

# Evolutionary outcomes should inform strategies to increase drought tolerance

**To the Editor** — Genome-assisted breeding and transgenic approaches to crop improvement are presently targeting phenotypic traits that may confer drought tolerance<sup>1</sup>. It has been suggested that these efforts are not proceeding at a sufficient rate considering the rapid pace of climate change<sup>2</sup>. Although the current and future demand for food may indeed warrant haste, efforts to improve plant performance in water-limited environments would benefit from first considering how natural selection has already solved the problem.

Angiosperm species from dry habitats are the products of an evolutionary legacy stretching back over 100 million years. As such, many of these species already possess the traits necessary to produce biomass efficiently, compete, and reproduce in water-limited environments. Under drought, the water-delivering conduits that make up the xylem come under tension and embolize, that is, they fill with gas, becoming useless until they can be repaired or replaced. Thus in dry habitats, the efficient transport of water by the xylem, as well as its resistance to embolization, are essential traits that allow plants to maintain growth<sup>3–7</sup>. It therefore seems likely that these traits could also prove beneficial in crop and forestry species. Indeed, the few studies that have quantified xylem efficiency and embolism resistance in crop species support the idea that efficient water transport and embolism resistance are necessary for maintaining growth in dry environments<sup>8–10</sup>.

It has long been thought that the efficiency and safety of water transport trade off against one another, such that

any change in xylem ultrastructure that increases efficiency should decrease embolism resistance, and vice versa. This idea is now known to be false, at least in the case of angiosperms: across the world's angiosperm species, xylem efficiency varies nearly independently of variation in embolism resistance<sup>11</sup>. It is therefore likely that modern breeding techniques could simultaneously improve both of these traits, providing there is sufficient heritable variation in each<sup>12</sup>.

The features of xylem tissue that confer high efficiency and high embolism resistance have been the subject of much study, nearly completely focused on wild plant species. Vessel dimension (width and length), as well as the permeability of the bordered pits (between adjacent vessels) and pit-membrane ultrastructures, contribute about equally to xylem efficiency<sup>13</sup>. In contrast, although embolism resistance can be measured accurately, the traits that engender it are still poorly understood, but likely include pit-membrane thickness, the size and quantity of pit-membrane pores, as well as the total number of bordered pits per vessel<sup>14,15</sup>. Taken together, xylem efficiency and embolism resistance arise from a complex interaction of vessel structure and connectivity, suggesting that the genetic complexity of these traits is also significant<sup>16,17</sup>. Nevertheless, xylem efficiency has been altered in wheat<sup>18</sup> and embolism resistance in maize<sup>9</sup>.

Despite the evident importance of the xylem in conferring drought tolerance in naturally occurring plant species, there remains a dearth of xylem research in crop species. Selection for xylem traits is likely

hindered by genetic complexities, such as when multiple genes code for a single phenotype, or when a single gene codes for multiple phenotypes<sup>19</sup>. However, these same difficulties have not thwarted selection for similarly complex traits in the past, such as grain yield and plant size. I suggest that, even considering these difficulties, the well understood association between xylem traits and drought tolerance demonstrates great potential for improving plant performance via manipulation of the xylem. □

## References

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Sean M. Gleason

USDA-ARS, Water Management Research,  
Fort Collins, Colorado 80526, USA.  
e-mail: sean.gleason55@gmail.com