



Drought tolerance in grapevine involves multiple interacting physiological mechanisms

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The past decade has produced some major advances in our understanding of how grapevines regulate their water use and tolerate drought. Numerous traits that are important for conferring drought tolerance have been identified and quantified across a range of cultivars¹. Nevertheless, arriving at a firm hierarchical rating of different cultivars' drought tolerance has eluded scientists. This short review seeks to explain how drought tolerance is dependent on multiple traits, all interacting within a particular environment and management context.

Drought tolerance cannot be determined by a single trait

In vineyards, grapevines function across a wide range of water availability. Of course, vines are most productive when they have ample water, but in most regions, and especially those that are dry-farmed, vines regularly experience water deficits. The real levels of water deficit are seldom quantified in dry-farmed vineyards because of the current lack of easy, inexpensive technologies to measure water potential. Typically, these water deficits can range from mild to moderate to severe. Across this spectrum, grapevines adapt their water use (and hence their productivity) to the constraints they face.

A grapevine's hydraulic system is essential for water use regulation and drought tolerance. Over the past decade numerous hydraulic traits that are involved in drought tolerance have been identified and quantified which has produced major advances in our understanding of how grapevines tolerate drought^{1 2 3 4 5}. This body of work has shown that drought tolerance cannot be determined by any single trait, and instead results from the complex interactions of many traits across the whole spectrum of water deficit (Figure 1). Even traits that act in the absence of any water deficit at all, like those that control a vine's maximum water use (i.e. maximum transpiration) and maximum water availability (i.e. root system size and distribution), are key traits in determining the time of survival under drought. For example, lower maximum transpiration and a larger rooting volume will delay the rate at which soil water is depleted.

Numerous other traits function as the vine experiences increasing water deficit intensity (Figure 1). Under mild to moderate deficits vines

decrease water use by changing leaf angle, partially closing stomata, and developing new leaves with lower stomatal densities while at the same time maintaining root growth. The water potential threshold for the onset of stomatal closure is an important drought tolerance trait that varies between cultivars. If the water deficit intensifies, photosynthesis stops and stomata close completely. Water deficits limit productivity and yield because vines must close stomata to prevent embolism. However, even under these more extreme conditions the canopy continues to lose water, which is why minimum leaf conductance is also a key trait, playing a role in leaf mortality and xylem embolism in particular. Under the most severe circumstances leaves, roots, and other perennial organs can experience xylem embolism, which can result in defoliation of the canopy and even vine mortality.

Drought tolerance is scenario specific

For a winegrower, the priority is to produce sufficient yields at sufficient quality to ensure economic sustainability. Because grapevines can adapt themselves to increasing water deficits, and because winegrowers manage vine water status through vineyard design and/or irrigation, the vascular system of grapevines almost always remains safely in the operating range of water deficit³ (see Figure 1).

However, studies also show that in dry-farmed regions some extremely hot and dry seasons have pushed grapevines to their hydraulic limits, resulting in defoliated canopies and very low yields. Grapevines tolerate these extremely stressful situations due to their hydraulic system's resistance to xylem embolism and vulnerability segmentation (i.e. hydraulic fusing). Vulnerability segmentation is where roots, leaves,

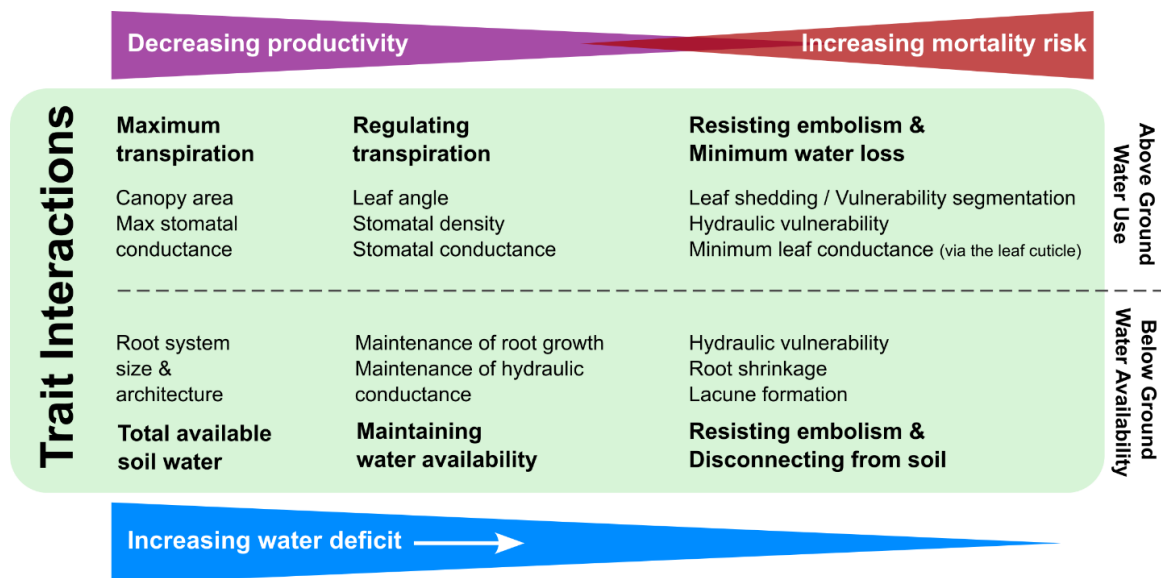


FIGURE 1. Grapevine response to water deficit is comprised of numerous traits (shaded green area) that all interact across the spectrum of water deficit.

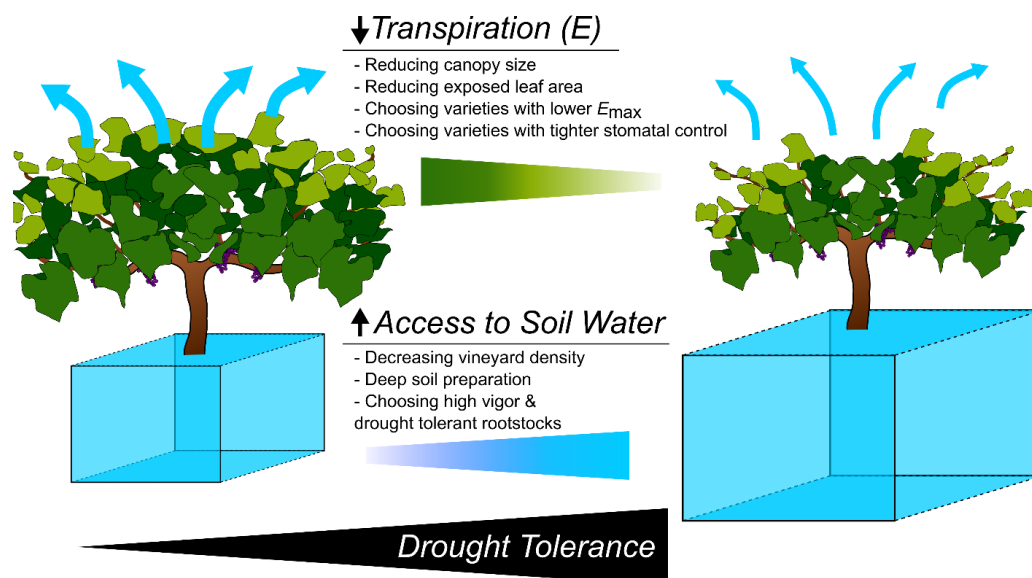


FIGURE 27. Among the trait conferring drought tolerance, some can be directly manipulated by growers via their management strategy.

and petioles are more vulnerable to embolism than perennial organs like canes, cordons, and trunks^{2,5}. Thus, the defoliation witnessed during these extreme seasons is adaptive, reducing canopy size and water use (at the expense of productivity and yield) while at the same time disconnecting leaves to prevent runaway embolism that could harm the perennial portions of the vine. Winegrowers want to avoid these situations at all costs, but in the context of climate change we can expect the frequency and intensity of extreme seasons to increase. Traits that protect vineyards from dramatically reduced productivity and grapevine mortality during such extreme events could become critical in the near future.

The situations above illustrate the reality that different scenarios rely on different drought tolerance traits and their interactions.

Some traits are beneficial for drought tolerance and can be managed by growers

So far we have seen that drought tolerance is a multi-trait, scenario dependent system. Even though this is true, there are some traits that research has shown are clearly beneficial for drought tolerance. Recent research^{1,4} suggest that conservative water use behaviors are extremely beneficial for drought tolerance. These traits include lower maximum transpiration (resulting from smaller canopy size, lower stomatal conductance, lower stomatal density, etc.), more conservative stomatal closure thresholds, higher resistance to embolism, and lower rates of minimal water loss. These are the qualities of the drought tolerant Spanish variety Grenache for example^{1,5}. Rootstock related traits that increase access to soil water are also beneficial, such as a larger and deeper root system^{1,6}. The important caveat is that it is the combination of traits that is important, and not any single trait. Not every trait needs to be optimal for the trait combination to confer a high level of drought tolerance¹. For example, Dayer *et al.* (2022)¹ showed that the variety Vidadillo exhibited very high maximum transpiration (under well-watered conditions). Intuitively, this would mean it would use more water, faster, and thus be less drought tolerant. However, because of its extremely conservative stomatal closure threshold it was one of the best performing cultivars under drought.

Importantly, some of the traits mentioned above are at least partially under grower's control (Figure 2). Growers can choose a vineyard design that decreases water use by choosing training systems, canopy management, and vineyard densities that decrease the amount of canopy area per hectare of vineyard. They can also choose cultivars with more conservative water use behaviors and/or more resistant to embolism as mentioned above. Decreasing planting density can also increase access to soil water along with use of high vigor, drought tolerant rootstocks.

Conclusions

Drought tolerance is a complex behavior resulting from the interaction of many traits. This is why a multi-trait approach is needed to create a hierarchical ranking of cultivar drought tolerance. Furthermore, different traits combinations will be critical under different scenarios and environment/management contexts. Despite this complexity, we suggest that cultivars with conservative water use behaviors will be the most drought tolerant under non-extreme conditions. In vineyards, growers can modify certain traits through management, such as decreasing maximum water use and maximizing soil water availability by favoring strong root system development during vineyard establishment. In the future, we need to determine which traits and in what combinations would be the best performing under specific scenarios, in order to tailor plant material and vineyard design to specific contexts and challenges. ■

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