Control of gas exchange: evidence for root–shoot communication on drying soil

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Decrease in leaf conductance (stomatal closure) with drying soil is a common phenomenon and has been reported in myriads of publications. Stomatal closure with soil drying generally occurs in parallel with a deterioration of plant water status. With a decrease in relative water content, leaf turgor and water potential in general decline. Since both leaf conductance and leaf water potential decrease more or less at the same time during a drying cycle, the decrease in leaf conductance is often explained as a function of the decrease in leaf water potential. During the last few years, increasing evidence has been accumulated that stomatal closure at drying soil is not only related to a deterioration in shoot water potential but also to changes in soil conditions. In this paper, we summarize the experimental evidence that led us to hypothesize a communication between root and shoot on drying soil.

Changes in plant performance with drying soil have been widely discussed during the last 50 years. Martin (1940), Veihmeyer and Hendrickson (1950), and Veihmeyer (1956) had previously concluded that the rate of transpiration was maintained until a critical soil water content was reached. With the introduction of thermodynamics in plant water relations and the development of more sophisticated measurement techniques, leaf water potential became the controlling factor in most experimental hypotheses. It was an obvious thought, because stomatal movements operate *via* changes in turgor of the guard cells and the surrounding epidermal cells (*e.g.*, Raschke, 1979). Also, in most experiments under normal conditions, we are unable to uncouple the decrease in leaf conductance and the decrease in water potential; both are common plant responses to drying soil. Leaf water relation parameters, however, failed to explain the stomatal response due to drought. Often there is no unique relationship between leaf conductance and leaf water potential for different species (*e.g.*, Schulze and Hall, 1982). Some species show a more linear relationship between the two, others an expressed threshold response, which means that, during a soil drying cycle, leaf conductance was maintained at a high value until a critical leaf water potential was reached (Turner, 1974; Ludlow, 1980). However, Bates and
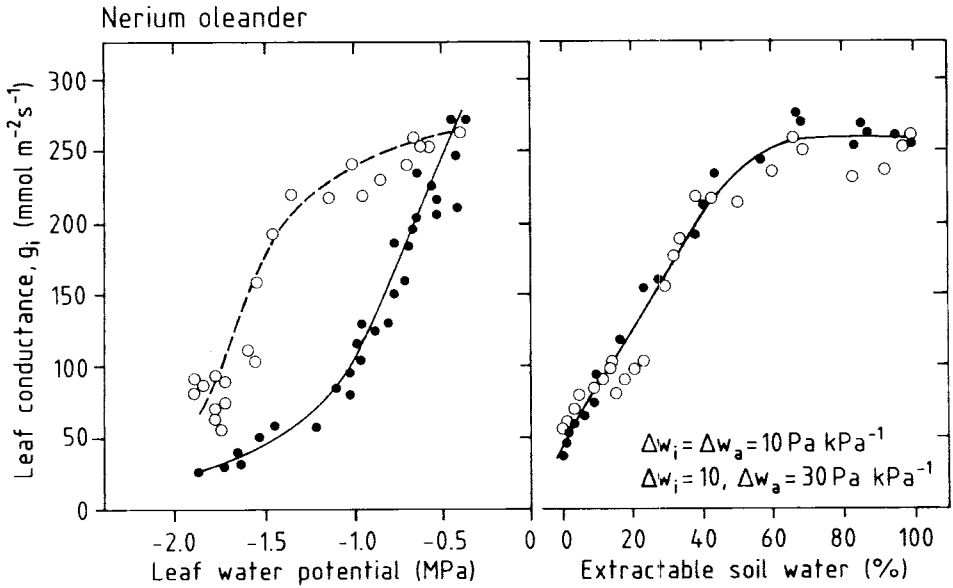
Nerium oleander

Fig. 1. Relationship between leaf conductance and (left) leaf water potential and (right) extractable soil water in a single leaf in a temperature- and humidity-controlled gas exchange cuvette at Δw_i = 10 Pa kPa^{-1}, while the remainder of the plant in a growth cabinet was at Δw_a = 10 Pa kPa^{-1} (low transpiration, ●) or at Δw_a = 30 Pa kPa^{-1} (high transpiration, ○). Δw = leaf to air vapor pressure difference.

Hall (1981) showed, that leaf conductance can decrease without any detectable changes in bulk leaf water potential. Turner et al. (1985) and Gollan et al. (1985) showed for a herbaceous and a woody species, that within one species there was no unique relationship between leaf conductance and leaf water potential with drying soil. In their studies, leaf conductance of a single leaf was measured at constant high humidity with the remainder of the plant being either at high or low air humidity (Fig. 1). Depending upon the humidity treatment, transpiration of the shrub was high at low humidity and vice versa. High rates of transpiration caused a decrease in leaf water potential of the whole shrub, and also in the single leaf. Leaf conductance, however, did not decrease, as would have been expected if a simple decrease in leaf water potential is a controlling factor for stomatal aperture. It

was surprising to see that the leaf conductance of the single leaf was independent of its leaf water potential related to the soil water content (Fig. 1).

The conclusion of their experiments was that the stomatal aperture is under the control of signals from the root system that experiences the drying soil and is mediated to the shoot via the transpiration stream.

The problem in working out controlling factors on stomatal conductance at drying soil is to uncouple soil and leaf water relations. Since there is a hydraulic link between water in the soil and in the leaf, leaf water potential will always decrease when the soil becomes dry and soil water potential decreases (pathway 1, Fig. 2). Besides possible reactions to leaf water potential or turgor, stomata might react to changes in leaf metabolism with decreasing leaf

water potential (pathway 2, Fig. 2), like the reduction in photosynthetic rate or the synthesis or accumulation of chemical substances like abscisic acid (*e.g.,* Pierce and Raschke, 1980).
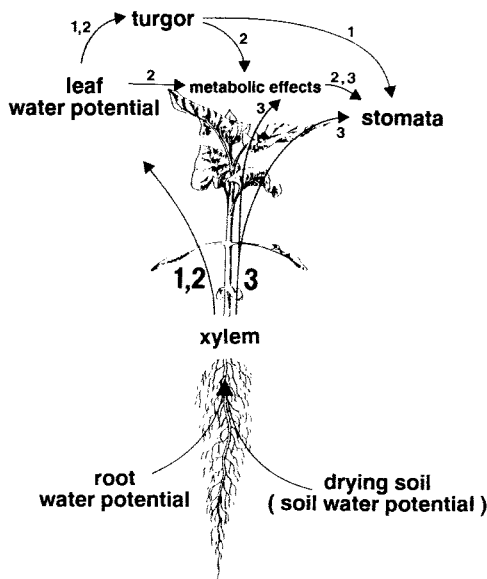
To study effects of drying soil on leaf behavior independent of leaf water status (pathway 3, Fig. 2) it is necessary to uncouple leaf and soil/root water relations. There are two experimental tools available that enable us to do this. Using the split root technique, the root system is divided and grown in two pots. Whereas the soil in one pot is permanently watered and thus supplying the shoot with enough water to keep leaf water potential high, the soil in the second pot is allowed to decrease in

Fig. 2. Possible pathways of communication between root and shoot on changes in the soil water status. **1**: a change in soil water potential is mediated to the stomatal complex *via* changes in xylem water potential, and in water potential and turgor of the leaf. **2**: the decrease in leaf water potential with drying soil causes metabolic reactions within the leaf that affect the stomata. **3**: the deterioration of soil water status is mediated to the shoot independent of changes in the xylem or leaf water potential by, *e.g.,* changes of the xylem composition.

water content. Blackman and Davies (1985), Zhang *et al.* (1987) and Zhang and Davies (1987) using such a system showed that leaf conductance decreased dramatically in such a situation even though leaf water potential did not change or may even have increased. This situation is similar to a plant living in soil with different water contents. Although the shoot does not experience changes in leaf water status, it reacts to reduced supply of water to part of the root system.
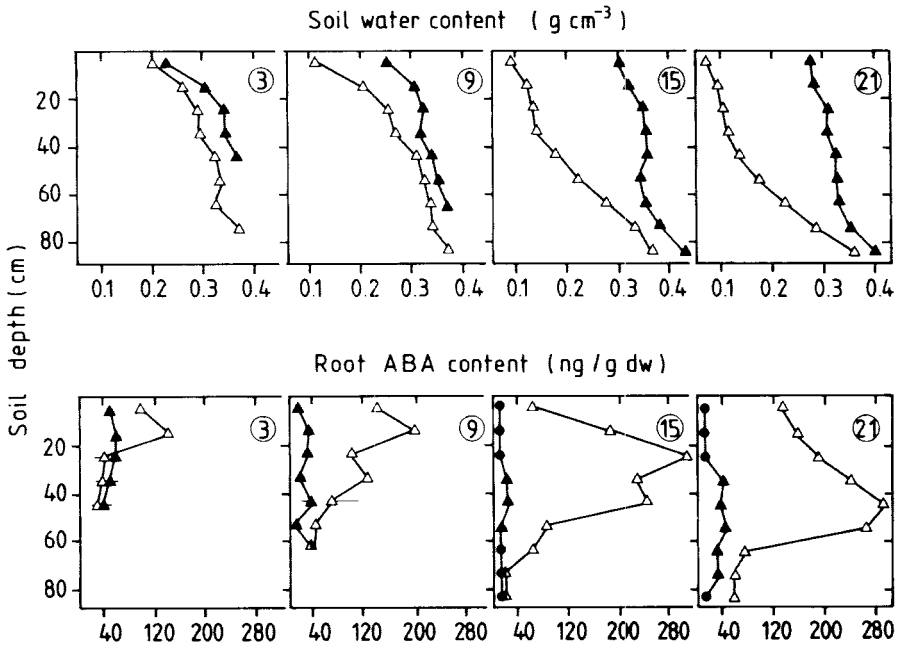
Using the split root technique, one might find slight changes in leaf water potential and therefore metabolic effects within the leaf cannot be completely excluded (pathway 2, Fig. 2).

In subsequent experiments, Zhang and Davies (1989) showed that the concentration of abscisic acid (ABA) increased in roots that experienced dry soil (Fig. 3). The increase in root ABA content in this experiment was correlated with the water content of the surrounding soil (Fig. 4). The ABA that accumulates in the root system could then be transported with the transpiration stream to the shoot. During the day, abscisic acid accumulates in the epidermal cells, whereas there is no detectable change in the abscisic acid concentration of the bulk leaf (Zhang *et al.,* 1987).

The second approach to separate shoot and root/soil water relations is an experimental design introduced by Passioura (1980). A plant is grown in special pots that can be placed in a pressure chamber with the root and soil inside and the shoot outside the chamber facing atmospheric pressure (Fig. 5). Applying pneumatic pressure inside the chamber to the soil and root system increases the xylem water potential in the shoot but does not alter water potential gradients in the root and the soil (Passioura and Munns, 1984). A cut through the xylem at any given position of the shoot is used to control the

Soil water content (g cm⁻³)

Soil water content (g cm^{-3})

## Root ABA content (ng / g dw)

Soil depth (cm)

Fig. 3. Soil water content and ABA content of maize roots in soil that was either well-watered (●, ▲) or last watered on day 0 (△). The encircled numbers in each graph indicate the day during the drying cycle. Adapted from Zhang and Davies (1989).

balancing pressure, *i.e.*, the pressure that is necessary to bring the hydrostatic pressure in the xylem of the shoot to atmospheric pressure. When balancing pressure is applied, a drop of water attached to the cut in the xylem will neither increase nor decrease in size. If the pressure is too high, xylem sap will bleed out of the cut, if it is too low, water will be sucked into the xylem. This feature is used by an electronic device to control the pressure in the pressure chamber within 0.005 MPa of the balancing pressure (Passioura and Tanner, 1985).

Fig. 4. Relationship between ABA content of maize roots and the bulk soil water content around those roots. Data are taken from the experiments in Fig. 3. ABA contents of roots in very dry soil (≤0.1 g·cm^{-3}) are not included since many roots died. Redrawn from Zhang and Davies (1989).
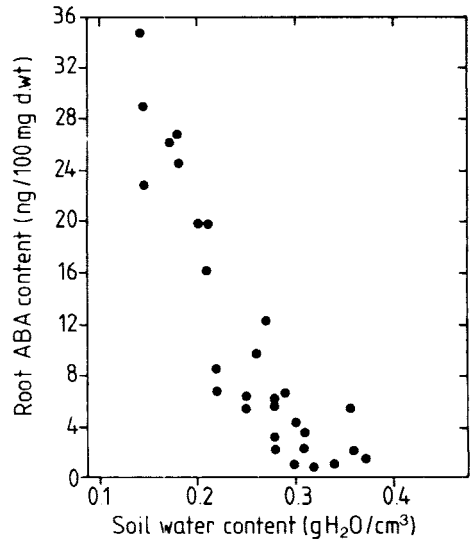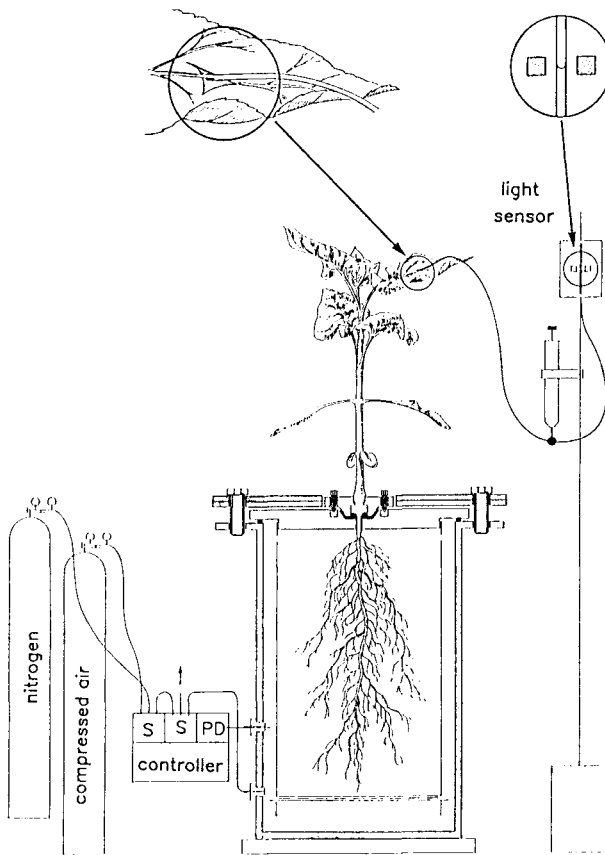
Fig. 5. A Passioura-type pressure chamber to control the hydrostatic pressure of the xylem sap to atmospheric pressure. Plants are grown in soil in pots that can be enclosed in a pressure chamber, and xylem water potential is increased by applying pneumatic pressure. The pressure in the chamber is controlled by an electronic device that includes a light sensor, which is connected to the xylem of the plant *via* a water-filled tube. Adapted from Gollan (1987), for details see Passioura and Tanner (1985).

When soil water potential decreases, the balancing pressure applied will increase and thus keep the xylem sap of the shoot at atmospheric pressure (about 0 MPa xylem water potential).

By applying the balancing pressure permanently throughout a drying cycle, the shoot never experiences any change in shoot water potential due to the drying soil. Even under such a condition, with the xylem water potential of the shoot being zero, leaf conductance decreased at the same soil water content as control plants that were allowed to decrease in leaf water potential (Fig. 6; Gollan *et al.,* 1986).

The pressure chamber system can be used to collect xylem sap from intact plants (Passioura and Munns, 1984; Gollan, 1987). This enables us to measure several components in the xylem sap of a plant throughout a drying cycle which might affect stomata, such as abscisic acid, inorganic ions or pH (reviewed by Schulze, 1986).
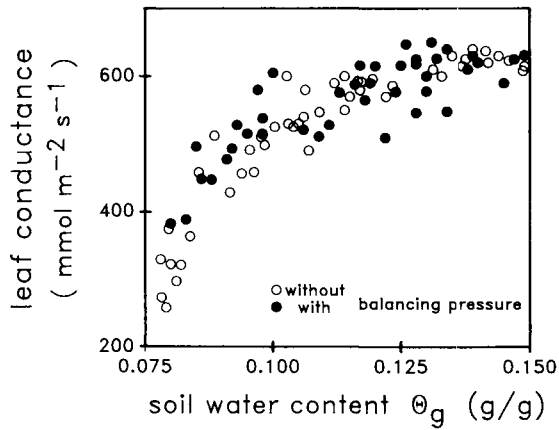
Fig. 6. Relationship between leaf conductance and soil water content in plants that were either kept fully turgid by applying a balancing pressure (●) or that were allowed to decrease in leaf water potential (o). Adapted from Gollan *et al.*, submitted.
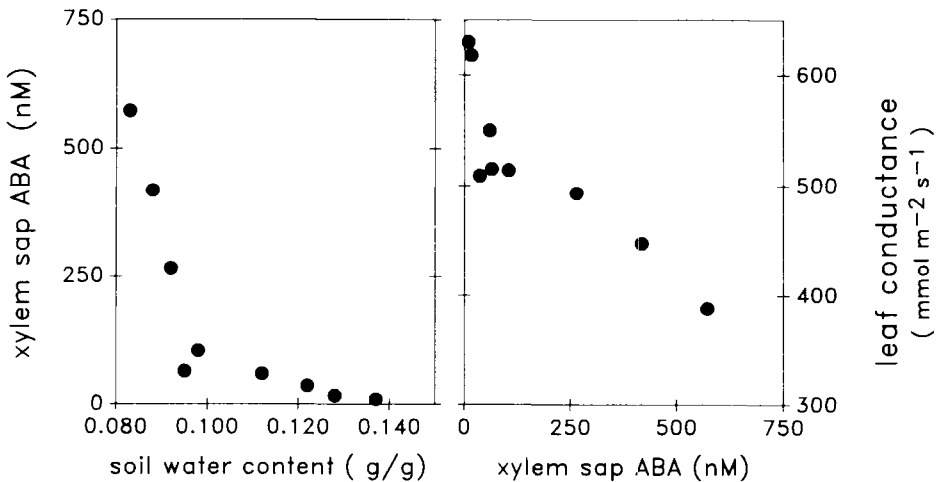
Fig. 7. Left: relationship between ABA concentration in the xylem sap and the soil water content in an individual sunflower plant (Gollan, 1987). Right: relationship between leaf conductance and ABA concentration the xylem sap of the same plant as above.

As one would expect from the results of Zhang and Davies (1989, Figs. 4 and 5) the increase in ABA content with drying soil appears not only in the root, but also in the xylem sap of the plant (Fig. 7). Abscisic acid increased several fold in the xylem sap of sunflower plants taken from the midrib of a leaf, and the decrease in leaf conductance was often linearly related to the increase in ABA concentration in the xylem sap of individual plants (Fig. 7). However, not only the ABA concentra-

tion changed with drying soil, but many other components in the xylem sap did as well (Gollan, 1987; Gollan et al., submitted; Schurr et al., submitted). While the change in the concentration of abscisic acid in the sap was the most evident, the effect of abscisic acid on stomatal aperture might be, e.g., synergistically altered by the presence of cations like calcium (De Silva et al., 1985). There is additional information from Munns and King (1988), who concluded that abscisic acid is not the inhibitor of stomatal opening in the xylem sap. In their experiments, they sampled xylem sap from plants in wet and in drying soils. Xylem sap of plants in dry soil had a higher abscisic acid content than that of plants in wet soil. Feeding xylem sap from 'dry' plants to detached leaves induced stomatal closure. However, the same sap also affected stomatal conductance, when abscisic acid was removed by passing the sap through an immunoaffinity-column before feeding. The xylem sap of drying plants had an inhibiting effect regardless of its abscisic acid content.

There is controversy in the literature about the more general aspects of root/shoot interaction on drying soil, e.g., in volume 11 (1988) of Plant Cell Environment. In different opinions on the subject, Kramer (1988) is worried about the shift in emphasis from traditional water relations to the idea of (bio-)chemical signaling in plants and increasing interest in root metabolism. The idea of root/shoot interaction and communication on drying soil does not exclude direct effects of a decrease in water potential on stomatal aperture, but rather includes an additional biochemical effect on the stomatal aperture independent of changes in leaf water relations (Schulze et al., 1988). 'The return (to emphasis on conditions in the soil) is not a circle. It is a helix.' (Passioura, 1988).

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