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Differential responses to K deficiency among soybean cultivars

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Abstract

The seed yield per unit of potassium applied differed for five soybean cultivars which were grown to maturity under different K regimes in a glasshouse. Whereas Dodds was the most responsive cultivar to moderate increases in K supply, the cultivar Bragg was the most efficient in its ability to produce seed with low levels of available K; Lee and Forest were the least efficient cultivars while Bossier and Dodds were of intermediate efficiency. The basis for the efficiency of cv. Bragg was that the growth of its tops, as indicated by mature stem weights and its roots, were less affected by reduced K supply than those of other cultivars. This enabled it to produce more pods under K-deficient regimes, resulting in a greater seed yield per plant. The percentage reduction in oil/protein ratios in the seed of the five cultivars under moderate K deficiency correlated closely with reductions in seed yield. However, changes in this ratio were poorly related to the K percentages in the seed. All cultivars experienced an impairment of plant senescence under K deficiency as evidenced by a reduction in leaf abcission and a delay in pod maturity. The existence of genetic diversity in K-use efficiency means that breeding programmes could utilize K-efficient germplasm in developing new cultivars for soils not naturally high in potassium.

Introduction

Previous work (Sale and Campbell, 1986) has shown how a reduction in K supply to soybean plants (*Glycine max* (L.) Merrill) of the cultivar Lee resulted in closely related reductions in both seed yield and the oil/protein ratio of mature seed. However, little is known about the response to reduced K supply of other soybean cultivars that are grown in coastal areas of Eastern Australia, USA or Brazil where K fertiliser applications are recommended. The choice of a cultivar which is better able to produce high seed yields in soils of low K status could be an alternative approach to the use of K fertilisers.

Differential responses among soybean cultivars to Fe deficiency (Brown and Jones, 1979), Zn deficiency (Rose *et al.*, 1981), Mn deficiency (Heenan and Campbell, 1980) and Mn toxicity (Heenan *et al.*, 1981) have been reported. However, possible differential responses among cultivars to K deficiency have not been investigated. It is reasonable to expect such differences to exist in soybeans as they have been reported to occur in snapbeans (Shea *et al.*, 1968), tomato (Gerloff, 1976) and in corn (Baligar and Barber, 1970).

The objectives of this experiment were to determine whether differential responses to K deficiency, in terms of changes in seed composition and yield, exist in a group of selected commercial cultivars. Measurements of seed yield components, top and root growth and plant development, were also made to provide an explanation of the basis for differences between cultivars.

Materials and methods

Growing conditions

The experiment was conducted in a glasshouse at Camden, New South Wales (34°S). Temperatures were controlled to maintain a diurnal range of 18° to 30°C (± 2°C). Seed of five commercial cultivars of soybeans comprising Lee, Forrest, Bragg, Dodds and Bossier, were sown in pots in mid-January and harvested four months later. Each pot contained 7.5 kg fo a fine-textured sand (FAO classification — Cambic Arenosol, FAO-UNESCO, 1974) in which 3000 mg N, 600 mg P, 900 mg Ca, 540 mg Mg, 720 mg S, 21 mg Fe (as iron sequestrene 138), 3.7 mg B (as boric acid), 18 mg Mn, 15 mg Zn, 3 mg Cu, 0.75 mg Mo (as ammonium molybdate) and 0.07 mg Co, had been uniformly mixed, together with the different K additions (112, 375, or 1875 mg K pot^{-1}). The macronutrients were supplied as NH_4NO_3, KNO_3, $Ca(NO_3)_2 \cdot 4H_2O$, KH_2PO_4 and $MgSO_4 \cdot 7H_2O$, while Mn, Zn, Cu and Co were added in the sulfate form. The low K regimes were achieved by substituting Na salts for K salts. Four seedlings were initially transplanted into 5 kg of this nutrient-enriched sand and, after one week, were thinned to one plant per pot. An additional 2.5 kg of sand plus nutrients, at the same sand to nutrient ratio described above, were added after 20 days. The pots were watered by maintaining a 1 cm-deep water table at the bottom of the sand in each pot by an inverted, water-filled bottle (Sale, 1981). All plants were harvested when plants of Bossier (the longest season cultivar) which had grown at the highest K rate, were mature.

Treatments consisted of the factorial combination of the five cultivars grown at 3 rates of K. The design was a randomized complete block with four blocks. Pots within a block were re-randomised regularly.

Measurements

Leaf abscission was determined by counting the number of nodes from which leaves had become detached and expressing that number as percentage of the total number of nodes. The first maturity index (FMI) of harvested plants was calculated using a previously developed, rapid, non-destructive method (Lindoo and Noodén, 1976).

Pods were shelled after counting and the seed weighed before drying to less than 2 percent moisture (fresh-weight basis) in an oven at 75°C for 24 hours. Oil levels in the seed fraction of each plant were measured by wide-line NMR spectroscopy (Collins *et al.*, 1967) and the Soil percentage was calculated on a dry-weight basis. The K concentration in the seed was measured using a flame photometer, following a $HNO_3/HClO_4$ wet digestion of subsamples from respective seed lots. Protein contents in the seed were calculated by multiplying the total N in the seed, determined by using a micro-Kjeldhal procedure (Yoshida *et al.*, 1972), by 6.25.

Results

Symptoms

Symptoms of potassium deficiency (Sale and Campbell, 1986) were first observed on the lower leaves twenty days after emergence of all cultivars grown at 112 mg K pot^{-1}. At the intermediate rate of applied K, symptoms were not apparent until late vegetative growth. Symptoms of potassium deficiency (leaf bubbling) became more severe during podfilling despite the fact that all cultivars were determinate in habit.

Seed yield and components of yield

Marked differences existed in the seed yield produced by different cultivars under K-deficient regimes (Table 1). Bragg was the only cultivar not to experience a significant reduction in yield when the K supply was reduced from 1875 to 375 mg K pot^{-1}. In addition, Bragg produced the highest absolute yield (g plant^{-1}) and relative yield (percentage of maximum seed yield) under moderate and severe K deficiency (375 and 112 mg K pot^{-1}, respectively). In contrast, Lee had the lowest absolute and relative yields at these two K regimes. Bossier, Dodds and Forrest had similar relative yields under severe K deficiency but, at the moderately deficient regime, the relative yield of Forrest was similar to that of Lee.

Cultivars fell into two groups with respect of pod and seed number. The more K-efficient cultivars, Bragg, Bossier and Dodds, did not experience a

Table 1. Seed yield and components of yield of mature plants of cultivars grown under different K regimes

Cultivars	K regime (mg K pot^{-1})	Pod no. (pod plant^{-1})	Seed no. (seeds plant^{-1})	Seed wt (mg seed^{-1})	Seed yield (g plant^{-1})
Lee	112	41a (41)[a]	84a (40)[a]	129a (70)[a]	10.9a (31)[a]
	375	61a (61)	134b (64)	185c (100)	24.8b (70)
	1875	100b	208c	170b (92)	35.4c
Forest	112	50a (36)	101a (34)	158b (100)	16.0a (40)
	375	85b (61)	181a (60)	155b (98)	28.0b (71)
	1875	139c	299b	132a (83)	39.5c
Bragg	112	64a (67)	135a (63)	130a (75)	17.5a (49)
	375	84ab (87)	196b (91)	174b (100)	33.4b (94)
	1875	96b	215b	165b (95)	35.5b
Dodds	112	63a (59)	126a (51)	110a (74)	13.9a (40)
	375	92ab (86)	204b (83)	148b (100)	30.2b (87)
	1875	107b	245b	141b (95)	34.5c
Bossier	112	90a (72)	183a (64)	91a (64)	16.7a (44)
	375	107ab (88)	225ab (78)	142a (100)	32.0b (85)
	1875	125b	287b	136b (96)	37.8c

[a] Relative pod and seed number, seed weight and seed yield (% of maximum) are given in parentheses.
Means within columns for each cultivar which are followed by different letters differ significantly ($P < 0.05$).

significant reduction in pod or seed number when K supply was reduced from 1875 to 375 mg K pot^{-1}, whereas Lee and Forrest produced fewer pods and, therefore, fewer seeds (Table 1). Under severe K deficiency Forrest experienced the largest reduction in pod number, producing about a third of the pods that were produced with adequate K. There was only a slight effect on seed number per pod for most cultivars under reduced K supply *viz.* fewer seeds per pod were set at the lowest level of potassium supply.

All cultivars tended to produce a heavier seed as K supply was reduced from an adequate to a moderately deficient regime (Table 1). However, under severe K deficiency, reductions in seed weight occurred with all cultivars, except Forrest. The ability by Forrest to produce large seed under severe K deficiency tended to offset the marked reduction in its pod and seed number and was resonsible for its relatively efficient K use at this K regime when compared with cultivar Lee (Table 2).

The efficiency of K use, defined as the seed yield produced per unit of K applied, varied by 60 percent between cultivars under severe K deficiency, with Bragg being the most efficient and Lee the least efficient cultivar (Table 2). Under moderate K deficiency, the difference in K-use efficiency between these two cultivars was 34 percent; there was no difference in efficiency of K use between these cultivars when the supply off potassium was adequate. Alternative criteria for K-use efficiency, which involve the notion of responsiveness to added K, would be the increase in seed yield as K supply was increased from 112 to 375 mg K pot^{-1} or the seed yield increase per unit of K increase. These criteria indicate that Dodds was the most efficient cultivar in responding to a moderate increase in K supply (Table 2).

Seed composition

Reducing the level of K supply resulted in lower oil and seed K concentrations and higher protein percentages in the seed of all cultivars (Table 3). However, the change in the oil/protein ratio was lowest at the moderately deficient K regime in seed of Bragg, the cultivar whose seed yield was least affected by this moderate reduction in K supply. In fact, the percentage reductions in the oil/protein ratio were closely correlated ($r = 0.99$, $n = 5$, $p < 0.01$) with percentage reductions in seed yield across cultivars under moderate K deficiency (Fig. 1A). In contrast, the percentage reduction in this ratio was poorly coorelated ($r = -0.3$) with the percentage reduction in K concentration in the seed of the different cultivars (Fig. 1B).

Reducing the amount of K added per pot from 375 to 112 mg K significantly lowered the K percentage in seed from all cultivars except Lee. This cultivar generally had the highest seed K percentage compared with the other cultivars, for each of the 3 K regimes under study. In fact, the differences

Table 2. Measures of K-use efficiency for cultivars

Cultivar	K regime (mg K pot^{-1})		Seed yield/ K applied (g g^{-1})	Δ Seed yield (K_2-K_1) (g plant^{-1})	Δ Seed yield/ Δ K applied (g g^{-1})[a]
Lee	K_1	112	97	13.9	52.9
	K_2	375	66		
	K_3	1875	19		
Forrest	K_1	112	143	12/0	45.6
	K_2	375	75		
	K_3	1875	21		
Bragg	K_1	112	156	15.9	60.5
	K_2	375	89		
	K_3	1875	19		
Dodds	K_1	112	124	16.3	62.0
	K_2	375	81		
	K_3	1875	18		
Bossier	K_1	112	149	15.3	58.2
	K_2	375	85		
	K_3	1875	20		

[a] The seed yield increase (K_2-K_1) per unit of K increase (K_2-K_1).

between the K percentage for Lee (1.7% K) and other cultivars (1.52, 1.52, 1.58 and 1.53% K for Forrest, Bragg, Dodds and Bossier, respectively) was highly significant ($p < 0.001$).

Stem, root growth and harvest index

The weight of stems of mature plants declined as K supply was reduced but the extent of the decline was considerably less with Bragg than with other cultivars (Table 4). In fact, Bragg had the highest yields with 112 and 375 mg K, relative to yields with 1875 mg K. Similarly, the smallest decline in both absolute and relative root weights under severe K deficiency occurred with Bragg, followed closely by Bossier, the second most K-efficient cultivar. Both Bragg and Bossier produced as much root weight under moderate K deficiency as they did with an adequate supply of potassium.

The more K-efficient cultivars, Bragg and Bossier, tended to have the lowest harvest indices (Table 4). Common to all cultivars was the trend of higher indices under a moderate K deficiency com-

Table 3. Concentration of oil, protein and K, and the oil/protein ratio, in seed of cultivars grown under different K regimes

Cultivar	K regime (mg K pot^{-1})	Seed composition (% of dry weight)			Oil/protein ratio
		Oil	protein	K	
Lee	112	21.4a	48.2a	1.3a	0.44
	375	22.3a	45.5a	1.4a	0.49
	1875	24.5b	38.2b	1.8b	0.64
Forest	112	22.4a	47.5a	1.0a	0.47
	375	24.2ab	39.1b	1.4b	0.62
	1875	26.8b	32.6c	1.6c	0.82
Bragg	112	23.5a	44.3a	1.1a	0.53
	375	26.1ab	40.9ab	1.3b	0.64
	1875	26.5b	37.1b	1.6c	0.71
Dodds	112	21.1a	48.2a	1.1a	0.44
	375	24.0ab	42.3ab	1.3b	0.57
	1875	25.4b	38.1b	1.7c	0.67
Bossier	112	25.0a	39.8a	1.1a	0.63
	375	26.3ab	36.5b	1.3b	0.72
	1875	27.1b	32.0c	1.6c	0.84

Means within columns for each cultivar that are followed by different letters differ significantly ($P < 0.05$).

pared to those occurring when K supply was adequate. Under severe K deficiency, however, harvest indices were generally less than those produced with an adequate K supply.

Phenology and senescence

A reduction in K supply appeared to have little effect on the time to floral initiation and the development of the first flowers, except for cultivar Lee which flowered early, and Bragg which had a delayed flowering under severe K deficiency (Table 5). However, the degree to which plants of all cultivars senesced at maturity, as assessed by the extent of leaf abcission, was influenced by K supply (Table 5). In all cultivars, K deficiency reduced leaf abcission, with the reduction increasing with the severity of the deficiency. The effect was less marked with cultivars Forrest and Bragg. Similarly, Forrest differed from other cultivars under severe K deficiency in the colour of its pods when all plants were harvested; its FMI had reached a maximum of 5.0 indicating that all pods were brown and dry, whereas a proportion of the pods of other cultivars had retained some green colour when the harvest was made.

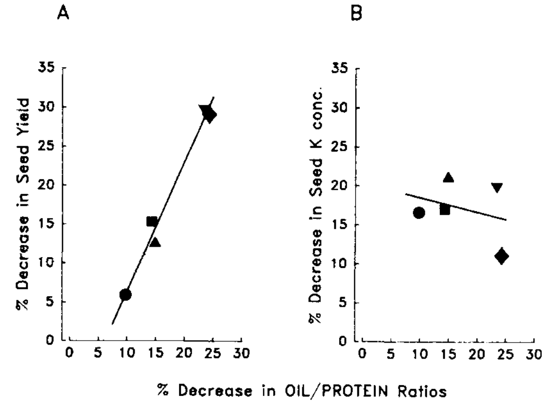

Fig. 1. Relationships between **(A)** the percentage decrease in the seed yield of Bragg (●), Bossier (■), Dodds (▲), Lee (◆) and Forrest (▼), and **(B)** percentage decrease in the K concentration in the seed of these cultivars, with the percentage reduction in the oil/protein ratios in the seed, under a moderate K deficiency. Lines of best fit were:

(A) $Y = -10.38 + 1.67(r = 0.99)$

(B) $Y = 20.4 - 0.19(r = -0.3)$

Discussion

Differences in the efficiency of K use existed amongst the five soybean cultivars that were compared in this study. While Dodds was the most

Table 4. Root and stem weights and harvest indices of mature plants of cultivars grown under different K regimes

Cultivar	K regime (mg K pot^{-1})	Root weight (g plant^{-1})	Stem weight (g plant^{-1})	Harvest index[a]
Lee	112	9.6a (54)[b]	5.4a (41)[b]	1.1a
	375	10.2a (58)	7.6ab (58)	1.5a
	1875	17.7a	13.1b	1.3a
Forrest	112	7.9a (40)	6.4a (30)	1.1a
	375	15.6a (79)	8.9a (41)	1.3c
	1875	19.6a	21.5b	0.9b
Bragg	112	17.0a (80)	11.2a (64)	0.8a
	375	21.1a	15.3a (88)	1.2a
	1875	17.2a (81)	17.4a	0.9a
Dodds	112	6.6a (35)	6.6a (38)	1.0a
	375	15.4ab (83)	11.4ab (66)	1.3a
	1875	18.6b	17.3b	1.1a
Bossier	112	17.2a (78)	13.5a (47)	0.6a
	375	22.1a	18.5a (65)	0.9c
	1875	22.1a	28.6b	0.8b

[a] Harvest index was calculated as the ratio of seed weight to stem and pod weight.
[b] Relative weights (% of maximum) are given in parentheses.
Means within columns for each cultivar which are followed by different letters differ significantly ($P < 0.05$).

Table 5. Effect of K regime and cultivar on days after sowing to first flower and the degree to which plants had senesced when harvested

Cultivar	Maturity[a] group	K regime (mg K pot^{-1})	Days to first flower	Degree of plant senescence	
				Leaf abscission (% of leaves)	FMI[c]
Lee	VI	112	33.0 (±0.0)	17.5 (±3.8)	4.7 (±0.12)
		375	33.0 (±0.0)	71.2 (±18.1)	5.0
		1875	35.2 (±0.6)	100	5.0
Forrest	VI[b]	112	38.0 (±0.4)	40.7 (±13.6)	5.0
		375	38.0 (±0.6)	96.5 (±3.5)	5.0
		1875	37.5 (±0.30)	100	5.0
Bragg	VII	112	40.5 (±0.5)	40.3 (±10.9)	4.8 (±0.06)
		375	39.2 (±0.2)	70.9 (±19.0)	5.0
		1875	38.7 (±0.2)	92.7 (±7.2)	5.0
Dodds	VI	112	40.0 (±0.4)	22.5 (±13.9)	4.9 (±0.04)
		375	40.0 (±0.6)	47.0 (±13.7)	5.0
		1875	39.5 (±0.6)	87.5 (±12.5)	5.0
Bossier	VII	112	47.5 (±0.5)	20.4 (±8.7)	4.7 (±0.11)
		375	45.2 (±1.9)	71.0 (±)	5.0
		1875	47.0 (±0.0)	98.5 (±1.5)	5.0

Where appropriate, means are followed by standard errors.

[a] Cultivars are classified into maturity groups according to length of growing period: the larger the group, the longer the growing season (Shibles, 1975).

[b] Forrest behaves as a group VI cultivar in New South Wales.

[c] Fruit Maturity Index.

responsive to moderate increases in K supply (Table 2), the cultivar Bragg was the most efficient in its use of limited quantities of available K, in that it produced the highest absolute and relative seed yields under moderate and severe K-deficiency regimes (Table 1). In contrast, the cultivar Lee produced the lowest yields and was the least efficient. The basis for Bragg's greater efficiency was that it was able to produce more pods than Lee under reduced K supply, resulting in a greater seed number being produced relative to the high K regime. Bragg was able to produce more pods because its stem growth was less affected by K deprivation than was the stem growth of Lee (Table 3). Bragg had a lower harvest index than Lee so its higher seed yields at low K regimes were not due to increased dry matter transfer from stem and pod to seed. These advantages of Bragg would more likely be due to a larger leaf canopy that was supported by the larger stems which, in turn, would result in larger supplies of assimilates for vegetative and reproductive growth.

A larger supply of assimilate for vegetative growth is certainly indicated by the root weights of Bragg which were least affected by K supply (Table 4). The importance of root growth in K uptake is highlighted by the sensitivity analysis (Silverbush and Barber, 1983) of parameters used in simulating K uptake with a mechanistic mathematical model. This analysis indicated that predicted K uptake by a soybean plant was influenced more by changes in root length and root radius than changes in any other parameter. Predicted K uptake by the model closely agreed with measured K uptake for soybean cultivars in a range of soil conditions (Barber, 1984). The ability of Bragg and Bossier to maintain root growth under K-deficient regimes would improve their capacity for K acquisition under such conditions and contribute to their superior seed yields at low levels of K supply.

Potassium deficiency resulted in lower oil and higher protein percentages in the seed from all five cultivars (Table 3). The reduction in oil/protein ratios in soybean seed under K deficiency (Sale and Campbell, 1986) is thus a general response to K deprivation and occurs independently of genotype. However, the smallest percentage reduction in the oil/protein ratio under moderate K deficiency occurred in the seed of Bragg, which had the lowest percentage reduction in seed yield under moderate K deficiency (Table 1). The close relationship between reductions in seed yield and oil/protein ratios across cultivars under the moderately deficient K regime (Fig. 1A) provides additional evidence to support the proposition (Sale and Campbell, 1986) that there is a casual relationship between these two effects. It is unlikely that the decline in the oil/protein ratio was caused by the level of K in the seed *per se*, as there was a poor relationship between seed K levels and the decline in this ratio of seed reserves (Fig. 1B). High K percentages in seed may be a useful indicator of low efficiency in K use, as Lee had the highest K concentration in its seed at each K regime, yet it was the lowest yielding cultivar under reduced K supply.

An impairment in the normal processes or plant senescence occurred under K deficiency (Table 5), as evidenced by reduced leaf abcission in all cultivars and a slower rate of chlorophyll loss from pods in all cultivars except Forrest. The degree of this impairment was not related to K use efficiency as it was similar for Lee and Bossier. It has been suggested that the senescence of the soybean plant results in retranslocation of nitrogen from vegetative tissue to the developing seed, leading to the so-called 'self destruction' of the leaf canopy due to loss of nitrogen (Sinclair and de Wit, 1975). The impairment in soybean senescence under potassium deficiency may therefore be linked to a reduced capacity to retranslocate nitrogen from the leaves. This notion is consistent with the results of numerous studies (Ashley and Goodson, 1972; Haeder *et al.,* 1973; Hartt, 1969; Mengel and Viro, 1974) which have found that phloem translocation, the means by which leaf N is transported to the seed (Pate, 1976), was impaired under K deficiency. However, the higher protein concentrations in the seed at low K supply (Table 3) indicate that N availability in the seed was not restricted under K deficiency. This could be explained by nitrogen movement to the seed proceeding via an alternative route such as the xylem, which is the path for ureide and amino acid transport from roots to shoots (Streeter, 1979).

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