



# Maternal environment regulates morphological and physiological traits in *Eucalyptus grandis*

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## ABSTRACT

The phenotype of a plant can be shaped by the biotic and abiotic conditions to which their parents are subjected. This phenotypic plasticity known as maternal environmental effect occurs regardless of the changes in the DNA sequences. Whereas the effect of the maternal environment on plant phenotype has been studied, its specific influence on plant physiology is less clear. This study considered the influence of the maternal environment on the regulation of plant morphology and physiology in progeny of *Eucalyptus grandis*. Plants were grown from seeds collected from two *E. grandis* clonal seed orchards that differed in environmental conditions (e.g. precipitation). Plant relative growth rate (RGR), leaf gas exchange and water use efficiency (WUE) were measured in the seedlings. RGR was 10% higher in the offspring from the maternal environment receiving higher precipitation levels. Leaf gas exchange, specifically leaves intercellular CO<sub>2</sub>, and intrinsic WUE were also influenced by maternal environments. Intrinsic WUE was significantly lower in the orchard that received lower precipitation levels. The results demonstrate that the maternal environment can regulate the physiology of *E. grandis* in the subsequent generation. These analyses are useful to optimise tree improvement in a changing environment. Moreover, in a scenario of climate change, maternal environmental effects may be a crucial mechanism for certain species to get acclimated to sudden changes in environmental conditions.

## 1. Introduction

The plant phenotype is mainly determined by its genetic inheritance and environment. However, the phenotype of a plant is also shaped by the biotic and abiotic conditions to which its parents are subjected (Roach and Wulff, 1987; Jablonka and Raz, 2009; Herman and Sultan, 2011; Holeski et al., 2012). These influences on the phenotypic expression of the seedlings are known as maternal environmental effects, and they are not caused by DNA mutations (Roach and Wulff, 1987; Rossiter, 1996; Rix et al., 2012). Rather, the maternal effects are induced by seed provisioning and by epigenetic mechanisms (Herman and Sultan, 2011; Rix et al., 2012). Since the description of maternal environmental effects three decades ago, a number of studies have demonstrated its influence on morphological changes and resistance responses of the plants in the subsequent generation (e.g. Roach and Wulff, 1987; Violle et al., 2009; Elwell et al., 2011; Luna et al., 2012; Rasmann et al., 2012; Vivas et al., 2013, 2017). However, little is known regarding the physiological adaptation underlying these

developmental and morphological changes.

Understanding maternal environmental effects is important from the perspective of predicting responses of plants to changing environments, as well as to harness their full productive potential through breeding programs. Failure to consider these effects could lead to misinterpretations of genetic studies in breeding programs. This is especially true in the light of climatic changes and the pressures these will place on natural distribution of plant communities and production areas alike (Allen et al., 2010; Koch et al., 1995). A relevant factor to consider in this regard, and that is expected to be influenced by maternal environments, is plant morphological and physiological responses to low water availability (Anderegg, 2015). Water availability is a key element shaping the distribution of current and future vegetation, as drought intensity and duration is expected to increase in many parts of the world (IPCC, 2014).

Water loss in plants is an inevitable consequence of photosynthesis, where CO<sub>2</sub> diffuses into the leaf and flux out water (i.e. leaf gas exchange). Minimizing water loss while maximizing CO<sub>2</sub> uptake (i.e.

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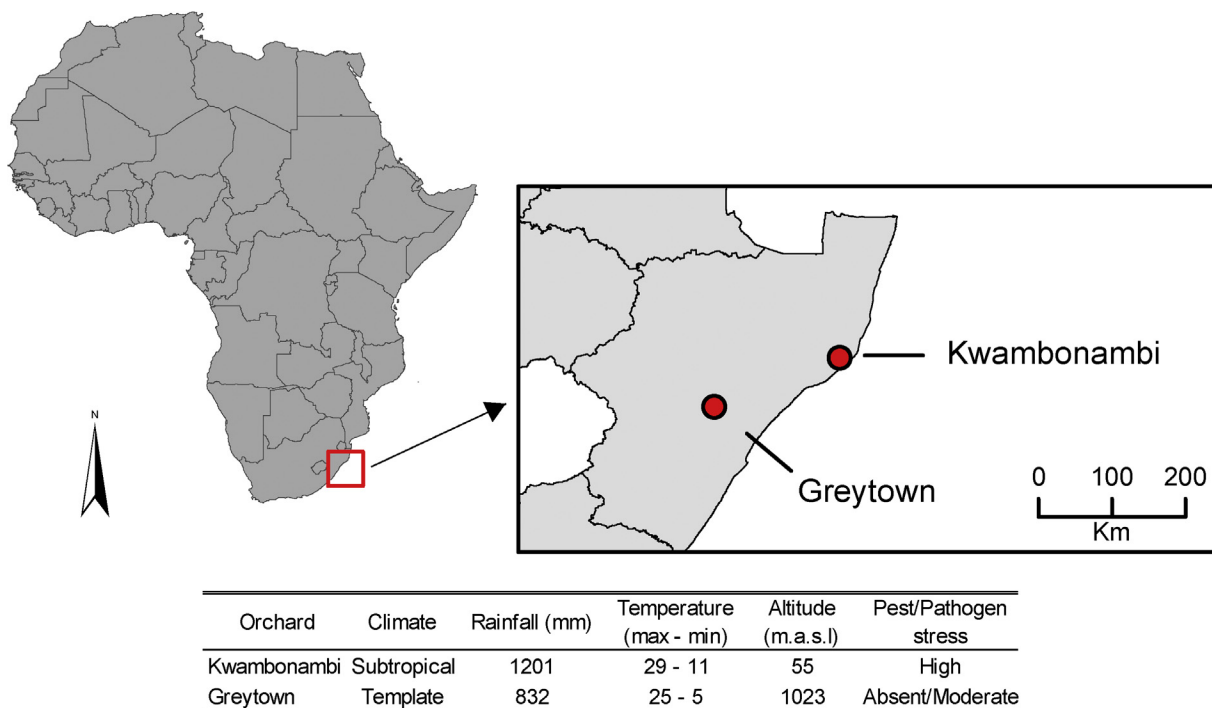


Fig. 1. Map showing the locations and the characteristics of the two *Eucalyptus grandis* orchards in South Africa. Data provided by the forest company.

increasing water use efficiency (WUE)) is a key physiological mechanism of plants adapted to low water availability (Gindaba et al., 2005; Choat et al., 2006). Plants achieve this by regulating the partial closure of the stomata (i.e. stomatal conductance ( $g_s$ )) to adjust leaf transpiration (Flexas and Medrano, 2002). The analysis of WUE evaluates plant biomass production as a function of water consumption (Monclus et al., 2006; Chamillard et al., 2011; Battie-Laclau et al., 2016). Water use efficiency can be estimated at multiple spatial and temporal scales: from short (the ration between net photosynthesis and stomatal conductance; intrinsic WUE (Medrano et al., 2009)) to long (based on the composition in stable carbon isotopes ( $\delta^{13}C$ ) (Farquhar and Richards, 1984)). This trait (WUE) typically has high within-species genetic variability and has therefore received substantial attention in tree breeding programs (e.g. Monclus et al., 2006; Aranda et al., 2012). However, the knowledge of how the maternal environment affects WUE in plant progeny, as well as related physiological traits such as stomatal control or net photosynthesis, remains limited (Latzel and Klimešová, 2009; Scotti et al., 2010).

Maternal effects on morphological traits of plants may result in changes in the relative growth rate (RGR) of the progeny, defined as the increase of dry mass production per unit of dry mass and time (Poorter and Werf, 1998). RGR can be divided into three components. Two of these are morphological components that describe how the plant allocates biomass to leaves (leaf mass ratio (LMR)), and how efficient the plant is in the construction of the leaf area (specific leaf area (SLA)). A third physiological component describes how plant biomass changes per unit leaf area and time (net assimilation rate) (Evans, 1972). Many studies have considered the relationship between RGR and its components in multiple plant species (e.g. Poorter and Remkes, 1990; Poorter and Werf, 1998; Loveys et al., 2002). However, the differences in RGR within a species are not well understood, and maternal environmental effects on RGR are less well-known. To understand the possible influence of maternal environments on plant morphology as well as its potential applications in plant breeding programs, it is necessary to consider the RGR within species.

*Eucalyptus* are widely used globally for the establishment of rapidly growing plantations and these are exposed to a wide variety of environmental conditions (Wingfield et al., 2015). Previous studies have

reported maternal effects in *Eucalyptus* species. For example, maternal environment influenced seed mass and seed germination of *Eucalyptus globulus* in two different studies (Lopez et al., 2003; Rix et al., 2012). Moreover, there is evidence in *Eucalyptus grandis* that the maternal environment influences progeny performance, resistance to pest and pathogens as well as the structure of fungal communities in the foliage of the subsequent generation (Vivas et al., 2017). A relevant case study would thus be to explore the impact of maternal effects on morphological and physiological traits related to growth potential and leaf gas exchange of offspring plants.

In this study, we measured morphological and physiological traits of *E. grandis* seedlings originating from two different maternal environments when grown in a common garden. Given the cosmopolitan distribution of *Eucalyptus* species, their morphological and physiological responses to a wide variety of environmental conditions are well known (e.g. Correia et al., 2014, 2018; Navarrete-Campos et al., 2013). However, little is known about the underlying role of maternal effects on *Eucalyptus* morphology and physiology. We hypothesized that trees having the same genotype would acquire different morpho-physiological strategies according to the availability of resources (e.g. water) of their maternal environments. In particular, we considered whether (1) growth rates of *E. grandis* trees depend on the maternal environment. And, if there are differences due to morphological (SLA and LMR) attributes. Furthermore, we considered whether (2) the physiology of *E. grandis* trees, specifically leaf gas exchange and WUE, reflect the conditions of the maternal environment.

## 2. Materials and methods

### 2.1. Plant material

Seed material was collected from *E. grandis* trees open-pollinated and located in two clonal seed orchards in South Africa. The two orchards, Greytown (29°11'56.73"S, 30°39'34.46"E) and Kwambonambi (28°35'41.45"S, 32°11'38.98"E), included the same genetic material with identical spatial design, but different abiotic and biotic conditions (Fig. 1). The Kwambonambi orchard represents more favourable abiotic conditions (e.g. higher rainfall and temperatures) for

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