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Soil moisture and potassium affect the performance of symbiotic nitrogen fixation in faba bean and common bean

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Abstract

Potassium (K) is reported to improve plant's 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 (0.1, 0.8 and 3.0 mM K) on symbiotic nitrogen fixation was evaluated with two legumes under high (field capacity to 25% depletion) and low (less than 50% of field capacity) water regimes. Plants were grown in single pots in silica sand under controlled conditions with 1.5 mM N (^{15}N enriched NH_4NO_3). The species were faba bean (*Vicia faba* L.), a temperate, amide producing legume and common bean (*Phaseolus vulgaris* L.), a tropical, ureide producing species. In both species, 0.1 mM K was insufficient for nodulation at both moisture regimes, although plant growth was observed. The supply of 0.8 or 3.0 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 faba bean and common bean 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.

Introduction

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

Potassium is an essential element for all living organisms. In plants it is an important cation involved in physiological pathways (Beringer et al., 1983; Duke and Collins, 1985). 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 upon many physiological, biochemical and biophysical interactions, require adequate K in the cell sap (Lindhauer, 1989; Marschner, 1995). In the tropics, where water is a major limiting factor for successful legume production (Wiersama and Christie, 1987), K may temper water stress due to its role in cell turgor control and metabolic activity (Beringer et

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al., 1983; Lindhauer, 1989). 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). 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 faba bean, an amide-producing temperate legume and common bean, a tropical ureide-producing species.

Materials and methods

Plant materials and growth conditions

Faba bean (*Vicia faba* L.) cv. "Herz Freya" and common bean (*Phaseolus vulgaris* L.) cv. "Wade" (Sri Lanka) were grown from seed in PVC pots (7 cm diameter, 25 cm height) containing 1.25 kg of air dried silica sand (diameter 0.7 - 1.2 mm) in growth chambers (PGR-15 Conviron Instruments Co, Winnipeg, Canada). Temperatures were 23 °C day/18 °C night, with a relative humidity of 80% ± 2% and a 16 hour day length. Photosynthetic photon flux density (PPFD) was maintained at 450 - 500 μmol photon m^{-2} sec^{-1} (400 - 700 nm wavelength) at plant height. The nutrient solution was similar to that of Hammer et al. (1978) containing 0.1 mM, 0.8 mM or 3.0 mM potassium. The nutrient solution contained 1.5 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 faba bean were inoculated with 4 mL of a broth containing *Rhizobium leguminosarum* biovar. *viciae* (strain 595; Swiss Federal Research Station for Agronomy, Reckenholz, Zürich) at two day intervals on five occasions, beginning the day after planting. The same procedure was carried out for common bean with an inoculum broth containing *Rhizobium tropicii* (Strain CIAT 899, Center for International Tropical Agriculture, Cali, Colombia). A prophylactic application of Benlate (concentration of 5 ppm) was carried out at 3, 8 and 14 days after planting to prevent fungal infections in common bean.

Regimes to control water supply

Prior to seeding, the water content of the planting medium at field capacity, 25% and 50% depletion of available moisture was determined by methods described by Black (1965). Plants were grown at high (field capacity to 25% depletion) and low (over 50% 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 90 to 95% 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 50% depletion. At this stage, equal quantities of the respective nutrient solutions were added to all pots with the quantities being determined by weighing, as above.

Faba bean were harvested at 23, 28, 33 and 38 days after seeding (DAS) and common bean at 17, 22 and 27 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 common bean at the V4/5 growth stage (25 DAS) using a Scholander pressure bomb.

Nitrogen and potassium determination

All plant material was dried at 65 °C for 48 hours 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 ^{15}N-atom-%-excess were determined by GC-MS (Europa Scientific, UK). The amount of nitrogen derived from symbiosis was calculated as follows: %Nsym = (1- ^{15}N-atom-% exc. in legume plant/^{15}N-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 common bean 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. 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 grown with 0.1 m*M* K in common bean and faba bean under both water regimes (Table 1). Such a finding, to our knowledge, has never been reported before. K 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 (Bordeleau and Prévost, 1994) and excess temperature (Sangakkara et al., 1996). 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 for infection, the presence of root hairs as the location of infection at the tap root of the germinating plant (Sprent and Minchin, 1985) 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 0.1 m*M* 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. The finding of Gober and Kashket (1987) 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 (Marschner, 1995). This leads to the reported K stress-induced accumulation of soluble nitrogen compounds such as amino acids, amines, amides and nitrate (Mengel and Helal, 1968), all molecules known or believed to suppress nodulation (Parsons et al.,1993; Streeter, 1988). Further work is required on this hypothesis.

Nodules were observed with the application of both 0.8 and 3.0 m*M* K in both species (Table 1). The application of 3.0 m*M* K resulted in higher nodule numbers compared to the 0.8 m*M* K supply. While in common bean nodulation under 3.0 m*M* K was increased more or less in proportion to the increased plant growth, in faba bean the beneficial effect of 3.0 m*M* 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 more nodules per plant dry weight under 3.0 m*M* K compared to 0.8 m*M* K in faba bean (Table 1). However, as evident from the unaffected percentage of nitrogen derived from symbiosis (^{15}N dilution), the reduced number of nodules per plant dry weight under 0.8 m*M* K in faba 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 N_2 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 0.8 m*M* K. Thus, the influence of K on symbiotic N_2-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 N_2 fixation, this effect is indirect, e.g. through a nitrogen feedback mechanism (Hartwig and Nösberger, 1994) rather than a specific K-effect on N_2 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 Benlloch (1980) and indicated here by the increased specific leaf weight (Table 2). In addition, a possible reduced protein synthesis under low K (Marschner, 1995) 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 con-

Table 1. Nodulation and biological nitrogen fixation by faba bean and common bean at flowering (R1; 38 DAS for faba bean, 27 DAS for common bean) 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 36 pots) are shown

Soil moisture	Potassium (m*M*)	Nodule plant^{-1} (nod)	Nodule plant^{-1} dry weight (nod g^{-1})	Nitrogen from symbiosis (mg)	Nitrogen fixed per nodule (mg N_{sym} nod^{-1})	% Ndfs
Faba bean						
Over 50% depletion	0.1	0	0	0	0	0
	0.8	21	22	25	1.16	84
	3.0	39	34	34	0.86	83
Field capacity to 25% depletion	0.1	0	0	0	0	0
	0.8	39	34	38	0.97	86
	3.0	68	42	55	0.80	88
p	Moisture (M)	<0.05	<0.005	<0.005	<0.05	<0.01
	Potassium(K)	<0.01	<0.005	<0.01	<0.05	ns
	M×K^{a}	<0.05	<0.05	ns	ns	<0.05
Common bean						
Over 50% depletion	0.1	0	0	0	0	0
	0.8	30	24	34	1.16	90
	3.0	46	28	48	1.09	90
Field capacity to 25% depletion	0.1	0	0	0	0	0
	0.8	41	28	44	1.07	92
	3.0	46	26	57	1.23	91
p	Moisture (M)	<0.005	<0.01	<0.005	<0.05	<0.01
	Potassium (K)	<0.005	<0.05	<0.01	<0.01	ns
	M×K^{a}	<0.05	<0.05	<0.05	<0.05	ns

^{a}The interaction was tested between 0.8 and 3.0 m*M* potassium supply only.

sistent 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 common bean under 3.0 m*M* 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). 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 common bean, in both water treatments, K could increase the water potential substantially. The values were -0.83, -0.56 and -0.27 MPa for 0.1, 0.8 and 3.0 m*M* K in the low water treatment and -0.31, -0.15 and -0.07 MPa for the high water treatment, respec-

Table 2. Influence of soil moisture and potassium on vegetative growth of faba bean and common bean. Relative growth rates were calculated from 0 over harvests at days 23, 28, 33 and 38 DAS in faba bean and from 0 over days 17, 22 and 27 DAS in common bean. All other parameters are from the last harvests (R1-stage)

Soil moisture	Potassium (m*M*)	Relative growth rate (g dry weight increase g^{-1} dry weight day^{-1})	RGR-ratio[a]	Total dry weight (mg)	Specific leaf weight (mg cm^{-2})	Shoot/root-ratio
Faba bean						
Over 50%	0.1	0.027 ± 0.014	1.00	679	5.1	1.31
depletion	0.8	0.051 ± 0.003	1.88	981	4.4	1.45
	3.0	0.063 ± 0.006	2.33	1146	3.4	1.71
Field	0.1	0.045 ± 0.003	1.00	909	4.4	1.38
capacity	0.8	0.062 ± 0.007	1.38	1142	3.6	1.52
to 25%	3.0	0.101 ± 0.012	2.24	1639	2.8	1.79
depletion						
p	Moisture (M)			<0.005	<0.005	<0.01
	Potassium (K)			<0.005	<0.005	<0.005
	M×K			ns	ns	<0.05
Common bean						
Over 50%	0.1	0.137 ± 0.007	1.00	1047	5.3	0.54
depletion	0.8	0.149 ± 0.002	1.08	1244	4.8	0.60
	3.0	0.174 ± 0.013	1.27	1575	4.1	0.66
Field	0.1	0.145 ± 0.007	1.00	1112	4.9	0.68
capacity	0.8	0.174 ± 0.012	1.20	1456	4.5	0.67
to 25%	3.0	0.192 ± 0.002	1.32	1756	4.0	0.68
depletion						
p	Moisture (M)			<0.05	<0.01	<0.005
	Potassium (K)			<0.005	<0.005	<0.005
	M×K			ns	ns	<0.05

[a] RGR-ratio = RGR of a treatment/RGR of 0.1 m*M* K.

tively. These data are consistent with those from Abd-Alla and Abdel Wahab (1995) and Mengel and 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 maintain the osmotic potential of plant cells, an increasingly critical problem with 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 faba bean the beneficial effect of 0.8 m*M* K compared to 0.1 m*M* 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 faba beans. This could be related to the effect of K in facilitating the translocation of photosynthates to the sinks (Lindhauer, 1989; Thomas and Hungria, 1988). 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

Table 3. Effect of soil moisture and potassium on nitrogen and potassium concentrations of faba bean (38 DAS) and common bean (27 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^{-1} dry weight)	K concentration (mg K g^{-1} dry weight)
Faba bean			
Over 50%	0.1	27.5	12.8
depletion	0.8	30.0	22.0
	3.0	35.6	33.4
Field	0.1	31.8	12.0
capacity	0.8	38.7	21.4
to 25%	3.0	44.2	26.0
depletion			
p	Moisture (M)	<0.005	<0.005
	Potassium (K)	<0.01	<0.01
	M×K	<0.05	<0.05
Common bean			
Over 50%	0.1	28.5	15.1
depletion	0.8	30.4	24.9
	3.0	33.7	32.0
Field	0.1	32.4	14.6
capacity	0.8	33.3	24.1
to 25%	3.0	35.0	30.8
depletion			
p	Moisture (M)	<0.005	<0.005
	Potassium (K)	<0.005	<0.01
	M×K	<0.05	<0.05

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 common bean 14 (V2; 14 DAS). Means of 3 replicates (blocks), each replicate containing 4 pots (total of 12 pots) are shown

Soil moisture	Potassium (m*M*)	Root hair density in the top 2 cm (root hairs)	Percentage of the tap root covered with hairs (%)
Over 50%	0.1	54	38
depletion	0.8	73	51
	3.0	80	95
Field	0.1	43	55
capacity	0.8	55	56
to 25%	3.0	69	90
depletion			
p	Moisture (M)	<0.05	<0.01
	Potassium (K)	<0.05	<0.1
	M×K	<0.01	<0.05

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 and Nösberger, 1994; Hartwig et al., 1994). This demand may be sensed from the intensity at which nitrogen is transported to the sink or from the amount of nitrogen recycled to the nodules (Heim et al., 1993; Oti-Boateng and Silsbury, 1993; Oti-Boateng et al., 1994; Parsons et al., 1993).

Conclusions

This study demonstrates that in both faba bean and common bean 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 N_2-fixation is not selectively limited by low K.

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