predominantly a potassium disorder caused by an imbalance of source and sink. Plant Soil 211:231–239. doi:10.1023/A:1004652728420

Xi S, Lihua R (1989) Effect of potassium fertilizer application on physiological parameters and yield of cotton grown on a potassium deficient soil. Z Pflanz Bodenk 152:269–272. doi:10.1002/jpln.19891520301

Yu G-R, Zhuang J, Yu Z-L (2001) An attempt to establish a synthetic model of photosynthesis-transpiration based on stomatal behavior and soybean plants grown in field. J Plant Physiol 158:861–874. doi:10.1078/0176-1617-00177

Zhao D, Oosterhuis DM, Bednarz CW (2001) Influence of potassium deficiency on photosynthesis, chlorophyll content, and chloroplast ultrastructure of cotton plants. Photosynthetica 39:103–109. doi:10.1023/A:1012404204910