

# Impact of Water Deficit Condition on Osmoregulation of the Brassica Species

**Khushboo Chandra**

*Agricultural Sciences, SGT University, Gurugram, Haryana, INDIA*

**Ashok Kumar**

*Agricultural Sciences, SGT University, Gurugram, Haryana, INDIA*

**ABSTRACT** – Oilseed rape and mustard are mostly grown on conserved soil water in the Indian sub-continent. These crops generally suffer from water stress at reproductive period of development. Thus, to obtain higher stable yields of Brassica species under routine stress conditions, it is essential to identify and understand the interactions of different morpho-physiological traits responsible for drought resistance. To explicate interaction of traits related to biochemical, physio-morphological factors for sustaining drought resistance in *Brassica species*. Dry mass production and partition in a plant is important when increased yield are sought. A osmometer like plant cell which allows only selective solutes to pass through elastic membrane, cell wall and the thin layer of cytoplasm and a vacuole containing an aqueous solution. To express drought tolerance turgidity of cells maintained by osmotic adjustments.

**Keywords:** Cell Turgor, Dry Mass, *Brassica Species*, Morpho-Physiological Traits, Free Energy

## I. Introduction

In different corners of world scarcity of water is problematic issue during crop production. In temperate regions, crops often suffer from water deficits during the summer. Production, productivity, stomata conductivity, leaf expansion and photosynthesis are direct and positively correlated to plant water relations. Drought affects the rate of dry mass production and the allocation to various plant parts (Turner and Begg, 1981; Passioura, 1983; Huck, Peterson, Hoogenboom and Busch, 1986). Under rainfed conditions production potential of *Brassica* is different and mechanism is still undefined.

Slatyer and Taylor (1960 and 1962) suggested a system of terms using the concept of free energy difference between a given state of water and a reference state which is taken as pure free water at the same temperature. The chemical potential of pure water and admixtures of solvent- solute differs which shows impact on energy differences which is notated as water potential. This terminology uses a number of assumptions. The parenchyma cells of leaf mesophyll approximate to the ideal osmotic cell. In the living tissue the cells and hence the water is connected to neighboring cells and water.

Slatyer (1967) used the concept of free energy for a comprehensive description of the water relations of plants. The water potential of pure water is zero as the difference with the reference pool is zero. Factors such as the addition of solutes, a matric force, negative pressure or tension in the xylem of transpiring plants and reduction in temperature decrease the water potential as free energy is reduced. Cell wall pressure and increase in temperature increase the water potential. Water movement occurs along gradients of decreasing total water potential. Briggs (1967) applied this concept to describe water movement through the plant. In a

cell or a tissue, the total water potential is the result of the presence of osmotic substances, cell wall pressure, colloids, matrices, and gravity, all of which influence the free energy of water (Begg and Turner, 1976). Hence under equilibrium conditions,

$$P = P_s + P_p + P_m + P_g$$

Where  $P_s$  is the solute potential due to the dissolved contents of aqueous solution,  $P_p$  the turgor potential due to the aqueous solution itself,  $P_m$  the matric potential due to the surface forces of the tissue adds to the energy state of water and  $P_g$  the gravitational potential due to the force of gravity.  $P$  is generally negative or zero. However, guttation and similar phenomena are supposed to result from positive  $P$  in the vascular elements (Slatyer, 1967).  $P_p$  may be positive or zero. Reports of negative  $P_p$  by Slatyer (1957 and 1960), Noy-Meir and Ginzburg (1967 and 1969) and Warren Wilson (1967a) are probably fallacious (Tyree, 1976). An underestimation of  $P_s$  by ignoring the apoplastic water may be one of the reasons for a negative  $P_p$  (Jones and Turner, 1978).  $P_s$  and  $P_m$  are always negative since solute and matrix reduce the chemical potential of water. Most often in experiments  $P_m$  and  $P_g$  are ignored (Begg, Bierhuizen, Lemon, Misra, Slatyer and Stern, 1964; Gardner and Ehlig, 1965; Kassam, 1971).  $P_m$  does not cause considerable variation in total  $P$  for changes in  $R$  in mesophyte parenchyma tissues (Wiebe, 1966; Miller, 1972). In xerophyte tissues and meristems of mesophytes,  $P_m$  always influences the sorption isotherm well before turgor falls to zero (Warren Wilson, 1967b; Alsaadi and Wiebe, 1973 and 1975).  $P_g$ , which is equivalent to the work required to bring the water to the height at which it is operational in the plant, is only about 0.01 MPa per meter height and can be neglected with only a small error in measurements on most crop plants. The following equation is then used for convenience (Weatherley, 1970):

$$P = P_s + P_p$$

P may also be assessed indirectly by establishing its relationship with R. R is water content difference at relative state of single tissue at full turgidity. It has been used to assess the water status of plants (Duniway and Durbin, 1971). R is far easier to determine. However, it has been suggested that R shows neutral indicator when there is negligible water deficiency.

(Hsaio, 1973). Assuming that a cell behaves as a perfect osmometer, R is a good approximation to cell vacuole volume and if a linear relation exists between R and Pp (Gardner and Ehlig, 1965; Warren Wilson, 1967c; Kassam and Elston, 1974; Elston, Karamanos, Kassam and Wadsworth, 1976) a number of empirical relations can be obtained.

The relationship between P and R, the sorption isotherm, has attracted the attention of several workers in the field of water relations (Weatherley and Slatyer, 1957; Slatyer, 1962; Jarvis and Jarvis, 1963; Noy-Meir and Ginzburg, 1967 and 1969; Jones, 1978; Richter, 1978). The sorption isotherm largely depends on the chemical and physical nature of the tissue (Kassam and Elston, 1974). These parameters in turn affect P and Pp which are the component potentials of P. P-R isotherm is influenced by the environment and the age of the tissue (Jarvis and Jarvis, 1963; Knipling, 1967). Kassam and Elston (1976) reported that the nature of P-R turgor maintenance is an important adaptation to maintain the processes of leaf enlargement, stomatal opening, photosynthesis and seed setting during drought (Jones and Turner, 1980; Ludlow, 1980; Morgan, 1983, 1984). To maintain turgor pressure into cell during water deficit condition osmoregulation is very much required process.

(Hsaio, Fereres, 1976). During stress condition change of leaf tissue elasticity, maintenance of turgor pressure and hike in solute concentration is involved as responsive mechanism (APP 1978). Ro decrease leads to Prolonged AR drought (Johnson, Nguyen and Croy, 1984; Schoenfeld, Johnson, Carver and Mornhinweg, 1988). It may bring advantage to a plant if cell can reduce water to manage cell tension. Moisture stressed environment plant with large and elastic cell wall adapt very quickly (Slatyer, 1967). Warren Wilson (1967b) suggested that the increased elasticity during stress is due to greater osmotic adjustment. Osmotic adjustment has been associated with dehydration tolerance in a number of species during the stress period (Blum, 1974; Kassam and Elston, 1974; Morgan, 1977 and 1983; Turner and Jones, 1980; Flower and Ludlow, 1986; Thomas, 1986; Schonfeld et al, 1988; Rada, Goldstein, Orozco, Montilla and Zabala, 1989) including some Brassica species (Kumar, Singh, Singh, Singh and Sharma, 1984; Kumar et al, 1987), the expression of which appears to depend on the rate of dehydration (Jones and Turner, 1978; Thomas, 1986). Most of the studies indicate that response of species towards water relations may vary accordingly towards subjected drought (Gutschick, 1987). The extent to which this occurs in Brassica species is little known and needs investigation.

A series of interdependent and interrelated processes justify the continuum soil-plant-atmosphere through water movement (Kramer, 1983). The difference in water vapour pressure between these two points constitutes forces which maintain water flow out from plants. Major resistances in pathway are the stomata, the cuticle, and the boundary layer surrounding leaves. Boundary layer resistance may be relatively important in still air. Under conditions of even moderate air movement, transpiration is effectively controlled by stomata. The term stomatal or leaf conductance ( $S_c$ ), the reciprocal of resistance, is now used because fluxes of  $CO_2$  and water vapour are linearly proportional to  $S_c$  (Burrows and Milthorpe, 1976). To regulate water loss and stress best mechanism is closure of the stomata. (Sung, 1981). Enhancement of economy of crop water can be achieved by lowering of low  $S_c$ . Positive turgor is believed to be necessary to maintain stomatal opening. Flexibility of stomatal opening and closure can be controlled by difference in turgor pressure of subsidiary cells and guard cells. At water deficit condition turgor dependent process is regulating osmotic adjustment (Hsaio et al, 1976; Turner and Jones, 1980; Morgan, 1984). Stomatal opening maintains during stress of water which regulates drought tolerant plants by lowering threshold P at stomatal closure time (Ludlow, 1980).

Drought stressed plant maintains water balance by closure and opening of stomata which lowers threshold P which is due to osmotic adjustment. This is vast correlation between drought and closure and opening of stomata in crop species from monocot to dicots. Turner and Begg (1978) also supported the same conclusion in relation to stomatal mechanism. Bulk Pp value points to zero, evidences the mechanics of stomata (Turner, 1974). Decline of P leads to less sensitiveness of stomata which is termed as adjustment of stomata (Ludlow, 1980). Significant variation in  $S_c$  to increasing water deficits in sorghum were thought to be due to the variations in osmotic adjustment (Ackerson, Krieg and Sung, 1980). Kumar et al (1984) observed a close association between  $S_c$  and the degree of osmotic adjustment in two Brassica species. In well-watered conditions, a genetic variability of 243% in  $S_c$  has been reported in Brassica species (Singh, Singh and Singh, 1982). In several studies, it is evident that that genotypes having longer duration of vegetative and reproductive phase the value of  $S_c$  is least variable.  $S_c$  declined with leaf age in a large number of plant species (Teare and Kanemasu, 1972; Jordan, Brown and Thomas, 1975; Turner and Heichel, 1977; Samsuddin and Impens, 1979; Schulze and Hall, 1982; Boller and Nosberger, 1985). In support of various reviews of scientists adaptive features and low value of P leads to stomatal mechanism more activated but Ludlow (1980) and Jones (1980) supported by saying that when elite genotypes subjected towards different vagaries of environments accordingly expresses water loss and water storage capacity at beneficial pace. However, osmoregulation alone has been considered responsible for stomatal adjustment. The response of stomata has been found to be independent of P in the reproductive period, but not in the vegetative period (Ackerson et al, 1980). Artificial manipulation of turgor has



shown that Pp does not control Sc in dry soil (Gollan, Passioura and Munns, 1986). Plant developmental changes, age of foliage and vagaries of environments are responsible factors for determination of stomatal mechanics at enhanced water deficit stage. So, this requires more attention towards search of another physiological mechanism which may contribute to stomatal adaptation and changes in its relation to water stress at various stages of plant development.

## II. Osmo-regulation approach to mitigate drought

Estimates of P made with different methods often do not correspond. It is difficult to determine which method is more accurate. It is mandatory to focus on consequences of limitations and assumptions before discussion of results of experiments. The thermocouple psychrometer method of measuring P has been considered to be the most accurate (Barrs, 1968). This method is expensive, often difficult to maintain, and unsuitable for studies where many determinations are needed. An alternative method was described by Scholander, Hammel, Hemingsen and Bradstreet (1964) in which the pressure chamber was used to measure P. This method quickly became very popular and has a number of advantages over the psychrometer. The two methods often provide different values when used to estimate P (Wright, Rahmianna and Hatfield, 1988; Hardgree, 1989). Therefore, caution should be exercised when a particular method is used. Methodology for measurements of P explained by Kassam and Warren Wilson put forwarded length change method.

Measurements derived from pressure chamber measurements agree well with those obtained from the length change method for *Vicia faba* (Kassam, 1971; Soman, 1980). This method is simple and quick, and observations can be replicated and so assessed statistically. The main source of error in this method is probably due to expansive growth of cells. This error was reduced as fully expanded young leaves were used for the measurements. The length of leaf strips of fully expanded leaf in mannitol solutions remained unchanged for 24 hours after having reached equilibrium. When regularly watered, the two Brassica species had similar P, Ps, Pso and Pp. Ps became significantly more negative during pod formation compared with floral bud appearance perhaps due to a buildup of solutes at later stages of growth, causing similar declines in P. In unstressed plants, similar decreases in Ps were reported in *Vicia faba* (Kassam and Elston, 1974), in soybeans (Sionit and Kramer, 1976) and in wheat (Morgan, 1980) in the field.

Here soil often becomes drier during the later stages. R and Ro is less in Indian Mustard as compared to *B.napus*. Values of APP AR, where increased APP AR indicates decreased tissue elasticity, were significantly greater in *B.napus* than in *B.juncea*. The parameters APP Ro and were significantly greater during full bloom and pod formation than AR at floral bud appearance (Elston et al, 1976). APP AR is related to Pso which decreased at later stages of growth, perhaps due to

transfer of organic solutes from the physiological older leaves to younger leaves. Higher Ro occurred when values of APP AR were high. *B.napus* (cv.Drakkar) took a longer time to mature than *B.juncea* (cv.Canadian Black). However, early and late maturing cultivars exist in the two species (Kumar et al, 1987). A particular maturity period is not confined to a particular species. Variations in drought resistance in crop species have often been attributed to the duration of growth (May and Milthorpe, 1962). However, in some Brassica species, it is not so (Richard and Thurling, 1978b). At different crop growth cycle significant variation within and between species of Brassica species respond differently as subjected to different drought conditions.

Seed yield and many physiological characters like osmotic adjustment and stomatal conductance were not related to the duration of growth in unstressed plants in Brassica species (Singh et al, 1985). Effect of drought is more impactful if it coincides with different growth stages of crop cycle. (Aspinall et al, 1964). Stress was imposed at several stages of plant development, covering both the vegetative and reproductive periods. Water shortage lowered the various expressions of water state. The extent of decline was different in the two species and three experiments. The water relations of the plants are dependent on the rate at which stress develops (Flower and Ludlow, 1986). Withholding water from plants growing in different media results in different rates of change in tissue water state. Water deficit developed slowly, probably because of the larger pots greater volume of available soil water and as compost were used, instead of the sand.

Drought made P, Ps and Pso more negative. The extent of depression varied with growth stages in the two species. The two species showed consistent differences. At wilting, P (P-Ps-Pso) was significantly more negative in *B.juncea* than in *B.napus* at all the stages of growth. The interaction species x growth stages x stress treatments were statistically significant. The plants reached zero Pp at higher P during full bloom than pod formation and floral bud appearance. The full bloom period in both species seemed to be the most susceptible to stress. Values of R at zero Pp were significantly smaller in *B.juncea* than *B.napus*. The interaction between species x stress treatments was not statistically significant but the interaction between species x growth stages was significant. In *B.juncea*, Ro was significantly lower at floral bud appearance than pod formation and full bloom. The lack of change in values of Ro at different growth stages in *B.napus* indicated that this species may have a specific dehydration tolerance. However, the response of one cultivar is not conclusive and should be tested further by including a number of cultivars. When drought was imposed for a shorter duration, P decreased by 0.1 to 0.3 MPa. The response of *B.juncea* was interesting in that there was a gradual change in P after an initial decline during the development of stress. In *B.napus*, there was a little change at the beginning and then it decreased rapidly as stress became severe. *B.juncea* delayed the development of more severe stress and was able to maintain a positive Pp for a longer time than *B.napus*. When stress was imposed until the plants showed visible wilting, the leaves of *B.juncea* took 1 to

3 days longer to reach zero Pp than did the leaves of B.napus. The rate of decline in Pp was 0.19 MPa per unit MPa P in B.juncea and 0.37 MPa per unit MPa P in B.napus. B.napus maintained a higher Pp but the leaves wilted after a comparatively smaller change in P. As P decreased below -1.0 MPa, B.juncea had a higher Pp than B.napus due to a greater decline in Ps. The total net difference in B.juncea was the maintenance of Pp. At zero Pp, P differed between the two species by 0.6 MPa.

Solute accumulation also occurred in B.napus but at a lower rate and to a more limited extent because a significantly smaller difference existed between Ps and Pso in B.napus than in B.juncea. This is mainly due to small augmentation in solute accumulation and which leads to slight changes in Ps before crop shows zero value of Pp. The rate of decline in Ps with R was statistically greater for B.juncea, 3.2 MPa per unit R, than for B.napus, 1.3 MPa per unit R. This would have a marked effect on the ability of the two species to maintain Pp as R decreases, B.juncea maintained a greater Pp over a wide range of R. The slight change in R value of Indian mustard directly change P, R fraction dissolves as Ro was very large. Therefore, the differences in Ro resulted from differences in changes in Ps and so differences in osmotic adjustment and tissue elasticity because APP, APP AR and Ro were significantly correlated in both species. Pp and Ps were statistically related only in B.juncea, therefore, drought resistance is mainly defined by elasticity of tissue and adjustment of osmotic pressure. Rewatering made P, Ps and Pso less negative. These became less negative in B.napus than in B.juncea. Therefore, there may be comparatively less advantage from previous stress cycles for B.napus in a subsequent period of stress. All values remained more negative at later stages of growth because the older tissues recovered less than the younger tissues.

Adjustment of osmotic pressure in roots, reproductive parts, hypocotyls and foliage of different crop species maintains partially or fully turgour pressure (Rada et al, 1989 and Morgan, 1984). This mechanism is less exposed towards researchers in *Brassica species*. Pp can be estimated approximately as P-Ps; when P-Ps the tissue would be at the point of incipient plasmolysis in laboratory measurements, and further lowering of P could result in physical damage. In B.napus, the decline in P was greater than the decline in Ps, indicating a lower degree of osmotic adjustment than in B.juncea. B.napus reached zero Pp at -1.8 MPa while B.juncea at -2.4 MPa. The decline in Pp with P s significantly greater in B.napus than in B.juncea. In an earlier study (Kumar et al, 1984), B.carinata showed a small decline in Pp from -1.6 to -2.4 MPa P, while Pp fell to zero at -2.8 MPa P in B.napus with a similar stress period for the plants grown in big containers.

Tugour pressure differs either difference arises during accumulation of solutes in cells and disparity at elasticity of cell wall (Richards and Turner, 1983). The outcome of osmotic pressure maintenance is R or water content continuance (Morgan, 1984). B.juncea with greater leaf dehydration resistance had low P at a given R (Ludlow, 1976). Weatherley and Slatyer (1957) explained that resilient plant

has more decline in P value as compared to R. This difference mainly due to cell wall elasticity (Johnson et al, 1984). Tissue turgidity is more in B. napus as compared to Indian Mustard. At zero Pp value of AR showed more R. The smaller values of for APP AR B.juncea than B.napus indicated a small change in Pp and P for a given change in R. Thus, the effect of cell volume on the gradient of P from soil in B.juncea will be small due to relatively small values of APP, Values of Ro in both species for AR watered treatments were greater than those for droughted treatments, a result expected when osmotic adjustment occurs (Turner and Jones, 1980) and represent an adaptation to drought stress (Elston et al, 1976). Ro was smaller in B.juncea than in B.napus.

The tissue water state components were correlated, and the relationships differed in the two species. So, B. juncea can develop a steeper P gradient from leaf to soil at a given R than B.napus (Coyne, Bradford and Dewald, 1982). The major statistical difference APP AR was that was related to R in B.napus and to P and Ps in B.juncea. B.juncea would have to lose less water in order to develop the necessary P gradient to extract water under limited availability situations. All physiological notations change if there is change from trait to trait. A decline in APP AR values of with a decrease in Ps observed in Indian mustard may be a mechanism to maintain Pp at least potentials of soil water. This would allow a large difference in P between leaves and soils to be produced with increase in uptake of water and loss of water in moisture stressed conditions.

### III. Conclusion

Rehydration seemed to have caused greater disappearance of solutes in B.napus than in B.juncea. B.juncea dehydration capacity is more than B.napus so that Indian mustard at low P easily maintains greater R. The maintenance of tugour pressure due to osmotic adjustment and elasticity of cell wall can be identified as integrated system. This clearly needs thought and should be investigated in future experiments.

### IV. References

- [1]. Ackerson, R.C., Krieg, D.R. and Sung, J.M. (1980). Leaf conductance and osmoregulation of field grown sorghum genotypes. *Crop Sci.*, 20, 10-14.
- [2]. Al-Saadi, H. and Wiebe, H.H. (1973). Survey of the matric water of various plant groups. *Plant Soil*, 39, 253-261.
- [3]. Al-Saadi, H. and Wiebe, H.H. (1975). The influence of maturity, season and part of plant on matric bound water. *Plant Soil*, 43, 371-376.
- [4]. Aspinall, D., Nicholls, P.B. and May, L.H. (1964). The effects of soil moisture stress on the growth of barley. I. Vegetative development and grain yield. *Aust. J Biol. Sci.*, 15, 729-745.
- [5]. Barrs, H.D. (1968). Determination of water deficit in plant tissues. In: *Water deficit and plant growth*. (ed. T.T. Kozlowski), vol. I, Academic Press, New York, London.



- [6]. Begg, J.E., Bierhuizen, J.F., Lemon, E.R., Misra, D.K., Slatyer, R.O. & Stern, W.R. (1964). Diurnal energy and water exchanges in bulrush millet in an area of high solar radiation. *Agric. Meteorol.*, 1, 294-312.
- [7]. Begg, J.E. and Turner N.C. (1976). Crop water deficits. *Adv. Agron.*, 28, 167-217.
- [8]. Blum, A. (1974). Genotypic responses in sorghum to drought stress. 1. Response to soil moisture stress. *Crop Sci.*, 14, 361-364.
- [9]. Boller, B.C. and Nosberger, J. (1985). Photosynthesis of white clover leaves as influenced by canopy position, leaf age, and temperature. *Ann. Bot.*, 56, 19-27.
- [10]. Briggs, G.E. (1967). Movement of water in plants. Blackwell Sei. Publ., Oxford, pp. 142.
- [11]. Burrows, F.J. and Milthorpe, FL. (1976). Stomatal conductance in the control of gas exchange. In: *Water deficits and plant growth*, Vol.4. (ed. T.T. Kozlowski). Academic Press, New York. pp. 103-152.
- [12]. Cowan, I.R. (1978). Stomatalbehaviour and environment. In: 'Advances in Botanical Research, Vol. 4'. (Eds. H.W. Woolhouse and R.D. Preston). Academic Press, London.
- [13]. Coyne, P.L., Bradford, J.A. and Dewald, C.I. (1982). Leaf water relations and gas exchange in relation to forage production in four asiatic bluestems. *Crop Sci.*, 22, 1036-1040.
- [14]. Duniway, J.M. and Durbin, R.D. (1971). Deterimental effect of rust infection on the water relations of bean. *Plant Physiol.*, 48, 69-72.
- [15]. Elston, J., Karamanos, A.J., Kassam, A.H. and Wadsworth, R.M. (1976). The water relations of field bean crops. *Phil. Trans. R. Soc. Lond. B.*, 273, 581-591.
- [16]. Flower, D.J. and Ludlow, M.M. (1986). Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeonpea (*Cajanuscajan* (L.) millsp.) leaves. *Plant Cell Enviorn.*, 9, 33-40.
- [17]. Gardner, W.R. and Ehlig, C.F. (1965). Physical aspects of the internal water relations of plant leaves. *Plant Physiol.*, 40, 705-710.
- [18]. Gollan, T., Passioura, J.B. and Munns, R. (1986). Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Aust. J. Plant Physiol.*, 13, 459-464.
- [19]. Gutschick, V.P. (1987). A functional biology of crop plants. Croom Helm, London and Sydney.
- [20]. Hardegree, S.P. (1989). Xylem water holding capacity as a source of error in water potential estimates made with the pressure chamber and thermocouple psychrometer. *Amer. J. Bot.*, 76, 356-360.
- [21]. Hsaio, T.C. (1973). Plant responses to water stress. *Annu. Rev. Plant Physiol.*, 24, 519-570.
- [22]. Hsaio, T.C., Fereres, E., Acevedo, E. and Henderson, D.W. (1976). Water stress and dynamics of growth and yield of crop plants. In: *Water and plant life-problems and modern approaches.*, *Ecol. Stud.*, 19, 281-305'. (eds. O.L. Lange, L. Kappen and E.D. Schulze). eds., Springer, Berlin, Heidelberg, New York.
- [23]. Huck, M.G., Peterson, C.M., Hoogenboom, G. and Busch, C.D. (1986). Distribution of dry matter between shoots and roots of irrigated and nonirrigated determinate soybeans. *Agron. J.*, 78, 807-813.
- [24]. Jarvis, P.G. and Jarvis, M.S. (1963). The water relations of tree seedlings. IV. Some aspects of the tissue water relations and drought resistance, *Physiol. Plant*, 16,501-516.
- [25]. Johnson, D.A., Richards, R.A. and Turner, N.C. (1983). Yield, water relations, gas exchange, and surface reflectances of near-isogenic wheat lines differing in glaucousness. *Crop Sci.*, 23, 318-328.
- [26]. Johnson, R.C., Nguyen, H.T. and Croy, L.I. (1984). Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. *Crop Sci.*, 24, 957-962.
- [27]. Jones, H.G. (1978). Modelling diurnal trends of leaf water potential in transpiring wheat. *J. Appl. Ecol.*, 15, 613-626.
- [28]. Jones, H.G. (1979). Stomatalbehaviour and breeding for drought resistance. In *Stress physiology in crop plants*. (eds. H. Mussell and R.C. Staples). Wiley Interscience, New York, Chichester, Brisbane, Toronto, pp. 407-428.
- [29]. Jones, H.G. (1980). Interaction and integration of adaptive responses to water stress: the implications of an unpredictable environment. In: *Adaptation of plants to water and high temperature stress'* (eds. N.C. Turner and P.J. Kramer). Wiley, New York, pp. 353-365.
- [30]. Jones, M.M. and Turner, N.C. (1978). Osmotic adjustment in leaves of sorghum in response to water deficits, *Plant Physiol.*, 61, 122-126.
- [31]. Jordan, W.R., Brown, K.W. and Thomas, J.C. (1975). Leaf age as a determinant in stomatal control of water loss from cotton during water stress. *Plant Physiol.*, 56, 595-599.
- [32]. Kassam, A.H. (1971). Some physical aspects of the water relations of *Viciafaba* L. Ph.D. Thesis, University of Reading. Kassam, A.H. (1972). Determination of water potential and tissue characteristics of leaves of *Viciafaba* L. *Hort. Res.*, 12, 13-23.
- [33]. Kassam, A.H. and Elston, J. (1974). Seasonal changes in the status of water and tissue characteristics of leaves of *Viciafaba* L. *Ann. Bot.*, 38, 419-429.
- [34]. Kassam, A.H. and Elston, J. (1976). Changes with age in the status of water and tissue characteristics of leaves of *Viciafaba* L. *Ann. Bot.*, 40, 669-679.
- [35]. Knipling, E.B. (1967). Effect of leaf ageing on water deficit-water potential relationships of dogwood

- leaves growing in two environments. *Physiol. Plant.*, 20, 65-72.
- [36]. Kramer, P.J. (1983). *Water relations of plants*. Academic press, Orlando.
- [37]. Kumar, A., Singh, D.P. and Singh, P. (1987). Genotypic variation in the responses of Brassica species to water deficits. *J. Agric. Sci. Camb.*, 109, 615-618.
- [38]. Kumar, A., Singh, D.P. and Yadav, S.K. (1987). Partitioning of dry matter accumulation in Aestivum and Durum wheats under irrigated and unirrigated conditions. *Indian J. Plant Physiol.*, 31, 104-106
- [39]. Kumar, A., Singh, P., Singh, D.P., Singh, H. and Sharma, H.C. (1984). Differences in osmoregulation in Brassica species. *Ann. Bot.*, 54, 537-541. Lang, A. and Thorpe, M.R. (1986). Water potential, translocation and assimilate J. *Exp. Bot.*, 37, 495-503.
- [40]. Levitt, J. (1972). *Responses of plants to environmental stresses*. Academic Press, New York.
- [41]. Ludlow, M.M. (1976). *Ecophysiology of C-4 grasses*. In: *Water and plant life problems and modern approaches*. (eds. O.L. Lange, L. Kappen and E.C. Schulze). Springer-Verlag, Berlin, pp. 364-386.
- [42]. Ludlow, M.M. (1980). Adaptive significance of stomatal response to water stress. In: *'Adaptation of plants to water and high temperature stress'*. (eds. N.C. Turner and P.J. Kramer), Wiley Interscience, New York.
- [43]. May, L.H. and Milthorpe, F.L. (1962). Drought resistance of crop plants. *Field Crop Abstr.*, 15, 171-179.
- [44]. Miller, L.N. (1972). Matric potentials in plants: Means of estimation and eco physiological significance. In: *Psychrometry in water relations research*. pp. 211-217.
- [45]. Morgan, J.M. (1977). Differences in osmoregulation between wheat genotypes *Nature*, 270, 234-235.
- [46]. Morgan, J.M. (1980). Differences in adaptation to water stress within crop species. In: *Adaptation of plants to water and high temperature stress*. (eds. N.C. Turner and P.J. Kramer). Wiley Interscience, New York, pp. 369-382.
- [47]. Morgan, J.M. (1983). Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.*, 34, 607-614.
- [48]. Morgan, J.M. (1984). Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.*, 35, 299-319.
- [49]. Noy-Meir, I. and Ginzburg, B.Z. (1967). An analysis of the water potential isotherm in plant tissue. I. The theory. *Aust. J. Biol. Sci.*, 20, 695-721.
- [50]. Noy-Meir, I. and Ginzburg, B.Z. (1969). An analysis of the water potential isotherm in plant tissue. II. Comparative studies on leaves of different types. *Aust. J. Biol. Sci.*, 22, 35-52.
- [51]. Passioura, J.B. (1983). Roots and drought resistance. *Agric. Water Manage.*, 7, 265-280.
- [52]. Rada, F., Goldstein, G., Orozco, A., Montilla, M., Zabala, O. and Azocar, A. (1989). Osmotic and turgor relations of three mangrove ecosystem species. *Aust. J. Plant Physiol.*, 16, 477-486.
- [53]. Richard, R.A. and Thurling, N. (1978a). Variation between and within species of rapeseed (*Brassica campestris* and *B.napus*) in response to drought stress. II. Growth and development under natural drought stresses. *Aust. J. Agric. Res.*, 29, 479-490.
- [54]. Richter, H. (1978). A diagram for the description of water relations in plant cells and organs. *J. Exp. Bot.*, 29, 1197-1203.
- [55]. Samsuddin, Z. and Impens, I. (1979). The development of photosynthesis rate with leaf age in *Hevea brasiliensis* Muell. Arg. clonal seedlings, *Photosynthetica*, 13, 267-270. Scheffe, H. (1953). A method for judging all contrasts in the analysis of variance. *Biometrika*, 40, 87-104.
- [56]. Scholander, P.F., Hammel, H.T., Hemingsen, E.A. and Bradstreet, E.D. (1964). Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proc. Nat. Acad. Sci. USA.*, 52, 119-125.
- [57]. Schonfeld, M.A., Johnson, R.C., Carver, B.F. and Mornhinweg, D.W. (1988) Water relations in winter wheat as drought resistance indicators. *Crop Sel*, 28, 526-531
- [58]. Schulze, E.D. and Hall, A.E. (1982). Stomatal responses, water loss and CO<sub>2</sub> assimilation rates of plants in contrasting environments. In: *Encyclopaedia of plant physiology II, New Series, Vol.12B'*. (eds. A. Pirson and M.H. Zimmermann). Springer-Verlag, Berlin. pp. 181-230.
- [59]. Singh, D.P., Singh, P. and Singh, M. (1982). Screening of genotypes of *Brassica juncea* L. for leaf conductance under field conditions. *J. Expt. Bot.*, 33, 381-387.
- [60]. Sionit, N. and Kramer, P.J. (1976). Water potential and stomatal resistance of sunflower and soybean subjected to water stress during various growth stages. *Plant Physiol.*, 58, 537-540.
- [61]. Slatyer, R.O. (1957). The influence of progressive increases in total moisture stress, on transpiration, growth and internal water relationships of plants. *Aust. J. Biol.Sci.*, 10, 320-336
- [62]. Slatyer, R.O. (1960). Aspects of the tissue water relationships of an important arid zone species (*Acacia aneura* F. muell) in comparison with two mesophytes. *Bull. Res. Coun. Israel*, 8D, 159-168.
- [63]. Slatyer, R.O. (1962). Internal water relations of higher plants. *Annu. Rev. Plant Physiol.*, 13, 351-378.
- [64]. Slatyer, R.O. (1967). *Plant water relationships*. Academic Press, New York. London.
- [65]. Slatyer, R.O. and Taylor, S.A. (1960). Terminology in plant and soil water relations. *Nature*, 187, 922-924.



- [66]. Soman, P. (1980). The effect of potassium and water stress on the water relations and growth of *Vicia faba* L. The Sutton. Ph.D. Thesis, University of Reading Stiles.
- [67]. Sung, F.J.M. (1981). The effect of leaf water status on stomatal activity, transpiration and nitrate reductase of sweet potato. *Agric. Water Manage.*, 4, 465-470.
- [68]. Teare, I.D. and Kanemasu, E.T. (1972). Stomatal-diffusion resistance and water potential of soybean and sorghum leaves. *New Phytol.*, 71, 805-810.
- [69]. Teare, I.D., Kanemasu, E.T., Powers, W.L. and Jacobs, H.S. (1973). Water use efficiency and its relation to crop canopy, stomatal regulation and root distribution. *Agron. J.*, 65, 207-211.
- [70]. Thomas, H. (1986). Effects of rate of dehydration on leaf water status and osmotic adjustment in *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. *Ann. Bot.*, 57, 225-235.
- [71]. Tumer, N.C. (1974). Stomatal behaviour and water status of maize, sorghum, and tobacco under field conditions. II. At low soil water potential. *Plant Physiol.*, 53, 360-365.
- [72]. Turner, N.C. (1979). Drought resistance and adaptation to water deficits in crop plants. In: 'Stress physiology in crop plants'. (eds. H. Mussell and R.C. Staples). John Wiley and Sons, New York, Chichester, Brisbane, Toronto. pp. 343-372.
- [73]. Turner, N.C. and Begg, J.E. (1981). Plant-water relations and adaptations to stress. *Plant Soil*, 58, 97-131.
- [74]. Turner, N.C., Begg, J.E. and Tonnet, M.L. (1978). Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. *Aust. J. Plant Physiol.*, 5, 597-608.
- [75]. Turner, N.C. and Heichel, G.H. (1977). Stomatal development and seasonal changes in diffusive resistance of primary and regrowth foliage of red oak (*Acer rubrum* L.). *New Phytol.*, 78, 71-81.
- [76]. Turner, N.C. and Jones, M.M. (1980). Turgor maintenance by osmotic adjustment: a review and evaluation. In: 'Adaptation of plants to water and high temperature stress. (eds. N.C. Turner and P.J. Kramer). Wiley Interscience, New York, pp. 87-103.
- [77]. Tyree, M.T. (1976). Negative turgor pressure in plant cells: fact or fallacy! *Can. J. Bot.*, 54, 2738-2746.
- [78]. Warren Wilson, J. (1967a). The components of leaf water potential. 11. Pressure potential and water potential. *Aust. J. Biol. Sci.*, 20, 349-357.
- [79]. Warren Wilson, J. (1967b). The components of leaf water potential. 1. Osmotic and matric potential. *Aust. J. Biol. Sci.*, 20, 329-347.
- [80]. Warren Wilson, J. (1967c). The components of leaf water potential. III. Effects of tissue characteristics and relative water content on water potential. *Aust. J. Biol. Sci.*, 20, 359-367.
- [81]. Weatherley, P.E. (1970). Some aspects of water relations. *Adv. Bot. Res.*, 3, 171-206.
- [82]. Weatherley, P.E. and Slatyer, R.O. (1957). Relationship between relative turgidity and diffusion pressure deficit in leaves. *Nature*, 179, 1085-1086.
- [83]. Wiebe, H.H. (1966). Matric potential of several plant tissues and biocolloids. *Plant Physiol.*, 41, 1439-1442.
- [84]. Wright, G.C., Rahmianna, A. and Hatfield, P.M. (1988). A comparison of thermocouple psychrometer and pressure chamber measurements of leaf water potential in peanuts. *Expl. Agric.*, 24, 355-359.