

CHAPTER - I

REVIEW OF LITERATURE ON POTASSIUM

A. INTRODUCTION

To provide adequate food for increasing population is a serious problem in front of agriculturist and scientists. This problem is especially acute in over populated Asian countries like India and China. In these countries there is a tremendous pressure on agricultural system. Severity of this problem can be partially minimized by modifying our cropping system in such a way that the crops can utilize properly the available resources in order to give higher yields. Plant nutrition forms an important aspect of plant production because high productivity can only be achieved if plants are properly fertilized. The beneficial effect of adding mineral elements to soil to improve plant growth has been recognized in agriculture for more than 2,000 years. By the end of nineteenth century, especially in Europe, large amount of potash, superphosphate, and later inorganic nitrogen were used in agriculture to improve crop growth and yield.

Soil gives support and provides water and reservoir for fourteen mineral elements essential for the normal development of plants. The term 'essential mineral' elements was coined by Arnon and Stout (1939). They concluded that, for an element to be considered 'essential', three criteria must be met :

- a) A given plant must be unable to complete its life cycle in the absence of the mineral element.
- b) The function of mineral element must not be replaceable by another mineral element.
- c) The element must be directly involved in plant metabolism

For example, as a component of an essential plant constituent such as an enzyme or it must be required for a distinct metabolic step such as an enzyme reaction. Clarkson and Hanson (1980), emphasized that mineral elements should be classified on the basis of their biochemical and physiological behaviours rather than according to their concentration. Accordingly elements required for plant growth have been classified into four major groups,

- i) elements that are covalently bonded into constituents or organic matter (C,H,O,N and S).
- ii) elements that occur as oxyanions or are esterified with native alcohol groups (P,B and Si)
- iii) elements that have non specific, osmotic and ionic balance function plus specific functions in enzyme conformation and catalysis (K, NA, Mg, Mn and Cl) and in elements that form metalloproteins, are present as structural chelates and participate in redox reactions or valency changes (Fe, Cu, Zn and MO).

B. POTASSIUM IN SOIL

Potassium is a major component of the earth's crust and is present in substantial quantities in most soils. Its availability to plants, however varies and is related in many ways to the physical chemistry and structure of soil minerals. Potassium is derived from primary minerals and from secondary minerals such as clays. Generally soils high in clay content tend to be relatively high in potassium.

Potassium is rather elusive in the soil with respect to plant availability. This is a consequence of the amount of type of clay in a given soil and the low hydration energy of the K ion which favours its entrapment in the lattice voids of the micaceous structure. The soluble, exchangeable and non exchangeable forms of K are in equilibrium. Hence removal of soluble K by leaching or cropping cause exchangeable K to go into solution to replace that removed. Also, as exchangeable K is used up, non-exchangeable K is released; though release may be an insufficient supplement of crop requirements due to limitation both in quantity and rate.

It is generally known that an equilibrium exist between the plant available potassium in the soil solution, exchangeable K and non-exchangeable K (Fig.1). According to Beringer (1985) in this equilibrium the diffusion

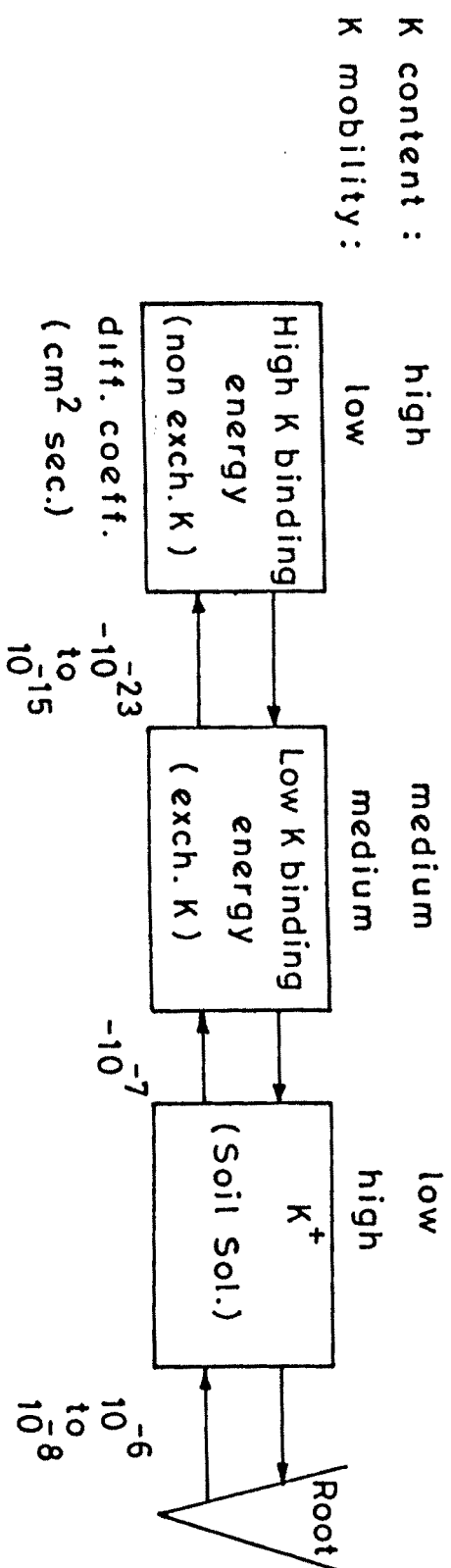


FIG. 1 - SCHEMATIC REPRESENTATION OF POTASSIUM DYNAMICS IN THE SOIL (AFTER BERINGER, 1985).

coefficients play a conclusive role. They indicate that the release of exchangeable K into the soil solution and from the soil solution to the root surface occurs almost at the same rate. Release of non-exchangeable K proceeds more slowly. So that plants cannot grow optimally when they have to rely on this fraction (Grimme, 1974). Nevertheless, part of the K uptake by the plant is covered from the non-exchangeable pool (Scheffer and Schachtshabel, 1982).

Inherent potassium status of soil largely depends on the rate and amount of non-exchangeable potassium release. Crop removal of potassium exceeds annual additions without any appreciable change in the available potassium status of soils, thereby suggesting that part of the non-exchangeable potassium becomes available to plants. The release of non-exchangeable potassium occurs when the level of exchangeable and soil solution potassium decreased by crop removal and leaching (Martin and Spark, 1983).

According to Bray and Turk (1938) and dynamics of K in the soil is characterised by an equilibrium between various forms of potassium such as non-exchangeable (fixed), exchangeable and solution K, Attoe and Troug (1946) observed that this equilibrium is controlled by mass action; or, between readily available, moderately available and difficulty available forms of potassium and the response of K equilibrium system to any stress such as K removal by

crops or addition of K fertilizers to soils. Drying and wetting, pH, nature and amount of clay minerals present in the soil, addition of potassium fertilizers and cropping, all affect this equilibrium. The availability of K in soil depends on many factors including kinds of parent materials, weathering conditions and clay minerals (Acquaye, 1974 and Kansal, 1976).

Geometrically Augite-Basalt, granites and gneiss form an important parent material for black soils. The important minerals noticed in these rocks are orthoclase feldspar, plagioclase feldspar, augite, magnetite, albite, apatite, olivine, microcline quartz, muscovite, biotite and hornblende of these parent materials orthoclase, microcline, muscovite and biotite are regarded as rich source of potassium as they release potassium on weathering.

Soils in the field do not have a constant potassium ion concentration throughout the year. The crop growing in the soil removes potassium continuously during its active period of growth, thus causing reduction in the exchangeable potassium in the soil; since rate of release of fixed potassium is appreciably slower than the rate of uptake, the exchangeable potassium falls during the growing season and then rises after crop growth has ceased which is typically in the winter in temperate regions. If a potassium

fertilizer is added to a soil, a part of added potassium will be converted to the fixed form, which will be greater, the greater the proportion that is not taken up by the crop (Bray, 1943).

The proportion of potassium ions added to a soil that is converted to the fixed form is increased by drying the soil, so that alternate wetting and drying in the root zone of a crop will tend to increase the amount of potassium that is converted to the fixed form. This effect of drying has the consequence that there need to be no close connection between the amount of potassium fixed and proportion of the exchangeable ions that are potassium, for this will depend on the intensity and frequency of the drying of the soil. Thus there can be no reversible equilibrium between the amounts of fixed and exchangeable potassium in a soil. The fixation of potassium takes place more readily in neutral soils than in acid soils and liming an acid soil increases its ability to fix potassium (Zende, 1978).

The potassium status of Indian soils has been investigated by some workers. There are few reports which indicate that the alluvial soils of India are generally rich in available K (Ramamoorthy, 1969; Misra, 1970 and Ali et al., 1976). According to Ramnathan and Krishnamoorthy (1976) red soils derived from the oldest geological formations are

poor in K bearing minerals. Ghosh and Hasan (1977) have done survey of Indian soils and observed that 20% of soils are poor in potassium, about 42% of soils have medium status of potassium and only 38% soils were having high potassium status. A good survey of fertility status of various soil types in India as obtained by the survey of various workers is presented by Alexander (1972) in the book 'Soils of India'. Thus in Kerala about 80% of the soils are deficient in potassium. In Orissa, about 66 to 75% of cropped area is low in available potash. ^{According to} Zende (1978), in Maharashtra, Karnataka, Tamilnadu and Andhra Pradesh 28.5 to 48% soils are high in potassium where as in Madhya Pradesh and Gujarath 71 to 100% soils are so characterised.

According to Kanwar et al. (1972) and Goswami et al. (1976) intensive cultivation of high yielding varieties and greater use of nitrogenous and phosphatic fertilizers, potassium deficiency has been reported to be fairly wide spread.

C. UPTAKE AND TRANSPORT OF POTASSIUM

Potassium is univalent cation with a hydrated ionic radius of .33/nm and hydration energy of 314/mol. Its uptake is highly selective and closely coupted to metabolic activity (Marschner, 1983). It is most dominant cations in plant tissues. One of the main features of K is the high rate at which it is taken up by plant tissues. Uptake of K

is in the form of monovalent cation K^+ . The K^+ absorption rate of the root is reliant on the root metabolism and particularly on respiration and thus on the carbohydrate content of the root (Mengel, 1967). Generally, younger plants have higher root carbohydrate contents than older plants, and even young root tips of older plants are less capable of absorbing K^+ than root tips of younger plants (Vincent *et al.*, 1979). Plant species and even cultivars of the same species are found to differ in their capability of exploiting soil K^+ . Glass and Perley (1980) observed a positive correlation between K uptake rate and growth rate in barley cultivars. Halevy (1977) studied root growth pattern of two cotton cultivars differing in their capability of exploiting soil K^+ . The cultivar with the higher uptake potential for soil K^+ was found to maintain vigorous root growth up to a later growth stage than the cultivar with the poor K^+ exploitation capability. Glass (1976) observed that K uptake rates are controlled by the internal K concentrations. According to Zimmermann (1978) it is ultimately cell turgor which control K uptake. Bowling (1976) has indicated the possibility that since K^+ is so mobile in plant tissues, passive diffusion may mask the activity of a K^+ pump. It is wellknown that K^+ uptake is selective in relation to other cations. It is therefore generally accepted that K^+ uptake involves the combination of a hypothetical carrier with a K^+ ion. This is believed

to take place in such a way that the intermediate ion-carrier complex formed at the outer part of the membrane is transported inward. At the internal side of the membrane the ion carrier complex breaks down, and K^+ is released inside the cell.

A carrier is not yet isolated from cell membranes. However, within the last 15 years organic compounds with highly complex structure have been discovered that are capable of transporting monovalent cations across membranes, and some bind very selectively with K^+ . These substances, which are antibiotics, are collectively called ionophores because of their property of acting as ion-carrying agents (Hinkle and McCarty, 1978). Two main groups have been recognised by Pressman (1968). The first group includes valinomycin, gramicidin, and the macrotetralide actins. These are all neutral and form complexes by acquiring the charge of the complexing cation. The second group includes nigericin, which contains a carboxyl group thus giving the molecule a negative charge, which is neutralized by the cation. All have lipophylic properties, so they are soluble in the lipid matrix of membranes. By selectively binding with K^+ they thus facilitate the transport of K^+ across biological membranes.

The selective properties of valinomycin in transporting alkali ions across a synthetic membrane were

investigated by Muller and Rudin (1967). Valinomycin was found to increase membrane permeability to K^+ so that the rate of K^+ transport was about 300 times higher than that of Na^+ .

Such or similar compounds may be responsible for K^+ selectivity in uptake by higher plants. If the process of K^+ complex formation and K^+ release were linked directly to metabolism to provide the energy for uphill transport against an electrochemical gradient, the system in effect would be that of active K^+ carrier transport on the other hand, passive K^+ transport may also be brought about by these selectively K^+ binding compounds by enabling K^+ to move down an electrical gradient from the outer solution into the cell.

An ion uptake model in which cation influx takes place down an electrochemical gradient has been proposed by Hodes (1973). As shown in Fig.2 cation uptake is regulated by an ATPase in the Plasma membrane. For each ATP molecule split by the ATPase, one H^+ is produced which is extruded from the cytoplasm into the outer medium, and one OH^- is generated in the cytoplasm. This process induces an electropotential gradient across the membrane, the cytoplasm being more negative compared with the outer medium. The cytoplasm thus attracts cations from the outer medium. Most of cation species are probably absorbed by this mechanism.

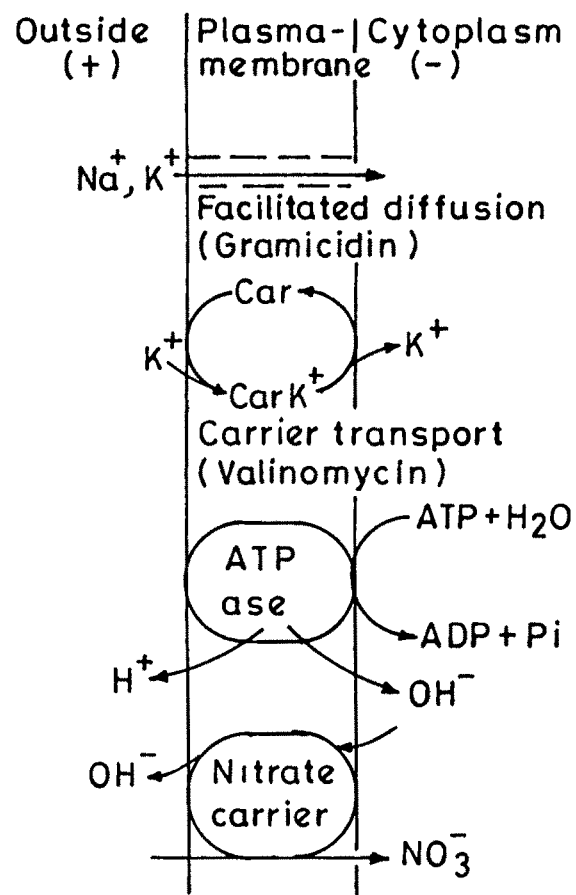


FIG.2 - SCHEME OF MEMBRANE-LOCATED ATPASE-DRIVING K^+ CARRIER TRANSPORT FACILITATED K^+ DIFFUSION AND CARRIER-MEDIATED NO_3^- UPTAKE (AFTER HODGES, 1973).

The substances like valinomycin or nonactin could induce selective uptake by preferential binding with K^+ in the downhill transport. This passive selective uptake has been called 'facilitated diffusion'. The findings of Ratner and Jacoby (1976) indicate that the high rate of K^+ uptake by plant cells can be accounted for in terms of an ATPase-driven facilitated diffusion of K^+ .

Watad et al. (1991) observed that K^+ uptake is appears to be linked to H^+ -ATPase. Such linkage could be mediated by a common transport mechanism e.g. cation/ H^+ exchanged or perhaps K entry could be passive through specific channels driven by the electrochemical potential gradient produced by the electrogenic H^+ -ATPase. According to Hoagland (1944), potassium uptake is active and translocation can be against strong electrical and chemical gradients. There is evidence that of all the essential mineral cation species, K is the only one which can be transported against an electrochemical gradient into plant cells (Ansary and Bowling, 1972). Potassium uptake is active at low K concentration in nutrient solution and the active uptake mechanism is inhibited by higher K concentrations (Cheeseman and Hanson, 1979). According to Jeschke and Pate (1991), salient features of the plant budget for K^+ were prominent deposition in leaves, high mobility of K^+ in phloem, high rate of cycling through leaves, and downward translocation of K^+ providing the root with a large excess

of K^+ . The reason why K is transported to young growing tissues is not well understood. Jacoby et al. (1973) postulated relationship of K to protein synthesis, growth rate and supply of cytokinins. K^+ in the plant is very mobile and the bulk of K^+ is mainly taken up during the vegetative growth stage (Mengel and Kirkby, 1982).

Recently it is generally accepted (on the basis of distinct properties such as kinetics, pharmacology, selectivity and specific dependence on the growth medium K^+ status) that the biphasic characteristic of K^+ uptake results from the operation of two independent transport mechanisms i.e. high affinity K^+ uptake system and low affinity K^+ uptake system (Maathuis and Sanders, 1996). According to them the high affinity system which on basis of its Michaelis-Menten like kinetics was assumed to be a 'carrier' has now been identified as a K^+/H^+ symport. On the other hand, the low affinity pathway mediating 'passive' K^+ uptake can now, at least partly be ascribed to a particular type of K^+ selective ion channel in root cells of *Arabidopsis thaliana* and to be associated with an inward current in the root hair cells in wheat. These two systems fundamentally differ in their mechanisms (Fig.3).

D. REDISTRIBUTION OF POTASSIUM

Lauchli (1972), Widders and Lorenz (1982) suggested that although the indispensability of potassium

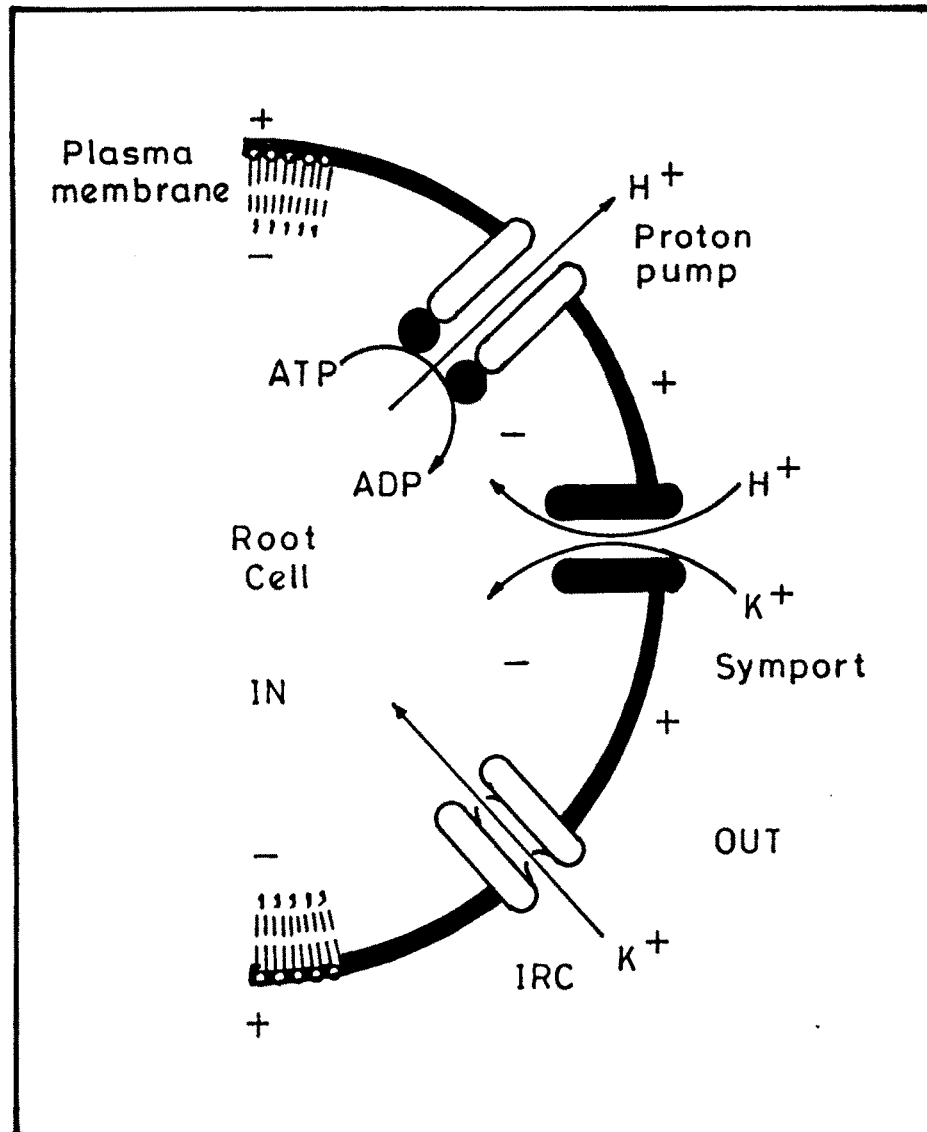


FIG.3 - SCHEMATIC OVERVIEW OF THE RELEVANT PLASMA MEMBRANE K^+ TRANSPORTING MECHANISMS IN A TYPICAL ROOT CELL (AFTER MAATHUIS AND SANDERS, 1996).

for plant metabolism is very well documented, it is observed that the accumulation pattern of this element in various plant parts may change along with the growth phases. Saxena and Krishnamurthy (1979) have noticed that K^+ content in leaf and stem of chickpea cultivars Annigeri, JG-62; and C-130 shows a decline after flowering. Rao et al. (1983) also observed that concentration of potassium declined with age of coriander plant. Wang et al. (1984) observed decrease in potassium in the vegetative organs during grain filling, suggesting redistribution of minerals to the seeds in the soybean. In kiwi fruits continuous influx of K into the fruit over the whole growing season has been reported by Fergusson (1980). Burridge et al. (1964) have shown that in *Theobroma cocoa* potassium is withdrawn from the leaves and supplied to the developing pods. According to Loneragan et al. (1976), the redistribution of K^+ takes place due to its quick mobility. Its main transport direction is towards the meristematic tissue. Greenway and Pitman (1965) observed translocation of K^+ from old to young leaves in oat plants. In view of Chamel (1969) translocation of K^+ in the plant system depends on the age of leaf. They also observed that, in lettuce more K^{42} was translocated from old leaves to young leaves, and the young leaves in turn transmitted K^{42} mainly towards the youngest part such as the meristem during the growth. Experiments of Ulrich and Hills (1969) also obtained same observations. Wolf et al. (1991) observed

that there is net loss of K^+ from the basal leaves, whereas young leaves increased in K^+ content. They claimed that direction of K export strongly depended on leaf age. According to them old basal leaves preferentially supplied the root and most of the K^+ retranslocated to the roots was transferred to the xylem and subsequently become available to the shoot. Upper leaves exported to the apex young organs were supplied by xylem and phloem, with xylem preferentially delivering Na^+ and Phloem most of K^+ . The potassium redistribution during senescence was evident in several experiments. Nimbalkar (1973) reported that during senescence of sugarcane leaves potassium decreases. Bhivare and Nimbalkar (1984) and Murumkar and Chavan (1985) observed the decrease in potassium in senescent leaves of bean and chickpea respectively. Taylor and Echlin (1986) found that in tobacco, potassium was greatest in juvenile and mature leaves and decreased as senescence progressed.

E. FACTORS INFLUENCING POTASSIUM UPTAKE

Potassium uptake is found to be influenced by several factors. Soil moisture and soil temperature conditions decide not only the availability of K, but also its uptake and movements in plant Nelson (1980). According to Wallace (1958), a number of investigations provide evidence of the restrictive effect of low soil moisture content on the uptake of potassium by crops. Potassium is not known to undergo any change in availability when the

soil moisture is increased from the aerobic to the anaerobic conditions, unlike Fe, Mn, Ca, Mg and Al, but potassium uptake is affected because according to Hoagland and Broyer (1936), potassium salts can enter the root rapidly only during active aerobic respiration of roots.

Farah (1981) observed that water shortage reduced the amount of leaf potassium throughout the growth period of bean. Batchelor et al. (1984) observed that potassium concentration in irrigated soybean plants were greater when K uptake is low. On the other hand K uptake and retention in plant cells are also competitively affected by H^+ , Ca^{2+} , Mg^{2+} and Na^+ (Elzam and Hodges, 1967) than those of water stressed plants. McQuate (1986) recently reported the declined total potassium concentration in the cell sap of soybean with decreasing water potential. Umar et al. (1991) confirmed that moisture stress reduced K uptake. Some reports indicates increase in potassium uptake due to moisture stress. Experiments of Takeshi (1966) demonstrated that water stressed leaves of *Brassica rapa* and *Vigna sinensis* contained more potassium. Singh and Singh (1970) observed an increase in potassium in the first period of growth of rice due to depleted soil water, but later the trend was reversed. Ford (1984) also observed similar trend in *Vigna mungo*, Cv. Regur, *V. unguiculata* CPI 2815 and *Glycine max* CPI 26671. Lower temperatures also hinder the uptake of K because root growth is affected at lower

temperatures. According to Nordin (1977), at low temperature membrane permeability is affected and thus uptake of K is reduced. Pedro and Uribe (1981) observed that the active ion transport system is also restricted by low temperature.

Chang and Loomis (1945) shown that high concentrations of CO₂ reduce the absorption of nutrients in the order K>N>P>Ca>Mg, and that potassium under these conditions was actually excreted from the roots. Absorption rate of other cations is especially enhanced. According to Grattan and Grieve (1992), potassium is present in relatively low concentrations in the saline and sodic soils. Because of the plants requirement for an adequate amount of K⁺, it is fortunate that the plasma membranes of root cortical cells have a high affinity for K⁺ over Na⁺.

Although plants selectively absorb and translocate K⁺ in preference to Na⁺, the degree of selectivity varies among species as well as among cultivars within a species. Kafkafi (1984) concluded that the roots of the salt tolerant species (beet) had a higher affinity for K⁺, in exchange for Na⁺ than the salt sensitive species (bean).

At the same time a decline in K uptake under saline conditions is observed in many plants (He and Cramer, 1992). Numerous studies have shown that the K concentration in plant tissue is reduced as Na⁺-salinity is increased

(Cramer et al., 1985; Janzen and Chang, 1987; Subbarao et al., 1990; He and Cramer, 1992). Rathert (1982) found that salinity reduced the concentration of K^+ in the leaves of the salt-sensitive cotton cultivar (Dandara) more than that in the salt tolerant cultivar (Giza-45).

There is evidence that Na^+ can partially substitute for K^+ in many glycophytic species without affecting growth. Marschner (1986) classified many crop species into four groups, depending upon the extent by which Na^+ can replace K^+ . Crop species in group A can replace a high proportion of K^+ by Na^+ (e.g. beets, turnip and swisschard) whereas in crop species in group D (e.g. Maize, bean and lettuce) no substitution of K^+ is possible. Rice has been classified as a group C crop where only a minor substitution of K^+ by Na^+ is possible and Na^+ has no specific effect on growth, unlike those crops in group A and B. Salim (1989) also found that decrease in K concentration in roots of mungbean, Red kidney bean, sunflower, tomato and *Atriplex spongiosa* due to increased salinity treatments. Blits and Gallagher (1990) noticed decrease in K content in roots of salt treated halophyte *Kosteletzkya virginica*. Ball et al. (1987) concluded that NaCl salinity produced a salinity induced K^+ deficiency in *Avicennia marina* by reducing the atrazine binding sites in isolated thylakoids. This caused a loss of functional photosystem II in the leaves of this mangrove species.

Evidence has been presented indicating that adaptation of glycophytes cells to NaCl results in increased capacity for K uptake and this enhanced capacity is even greater under saline conditions (Watad et al. 1991). The principal effect of such an adaptation is to regulate intracellular K concentration (Jeschke, 1984). This is an adaptive mechanism that contributes to the ability of NaCl adapted glycophyte cell to maintain intracellular levels of K sufficient for survival and growth in saline environments (Watad et al., 1991).

F. POTASSIUM STATUS OF PLANTS

Epstein (1972) has suggested 1% of dry weight as an optimal level of potassium in plants. According to Ulrich and Hills (1967), a 'critical' concentration of K^+ can be determined which can be defined as the concentration at which 90% of maximum yield is obtained. Leigh and Wyn Jones (1984) observed that above this concentration (1% K in dry matter) growth shows little response to increased tissue K^+ but at lower concentrations it declines rapidly. According to Asher and Ozanne (1967) for many plants the critical K^+ concentration is in the range of 0.5 to 2% in dry matter. Besford (1975), Spear et al. (1978) and Smith et al. (1982) mentioned the critical concentrations of K^+ for the growth and the maximum percentage of K^+ in dry matter in *Lycopersicum esculantum* (1.0 and 4.1%), *Helianthus annus*

(2.2 and 10.0%) and in *Medicago sativa* (1.9 and 6.0%) respectively. Flower et al. (1977) reported high values of potassium (5 to 10% of dry matter) for halophytes. Grubben (1976) reported very high level of K^+ (upto 7.7% dry weight) in *Amaranthus* foliage. Gaikwad (1995) from our laboratory noticed that the K^+ contents in different parts ranged from 2.0 to 9.0% of dry matter in the *A. caudatus*, *A. hypochondriacus* and *A. paniculatus*.

G. ROLE OF POTASSIUM IN PLANTS

According to Barker and Maynard (1969) potassium is an indispensable for plant growth, influencing a number of physical, physiochemical and metabolic pathway at the cellular level and thus affecting the ultimate growth and productivity of the plant. Unlike nitrogen and phosphorus, it does not enter into the composition of any plant product. But an extensive survey of literature on K reveals that it has an important role, either direct or indirect, in major plant processes such as photosynthesis, respiration, growth, osmoregulation, development and yield. Potassium has differential influence on various components of each process.

a. Water Uptake and Transport

Potassium nutrition influences the uptake and translocation of water. Blanchet et al. (1962) observed better extraction of moisture from the soil with high supply

of K^+ . According to Rogaler (1958), permeability of root cells increases with increasing potassium in soil. Weatherly (1969) observed that the movement of water from the surrounding cells of the root into xylem vessel is regulated by the presence of potassium. According to Mengel and Pfluger (1969), the movement of water within the plant is also influenced by potassium. Graham and Ulrich (1972) have clearly shown the effect of K on the root permeability. Mengel and Simic (1973) noticed that the quantity of water moved upwards by root pressure was reduced with lower concentrations of potassium in the root medium. A high rate of potassium uptake by root cells depress the osmotic potential in the cells and this induces water uptake. Umar et al. (1993) and Dwivedi (1993) also noticed that potassium lowers the osmotic potential and increase the water uptake. Hence Mengel and Kirkby (1980) concluded that uptake of water by roots and the ability of plant to exploit soil water, depends on the potassium nutritional status of the plant. Nelson (1980) also emphasized that potassium influences the water economy and crop growth through its effect on water uptake. Polizotto (1986) and Umar et al. (1990) observed that adequate potassium nutrition promotes root growth that results in better uptake of nutrients and water.

b. Osmoregulation

In higher plants potassium plays a prominent role

in osmoregulation. Blanchet (1958) noticed that, improved potassium nutrition resulted in lowering of osmotic potential in plant organs. Morard (1974) also observed that the potassium shows the effect on osmotic potential. Observations of Dela-Guaradia and Benlloch (1980) emphasize the essential role of K for turgor maintenance and stem elongation in young sunflower plants. Arneke (1981) observed a relationship between the K content of leaves and osmotic and turgor potential in *Phaseolus vulgaris*. According to Balasubramanian (1975), K helps to maintain turgor in plant and found in higher concentration in cell sap than any other cation and serves as an osmoticum. In view of Cram (1976) K^+ is a chief osmotic gradient regulator in glycophytes and glycohalophytes. Mac Robbie (1977) observed that most of glycophytes typically accumulate high concentrations of K^+ in plant tissue and most of the cellular K^+ is present in the vacuole as a simple salts (e.g. KNO_3 , KCl , K-malate) which make major contribution to the osmotic potential of the cell sap and hence are important in the generation of turgor. According to Mengel (1977), K^+ is the most important inorganic solute in plants as this element is osmotically active and thus this ion forms an integral component to a wide range of turgor mediated responses in plants including stomatal and leaf movements. Wyn Jones et al. (1979) reported that the leaves of glycophytes contain 200 mM K (or approximately 6% of K in D.M.) and the osmotic potential of

the K salts in the vacuole will be about -9 bar which represents a major proportion of the osmotic potential of the sap. According to them K maintains a balance between osmotic potential of the plant and its surrounding. Ortiz et al. (1994) concluded that K is the main inorganic osmoticum in plants probably because it is energetically 'cheaper' than organic metabolites.

c. Stomatal Regulation

Stomata regulate gaseous exchange on one hand and water loss by way of transpiration on the other hand. Thus stomatal behaviour is very important with respect to various plant processes. Now wellknown that K^+ plays important role in opening and closing of stomata. Investigations of Fisher and Hsiao (1968) and Hsiao (1976) have revealed that K plays a significant role in stomatal opening and closing. According to Humble and Hsiao (1969), K is accumulated in the guard cells in the considerable concentration, thus resulting in high turgor pressure which causes the opening of stomata. Raschke (1971) clearly showed the relationship between K content in the guard cells of *Vicia faba* and the opening and closing response. Humble and Raschke (1971) suggested that an organic acid like malate is the anion balancing K. Graham and Ulrich (1972) observed that in *Beta vulgaris*, the stomatal aperture was shown to be strongly related to leaf K content. Mengel and Kirkby (1980) stated

that in most plant species, potassium plays a very specific role in stomatal opening and closing and cannot be replaced by any other univalent cation. Beringer (1982) also supported this view. Wilson et al. (1978) found that increased KCl concentrations resulted in increased stomatal aperture even in presence of ABA, a phytohormone generally responsible for stomatal closure. Smith and Stewart (1990) also made similar observations in hemiparasite *Striga hermonthica*. Experimental results of Ridolfi and Jean (1994) indicated the existence of three alternative mechanisms of osmotic accumulation in guard cells, including K^+ -uptake, starch breakdown and photosynthetic sugar production. Movement of leaves in nyctinastic (night-closing) plants is caused by turgor changes in motor cells and is also associated with large K^+ fluxes (Satter and Galston, 1981).

d. Photosynthesis and Respiration

Significance of K^+ in photosynthesis and respiration was firstly admired by Jackson and Volk (1968). K is highly essential to maintain structural integrity of chloroplast and plastids. Marschner and Mix (1974) observed that, the enhanced leakage of K^+ caused by antibiotics also induces severe changes in the fine structure of chloroplasts and proplastids. According to Marschner and Possingham (1975), potassium influences the photosynthetic process by controlling chlorophyll synthesis. Wolf et al. (1976) found

that potassium serve a vital role in photosynthesis by directly increasing growth and leaf area index and hence CO₂ assimilation and increasing outward translocation of photosynthate. Gross and Prashner (1974) indicated that monovalent cations, especially K⁺, are necessary at a concentration of 60 to 150 mM for high efficiency of energy transfer between the two photosystems. Uribe (1973) and McCarthy (1976) have shown that K⁺ is essential for ATP formation through electron transport chain in thylakoid membrane of chloroplast. Thus in view of Lauchli and Pfluger (1978) the principle role of K⁺ in the primary reactions of photosynthesis seems to be to serve as a counter ion to H⁺ in ion transport across the thylakoid membrane. According to Huber and Maury (1980), the requirement of external K⁺ may be related to maintenance of alkaline pH in the stroma by a Mg²⁺ activated K⁺H⁺ antiporter in the chloroplast envelope. Huber (1984) has opined that although K⁺ is not involved specifically in photosynthetic metabolism, it is required in relatively in high concentrations for other physiological and biochemical processes which influence photosynthesis. Behboudian and Anderson (1990) also observed reduced photosynthesis rate due to low levels of K in tomato.

Similar to photosynthesis, respiratory process also demands potassium and its essentiality has been proved in several processes like CO₂ liberation (Jackson and Volk, 1968; Barankiewicz, 1978) O₂ uptake (Walker and Ward, 1974)

as well as activities of TCA cycle enzymes oxidative phosphorylation (Okamoto, 1969).

e. Translocation of Photosynthates

Burr et al. (1957) demonstrated that potassium plays important role in translocation of photosynthates from the leaves of sugarcane. Experiments of Hartt (1970), Amir and Reinhold (1971) also showed that phloem transport of carbohydrates could be reduced in potassium starved plants. Mengel and Haeder (1977) have shown a promotive effect of potassium on phloem exudation from castor bean while Malek and Baker (1977) found potassium enhanced the uptake of ^{14}C -labelled sugars in castor bean petioles. Doman and Geiger (1979) demonstrated a promotion in the export of ^{14}C -labelled assimilates from sugarbeet leaves by exogenously applied potassium. Malek and Baker (1977) suggested loading of sucrose into sieve elements is mediated through a proton-sugar cotransport system which is linked with potassium movement between the apoplast and the sieve element. Similar proposal have been made by Giaquinta (1977). Mengel (1980) also stated that potassium plays important role in translocation of photosynthates.

f. Protein Synthesis

It is now known that K is essential for protein synthesis in higher plants (Hasio and Lauchli, 1986). According to Leigh and WynJones (1984), in vitro protein

synthesis needs 100 to 150 mM K (approximately 3 to 4.5% of K of D.M.) and high K/N ratio. According to Franks and Eagland (1975), as the principal inorganic constituent of the cytosol, K^+ is the dominant counterion for the excess of negative charge on proteins and nucleic acids. The relatively low charge : mass ratio of K^+ (in comparison with say Na^+) results in a small hydration shell, a low tendency to order water and hence compatibility with the conformational integrity of proteins when the ion is present high concentration. Typically in Plants, as in animals, cytosolic K^+ levels are of the order of 80 to 120 mM (Maathuis and Sanders, 1993 and Walker *et al.*, 1995).

g. Enzymes

According to Suelter (1970), there are more than 50 enzymes which either completely depend on or are stimulated by K. Potassium activates enzymes by inducing conformational changes in the enzyme proteins. The main function of K in biochemistry is its activation of various enzymes (Evans and Sorger, 1966) such as pyruvate kinase, phosphofructokinase, glutathion synthetase, fructose biphosphate aldolase (Suelter, 1970), starch synthetase (Nitsos and Evans, 1969), Nitrate reductase (Umar *et al.* 1991; Gutierrez *et al.* 1992b), Glutamine synthetase (Gutierrez *et al.*, 1992a) and RuBP carboxylase (Peoples and Koch, 1979). According to Hartt (1929), potassium seems to be a specific activator of invertase in sugarcane. Sorger *et al.* (1965) suggested that

potassium imparts a specific structure to the enzymes it activates. The experiments of Buczek (1979) shows that the presence of K^+ ions in the induction medium is essential for maintenance of NR activity in the cotyledons, and the effect of K^+ cannot be replaced by Na^+ or NH_4^+ .

h. Drought Resistance

Shchukina (1965) emphasized that potassium as fertilizer and also presowing hardening treatment increased drought resistance in maize. According to Umar et al. (1991), among various nutrients, potassium works efficiently in drought conditions and promotes a number of physiological activities in plants that tends to improve their drought tolerance.

i. Salt Tolerance

According to Shimose (1973), and Storey and Wyn Jones (1978) salt tolerance capacity is dependent upon efficient potassium uptake mechanism in presence of salt. Preferential uptake of potassium over sodium has been demonstrated in many marine algae and mangroves (Joshi, 1976).

j. Disease Resistance

Potassium is also involved in the process of disease resistance of crop plants. According to Hall and Loomis (1972), disturbed K metabolism is a pathogenic effect of beet yellow virus infection on the sugarbeet. Russel

(1969) has observed that a possible correlation in the storage root and tolerance for beet yellows virus exists in sugarbeet. Generally K fertilization reduces the intensity of several infections diseases; and this occurs with diseases caused by facultative parasites like *Puccinia gramineae*, *Alternaria solani*, *Fusarium oxysorum*, *Xanthomonas oryzae* and *Tobacco mosaic virus*. It has been frequently observed that K reduces the incidence of, or damage from various diseases, such as bacterial leaf blight in cotton; cercospora leaf spot in cassava; tikka leaf spot in peanut; red rust in tea; cercospora leaf spot in mungbean (*Vigna radiata* L.) and seedling rot caused by *Rhizoctonia solani* in mungbean and cowpea (Tandon and Sekhon, 1989). Usherwood (1980) draw the following conclusions :

- i) Potassium improved plant health in 65% of the studies and was deleterious 23% of the time.
- ii) Potassium reduced bacterial and fungal diseases 70% of the time, insects and mites 60% of the time and the effects of nematodes and viruses in a majority of the cases.
- iii) Fungal disease infection was reduced by K and average of 48% in soils tested low in K and 14% where soil test levels were unknown.
- iv) The influence of K on crop yield varied according to the parasite group. The average increase in yield or

growth was 48% for fungal diseases, 99% for viruses, 14% for insects and mites and 70% for bacteria.

- v) The balance between N and K affects disease susceptibility of plants.

The nature of the action of K in controlling the severity of plant diseases is still not understood. It may relate, in part, to the effect of K in promoting the development of thicker outer walls in epidermal cells, thus preventing disease attack. In addition plant metabolism is much influenced by K, and some plant diseases may be favored by changing in metabolism associated with low K contents in the plant (Mengel and Kirkby, 1978). Thus experiments of Hillocks and Chinodya (1989) indicated that the cotton plants with very low level of potassium at the stage of flowering became susceptible to *Alternaria* leaf spot disease.

k. Growth and Yield

The necessity of potassium for optimal growth and yield of crops, vegetables, fruit and tuber crops has been recognized by many workers. The role of potassium is associated with starch synthesis leading to promotion of tuber growth through the accelerated translocation of photosynthates from leaves to tubers (Mukhopadhyay et al., 1992). Tsuno and Fujise (1968) reported that liberal supply of potassium was a key factor for increasing sink capacity

and photosynthesis. Potassium in higher level also increased leaf area duration and excessive leaf growth was suppressed, resulting in higher root yield (Hann, 1977). Roy et al. (1991) observed that with increasing rates of K application, grain and stalk yield of maize also increased. Singh and Verma (1991) observed a significant increase in the growth parameters like height and number of branches per plant with increasing levels of potassium upto 120 kg/ha. Umar et al. (1991) found that application of K increased dry matter accumulation and helped in partial linear recovery of seed yield and oil content. According to Mondal et al. (1990), potassium fertilization improved the different yield parameters, seed yield as well as oil content in mustard. Bohra and Doerffling (1993) observed that potassium application significantly increased potential photosynthetic activity, percentage of filled spiklets and yield in Rice. Singh and Tomar (1991) also observed similar effects in wheat. Potassium is found to be highly essential for the maintenance of growth and leaf area in tomato (Behboudian and Anderson, 1990) and biomass of sunflower and bean (Benlloch et al. 1994).

Sinha and Nair (1971) also observed that more leaf area formation and its retention during drought period resulted in higher yields due to K application in tapioca. Rama Rao (1986) also observed favourable effects of K on pearl millet yield under moisture stress. Umar et al. (1993)

found that moisture stress adversely affected dry matter and yield. This could be overcome to a certain extent by potassium application (upto 60 ppm) in all the situations.

H. POTASSIUM DEFICIENCY SYMPTOMS

Potassium deficiency symptoms of various plant species have been described in details by Busster (1964) and Ulrich and Ohki (1966). K deficiency does not immediately results visible symptoms. At first there is only reduction in growth rate and then chlorosis and necrosis occur. These symptoms generally begin in the older leaves due to the fact that these leaves supply the younger ones with K. In most plant species chlorosis and necrosis begin in the margins and tips of the leaves but in some species such as cloves, irregularly distributed necrotic spots occurs in the leaves (Morard, 1973). There are many reports which shows that K deficiency results in weakening of leaves, chlorosis, necrosis and rolling of leaves. Humbert and Martin (1955) observed that in sugarcane potassium deficiency induce yellowing and spotting of older leaves. Sircar and Datta (1959) reported that in rice K deficiency induced scorching of leaves with red patches on margins and dry tips and development of minute brown streaks on stem. According to Treshow (1970), due to K deficiency chlorotic and necrotic leaf symptoms appears initiating from older leaves. Tanaka and Yoshida (1970) noticed that in rice leaves short, droopy and dark green due to K deficiency. On lower leaves

yellowing takes place at the interveins starting from the tip. The panicle becomes sterile. In many cases blackened reddish brown or rotten roots occur. Park et al. (1971) also observed severe root rot in rice due to K deficiency. Epstein (1972) reported that K deficiency in many species cause leaves to be dark green or blue green. Chavan (1980) observed drying of leaf lamina from tip in *Eleusine coracana* due to K deficiency. Karadge (1986) also reported drying of old leaves of peanut plants from the margins due to K deficiency.