
Potassium and Abiotic Stresses in Plants

SURYA KANT AND UZI KAFKAFI

*The Hebrew University of Jerusalem, Faculty of Agricultural, Food and
Environmental Quality Sciences,
Rehovot, Israel*

Introduction

Potassium is the cation present in the plants in concentrations ranging from 50–150 mM in the liquid parts, the cytoplasm and the vacuole (Leigh and Wyn Jones, 1984). The concentration of K^+ in the cytoplasm is usually constant about 50 mM, (Leigh, 2001) while the concentration in the vacuole may vary quite substantially. Under cold stress plants performs better when the K^+ concentration in the plant is usually in the category of “Luxury consumption concentration range” (Bergmann and Bergmann, 1985). Kafkafi (1990) have suggested that accumulation of K^+ by plants before initiation of stress is not luxury but rather an insurance strategy to allow the plant survive a sudden environmental abiotic stress. When a short supply in K^+ exists in the early vegetative stages of plant growth, the plant whole structure suffers and may express itself in lodging, and frost damage to much higher proportions that expected from fully healthy plant. The following review is trying to emphasize that accumulation of K^+ in the plant prior to stress events like water shortage, lodging, cold stress and salinity stress is a survival policy for the plant.

Potassium and Water Stress

The major limiting factor for crop yield in arid and semi-arid regions is the amount of soil moisture available to plants during the growing season. Soil moisture influences K^+ uptake by plants by affecting root growth rate and the rate of K^+ diffusion in the soil towards the root. Mackay and Barber (1985) tried to resolve the effects of actual root growth as compared with the K^+ diffusion rate as affected by moisture. At the lower side of the optimal soil moisture content increasing soil moisture increased the effective diffusion coefficient of K^+ and therefore increased K^+ uptake. Increasing the moisture content above the optimum resulted in slow root growth due to oxygen

shortage. The reduction in root elongation was reflected in lower K^+ uptake. The rate of root elongation is a crucial parameter in the uptake of nutrients that are strongly adsorbed to the soil and their concentration in the soil solution is usually very low (Kafkafi, 1991). Combined effects of low temperatures and low moisture can be alleviated by increasing the concentration of K^+ in the soil (Kafkafi, 1990).

Potassium (K^+) has substantial effect on enzyme activation, protein synthesis, photosynthesis, stomatal movement and water-relation (turgor regulation and osmotic adjustment) in plants (Marschner, 1995). Increased application of K^+ has been shown to enhance photosynthetic rate, plant growth, yield and drought resistance in different crops under water stress conditions (Sharma *et al.*, 1996; Tiwari *et al.*, 1998; Yadav *et al.*, 1999; Egilla *et al.*, 2001). K^+ -fed plants maintained higher leaf water potential, turgor potential and relative water content and lower osmotic potential as compared to untreated plants of *Vigna radiata* (Table 1) (Nandwal *et al.*, 1998), maize (Premachandra *et al.*, 1991), and wheat (Pier and Berkowitz, 1987; Sen Gupta *et al.*, 1989) grown under water stress. Nodulation, nitrogenase activity and dry matter yield increased with incremental K^+ supply in broad bean grown at moisture level of only 1/4 of field capacity (Abd-Alla and Wahab, 1995). K^+ is predominant in accumulating solute during drought in tropical grasses (Ford and Wilson, 1981), soybean (Itoh and Kumura, 1987) and maize (Premachandra *et al.*, 1991) and significantly contributed to osmotic adjustment.

The function of stomata is to control water loss from the plant via transpiration. When K^+ is deficient, the stomata can not function properly and water losses from plant may reach damaging levels (Gething, 1990). This has been demonstrated in field experiment in barley in which plants were exposed to hot wind (Fig. 1). This caused an immediate increase in transpiration rate, more severe in K^+ deficient plants which took long time to

Table 1: Effect of K^+ on water and osmotic potentials and relative water content in *Vigna radiata* leaves under water stress condition.

K^+ application (mmol dm ⁻³)	Water potential (-MPa)		Osmotic potent (-MPa)		RWC	
	control	stress	control	stress	control	stress
0.65	0.55	0.84	1.34	1.55	80.9	72.3
3.20	0.47	0.78	1.30	1.76	84.2	74.7
4.50	0.50	0.79	1.22	1.73	86.1	76.9

Source: Nandwal *et al.*, 1998

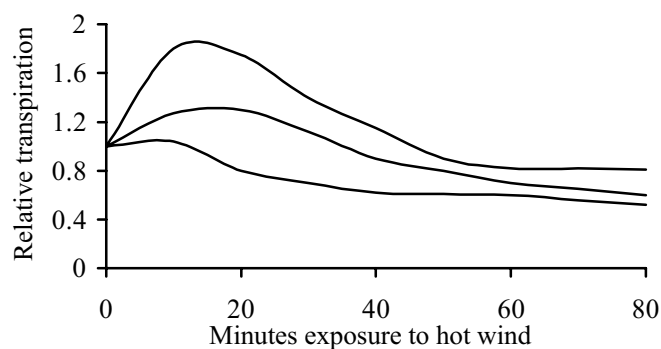


Fig. 1: Control of water stress effects by K^+ supply
Source: Gething, 1990

react by closing stomata, while the K^+ supplied plants respond quickly in closing stomata and preserved internal moisture. The stomata close in response to water stress, thereby reduction in carboxylation efficiency of the chloroplasts. Stomatal closure for long time leads to photoreduction of O_2 to toxic O_2 species. This effect of drought can be more severe when plants are grown with inadequate supply of K^+ , as K^+ itself is required for stomatal movement (Humble and Raschke, 1971). The larger K^+ requirement of water stressed plants can be related to the protective role of K^+ against stress induced photo-oxidative damage. The protective role of K^+ in plants suffering from drought stress has been well documented (Pier and Berkowitz, 1987; Sen Gupta *et al.*, 1989). Under water stress, the photosynthetic efficiency of plants is reduced drastically (**Table 2**) as a consequence of chloroplast dehydration (Sen Gupta and Berkowitz, 1987; Berkowitz and Kroll, 1988). The chloroplasts lose large amounts of K^+ with a simultaneous decrease in photosynthesis. Hence, application of more K^+ than that usually applied for irrigated plants was necessary to maintain photosynthetic activity (Sen Gupta *et al.*, 1989). In

Table 2: Effect of water stress and K^+ supply on net photosynthesis rate in wheat leaves.

K^+ application (mM)	Photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)		
	Water stress in leaves		
	low	mild	severe
0.2	38	11	2
2.0	47	42	21
6.0	46	45	28

Source: Sen Gupta *et al.*, 1989

wheat experiments, Pier and Berkowitz, (1987) observed 66-113% higher photosynthetic rates in plants fertilized with above normal K^+ than those under standard fertilization, indicating that leaves of plants grown in very high internal K^+ levels have partially reversed the dehydration effects on photosynthesis.

The plant's K^+ status also affects the ease with which it can extract water from soil. Plants adequately supplied with K^+ can utilize the soil moisture more efficiently than K^+ deficient plants (El-Hadi *et al.*, 1997). Cell elongation, the basic event of plant growth, is initiated by wall relaxation, causing osmotic potential-driven water uptake and turgor-driven cell expansion, consequently enhanced by K^+ application (Lindhauer, 1989). Improved cell expansion and growth, set up a pressure gradient between the root and its surrounding which causes water to be taken up (Gething, 1990). Lindhauer (1985) showed that K^+ fertilization besides increasing dry matter production and leaf area development greatly improved the retention of water in the plant tissues even under conditions of severe water stress. The K^+ is found in the plant cell in two distinct compartments (Leigh, 2001), the cytosol and the vacuole. It is now clear that K^+ transport through plant cell membranes is done through specific protein channels (Maathuis *et al.*, 1997). Not only K^+ but also water moves through membranes in pores that are now called "aquaporin" (Steudle, 2000). Any shortage of water cause plants to lose turgor. K^+ -deficient roots have lower sap osmotic pressure and turgor. Stretch activated K^+ channels could provide turgor-responsive transport pathway for K^+ (Leigh, 2001).

Potassium and Salinity

Saline soils generally have higher concentrations of Na^+ than K^+ and Ca^{2+} this may result in passive accumulation of Na^+ in root and shoot (Bohra and Doerffling, 1993). High levels of Na^+ can displace Ca^{2+} from root membranes, changing their integrity and thus affecting the selectivity for K^+ uptake (Cramer *et al.*, 1985, 1987). Xylem loading of K^+ is regulated by K^+ uptake from external solution (Engels and Marschner, 1992). This indicates that Na^+ salinity beside reducing the K^+ uptake rate, also interfere to a greater extent in K^+ translocation from root to shoot, which results in a lower K^+ shoot content and a higher K^+ root content (**Table 3**). The inhibitory effect of salinity on K^+ translocation was stronger with low K^+ concentration in the nutrient solution, when compared at two levels of K^+ supply in maize seedlings i.e. 0.1 and 1 mmol/L (Botella *et al.*, 1997). Thereby, salinity did not affect root dry weight,

Table 3: Concentration of Na⁺ and K⁺ (mmol kg⁻¹ DW) in shoot and root of 19 days maize seedlings in response to salinity and potassium applications

	NaCl (1 mM) KNO ₃ (mM)		NaCl (100 mM) KNO ₃ (mM)	
	0.1	1	0.1	1
		Shoot		
K ⁺	630	1310	426	731
Na ⁺	33.8	34.4	2128	1625
K ⁺ /Na ⁺ ratio	20.8	42.5	0.21	0.45
		Root		
K ⁺	396	689	630	813
Na ⁺	89	72	1447	1203
K ⁺ /Na ⁺ ratio	4.48	9.82	0.44	0.68

Source: Botella *et al.*, 1997

but low level of K⁺ in the nutrient solution significantly reduced shoot dry weight. Similar responses have been found in spinach plants, which responded to an increasing K⁺ concentration, reducing the differences in shoot growth between plants grown in low and high salinity (Chow *et al.*, 1990). The salinity-induced inhibition of shoot growth at low level of K⁺ in root medium was attributed to the effect of K⁺ deficiency and/or Na⁺ toxicity on the plants.

Any stress that is causing K⁺ leakage out of the cell will eventually lead to reduction in cell growth. Ben-Hayyim *et al.* (1987), have shown that growth was linearly correlated with K⁺ content in callus cells of citrus roots. Increasing levels of Na⁺ in the external medium reduced K⁺ in the cell. Salt tolerant cells were able to hold the K⁺ in the vacuole against leakage when Na⁺ was increased in the external medium. Termaat and Munus (1986) also suggested that salt stress might result in limited transport of essential nutrients to the shoot. They have shown that the net transport of K⁺, Ca²⁺, Mg²⁺ and total nitrogen to the shoot was lower in NaCl-grown plants.

Salt tolerance has been partially linked to the regulation of leaf Na⁺ concentration (Taleisnik and Grunberg, 1994) and to selectivity for K⁺ over Na⁺ (Cuartero *et al.*, 1992). The plants have different pathways to avoid Na⁺ from reaching to the leaves: by controlling Na⁺ influx at the plasmalemma of root cells (Jacoby and Hanson, 1985); by removing Na⁺ from the xylem stream and sequestering Na⁺ in parenchyma cells of roots and lower part of stem

(Johanson and Cheesman, 1983); by retranslocating Na^+ from shoots to roots via phloem (Jacoby, 1979). In suspension cells of *Brassica napus*, increased tolerance to NaCl arises by alteration of K^+ uptake system (Lefebvre, 1989); tobacco cell cultures show enhanced K^+ uptake capacity when adapted to NaCl (Wataad *et al.*, 1991). Salt tolerant cultivars of wheat translocate less Na^+ from roots to shoots than salt sensitive genotypes (Schachtman *et al.*, 1989). The differences within plant species in their capacity to satisfy metabolic requirements for K^+ , higher K^+ fluxes and lower Na^+ fluxes in the presence of salinity is related to differences in salt tolerance (Cerda *et al.*, 1995). Taleisnik and Grunberg, (1994) observed that, K^+/Na^+ selectivity ratio was higher in tomato cultivar 'Edkawi' than in 'Ace' (Table 4). The difference between the cultivars was due to greater replacement of K^+ contents by Na^+ in all the plant parts of cultivar Ace. This indicates that Edkawi has higher capacity to retain K^+ under salinity, a feature that may contribute to its salt tolerance.

Photosynthetic capacity and quantum yield of oxygen evolution were sharply reduced under high salinity condition with decreasing K^+ supply in spinach plants due to malfunctioning of photosystem II (Chow *et al.*, 1990). Their results suggest that there was higher K^+ requirements for shoot growth under high salinity (250 mM NaCl) than low salinity (50 mM NaCl) conditions. By increasing total salt content with addition of K^+ supply to roots one can

Table 4: Net uptake rates of K^+ and Na^+ in whole plant and translocation to shoot ($\mu\text{mol g}^{-1}$ root FW day^{-1}) in tomato cultivars grown for 10 days under different salt treatments

Treatment	Ace		Edkawi	
	whole plant	stem	whole plant	stem
		K^+		
Control	96.7	64.5	108.2	94.3
25 mM NaCl	36.1	25.0	69.9	60.6
100 mM NaCl	37.7	41.5	60.4	53.0
		Na^+		
Control	3.3	2.9	5.5	4.2
25 mM NaCl	43.6	29.3	49.5	37.7
100 mM NaCl	69.2	56.4	53.5	41.0
		K^+/Na^+ ratio		
25 mM NaCl	6.7	5.4	11.6	13.6
100 mM NaCl	18.7	23.9	38.0	43.5

ameliorate reductions in plant and shoot biomass imposed by an increase in salinity and overcome Na^+ toxicity. The higher Na^+ accumulation in leaves may help in turgor maintenance, but cannot substitute for adequate K^+ levels in leaves, because K^+ is specifically required for protein synthesis and enzymes activation (Marschner, 1995). Therefore, maintenance of adequate cytoplasmic levels of K^+ and K^+/Na^+ ratios in the cell is essential for normal functioning under saline conditions (Greenway and Munns, 1980; Chow *et al.*, 1990). Addition of K^+ to a saline culture solution has been found to increase the plant dry weight and K^+ content with a corresponding decrease in Na^+ content in rice and bean plants (Muhammed *et al.*, 1987; Benlloch *et al.*, 1994).

Since Na^+ in most of the natural salinity cases is accompanied with chloride, competition with nitrate was suggested as a practical agricultural method to prevent salt damage to tomato (Kafkafi *et al.*, 1982), and Avocado (Bar *et al.*, 1997). A general review on Cl behavior in plants is reported by Xu *et al.* (2000).

Potassium and Cold Stress

Chilling effects in the range of +5 to +10 °C are commonly occurring in plants of warm climates. The temperature decline results in sudden change in membrane fluidity; this change is specific to each cell and dependent on the relative composition of the various phospholipids (Beringer and Troldenier, 1980). The balanced proportion of fatty acids is also involved in reducing the plant sensitivity to chilling. The higher the ratio of unsaturated/saturated fatty acids in the cell membrane the more tolerant is the tissue to low temperatures (McKersice and Leshem, 1994). Maximum growth response and chilling resistance in tomato, eggplant and pepper plants with the addition of K^+ were associated with increase in phospholipids, membrane permeability and improvement in biophysical and biochemical properties of cell (Hakerlerker *et al.*, 1997).

The effect of increasing K^+ concentration on yield and chilling damage was studied by Yermiyahu and Kafkafi, (1990) in the carnation cultivar standard (*White Candy*) grown on a sandy loam soil. The percentage of stem brittle incidence increased 5-6 weeks after cold night events below 8°C followed by clear sunny days. The weekly loss of broken stems was lower with the increasing K^+ concentration in the irrigation water (**Fig. 2**). When the K^+ in the 5th leaf from the apex was below 4%, an overall seasonal average

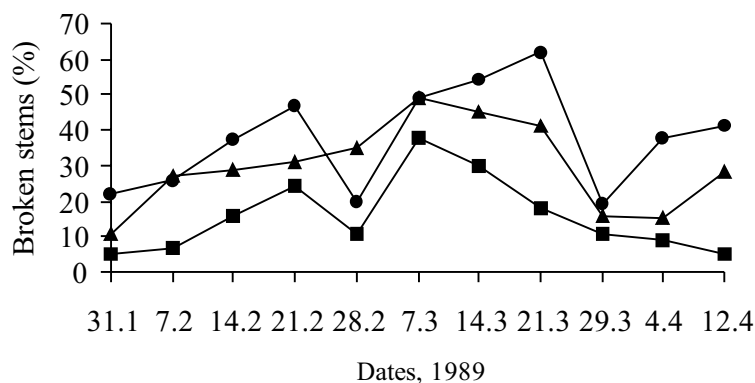


Figure 2 : Broken stems of carnation cv. *White Candy* during the growing season on three levels of K⁺ in irrigation water: —●93; —▲252; —■378 g K⁺ m⁻³.
Source : Yermiyahu and Kafkafi, 1990

of about 31% stem brittle was recorded with heavy losses to the farmer. It was only 18% loss when the K⁺ content in the plant 162 days after planting was greater than 4%. Stem brittle susceptibility was significantly reduced by supplying high levels of potassium to the irrigation water at the same level of total N concentration from the beginning of the growing season. As long as the temperature did not drop below 12°C the high doses of K⁺ would have been regarded as “Luxury” or waste. The economical saving to the farmer after only one night event of low temperature is more than the entire price paid to the fertilizer in the whole season. The fact that the K⁺ effect is detected only about 5 weeks after the cold events probably explains why such K⁺ effects are not reported more frequently. The continuous supply of potassium at a much higher concentration in the soil solution than that regarded as “sufficient” for maximum yield might prove as an “insurance” against unexpected climatic events.

The susceptibility to such cold events is also dependent on the plant variety. K-stressed potato plants may be more susceptible to frost. Applying high rates of K⁺ fertilization can effectively increase the frost resistance of some of the frost-sensitive genotypes (Roberts and Mc-Dole, 1985). The effects of nitrogen and potassium on spikelet sterility induced by low temperature (15/15°C: day/night, for two duration of 3 and 5 days) at reproductive stage of two rice cultivars were studied by Haque (1988). The spikelet sterility decreased with the increase of K⁺ supply and increase of K/N ratio in the leaves of cultivars *Fujisaka-5* and *IR36*. However, the effect of K⁺ in reducing the spikelet sterility was more conspicuous in cultivar *Fujisaka-5* than *IR36*

(Fig. 4). The changes in varietal response to chilling effects might be due to differences in the fatty acid composition of their root membranes. The root membrane composition have effects on the rates of ion and water transport in the root, carbohydrate content of the plant or translocation of nutrients and metabolites in the plant (Marschner, 1995).

The effect of soil temperature around the crown node of wheat on growth and nutrient translocation was studied by Boatwright *et al.* (1976). Careful chilling of the crown zone only enabled them to demonstrate that the cold zone restricted translocation of ^{86}Rb and, by inference, also of potassium to the top (Fig. 3). It is the actual transport through the chilled zone that influenced the wheat yield. Since the roots and the top were exposed to optimal temperatures it is probable that the changes in membrane fluidity is the cause for low transport of ions through that barrier. The effects of the high K^+ content of the cell in increasing frost tolerance have also been related to regulation of osmotic and water potential of the cell sap and reduction of electrolyte leakage caused by chilling temperature (Beringer and Troldenier, 1980; Singer *et al.*, 1996).

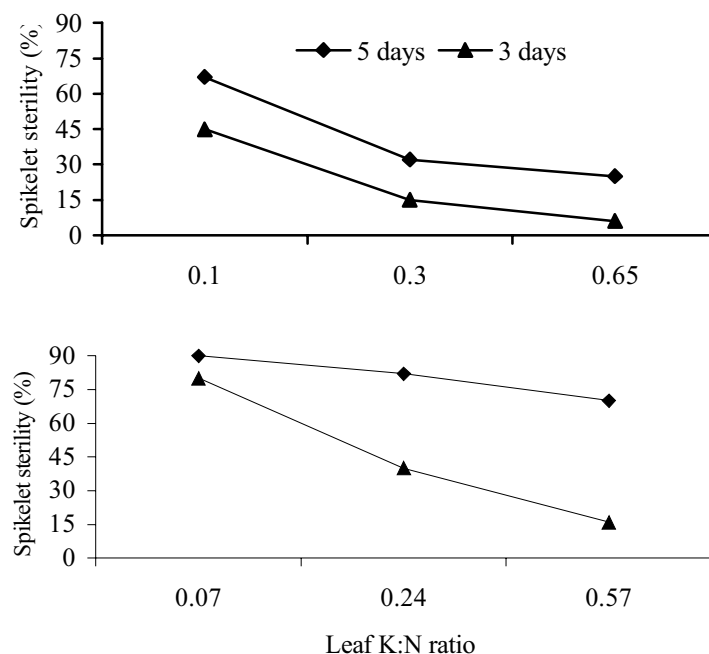


Figure 3: Relationship between leaf K:N ratio and spikelet sterility induced by low temperature (15°C) at booting stage of rice cultivars *Fujisaka 5* (A) and *IR 36* (B). Source: Haque, 1988

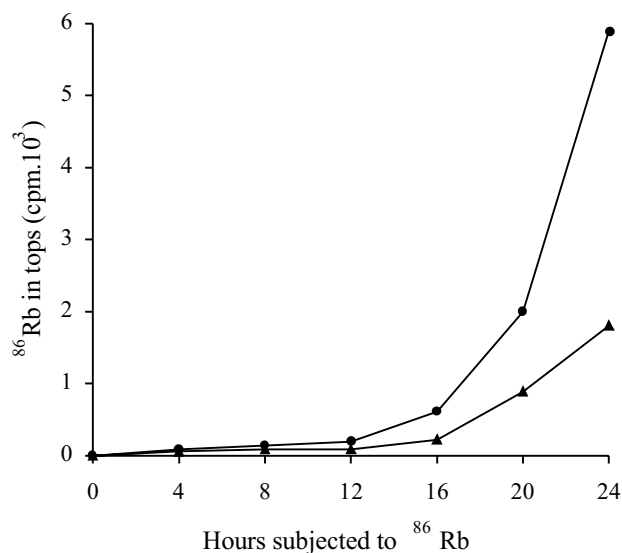


Figure 4: Effect of crow-zone temperature on translocation of ^{86}Rb from roots to tops of wheat at: —●22°C; —▲11°C

Source: Boatwright *et al.*, 1976

Potassium and Lodging

Lodging is the displacement of stems from their upright position. It may be permanent or partly reversible, depending upon the extent of bending. Two types of lodging are recognised: a) *stem lodging* – bending of lower culm internodes, b) *root lodging* – leaning from the crown due to disturbance of root system (Pinthus, 1973). This problem generally occurs in cereal crops. Heading and early grain development stages are the crucial stages of yield loss by lodging. It may result from the interactive effects by environmental and soil conditions, plant type and nutrient management. In K-deficient plants, the diameter of stem is reduced making the plant susceptible to lodging. Sclerenchyma fiber cell and woody parenchyma cells in the stems of K-deficient plants form thin and poorly lignified cell walls resulting reduced stem diameter (Mulder, 1954; Wakhloo, 1975)

Increase in the thickness of sclerenchyma tissue layers by optimum potassium nutrition has been reported for rice (Vaithilingam and Balasubramanian, 1976). Cross section of wheat internode (Plate 1) show that plants of better K^+ nutrition has thick stalk wall. Higher stem stability and improved thickness might be associated with a less senescing pith parenchyma

and more active general defense mechanism under optimum K supply (Abney and Foley, 1971).

The addition of K^+ reduces the per cent of senescent stalks and stalk lodging in corn grown on K-deficient soils (Plate 2). Crushing strength and rind thickness increases with K^+ application. The influence of K^+ on senescent stalks varies with hybrids (Welch and Flannery, 1985). The high yielding corn hybrids have the ability to translocate the photosynthates from leaves and stalk to grains. They may have greater lodging probably due to increased mechanical stress on the stalk by greater ear weight and photosynthate translocation from stalk structurally weakens the stalk and premature parenchyma breakdown (Campbell, 1964; Liebhardt *et al.*, 1968). Measurements made by Campbell (1964) indicated that there was an inverse relationship between ear weight and soluble solids in stalk juice. Potassium sufficient plants produce photosynthate at a faster rate for longer time than K-deficient plants. This extra photosynthate would help in preventing the soluble solid concentration in stalk from becoming too low during grain development (Welch and Flannery, 1985). Potassium deficiency increases respiration and transpiration rate and decreases photosynthesis, accumulation of starch and cell wall substances, such as holocellulose, that influence stem strength in rice. A close correlation exists between the K^+ content of basal part of the culm and the breaking strength of the stem, implying that proper K^+ nutrition is closely associated with lignification of sclerenchyma cells and vascular bundles and strengthening culms, thereby, increase lodging resistance (Datta and Mikkelsen, 1985). Melis and Farina (1984) conducted experiment on lodging susceptible maize cultivar. The percentage of total lodging reduced with the incremental dose of K^+ from 50 to 200 kg ha⁻¹ (Fig. 5). The root lodging was higher without K^+ application, but stalk lodging was significantly lower. Low incidence of stalk lodging in control plots was associated with poor ear development and consequently absence of sink to translocate photosynthates. Lodging resistance is primarily governed genetically and adequate potassium application further decrease the lodging tendencies in different crop varieties and hybrids (Parks, 1985). Role of potassium for increased resistance to lodging has been well documented in different crops such as corn (Welch and Flannery, 1985, Csatho, 1991); rice (Datta and Mikkelsen, 1985); wheat (Beaton and Sekhon, 1985, Khurana and Bhaya, 1990) and oilseed rape (Sharma and Kolte, 1994).

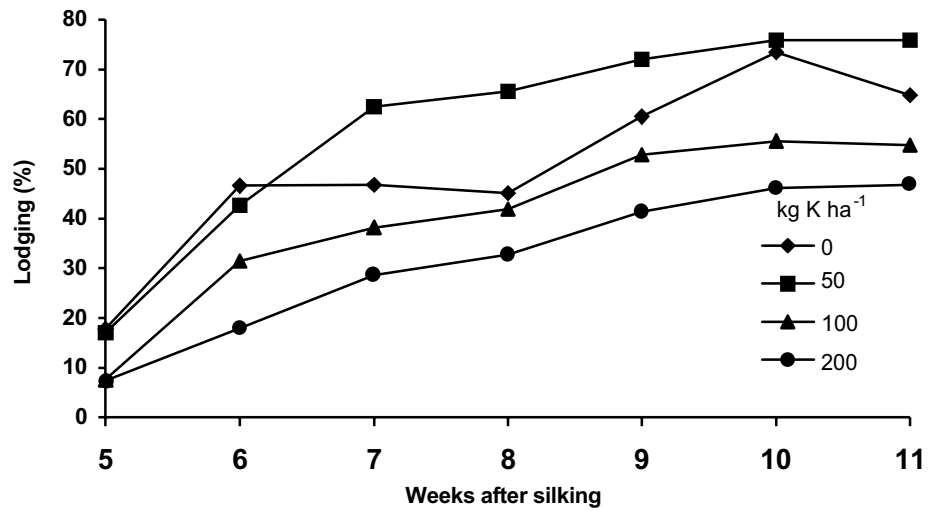


Figure 5: Effect of K⁺ application on lodging in a susceptible maize cultivar. Source: Melis and Farina, 1984

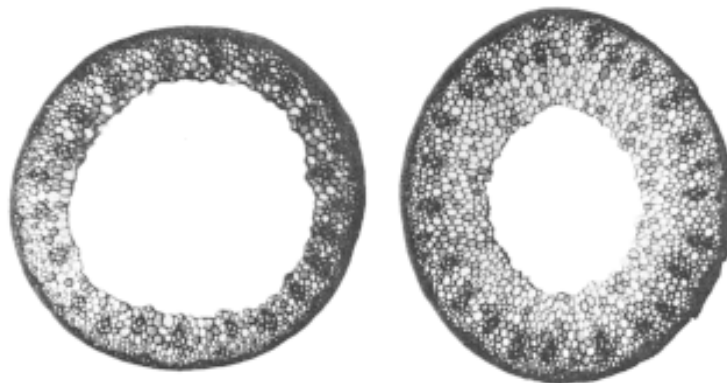


Plate 1: Cross-section of 3rd internode of wheat plant with low (left) and high (right) K⁺ nutrition.



Plate 2: Effect of K⁺ supply on maize plant.

Conclusions

Potassium is needed at high concentrations inside the plants from early stages of vegetative growth phase. High internal K^+ concentration can dampen extreme sudden environmental events like cold, frost, late season rains, high salt stresses and heat waves. The whole structure of proteins and protein activity needs high concentrations of K^+ in the cytosol for optimum plant functions. However, to withstand stresses that causes osmotic stress and unusual physical burden, prior accumulation of K^+ is shown to reduce the damage to plants.

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