

Effect of Water Shortage and Potassium on Efficiency of Symbiotic Nitrogen Fixation in Some Legumes

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POTASSIUM (K) is reported to improve plants resistance against environmental stress. A frequently experienced stress for plants in the tropics is water shortage. It is not known if sufficient K supply would help plants to partially overcome the effects of water stress especially that of symbiotic nitrogen fixation which is often rather low in the tropics when compared to that of temperate regions. Thus, the impact of three levels of fertilizer potassium (0.2, 1.0 and 3.3 mM) on symbiotic nitrogen fixation was evaluated with two legumes under high (field capacity to 23% depletion) and low (less than 46% of field capacity) water regimes. Plants were grown in single pots in silica sand under controlled conditions with 1.3 mM N (^{15}N enriched NH_4NO_3). The species were broad bean (*Vicia faba* L.) variety Giza blanca, a temperate, amide producing legume and pea (*Pisum sativum* L.) variety little marvel, a tropical, ureide producing species. In both species, 0.2 mM K was insufficient for nodulation at both moisture regimes, although plant growth was observed. The supply of 1.0 or 3.3 mM K allowed nodulation and subsequent nitrogen fixation which appeared to be adequate for respective plant growth. High potassium supply had a positive effect on nitrogen fixation, on shoot and root growth and on water potential in both water regimes. Where nodulation occurred, variations caused by either K or water supply had no consequences on the percentage of nitrogen derived from the symbiosis. The present data indicate that K can apparently alleviate water shortage to a certain extent. Moreover, it is shown that the symbiotic system in both broad bean and pea is less tolerant to limiting K supply than plants themselves. However, as long as nodulation occurs, N assimilation from the symbiotic source is not selectively affected by K as opposed to N assimilation from fertilizer.

Keywords: Water stress, Symbiotic nitrogen fixation, Potassium fertilization, Nodulation, Peas, Broad bean.

Grain legumes are an important component of the food production systems in tropical agriculture (Carangal *et al.*, 1987 and Kramer & Boyer, 1995). These crops are very adaptable, produce protein-rich edible material and fix atmospheric nitrogen through symbiosis (Wood & Myers, 1987 and Maurel, 1997). In Asia and Africa, the principal regions cultivating legumes for direct human consumption, yields are generally low (FAO, 1995 and Schaffner, 1998). The principal factor affecting growth, yields and nitrogen fixation of most food legumes in the tropics is considered to be soil moisture (APO, 1980; Patanothaia & Ong, 1987 and Moreshet *et al.*, 1996).

Potassium is an essential element for all living organisms. In plants, it is an important cation involved in physiological pathways (Beriner *et al.*, 1983; Duke & Collins, 1985 and Steudle, 1994). In particular, the ability of ATPases in membranes to maintain active transport is highly dependent on adequate K supply. Thus efficient cell development and growth of plant tissues, translocation, storage of assimilates and other internal functions, which are based on many physiological, biochemical and biophysical interactions, require adequate K in the cell sap (Lindhauer, 1989; Marschner, 1995 and Ruggiero *et al.*, 1999). In the tropics, where water is a major limiting factor for successful legume production (Wiersama & Christie, 1987 and Steudle & Peterson, 1998), K may temper water stress due to its role in cell turgor control and metabolic activity (Beringe *et al.*, 1983; Lindhauer, 1989 and Abou-Arab *et al.*, 1998). However, in most tropical soils, K contents are low.

The influence of K on growth and yields of food legumes has been demonstrated (Hanway and Johnson, 1985; Sangakkara, 1990, and El-Sayed & Ghaly, 1996 a&b). However, little is known about the importance of K in partially overcoming its effects of moisture stress in temperate and tropical food legumes, and on the process of symbiotic nitrogen fixation. Thus a study was undertaken to evaluate symbiotic nitrogen fixation and vegetative growth in a temperate and in a tropical legume under three K fertilizer regimes under high and low soil moisture conditions. The species selected were broad bean, an amide-producing temperate legume and pea, a tropical ureide-producing species.

Material and Methods

plant materials and growth conditions

Broad bean (*Vicia faba* L.) variety Giza blanca and pea (*Pisum sativum* L.)

variety little marvel were grown from five seed in PVC pots (10 cm diameter, 30 cm height) containing 1.50 kg of air dried silica sand (diameter 0.7-1.2 mm) in growth greenhouse of Faculty of Agriculture in Assiut, Al-Azhar University, during the winter season 2000/2001. The nutrient solution was similar to that of Hammer *et al.* (1978) containing 0.2 m *Mf*, 1.0 mM or 3.3 mM potassium. The nutrient solution containing 1.3 mM N in the form of ^{15}N labeled NH_4NO_3 at 1.0% ^{15}N -atom excess. The planting medium of pots containing broad bean were inoculated with 4 ml of a broth containing *Rhizobium leguminosarum* biovar. *Viciae* (strain 482; ICARDA) was obtained from Microbiology Research Center, Cairo Mircen, Egypt (EMCC), Fac. of Agric., Ain Shams Univ., Cairo, Egypt, at two day intervals on five occasions, beginning the day after planting. The same procedure was carried out for pea with an inoculum broth containing *Rhizobium tropicii* (Strain ARC 203; was obtained from Microbiology Research Center, Cairo, Mircen, Egypt (EMCC), Fac. of Agric., Ain Shams Univ., Cairo, Egypt). A prophylactic application of Benlate (concentration of 5 ppm) was carried out at 5, 10 and 16 days after planting to prevent fungal infections in pea. Number of pods plant⁻¹ and number of grains pod⁻¹ in peas and broad bean were recorded.

Regimes to control water supply

Prior to seedlings, the water content of the planting medium at field capacity, 23% and 46% depletion of available moisture was determined by methods described by Black (1965); Evenhuis & De Waard (1978) and Cottenie *et al.* (1982). Plants were grown at high (field capacity to 23% depletion) and low (over 46% depletion) soil moisture regimes from the moment the cotyledons appeared. Randomly selected pots (three per replicate per treatment) were weighed daily and deionized water was added to bring the planting medium of pots maintained at a high soil moisture content to 83 to 88% of field capacity. Any drainage was prevented. Pots designated to be maintained at a low soil moisture regime received no liquid until the planting medium reached a soil moisture of over 46% depletion. At this stage, equal quantities of the respective nutrient solutions were added to all pots with the quantities being determined by weighting, as above.

Broad bean were harvested at 25, 30, 35 and 40 days after seedling (DAS) and peas at 19, 24 and 29 (DAS). Relative growth rates were calculated over the entire experimental period using methods described by Hardwick (1984).

Measurement of water potential

Water potential was determined in peas at the V4/5 growth stage (27 DAS) using a Scholander pressure bomb.

Nitrogen and potassium determination

All plant material was dried at 65°C for 48 hr in a drying oven. Total K content of plants was determined from the final harvests by flame photometric analysis (PFP-7 flame photometer, Jensons Scientific, UK). Total nitrogen and ¹⁵N-atom -%- excess were determined by GC-MS (Europa Scientific, UK) (FAO, 1980 and Page *et al.*, 1982). The amount of nitrogen derived from symbiosis was calculated as follows: % N_{aym} = (1 - ¹⁵N-atom-% exc. in legume plant / ¹⁵N-atom-% exc. in nutrient solution) * 100.

Statistical analysis

The experiments were laid out as a randomized block design. The first experiment, using both legumes, had 3 replicates (blocks) each replicate consisted of 6 pots (total of 18 pots). For the last harvest, 12 pots per replicate (block) were used (total of 36 pots). The second experiment with peas had 3 replicates (blocks), each one containing 4 pots (total of 12 pots). Data were analyzed using the general linear model technique of SAS with a 2-factor factorial design to identify the significance of treatment differences and interactions (SAS Institute Inc., 1988, Snedecor & Cochran, 1967). Nodulation at the various K nutrition levels was double checked twice.

Results and Discussion

Effects of potassium supply on symbiotic nitrogen fixation and plant growth

Unexpectedly, nodulation was completely prevented in plants growth with 0.2mM K in broad bean and peas under both water regimes (Table 1). Such a finding has never been reported before. Potassium supply, although sufficient for plant growth (Tables 2 and 3), was not sufficient to support the development of a symbiosis. These data support the concept that the ecological range of the symbiosis is narrower than that of the plant itself as also reported for low temperature (Hirasawa & Ishihara, 1991; Hazaizeh *et al.*, 1992; Bordeleau & Prevost, 1994, Abou-Arab *et al.*, 1998) and excess temperature (Cruz *et al.*, 1991, Huang *et al.*, 1991; Sangakkara *et al.*, 1996 and El Sayed, 1998 a & b). The symbiosis ceases when it is exposed to extreme conditions.

Since viable rhizobia were used as inoculum it is suggested that either the infection process or the subsequent nodule development was obstructed at a certain stage due to the low K supply to the plant. As an important pre-requisite

TABLE 1. Nodulation and biological nitrogen fixation by broad bean and peas at flowering (R1; 40 DAS for broad bean, 29 DAS for peas) as affected by soil moisture and potassium. Symbiotic nitrogen fixation was quantified from ^{15}N -isotope-dilution. Means of 3 replicates (blocks), each replicate containing 12 pots (total of pots) are shown.

Soil moisture	Potassium (mM)	Nodule/plant (nodule)	Nodule/plant dry weight (nodule/g)	Nitrogen from symbiosis (mg)	Nitrogen fixed per nodule (mg/N sym/nodule)	No. of pods/plant	No. of grains/pod	% Ndfs
Pea Over 46% depletion	0.2	0	0	0	0	0	0	0
	1.0	29	23	33	1.15	115.60	3.6	89
	3.3	45	27	47	1.08	76.80	3.4	89
Field capacity to 23% depletion	0.2	0	0	0	0	0	0	0
	1.0	40	27	43	1.06	78.9	3.2	91
	3.3	45	25	56	1.22	71.7	3.2	90
P	Moisture (M)	<0.005	<0.01	<0.005	<0.05	<0.01	<0.05	<0.01
	Potassium (K)	<0.005	<0.05	<0.01	<0.01	<0.05	<0.01	N.S
	MxK ^a	<0.5	<0.05	<0.05	<0.05	<0.05	<0.05	N.S
Broad bean over 46% depletion	0.2	0	0	0	0	0	0	0
	1.0	20	21	24	1.15	81.20	3.1	83
	3.3	38	33	33	0.85	70.60	3.2	82
Field Capacity to 23% depletion	0.2	0	0	0	0	0	0	0
	1.0	38	33	37	0.96	69.5	3.4	85
	3.3	67	41	54	0.79	61.7	3.3	87
P	Moisture (M)	<0.05	<0.005	<0.005	<0.05	<0.01	<0.05	<0.01
	Potassium (K)	<0.01	<0.005	<0.01	<0.05	<0.05	<0.01	N.S
	MxK ^a	<0.05	<0.05	N.S	N.S	<0.05	<0.05	<0.05

^aThe interaction was tested between 1.0 and 3.3 mM potassium supply only.

TABLE 2. Influence of soil moisture and potassium on vegetative growth of broad bean and peas. Relative growth rates were calculated from 0 over harvests at days 25, 30, 35 and 40 DAS in broad bean and from 0 over days 19, 24 and 29 DAS in peas. All other parameters are from the last harvests (R1-stage).

Soil moisture	Potassium (mM)	Relative growth rate (g dry weight increase/g dry weight/day)	RGR-ratio ^a	Total dry weight (mg)	Specific leaf weight (mg/cm ²)	Shoot/root ratio
Pea Over 46% depletion	0.2	0.136±0.007	1.00	1046	5.2	0.53
	1.0	0.148±0.002	1.09	1243	4.7	0.59
	3.3	0.173±0.012	1.27	1574	4.0	0.65
Field capacity to 23% depletion	0.2	0.144±0.007	1.00	1111	4.8	0.67
	1.0	0.173±0.011	1.20	1455	4.4	0.66
	3.3	0.191±0.002	1.33	1755	3.9	0.67
P	Moisture (M)			<0.05	<0.01	<0.005
	Potassium (K)			<0.005	<0.005	<0.005
	MxK			NS	NS	<0.05
Broad bean over 46% depletion	0.2	0.026±0.013	1.00	678	5.0	1.30
	1.0	0.050±0.003	1.92	980	4.3	1.44
	3.3	0.062±0.006	2.38	1145	3.3	1.70
Field Capacity to 23% depletion	0.2	0.044±0.003	1.00	908	4.3	1.37
	1.0	0.061±0.007	1.39	1141	3.5	1.51
	3.3	0.100±0.011	2.27	1638	2.7	1.78
P	Moisture(M)			<0.005	<0.005	<0.01
	Potassium (K)			<0.005	<0.005	<0.005
	MxK			NS	NS	<0.05

^a RGR - ratio = RGR of a treatment / RGR of 0.2 mM K.

for infection, the presence of root hairs as the location of infection at the tap root of the germinating plant (Sprent & Minchin, 1985; Husain *et al.*, 1990; Rieger & Motisi, 1990; Lafolie *et al.*, 1991 and El-Sayed & Abdel-Mawly, 1999) was evaluated. Although root hair density and percentage of the tap root covered with root hairs was reduced with low K (Table 4), potential infection sites were still present under 0.2 mM K. Nevertheless, nothing resembling nodule structures appeared. Thus it is very likely that nodule development was obstructed either before infection, at infection or very shortly after rhizobia invaded root hairs.

TABLE 3. Effect of soil moisture and potassium on nitrogen and potassium concentration of broad bean (40 DAS) and peas (29 DAS). Means of 3 replicates (blocks), each replicate containing 12 pots (total of 36 pots) are shown.

Soil moisture	Potassium m M	N concentration (mg N/g dry weight)	K concentration (mg K/g dry weight)
Pea Over 46% depletion	0.2	28.4	15.0
	1.0	30.3	24.8
	3.3	33.6	31.9
Field capacity to 23% depletion	0.2	32.3	14.5
	1.0	33.2	24.0
	3.3	34.9	30.7
<i>P</i>	Moisture (M)	<0.005	<0.005
	Potassium (K)	<0.005	<0.01
	MxK	<0.05	<0.05
Broad bean Over 46% depletion	0.2	27.4	12.7
	1.0	29.9	21.9
	3.3	35.5	33.3
Field capacity to 23% depletion	0.2	31.7	11.9
	1.0	38.6	21.3
	3.3	44.1	25.9
<i>P</i>	Moisture (M)	<0.005	<0.005
	Potassium (K)	<0.01	<0.01
	MxK	<0.05	<0.05

The finding of Gober & Kashket (1987) and El-Sayed (1997) that sufficient K supply is essential for bacteroid development in cowpea *Bradyrhizobium*, emphasises the importance of K for the development of the symbiosis. One link to explain the complete suppression of nodule formation could be that K is used in higher concentrations for protein synthesis than for enzyme activation (Davies & Zhang, 1991; Marschner, 1995, Abdel-Mawly & El-Sayed, 1999). This leads to the reported K stress-induced accumulation of soluble nitrogen compounds such as amino acids, amines, amides and nitrate (Hirasawa *et al.*, 1991; Sarkar & Kar, 1992 and DePascale & Barbieri, 1997), all molecules known or believed to suppress nodulation (Parsons *et al.*, 1993; Streeter, 1988 and Steudle, 1994). Further work is required on this hypothesis.

TABLE 4. Effect of soil moisture and potassium on the root hair density and the percentage of the tap root covered with root hairs in peas 16 (V₂; 16 DAS). Means of 3 replicates (blocks), each replicate containing 4 pots (total of 12 pots) are shown.

Soil moisture	Potassium (mM)	Root hair density in the top 2 cm (root hairs)	Percentage of the tap root covered with hairs (%)
Over 46% depletion	0.2	53	37
	1.0	72	50
	3.3	79	94
Field capacity to 23% depletion	0.2	42	54
	1.0	54	55
	3.3	68	89
<i>P</i>	Moisture (M)	<0.05	<0.01
	Potassium (K)	<0.05	<0.1
	M x K	<0.01	<0.05

Nodules were observed with the application of both 1.0 and 3.3 mM in both species (Table 1). The application of 3.3 mM K resulted in higher nodule numbers compared to the 1.0 mM K supply. While in peas, nodulation under 3.3 mM K was increased more or less in proportion to the increased plant growth, in broad bean the beneficial effect of 3.3 mM K in establishing nodules appeared to be consistently greater than expected from plant growth (nodule number per plant dry weight; Table 1). This led to produce more nodules per plant dry weight under 3.3 mM K compared to 1.0 mM K in broad bean (Table 1). Number of pods plant⁻¹ and number of grains pod⁻¹ in peas produced more pods and grain per plant than broad bean. However, as evident from the unaffected percentage of nitrogen derived from symbiosis (¹⁵N dilution), the reduced number of nodules per plant dry weight under 1.0 mM K in broad bean appeared to be compensated by a higher nitrogen fixing activity per nodule (Table 1). Similar results were reported by Chalamet *et al.* (1987) and Cadisch *et al.* (1993). This is in notable contrast to the response of N₂ fixation to phosphorus, where the percentage of nitrogen from fixation decreased with decreasing phosphate supply (Cadisch *et al.*, 1993) indicating increased preference for nitrogen assimilation from mineral sources under low phosphorus. Obviously, in the present experiment, the reduced nodulation still allowed adequate nitrogen fixation as demanded by the relatively poor growth under 1.0 mM K. Thus, the

influence of K on symbiotic N₂-fixation was to improve nodulation rather than the activity of established nodules. The present finding that K does not affect the percentage of nitrogen from fixation is consistent with the observation that specific nitrogenase activity was not affected by K supply in alfalfa (Barta, 1982). These data indicate that, if low K reduces total N₂ fixation, this effect is indirect, *e.g.* through a nitrogen feedback mechanism (Hartwig and Nosberger, 1994; Hallgren *et al.*, 1994 and Kramer & Boyer, 1995) rather than a specific K-effect on N₂ fixation.

The decreased nitrogen concentrations with decreasing K supply (Table 3) may at least in part, be interpreted as dilution effects of nitrogen through accumulating nonstructural carbohydrates, a phenomenon reported by Guardia and Benloch (1980) and indicated here by the increased specific leaf weight (Table 2). In addition, a possible reduced protein synthesis under low K (Grashoff, 1990 and 1991; Marschner, 1995; Moreshet *et al.*, 1990 & 1996 and Tyree, 1997) could have contributed to this. Compared to nitrogen, K concentrations were reduced much more due to the low K supply suggesting that K limited growth. This would be consistent with the observation that high application of K increased shoot: root ratios (Table 2). Nevertheless, it is noteworthy that even a reduction in K concentration by a factor of 2 to 3 still allowed growth. The plasticity of growth in the selected plant species to variations in K concentrations seems to be extremely high compared *e.g.* to the nitrogen plasticity.

Effects of water supply on symbiotic nitrogen fixation and plant growth

Nodulation was generally reduced by low water supply in both species except in peas under 3.3 mM K (Table 1). As evident from nodules per plant dry weight, in the other cases, the reduction in nodulation was more severe than would have been expected from growth (Tables 1 and 2), an observation previously made in soybean (Khanna-Chopra *et al.*, 1984; El-Sayed and Ghaly, 1996 a & b and Schaffner, 1998). However, in the case of reduced nodulation, increased nitrogen fixation per nodule could apparently compensate for the relatively low nodule numbers (Table 1). This is also evident from the unaffected percentage of nitrogen derived from symbiosis (Table 1).

Does high K supply alleviate water stress on symbiotic nitrogen fixation and growth?

Clearly, high K supply stimulates growth and nodulation also under water limiting conditions (Tables 1 and 2). With peas, in both water treatments, K

could increase the water potential substantially. The values were -0.81, -0.54 and -0.25 MPa for 0.2, 1.0 and 3.3 mM K in the low water treatment and -0.29, -0.13 and -0.05 MPa for the high water treatment, respectively. These data are consistent with those from Abd-Alla & Abdel Wahab (1995) and Mengel & Arneke (1982) indicating that high K fertilization can at least in part compensate water shortage. This conclusion is also in agreement with Robin *et al.* (1989) who demonstrated that K is an essential factor determining plant resistance to water stress. This would support the view that K helps to maintain the osmotic potential of plant cells, an increasingly critical problem by increasing water stress (Beringer *et al.*, 1983). The beneficial effect of high K supply on growth was generally similar in both water treatments with the exception that in broad bean the beneficial effect of 1.0 mM K compared to 0.2 mM K was more pronounced in the low water treatment than in the high water treatment (Table 2). The beneficial effect of high K under water stress can certainly, in part, be explained by the fact that under conditions of restricted water flow into the roots, an increase in nutrient concentration will lead to an increased nutrient intake per unit of water uptake (Fick's Law).

Specific leaf weights were higher when both species were grown at a lower soil moisture, thus indicating the effect of water stress in restricting the movement of photosynthates from leaves to the sinks (Munns and Weir, 1981). Application of K reduced specific leaf weights significantly, and the impact was more prominent in broad bean. This could be related to the effect of K in facilitating the translocation of photosynthates to the sink (Lindhauer, 1989; Thomas & Hungria, 1988 and Steudle & Peterson, 1998). As evident from the strongly adverse effect of both water shortage and low K supply on nodule formation, this process seems to be highly dependent on efficient transport conditions in the plant. On the other hand, in the present study, nitrogen fixation appeared to be similarly affected by the adverse conditions as plant growth itself. This meets the concept that nitrogen fixation is tuned to the demand for symbiotically fixed nitrogen (Hartwig & Nosberger 1994; Hartwig *et al.*, 1994 and Ruggiero *et al.*, 1999). This demand may be sensed from the intensity at which nitrogen is transported to the sink from the amount of nitrogen recycled to the nodules (Heim *et al.*, 1993; Oti Boateng & Silsbury, 1993; Oti-Boaten *et al.*, 1994; Parsons *et al.*, 1993; Ruggiero & Fagnano, 1996 a&b & Maurel, 1997).

Conclusions

This study demonstrates that in both broad bean and peas the plasticity for nodulation, thus to potentially establish a nitrogen fixing symbiosis, for K shortage is smaller than that for plant growth itself. However, as long as effective nodules get established, symbiotic N₂-fixation is not selectively limited by low K.

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تأثير نقص الماء والبوتاسيوم على كفاءة تثبيت النيتروجين حيويًا في بعض البقوليات

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يعمل عنصر البوتاسيوم على تحسين مقاومة النباتات ضد ظروف البيئة السيئة، مثل الانخفاض المائي (النقص الرطوبي) في المناطق الاستوائية. وجود البوتاسيوم بمقدار كبير في التربة يساعد النباتات في التغلب على الانخفاض المائي (النقص الرطوبي) خاصة في النباتات البقولية التي تقوم بتثبيت النيتروجين حيويًا والتي تكون منخفضة في المناطق الاستوائية عند مقارنتها بالمناطق المعتدلة.

تم دراسة تأثير ثلاثة مستويات من التسميد البوتاسي هي (٢، ١، ٣، ٣، ٣ ملليمول بوتاسيوم) على تثبيت النيتروجين حيويًا في النباتات البقولية تحت مستويين مختلفين من السعة الحقلية (٤٦٪، ٢٣٪).

تم نمو الفول صنف جيزة بلانكا وهو يمثل المناطق المعتدلة، والبسلة صنف لتل مارفل وتمثل المناطق الاستوائية في أسس مستعملا تركيز ١.٣ ملليمول نيتروجين مشع على هيئة نترات امونيوم.

تشير النتائج أنه عند الانخفاض المائي (النقص الرطوبي) وعند تركيز ٠.٢ ملليمول بوتاسيوم حدث نقص في تكوين العقد البكتيرية، وعند زيادة تركيز البوتاسيوم إلى ٣.٣، ١، ٣ ملليمول بوتاسيوم لوحظ زيادة في تكوين العقد البكتيرية وبالتالي النيتروجين المثبت حيويًا، إضافة البوتاسيوم بكميات كبيرة في وجود الانخفاض المائي كان مشجعاً لنمو السيقان والجذور والعقد البكتيرية وزيادة النيتروجين المثبت حيويًا، كذلك زاد عدد القرون لكل نبات، وعدد الحبوب في كل قرن في البسلة صنف لتل مارفل عنها في الفول صنف جيزة بلانكا.

أوضحت النتائج أن إضافة البوتاسيوم يعمل على تخفيف الانخفاض المائي (النقص الرطوبي) وكذلك زيادة قدرة كل من الفول والبسلة على الاحتمال وزيادة كمية النيتروجين المثبت حيويًا.