

An overview of adaptative responses to drought stress in *Eucalyptus* spp.

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Abstract. *Eucalyptus* is a plant frequently present and cultivated in arid regions because of its high adaptation to drought. Furthermore, it is known by its numerous species which represents a great opportunity to choose several tolerant species with variable uses. Therefore, the choice of species, hybrids or genotypes resistant to aridity becomes a necessity before any plantation in regions and countries characterized by semi-arid, arid and Saharan climates. Our review shows an important effect of drought on anatomical, physiological and biochemical parameters of *Eucalyptus* spp. Indeed, water stress acts directly on growth, yield and response to pests. However, the response to drought varies significantly among species, genotypes, hybrids and clones. This result represents a field for the selection of eucalypts tolerant and adapted to water deficit or climate change.

Key words: *Eucalyptus* spp., drought, adaptation, essential oil, pests.

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Introduction

Eucalyptus L'Hér. species (Myrtaceae) are native to Australia, with a few native species from Papua New Guinea, Indonesia and the Philippines (Leicach et al., 2012). The Eucalyptus genus contains 747 species distributed in a big range of environments (Beech et al., 2017). Eucalypts are the world's most widely planted hardwood trees (Myburg et al., 2014). Today, it is found in over 90 countries and spread over more than 22 million hectares planted around the world and 11 million hectares of native Eucalyptus in Australia, which represent 12% of global forest plantations, 13 million hectares of planted Eucalyptus have interest for industrial production (ENCE, 2009). Eucalyptus have been successfully introduced worldwide; it is used for ornamentation, afforestation, or to obtain timber, gum, pulp and paper and it's known by its cosmetic and medicinal values. Essential oil is used in food, perfumery, beverage and pharmaceutical industry (Batish et al., 2008; Leicach et al., 2012; Vecchio et al., 2016). Indeed, Eucalyptus shows the greatest diversity of genes for particular metabolites such as terpenes that act as chemical defence and provide unique pharmaceutical oils (Myburg et al., 2014). Eucalyptus oil and its major component, 1,8-cineole, have antimicrobial effects against many bacteria, viruses, and fungi. There are also immune-stimulatory, antiinflammatory, antioxidant, analgesic, and

spasmolytic effects (Sadlon & Lamson, 2010; Vecchio et al., 2016).

Eucalyptus is a fast-growing forest tree with high potential biomass carbon sequestration and soil nutrient depletion; its development in mixed forest communities would improve the ecological function of Eucalyptus plantations (Du et al., 2015; Fladung et al., 2015). In addition, several factors contribute to the success of Eucalyptus; the ability to grow in a wide range of environments and soils, the fast growth rate and large biomass production, good wood quality for solid wood products and short cellulose fiber, suitable for pulp production, particularly for paper and tissue (Labate et al., 2008). Hence, several species are known for their growth and adaptation to arid, tropical or temperate regions; E. grandis W.Hill ex Maiden, E. globulus Labill., E. camaldulensis Dehnh. and their hybrids predominated in arid regions and used as commercial plantations, E. grandis, E. urophylla S.T.Blake and their hybrids for tropical and subtropical regions and E. globulus known for temperate climates (Potts, 2004).

Drought is one of the environmental problems that affect directly plant growth and yield; it's the most common factor limiting plant productivity. Global climate change is increasing the frequency of severe drought conditions (Basu *et al.*, 2016). In this review, we aim to analyze the resistance of *Eucalyptus* to drought through various parameters that explain the behaviour of the plant under water stress conditions, thus, intra and interspecific variations are studied.

Eucalyptus water demand and efficiency

Plant-water relationship in *Eucalyptus* is specific, because of its high water uptake ranging from 50 to even 90 L/day/plant and the particular tolerance of several eucalypts to drought (Joshi & Palanisami, 2011). The cumulative annual water use by *E. urophylla* in sandy soil is about 3200

L/tree; the parameters that explain this high water consumption are in order: root uptake, leaf transpiration and soil evaporation (Ouyanga et al., 2016). In two arid plantations of the southern China, Morris et al. (2004) estimated annual water use by E. urophylla about 542 and 559 mm in limiting soil water and 916 and 815 mm without limiting soil water. The effect of *Eucalyptus* species on water reserves depends on root architecture, root depth, leaf area, age, climatic conditions and management regime (FAO, 2011). Joshi & Palanisami (2011) reported that, eucalypt roots can grow even up to 6-9 m in stress conditions and extract more water. Indeed, Roots of some species can grow to 30 m in depth and extract the ground water (FAO, 2011). In fact, Laclau et al. (2013) concluded that all the water stored down to a depth of 6-7 m and available for trees is withdrawn by tree roots of E. grandis within 1.1 year of planting.

Generally, eucalypt drought-tolerant clones under water deficit have high uptake efficiency and low nutrient use efficiency, whereas drought-sensitive clones have low uptake efficiency, low nutrient use efficiency for root formation and high use efficiency for leaf formation (Hodecker, 2015). Stape et al. (2004) mentioned that a 15% irrigation supplement increases wood production by 52% in 3.4 to 5.4year-old plantation of E. grandis × E. urophylla in the North of Brazil. Indeed, Potential productivity in *Eucalyptus* is high but maximum rates are rarely achieved because of limitations due to nutrient availability and drought (Whitehead & Beadle, 2004).

Eucalyptus plantings have elicited environmental concerns for two primary reasons; its water demand and effect in the reduction of biodiversity (Williams, 2015). The increased water use by Eucalyptus may lead to desertification, lowering ground water and scarcity of aquifer resources for irrigated-agriculture in arid and semiarid regions (Zahid et al., 2010). Its introduction causes the dryness of water sources, the lowering of the water table, the exploita-

tion of groundwater and competition with the species of the maquis (Bilal et al., 2014).

Mechanisms and strategies of resistance to drought

Morphological adaptations

In Eucalyptus, leaf area index (LAI), vertical leaf arrangement and deep rooting ability change between seasons; these parameters are mechanisms for drought avoidance (Whitehead & Beadle, 2004). Fast downward growth of roots and the exploration of deep soil layers provide access to large amounts of water stored in deep soil layers after wet seasons. Indeed, deep roots can reach a depth of almost 20 m within a rotation cycle of 5-7 years in E. grandis planted forests, giving access to large water stocks (Christina et al., 2017). Eucalyptus presented investment in the root system to access water (e.g. E. urocan) (Matos et al., 2016). Susiluoto & Berninger (2007) studied the response of *E. microtheca* F.Muell. to water stress and observed an increase in root/shoot ratio and a decrease in the ratio of coarse and fine root mass. The changes in root/shoot ratio are considered the primary reactions of the species to drought. Roots of *Eucalyptus* trees are consistently dimorphic, comprising a widely spreading lateral system just below the soil surface and a deep taproot system. Although the numbers of fine roots were decreased with depth, they were important for survival by absorbing water during seasonal droughts. The vertical distribution of fine root system differs between wet and dry periods in E. grandis × E. urophylla, about 70% of fine roots were found within the upper 30 cm in winter and only 30% in summer.

Five morphological variables (height, increase in height, diameter, stem density and leaf area) present good markers to the genetic improvement of *Eucalyptus* aiming dieback and water deficit tolerance; among eight morphological variables assessed in thirteen clones belonging to *E. grandis* × *E.*

urophylla, E. grandis × E. pellita F.Muell., E. grandis, E. urophylla and E. pellita. For Corrêa et al. (2017), height, increase in height, stem density, diameter and N content show the highest heritability. A study of drought effect for six genotypes, three from E. camaldulensis and three from E. globulus indicated a reduction in total biomass, root biomass and leaf area for all *Eucalyptus* provenances. In addition, RGRmax (maximum relative growth rate) genotypes, characterized by the higher relative growth rate, maintain both leaf area and water transport capacity (leaf-specific hydraulic conductivity), whereas low RGRmax genotypes have a higher reduction of both leaf area and water-transport capacity under drought (Maseda & Fernández, 2016)

Physiological and nutritional adaptations

Drought resistance is the set of plant adaptive features for escape, avoid, or tolerate drought stress (Basu et al., 2016). Eucalyptus closes their stomata for longer periods in the day to prevent loss of water. Also, osmotic adjustment, intercellular storage of water and process of hardening can be used by *Eucalyptus* for tolerate water stress (OECD, 2016). Under hydric deficit conditions, E. urocan plants reduced the breathing rate and turgor maintenance sufficient to sustain growth (Matos et al., 2016). Merchant et al. (2007) analyzed the response of six eucalypt species (E. obliqua L'Hér, E. rubida H.Deane & Maiden), E. camaldulensis, E. cladocalyx F.Muell., E. polyanthemos Schauer and E. tricarpa L.A.S.Johnson L.A.S.Johnson & K.D.Hill) to water deficit, and showed that osmotic adjustment is a common response to water deficit in these six species and explained the level variation observed between species by the environment of plant origin. The same result is found by Silva et al. (2016b) after the study of 12 Eucalyptus species. Lima et al. (2003) concluded a decrease in stomatal conductance, photosynthesis and transpiration rates under drought stress of five eucalypt species (E. grandis, E. urophylla, E. camaldulensis, E. torelliana F.Muell. and E. phaeotrica Blakely & McKie). For E. globulus and E. cladocalyx, net carbon assimilation, stomatal conductance and sub-stomatal carbon concentration reduced in drought conditions (Spokevicius et al., 2017).

Shvaleva et al. (2005) studied the metabolic responses of leaves and roots of two *E*. *globulus* clones under severe drought; they observed a general decrease in growth and osmotic potential. For two other genotypes of E. globulus, at the end of the 7-week of drought, the treatment reduced height, biomass, water potential, non-photochemical quenching (NPQ) and gas exchange are registered for these both genotypes. Contrarily, the levels of pigments, chlorophyll fluorescence parameters Fv/Fm (maximum photochemical efficiency of PSII) and φPSII (photochemical yield of photosystem II), MDA (malonyldialdehyde) and ABA (abscisic acid) increased. During recovery, MDA, ABA, E (transpiration rate), gs (stomatal conductance), and pigments are recovered, while other parameters are not restored (φPSII, NPQ) (Correia et al., 2013). *Fv/Fm* is found to be a reliable tool facilitating the selection of eucalypt species tolerant to drought; sensitive clones reveal the largest decreases in Fv/Fm values under water stress regime (Silva et al., 2016a). Therefore, variation level differs between clones, genotypes and species; minimal variation in physiological characteristics shows an ability to overcome physiological stresses and adapt to varying climatic conditions (Warrier et al., 2013).

Martorell *et al.* (2013) examined the dynamics of leaf gas exchange and xylem function in *E. pauciflora* Sieber ex Spreng. plants under severe water stress and recovery after re-watering. Stomatal closure and leaf turgor loss occurred at water potentials that delayed the extensive spread of embolism through the stem xylem. Stem hydraulic conductance and stomatal conductance recovered within 6h and 10 days after a return to water availability. Indeed, changes in stomatal conductance may be

used as signs and good indication of water stress (Valadares et al., 2014). In hydroponic culture, Granda et al. (2011) registered a specific model of ABA and pH in response of *E. globulus* to water restriction regime. Indeed, pH acts as an early signal, whereas later xylematic ABA becomes the main signal. These signals cause fast responses such as changes in stomatal conductance. Mitchell et al. (2013) registered a decrease in starch and soluble sugar concentrations in the roots of *E. globulus* and *E.* smithii R.T.Baker under lethal drought. In the same species, Shvaleva et al. (2005) observed high decrease in roots growth and increase in concentrations of soluble sugars and proline in leaves and roots. In the last, glutathione reductase activity increased in response to water deficit, suggesting that this enzyme plays a protective role in roots during drought stress by catalyzing the catabolism of reactive oxygen species.

Corrêa et al. (2017) evaluated N, P, K, Ca, Mg, S, Fe, Zn, Cu, Mn and B in 13 clones of Eucalyptus and showed high heritability for N content and moderate for K and B content; these markers can be used in the early selection of tolerate clones to drought. Hodecker (2015) studied the effect of Boron (B) to maintain the normal growth and development of five eucalyptus species: E. grandis, E. urophylla, E. melliodora A.Cunn ex Schauer, E. camaldulensis, E. globulus and E. cladocalyx. He observed a strong increment on instantaneous water use efficiency in stressed plants supplemented with B, due to the combination of higher photosynthetic rate, higher K concentration in leaves promoting faster stomatal closure, lower water loss and a higher translocation of sugars and B to root growth. Conversely, P fertilization increases growth when water is not limiting, but has no promotive effect under drought conditions; fertilization with P may increase drought susceptibility in young E. grandis plants (Graciano et al., 2006).

Spokevicius *et al.* (2017) identified key genes responsible for the differences between eucalypts of humid and arid climates; these key genes that differentiated species responses were linked to photoprotection/redox balance, phytohormone/ signalling, primary photosynthesis/cellular metabolism and secondary metabolism based on metabolic pathway. This suggests that eucalypt species has metabolic mechanisms resulting in a broad scale modification of their biochemistry to reduce water loss. Additionally, a gene named EgPHI-1, was identified in Eucalyptus and introduced in tobacco; its overexpression enhances tolerance to osmotic stress in comparison with wild-type plants. EgPHI-1 transgenic plants showed a increase in root length and biomass dry weight (Sousa et al., 2014). In addition, a tolerance to drought is reported in *E. grandis* × *E. urophylla* transformed with DREB1A transcription factor of Arabidopsis thaliana (L.) Heynh. (McDonnell et al., 2010)

Anatomical adaptations

The anatomy of 28 Eucalyptus species distributed in wide gradient of aridity is studied in Australia. With increasing aridity, vessel diameters narrow, their frequency and sapwood density increase and hydraulic conductivity declines. Differences in these traits appear largely genotypic; indeed, the data reflect an adaptation of anatomy to water availability. In the case, climate change presents a challenge to the capacity of eucalypts to adapt their vasculature (Pfautsch et al., 2016). Adaptations to drought concern leaf anatomy; in E. alba Reinw. ex Blume, E. maculata Hook and E. microtheca, thicker epidermis reflect an adaptation to water limited environments and larger vascular tissue. This character allows the survival of the plant under variable conditions (Ali et al., 2009). For juvenile individuals of three Eucalyptus species (E. grandis, E. sideroxylon A.Cunn ex Woolls and E. occidentalis Endl.) studied in waterlimitation, the results of wood anatomy obtained show that vessel lumen area are

reduced and vessel frequency is greater in water-limited plants. Consequently, conduit efficiency is lowest in the *Eucalyptus* water-limited plants (Searson *et al.*, 2004). Wide zone of secondary thickening xylem is observed for *E. globulus* in various stages of lignification. This structure is explained by its interest in wood elasticity; it's an additional water storage like the bark and the water transport efficiency (Zweifel *et al.*, 2014). In *E. marginata* Donn ex Sm., pressure-volume curves showed that cell-wall elasticity of leaves increased in response to drought (Szota *et al.*, 2011).

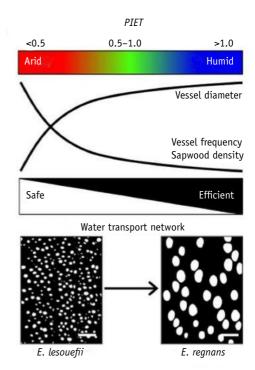


Figure 1. Changes in hydraulic traits along a gradient of aridity, represented as ratio P/ET (annual precipitation over potential evapotranspiration), and binary micrographs of diffuse porous sapwood collected from the base of Eucalyptus lessouefii in the driest site and E. regnans in the wettest (Pfautsch et al., 2016).

Inter and intraspecific variation in *Eucalyptus* tolerance to water stress

Eucalyptus genus is very heterogeneous group; it contains very high number of species and hybrids, which behave very differently with drought. Lin (2012) studied photosynthetic versus stomatal responses to water availability for *Eucalyptus* species; interspecific differences were observed, E. dunnii Maiden and E. saligna Sm., both fastgrowing species, maintain lower soil-toleaf water potential to prevent water loss via closing stomata during dry days. While E. melliodora, slow-growing species, shows the same response in dry and wet days. In addition, two months of partial drought have a greater impact on photosynthesis in E. camaldulensis than E. occidentalis. But, after four months, the responses to partial drought are not different among both species; four months of drought allowed the photosynthetic acclimation that involves hydraulic adjustments to reduce water loss while maintaining photosynthesis (Zhou et al., 2016).

In South Africa, after the examination of 52 species, 11 among them were considered resistant to drought; there are: E. lehmannii (Schauer) Benth., E. sideroxylon, E. torquata Luehm., E. melliodora, E. paniculata Sm., E. polyanthemos, E. bridgesiana R.T.Baker, E. camaldulensis, E. citriodora Hook., E. cladocalyx and E. crebra F.Muell. Other species are considered to be very sensitive to water stress, as E. fraxinoides H.Deane & Maiden (FAO, 1982). du Toit et al. (2017) tested the survival and growth of several eucalypt species and hybrids in semi-arid conditions in South Africa. E. gomphocephala DC., E. camaldulensis and E. tereticornis Sm., and hybrids of these last two species with *E. grandis* survived and grew well. However, E. cladocalyx survived well and attained competitive growth rates only on the wettest site. Some hybrids are more resistant to drought than one or both parents, for example, E. grandis × E. tereticornis showed a higher resistance than E. grandis, but lower than E. tereticornis (FAO,

1982). Lundqvist *et al.* (2017) compared three drought-tolerant eucalypt genotypes selected in South Africa on previous studies for their good potential to tolerate arid conditions, reasonably good volume growth and straightness of stems. The three genotypes are E. grandis × E. camaldulensis hybrid, E. gomphocephala and E. cladocalyx. The two last presented the high wood densities and stiffness values. In Morocco, in areas characterized by rainfall between 200 and 400 mm, E. brockwayi C.A.Gardner, E. loxophleba Benth., E. salmonophloia F.Muell. and E. striaticalyx W.Fitžg. are recommended for the production of firewood and protection, and E. salubris F.Muell., E. stricklandi Maiden. and E. torquata, for reforestation protection (FAO, 1982). In arid region of Southern Africa, 46 species and hybrids are tested; some individuals of E. grandis × E. camaldulensis, E. gomphocephala and E. cladocalyx presented the highest growth and important lumber production (Wessels et al., 2016). Khouja et al. (2001) followed the behaviour of 117 Eucalyptus species introduced in Tunisia and distributed from humid bioclimate to the Saharan (Mediterranean climate); seven species are judged drought-resistant: E. gracilis, E. salmonophloia, E. lesouefii, E. occidentalis, E. astringens, E. torquata, and E. microtheca. In Brazil, Gonçalves et al. (2017) indicated three Eucalyptus hybrids for the region with high water deficit (200-400 mm/year), there are E. grandis \times E. canaldulensis (grancam), E. tereticornis × E. brassiana S.T.Blake and E. urophylla \times E. tereticornis. But under moderate water deficit (100-200 mm/year), the tolerant hybrids are in order of increasing E. urophylla × E. grandis, E. grandis × E. camaldulensis (grancam), E. urophylla × E. camaldulensis (urocam), and the species are *E. urophylla*, *E. camaldulensis* and E. tereticornis. Indeed, E. urophylla has high adaptability to several regions and has much higher volumetric growth than E. camaldulensis.

Granda *et al.* (2014) studied intraspecific variation between nine *E. globulus* clones and reported two models of responses to

water stress; the first group behaves as water saver, maintaining high water content, showing high stomatal adjustment, and reducing their aerial growth to a great extent. The second group behaves as water spender, reducing their water content drastically and presenting osmotic adjustment. Also, it maintains high growth rate under stress conditions. In the same species, drought-tolerant genotypes presented smaller seeds, higher desiccation in the mature state, developed root system, high endogenous content of free and conjugated abscisic acid (ABA and ABAGE (abscisic acid-glucose ester)) (Valdés *et al.*, 2013).

Effect of drought in essential oil yield and composition

Drought stress is able to change allelochemical abundances, including essential oil yield and composition. Changes in essential oil production and composition have been observed for E. camaldulensis seedlings submitted to drought. Total amount of non-oxygenated terpenes decreases by 44%, whereas some oxygenated sesquiterpenes are doubled, and 1,8-cineole content are enhanced by 28.3% (Leicach et al., 2010). Emara & Shalaby (2012) studied the effect of seasonal variation and environmental factors on the metabolism of essential oils in E. camaldulensis and E. cinerea. They obtained high yield in summer, and suggested a relationship with water stress; that causes the secretion of different defence components called secondary metabolites essentially terpenoid compounds which play the role of protecting agents. Manika et al. (2012) observed a high yield and a different complementation related to the rainy season in *E*. citriodora. However, drought stress reduced essential oil yield of leaves up to 5 months of age in E. camaldulensis, with stability in the equilibrium between synthesis and removal of oils at leaf maturity (Doran & Bell, 1994). Low irrigation levels are responsible for the greatest essential oil content for *E*.

globulus; 50% and 75% ET (evapotranspiration) provides the greatest mean content of essential oil, with 4.43% and 4.09%, respectively (Queiroz *et al.*, 2017). For the same authors, analysis of chemical compounds of the essential oil, showed difference in constituents according to water regime; β -myrcene appears in accordance with 75% of the reference evapotranspiration and 125% for α -gurgujeno, alloromadendreno and varidiflorene.

McKiernan *et al.* (2016) found only a limited impact of drought on concentrations of plant secondary metabolites (terpene and formylatedphloroglucinol compounds and condensed tannins) in two eucalypt species, *E. viminalis* and *E. globulus*. For the last species, total oil concentration are lower in stressed juvenile plants leaves, nevertheless 1,8-cineole, α -pinene, aromadendrene, globulol and limonene are constant (McKiernan *et al.*, 2017). Consequently, the variation on the yield and the composition of essential oils of the plant under water deficit acts on its biological activities (Hojjati & Barzegar, 2017).

Effect of drought in *Eucalyptus* response to pests

In forest, drought and pests are the main factors affecting the establishment and productivity of Eucalyptus plantations worldwide. It's interesting to explore drought × disease interaction in *Eucalyptus* by the study of plant growth, physiological responses, including relative water content, water potential, photosynthetic pigments and lipid peroxidation involved in plant performance. In *E. globulus*, water-stressed plants were more susceptible to Neofusicoccum eucalyptorum Crous, H.Sm. ter & M.J.Wingf. than non-stressed ones. However, the comparison between droughtprimed and non-primed plants in drought resistance showed slightly resistance to fungal infection for drought-primed plants (Barradas et al., 2017). Ralstonia solanacearum

Smith and *R. pseudosolanacearum* are well known pathogens of *Eucalyptus* crops always associated with trees that have been subjected to severe stress (Coutinho & Wingfield, 2017).

Drought is an important factor of tree susceptibility to forest insects as reduced water availability compromises tree defences and vigour (Ramsfield et al., 2016). Drought and heatwaves can trigger outbreaks of woodboring beetles by compromising host defences and creating habitat conducive for beetle development. Indeed, heavy infestations can cause leaf drop, may weaken trees, and may increase tree susceptibility to adverse climatic conditions, including drought (Schühli et al., 2016). Phoracantha semipunctata Fab. is a major pest of Eucalyptus species; drought-affected individuals are vulnerable to this xylophagous attack. In fact, the effect of this beetle is largely restricted to trees severely affected by drought (Seaton et al., 2015). Caldeira et al. (2002) examined the effects of water deficits in the host trees of E. globulus on the mortality and growth of P. semipunctata larvae; they registered low larvae mortality in water stressed trees and the absence of survived larvae in irrigated trees. Their results suggest that water stress had a major role on the survival and growth of the larvae. Wills & Far (2016) examined the effects of temporal variation in regional temperature and rainfall anomalies on the dynamic populations of Uraba lugens Walk. in E. marginata forests in West of Australia. Synchronous *U. lugens* outbreaks coincided with a combination of long-term drying trends and autumn and winter drought.

Conclusions

Eucalypt species are generally characterized by a great ability of water absorption, as well as a great resistance to the dry conditions. This quality is manifested in morphological and physiological parameters, including root development and changes

in osmotic potential, stomatal conductance, gas exchange, transpiration rates and photosynthesis. Furthermore, biochemical changes were reported in concentrations of sugars, proline and total protein. Detailed knowledge about the growth behaviour, ecophysiological and biochemical responses and the subspecific variation of eucalypt in water stress conditions could contribute to the selection of promising species and the success of reforestation programs. However, after the selection of resistant species, we can plant them in arid regions on marginal soils using treated wastewater for irrigation (De Almeida et al., 2017) because wastewater irrigation can improve the growth and productivity of *Eucalyptus* plantation wood (Minhas et al., 2015).

Thus, silvicultural practices tailored to improve tree behaviour under stress conditions should be considered. Finally, the use of *Eucalyptus* for reforestation under reduced water conditions, essentially with climate change impacts, would pose problems related mainly to its water consumption, biodiversity reduction and environment degradation (Zhang, 2012). With its advantages and disadvantages, eucalypt remains a world forest heritage of great interest.

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