Editorial

https://doi.org/10.1038/s41477-024-01661-8

Salts out, water in

Check for updates

Research on apoplastic diffusion barriers may help to better understand sensitivity to drought and salinity, two of the most pressing problems in agriculture.

Spain is currently suffering one of the most severe droughts in a hundred years, and the region of Catalonia recently declared a drought emergency[1]. This situation did not develop unexpectedly since precipitation had already been decreasing in the last years and is expected to decrease further due to climate change. Of all the countries in the European Union, Spain is most threatened by desertification, and a drier climate in future will aggravate this problem further. However, desertification is also dependent on the type of land use and on soil fertility, salinization and erosion. Common strategies to counteract desertification include reforestation and soil amelioration, but the most frequently used strategy is irrigation to maintain agricultural productivity. While good irrigation practices can contribute to retention of fertility in arid climates, the question remains as to whether such practices are sustainable in all cases.

Soil salinization can be a consequence of non-sustainable irrigation, for example by the intrusion of seawater into the groundwater of coastal regions or by inappropriate water quality. In addition, excessive application of mineral fertilizer can contribute to soil salinization in regions of intensive agriculture. However, most saline soils develop by primary salinization in arid regions due to factors such as precipitation, evaporation and soil geochemistry. Soil salinization poses a major threat to crop productivity and hence food security, and climate change is predicted to shift the hotspots of primary salinization, increasing the challenges for regions such as the aforementioned Spain[2]. Therefore, it is unclear whether currently used agricultural practices can be maintained everywhere without the risk of land degradation.

Another way to address this problem is from the point of view of cultivated crop species and varieties. Sorghum and millet are more drought tolerant in arid and semi-arid climates than wheat, and breeding efforts could result in varieties with similar yields per hectare. Whether consumer-oriented markets can easily replace wheat with more drought-resistant crops is uncertain, unless large parts of the European and North American populations change their habits of having continental breakfast and replace bread and pastries with millet gruel. Since this is unlikely to happen, it will be necessary to investigate the basis for drought resistance and salt tolerance, and try to use this knowledge to engineer or breed more resilient varieties of otherwise vulnerable species.

One plant structure that contributes to both drought resistance and salt tolerance is the Casparian strip. Located in the root endodermis of vascular plants (and the exodermis in some species), this lignified structure seals the interior of the stele from the outer apoplastic space and thus prevents passive diffusion of water and salts through the apoplast into the stele. In addition, suberin lamellae form a hydrophobic barrier that prevents diffusion of water and salts between the apoplast and endodermal cells. It is therefore not surprising that both the Casparian strip and suberin lamellae have recently been found to be important players in drought resistance and salt tolerance.

It was shown, some time ago, that the correct formation of the Casparian strip is essential for salt tolerance in maize[3]. It was found that a dirigent protein – a protein that affects the stereochemistry of a compound synthesized by other enzymes – is required for correct lignin deposition during Casparian strip development. Mutants without the dirigent protein display transpiration-dependent salt hypersensitivity due to leakage of sodium ions into the stele. The mutation occurred in a maize inbred line, suggesting that varying levels of salt tolerance in cultivated crop varieties could be partly due to non-optimal alleles of genes involved in Casparian strip formation. This underlines the importance of uncovering new factors involved in Casparian strip formation to study the genetic basis of salt tolerance in crops.

Other factors involved in the development of Casparian strips have been recently identified. Proteins with a glycine, alanine, proline-rich domain, a lectin domain and a secretory signal peptide, short GAPLESS, are important for tethering the lignified Casparian strip to the endodermal plasma membrane in rice, thus forming a junction called the Casparian strip membrane domain[4]. Without these proteins, the plants suffered from disturbed nutrient homeostasis, likely due to leakage of nutrients between the stele and the outer apoplast. Whether these proteins are also involved in salt tolerance will be a question for future investigations.

While Casparian strips were already present in non-seed plants such as ferns and lycophytes, suberin lamellae only evolved in the more drought-adapted seed plants[5]. This suggests that the emergence of suberin lamellae in seed plants during a period of drier climate in the late Carboniferous may have laid the groundwork for their success and later dominance over ferns and lycophytes. Indeed, *Arabidopsis* mutants defective in the formation of suberin lamellae are highly drought sensitive, confirming their function in drought resistance though prevention of water leakage from the stele[5]. While the presence of suberin lamellae seems conserved in seed plants, its location is more variable. In tomato, suberization occurs not in the endodermis but in the exodermis and retains the same essential function for drought resistance[6].

Such diffusion barriers may also be adapted to different roles aside from those in roots. In this issue, Ning Hao from the University of Tokyo and colleagues show that a lignified structure resembling Casparian strips also occurs around the neck cells of glandular trichomes in cucumber[7]. The biogenesis of this structure, called the neck strip, involves factors that are homologous to those involved in Casparian strip formation, suggesting that they share a common genetic basis. This barrier prevents backflow of stored compounds through the apoplast of the neck, allowing their accumulation in the gland cells.

Apoplastic diffusion barriers remain relatively poorly understood. Insights into their biogenesis across species and varieties may help to clarify the variable nature of their actions in transport and storage of water, nutrients, solutes and metabolites, and the physiological consequences when under conditions of abiotic stress.

Published online: 21 March 2024

References

1. Llach, L. Barcelona declares drought emergency, with big fines for breaking water rules. *euronews. green* https://www.euronews.com/green/2024/02/01/spain-expected-to-declare-drought-emergency-today-with-big-fines-for-breaking-water-rules (2024).
2. Hassani, A. et al. *Nat. Commun.* **12**, 6663 (2021).
3. Wang, Y. et al. *Nat. Commun.* **13**, 2222 (2022).
4. Song, T. et al. *Nat. Plants* **9**, 1749–1759 (2023).
5. Su, Y. et al. *Nat. Plants* **9**, 1968–1977 (2023).
6. Cantó-Pastor, A. et al. *Nat. Plants* **10**, 118–130 (2024).
7. Hao, N. et al. *Nat. Plants* https://doi.org/10.1038/s41477-024-01626-x (2024).