INTERDROUGHT

INTEGRATED STUDY ON DROUGHT TOLERANCE OF HIGHER PLANTS

FIRST INTERNATIONAL MEETING

PROCEEDINGS

August 30th - September 2nd 1995
MONTPELLIER - France

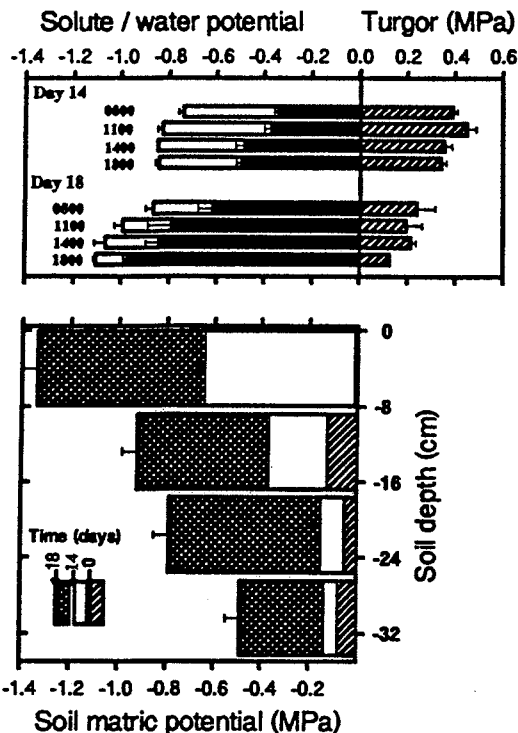# Does soil nutrient uptake control drought perception in plants?

Urs Schmidhalter, Institute of Plant Sciences, ETH Zürich, Switzerland

Recent discussion of drought perception in plants has focused on chemical messages originating from dehydrating roots (e.g. Davies and Zhang, 1991) and more recently on the integration of hydraulic and chemical signals which control stomatal conductance of plants in drying soils (Tardieu and Davies, 1993). This seems to be adequate for non-growing tissues. However, the growth process per se reacts even more sensitive to reduced water supply from the soil. Hence drought will be sensed first in growing organs. The question where and how drought is perceived becomes then what limits the growth process. In monocotyledonous plants, to which the discussion is restricted to, the growth process is confined to a well-defined zone, about 30 mm in length in maize and wheat plants, enclosed within a whorl of encircling leaf sheaths. It is generally accepted that reduced leaf elongation is one of the most sensitive processes in monocots subjected to drought. Therefore, limiting factors in leaf elongation will be outlined. In this context basic properties like leaf extensibility and yield turgor threshold and their modification by drought will be discussed. It is important to distinguish between water status in the elongated part of the leaf and in the elongating part. Although properties like turgor may be similar in both tissues, the measurements have to be interpreted carefully. Maintenance of turgor must not mean that growth is not restricted, and for the growth process it is essential to consider the yield turgor threshold or effective turgor and not the turgor. This presentation will be completed by an analysis of growth kinematics showing that nutrient uptake under water stress could limit growth and hence sensed as primary information of drought stress.

Drought perception in a plant physiologist's view might mean a primary reaction of a plant to a beginning drought, whereas an agronomist rather thinks of the resulting response of drought. The sites were plants perceive drought is a matter of discussion. Are roots really sensors of drought? Some shortcomings in the present discussion about drought sensing from dehydrating roots are pointed out. Recent questions regarding measurements of root water status will be addressed. For the measurements of root water status we have adopted the pressure chamber technique (Schmidhalter et al., 1992a). The information obtained from these studies is used to raise some questions which are not adequately answered.

Are roots sensors of soil dryness? Measurements of soil water uptake from spatially variable soil matric potentials have shown that water uptake occurs from zones with high soil matric potentials as long as the evaporative demand can be met by roots present there (Fig. 1) (Schmidhalter et al., 1992b). If the evaporative demand exceeds the amount of water supplied by roots, leaf and root water potentials decrease, thus enabling the roots to extract water from drier zones, provided that a sufficiently steep gradient exists from the soil to the leaves.

Is the root water status in zones with different soil matric potentials different? Pre-dawn measurements of the water status of roots present in moist and dry soil layers show that roots in dry zones are supplied with water from roots growing in wet zones (Fig. 2) (Schmidhalter et al., 1992b). The well-known phenomenon of hydraulic lift supports this assumption. Roots are hydraulically connected. Signals produced in "dry" roots would thus be diluted. In split-root experiments it was

Solute / water potential   Turgor (MPa)

-1.4 -1.2 -1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6

Soil depth (cm)

-1.4 -1.2 -1.0 -0.8 -0.6 -0.4 -0.2
Soil matric potential (MPa)

found that the water potential in the root tip+2 cm was comparable or higher in the unwatered pot than in the watered pot, whereas the root tip water potential was clearly lower in stressed roots (Davies et al., 1986). Water (chemical message) transport could occur against a positive water potential gradient because of root pressure induced during the night.The above findings rather point to roots sensing first wetness and then dryness. A critical root mass present in moist layers will largely determine water uptake. If water loss from leaves exceeds uptake and with subsequently decreasing root water potentials, roots in drier zones will contribute to water uptake. If plants tend to "maintain" the water status of roots extending in dry zones, why then ABA e.g. could be produced there? Growth reduction might induce a production of chemical signals.

Fig. 1. *Diurnal variation in the leaf water potential components of water stressed maize plants, 14 and 18 days after beginning the experiment. Soil matric potentials at different soil depths are shown in the bottom.*
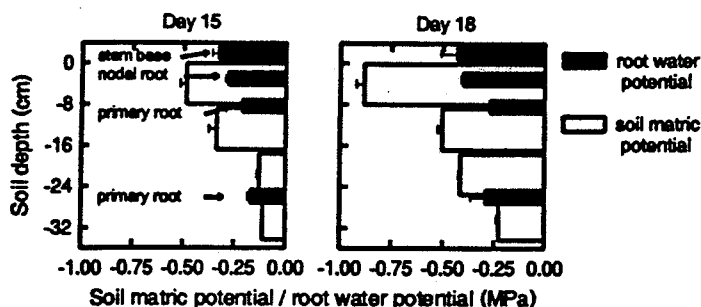

Soil depth (cm)

-1.00 -0.75 -0.50 -0.25 0.00 -1.00 -0.75 -0.50 -0.25 0.00
Soil matric potential / root water potential (MPa)

Fig. 2. *Soil matric potentials and root water potentials measured in different soil depths 15 and 18 days after beginning the experiment. Horizontal bars indicate standard errors.*

Is the soil matric potential in the vicinity of roots different from the bulk soil water potential? Experiments carried out with seedlings of four different species grown in a silt loam soil show that significant gradients between bulk soil and rhizoplane soil were only found at soil matric potentials lower than -0.22 MPa.

ABA is synthesized by dehydrating roots (Walton 1976). **When do roots get dehydrated and to which degree?** Capacitance and elasticity are significantly higher in roots than in shoots (Evéquoz et al., 1992). The drop in water potential from a decreased relative water content is much more gradual in roots than in shoots of maize plants (Fig. 3) (Schmidhalter and Evéquoz, 1994). However, water potentials of shoots oscillate much more than in roots (Burucs and Schmidhalter, 1995, unpublished). We frequently observed that root water potentials decrease only little if plants are subjected to mild or moderate water stress. Roots are normally only little dehydrated.
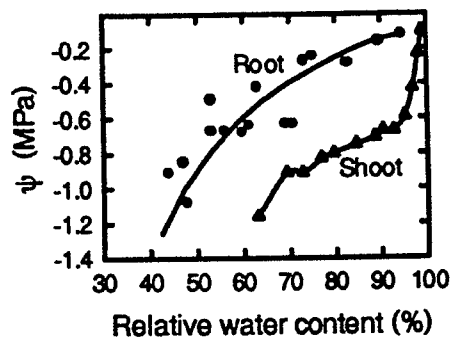
Fig. 3. *Moisture release curves of shoot and roots of soil grown maize plants.*

Does increased hydraulic resistance in roots control stomatal conductance in leaves?
Resistances in roots and shoots can be constant as well as variable. Whereas in shoots a threshold value seems to be involved, that means that the drop in water potential across the shoot is sometimes insensitive to transpiration rate, roots are characterized by gradually increasing resistances at relatively high water potentials (Schmidhalter, 1995, unpublished data). A theoretical analysis based on soil moisture release curves of shoot and roots showed that increases in root resistance are observed at high water potentials (2fold increase at -0.05 MPa, 10fold at -0.16 MPa, 100fold at -0.5 MPa) whereas in shoots a 0.1fold increase was found at -0.5 MPa, 2fold increase at -0.63 MPa, 10fold increase at -0.8 MPa, and 100fold increase at -1 MPa. It is not the absolute value which interest us, but rather the different behaviour of root and shoot tissues.
Stronger reductions of hydraulic resistance at decreased water availability in roots as compared with shoots could be a sensitive factor involved in signalling drought stress. However, at mild and moderate water stress root water status is normally maintained at relatively high water potentials. Possibly cavitation events occur earlier in roots than in shoots. Increasing cavitation could also be a mechanism to prevent further water losses.

Is early drought stress reflected in changed water status? We do not elaborate this issue, because there is ample evidence that under mild water stress water status in shoots and in roots (unpublished own data) must not be changed. However, water status can change fast and may be highly backregulated. Hydraulic signals precede chemical signals. A short term shrinkage of roots or increased hydraulic resistance resulting from embolisms might affect the degree of stomatal opening. Reductions in the amount of water lost by transpiration can then again result in increased water potential. With mild water stress it can be observed that turgor is maintained although leaf elongation is reduced. Increased osmotica concentration may simply result from reduced growth. Interpretation of the water status and the growth process based on osmotica concentration alone can be misleading. Growth is better characterized by the effective turgor, that means turgor above a threshold value, which induces plastic deformation. Water stress modifies this property and differently in several varieties. Modifications in the yield threshold turgor seem to be more growth limiting than changes in leaf extensibility.

Is drought initially perceived in monocotyledonous plants as reduction in leaf elongation? It is generally accepted that reduction in leaf elongation in monocotyledonous plants is one of the most sensitive reactions of plants to beginning drought stress. These changes can occur before significant differences in water potential, osmotic potential and turgor of roots and shoots, or assimilation are observed. Drought was expressed as reduced leaf elongation before differences in stomatal conductance or transpiration were observed. Reduced leaf elongation results from decreases in the segmental elongation rate in the growth zone and from reduced length of the growth zone (Fig. 4).
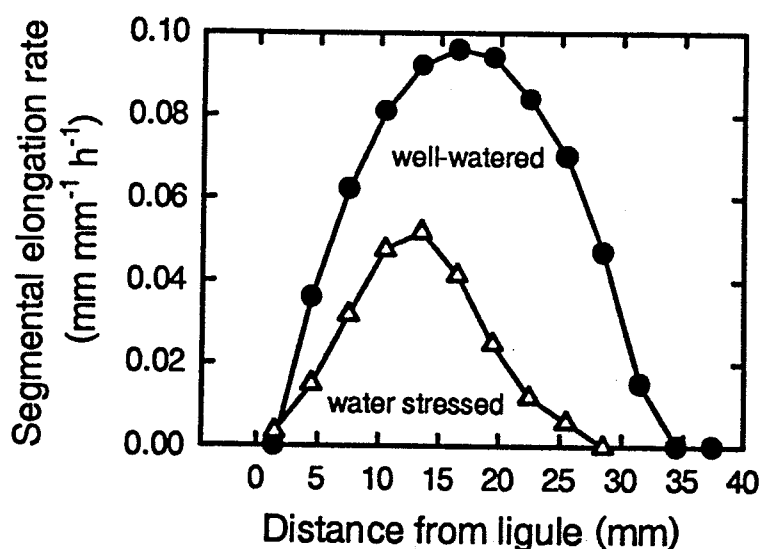

Fig. 4. *Segmental elongation rates within the elongation zone in well-watered and water stressed maize plants.*

Net deposition rate of water parallels the observed reductions in segmental elongation rate. Half-time rates of water exchange occur much faster than solute uptake. The amount of water which is used for the expansion of cell volume is small as compared with the total amount which is lost by transpiration. The growth process may be more limited by solute uptake than by water uptake. Solutes are not only required to fulfill the demand for increased cell volume but limit growth by specific roles played in the metabolism. Higher concentrations of water soluble carbohydrates and similar amounts of ions were found in the growth zone of water stressed maize plants as compared with well-watered plants (Fig. 5). These findings could easily be misinterpreted. A better understanding is obtained by quantifying the deposition rates of various compounds in the growth zone. It can be shown that carbohydrate probably do not limit growth under water stress, whereas the net deposition rates of several ions is clearly reduced (Fig. 5; Evéquoz and Schmidhalter, 1995, unpublished results). Reductions in net deposition rate were found for Ca, Mg, Na, P, K. However, growth reduction could not be explained by the total of these ions. In this experiments nitrate are nitrogenous compounds were not measured. There is indirect evidence from other experiments that these compounds might be causally involved in reduced leaf elongation. By varying the supply of nutrients to water stressed maize plants the highest shoot biomass production was obtained with optimal N supply or the combination of N+P (Studer and Schmidhalter, 1995, unpublished). It is possible that changes in the yield turgor threshold which are observed under water stress result from metabolic limitations which reduce cell volume growth. In drying soils the delivery of nutrients is strongly decreased. Roots are probably better supplied with inorganic soil nutrients and thus also represent stronger sinks for organic compounds leading finally to increased root/shoot ratio. Improving the fertility status of a soil may increase production under drought stress, but eventually

exerts only a small effect, because water may be available in lower soil depths, but nutrients are not available in dry top soil layers. Therefore, one strategy could be to improve the subsoil fertility level or to select plants with root systems showing better affinities for nutrient uptake.
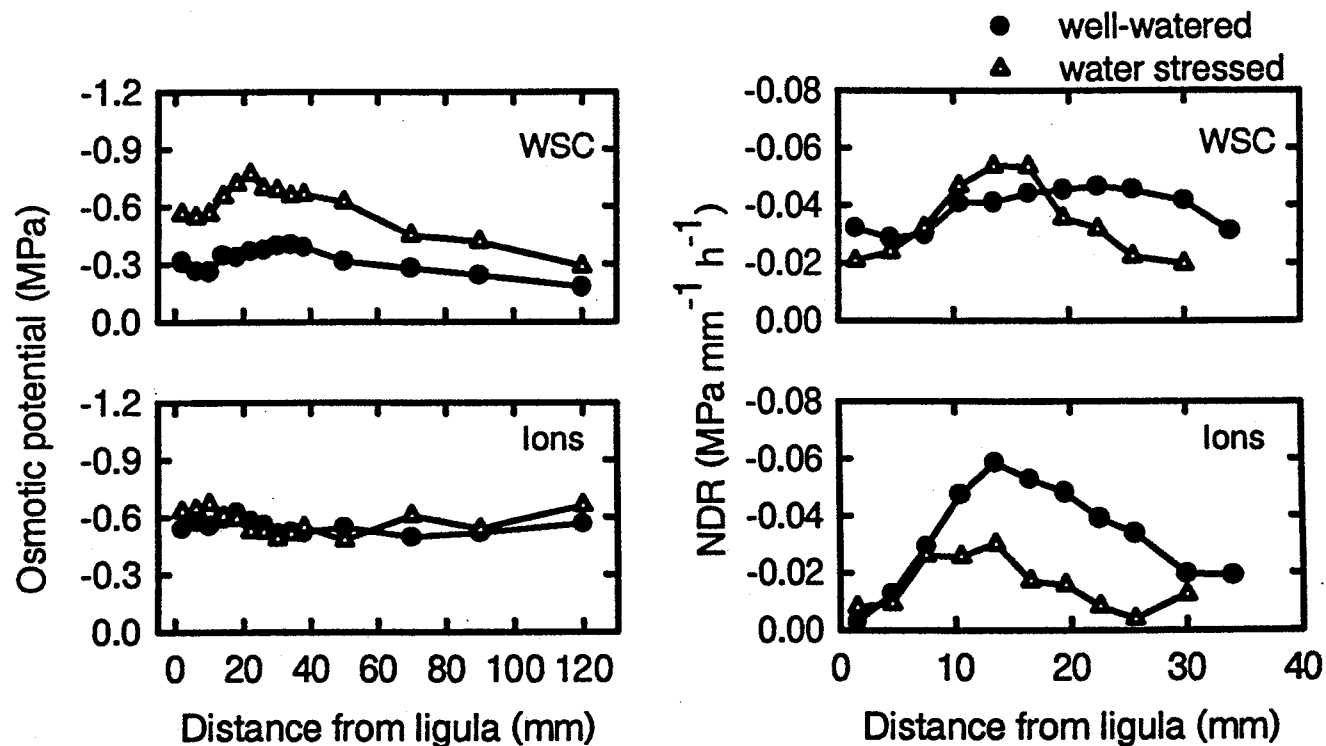

Fig. 5. *Spatial distribution of osmotic potential and net depostion rates (NDR) of water soluble carbohydrates (WSC) and ions within and distal to the elongation zone of well-watered and drougth stressed maize leaf blades.*

References

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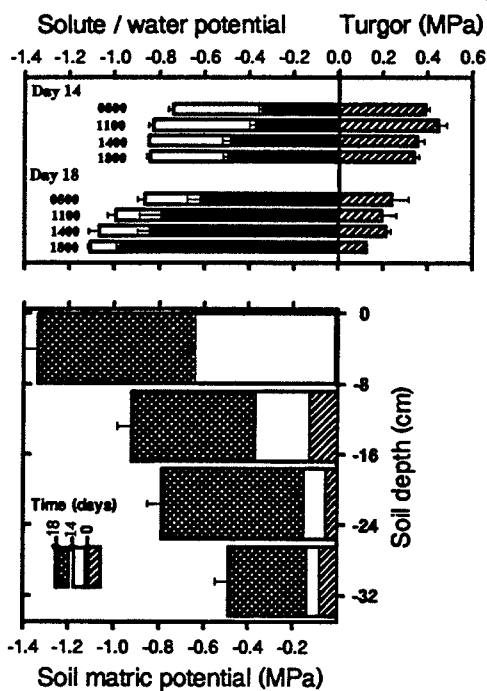
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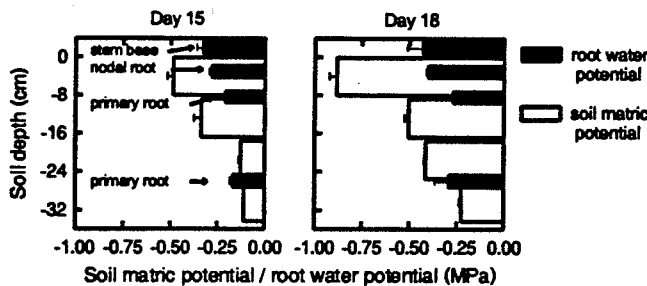

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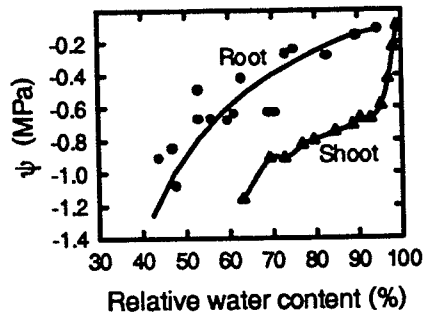
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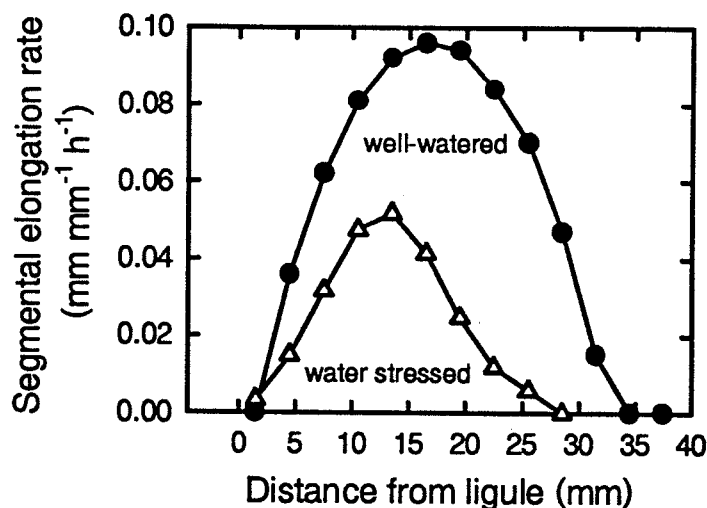

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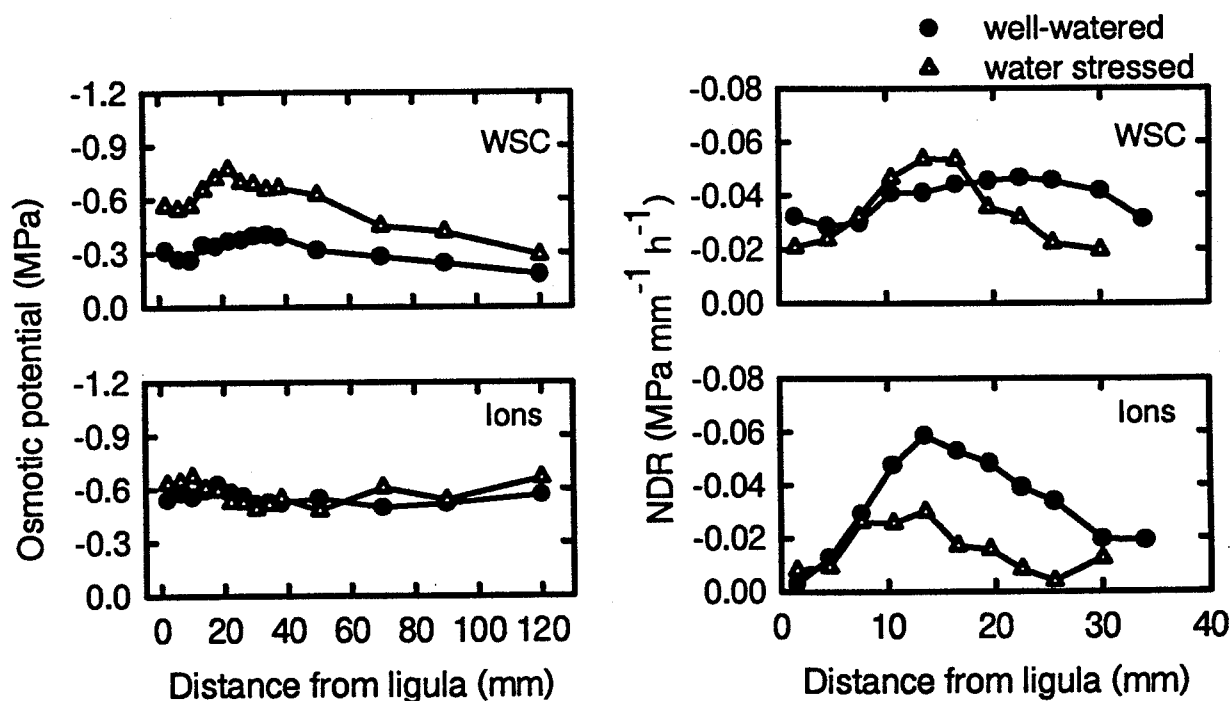

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