



Complex Analysis of Physiological, Biochemical and Molecular Mechanisms of Drought Adaptation in Apple (*Malus domestica* Borkh.): A Review

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ABSTRACT

Drought is one of the most critical abiotic stresses limiting apple (*Malus domestica* Borkh.) growth, productivity and fruit quality worldwide. Understanding the complex physiological, biochemical and molecular mechanisms underlying drought tolerance is essential for developing stress-resilient cultivars. The present review highlights integrated responses of apple varieties to drought stress, focusing on water relations, gas exchange, osmotic regulation, antioxidant defense and hormonal signaling. Physiologically, drought-tolerant genotypes maintain higher relative water content, stomatal conductance and water-use efficiency. Biochemically, accumulation of osmolytes (proline, soluble sugars, glycine betaine) and enhanced activity of antioxidant enzymes (SOD, CAT, POD, APX) mitigate oxidative damage. Molecular mechanisms involve activation of drought-responsive transcription factors (AREB/ABF, DREB, NAC, MYB), signal transduction through ABA pathways and upregulation of stress-protective genes. Integration of these responses enables better nutrient and water uptake, osmotic adjustment and improved photosynthetic performance under water deficit. Future research should focus on genome editing, marker-assisted selection and omics-based approaches to accelerate the breeding of drought-resilient apple cultivars.

Key words: Antioxidant defense, Biochemical mechanisms, Drought stress, *Malus domestica* Borkh, Molecular responses, Physiological adaptation, Transcription factors.

Apple (*Malus × domestica* Borkh.) is one of the most widely cultivated and economically important fruit crops globally, valued for its nutritional content, industrial use and contribution of over 73 billion USD to the global economy (FAOSTAT, 2020). In Uzbekistan, apple is the leading fruit crop, where intensive production largely relies on high-yielding commercial cultivars. However, these modern varieties often lack adaptability to local environmental stresses.

Due to global climate change, decreasing water availability, unpredictable rainfall patterns and rising temperatures pose serious threats to agricultural systems worldwide. Among fruit trees, apple (*Malus × domestica* Borkh.) is particularly vulnerable to drought stress, which adversely affects not only vegetative growth but also fruit yield and quality. In drought-prone regions, such as the Mediterranean, Central Asia and parts of Uzbekistan, these stresses directly impact the economic viability and sustainability of apple production.

Identifying drought-tolerant cultivars and rootstocks and understanding their physiological and molecular mechanisms of stress response, is therefore of both scientific and practical significance. Such knowledge enables the development of resilient apple varieties better adapted to climate change, while also supporting improved agronomic practices and resource-efficient production systems. In Uzbekistan-where apples are the most cultivated fruit and water scarcity is an increasing concern-the

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preservation and study of traditional apple germplasm offer a promising avenue. These varieties, often naturally adapted to local environmental conditions, can serve as valuable genetic resources for breeding drought-tolerant, high-quality cultivars.

This research provides an essential foundation for modern breeding strategies by elucidating the physiological, biochemical and genetic basis of drought tolerance in apples. The findings have the potential to contribute significantly to sustainable fruit production and food security in water-limited environments.

Due to climate change, apple production faces increasing threats from abiotic stress factors such as drought, extreme heat and salinity. These stressors negatively affect physiological and molecular processes, including photosynthesis, stomatal conductance and oxidative balance, ultimately reducing fruit yield and quality (Berger *et al.*, 2016; Pérez *et al.*, 2008). As agriculture consumes over 70% of the world's freshwater, the need for drought-resilient cultivars is more urgent than ever.

Traditional apple cultivars, though underutilized, are better adapted to local conditions and often show enhanced resistance to environmental stresses. They contain higher levels of bioactive compounds and demonstrate stable performance under drought (Donno *et al.*, 2012; Cvetković *et al.*, 2012). Therefore, understanding and utilizing their genetic potential is critical for future breeding strategies.

This study aims to comprehensively examine the physiological, biochemical and molecular responses of apple plants to drought stress. Special focus is given to identifying drought-responsive genes and pathways that contribute to improved stress adaptation. The findings will provide a basis for developing high-performing, drought-tolerant apple varieties to ensure sustainable production in a changing climate.

The effect of drought stress on the physiological, biochemical and molecular mechanisms of apple plants

Drought is a major limiting factor in crop production. Due to increasing global temperatures and limited water resources, drought has become a global issue threatening future crop production (Zhao *et al.*, 2020; Botirov *et al.*, 2021). Naturally, plants have developed multiple molecular and physiological mechanisms to withstand stress. Drought activates key regulatory genes that control physiological processes such as stomatal closure (Taiz *et al.*, 2002) and detoxification of reactive oxygen species (ROS) (Sun *et al.*, 2018; Chen *et al.*, 2019). Additionally, heat and drought conditions generate ROS, leading to membrane damage and oxidative stress.

Recent studies published in ARCC journals have highlighted the importance of integrating physiological, biochemical and molecular approaches for improving drought tolerance in horticultural crops. These studies emphasize the role of antioxidant systems, transcription factors and stress signaling networks in enhancing plant resilience under water deficit conditions, which is essential for developing climate-resilient fruit production systems (Kumar *et al.*, 2021; Singh *et al.*, 2020; Patel *et al.*, 2019; Sharma *et al.*, 2022).

Water deficiency in plants induces oxidative stress (Lei *et al.*, 2006; Noctor *et al.*, 2014), including excessive

production of reactive oxygen species such as superoxide radicals (O_2^-) and hydrogen peroxide (H_2O_2) resulting in lipid peroxidation and damage to membranes, proteins, chlorophyll, nucleic acids and ultimately cell death (Scandalios, 1993). Drought can significantly reduce photosynthesis and cause chlorophyll degradation (Viljevac *et al.*, 2013; Bhusal *et al.*, 2019). According to Chaves *et al.* (2002), the negative effects of drought on plant physiology depend on the intensity and duration of the drought stress as well as the plant's ability to adapt and survive under such conditions.

To withstand drought stress and protect against oxidative damage, plants have developed antioxidant defense mechanisms, including antioxidant enzymes such as peroxidase (POD), superoxide dismutase (SOD), catalase (CAT) and non-enzymatic antioxidants such as phenolic compounds, ascorbic acid, glutathione and carotenoids (Asensi, 2010; Farooq *et al.*, 2012). Some plants accumulate osmolytes like proline, glycine betaine and soluble sugars to protect themselves and mitigate drought stress (Shehab *et al.*, 2010; Xu *et al.*, 2018; Dien *et al.*, 2019). Recent studies have shown that certain plant organ compounds like terpenes (Mahdavi *et al.*, 2020) and phytohormones like brassinolide (Naservafaei *et al.*, 2021) can alleviate drought effects by enhancing the plant's defense systems.

Chlorophylls, as the main photosynthetic pigments in plant leaves, reflect the photosynthetic capacity and overall vitality of plants. The chlorophyll content in leaves is considered a good indicator of stress tolerance in various crops, including drought tolerance (Arunyanark *et al.*, 2008). Previous studies have documented that drought stress negatively affects chlorophyll accumulation in apple rootstock cuttings (Alizadeh *et al.*, 2011; Bolat *et al.*, 2014). Under drought conditions, a decrease in chlorophyll content has been observed in plants, with a greater decrease recorded in the commercial cultivar 'Golden Delicious Reinders' compared to 'Crenka' (Mihaljević *et al.*, 2021). These results are consistent with observations by Bhusal *et al.* (2019), where a smaller decrease in total chlorophyll content was found in the drought-tolerant 'Fuji' apple compared to the 'Hongro' apple.

Carotenoids play an essential role in photosynthesis, as they protect photosystem II from photooxidative damage (Cogdell and Gardiner, 1993); Khoyardi *et al.* (2016) reported that high carotenoid content in pistachio cultivars leads to greater drought tolerance.

Under drought conditions, the decline in photosystem II activity is associated with oxidative stress and cell membrane damage caused by increased lipid peroxidation (Benhassaine *et al.*, 2002). Malondialdehyde (MDA) is a product of lipid peroxidation and is commonly used to assess oxidative stress during drought (Farooq *et al.*, 2010). Various abiotic stresses, including drought, induce the generation of ROS such as H_2O_2 which damages membrane lipids (Kocsy *et al.*, 2005). Our findings indicate that higher MDA concentrations under drought stress are

associated with elevated H_2O_2 levels in plants. During drought stress, significant increases in MDA and H_2O_2 contents were observed in both the 'Golden Delicious Reinders' and 'Dugara' cultivars, indicating oxidative damage in both. As the intensity of stress increased, so did the levels of H_2O_2 and consequently MDA. Møller *et al.* (2007) suggested that higher MDA levels indicate more severe oxidative damage.

In our study, the commercial 'Golden Delicious Reinders' cultivar exhibited a faster increase in MDA and H_2O_2 concentrations compared to the traditional 'Dugara' cultivar and significant early-stage changes in H_2O_2 suggest that 'Dugara' is more drought-tolerant. Several researchers have reported increased MDA and H_2O_2 levels under drought stress in plants (Petridis *et al.*, 2012; Yang and Miao, 2010). In the traditional 'Crvenka' cultivar, MDA content remained stable under drought, while H_2O_2 levels decreased after 12 days of drought, consistent with earlier findings (Umar and Shaheed, 2018), suggesting that reduced H_2O_2 production is likely associated with increased antioxidant enzyme activities, particularly CAT.

Leaf water content (WC) is an indicator of plant water status and is used to evaluate drought tolerance (Bandurska and Joswiak, 2010). After 12 days of stress, a significant decrease in leaf water content in response to drought stress was observed only in the 'Golden Delicious Reinders' cultivar, which had the lowest photosynthetic efficiency. In contrast, the traditional cultivars maintained better photosynthetic efficiency and stable water content. Similarly, Tounekti *et al.* (2018) found that a drought-tolerant coffee cultivar exhibited higher water content along with better photosynthetic efficiency under drought conditions. These observations, confirmed by photochemical parameters, highlight the better drought tolerance of traditional cultivars.

Proline is an important organic osmolyte that accumulates and increases under drought conditions and also acts as a ROS scavenger (Sumera and Asghari, 2010; Liang *et al.*, 2013). Numerous previous studies have reported higher proline accumulation in drought-tolerant plants (Anjum *et al.*, 2016; Man *et al.*, 2011). However, our results showed that proline measurement was not a reliable screening method for determining drought tolerance in the studied apple cultivars. The proline content in the drought-tolerant 'Crvenka' was not higher than that in the drought-sensitive 'Golden Delicious Reinders'. The lower proline accumulation in 'Crvenka' may suggest the activation of other drought defense mechanisms. Rampino *et al.* (2006) also reported that drought-tolerant wheat plants exhibited higher relative water content (RWC) and lower proline accumulation.

Plant phenolic compounds are secondary metabolites that serve as antioxidants and have been described as indicators of abiotic stress tolerance in plants (Blokchina *et al.*, 2003; Quan *et al.*, 2016); Hura *et al.* (2009) found that in triticale plants, higher phenolic content was associated with better photosynthetic activity. However, this does not align with our findings, as the total phenolic content accumulated in the leaves of the studied apple cultivars

was highly variable, with the highest phenolic content observed in the commercial cultivar "Golden Delicious Reinders." These results suggest that phenolic compounds may not play a major role in the defense responses of the studied apple cultivars. Similarly, Puente-garza and colleagues reported that total phenolic content was not correlated with antioxidant activity in Agave plants.

Although we hypothesized that higher concentrations of proline and secondary metabolites (phenolics) would improve osmotic adjustment and drought tolerance, this hypothesis was not supported. This likely indicates that antioxidant enzyme systems were activated as a protective mechanism in this study. According to Mihaljević *et al.* (2021), there are significant differences among cultivars in their physiological and biochemical responses to drought stress. The most drought-tolerant cultivars showed high photosynthetic efficiency, high chlorophyll content and strong membrane stability, whereas the commercial cultivar "Golden Delicious Reinders" was found to be the most sensitive under the studied conditions. The good quality traits of "Crvenka" (Jakobek *et al.*, 2020) and its high drought tolerance make it a promising cultivar for cultivation under dry conditions in the region. These cultivars could be used to update the production assortment and support the development of fruit cultivation. Preserving traditional cultivars is also important for maintaining genetic material for breeding purposes; therefore, the results of this study could provide valuable information for future breeding programs.

Plants have developed morphological, physiological and molecular resistance mechanisms in response to abiotic stress. Among these molecular mechanisms are the regulation of gene expression through transcription factors (TFs) and the roles of specific functional genes. NAC genes are plant-specific transcription factors that influence plant growth and development and participate in the transcriptional regulation of responses to various abiotic stresses such as drought, salinity, cold and pathogen infection (Sun *et al.*, 2012; Tak *et al.*, 2017). Members of the NAC gene family are differentially expressed in response to abiotic stress.

Here, we isolated the MdNAC29 gene, a NAC transcription factor, from apples. Our results showed that MdNAC29 is localized in the nucleus and responds to drought stress. Overexpression of MdNAC29 was found to negatively regulate drought tolerance in transgenic apple plants, callus and tobacco plants.

Moreover, genes such as MdERD5, MdRD22, MdRD29A, MdAREB1, MdDREB2A and MdMYB46 have been reported to be extensively involved in improving drought tolerance in plants (An *et al.*, 2018; Chen *et al.*, 2019; Li *et al.*, 2022; Liu *et al.*, 2022). We hypothesize that MdNAC29 regulates the expression of these drought-responsive genes. qRT-PCR results showed that the overexpression of MdNAC29 significantly downregulated the expression of these genes in apple trees.

Drought in apple trees is generally understood as a persistent water deficit due to an imbalance between water

supply and demand or a low water budget throughout the growth cycle. This leads to leaf wilting, yellowing and premature leaf drop, as well as early fruit ripening and fruit drop (Yang *et al.*, 2021). In apple trees, drought stress can temporarily inhibit shoot growth due to reduced leaf area, stomatal closure and disruption of the plant's carbon balance caused by hydraulic failure (Lauri *et al.*, 2016). During hot summer months, drought stress, often combined with heat stress, can cause leaf scorch. Frequent drought stress events caused by dry weather conditions resulting from global warming have significantly reduced apple yield and quality (Aras and Keles, 2019). Therefore, apple trees must sense soil water availability and activate appropriate molecular stress responses to survive under such conditions.

Research has shown that one of the key genes involved in improving drought tolerance in apple trees is MdDREB2A. Overexpression of this gene activates stress-responsive genes under stress conditions, thereby enhancing drought tolerance. Furthermore, other transcription factor families, such as NAC, MYB and ERF, also participate in forming drought adaptation responses, but many studies particularly emphasize the importance of MdDREB2A. To date, many genes from the APETALA2/ethylene-responsive factor (AP2/ERF), ZFP, bHLH, MYB and NAC families have been identified and characterized for their roles in apple drought responses (Fig 1).

In the study by Sun *et al.* (2018), overexpression of the MdATG18a gene in apple trees enhanced their drought tolerance. These processes help degrade aggregated proteins and limit oxidative damage. Another important agricultural practice to improve drought tolerance is the inoculation of plants with arbuscular mycorrhizal fungi (AMFs) (Chitarra *et al.*, 2016). AMFs are well-known symbionts of many terrestrial plants and play critical roles in adapting to various stresses (Huang *et al.*, 2020). The effects of AMFs on plant drought tolerance are highly complex, involving multiple metabolic pathways. They assist

in drought adaptation by improving nutrient and water uptake and transport, enhancing osmotic regulation, inducing hormone signaling, improving gas exchange capability, increasing water use efficiency and strengthening antioxidant capacity (Yang *et al.*, 2014).

Moreover, during drought conditions, MAPK signaling genes are highly expressed, facilitating the interaction between AMFs and apple trees and enhancing drought tolerance (Huang *et al.*, 2020). Plant transcription factors (TFs) also play important roles in regulating stress responses (Century *et al.*, 2008). Among these TFs, the homeodomain-leucine zipper (HD-Zip) family is particularly important in regulating drought responses (Yang *et al.*, 2014). In apples, the HD-Zip gene MdHB-7 leads to the accumulation of endogenous abscisic acid (ABA) in response to drought, promoting ROS detoxification and stomatal closure, while RNA interference (RNAi) lines of this gene showed opposite effects (Zhao *et al.*, 2020).

Additionally, ethylene response factors (ERFs) influence anthocyanin biosynthesis. The well-characterized ERF protein MdERF38 participates in anthocyanin biosynthesis induced by drought stress. Molecular experiments showed an interaction between the ERF protein (MdERF38) and the positive regulator of anthocyanin (MdMYB1), which promotes drought tolerance. MdMYB88 and MdMYB124 also act as positive regulators of drought tolerance (Li *et al.*, 2020). In apple, 42 apple-specific miRNAs have been identified, among which miR156, miRn249, miR408 and miR395 act as positive regulators of drought tolerance (Li *et al.*, 2020).

The drought-responsive gene families and their regulatory roles in stress adaptation in apple are illustrated in Table 1. The schematic depicts the major drought-responsive gene families in apple and their roles in physiological and molecular pathways of stress adaptation. Abbreviations: NAC - NAM/ATAF/CUC transcription factors; DREB - dehydration-responsive element-binding proteins; ERF - ethylene response factors; MYB - MYB transcription factors; HD-Zip - homeodomain-leucine zipper proteins.

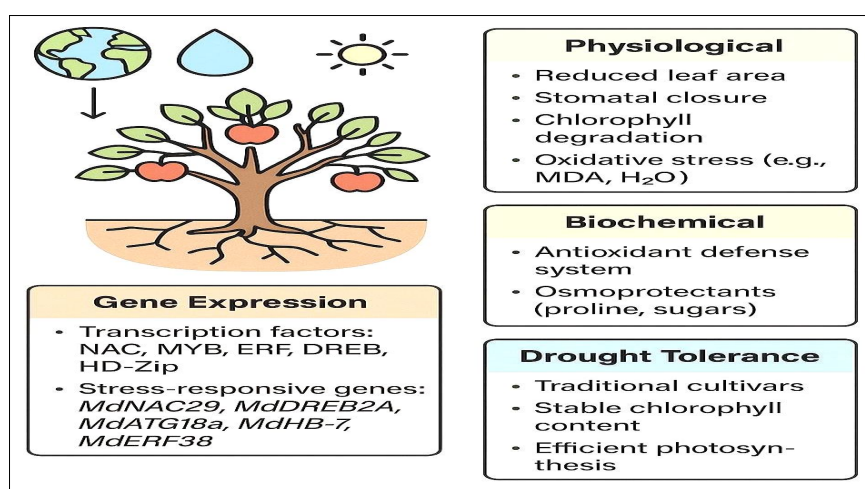


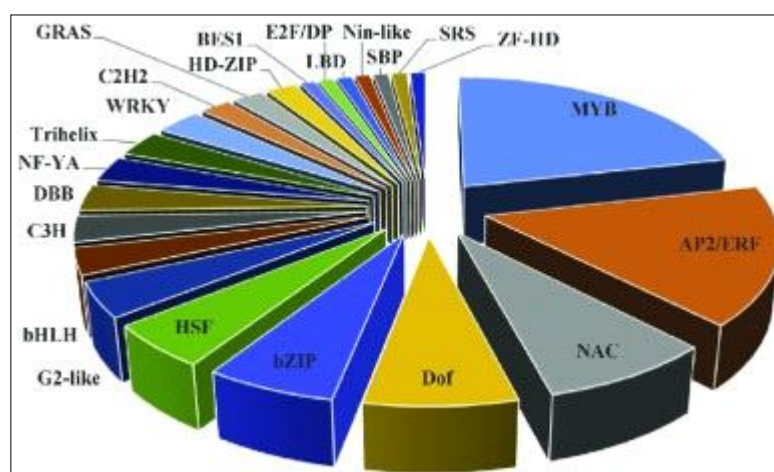
Fig 1: Effects of drought on apple (*Malus domestica* Borkh.): physiological, biochemical and molecular responses.

Table 1: Specific gene families in apple are involved in stress responses.

The name of the gene family	Gene	Function	References
NAC	MdNAC1, MdNAC2, MdNAC3	Stress resistance, growth and development	Jiang <i>et al.</i> , 2016
MYB	MdMYB1, MdMYB2, MdMYB3	Phytoalexin production, pigmentation	Zhang <i>et al.</i> , 2012
ERF	MdERF1, MdERF2, MdERF3	Ethylene response, stress tolerance	Zhang <i>et al.</i> , 2013
DREB	MdDREB1A, MdDREB2A	Drought and cold tolerance	Zhao <i>et al.</i> , 2016
HD-Zip	MdHB1, MdHB2, MdHB3	Growth and development, stress response	Liu <i>et al.</i> , 2014

Notes:

- NAC Family: Genes in this family play an important role in growth, stress tolerance and development. For example, the MdNAC1 and MdNAC2 genes enhance drought tolerance.
- MYB Family: Genes in this family are involved in pigmentation, phytoalexin production and stress response. The MdMYB1 and MdMYB2 genes are crucial for determining the color of apple fruits.
- ERF Family: Genes involved in the ethylene response, which contribute to stress tolerance. The MdERF1 and MdERF2 genes regulate the stress response in apple plants.
- DREB Family: Genes in this family enhance drought and cold tolerance. The MdDREB1A and MdDREB2A genes regulate the drought response in apple plants.
- HD-Zip Family: Genes in this family participate in growth and development. The MdHB1 and MdHB2 genes regulate the growth of apple plants.

**Fig 2:** Stress-responsive specific gene families.

The pie chart (Fig 2) illustrates the percentage distribution of genes across different transcription factor (TF) families. The largest portions are represented by the MYB, AP2/ERF and NAC families, which play critical roles in gene expression. Other families, such as bZIP, HSF, bHLH, Dof and G2-like, occupy relatively smaller proportions. The smaller segments include transcription factor families such as WRKY, GRAS, C2H2, Trihelix, NF-YA, DBB, C3H, BES1, HD-ZIP, E2F/DP, LBD, Nin-like, SBP, SRS and ZF-HD.

This distribution visually represents the allocation of transcription factor families within the plant genome and analyzing their expression profiles provides deeper insights into stress responses, development and molecular regulatory mechanisms in plants. The highly represented MYB, AP2/ERF and NAC families constitute major regulatory

genes in plants, making them central targets for molecular biology and breeding research.

CONCLUSION

This study analyzed drought resistance mechanisms in apple plants at physiological, biochemical, and molecular levels. The results indicate that apples adapt to drought through stomatal closure, reduced leaf area, osmoprotectant synthesis, and activation of antioxidant enzymes such as SOD, CAT and POD, which mitigate oxidative damage caused by ROS. At the molecular level, stress-responsive genes including *MdNAC29* and *MdDREB2A* regulate signaling pathways and activate downstream defense mechanisms. The findings suggest that combining the natural drought tolerance of traditional varieties with transgenic approaches offers strong potential

for breeding resilient apple cultivars capable of maintaining yield and fruit quality under climate change.

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Author contribution

Farhod Abdurasulov conceived and structured the study, conducted the literature search and selection and drafted the initial version of the manuscript. Farhod Abdurasulov and Jaloliddin Shavkiev contributed to the critical analysis of the literature and the revision of the manuscript. Sherzod Rajametov assisted in data organization.

Data availability

The data supporting the findings of this review are entirely derived from peer-reviewed publications and publicly available databases, including PubMed, ScienceDirect, Scopus and Web of Science. A comprehensive list of these sources is provided in the References section. No proprietary or unpublished data were used.

Ethical approval

Not applicable to this study.

Conflict of interest

The authors declare no conflicts of interest.

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