CP174

1580

pp1-15

Potash Review

Monthly communications by the International Potash Institute Berne (Switzerland)

Subject 16

Potash Fertilizers and Manuring
102nd suite.

No. 5/1985

The role of potassium in drought tolerance[1]

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Summary

Water stress effects are severe in semi-arid environments where droughts are unpredictable and cause instability in 'production'. Efforts are being made to improve drought tolerance by plant breeding but it will be some time before a solution is found.

Studies of the role of potassium in water uptake and the regulation of its loss through stomatal control in controlled experiments and field studies of yield response to potassium in limiting soil water environments indicate that it may improve water relations of plants and water use efficiency and maintain yields under water stress. Further study is needed of the effects of potassium in relation to drought in field experiments under diverse agroclimatic conditions on soils deficient and sufficient in potassium. Attention should be paid to the economics of potassium response under drought conditions.

1. Introduction

Drought is a complex and variable phenomenon and progress in drought research has been slow, though, judging from the number of workshops and symposia held and books published (*Turner* and *Kramer*, 1980; *Paleg et al.* 1981; *Mussell* and *Staples*, 1979; *Christiansen* and *Lewis*, 1982; *Irri*, 1981), the subject has been receiving priority attention. Progress via plant breeding will be very difficult (*Arnon*, 1980) and success is difficult in the near future.

Improved crop, soil and water management, by increasing root penetration, regulating transpiration, and improving water use efficiency can increase and stabilize yields under drought conditions.

The uptake of nutrients is one of the processes that is affected by water stress. Nutrient content in the leaf cell contributes to osmoregulation and is important in drought tolerance (*Pitman*, 1981).

This paper does not pretend to be a comprehensive treatment of the role of potassium, as there are a number of good reviews of the subject; it concentrates on a few selected cases.

[1] Approved as C.P. No. 174 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)

In an early review, *Achitov* (1961) distinguished between direct effects of potassium which either increase uptake of water or reduce its loss through plants or create any other internal condition of drought resistance and indirect effects when it increases yield without affecting water relations. It is the former which are of the greater interest to plant physiologists and which are discussed here. The effects of deficiency and sufficiency of potassium on a number of plant processes including stomatal movement and transpiration loss, translocation of metabolites, dry matter production and water use efficiency have been extensively studied. However, there are relatively few reports which deal with such effects on crops growing on sites where soil potassium is not at deficiency levels. Since soil moisture content affects the mobility of potassium in the soil and hence its availability to plants it is not easy to say whether responses to K fertilizer under dry conditions are due to effects on soil K availability or to improvement of drought tolerance by the plant.

2. Effects on roots and uptake of water

Baker and *Weatherley* (1969) showed that water movement from the outer cells of the root into the xylem is regulated by potassium. *Mengel* and *Simic* (1973) showed that the quantity of water moved upward by root pressure in decapitated sunflowers was reduced as K concentration in the rooting medium was lowered. *Rogaler* (1958) suggested that added K increased the permeability of root cells to water. The osmotic potential of root cells was lowered when K uptake was high, thus increasing water uptake (*Mengel* and *Kirkby*, 1980).

Adequate nutrient supply encourages root proliferation and deeper penetration so that water can be taken up from depth which is obviously advantageous under drought conditions. *Edward* (1981) in Illinois, found that maize roots penetrated 60 cm deeper when receiving K fertilizer, giving access to an extra 10 cm of water. Adequate nutrients decreased shoot/root ratio as well as improving the water uptake potential of plants (*Beringer* and *Trolldenier*, 1978), but *Brag* (1972) found with wheat and peas a negligible effect of potassium content of leaves on shoot/root ratios.

It has been suggested that efficient water uptake from the soil and its transport upwards are more important than stomatal conductance in determining drought resistance by sorghum and cotton (*Ackerson* and *Krieg*, 1977).

2.1 Loss of water by transpiration

Treatments which could reduce transpirational loss would be valuable in moisture stress. Early work reviewed by *Achitov* (1961) suggests that K supply reduces transpiration and increases water uptake and, further, improves water use efficiency. A number of observations of reduced transpiration with potassium were mentioned in a review by *Hoefner* (1971). *Wastermann* (1942) found with 12 species in water culture that potassium increased transpiration whereas calcium reduced it. In another experiment, he found that K reduced transpiration in plants with a restricted water supply. *Rogaler* (1958) with sunflower, wheat, barley, maize and clover grown in water culture and in soil in pot experiments found plants lacking K to transpire much water and that the addition of a small amount of K greatly reduced transpiration. *Brag* (1972) found transpiration reduced when enough K was applied to increase tissue K content (fig. 1) and recently, *Bo Larsen* (1981) showed that K reduced both day and night transpiration in Douglas fir (fig. 2). On the other hand, *Achitov* (loc. cit.) quotes reports of the reverse effect and

Christersen (1976) found that though K increased transpiration in pine, the plants survived drought better due to efficient osmoregulation. It thus appears that there is some uncertainty in these matters and that the results were affected by the initial K level in the soil.

2.2 Stomatal regulation

Mengel and *Kirkby* (1981) say that K plays a specific role in most plant species in opening and closing of stomata – a role which cannot be played by any other cation. This has been investigated and discussed by many workers. *Fisher* and *Hsia* (1968); *Humble* and *Raschke* (1971); *Trolldenier* (1971) *Skogley* (1976) showed that barley well supplied with K closed its stomata in 5 minutes and so reduced water loss while K deficient barley required 45 minutes (fig 3)

3. Effect on plant turgor

Using *Phaseolus vulgaris* in solution culture *Arneke* (1981) showed the effect of K on various aspects of water regulation (fig 4). He found that total water potential of upper and lower leaves reacted differently to K, plants well supplied

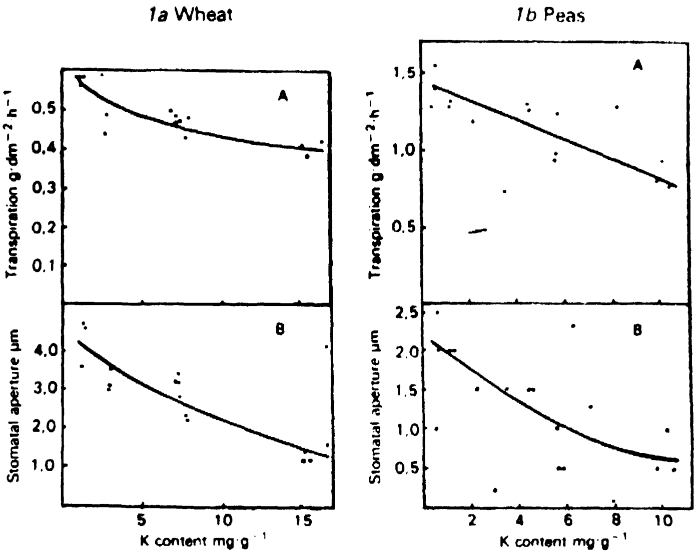

Fig. 1 The transpiration rate (A) and stomatal opening (B) of *Triticum aestivum* and peas, grown in a nutrient solution of different potassium concentrations. The stomatal opening is expressed as the width of the broadest part of the guard cells minus the same width of closed stomata. Abscissa: concentrations of potassium in the shoot (mg per g fresh weight). Each dot represents the transpiration per leaf area of ten plants in one growth vessel or the mean value of ten stomata (after *Brag et al.*, 1962).

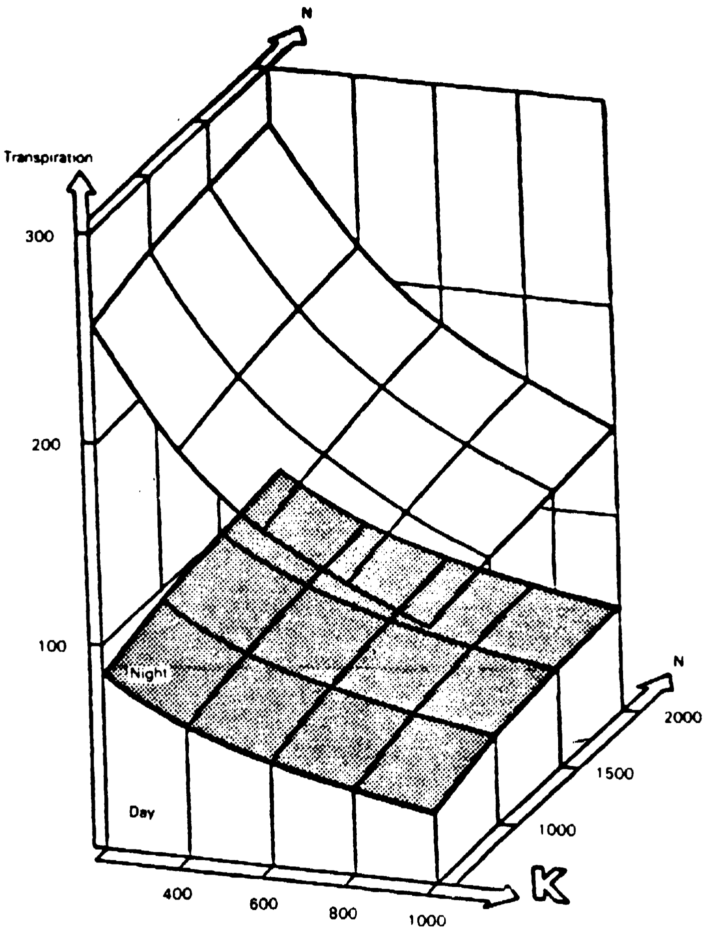

Fig. 2 The rate of transpiration (mg / g needle dry matter and hour) in relation to the N and K level (mg / 100 g needle dry matter) (after *Bo Larsen*, 1981).

having a higher water potential in the upper leaves than deficient plants, while the reverse held for the lower leaves. The mean osmotic potential of upper and lower leaves was lowered from −7.62 to −9.11 bar by increased K concentration. The turgor potential of lower leaves was not affected by K but that of younger leaves changed from 5.05 to 7.17 bar.

In his work quoted above *Bo Larsen* found that overall drought resistance (the sum of avoidance and tolerance) increased with increasing K level.

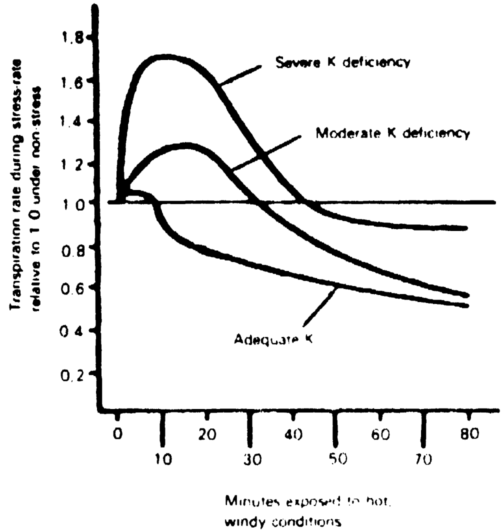

Fig. 3 K deficiency on barley results in a high and prolonged transpiration loss under hot, windy conditions (after *Skogley*, 1976).

4. Effects of dry matter production

Mengel and *von Braunschweig* (1972) found that at low soil moisture tension, about 17 mg/100 g exchangeable K was needed to produce 6 g dry matter compared with 46 mg at high soil moisture tension, concluding that higher levels of exchangeable K are needed under stress conditions. The effect is explained by the greater mobility of soil K under moist conditions (fig. 5). However, it appears that there was a large response to K even at field capacity, suggesting that the soil was actually deficient in K.

5. Effects on maturity

Early maturation is advantageous in drought avoidance. In a review by *Darst* (1980) it is stated that application of K to potassium deficient maize hastened silking and lengthened the grain filling period. Effects on soybean were inconsistent.

6. Effects on yield

There are many reports of yield response to K fertilizer on soils low in K but there are few reports of response under dry conditions. Indeed, *Mengel* and *Kirkby* (1980) suggest that such responses occur when N and water are not limiting. If the main effect of water shortage is to reduce availability of K in the soil, then K

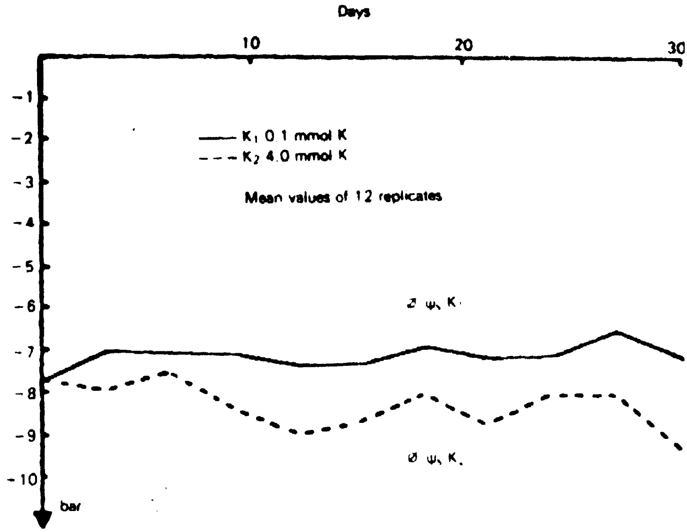

Fig. 4a Mean osmotic potential (Ø ψ_s) of leaves with two levels of potassium nutrition (lower and upper leaves combined) (after *Arneke*, 1981).

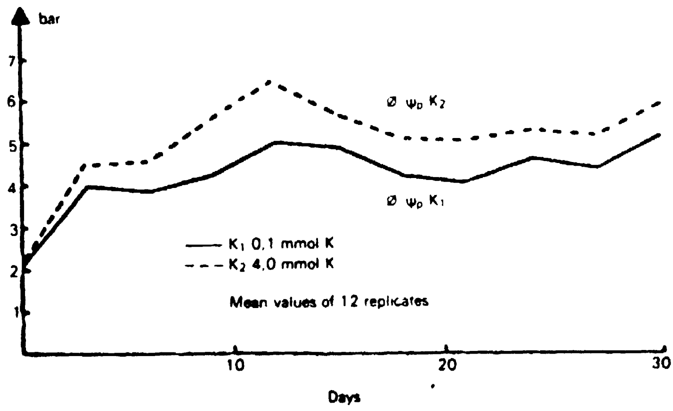

Fig. 4b **Mean turgor potential (Ø ψ_p) of leaves with two levels of potassium nutrition (lower and upper leaves combined) (after *Arneke*, 1981).**

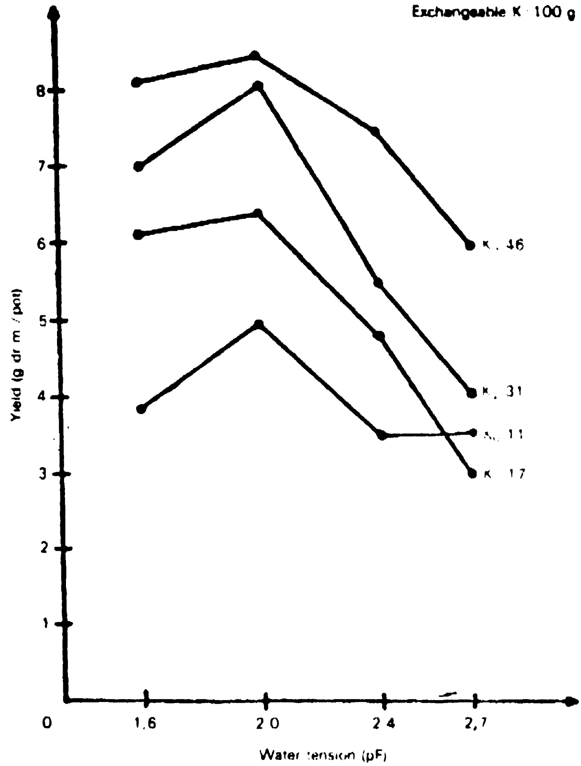

Fig. 5 Importance of soil moisture and exchangeable potassium in soil for the growth of maize seedlings (after *Mengel* und *Braunschweig* 1972)

fertilizer would be expected to ameliorate the apparent shortage of soil K and to increase yield. Response to K would vary with the year, depending on rainfall and this is seen in results reported by *van der Paauw* (1958).

Van der Paauw compiled a report on fertilizer response by potato, wheat, grass and beans over the 15 years from 1935 to 1949 Crops differed in their responsiveness to K and the optimum level differed with crop If there were more than 46 rainless days after planting, potato yield declined in proportion to the number of rainless days on the Ko treatment but was maintained if the K supply was good (fig. 6 and 7). K uptake was reduced in dry years. Wheat was much less responsive than potatoes and here K increased yield only in dry years (fig. 8). Such effects were not evident with grass and beans.

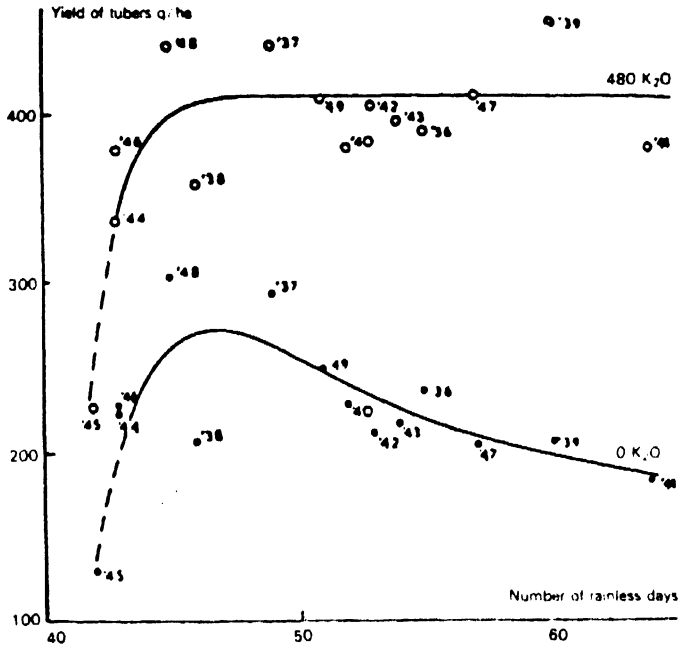

Fig. 6 Relation between the number of rainless days (May—July) and the yield of potato tubers in the presence and absence of heavy applications of potash (480 and 0 kg K_2O per ha) (after *van der Paauw,* 1958).

Boulay (1976) found that drought resistance in vines was increased by a heavy preplanting application of K. *Beringer* and *Trolldenier* (1978) state that crops liberally treated with K remain turgid and green for a longer time

Water stress also occurs if soil water is excessive and *Barber* (1967) recorded responses by maize to K under both dry and wet conditions in a 3 year experiment (table 1). Later (1971) he found that K response by soybean depended on rainfall in the 12 weeks following planting (fig. 9); if rainfall was below 380 mm, response to K was nearly linear.

On soils of medium K availability in Ohio, response by maize in dry years was as much as 2700 kg/ha compared with only 198 kg/ha in years with optimum rainfall (*Johnson,* 1979). *Hernando* and *Orihuel* (1977) found tomatoes to be more K responsive with drier watering schedules.

7. Water use efficiency

Transpiration coefficient (water consumed/D.M. produced) can be reduced either because yield is increased or because water consumption is reduced or both. The former seems to be the case in work reported by *Blanchet et al.* (1962)

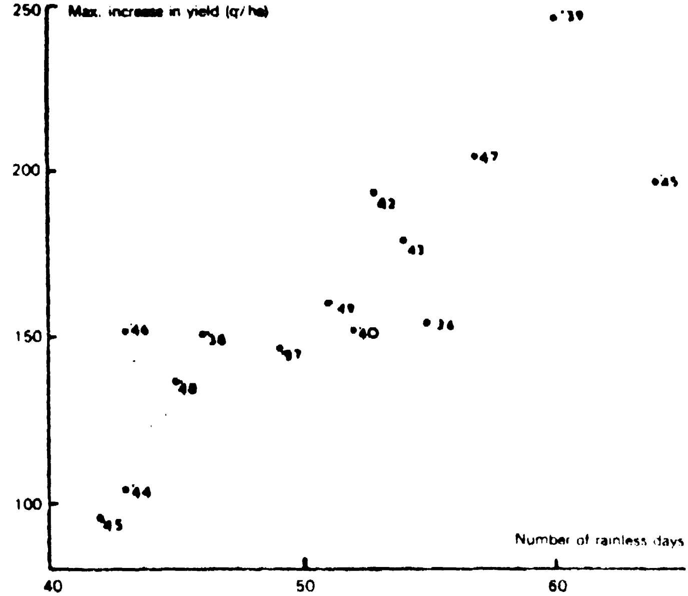

Fig. 7 Relation between the number of rainless days (May–July) and the maximum increases in yields of potato tubers obtained after applications of potash (after *van der Paauw,* 1958)

who found water use efficiency to be high in lucerne when tissue K content was 1.3% K but low when it was 0.8% or less, but this may have been due to restriction of D.M. production by K deficiency (fig. 10).

In *Herwig's* (1970) work quoted by *Hoefner* (1971) increasing K increased water consumption in the early stages of growth of oats but the greater accumulation of dry matter resulted in lower transpiration coefficients (table 2). However, at harvest, transpiration coefficients were similar in both treatments. Lower transpiration coefficients in flax well supplied with K were observed by *Linser* and *Herwig* (1968) but this was due to greater D.M. accumulation rather than reduced water consumption (table 3). On the other hand, high K plants at low soil moisture consumed less water giving lower transpiration coefficients. High K plants (2.6% K in tissue) at 40% field capacity produced much the same D.M. as low K plants (0.4%) at 80% F.C. The former also consumed less water. This, showing that high tissue K may reduce water consumption, is interesting evidence.

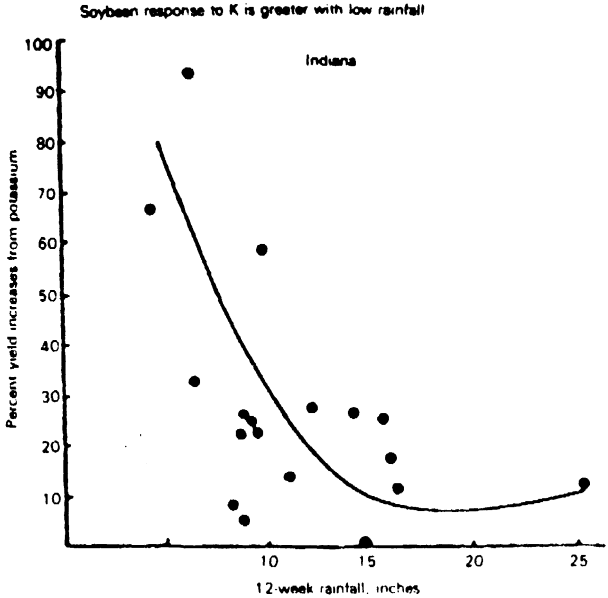

Fig. 9 The less the rainfall for the 12-week period after planting the greater the percent yield increase of soybeans from K on a low K soil (after *Barber*, 1971)

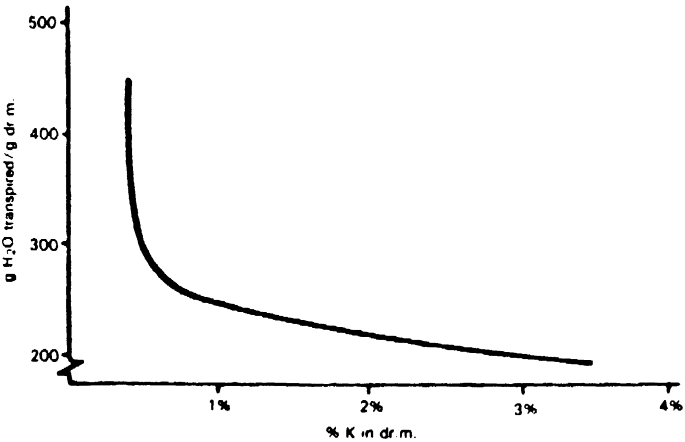

Fig. 10 Relationship between K content in lucerne leaves and transpiration/g dry matter produced (after *Blanchet et al.*, 1962).

Table 2 Influence of K on the transpiration coefficient of oats (*Herwig*, 1970: unpublished data)*

Growing period	K_1 yield (g)	Water consumption (ml)	Transpiration coefficient	K_2 yield (g)	Water consumption (ml)	Transpiration coefficient
4–6 to 19–6	21.6	6 435	298	28.8	8 042	279
19–6 to 27–6	16.8	4 893	291	20.3	5 309	282
27–6 to 3–7	10.8	4 717	437	10.1	5 145	509
22–5 to 31–7	75.0	26 742	393	84.1	30 269	393
(Harvest)	(36.9 grains)		725	(40.9 grains)		740
	(38.1 straw)		702	(43.2 straw)		701

K_1 = 0.42 g K_2O/pot K_2 = 20 g K_2O/pot Water supply = 80% water capacity

* After *Höfner*, 1971

Table 3 Influence of K nutrition on the transpiration coefficient of flax at two water regimes (*Linser* and *Herwig*, 1968)

	40% field capacity		80% field capacity	
	−K	+K	−K	+K
Dry matter (g).	58.5	65.6	64.6	80.4
Leaf-K (% dry matter)	0.4	2.6	0.4	2.9
Water consumed l/pot	34.0	30.1	40.3	40.5
Transpiration coefficient	581	459	624	504

8. Looking ahead

It seems well established that potassium is important in stomatal regulation and has effects on water potential but most of the data come from short term experiments in pots or nutrient solution and as *Beringer* and *Trolldenier* (1978) say relationships established under controlled conditions may have little relevance to field conditions. Effects are difficult to interpret because crops are more sensitive to water stress at certain stages than at others. It does seem to be important to collect more data from field experiments and it is important that such experiments should cover soils with low, medium and high K. Further work should include full growth analysis and assessment of the economics of treatment.

Looking ahead: sum up

I

- Results from controlled pot and nutrient culture experiments are mostly not applicable to field conditions
- Further experimentation in the field is necessary on
  - different soil types
  - soils low and high in exchangeable K
- Close monitoring of soil and climate essential

II

1. Roots and root growth
2. Water uptake
3. Transpiration
4. Maintenance of turgor
5. Stomatal conductance

III

1. LAI LAD CGR
2. Dry matter production
3. Water use and water use efficiency
4. Maturity
5. Yield and yield components

IV

- Correlating results from II and III
- Comparison of responses to K with other factors affecting water relations
- Economics of response to K

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