

The future of water relations of plants

Ulrich Zimmermann

ZIM Plant Technology GmbH, Neuendorfstr. 19, D-16761 Hennigsdorf, Germany.

*Corresponding author: zimmermann@zim-plant-technology.de

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Water shortage will increase dramatically in the near future due to climate change and the increased demand for crop production to feed the world's fast growing population. Agriculture is the largest consumer of water. For growers it is frequently more cost-efficient to over-irrigate than to risk the crop being stressed either early or at a later stage of growth. However, over-irrigation wastes water, energy, labour and leads to the progressive salinization of arable land (particularly in arid regions). Furthermore, it leaches expensive nutrients below the root zone out of reach of plants, reduces soil aeration and thus crop yields.

Optimum irrigation scheduling implies determining precisely both the timing of irrigation and the quantity of water to apply. Irrigation scheduling decisions are frequently based on the determination of soil moisture content or soil moisture tension. These sensors give only limited information because of the large variations of plant/crop responses to water deficits. The complex hydraulic architecture of plants is still not sufficiently understood. A very good example for our inadequate understanding of plant water relations is the anti-gravitational water ascent. The Cohesion Theory assumes that xylem vessels are continuously filled with water and that negative pressure gradients are generated in the vessels due to transpiration (up to -15 MPa) which drives exclusively long-distance water transport. Even though water under negative pressure (tensions > 0.1MPa) is in a metastable state, the Cohesion Theory has prevailed largely unmodified

for > 100 years, a somewhat unusual situation for a scientific paradigm explaining a fundamental process as stated by Meinzer et al. (2001). Beginning 1990s, however, the introduction of the xylem pressure probe and other new techniques (e.g. ^1H nuclear magnetic resonance imaging, the gas-bubble-based jet discharge method etc.; Zimmermann et al. 2004, Westhoff et al. 2009a) has challenged the Cohesion Theory as the whole mechanism by which water ascends and have stimulated a lively debate in a field previously characterized by a dangerous degree of complacency (Meinzer et al. 2001).

Turgor pressure measurements using the highly sophisticated cell turgor pressure probe and direct xylem vessel probing by using the xylem pressure probe have shown (literature quoted in Zimmermann et al. 2004) that transpiration-induced tension (in co-operation with the water relation parameters of the adjacent tissue cells) obviously plays a crucial role in water lifting as long as water continuity in the vessels is maintained. However, the absolute maximum magnitude of negatives pressures measured in herbaceous plants of laboratory-size subjected to drought was about -0.6 MPa and thus much less than needed for water lifting in taller trees.

Today, a bulk of results disclosed no evidence for continuous water filled vessels, particularly in trees (e.g. Westhoff et al. 2009a). The data suggest that trees use a broad spectrum of complementary strategies for anti-gravitational water ascent to cope with water deficiency without the

necessity of developing incredibly negative pressures. Driving forces include — among other forces — mucilage-supported water ascent and mucilage-supported reverse transpiration. These gel-mediated driving forces play an important role in water lifting of plants subjected to drought and salinity (Zimmermann et al. 2004, Westhoff et al. 2009b). Gradients of filamentary gel structures in the vessels of stressed plants can be visualized by precipitation with the dye alcian blue (Figure 1A). Mucilage gradients overcompensate the gravitational term and generate, in turn, a driving force from the roots to the leaves. Epistomatal mucilage plugs (Figure 1B) are involved in moisture uptake from the atmosphere (reverse transpiration) and buffering leaf cells against complete turgor pressure loss at low humidity.

These and other results demonstrate the complexity of the hydraulic network in maintaining the water balance of higher plants. The introduction of the small, non-invasive magnetic leaf patch clamp pressure probe (so-called ZIM-probe) for measuring relative changes in turgor pressure has opened up numerous possibilities to reveal the spatial and temporal dynamics of the water relations of small laboratory-sized plants up to tall trees (e.g. by multiple probe readings). Moreover, the magnetic probe represents a user-friendly and field-suitable monitoring system that allows the continuous measurement of the water supply of plants under field conditions in real time and with high precision (see e.g. Figure 2 and the examples in the review article of Zimmermann et al. 2013) over an entire vegetation period. It can be applied to all leafy plant species. Data are sent wireless by telemetric units to a GPRS modem which is linked to an Internet server *via* a mobile phone network from which the data can be downloaded by smartphones, tablets or laptops. Thus, drought, salinity or irrigation effects on the plants are available for the researcher or grower in real time.

A further quantum leap in elucidation of the water relations of plant and trees under outside conditions as well as of agricultural water management is expected if the ZIM-probe technology is combined with satellite or aerial remote sensing technology. Vegetation images of crop growth from planting to harvest are valuable, but need to be interpreted. ZIM-probes are certainly one of the key technologies which will provide a straightforward interpretation of satellite imagery data taken at different spatial, spectral and temporal resolutions.

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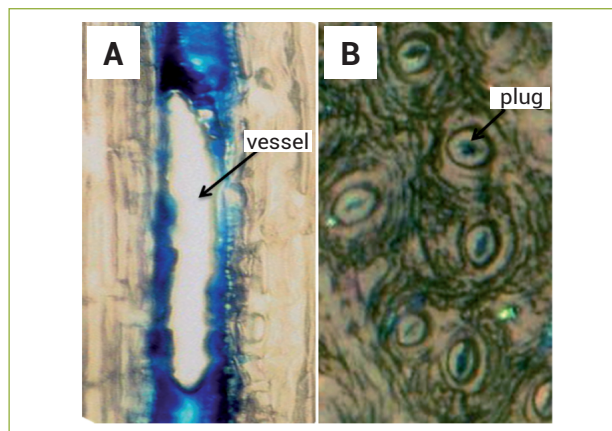


Figure 1. Evidence for mucilage in xylem vessels (A) and epistomatal mucilage plugs extending into the substomatal cavity (B) verified by 24 h-exposure of leaves of drought-stressed plants to an alcian blue solution.

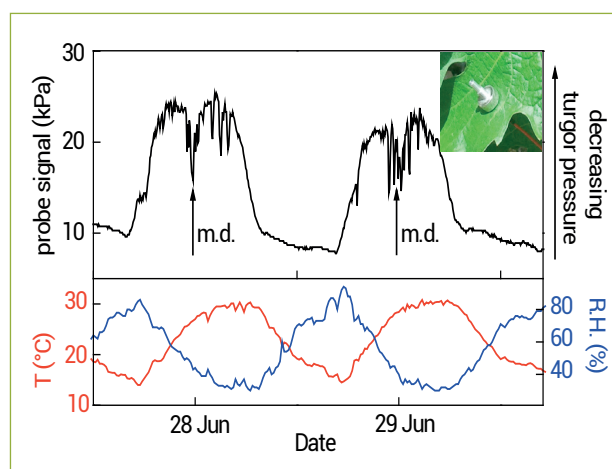


Figure 2. Typical diurnal changes of the signal of the ZIM-probe (inversely correlated with turgor pressure measured on grapevine on a hot day). Note that the midday depression (m.d.; closure of the stomata) is recorded by the probe with high precision. For more details, see Zimmermann et al. (2013).

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