

Review

Adaptation Mechanisms of Olive Tree under Drought Stress: The Potential of Modern Omics Approaches

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Abstract: Olive (*Olea europaea* L.) is a crop of enormous economic and cultural importance. Over the years, the worldwide production of olive oil has been decreasing due to various biotic and abiotic factors. The current drop in olive oil production resulting from climate change raises concerns regarding the fulfillment of our daily demand for olive oil and has led to a significant increase in market prices. In the future, there will be a higher chance that we will face a severe shortage of olive oil, which could harm both the economic sector and the food supply. As olive groves cover more than 5 million hectares in the European Union alone, the need to preserve the crop in the context of extreme climatic events is imperative. As drought is considered one of the most limiting factors in agriculture, drought-resistant varieties and sustainable irrigation strategies are being developed to mitigate the impact of drought on crop productivity and secure the future supply of olive oil. This review focuses on recently gained insights into drought stress in olive trees through omics and phenomics approaches to unravelling mechanisms that may lead to developing new varieties that are tolerant against drought elicited by changes in growing systems.

Keywords: *Olea europaea*; climate change; water deficit; stress memory; priming



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1. Introduction

The olive tree (*Olea europaea* L.) is one of the most iconic crops in the Mediterranean Basin [1,2], with fundamental importance for primary production, not only for its economic and nutritional value but also for its profound cultural and ecological significance. Olive products, such as table olives and olive oil, have many health benefits, which have increased consumer demand [3]. As a result, this has expanded the income of producers and resulted in the creation of more employment prospects within the industry [4]. The European Union produces more than 93% of global olive oil production, and Spain is the largest producer and exporter of olive oil in the world, followed by Italy and Greece [3]. The presence of olive trees in the Mediterranean Basin since the Bronze Age, as confirmed by palynological analysis and the discovery of olive tree remains at archaeological sites, confirms that olive trees are unequivocally regarded as one of the most suitable and best-adapted species to thrive in the Mediterranean-type climate [2,4]. Despite being well suited to the Mediterranean Basin, olive trees face increased drought risk due to rising temperatures and limited precipitation. According to future model forecasts, considerable warming and drier conditions are expected in numerous regions worldwide due to climate change [5].

These projections indicate that areas that were already vulnerable to drought and heat increase the likelihood of these conditions worsening. Such conditions could have adverse effects on agriculture, water resources, and overall ecosystems that would contribute to the weakening of and threat to olive-growing areas by reducing productivity as well as the quality of the olive fruit [6]. To ensure the future of this significant species and increase its profitability, it is necessary to understand how olive trees respond to drought stress, identify tolerant traits effective in breeding programs, and develop accurate adaptation strategies to stress conditions. An integrated approach of omics technologies, including phenomics (morpho-physiological measurements), genomics, transcriptomics, metabolomics, proteomics, and epigenomics, could aid in deconstructing and understanding the drought effect and the mechanisms that olive trees utilize to overcome this threat (Figure 1). In the following study, we will explore the recent findings in the use of omics approaches underlying drought stress in olive trees, aiming for the development of climate-resilient olive varieties.

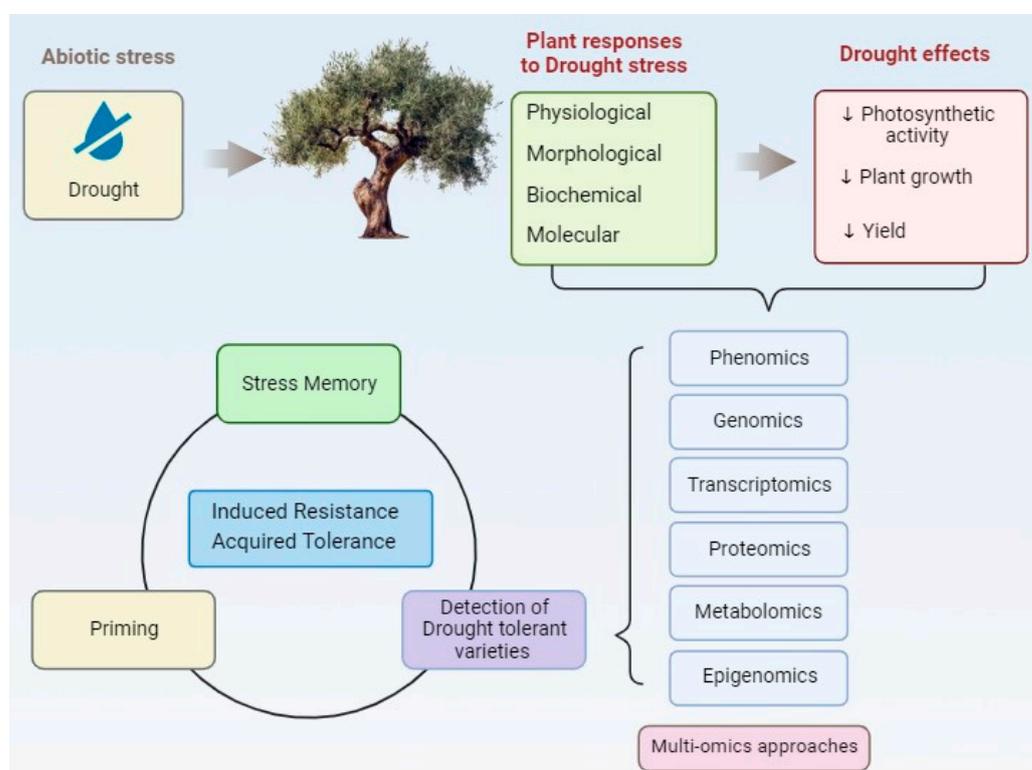


Figure 1. Prolonged drought stress results in a decrease in photosynthetic activity, plant growth and reduced production. Multi-omics approaches, priming and stress memory strategies enhance drought stress tolerance in olive crop.

1.1. Olives and Drought in a Changing Climate

Among all environmental stresses (extreme temperatures (high/low), lack or excess of water, salinity, heavy metals, lack of nutrients, oxidative stress), drought has been recognized as the most devastating, affecting agriculture globally and leading to the greatest reduction in production [6–12]. Extreme weather events, such as high/low temperatures, prolonged droughts, more frequent floods, accelerated sea level rises, and storm surges, are already being witnessed in many regions, with increased frequency [13–15]. In the latest report of the World Meteorological Organization (WMO) published in November 2023, data indicated that the year 2023 was the warmest in the 174-year observational record, exceeding the previous joint warmest years, 2016 at $1.29 (\pm 0.12) ^\circ\text{C}$ above the 1850–1900 average and 2020 at $1.27 (\pm 0.13) ^\circ\text{C}$ [16]. In 2023, extreme heat and drought, as well as wildfires, had significant consequences for all inhabited continents, threatening

water resources and food security. As stated in “The Sustainable Development Goals Report 2022”, medium- to large-scale disasters will increase by 40% from 2015 to 2030, while drought is estimated to displace 700 million people by 2030 [17]. In some areas, such as the Mediterranean region, medium- or long-drought periods increased eight times more than in the past [17]. Such conditions would have major consequences for crops, as water availability is a critical factor in agricultural productivity, while drought events have already caused significant damage to olive cultivation. Although olive trees are considered drought-tolerant species [18], water stress can possess a wide variety of negative effects and physiological processes, including nutrient uptake, carbon assimilation, reduced flower and fruit setting, canopy dimension, flower abortion, and cluster abscission [2,19]. These projections may result in an overall decrease in yields until 2080 [2]. Currently, world olive oil production for the marketing year 2022/23 is estimated at 2555 tonnes (1392tn EU and 1163tn non-EU), while for 2023/24 it is expected to remain lower, around 2414 tonnes (1413tn EU and 1002tn non-EU), as production in non-EU countries decreases by 14% and EU production remains below average [20]. Drought and extreme weather in the EU’s south in 2023 significantly impacted olive yields, as the EU’s olive oil production level reached its lowest level since 1994/95 [20]. To reduce the impact of drought on food security and address climate change, comprehensive research on how olive trees respond to drought stress, along with the exploitation of genetic diversity to promote drought tolerance, is beyond critical.

1.2. Drought Stress Tolerance and Adaptation Mechanisms

Olives, as a high-value crop grown in 28 countries around the globe, have more than 2000 varieties [21,22]. The distribution and development of these varieties are significantly affected by climate change due to their adaptability to specific environments. The species has evolved effective physiological, biochemical, and morphological tolerance mechanisms, leading to improved drought adaptation [23]. In general, plants exhibit various response mechanisms under drought stress to minimize negative effects. These strategies include the responses of evasion, escape, tolerance, and recovery, all of which play an important part in the plant’s capacity to tolerate and adapt to water scarcity, and are being extensively studied [24]. In addition to these stress management strategies, plants may develop mechanisms that allow them to recognize a re-exposure to a similar stressor and respond more effectively [25]. Through these mechanisms, plants may “remember” the stressor, and defend themselves more effectively relative to the first time/stressful event, a process known as stress memory [26]. Priming and stress memory are defined differently by different authors and areas within plant science [27]. In the context of biotic stress, priming is widely used to describe the sensitization of inducible defense mechanisms. It arises after being exposed to biotic stimuli and creates a recurring stress reaction that causes a quicker and/or greater defensive response, whereas abiotic stress adopts a broader concept of priming, also known as acclimatization or hardening, in which priming leads to either permanent upregulation (Type I) or sensitization (Type II) adaptive responses [27]. The information imprinted into the cells of the plant, after a previous environmental stimulus, can provide an improved reaction to recurrent stress factors. As a result, stress memory can emerge during the phase of a priming event, and the duration of the stress memory varies, depending on the intensity of the priming event, as well as on genetic characteristics that influence stress tolerance [28]. Today, the focus of crop breeding approaches in agriculture regarding climate change is priming and stress memory. A range of priming strategies such as posttranslational modifications via epigenetic mechanisms, the accumulation of various cellular compounds, and the phosphorylation of mitogen-activated protein kinases (MAPKs), have been identified [29]. Priming might be implemented at any developmental stage or tissue to promote tolerance exposure and can be achieved through biological stress factors (elicitors and bio stimulants) and non-biological forces (physical forces or chemicals) [30]. These external stressors can be captured as core memories, through somatic memory maintained in the same generation through mitosis (somatic memory)

and/or long-term memories transmitted between generations (inter-generational and trans-generational) [25]. Even though research groups are focusing on networking mechanisms to trigger and sustain stress memory via priming events, the molecular basis regulating these pathways is as yet unclear. Further study of these processes, as well as the identification of the most effective pathways to acclimatization and acquired tolerance, might lead to novel approaches to stress management. Already in the 1990s, researchers began to focus on abiotic stress in olive tree cultivation, particularly drought [6–8]. However, drought stress memory and priming mechanisms, especially in woody species, have not been widely investigated. In the context of olive trees, there is evidence of priming processes that facilitate the promotion of stress memory. In 2017, Abdallah et al. studied the priming effect of drought, using the olive drought-sensitive variety Chétoui, one of the most cultivated olive varieties in Tunisia [31]. In their study, they employed two drought events with an intermediate phase of rewatering. They found that, in comparison to the plants that had not previously experienced drought, the plants that had gone through drought before had improved stress tolerance mechanisms and overall improved growth and survival rates [31]. This indicates that plants could exhibit an adaptive mechanism to handle consecutive periods of drought, hence improving their ability to tolerate drought as well as recuperate in regions prone to drought. The same research group, in another experiment in 2022 using the same olive variety (Chétoui), employed salt priming as a stimulus to promote drought stress memory (cross-priming) [32]. Their study indicated that salt priming induces noteworthy impacts on the physiological and biochemical reactions of olive plants under drought conditions. They discovered the buildup of osmotic compounds, improved removal of reactive oxygen species (ROS), and increased leaf density and structural lipid content, highlighting cross-priming as an alternative option for the induction of olive stress memory. Furthermore, these results emphasize the need to understand plant responses to numerous drought events, which could potentially help develop strategies related to water scarcity and improve crop productivity [30]. There are many studies regarding drought priming that has been shown to improve drought tolerance in important plant species, through different water regimes and recovery phases [33–35] or through seed priming [36–38]. However, these strategies are not widely investigated in woody/tree crops, with a few exceptions such as the *Populus* sp. [39,40]. To thoroughly investigate these drought management strategies, the entire range of functions of olive plants that are exposed to drought and/or recovery should be considered. This review presents recent knowledge on the impact of abiotic stresses on the physiology, morphology, and omic level of olive cultivation, especially under drought conditions. By studying these different aspects, we can develop strategies to mitigate the negative effects of abiotic stress on olive production and ensure the sustainability of this crop.

2. Morphophysiological and Biochemical Responses of Olive Tree under Drought Stress

As stated previously, the olive tree is considered a drought-tolerant species. However, the ongoing rise in temperature, along with limited precipitation, may lead to catastrophic outcomes. This drought tolerance can be exhibited through various genetic factors, as specific genes can regulate water uptake and enhance tolerance [5]. For instance, ER, G protein α -subunit 1 (GPA1), carbonic anhydrase 1 and 4 (CA1/4), HOMEODOMAIN GLABROUS 11 (HDG11), GT-2-LIKE 1 (GTL1), ANGUSTIFOLIA 3 (AN3), AUXIN RESPONSE FACTOR2 (ARF2) and AINTEGUMENTA (ANT) and EPFs are the genetic factors in *Arabidopsis* and crops that control the adjustment of drought tolerance and water usage efficiency [41]. The development of a deep-root system can facilitate the absorption of water from deeper soil sources when water availability is limited, reducing water loss through transpiration [42]. In terms of physiological processes, plants can regulate stomatal closure to control the transpiration rate. SDD1 (STOMATAL DENSITY AND DISTRIBUTION), a subtilisin-like serine protease, has a major impact on stomatal development [41]. In addition, the number of stomata in developing *Arabidopsis* leaves is controlled by genes belonging to the EPF (EPIDERMAL PATTERNING FACTOR) and EPFL (EPIDERMAL PATTERNING FACTOR-LIKE) families [41]. Likewise, the production of osmo-protectants and

antioxidant compounds can enhance protection from cellular damage caused by limited water availability [43]. Thorough research has been conducted on each of these features in the olive crop, in different water regimes, posing different scales of tolerance in the different varieties used [44]. Olive plants exhibit specific features that enable them to retain their vital functions, even in conditions of extreme water scarcity [45]. Various morphological and physiological characteristics have been linked to drought adaptation [46]. Olive varieties that perform better under drought conditions usually exhibit reduced leaf area and leaf water potential as well as lower stem growth, in comparison with well-irrigated conditions [47]. Characteristics such as the waxy leaf surface, the trichome's density/diameter and the petal elasticity have also been identified as characteristics that enhance drought tolerance in the olive tree, through reduced transpiration [45,48]. Undoubtedly, olive varieties that develop a longer and deeper root system have the capacity to penetrate deeper into the soil layers, where water is accessible. Olive root growth and distribution depend largely on the soil conditions. Another way to control the water loss is through the regulation of stomatal closure, which is recognized as an adaptative response mechanism to water limitation [49,50]. This controls not only the water loss but the CO₂ exchange as well [51]. During periods of water deficit, the stomata close, to regulate water loss, through transpiration [49] and as expected, reductions in stomatal conductance have been reported in olive leaves as well [8,52]. Further, an increased stomatal density is a disadvantageous trait for drought tolerance since it leads to greater water loss through transpiration [53], whereas the stomatal density in olive leaves also displays a negative correlation with stomata size. In the case of moisture restoration after stress (recovery), stomatal conductance exhibits lower reset values compared to net assimilation [54]. The stomata on olive leaves are small and exclusively located on the lower surface (hypostomatous). In conditions of water scarcity, the stomata become even smaller, enhancing the regulation of water loss by transpiration [54]. However, the regulation of stomatal closure is a complex characteristic that is influenced both by the genetic background and environmental factors such as light, humidity, water supply, and CO₂ concentration. Following stomatal closure, if the stress event persists, there can be further negative effects on leaf photochemistry and carbon metabolism, ultimately impacting photosynthesis [30,55]. Many researchers confirm that the photosynthetic rate of olive varieties decreases during drought events. In their study, Baccari et al. (2020) reported a significant reduction in net photosynthesis (A_n), stomatal conductance (g_s), and transpiration rate (E) across all olive varieties (Chemlali, Chetoui, Zarrazi, and Oleaster) when comparing rooted cuttings with seedlings after 60 days of drought stress [56]. Despite the decrease in the photosynthetic rate, the plants were still able to perform photosynthesis, even when the leaf water potential dropped to a very low range of −4 to −6 MPa [56]. Additionally, reductions in F_v/F_m values are common in drought events. Ennajeh et al. (2009) examined olive tree varieties that were both tolerant and sensitive to drought and found a decline in F_v/F_m as desiccation became more severe [57]. Reductions in F_v/F_m imply reduced efficiency of the photochemical conversion process, which may suggest possible damage to and inhibition of PSII activity [58]. In general, a strong correlation between net photosynthesis and stomatal conductance has been reported in olive varieties [11,59]. However, according to Brito et al. (2018), olive trees that have been under water deficit exhibit a quicker recovery of the photosynthetic rate compared to stomatal conductance, even if they have been pre-exposed to drought conditions before [54]. Therefore, the speed of photosynthetic rate recovery could be an indicator for drought-tolerant varieties. Subsequently, after the stomata are closed, the limited CO₂ in the intercellular spaces of the leaf may affect the biochemical responses. Olive plants use a series of biochemical processes to cope with stressful conditions. These processes refer to the production of osmoprotectants such as sugars, proteins, amino acids (proline, aspartic acid, and glutamic acid), and their derived compounds [60]. Sugars are the initial molecules responsible for osmoregulation in leaves, whereas amino acids develop gradually [61]. Water scarcity affects not only transpiration but also triggers the overproduction of reactive oxygen species (ROS) and oxidative stress, resulting in damage

to lipids, nucleic acids, and proteins [62]. Phytohormones are key players in regulating the most essential processes during plant growth and development [63]. During stressful conditions, plant hormones are produced such as Abscisic acid (ABA), Jasmonic acid (JA), Ethylene (Eth), Gibberellins (GA), Auxins (Aux), Salicylic acid (SA), and Cytokinins (CK), to control plant growth development and responses to water deficit conditions [64].

3. Omics Approaches in Regulation of Drought Tolerance

Research on the genome, transcriptome, proteome, metabolome, and epigenome of plants has provided vital knowledge about the systems that regulate cellular processes in response to different environmental stresses [55,56]. In addition, advanced omics techniques have been used to identify genes that are expressed differently (differentially expressed genes or DEGs) and can be used as biomarkers to indicate agricultural plants that are resistant to drought [65,66]. As plants have evolved many morphological, physiological, and biochemical mechanisms to effectively respond and adapt to stressful environments over time, following exposure to a stress stimulus, individuals can exhibit various molecular responses at multiple levels, including the genome, transcriptome, proteome, metabolome, and epigenome.

3.1. Genomics

Plant genomics refers to the sequencing, description, and analysis of the genetic compositions, structures, functions, and interactions/networks of an entire plant genome [67]. The progression and evolution of this field are intricately linked to the aforementioned omics approaches. In the realm of cost-effective, high-throughput sequencing technology, plant genomics has posted important achievements during the past three decades, successfully sequencing more than 100 plant genomes. In reference to the olive crop, *Olea europaea* is a diploid species with 23 chromosomes ($2n = 2x = 46$). Through shotgun sequencing, the first draft genome of a 1000-year-old tree of the Spanish Farga was publicly available in 2016, consisting of 1.38 GB (Table 1) [68]. A year later, in 2017, the genome of the wild olive or oleaster, *Olea europaea* L. subsp. *sylvestris*, from a Turkey-located individual, was released, consisting of 1.46 GB [69]. In 2020, the DNA of the Picual variety was sequenced by shotgun, using two sequencing technologies (Illumina short reads and PacBio long reads), resulting in a larger genome size ranging from 1.63 to 1.81 Gb [70]. In 2021, an enhanced draft genome of the Spanish variety Arbequina was released using Oxford Nanopore third-generation sequencing and Hi-C technology, resulting in a final genome of 1.30 Gb [71]. Rapid advances in sequencing technologies are providing critical information about the extensive genetic background of olive cultivation. This is extremely important, as breeding practices increasingly focus on developing varieties that are resistant to unpredictable environmental conditions. However, the distinction between olive varieties based on morphological characteristics is particularly difficult. As the only reliable method for distinguishing varieties is DNA identification, many molecular tools have been developed and evolved in the past 20 years. The molecular markers employed most often are SSRs (simple sequence repeats) and SNPs (single nucleotide polymorphisms) [72]. In many studies, SSR and SNP markers have been used to discriminate different olive varieties in reference to their origin as well as morphological and biochemical traits [72–76]. Recent studies include the development of the most complete genomic variation map and the most thorough resource of molecular variation until today, through SNP and genome-wide association studies (GWAS), for 89 olive tree genotypes derived from the Mediterranean Basin [77]. Current developments in genetics are enhancing the progress in quantitative trait loci (QTL) research, GWAS, and genomic selection for the improvement of varieties tolerant to abiotic stresses and especially drought [78]. The assessment of genetic variability is critical for the olive crop, especially when studying traits such as drought tolerance. Regarding the evaluation of genetic variability, several distinct varieties have been tested in drought experiments. Razouk et al. (2022) examined 32 olive varieties and evaluated their drought tolerance, using leaf macro-characteristics [45]. They observed that the varieties

Lechin de Sevilla and Azeradj were the most drought-tolerant, as opposed to Moraiolo, Vernina, and Frantoio, that were the most susceptible. These findings highlight the potential of using QTL research and GWAS in genetic selection to detect drought-tolerant and susceptible varieties, offering valuable insights for breeding programs focused on crop resilience under abiotic stresses.

Table 1. Summary of Olive Varieties, Genome Size, and Sequencing Technology.

Species/Variety	Genome Size (GB)	Sequencing Technology	Year	References
<i>Olea europaea</i> L. cv. Farga	1.38	Illumina MiSeq—HiSeq	2016	[68]
<i>Olea europaea</i> L. subsp. <i>Sylvestris</i>	1.46	Illumina HiSeq 2000	2017	[69]
<i>Olea europaea</i> L. cv. Picual	1.63 to 1.81	Illumina short reads, PacBio long reads	2020	[79]
<i>Olea europaea</i> L. cv. Farga	1.31	Illumina HiSeq 2000	2020	[80]
<i>Olea europaea</i> L. cv. Arbequina	1.30	Oxford Nanopore third-generation sequencing, Hi-C technology	2021	[71]
<i>Olea europaea</i> L. cv. Farga	1.31			
<i>Olea europaea</i> L. cv. Leccino	0.54	Illumina HiSeq 2000, Roche 454	2022	[81]
<i>Olea europaea</i> L. cv. Ayvalik	0.93			

3.2. Transcriptomics

Transcriptomics is the study of the “transcriptome”, i.e., the set of ribonucleic acid (RNA) molecules within a biological entity, like a cell, tissue, or organism [82]. Shortly after 2008, recognition of RNA sequencing increased, due to the development of new Solexa/Illumina technologies in San Diego (CA), and many research groups around the world began to investigate the transcriptome more thoroughly [82]. Exposure to stressful environmental conditions may lead to major modifications at the molecular and physiological levels in plants. Such modifications include rapid adjustments in gene expression and metabolic processes, resulting in various outcomes. Many studies have been conducted on the transcriptome of many important organisms in the field of agriculture, under stressful conditions. Notably, the limitations of water can lead to gene malfunctions. Drought experiments on the model organism *Arabidopsis thaliana* indicated a great difference between the responses of roots of soil-grown plants compared to stems, unveiling unique genes that may regulate the stress response in roots [83]. In a recent work by Öztürk Gökçe et al. (2022), studying the drought stress response of the purple carrot, RNA-seq analysis revealed higher upregulation of differentially expressed genes in the tolerant carrot line (B7262A), including the transcription factor MYB75 and ethylene responsive factor RAP2-3, which were uniquely upregulated in the tolerant line [84]. As for trees, it has also been found that abiotic stressors can affect the transcriptome of poplar, by alternative splicing, differential intron retention, and isoform ratio switching [85]. Regarding the olive crop, there are numerous transcriptomic studies, investigating the origin of the olive tree and its domestication [86,87], the early development of the plant [88], the processes during ripening [89,90], the plant architecture [91], as well as the different expression patterns in olive tree organs [79,92,93]. Apart from the aforementioned studies, the transcriptome of the olive tree has also been investigated under various biotic and abiotic stresses (Table 2). Regarding the biotic stressors, Marchese et al. (2023) worked on a comparative transcriptomic analysis (RNA-seq) of leaf tissues from two varieties, Koroneiki (low susceptible) and Nocellara del Belice (high susceptible), infected by the obligate fungal pathogen *Spilosea oleagina* [94]. In their study, they reported significant differences between the two varieties including the early signaling and defense responses of Koroneiki and the expression of unique genes compared to Nocellara del Belice [94]. Another research group examined the Verticillium wilt of two olive varieties, Frantoio (tolerant) and Picual (susceptible),

in the root tissue, resulting in significant differences in both varieties in the absence and presence of the pathogen [95]. Moreover, regarding abiotic stresses, the varieties Kalamon (salt-tolerant) and Chondrolia Chalkidikis (salt-sensitive) were treated with 120 mM NaCl, resulting in a significant absence of transcriptional activation of the latter compared to Kalamon, explaining the sensitivity at the gene expression level [96,97]. Similarly, under salinity conditions the following varieties, Koroneiki, Picual, Royal de Cazorla, and Fadak86, were studied by Mousavi et al., 2021 [98], and Leccino (salt-sensitive) and Frantoio (salt-tolerant) were studied by Rossi et al., 2016 [99]. A transcriptomic study, published in December 2023, examined the salinity tolerance of olive trees in relation to PGPB Bacillus G7 and resulted in improved performance in the G7-treated plants compared to the control [100]. Besides salinity studies, over the years several researchers have investigated the effects of cold in olive crops, reporting specific features characterizing the cold response of olive tree, including unigenes differentially expressed in response to stress [101–103]. Although there is extensive literature on drought stress, the level of coverage for olive crops is quite limited. An RNA-seq meta-analysis conducted by Benny et al. (2020) examined five fruit tree crops from six published studies, including olive trees, under drought and salinity stress [104]. 26 RNA-seq samples were analyzed, and 683 genes were identified as commonly regulated among the three drought studies. A comparison was also employed on the genes that were common, among both salinity and drought, resulting in 82 genes, of which 39 were regulated with the same trend of expression [104]. The following year, in 2021, a study was published regarding olive trees (cv. Souri) and water stress on nonstructural carbohydrates (NSC) and starch regulation, suggesting a group of stress-related starch metabolism genes, correlated with NSC fluctuations during drought and recovery [105]. In 2023, an Olive Atlas was published, containing 70 RNA-seq experiments [106]. The experiments related to drought in the Olive Atlas were based on the Souri variety and included a total of three experiments. The Souri drought experiments were conducted using RNA-seq technology, and the data were analyzed using the Picual genome sequence and gene annotation as a reference. To obtain detailed information about the genes identified in the framework of the Olive Atlas, a public platform was released in 2023 (<https://www.oliveatlas.uma.es/>, accessed on 24 February 2023). These findings indicate that plants, upon detecting changes in environmental conditions, may activate distinct genetic pathways to initiate adaptive responses.

Table 2. Omics Studies in Olive Crop Regarding Abiotic Stresses.

Approach	Type of Abiotic Stress	Varieties	Tissue	References
Transcriptomics	Salinity	Kalamon Chondrolia Chalkidikis	roots leaves	[96,97]
		Koroneiki Picual Royal de Cazorla Fadak86	leaves	[98]
		Leccino Frantoio	roots stems leaves	[99]
		Arbequina	leaves	[100]
		Kalamon	roots	[104]
	Cold	Leccino	leaves	[101]
		Picual	leaves	[102]
		Frantoio	seed coats embryos	[103]
	Drought	Souri	Branches roots	[105]
		Souri	branches	[106]

Table 2. Cont.

Approach	Type of Abiotic Stress	Varieties	Tissue	References
Proteomics	Salinity	Chondrolia Chalkidikis	roots leaves	[107]
		Chetoui	leaves	[108]
Metabolomics	UV-B radiation/heat shock	Cobrançosa	leaves	[109]
		Koroneiki	leaves	[110]
	Drought	Cobrançosa	leaves	[111]
Epigenomics	Salinity	Koroneiki Royal de Cazorla Arbequina Picual	leaves	[112]

3.3. Proteomics

Proteomics refers to the analysis of the protein complement of a cell or organism [113]. Proteomics has an edge over other “omics” technologies since proteins play a crucial role in most biological activities [114]. Proteomic studies in drought conditions have revealed the involvement of various proteins in responding to water scarcity. Skodra et al. (2023) conducted a study on the olive variety Chondroelia Chalkidikis, exposing stress to salt concentrations of 75 and 150 mM (Table 2) [107]. Through transcriptomic and proteomic investigation, they discovered multiple genes and proteins, including known and putative regulators, that reported significant proteomic and transcriptomic changes between primed and non-primed plants [107]. In 2018, Abdallah et al. published a comprehensive analysis of the Chétoui olive plant’s response to drought and salinity conditions, studying the plant’s growth, the oxidative damage and the osmolyte accumulation in leaves, as well as the physiological parameters and proteome. [108]. However, the literature on the field of olive proteomics under drought stress is as yet limited, even though drought stresses have been extensively studied at the protein level in many crops such as amygdalus [115] rice [116], maize [117], wheat [118], barley [119], sorghum [120], and soybean [121]. Proteomics is a powerful analytical technique, which significantly contributes to our understanding of the molecular mechanisms involved in plant development, growth processes, and plant stress tolerance and should be exploited more regarding olive crops.

3.4. Metabolomics

Metabolomics refers to the systematic identification and quantitation of all metabolites in an organism or biological sample [122]. Abiotic stress induces metabolic regulation in plants, to protect the osmotic potential of plant cells. Profiling plant metabolites throughout this process is useful for studying changes in the plant metabolome under stress [123]. Plant metabolomics provides an in-depth knowledge of how plant metabolism responds to different stressors. Considerable accumulation has been shown for various metabolites formed during important cellular metabolic processes in individuals with drought stress. Drought conditions often result in a spike in sugar concentration within the cytosol, leading to a drop in osmotic potential. This, in turn, contributes to preserving cell turgor, as shown by Razavi et al. in 2011 [124]. Water scarcity may increase flavonoids in olive leaves, especially the catechol B-ring substituted flavonoids (e.g., quercetin 3-glycoside) (Table 2) [109]. During stressful conditions, olive plants regulate reactive oxygen species (ROS) by upregulating antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione reductase (Gr), and guaiacol peroxidase (GPOX) [110,125]. Secoiridoids, such as oleuropein, are a group of polyphenols with high antioxidant activity that can only be found in the Oleaceae family [126]. Araujo et al. (2021) studied the antioxidant adjustments of olive trees under field stress conditions and observed high ROS levels of hydrogen peroxide (H₂O₂) and superoxide radical (O₂) [111]. Flavonoids like kaempferol

and quercetin were found to be boosted in dry conditions, effectively contributing to the detoxification of H₂O₂ molecules [127]. Moreover, the rapid accumulation of anthocyanins and flavones may serve as vacuole reactive oxygen species (ROS) scavengers in reaction to water deficits, as stated by Fàbregas and Fernie in 2019 [128]. In other tree species, such as in eucalypt, metabolic analysis distinguished the drought-tolerant clones from the sensitive ones [129]. Jia et al. (2019) discovered a total of 69 and 53 differentially accumulated metabolites in drought-tolerant *Populus simonii* and sensitive *Populus deltoides* cv. Danhong, respectively, where *Populus simonii* exhibited specific metabolic changes that improved antioxidant levels, balanced carbon/nitrogen levels, and controlled wax production [130]. You et al. (2019) examined drought-tolerant (DT) and susceptible (DS) sesame genotypes, revealing higher levels of ABA, proline, arginine, lysine, aromatic, and branched chain amino acids GABA, saccharopine, 2-aminoadipate, and allantoin in DT under stress conditions, compared to DS [131]. Soliman et al. (2019) listed the compounds that exhibited a substantial rise in response to water deprivation in *Cleome Amblyocarpa* including 2-naphthalene methanol, heneicosane, caryophyllene oxide, heptadecanal, tetratetracontane, heptatriacotanol, tetracosane, 1-heptacosanol, phytol, n-nonadecanol-1, n-pentadecanol, octacosyl acetate, octadecanoic acid, and hexatriacontane [132]. Through metabolomic studies, crucial stress metabolites can be identified and serve as indicators of a plant or species' ability to adapt and detect changes in groups of compounds that play a role in mediating stress tolerance and investigate a species' capacity to reorganize its main metabolic pathways [55]. Assessing the alterations in the profiles of these metabolites in response to severe climate change circumstances will aid in the detection of olive varieties that are better suited to the changing environment.

3.5. Epigenomics

An epigenetic change describes the biochemical alteration in DNA that can regulate gene expression without changing the DNA sequence, and can be achieved through DNA methylation, histone modifications, and RNA interference [133–135]. Through DNA methylation, plants can adapt to various abiotic stresses, especially in drought conditions [136]. Badad et al. (2021) studied the methylation status of the olive genome in secondary metabolism during fruit ripening, in the wild *Olea europaea* ssp. *europaea* var. *sylvestris* and the cultivated variety Ayvalik [137]. They also discovered different methylation levels between leaves and fruits, with leaves exhibiting a higher frequency [137]. Regarding abiotic stresses, Mousavvi et al. (2019) discovered epigenetic changes in olive varieties (Koroineiki and Royal de Cazorla) after salt stress (Table 2) [112]. The study showed that four out of six differentially methylated genes of the tolerant cv. Royal de Cazorla were downregulated (reduced growth after stress), whereas the susceptible one (Koroineiki) had no significant changes in gene expression (normal growth until withering after stress) [112]. While extensive research has been conducted on epigenetic regulation in various plant species (e.g., arabidopsis, maize, rice, faba bean, tomato) [138–143], there is a scarcity of studies focusing on the drought of woody species such *Populus* sp. [40,144] and fruit trees (citrus, apples), [145–147]. Furthermore, the number of publications dedicated to epigenetics in olives is even lower [137]. Understanding the epigenetic regulation in plants in response to intensified environmental stresses could enhance the disclosure of genetic variation to improve productivity, resilience, and adaptation to stress conditions. Through such insights, modern proactive crop breeding will provide more productive, resilient, and ready-to-transcend varieties.

3.6. Multi-Omic Approaches

Multi-omic approaches such as genomics, transcriptomics, proteomics, metabolomics, epigenomics, etc., offer a wide array of data for a further understanding of all biological processes in plants under any condition [148]. By merging information from these different levels, we can gain a complete overview of complex processes and detect important molecular factors involved in plant responses. Such approaches have been widely employed

in numerous crops to examine the molecular mechanisms behind abiotic stress tolerance responses, required to establish resistant crop varieties [149]. *Vitis vinifera* is a well-studied species in terms of integrated omics, with modern breeding tactics focused on creating climate-resilient varieties [150]. Multi-omic methods have been used to study drought responses in various plant species, including *Populus trichocarpa*, a model species for woody plant genomics [151]. These methods have identified important genetic pathways and regulatory networks that help plants respond to drought. An integrated analysis of the oil palm transcriptome, proteome, and metabolome in response to salinity and drought, discovered enzymes and metabolites that were highly related to cysteine and methionine metabolism pathways affected by osmotic stress [152,153]. Transcriptomic, proteomic, and metabolomic analysis from *Quercus ilex* seedlings subjected to drought-like conditions revealed key processes such as transcriptional control, and identified a key function of transcription factors, such as DREB2A, WRKY65, and CONSTANS, in the early metabolomic response to drought [154]. Regarding olive crops, our knowledge of multi-omics is not as extensive as it is for other model crops, particularly when focused on drought. Quiles et. al (2022), investigated the origin of the chlorophyll content in virgin olive oil of the Arbequina variety by chemical (HPLC-hrMSn), biochemical (enzyme activity), and molecular biology (qRT-PCR) methods, where they discovered that the highest chlorophyll biosynthetic capacity in olive fruits is induced by the enzyme protochlorophyll reductase, while chlorophyll degradation occurs through the stay-green and pheophytinase pathways [155]. Sirangelo et al. (2023), with a combined transcriptomic and metabolomic analysis on three olive varieties, Cellina di Nardò, Ruveia, and Salella, revealed a direct correlation between a higher expression of the main flavonoid genes and the high content of metabolites in Cellina di Nardò [156]. While extensive multi-omics investigations have been conducted on numerous plant and tree species in relation to abiotic stresses, there are still substantial knowledge gaps concerning the molecular mechanisms underlying drought tolerance in the olive crop. Olive-specific comparative and integrative multi-omics investigations may yield significant knowledge regarding the intricate molecular pathways and regulatory networks that control responses to drought stress (Figure 1).

4. Future Perspectives and Challenges

One of the biggest challenges today is the achievement of “zero hunger” while making agriculture and food systems sustainable [157]. However, the population growth rate has always raised concerns regarding food security and availability. Today, climate change threatens crops more than ever, particularly due to drought events. Future projections indicate that we will witness an escalation in the intensity and severity of drought. However, advanced breeding technologies and biotechnological tools, such as genomics, transcriptomics, proteomics, metabolomics, epigenomics, and genome editing have made considerable progress in understanding drought stress tolerance. The discovery of novel genes and their associated pathways and stress-responsive mechanisms, holds great potential to manage the changing environment and safeguard vital crops like the olive. Early detection of stress-tolerant varieties through rapid screening can significantly contribute to the sustainability of agriculture and food security. By using these advanced methodologies, breeders will be able to detect and select plant crops that have superior adaptability to drought conditions, leading to increased productivity. The identification of stress-resistant varieties and the exploitation of stress memory combined with the acquired tolerance through priming, will result in the protection and conservation of valuable genetic resources, ensuring the long-term viability of the olive and other important crop species.

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