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Consequences of saline-dry conditions to the soil–plant–air continuum

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Studies on co-occurring stresses have substantially increased in past decades as researchers have acknowledged that plants are rarely challenged by a single stress in natural settings. High salinity occurs in over one-third of the agricultural lands across the globe, resulting in major yield losses (Abbas et al., 2013). Simultaneously, soil droughts are expected to increase in frequency and intensity in the near future due to climate change (Trenberth et al., 2014). These future droughts are anticipated to threaten plants in several regions of the world, but especially in regions with saline soils. Therefore, the impact of saline-dry conditions on the plant hydraulic system represents a topic of considerable scientific interest at many levels.

Within the soil–plant–air continuum, both salinity and drought limit soil water absorption, thus reducing plant water status and impairing plant function (Chaves et al., 2009). The water status of a plant organ or tissue is indicated by its water potential, a measure of the potential energy of water solutions relative to that of pure water. By convention, the water potential of pure water is designated as zero at atmospheric pressure and ambient temperature, and water potentials in various circumstances can either be equal to, higher, or lower than zero.

In plants, water is transported alongside other organic and inorganic molecules through a very specialized tissue called xylem. Within the xylem, water moves from the roots to the aboveground tissues, down its potential gradient, under negative water potentials developed due to leaf water loss. During drought, further declines in plant water potential can occur given the low water content in the soils and decreased ability of plants to transport water (quantified as hydraulic conductance). During soil salinity, high ion content in the soil water solution decreases the water potential of the soil, thus making water less available for plant absorption. Limitations in root water uptake under high salinity are also associated with ion accumulation inside root tissues and a decline in root hydraulic conductance. Ions have also been suggested to accumulate on the root surface in saline soils, and if that is the case, how might we understand the mechanism for this process, and how could this process influence water flux through the soil–plant–atmosphere continuum?

In this issue of *Plant Physiology*, Abdalla et al. (2022) address these critical knowledge gaps by combining a noninvasive root pressure chamber system with mathematical models of soil–plant water flow and salt transport. The authors recorded leaf transpiration and leaf water potential (Ψ_{leaf}) simultaneously by placing plants with attached roots within a pressure chamber, while the shoots were enclosed in a cuvette with a light source [see a photograph and a comprehensive diagram of this system in Cai et al. (2020)]. Pressure was applied to the soil and roots to bring water in a cut leaf to atmospheric pressure. At this point, the pressure applied (namely balancing pressure) corresponded to Ψ_{leaf} prior to pressurization. Transpiration rates were obtained by multiplying the airflow in the cuvette by the difference between the outgoing and ingoing air humidity measured with sensors. Under pressurization at balancing pressures, however, the actual Ψ_{leaf} was very close to zero, and the authors could assess potential transpiration and Ψ_{leaf} values that would have been obtained if the aboveground tissues were fully hydrated, even under saline-dry conditions.

Abdalla et al. (2022) found that high salinity aggravated drought-induced impairments in tomato (*Solanum lycopersicum*) plants. Their modeling revealed that water flow led to ion accumulation around the roots under saline-dry conditions (Figure 1). Salt accumulation on the root surface was

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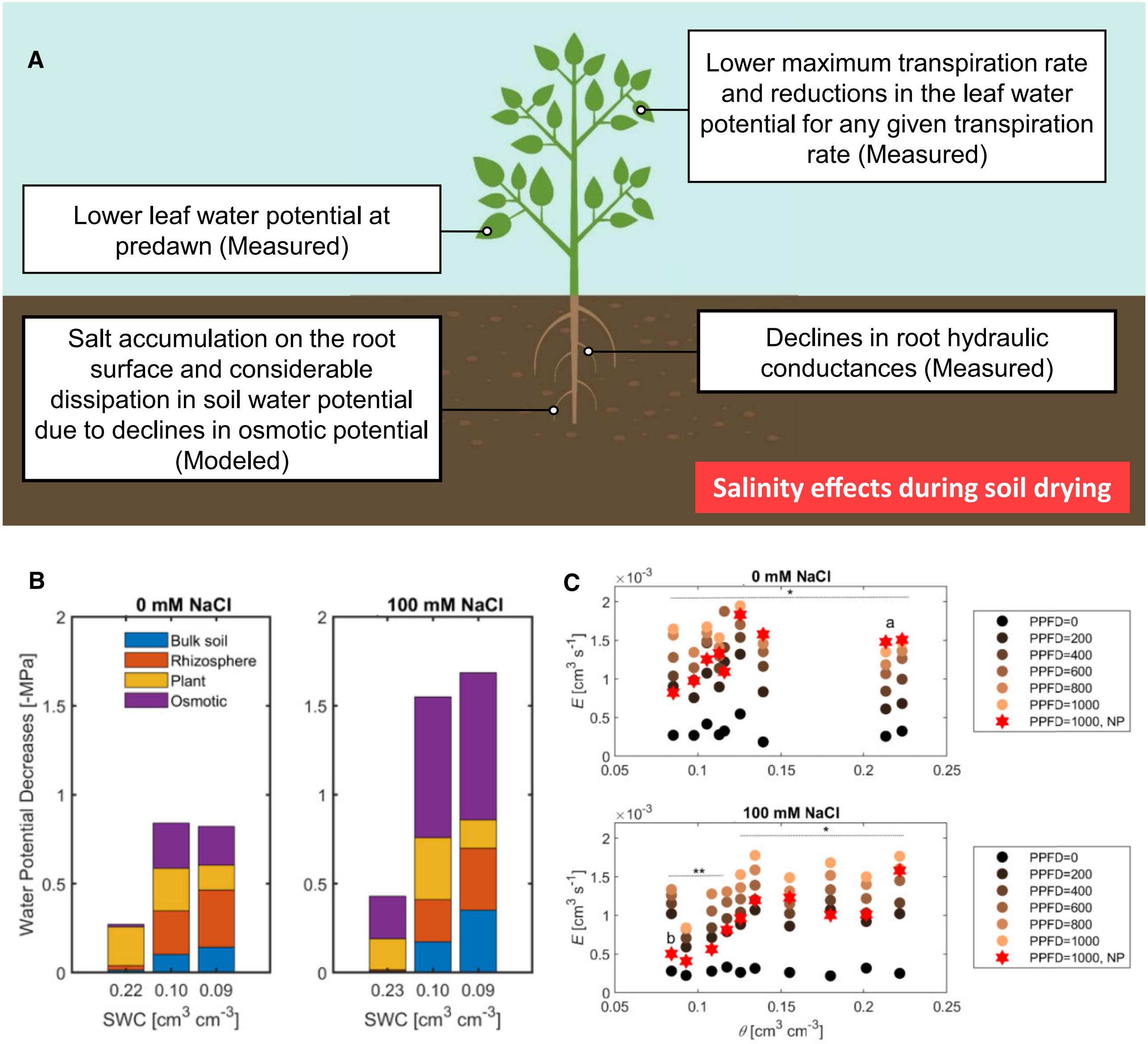

Figure 1 The consequences of increased salinity associated with soil drought on the soil–plant–air continuum. A, Main findings of Abdalla et al. (2022) regarding these consequences using tomato plants as a model species. Collected and modeled data are included. B, Dissipation in water potential throughout the soil–plant continuum under nonsaline and saline conditions at three soil water contents (SWCs) [Adapted from Abdalla et al. (2022), Figure 9]. C, Transpiration rate (*E*) at different SWCs (θ) and photosynthetic photon flux densities (μmol m^{-2} s^{-1}) in nonsaline and saline-treated plants. *E* was obtained with (closed symbol) and without (red stars; NP) plant pressurization [Adapted from Abdalla et al. (2022), Figure 2].

simulated by the soil–plant model, and the results were confirmed through the match between measured and simulated dynamics of Ψ_{leaf} over time. The model also suggested that ion accumulation on the root surface considerably reduced the soil osmotic potential, which was then identified as the main component responsible for soil water potential dissipation (Figure 1). Salinity also caused a slight reduction in root hydraulic conductance that, together with declines in soil water potentials, likely explain the lower Ψ_{leaf} at predawn.

Abdalla et al. (2022) also demonstrated that salinity resulted in reduced maximum transpiration for all soil water contents and considerably lower Ψ_{leaf} for any given transpiration rate, given the lower water availability for plants (Figure 1). In wet and nonsaline conditions, maximum transpiration rate in nonpressurized plants was similar to that of pressurized plants. In saline conditions, however, maximum transpiration rate in nonpressurized plants was always lower than that of pressurized plants, with a higher difference between pressurized and nonpressurized plants under saline-dry conditions than under saline-wet conditions. The difference in maximum transpiration rate between pressurized and nonpressurized plants in the study of Abdalla et al. (2022) can be interpreted either as declines in root hydraulic conductance or as ion-induced damage to the leaves, which can include damage to the leaf hydraulic system. Although declines in root hydraulic conductance were indeed confirmed by the authors, potential declines in leaf hydraulic conductance and/or mesophyll damage were not assessed.

The salinity-induced declines in Ψ_{leaf} observed in this study would be expected to cause major alterations in leaf function in tomato, unless accompanied by osmotic adjustment. Osmotic adjustment is a very important mechanism that guards against drought damage and is represented by shifted turgor loss point to lower water potentials. This shift is important because when plants exhibit lower water potentials, they can maintain cell turgor and function at lower water status, including maintaining transpiration and soil water absorption in drier soils (Blum, 2017; Cardoso et al., 2018). In the study of Abdalla et al. (2022), the minimum predawn Ψ_{leaf} experienced by plants during drought in saline soils was ca. −0.9 MPa (versus ca. −0.6 MPa for nonsaline soils). A Ψ_{leaf} of −0.9 MPa (equivalent to 9 bar or the water potential of a 250-mM solution of KCl) is more than enough to cause tomato leaves to lose turgor (Andrade et al., 2022). That means that tomato plants exposed to this water status would not be able to maintain open stomata during the day to photosynthesize without osmotic adjustments (Cardoso et al., 2020). The presence of minor transpiration rates in saline-dry soils (higher than the minimum transpiration rates in the absence of light) (Figure 1), however, clearly indicates that tomato plants were able to slightly open their stomata, likely due to leaf osmotic adjustment.

At −0.9 MPa, tomato plants would also be expected to experience minor levels of leaf embolism (i.e. when gas enters the xylem and reduces hydraulic conductance) (M.T. Andrade and A.A. Cardoso, unpublished data). Thus, it is possible that embolism induced declines in leaf hydraulic function and contributed to the reductions in maximum transpiration rates under saline-dry conditions. Leaf embolism and declines in leaf hydraulic function, however, have never been explored in response to salinity, and further studies are necessary to test whether these processes play a role in defining leaf gas exchange in addition to the belowground component of the soil–plant–air continuum. In conclusion, the results obtained by Abdalla et al. (2022) not only demonstrate the key role played by the soil-root component in defining leaf hydration levels and gas exchange in saline-dry soils, but also shed light on the importance of leaf osmotic adjustment under this condition.

Conflict of interest statement. The author has no conflicts of interest to declare.

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