Response to Dr P. J. Kramer's article, 'Changing concepts regarding plant water relations', Volume 11, Number 7, pp. 565–568

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Looking back on a more than 50 year's experience in the field, Kramer is concerned that certain sound principles of plant water relations seem to be questioned which, in his opinion, has no adequate basis. Physical concepts tend to be modified or replaced by 'weaker' physiological or biochemical principles. To clarify his concern, Kramer questions the value of four topics which have been raised recently:

(1) Cell volume or relative water content may be better parameters expressing metabolic effects on water status than water potential (ψ). He suggests that water potential should be used because it is the wider concept based on thermodynamic laws.

(2) Growth may occur despite turgor loss. Kramer reminds that this is not a new concept, since growth has always been considered to depend on both, water status and cell wall extensibility.

(3) The importance of hydraulic vs biochemical effects of water stress, especially with respect to stomatal response.

(4) The role of root vs shoot as the primary sensor for water stress. He thinks that observations of root signals result from very special experimental conditions which do not generally apply to situations in the field.

The considerations of Kramer are very useful in that they focus on recent issues in plant water relations from a long-term perspective. Nevertheless, his concern may also reflect a change in scientific thinking. While previously we were used to looking for the 'most important factor', we are trained today to consider multifactorial systems, non-linear processes and changes in the optimum response. This may contribute to the discrepancies discussed.

Water status of plants: cell volume vs water potential

The discussion of the issue is not new. When the concept of water potential was introduced by Slatyer (1967) and others, some physiologists opposed (e.g. Walter & Kreeb, 1970) by pointing out that water potential may not be the best parameter for describing physiological processes. There is now a general agreement that water potential gradients are the driving force for the water transport in plants although modifications of the driving force may occur in the pres-

ence of interactions between water and solute flows which may be expressed by the formalism of irreversible thermodynamics (Dainty, 1963; Zimmermann & Steudle, 1978). Usually, these coupling effects are not very important for mature plant cells, but should be important for the uptake of nutrients into roots, for growth, and for phloem transport (Fiscus, 1975; Steudle, 1985; Steudle, Oren & Schulze, 1987). However, in spite of this, we agree with Kramer that the term water potential is a useful one. Of course, this does not mean that the availability of water as expressed by ψ will limit any metabolic reaction in the living plant. The terms relative water content and cell volume are also useful and should not be omitted.

In our opinion, it would be much more important, to work out the mechanisms by which plants respond to changes in water potential, relative water content, cell volume or other physiological variables rather than to erect a hierarchy of different parameters. For example, during osmoregulation, plants adjust to changes in water potential by varying their internal osmotic pressure in order to maintain (within certain limits) a constant turgor and/or volume. For algal cells both types of regulation (turgor and volume regulation) exist (Kauss, 1977; Zimmermann, 1978). It has been shown that physical parameters such as membrane stretching and compression transform changes of water potential, turgor, and volume into metabolic responses such as active membrane transport (Coster, Steudle & Zimmermann, 1977).

There are also examples of pressure dependent transport in higher plants (e.g. Steudle, Zimmermann & Zillikens, 1982; Steudle & Zimmermann, 1984). Nevertheless, there is not doubt that there is an active response of living cells or organs, such that they can maintain their metabolism in the presence of an adverse water potential in the surroundings.

Growth: turgor vs wall extensibility and solute transport

According to Lockhart (1965), growth is the result of a viscous flow of matter and a concomitant flow of water whereby the former needs a certain minimum wall stress (yield) to occur. Hence, both the hydraulic conductivity or the wall extensibility could, in principle, become rate limiting (Molz & Boyer, 1978; Steudle, 1985; Cleland, 1986). In the experiments of Boyer, Cavalieri & Schulze (1985), both parameters were

equally important. There are situations which do not allow growth despite sufficient turgor or which allow growth despite turgor loss. The recent experiments cited by Kramer only point to the fact, that 'extremes' may be more common than previously thought. In the basic experiments of Green, Erickson & Buggy (1971) on individual cells of *Nitella,* it became already clear that despite the limitation of growth by wall extensibility there was also a metabolic control of growth. This control could, in principle, work through a shift in the yield threshold or *via* solute transport, which, in turn, results in a coupling between water and solute flows (Steudle, 1985). Recent unpublished experiments of Dr Hsiao carried out at Bayreuth on elongating maize roots support this view. Experiments with *Vigna* showed that growth was reduced when plants were grown at different air humidities despite higher leaf water contents in dry air (Nagarajah & Schulze, 1983). Again, growth appears to be not a purely physical process only driven by turgor and depending on wall mechanics. It seems to be regulated by physical *and* metabolic processes, whereby in a complex tissue or organ the decision which of the processes is rate limiting, is not easy and a more advanced model than that of Lockhart (1965) will be required in future (Shackel, Matthews & Morrison, 1987).

Water stress: hydraulic vs biochemical effects

Improved analytical methods show that many processes which were previously thought to be purely hydraulic in nature are in fact related to metabolism. In many cases, changes in plant water status are converted into ion fluxes. Stomatal response may be taken as an example. From the observation of Hsiao (1973) on potassium transport in guard cells, it is clear that most stomatal responses are associated with ion fluxes (Raschke, 1979). Even the stomatal responses to humidity, which were initially interpreted to be purely hydraulic (Lange *et al.,* 1971) are linked to potassium transport (Lösch, 1978). Only *transient* responses following perturbations appear to follow a 'pipe model' of plant water relations but they are generally regulated again by some metabolic action (Schulze, 1986).

Schulze & Hall (1982) pointed out that the same water potential may be reached by strongly transpiring well-watered plants at high photosynthesis or by water-stressed plants at low transpiration rates. The hydraulic effect in the well-watered plant was reversible and had no effect on plant performance, i.e. stomata were most widely open at the lowest potential. In contrast, the response to soil drought was non-reversible and indicated biochemical effects due to changes in root water status.

Primary signals of water stress: root vs shoot

The cuticle exhibiting a very low hydraulic conductivity (by a factor of 10^4–10^6 less than a cell membrane;

Schönherr, 1982) uncouples the leaf from its environment. Thus, the response time of roots to changes in water potential of the environment should be much smaller than that of leaves. The initial observation on root effects was made in field experiments, where leaf conductance did not correlate with leaf water potential (Schulze *et al.,* 1980; Bates & Hall, 1981). Running (1980) correlated stomatal conductance with predawn ψ as a measure of root water status. Turner, Schulze & Gollan (1985) and Gollan, Turner & Schulze (1985) found that stomatal conductance of a leaf in an environment of constant humidity did not respond uniformly to changes in bulk leaf water potential. If ψ was changed by transpiration of the whole plant, the stomatal response to ψ was less than the response to water potential at dry soil.

Even in plants where xylem water potential was close to zero and did not change while the soil was drying, leaf conductance decreased even though the leaves remained fully turgid (Gollan, Passioura & Munns, 1986). In these experiments, the root system was the only part that experienced a decrease in water potential. There was no difference in the initial phase of stomatal closure at drying soil between plants with or without controlled xylem water potential. Only at very dry soil there was an addititional direct effect of leaf water potential on leaf conductance (Gollan, unpublished data).

The nature of the root to shoot communication of drying soil is still unclear but is not necessarily a hydraulic transmission. The ionic composition and the pH of the xylem sap changed with drying soil (Gollan, 1987). This could cause a release of ABA from the leaf internal storage into the apoplast (Cowan *et al.,* 1982). Also, at dry soil ABA is transported in the xylem sap at concentrations 100 times higher than at wet soil (Schurr, 1987). Associated with the increase in ABA concentration, stomatal conductance decreased but the sensitivity of the response was modulated by the ionic composition of the xylem sap (Gollan, 1987).

The time lag for the transmission of a root signal is important. In herbaceous species the xylem water stream may reach velocities of $100\ \mathrm{mh^{-1}}$ (Ziegler, 1982). Due to the high conductance and rigidity of the xylem system changes in water potential will be transmitted rapidly. In contrast, the time lag for solutes to appear in the shoot of trees should last much longer. In conifers water moves at a rate of about $1\ \mathrm{mh^{-1}}$. In this case, a hydraulic signal may be faster. Nobel (1983) showed that xylem and phloem water relations parameters are linked. If ψ decreases in the leaf, the turgor of sieve elements will also decrease. Plants may balance the change in ψ by increasing phloem loading. If a decrease of leaf water potential would lower the pressure in the phloem, a reversed phloem flow could occur, which was not observed using $^{11}CO_2$ (Goeschl *et al.,* 1988). However, it has been observed that the sap flow in the phloem stops in drying soil, probably, because of an influence on the unloading process in

the root. This would create an immediate signal to the leaves, even in conifers. Again, the originating site for this signal would be the root. The indication that such regulative mechanisms exist in the field was supported by the observation that the range between maximum and minimum water potential shift during the day even when the soil dries (Kappen et al., 1975).

The term water stress if often used in a very general sense. Water stress situations in field and laboratory experiments differ in terms of duration, periodicity, severity of stress and in the stressed organ. In each case the relevance of chemical versus hydraulic signals has to be evaluated. We think that root signals are important in the field and in the forest, even if the water potential of the leaves is lower than that of the roots. Especially in situations where stress develops slowly, stress-induced metabolic signals could be integrated, which is hard to envisage for hydraulic signals. One example for such an integration is the fact that ABA concentration does not only increase in dry soil but also in plants with low nitrate nutrition irrespective of soil water status (Gollan, 1987). Therefore, root-to-shoot signals may be important in environments with periodically changing soil conditions as defining the thresholds for short-term responses (metabolic or hydraulic). Structurally these thresholds could be due to morphological changes (e.g. stomatal frequency) or to changes of the sensitivity of stomata (Gollan, 1987), especially if one proposes plant growth regulators to be involved in root to shoot communication (Schurr, 1987). In this context, stress intensity has to be considered. If roots are stressed so severely that hydraulic effects do occur in the shoot, other than metabolic effects in the root will also cause changes in the shoot. One has to think about 'hydraulic' and 'metabolically' communicated stresses, whereby the relative importance of the different signals depend on the physiological state of the plant.

Conclusions

We see that numerous hydraulic effects are interrelated with ionic or biochemical events. The nature of the primary sensor could, in principle, be both hydraulic (turgor, hydraulic conductivity, elasticity etc) or metabolic (rate of biochemical reaction, active membrane transport, translocation etc). Changes in the nutrient supply may occur prior to or in parallel with changes in water relations. In spite of this, we cannot see that the concept of water transport based on thermodynamic principles is getting lost during this discussion. However, the complementation of these concepts seems to be necessary in order to relate plant hydraulics with solute relations and metabolic events. New experimental and theoretical approaches seem to be necessary in order to arrive at a more integrative view of plant water relations. If this is done properly, the result should not contradict the sound physical basis of water transport.

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