

Anatomical, physiological, biochemical and molecular responses of *Eucalyptus* spp. under water deficit conditions and characteristics of Tunisian arid species: an overview

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Abstract

The genus *Eucalyptus* occurs in a large range of environmental conditions, mainly arid/semi-arid areas. It includes species with high capacity to survive with extremely low water potential. For that, our review shows an important effect of drought on *Eucalyptus* spp. plants' resistance mechanisms and management strategies. In fact, water stress acts directly on growth, productivity, yield, it affects also response to pests and diseases, disturbs wood formation and essential oil yield. However, the general patterns of response to water stress varied among species, genotypes, hybrids and clones. To assume, reducing water loss in eucalyptus species is manifested by reducing leaves area, reducing gas exchange, increasing water uptake thanks to a prolific and deep root systems. A greater accumulation of osmolytes that gives rise to osmotic adjustment including carbohydrates especially cyclitols and quercitol, other amino acids and organic acids, also some proteins which play a vital role in sustaining cellular functions under drought conditions. More than that, water stress increases mainly the levels of pigments, chlorophyll fluorescence parameters, malondialdehyde (MDA), abscisic acid (ABA) and the biosynthesis of triacylglycerols (TAGs) in *Eucalyptus* species.

Keywords: drought; *Eucalyptus*; water deficit; tolerance mechanisms; Tunisian arid zones

Introduction

In arid and semi-arid areas, evaporative demands change considerably throughout the year and plants must constantly acclimatize (Carignato *et al.*, 2020). Those climate fluctuations associated with increases in

the duration, frequency and/or severity of drought could essentially affect forest sustainability, alter the structure, composition and biogeography of forests (Ferraz *et al.*, 2013; Gonçalves *et al.*, 2017). In recent years, environment is putting stress on many *Eucalyptus* plantations, due to frequent severe climatic events.

For instance, *Eucalyptus* spp. belongs to the Myrtaceae family and consists of 747 species (Beech *et al.*, 2017) is a native genus from Australia, represents 95% of Australian forest with a few native species from Papua, New Guinea, Indonesia and the Philippines (Leicach *et al.*, 2012; Elaieb *et al.*, 2019). *Eucalyptus* is frequently present and cultivated in arid regions with low soil water and nutrient availability mainly for its high adaptation to drought (Saadaoui *et al.*, 2017; Mateus *et al.*, 2021). So, it has been successfully introduced worldwide, including Tunisia (Elaieb *et al.*, 2019; Mecherghi *et al.*, 2019). It was adopted in more than 100 countries across six continents, with a total planted area of over approximately 20 million hectares worldwide (White *et al.*, 2014; Correia *et al.*, 2018; Barradas *et al.*, 2018). This genus is the second largely planted multipurpose woody tree species in tropical and

Mediterranean climate regions and together with *Pinus*, represents 98% of the world's forestry production (Carignato *et al.*, 2020). Its high adaptability to wide range environments (Martins *et al.*, 2020), together with its fast growth, superior wood properties, low susceptibility to pests and diseases, high productivity and adequate fiber quality for the industry explain the expansion of commercial *Eucalyptus* tropical plantations worldwide (Attia *et al.*, 2019; Elli, 2020).

In Tunisia, droughts are a recurrent phenomenon and seem to be becoming more frequent. Since 1990, drought has been officially declared in 1994, 1995, 1997, 2000, 2001, 2002, 2008, 2010, 2013, and 2016 and the most severe drought in 50 years took place for three consecutive years from 2000 to 2002 (Verner *et al.*, 2018). In this country, the forests of *Eucalyptus* occupy an area of 41397 ha, the third place after those of pine and cork oak. It is the first introduced forest species used in afforestation (ONAGRI, 2019).

Throughout the country, 117 species have been identified by Khouja *et al.* (2001). However, 15 species and one hybrid have been cited in the arid region (Saadaoui *et al.*, 2022). In this work, we aim to understand the mechanisms of drought response and resistance strategies for *Eucalyptus* species at global and national scales, precisely in the Tunisian south where the periods of drought are frequent and the bioclimatic conditions are semi-arid and arid.

Drought-tolerant *Eucalyptus* species

The ecological interval of *Eucalyptus* genus occurs in a vast range of different soil and environmental conditions, as well moist temperate zones, rainforests, subalpine and arid/semi-arid region (Merchant *et al.*, 2006). Variations in response to low water potential are reported between *Eucalyptus* species (Myers and Neales, 1986), its provenances (Li, 1998) and between clones (Pita and Pardos, 2001).

For instance, the species of subgenus *Symphyomyrtus* are widely distributed across the continent, particularly in more arid habitats and regions subject to prolonged periods of water deficiency (Merchant *et al.*, 2006). It regroups various species that are adapted to water shortage conditions, especially *E. grandis*, *E. urophylla*, *E. globulus*, *E. camaldulensis* and their hybrids and account for 80% of plantations globally (Amrutha *et al.*, 2019). Other *Eucalyptus* species had screened also for their tolerance to drought such as *E. bebriana*, *E. microcarpa* and *E. polyanthemus* (Myers and Neales, 1986); *E. microtheca* (Tuomela, 1997; Li, 1998), *E. camaldulensis* (Lemcoff *et al.*, 1994; Farrell *et al.*, 1996; White *et al.*, 2000); *E. nitens* (White *et al.*, 1996), *E. melliodora* (Clayton-Greene, 1983), *E. grandis*, *E. viminalis* and *E. tereticornis* (Lemcoff *et al.*, 1994), *E. saligna*, *E. leucoxylon* and *E. platypus* (White *et al.*, 2000) and *Eucalyptus* hybrids (Eksteen *et al.*, 2013).

FAO (2002) indicated that in the Mediterranean region, *E. camaldulensis*, *E. globulus* and *E. gomphocephala* are the most commonly used species, also shown that in arid region a high tolerance level and flower abundance for three species of *E. camaldulensis*, *E. torquata* and *E. salubris*. For Metro (1970), the species that seem best adapted to the severe conditions of the arid region in the southern provinces of North Africa are the following: *E. brockwayii*, *E. salmonophloia*, *E. flocktoniae*, *E. torquata*, *E. microtheca*, *E. oleosa* var. *longicornis*, *E. occidentalis* and *E. sideroxylon*. In the three arboreta of the southern Tunisian, seven species are considered drought resistant: *E. gracilis*, *E. salmonophloia*, *E. lesouefii*, *E. occidentalis*, *E. astringens*, *E. torquata* and *E. microtheca* (Khouja *et al.*, 2001; Saadaoui *et al.*, 2017).

Recent studies conducted by Souden *et al.* (2020) in the same region focused on *E. camaldulensis* and *E. torquata*, shows high resistance to drought of these two species. More than that, Johannsmeier (2016) studies indicated that *E. microtheca* is a rare eucalypt encouraged in dry regions thanks to its resistance to drought and frost, and tolerances to brackish conditions. All these data on drought tolerant species and their intraspecific diversity by adaptive traits are key factor in determining their ability to survive under stressful conditions.

Morphological and anatomical response

As reported by several studies maintained on some *Eucalyptus* species, shown a reduction in growth and biomass under water stress conditions for *E. globulus* (Silva *et al.*, 2004; Coopman *et al.*, 2008; Correia *et al.*, 2014), *E. camaldulensis* (Maseda and Fernández, 2015) and *E. microtheca* (Li, 1998). Reported also by other studies maintained on *E. globulus* in which drought hardening treatments of -1.3 MPa and -2.4 MPa significantly reduced plant growth, height, leaf area and specific leaf area respectively (Pita and Pardos, 2001; Silva *et al.*, 2004; Shvaleva *et al.*, 2006). Hence, reduction of area in water-deprived conditions is a response in all eucalypt species as reported in *E. camaldulensis* (Maseda and Fernández, 2015; Amrutha *et al.*, 2019), *E. microtheca* (Susiluoto and Berninger, 2007), and *E. tereticornis* (Amrutha *et al.*, 2019).

Other authors such as Tuomela (1997) have pointed out that the high capacity of drought tolerance of *E. microtheca* may be related to foliage area (or foliage dry weight) per sap wood area because of low rates of water loss per unit leaf area (or leaf dry weight). Moreover, Merchant *et al.* (2006) results showed that others structural mechanisms displayed by *E. viridis* and *E. oleosa* such as thick cuticles, high leaf surface/volume ratios and sunken stomata. For Coopman *et al.* (2008), reported that root growth of *E. globulus* is less affected by drought than shoots and stem, whereas it stimulates formation of new roots. In fact, both the average length of the three longest roots and the number of new roots and from treatment -1.3 MPa increased from the beginning until day 28 having values 41 and 47% higher than treatments at -0.2 and -2.4 MPa respectively. Similar studies of Silva *et al.* (2004) shown also a higher root length in water stressed clones of *E. globulus* compared to well irrigated plants. For Pita and Pardos (2001) shown that plants of *E. globulus* exhibited only an 11 and 19% reduction of root biomass in plants treated at -1.3 and -2.4 MPa.

Studies by Gibson *et al.* (1991), based on an experiment made with *E. camaldulensis* seedlings from dry tropics, proposed that the seedlings depend much more upon to the reduction in leaf area to conserve water. Moreover, other research reported by Pita *et al.* (2003) and Teulieres *et al.* (2007), showed that the most drought resistant clone eucalypt presented significantly smaller leaves than other clones. Furthermore, roots of *Eucalyptus* trees are usually well developed in the dry areas and the depths of the soil roots are penetrating in which enables them to take out the water stored deep in the soil during stressful conditions. Also, Joshi and Palanisami (2011) confirmed this data and showed that eucalypt roots could grow even up to 6–9 m in stress conditions to extract more water.

In fact, Laclau *et al.* (2013) concluded that tree roots of *E. grandis* withdraw all the water stored down to a depth of 6-7m and available for trees within 1.1 year of planting. Other studies made by Hodecker (2015) demonstrated that under water deficiency eucalypt drought-tolerant clones had a high uptake efficiency and

low nutrient use efficiency, whereas drought-sensitive clones exhibited low uptake and low nutrient use efficiency for root formation and high use efficiency for leaf formation.

In the same way, Susiluoto and Berninger (2007) research indicated that *E. microtheca* seedlings used allocation between roots and foliage as a key mechanism to survive under water shortage conditions. They increased their root/shoot ratios and there was a shift in root mass towards finer roots that take up the water. This higher biomass allocation to roots may increase the amount of soil water accessible to a plant. For this drought stressed seedlings *E. microtheca* indicated a higher fine root/leaf area ratio than non-stressed seedlings. Other data of Silva *et al.* (2004) maintained on *E. globulus*, showed that successful drought acclimation of this species may be the result of changes in root biomass coupled with changes in hydraulic properties of the root systems. Higher hydraulic conductance and significant allocation of biomass to roots made it possible to prolong the water-stress period for active carbon assimilation in the clone that was at least susceptible to drought. These developmental changes, which maintained the balance between absorption and transpiration areas when soil water availability declined, seemed to be the key determinant of performance under drought conditions. In addition, Pfautsch *et al.* (2016) studies indicated a strong relationship between wood traits and the aridity index with the evaluation of 28 species of *Eucalyptus* in Australia, they showed that as dryness index increases, it results in smaller vessels diameter, higher frequency of occurrence of vessels, higher wood density and lower hydraulic conductivity. More than that, studies of Searson *et al.* (2004) focused on wood anatomy of juvenile individuals of *E. grandis* and *E. occidentalis* showed that the conduit efficiency is lower in eucalypt stressed plants, manifested by a reduced vessels lumen area and greater vessels frequency. Other results of Zweifel *et al.* (2014) research maintained in wood elasticity, showed a special structure of wide zone of secondary thickening xylem in various stages of lignification in *E. globulus* which used for additional water storage.

Physiological response

In response to stimuli such as light radiation, photoperiod, temperature, drought, and evaporative demand eucalyptus plants use several mechanisms to acclimatize to those stressful conditions. On the one hand, during water-deprived conditions a significant change in stomatal function (Silva *et al.*, 2004; Macfarlane *et al.*, 2004), cell turgor adjustment (White *et al.*, 1996), in biomass allocation (Rawat and Banerjee, 1998), osmotic potential, gas-exchange parameters, chlorophyll and carotenoid contents (Michelozzi *et al.*, 1995) have all been observed in leaf tissues of eucalypt (Amrutha *et al.*, 2019) as responses to arid conditions. A review of previous investigations revealed that inherently lower water potentials are commonly observed in eucalypt growing in low-rainfall environments, including *E. melliodora*, *E. microcarpa* (Clayton-Greene, 1983), *E. polyanthemos*, *E. behriana*, *E. macrocarpa* (Myers and Neales, 1986), *E. microtheca* (Tuomela, 1997) and *E. leucoxylon* (White *et al.*, 2000; Merchant *et al.*, 2006). Research reported by Pita *et al.* (2003); Teulieres *et al.* (2007), showed that the most drought resistant clone eucalypt exhibit higher values of predawn leaf water potential, higher reductions in maximum permeability. Other studies have also detected significant decreases in transpiration and stomatal conductance in *E. globulus* under drought conditions (Pita and Pardos, 2001; Pita *et al.*, 2003; Merchant *et al.*, 2006).

According to Zhou *et al.* (2016) studies based on photosynthetic versus stomatal responses to water availability in some *Eucalyptus* species *E. dunnii* and *E. saligna*, two fast growing species showed that both of them maintained lower soil to leaf water potential to prevent water loss via closing stomata during dry days. While *E. melliodora*, slow-growing species showed the same response in dry and wet days. Furthermore, Souden *et al.* (2020); and Souden (2021) showed that during the dehydration phase plant water status, cell turgor, net photosynthetic rate and photosynthetic machinery integrity are less affected in *E. camaldulensis* and *E.*

torquata. However, for Amrutha *et al.* (2019) photosynthetic parameters including transpiration rate, stomatal conductance and photosynthesis were decreased in both genotypes of *E. tereticornis* and *E. camaldulensis* in drought conditions. In addition, relative water content (RWC) decreased in several eucalypt species including *E. globulus* (Pita and Pardos, 2001; Carignato *et al.*, 2020), *E. oblique*, *E. rubida*, *E. polyanthemos*, *E. tricarpa* (Merchant *et al.*, 2007), *E. grandis* × *E. urophylla* (Valadares *et al.*, 2014), *E. camaldulensis* and *E. tereticornis* (Amrutha *et al.*, 2019) during water stress. Carignato *et al.* (2020) indicated that the clones of *E. globulus* showed significant seasonal variations in stomatal size and density, specific leaf area (SLA) and leaf relative water content (RWC). For that, the maintenance of balance between the areas involved in transpiration and absorption is a key determinant of survival and productivity as reported in *E. globulus* (Silva *et al.*, 2004; Amrutha *et al.*, 2019). The same study of Carignato *et al.* (2020) showed that stomatal density (d) is often negatively related to stomatal size, in which a signalling mechanism seems to exist from the mature leaves to the developing leaves, leading to the optimization of d and of stomatal size to face the changes to come in future environmental conditions. Moreover, studies of Silva *et al.* (2004) carried also on *E. globulus* showed that the drought-resistant (CN5) clone maintained higher leaf water status (higher predawn and midday leaf water potentials), sustained a higher growth rate (new leaf area expansion and root growth) and displayed greater carbon allocation to the root system and lower leaf-to-root area ratio than the drought-sensitive (ST51) clone. However, Correia *et al.* (2014) showed that for two genotypes of *E. globulus* (AL-18 and AL-10) submitted to a 3-week water stress period at two different intensities (18 and 25% of field capacity), drought reduced height, biomass, water potential, gas exchange in both genotypes and increased the levels of pigments, chlorophyll fluorescence parameters, malondialdehyde (MDA) and abscisic acid (ABA). In *E. marginate*, pressure-volume curves showed that cell-wall elasticity of leaves increased in response to drought (Szota *et al.*, 2011; Saadaoui *et al.*, 2017). As well as plant survival depends on the maintenance of xylem integrity as a hydraulic conducting system (Sperry *et al.*, 2002). However, as water stress became more severe, root hydraulic conductance and leaf specific hydraulic conductance decreased which affect hydraulic conducting system and increases tension of xylem sap leading to embolism when a specific threshold is reached (Sevanto, 2018). The dysfunction of xylem vessels results in the death of some parts or the whole tree (Brodersen and McElrone, 2013). Root and leaf-specific conductance are generally lower in drought-adapted species than in more water-demanding species (Nardini *et al.*, 2011). Both *Eucalyptus* species *E. camaldulensis* and *E. torquata* are noticeably resistant to xylem embolism having Ψ_{50} values more negative than -4.5 MPa. Curves of vulnerability to xylem embolism show interspecific differences between the two species, *E. camaldulensis* is less vulnerable to xylem cavitation than *E. torquata*. The value of Ψ xylem which induced 50% PLC (Ψ_{50}) is -5.5 MPa in *E. camaldulensis* and -4.6 MPa in *E. torquata* (Souden *et al.*, 2020).

Biochemical response

Adjustment of internal osmotic potential in response to stressful conditions has been illustrated across many *Eucalypts* species (Tuomela, 1997; Li, 1998; White *et al.*, 2000; Pita and Pardos, 2001). Several studies such as those of Merchant *et al.* (2010); Warren *et al.* (2011) agreed that osmotic adjustment is a common response to water deficiency within this genus by accumulating compatible organic compounds in which carbohydrates dominates leaf metabolite profile of *Eucalyptus* from dry areas. Those one has an important role in osmoregulation to maintain cell turgor, and in osmoprotection of vital cell constituents (Chen *et al.*, 2011). The osmotic contribution of stress induced accumulations of major inorganic ions (K⁺, Na⁺, Ca²⁺, Mg²⁺) and/or carbohydrates involved in primary metabolism (sucrose, glucose or fructose) (Merchant *et al.*, 2006). Moreover, other results indicated that quercitol is one of the most accumulated compounds in *Eucalyptus* spp, it correlated well with environmental adaptation. In addition, species from xeric environments accumulate

much more quercitol in response to drought than species from mesic environments (Merchant *et al.*, 2007). Furthermore, Shvaleva *et al.* (2006) studies observed that the concentrations of soluble sugars, proline and glutathione reductive activity increased in leaves and roots of clones *E. globulus*, this enzyme plays a protective role in roots by catalysing the catabolism of reactive oxygen species in response to drought conditions. Other research by Warren *et al.* (2011), also confirmed these results in *E. globulus*, *E. dumosa* and *E. pauciflora* and showed that these species respond to severe water stress by accumulating osmotically active solutes in their leaves and keeping their Ψ s low. For that, after 6 days of water stress imposition, results of Amrutha *et al.* (2019) studies showed that total sugars, flavonoids, phenols, proline and phytohormones (indole acetic acid and abscisic acid) increased seriously in both genotypes *E. tereticornis* and *E. camaldulensis*, except flavonoid content which decreased in *E. camaldulensis* while it increased in *E. tereticornis*. For Souden *et al.* (2020), both *E. torquata* and exclusively *E. camaldulensis* accumulate large quantities of soluble carbohydrates especially cyclitols in their leaves during moderate and severe dehydration, which are involved in osmoregulation and osmoprotection and made these species less vulnerable to drought-induced xylem embolism and had higher ability of xylem refilling. The same study illustrated that glucose, fructose, quercitol and myoinositol are the main soluble sugars extremely accumulated by *E. camaldulensis* and *E. torquata* under severe water stress (from Ψ_{pd} lower than -5.5 MPa). For Merchant *et al.* (2006), results indicated that under drought conditions significant concentrations (up to 150 mmol L⁻¹) of quercitol are found in leaves of *E. polyanthemos*, *E. tricarpa*, *E. cladocalyx*, *E. astringens*, *E. viridis* and *E. oleosa*. Results of Singh *et al.* (2020), showed a higher level of proline and sugar accumulation in 'KE8' and 'Y8' clones of *E. tereticornis* coupled with an important activity of antioxidant enzymes such as catalase, peroxidase, ascorbate peroxidase and superoxide dismutase (SOD). Furthermore, Marchin *et al.* (2017), suggested that in leaves of water-stressed plants and in oxidative stress conditions the biosynthesis of triacylglycerols (TAGs) may specially increase, this mechanism is for dissipating excess radiation energy. In fact, TAG concentrations decline with drought, the degradation of foliar TAGs may represent an early adaptive response to water deficit in drought-sensitive plants, which is then followed by accumulation of TAGs as water deficiency becomes more severe. Comparative proteomics results of Martins *et al.* (2020), in *E. saligna* and *E. tereticornis* suggested that such proteins may play a crucial role as potential markers of water stress tolerance. For this, results allowed to identify four proteins (ATP synthase, gamma, alpha, glutamine synthetase and vacuolar proteins) that were more abundant in drought-tolerant species of *E. saligna* and simultaneously less abundant or unchanged in the drought-sensitive species of *E. tereticornis*. In addition, ten proteins were only induced in *E. saligna* in response to water stress, which are plastid-lipid, rubisco activase, ruBisCO, protease ClpA, transketolase, isoflavone reductase, ferredoxin-NADP reductase, malate dehydrogenase, aminobutyrate transaminase and sedoheptulose-1-biophosphatase. Bedon *et al.* (2011) also examined the proteome of *E. globulus* roots under water stress and identified a greater accumulation of proteins related to the cellular processes, transport, cell protection, and stress defense in the tolerant genotype. The leaf proteome of *E. globulus* under contrasting water stressed conditions identified such proteins related mainly to the photosystem II (PSII) and the Calvin cycle. Another recently research of Fernando *et al.* (2021) indicated that the microprobe data provide evidence of drought tolerance by demonstrating that extended conditions of lack of water to trees do not elicit neither changes in leaf anatomy nor in leaf cellular storage of these elements, for this, foliar Na concentrations of ~2000-6000 mg kg⁻¹DW are found co-localized with Cl in mesophyll and dermal cells of young and mature leaves, suggesting vacuolar salt disposal as a detoxification strategy.

Molecular response

Understanding the genetic and molecular basis of water stress response is of main importance for the sustainability of the planted forests in areas where soil water availability is already restricted. Under drought

conditions, plants sense and transmit the stress signals which regulate the expression of numerous genes and help them to optimize their growth and development (Singh and Laxmi, 2015). The same studies indicated that “signalling mechanism” is based on the phytohormone abscisic acid (ABA) in which both ABA-independent and ABA-dependent regulate transcriptional response in plants to water deficiency. Moreover, genomic and molecular investigations indicated the existence of cross talk between those two transcription factors operating under drought stress conditions (Shinozaki and Yamaguchi-Shinozaki, 2007). This crosstalk affects one or many regulons (Nakashima *et al.*, 2009; Singh and Laxmi, 2015), such as abscisic acid-responsive element binding protein (AREB)/ABF (ABRE binding factor) regulons function in ABA-dependent regulation of gene expression and Dehydration-responsive element binding protein 1 (DREB1)/CBF (C-repeat binding factor) regulons function in ABA-independent which are the major regulators governing drought response (Nakashima *et al.*, 2009; Agarwal and Jha, 2010; Amrutha *et al.*, 2019).

Moreover, other authors Bartels and Sunkar (2005); Wang *et al.* (2006) and; Morran *et al.* (2011) studies indicated that other elements play a pivotal role in cellular protection and stress alleviation such as dehydrins, molecular chaperones, water channel proteins, transporters and biosynthetic enzymes, growth regulators, protein phosphates, phospholipid metabolic proteins and protein kinases. In *Eucalyptus*, extensive studies on morpho-physiological and biochemical response to water stress condition is reported, while molecular response is limited to transcriptome-wide response in *E. globulus* and *E. cladocalyx* (Spokevicius *et al.*, 2017), *E. camaldulensis* (Thumma *et al.*, 2012), *E. alba* hybrid and *E. urophylla* × *E. grandis* (Villar *et al.*, 2011), and *E. grandis* (Ghosh Dasgupta and Dharanishanthi, 2017). In this genus, the major transcription factors which regulate water stress include zinc finger transcription factor family protein (Villar *et al.*, 2011), such as MYB, NAC, ERF, HB12 (Thumma *et al.*, 2012) and HSFs, DREB2A, DEAR3 (Ghosh Dasgupta and Dharanishanthi, 2017). For Amrutha *et al.* (2019), a high expression of water responsive transcripts like osmotin (OSM34) has registered in *E. tereticornis* and *E. camaldulensis*, indicating that level of osmotin can act as an indicator in screening water-responsive genotypes, added to that, dehydration responsive element binding proteins DREB/CBF, C-repeat/DRE-binding factor (CBF1c and CBF2), glutathione peroxidase (GPX6), and raffinose synthase family protein (SIP) showed also significant up-regulation. Expression of osmotin during water deficiency condition reported also in *E. cladocalyx* (Spokevicius *et al.*, 2017) and *E. grandis* (Ghosh Dasgupta and Dharanishanthi, 2017). For instance, *E. camaldulensis* revealed a high genetic variation related to considerable variation in growth, wood quality and tolerance to three environmental factors: salinity, drought and frost (Yang *et al.*, 2017). In addition, *E. globulus* offers certain genotypes that potentially tolerate environments with low water availability (Carignato *et al.*, 2020). Results of Correia *et al.* (2018) on *E. globulus* showed that a strong realignment of gene expression resulting from an overwhelming of physiological adjustments to water limitation, a number of transcripts exhibited altered abundance after the acute water stress: reduction of RuBisCO activase, mitochondrial glycine cleavage system H protein and increase of isoflavone reductase. For malate dehydrogenase, dehydration response element B1A and potassium channel GORK, it showed a different abundance pattern in each clone.

Upstream of these cellular changes induced by drought stress are alterations of gene expression and synthesis of the corresponding proteins. Other research of Amrutha *et al.* (2019), revealed that genome wide analysis in *E. grandis* revealed the presence of 17 DREB1/CBF genes and 6 DREB2-type transcription factors, which were highly induced in response to osmotic stress conditions and have considered to be involved in DRE mediated gene transcription in response to water deficiency (Liu *et al.*, 1998; Dhriti Singh and Laxmi, 2015). Andrade *et al.* (2007) indicated that root proteome has changed for six-month-old plantlets of *E. grandis* a drought resistant species, seven days of drought later they mentioned that 66 proteins showed significant changes in spot volumes with 49 have increased abundance and 17 have reduced their expression level. The functional categories of these proteins have been identified as defense, energy, metabolism, cell structure and signal transduction. Moreover, Zhang *et al.* (2020) indicated that a total of 40 Eg HD-Zip genes have been

identified in *Eucalyptus* species in which HD-Zip proteins are plant-specific transcription factors that play a significant role in plant development and response against various stresses.

Eucalyptus in arid region of Tunisia: resistance and adaptation

Climatic conditions of the region

Due to its geographic location, Tunisia is a transitional zone between the dry North African desert climate and the humid South European climate. In this Mediterranean country, rainfall is highly variable in space and time. Average annual rainfall ranges between 1500 mm in the northwest and less than 100 mm in the extreme arid southwest, the Sahara (Arnould and Horyat, 2003; Souden *et al.*, 2020). Southern Tunisia is a dry region characterized by an arid or Saharan bio-climate and severe edaphic conditions heavily affected by wind erosion, with very limited rainfall where drought can be frequent (Verner *et al.*, 2018). Approximately 25% of Tunisia territory is affected by desertification, for this several indigenous and autochthonous species becoming endangered (DGF, 2007; Souden *et al.*, 2020). The risks of a significant declines in water resources (28% for groundwater resources and -5% for surface water), and degradation of irrigation water quality (higher salinity) have been mentioned by several national and regional studies in southern Tunisia (MEE, 2013; Mahdhi *et al.*, 2019).

Eucalyptus in Tunisian arid: species and behavior

Eucalyptus is a very important reforestation species in Tunisia, it is from North to South of the country (Mechergui *et al.*, 2019). Since 1957, *Eucalyptus* is the most widely used exotic species for the rehabilitation of affected areas in Tunisia, 117 species of the genus *Eucalyptus* have been introduced and acclimated into 30 arboreta distributed from the north to the south of the country (Khouja *et al.*, 2001). According to the latest forest inventory in Tunisia, the area of *Eucalyptus* accounts for 6% of the national forest cover (DGF, 2010). This preference for *Eucalyptus* is principally related to its high drought tolerance. In fact, they have a growth adaptation in the arid region and show rapid growth, tolerance to salinity, tolerance to drought and intense flowering (Saadaoui *et al.*, 2017; Maaloul *et al.*, 2019). Given the importance of this taxa, this area should be protected and valued for the multiple use of these species, *E. camaldulensis* and *E. gomphocephala* account for more than 80% of the *Eucalyptus* stand (Mechergui *et al.*, 2019). In the south, arid and Saharan regions, fourteen species and one hybrid have been identified (Khouja *et al.*, 2001; Saadaoui *et al.*, 2022). There are *E. camaldulensis*, *E. gomphocephala*, *E. torquata*, *E. microtheca*, *E. occidentalis*, *E. oleosa*, *E. lesouefii*, *E. salubris*, *E. salmonophloia*, *E. gracilis*, *E. flocktonia*, *E. brokwayii*, *E. astringens* and *E. diversifolia*. The most frequent species are *E. camaldulensis*, *E. occidentalis*, *E. torquata*, *E. microtheca* and *E. gomphocephala* (Saadaoui *et al.*, 2022). Seven species are judged drought-resistant such as *E. gracilis*, *E. salmonophloia*, *E. lessouefii*, *E. occidentalis*, *E. astringens*, *E. torquata*, and *E. microtheca* (Khouja *et al.*, 2001; Saadaoui *et al.*, 2017). This high number of *Eucalyptus* species in this arid region shows an enormous ecological importance, mainly to select promising species for combating desertification and protecting the soil. In addition, the vast majority of eucalypt species have important melliferous interests (Saadaoui *et al.*, 2022). The level of presence of all eucalyptus species presents in the Tunisian arid region, as well as the level of tolerance to water deficiency have been summarized in the following (Table 1).

Table 1. Comparison between eucalyptus species presents in the Tunisian arid region

Species	Presence in arid Tunisia (-, +, ++)	Drought resistance (-, +, ++)	Adaptation strategies	Interests	References
<i>E. camaldulensis</i>	++	+++	<p>Osmotic adjustment accumulation of soluble carbohydrates (especially cyclitols)</p> <p>Resistance to xylem embolism: higher ability to restore its xylem conductivity after rehydration</p>	<p>Silvicultural tree.</p> <p>A nectar plant: High level of flowering (9 months from February to October).</p> <p>Reforestation interest (used to stabilise the costal dunes, reduce erosion and protect the roadsides).</p> <p>Frequently used for wood production (high resistance to rot and high density about 0.90 g/cm³).</p> <p>Several uses: in heavy construction, railway ties, floors, structural beams, fences, turned wood, in the production of firewood, coal and in the manufacture of plywood.</p> <p>Important ethno-medicinal plant</p> <p>Extraction of essential oil: Aromatherapy agents used in medicine for their biological activities (anti-inflammatory, antibacterial and antioxidant potential)</p>	<p>(Souden <i>et al.</i>, 2020)</p> <p>(Abed <i>et al.</i>, 2015)</p> <p>(Ayepola and Adeniyi, 2008)</p> <p>(Elaieb <i>et al.</i>, 2019)</p> <p>(Ghasemian <i>et al.</i>, 2019)</p> <p>(Iwakiri <i>et al.</i>, 2019)</p> <p>(Limam <i>et al.</i>, 2020)</p> <p>(Saadaoui <i>et al.</i>, 2017)</p> <p>(FAO, 2002)</p>
<i>E. torquata</i>	+	+++	<p>Osmotic adjustment: accumulating soluble carbohydrates, (especially cyclitols)</p> <p>Resistance to xylem embolism: higher ability to restore its xylem conductivity after rehydration</p>	<p>A nectar plant: High level of flowering (9 months from February to October)</p>	<p>(Souden <i>et al.</i>, 2020)</p> <p>(Saadaoui <i>et al.</i>, 2017)</p> <p>(FAO, 2002)</p> <p>(Eisikowitch <i>et al.</i>, 2012)</p>
<i>E. occidentalis</i>	++	++	<p>Reduction in foliage photosynthetic characteristics</p> <p>Increase the emissions of volatiles from the</p>	<p>A nectar plant: present a high level of flowering (9 months from February to October)</p> <p>Essential oil: used as a natural repellent, insecticide and a fumigant toxicity for stored-product insect pests.</p>	<p>(Bande-Borujeni <i>et al.</i>, 2018)</p> <p>(Saadaoui <i>et al.</i>, 2017)</p> <p>(Jeddi <i>et al.</i>, 2009)</p>

			lipoxygenase (LOX) pathway.		
<i>E. gomphocephala</i>	++	++	Anisohydric plant	Frequently used for wood production	(McDowell <i>et al.</i> , 2008) (Souden <i>et al.</i> , 2020) (Saadaoui <i>et al.</i> , 2017) (FAO, 2002)
<i>E. torwood</i>	-	++	No information	A nectar plant	(Eisikowitch <i>et al.</i> , 2012)
<i>E. diversifolia</i>	+	+	No information	A bee plant: high level of flowering	(Saadaoui <i>et al.</i> , 2017)
<i>E. flocktoniea</i>	-	++	No information	Extraction of essential oil	(Bignell <i>et al.</i> , 1995)
<i>E. microtheca</i>	++	+++	Transpire less Grow less Increase their root/ foliage ratio: changes in allocation to the root system high activities of Rubisco. Reduction of photosynthesis Thicker epidermis of leaves Larger vascular tissue	Mostly grown for fuel, also useful for low-grade posts and poles, shelterbelts Soil stabilization. A bee plant: medium to good source of nectar and pollen, honeydew and propolis for honeybees	(Li and Wang, 2003) (Johannsmeier, 2016) (Tuomela, 1997)

Disease and drought in eucalyptus plants

In nature, plants are simultaneously exposed to diverse environmental stresses (Negahdarsaber, 2019). Among a wide variety of abiotic and biotic factors, drought and bio-aggressors are important stressors affecting forest and tree health. Since both infection and drought act at the same time as stressors, reducing the plant's capacity for plastic response. It is likely that their combined occurrence has additive deleterious effects and may lead more rapidly to exhaustion. In most cases, a trend of increasing disease severity with increasing water stress is observed (Desprez-Loustau *et al.*, 2006). In *Eucalyptus*, the family Botryosphaeriaceae are well-known opportunistic pathogens that cause serious diseases in stressed *eucalyptus* plants and causing high economic losses (Chen *et al.*, 2011; Barradas *et al.*, 2018). In fact, it has been recognized that water deprivation increases the susceptibility of woody plants to these fungi (Sherwood *et al.*, 2015; Barradas *et al.*, 2018).

In addition, *Neofusicoccum eucalyptorum* is a pathogen and endophyte in non-native and native *eucalyptus* trees, it is one of the most frequent Botryosphaeriaceae species associated with *Eucalyptus* Portuguese

stands which induced canker and necrotic lesion formation on 6-month-old *E. globulus* plants (Barradas *et al.*, 2018). Diseases caused by *N. eucalyptorum* have been reported also as a threat for *eucalyptus* plantations worldwide (Pérez *et al.*, 2009). Moreover, (Naidoo *et al.*, 2014; Wingfield *et al.*, 2008) indicated some examples of pests and pathogens that currently posing a threat to *Eucalyptus* include the myrtle rust pathogen *Puccinia psidii*, the stem canker pathogen *Chrysosportheaustro africana*, the root rot pathogen *Phytophthora cinnamomi* and the insect pest *Leptocybe invasa*. Studies of Barradas *et al.* (2018) focused on *E. globulus* indicated that water-stressed plants were more susceptible to *N. eucalyptorum* than non-stressed plants. Whereas, this response is particularly relevant when the plants are inoculated while water limitation is already occurring. Moreover, drought-primed plants are slightly more resistant to fungal infection than the non-primed ones (Barradas *et al.*, 2018). A large majority of published studies referred to a positive association between drought and disease, disease favored by drought or drought and disease acting synergistically on tree health status, with a predominance of canker/dieback diseases, caused by pathogens like *Botryosphaeria*, *Sphaeropsis*, *Cytospora* and *Biscogniauxia* (Hypoxylon). The type of disease-related variables (incidence vs. severity) and the intensity and timing of water stress are shown to be significant factors affecting the drought-infection interaction (Desprez-Loustau *et al.*, 2006). Indeed, drought influences the physiological status of the plants by changing their predisposition to disease and favouring the attack by pathogens on one side (Bostock *et al.*, 2014). On the other, pathogen attack leads to changes in plant physiological processes, such as primary and secondary metabolism related to the induction of defense responses, which affect the growth and development of the plant (Berger *et al.*, 2007; Barradas *et al.*, 2018).

Findings results reinforce the concept that drought leads to plant predisposition to diseases (Bostock *et al.*, 2014). The same idea is shared by Barradas *et al.* (2018) indicates that plant susceptibility to fungal diseases increases when inoculation occurs under water deprivation conditions, indicating that pre-established water deficit weakens basal defenses and facilitates successful pathogen infection (predisposition). However, Desprez-Loustau *et al.* (2006) mentioned that direct effects of drought on pathogens are generally negative, although most fungal pathogens exhibit an important plasticity and can grow at water potentials well below the minimum for growth of their host plants. Many species can sustain significant growth (more than 50% of optimal) at water potentials as low as -2 MPa. The same research of Desprez-Loustau *et al.* (2006) indicated that pathogens that cause increased damage in plants predisposed by stress are habitually present on or in their host before stress, as saprophytes or endophytes. It is well established by Kendig *et al.* (2000) studies that carbohydrate and protein metabolisms are very sensitive to changes in plant water status, changes may then provide compounds that stimulate metabolism and growth of pathogens or decrease toxic or inhibitory contents. It appeared also that early exposure of plants to drought stress results in the beginning of drought stress responses such as increased reactive oxygen species (ROS) levels and induction of PR-protein and ABA encoding genes which play antagonistic role in suppressing or minimizing the effect of pathogen infection and contributed for disease resistance in combined stressed *Eucalyptus* plants (Fujita *et al.*, 2006; Negahdarsaber, 2019).

Drought effects on essential oil from eucalypt

About 300 species of genus *Eucalyptus*, contain volatile essential oils in their leaves. Around 20 species have a very high content of 1,8-cineole that are economically favourable and extensively used in number of marketable products of commercial importance (Kainat *et al.*, 2019). Whereas nursery conditions mainly biotic stresses such as disease or herbivory and abiotic stresses like nutrient deficiency and especially drought can affect leaf quality by modulating their chemical composition, this affects essential oil quantity, quality, yield and composition (Leicach *et al.*, 2008; Leicach *et al.*, 2010; Llorens-Molina and Vacas, 2017).

For instance, studies of Rad *et al.* (2014) based on three treatments including 100,70, and 40% field capacity maintained on *E. camaldulensis* species which are considered as a rich source of essential oils especially 1,8-cineol. For this, results showed that essential oil production increase with soil moisture. Whereas mild drought stress improved the production of 1,8-cineol, however it decreased or stopped the production of many other compounds. The percentage of 1,8-cineol in the treatments of 100,70 and 40% of field capacity, were 69.33, 78.13 and 51.87.

Drought effects on wood formation

Wood formation in trees is a dynamic process that is strongly affected by environmental conditions, including nutrient availability (Puech *et al.*, 2000; Wind *et al.*, 2004), atmospheric CO₂ concentration (Luo *et al.*, 2005) and climatic factors (Deslauriers and Morin, 2005; Rossi *et al.*, 2006; Arend and Fromm, 2007). Wood development processes and properties such as wood density and fiber radial diameter were sensitive to water availability and may be markedly altered directly or indirectly via physiological responses in the cambial zone when the processes of cell expansion and wall thickening are limited by water availability (Arend and Fromm, 2007). For instance, abiotic stress such as drought can affect wood growth, directly, through effects on cambial cells and their derivatives or, indirectly, through an effect on photosynthesis and the translocation of assimilates in which cambial activity and wood cell development are strongly dependent on their availability (Krabel, 2000). Moreover, studies of Arend and Fromm (2007) indicate that drought induced changes in the anatomy of developing xylem cells, significantly reduced the length and cross-sectional area of newly formed fibers and vessel elements. For *Eucalyptus* species, study of Drew *et al.* (2009), realized on *E. globulus* species indicate that wood density increased significantly whereas fiber radial diameter and microfibril angle MFA decreased in response to water stress. However, when water was available, wood density in *E. globulus* was positively correlated with temperature. This result is confirmed also by another study of Thomas *et al.* (2004) realized on *E. camaldulensis* which proposed the existence of positive relationship between temperature and wood density. In fact, results showed that wood density increased with a rise of temperature whereas was negatively related to hydraulic conductivity. The reduction in vessel area per cross-sectional area of wood at higher temperature was in part a result of a shift towards smaller diameter vessels. Moreover, results obtained by Downes *et al.*, (2004); Wimmer *et al.*, (2002) indicated also that wood density in *E. nitens* declined when water availability increased and Wimmer *et al.* (2002) demonstrated that MFA in *E. nitens* increased when water stress was released. Moreover, Drew and Pammenter (2007); Drew *et al.* (2009) observed that cambial width and meristematic activity increased in relation to increased water availability in two sub-tropical hybrid *Eucalyptus* clones. The same results of Eilmann *et al.* (2011) showed that in pine stressed plants, water conduction cells were significantly enlarged, had significantly thinner cell walls and have a short growth period, in this period wood formation actually takes place can be much shorter under drought than the 'potential' period, meaning the phenological growth period. In addition, various studies revealed a distinct correlation between potassium nutrition and wood formation in *Eucalyptus*. It is suggested that potassium (K) is considered as a key player in wood formation (Fromm, 2010). For that, K modulates xylem hydraulic conductance and improves water use efficiency for biomass production in *Eucalyptus* plants (Battie-Laclau *et al.*, 2016), possibly by interacting with pectins in inter-vessel pits, to enhance tree resistance to drought (Nardini *et al.*, 2011; Jansen *et al.*, 2011). Results of Wind *et al.* (2004) indicated a key role for potassium in the regulation of cambial growth and wood formation of poplar plants, due to its strong impact on osmoregulation in expanding cambial cells. They also demonstrate involvement of ABA in regulation of potassium-dependent cambial growth. Therefore, the $\delta^{13}\text{C}$ signatures of wood may become useful indices of drought-susceptibility in plantations within a few years of establishment. The seasonal pattern of $\delta^{13}\text{C}$ of wood appeared to reflect seasonal variation in water availability and duration of cambial activity. $\delta^{13}\text{C}$ of wood across

boundaries of growth-rings suggested that drought stopped cambial activity resulting in less production of late wood and less dense wood (Macfarlane and Adams, 1998). Furthermore, the effects of availability of water on tissue development will affect wood density and we might expect that the $\delta^{13}\text{C}$ of wood could be related to its density (Kozłowski *et al.*, 1991; Macfarlane and Adams, 1998). The same study of Macfarlane *et al.* (1998) showed that throughout the 6 years of *E. globulus* development the abundance of ^{13}C (expressed as $\delta^{13}\text{C}$) in wood of trees growing on the drought-prone site ($-24.8\text{‰} \pm 1.4$) is greater than in other trees well-watered (-25.8‰) moreover basic density of wood of trees growing on the more drought-prone site ($496 \pm 14.0 \text{ kg m}^{-3}$) is reduced compared to other trees (554 kg m^{-3}).

Conclusions

Based on this study, insights into the effects of water availability might change dramatically on *Eucalyptus* Spp. For that, a large scale of strategy and mechanisms are used by eucalyptus to cope with stressful conditions of Arid and semi-arid zones. This paper showed a variety collection of successful drought acclimation *Eucalyptus* species able to cope with a lack of water availability and showed enormous ecological importance of those exotic species with a strong interest in *Eucalyptus reforestation* mainly in southern Tunisia especially for *E. microtheca*, *E. occidentalis*, *E. torquata* and *E. camaldulensis*.

Authors' Contributions

The manuscript writing was done by C.I. under the guidance of the coauthors. S.B. and S.B.R. helped to shape the research. Species verification and prospecting were performed by C.b.R. and N.M. K.b.Y. proofread and refined the manuscript. the work in its various stages is carried out under the direction of E.S.

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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