



Review Article

An Overview of Drought Stress in Grapevine

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ABSTRACT

Grapevine is an important fruit crop globally. Drought-resistant cultivars are attracting more attention from researchers and growers. The major purpose is to develop a favourable rootstock that can influence productivity and scion growth during drought conditions. It can help conserve water by minimizing the need for irrigation and lowering negative returns. Rootstocks play a substantial impact on the structure of the vine (e.g., stomatal conductance, water status and photosynthesis), growth and drought tolerance. Absciscic acid (ABA) is regarded as a key component in the mechanism of drought tolerance in plants. Various transcript families are directly or indirectly involved in regulating abiotic stress, particularly drought stress in horticultural plants. Most transcripts are linked with ABRE/ABF, WRKY, and ABA-independent AP2/ERF families. The present report aims to overview the physiological and molecular processes associated with drought stress in grapevines.

Keywords: Drought, grapevine, ABA, transcript, rootstock.

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INTRODUCTION

Globally, grapevine is one of the most commercially important perennial fruit crops. Grapevine has become a model perennial fruit crop due to its economic significance around the globe, widely adapted to climate (Alsina et al., 2007). One of the most important limiting factors for sustainable agriculture is water availability for irrigation. Uneven precipitation plays a vital role in the occurrence of drought stress in many agro-based regions. As our planet contains limited water fit for agriculture, a sustainable solution to mitigate drought stress is either identifying new crops which can be grown in drought conditions or improving existing crops through breeding programs. It has been observed that grapevine (*Vitis vinifera*) has emerged as a major fruit crop that can sustainably grow under drought stress in the recent past (Gambetta et al., 2020). Because grapevines are drought-tolerant, some agricultural practices focus on enforcing moderate soil water deficits to maximize berry quality, minimize yield reduction, and promote the formation of

flavonoids, sugars, polyphenols, and carotenoids (Alsina et al., 2011). Grapevines appear to be unaffected by drought or moderate water limitations has a good impact on yield despite its negative impact on fruit yield. Most grapevines are grafted and grown from woody cuttings vegetatively (Zhang et al., 2016). The most common rootstocks are crossbreeds between the natural *Vitis riparia*, *Vitis rupestris*, and *Vitis berlandieri* vines found in North America.

Rootstocks are preferred based on the specific parameters. The roots (xylem) are associated with anchoring the plant for both water and nutrient uptake. The system's foundational architecture is carefully managed to maximize the utilization of available resources (Zhang et al., 2016). Drought stress (abiotic) on plants is caused by lack of rain, rising temperature, and limited water availability, and it is becoming increasingly problematic due to the change in climate (Dubois et al., 2013).

Absciscic acid (ABA) is a phyto-hormone that is abruptly replaced in response to many stress stimuli, plants adapt to drought stress through various mechanisms that help improve their tolerance to dehydration. PYR/PYL receptors detect ABA and activate abbreviated transcription factors (TFs) such as ABA-responsive element (ABRE)-binding proteins (AREBs)/ABRE binding factors (ABFs) via cascade kinase events. Woody plant species, like *Arabidopsis*, can be affected by drought stress, with lower development of plants, inhibited formation of wood, and increased water stress as well as increased susceptibility to infections. In literature, the response of woody plants has found several essential TFs using genetics and omics approaches, and the transcriptional control of drought response is only slowly

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being explored (Yao et al., 2021).

Despite accounting for over 60% of global grape production, about 10% of vineyards in the European Union were irrigated in 2016. Grapevines have been adapted to survive drought, and several typical agricultural practices rely on imposing soil water limitations to enhance berry quality, reduce yield decline, and encourage the synthesis of carbohydrates, carotenoids, polyphenols, and antioxidants.

In the kingdom Plantae, ABA is a ubiquitous hormone that has been shown to regulate physiological responses. It controls many physiological functions in plants, including fruit ripening, cambium activity, seed dormancy, and organ development (Dash et al., 2017).

Water shortages reduce growth and yield but can increase wine and grape quality until they become severe. To find variations in drought tolerance among grapevine genotypes, much research has focused on basic agronomic variables like yield and composition (fresh fruit caliber). The control of stomatal conductance, carbon absorption, and other fine-scale physiological processes has, nevertheless, been the primary focus of research (Gambetta et al., 2017).

IMPACT OF DROUGHT ON PLANT GROWTH AND YIELD

The role of climate is crucial. Water accessibility is important for the growth of vines through optimal renewable needs. Radiation intensities and scope may be a risk to plant growth, yield, and quality during the development cycle (Orduna, 2010). Plant reactions to abiotic factors can be attributed to a succession of internal occurrences. The first growth inhibition, however, happens considerably earlier. The ability of plants to osmotically adaptor conduct water can control expansion, implying that Metabolic and morpho-anatomical alterations will take place over time (Deluc et al., 2011). During the growing cycle, the structural dynamic of the grapevine canopy is intimately linked to the development and growth of high-quality prospective flowers. Enhanced penetration of sunlight into the tree's canopy could have negative consequences. When reaching environmental thresholds, older to younger leaves ratio has a critical impact on the softening point of berries. The vegetative growth and reproductive growth of the plant will be affected due to these effects (Farooq et al., 2009).

Yield

Water stress reduces production by inhibiting photosynthesis, which means that only a small portion of the crop is harvested as many berries do not reach full maturity (Zulini et al., 2007). Determine harvest return throughout nitric growth, affected by various critical stages of phenology and seasonal conditions. During ripening, the berry fruit mechanism varies due to abiotic stresses (Leeuwen and Destrac-Irvine, 2017).

Photosynthesis

Plant physiology can be greatly affected by stress, which can affect the photosynthesis rate caused by the photo-inhibition of photosystem II and a decrease in the conductance of guard cells

(Dinis et al., 2016). Studies have shown that high temperatures can cause anatomical and structural changes in the photosynthetic membranes (chloroplasts), resulting in a decrease in photosynthetic respiratory mechanisms (Zhang et al., 2015).

ROLE OF HORMONES IN DROUGHT STRESS

Hormones like Absciscic acid (ABA), ethylene, and auxins are important regulators of plant stress mechanisms (Pieterse et al., 2009). Abiotic stress is linked to changes in ABA levels. Biotic stress responses are mediated by the regulation of salicylic acid, ethylene, and other hormones acid (Rejeb et al., 2014). Increase in its concentration in the xylem vessels and altering water relations in grapevines, ABA has a key function in modulating water relations, embolism, hydrostatic conductance, and aquaporin gene expression (Schachtman and Goodger, 2008). Studies revealed that ABA and sucrose have a synergetic effect on anthocyanin accumulation in grapevine. ABA is of great significance in grape ripening (Pirie and Mullins, 1976). ABA is likely linked to genes that regulate the expression of stress-adaptive genes, which are essential for plant survival (Sah et al., 2016; Ferrandino and Lovisolo, 2014). ABA modulates the starch-to-sugars pathway by up-regulating carbohydrate metabolism enzymes (e.g. amylase and vacuolar invertase). Various studies suggested that it may play a crucial role in carbohydrate mobilization and response during recovery. Exogenous ABA application decreases starch and increases soluble sugars.

IMPACT OF ROOTSTOCKS ON SCION RESPONSIVENESS TO DROUGHT

Unfavourable conditions for growing (e.g., drought, salinity, nutrient deficit, frost) can cause stress in cultivated grapevines. As a result, drought can have a severe impact on vine development and yield. Water and the root system are intricately linked. With a drying soil's availability rootstocks play a role in drought-induced scion transpiration control (Iacono et al. 1998; Padgett-Johnson et al., 2000) Although the exact drought mechanisms are still unknown (Marguerit et al., 2012), The assumption is that it includes a mix of signalling from the root to the shoot (Lovisolo) a genetic component of rootstock regulation. Hormone signalling and scion transpiration lay the groundwork for breeding rootstocks that are resistant to drought (Soar et al., 2006; Zhang et al., 2016).

BREEDING DROUGHT RESISTANT ROOTSTOCKS

The main objective is to sustain production and yields in the face of stress, while also considering the vine's ability to safeguard its hydraulic function against potential long-term harm. Genetic factors impact stomatal conductance and other traits related to drought tolerance (Street et al., 2006). The genetic foundation of scion qualities, such as transpiration and whole-plant hydraulic conductivity, may result in differences when grafted onto a common rootstock (Coupel-Ledru et al., 2014).

FRUIT METABOLISM UNDER DROUGHT

Berry metabolism is substantially influenced by a lack of water.

According to [Mirás-Avalos and Intrigliolo \(2017\)](#), reducing sugars and organic acids have a negative and positive relationship with berry quality. Berries, like leaves, collect osmolytes in response to water shortage. When studying the adjustment of berry osmotic potential during drought, it is important to consider the role of amino acids. This should be done in conjunction with our existing knowledge of the primary molecules that influence berry osmotic potential during ripening, which include malate, tartrate, glucose, fructose, and potassium before véraison. After véraison, the main contributors are primarily glucose and fructose ([Wada et al., 2008](#)).

Flavonoids

The most important metabolites influencing grape flavour and quality are flavonoids and volatile organic compounds. It was found that the phenolic profile of 279 *Vitis vinifera* cultivars responds differently to water shortage, with unique molecular families impacted positively or adversely ([Pinasseau et al., 2017](#)). Water scarcity reduces the growth of tree canopy and exposure to sunlight, as well as has a direct impact on berry metabolism ([Castellar et al., 2007b](#)). Light and UV radiation have a particularly strong effect on flavanol synthesis. [Deluc et al. \(2009\)](#) proposed that the change in flavanols seen in white varieties (e.g., Chardonnay) treated with water stress might serve as a potential method for photo-protection, as white berries do not contain anthocyanins ([Gambetta et al., 2020](#)).

EXTREME DROUGHT

Plant mortality can result from drought in perennial organs, known as 'hydraulic failure' ([McDowell et al., 2008](#)). Although their vulnerability segmentation shields them from harm, in terms of carry-over effects from one season to the next, even less significant water deficiencies might sometimes contribute to lower fruit output.

EFFECT OF DROUGHT ON FRUIT QUALITY AND TASTE

Abiotic stress, particularly high temperature, can produce chemical changes in grapes, resulting in overripe fruits with low titratable acidity, high sugar contents, and hence higher levels of alcohol, along with changes in aroma and colour ([Pons et al., 2017](#); [Orduna, 2010](#)). The exposure of grape clusters to sunlight induces the production of secondary metabolites, which have a significant impact on the potential quality of the fruit, as long as they remain within specific limits ([Cohen et al., 2008](#)). [Pons et al. \(2017\)](#) suggested that the berry ripening at high temperatures could be linked to the absence of herbaceous aromas in wines. Because many metabolic processes are temperature and light-sensitive, sunlight has an impact on the composition of grape berries. The most frequent are malic and tartaric acids. Malic acid is digested and utilized and hence remains stable throughout the ripening phase as a source of energy ([Rienth et al., 2016](#)). Furthermore, greater pH is usually associated with lower overall grape acidity. Climate change has posed a serious threat to the grape industry, owing to changes in grape formation and conditions, like increased warmth of grapes at harvesting time and increased ambient temperatures ([Orduna, 2010](#)).

WATER SCARCITY DURING GROWTH AND DEVELOPMENT

Water is essential for viticulture's long-term viability, as output, quality, and profitability depend on it ([Flexas and Medrano, 2002](#)). A lot of time and effort had gone into determining the impact of water status on the composition of berries, primarily on genotypes grown in semi-arid climates. Titratable acidity, TSS, malic and tartaric acid are present, although pH is not one of them. Phenolics, anthocyanins, and tannins have all been studied ([Leeuwen and Destrac-Irvine, 2017](#)). The severity and time of water stress during the grapevine development cycle are critical. Water stress causes severe phenotypic and metabolic changes in fruit, which can be preserved by following re-watering ([Shellie, 2014](#); [Zhang and Keller, 2015](#)). Water stress also affects berry weight. Total soluble solids, anthocyanins, and titratable acids will rise, but total soluble solids, anthocyanins and phenolics of red grapes improve the quality of the berries.

Drought forces the grapevine to modulate its growth. Several secondary metabolic processes affect the number of involved transcripts and metabolites in phenyl propanoid isoprenoid, carotenoid, amino acid, and fatty acid.

TRANSCRIPTIONAL PATHWAY ASSOCIATED WITH DROUGHT STRESS

There are two types of transcriptional pathways:

1. ABA-dependent drought response pathway.
2. ABA-independent drought response pathway.

ABA-dependent drought response pathway

ABA Indicating PYR/PYL/RCARs create a trimetric complex with PP2Cs when activated by ABA, which suppresses PP2Cs' phosphatase activity. PP2Cs are then used to liberate SnRK2s from the association. Consequently, the transcription factors (TFs) and ion channel proteins located downstream are phosphorylated ([Yoshida et al., 2015](#); [Ma et al., 2009](#); [Park et al., 2009](#)). The TFs of the ABA signalling pathway, AREBs/ABFs, are one of SnRK2's targets. Many other TF families participate in drought response and adaptation, such as WRKY and MYB ([Singh and Laxmi, 2015](#)).

AREBs/ABFs and WRKYs

Finally, ABA synthesis and the ABA signalling system are crucial for woody plants to respond to drought stress. Water deprivation and ABA promote the expression of many WRKY family genes such as WRKY18, WRKY40, and WRKY60. According to [Liu et al. \(2015\)](#) and [Lee et al. \(2010\)](#), ABA enhances the ABAR/WRKY40 interaction, which counteracts the unfavourable effect of WRKY40 on ABI5 expression.

ABA-independent drought response pathway

Even though ABA activates many TFs and participates in the pathway of ABA-dependent signalling, several TFs are substantially stimulated by a shortage of water but are not primarily mediated by ABA production ([Yoshida et al., 2015](#)).

AP2/ERFs

The DRE (A/GCCGAC) element in drought-responsive genes is recognized by DREB2 proteins, such as DREB2A and DREB2B, which belong to the AP2/ERF transcription factor family. Dehydration-responsive The DRE (A/GCCGAC) element is located in many drought-responsive genes, and DREB2 proteins are well aware of it. DREB2A and DREB2B belong to the AP2/ERF (Apetala2 and ethylene-responsive facets) transcription factor family. The expression of DREB2A is slightly elevated by ABA but strongly induced by dehydration, demonstrating that drought stress is mediated in an ABA-independent way (Kim et al., 2013). Arabidopsis TINY is part of the AP2/ERF family. TINY promotes drought response and ABA-mediated stomatal closure by interacting with BES1 in the BR signalling pathway (Xie et al., 2017). Other ERF/AP2TF relatives, such as HARDY (HRD), TG/RAP2.4A, and AtERF74, have been demonstrated to improve drought tolerance, whilst AtRAP2.1 has been shown to reduce drought responsiveness (Dong and Liu, 2010; Zhu et al., 2014; Yao et al., 2017).

CONCLUSION

In the last few years, our understanding of grapevine drought stress physiology has vastly improved. However, many drought responses still lack a mechanistic explanation, preventing precise simulations under future climate situations. ABA has been studied extensively in recent decades due to its role in regulating a variety of physiological systems, including abiotic stress responses. The tripping system of ABA signalling continues to be questioned as the biosynthetic pathway is further understood. Although the assumption that ABA is predominantly synthesized in the root system is widely recognized in grapevine, a growing body of evidence supports the hypothesis that drought-induced stomata closure is mediated by ABA produced in the leaf. Hydrostatic integration, genetic element exchange, structural alterations at the graft interface, and hormonal communication are all intricately interwoven.

Declaration of competing interests

The authors declare no competing interests.

Author contribution statement

Muhammad Abi Waqas: Wrote the first draft of the manuscript.
Amina Shahid, Fatima Rasool: Revised the manuscript. All authors approved the final draft of the manuscript.

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