

Title	Environmental effects on growth phenology of co-occurring <i>Eucalyptus</i> species
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## **Abstract**

Growth is one of the most important phenological cycles in a plant's life. Higher growth rates increase the competitive ability, survival and recruitment and can provide a measure of a plant's adaptive capacity to climate variability and change. This study identified the growth relationship of six *Eucalyptus* species to variations in temperature, soil moisture availability, photoperiod length, and air humidity over 12 months. The six species represent two naturally co-occurring groups of three species each representing warm-dry and the cool-moist sclerophyll forests respectively. Warm-dry eucalypts were found to be more tolerant of higher temperatures and lower air humidity than the cool-moist eucalypts. Within groups, species-specific responses were detected with *E. microcarpa* having the widest phenological niche of the warm-dry species, exhibiting greater resistance to high temperature and lower air humidity. Temperature dependent photoperiodic responses were exhibited by all the species except *E. tricarpa* and *E. sieberi*, which were able to maintain growth as photoperiod shortened but temperature requirements were fulfilled. *Eucalyptus obliqua* exhibited a flexible growth rate and tolerance to moisture limitation which enables it to maintain its growth rate as water availability changes. The wider temperature niche exhibited by *E. sieberi* compared to *E. obliqua* and *E. radiata* may improve its competitive ability over these species where winters are warm and moisture does not limit growth. With climate change expected to result in warmer and drier conditions in south-east Australia, the findings of this study suggest all cool-moist species will likely suffer negative effects on growth while the warm-dry species may still maintain current growth rates. Our findings highlight that climate driven shifts in growth phenology will likely occur as climate changes and this may facilitate changes in tree communities by altering inter-specific competition.

**Keywords:** *Eucalyptus*, phenology, climate, soil moisture, photoperiod

## 1    **Introduction**

2    The impact of recent climate change on plant phenology has increasingly been documented  
3    over the last 15 years (Hughes 2000; Root and Hughes 2004; Linares et al. 2012). Changes in  
4    phenology can have direct and/or indirect impacts on plant diversity (Post and Stenseth 1999;  
5    Post et al. 1999; McCarty 2001) and plant distribution (Chuine and Beaubien 2001). Due to  
6    the sensitivity of plant phenology to climate variability and the influential nature that it can  
7    have on species distributions, understanding the response of species phenology to climate  
8    variability and change is important (Hobbie and Chapin 1998; Menzel 2002). Of particular  
9    importance for predicting a species response to climate change, is an understanding how  
10   growth phenology interacts with climate (Linares et al. 2012).

11   Phenological events of plants are typically controlled by environmental factors (Hopp 1974)  
12   and are influenced by each other (Primack 1987). Environmental factors that mainly affect  
13   phenological events are temperature, moisture availability, soil and light (Scurfield 1961;  
14   Ashton 1975ab; Primack 1987; Kozlowski and Pallardy 1997; Keatley and Hudson 2000;  
15   Badeck et al. 2004). Recruitment and plant growth are highly dependent on moisture  
16   availability and temperature (Kozlowski and Pallardy 1997; Cochrane et al. 2011) the latter  
17   playing a significant role in vegetative and reproductive phenology (Valdez-Hernández et al.  
18   2010). Photoperiod length, defined as the duration of day light or sun hours that plants  
19   receive in a day (Garner and Allard 1920) is also important for growth (Vaartaja 1963),  
20   typically following temperature, in the phenological cycle (Saxe et al. 2001; Badeck et al.  
21   2004). The effect of photoperiod length (i.e. longer or shorter day) on plant phenology in  
22   *Eucalyptus* species, however, has been found to be a limited (Ashton 1956; Cremer 1960;  
23   Vaartaja 1963). Vaartaja (1963) suggested that most tree species from warmer climates are  
24   not responsive to changes in photoperiod length compared to species from cold climate  
25   regions. South-east Australia occurs at the transition between warm and cold climate species  
26   as defined by Vaartaja (1963). Air humidity is another factor that has been found to affect  
27   plant growth (Marsden et al. 1996; Nataraja et al. 1998).

28   The seedling stage of a plant is the critical phase as seedlings exhibit a high sensitivity and  
29   low tolerance to environmental conditions (Rehfeldt et al. 1999; Green 2005; Chhin and  
30   Wang 2008; Morin et al. 2010). As seedlings are limited in their access to soil nutrients and  
31   moisture, higher growth rates can facilitate access to these resources and in turn increasing

32 their competitive ability and survival (Wright et al. 2004; Vitasse et al. 2009). Growth rate is  
33 therefore regarded as an important characteristic that measures a plant's capacity to adapt to  
34 climate variability and change (Green 2005), and has a strong impact on survival and long-  
35 term persistence (Vitasse et al. 2009). Measures such as height, diameter, and biomass  
36 growth along with growth cessation are typically interconnected with each other and as such  
37 a detailed understanding of a species phenological response to environmental heterogeneity  
38 may provide insights into a species' adaptive capacity to predicted climate change (Green  
39 2005, 2007; Cochrane et al. 2011). In addition, understanding the phenological responses of  
40 co-occurring and adjacent species may shed light on the impacts of climate change on the  
41 competitive ability of these species as a mechanism for instigating changes in community  
42 composition (Menzel and Sparks 2006).

43 Although the effect of climate change on plant flowering phenology is well documented in  
44 the northern hemisphere, in Australia, documenting the impacts of climate change on species  
45 phenology is limited due to the lack of long-term datasets (Chambers 2006; IPCC 2007).  
46 Predicted climate change for south-east Australia by the 2080s is for temperatures to increase  
47 by 2–4°C and precipitation to decline by 5–10% leading to an increase in moisture deficits  
48 along with an increase in drought events (CSIRO and the Bureau of Meteorology 2007).  
49 Significant changes in plant communities are expected for Australia; and in particular for the  
50 genus *Eucalyptus*, with many species occurring within a narrow temperature and moisture  
51 range (Hughes et al. 1996; Hughes 2003).

52 For the eucalypt species of south-east Australia, there have been few studies on growth-  
53 climate relationships with the majority of research focussed on flowering phenology (Keatley  
54 et al. 2002). A few studies have identified phenological observations around growth initiation  
55 and cessation (Ashton 1975a; Cremer 1975), however, comprehensive studies on the  
56 relationship between climate and growth phenology are non-existent. Ashton (1975a) found  
57 that the active height growth period for *E. regnans* is from spring to mid-summer with growth  
58 rate strongly correlated to mean maximum temperatures. Cremer (1975) also found that  
59 vegetative shoot growth and development of young *E. regnans* seedlings was directly  
60 controlled by air temperature. A population study on seedlings of *E. obliqua* by Wilkinson  
61 (2007), however, found difference in growth rates between gully, ridge and mid slope sites  
62 with lower growth exhibited on warmer and drier ridge sites, which suggests that both  
63 temperature and moisture are influencing growth. The limited studies conducted to date on

64 eucalypts in south-east Australia therefore suggest that temperature and in some cases  
65 moisture are the important drivers of seedling growth and survival.

66 Understanding the growth-climate relationship of species, particularly at the seedling stage, is  
67 an important component for inferring future species distributions and community  
68 compositions (Chhin and Wang 2008). A species' capacity to persist in a given location may  
69 be governed by its phenological plasticity as inter and intra population variation has been  
70 found to affect the ability of species to cope with variable and contrasting precipitation  
71 regimes and growing season durations (Linares et al. 2012). This study explores the effect of  
72 environmental variability on seedling growth phenology of co-occurring eucalypts from two  
73 distinct climatic regions of south-east Australia. The study focuses on examining the growth  
74 traits of plants in response to variation in temperature, photoperiod, soil moisture availability,  
75 and air humidity. The study ultimately seeks to identify the temperature range/niche in  
76 interaction with soil moisture availability at which the eucalypt species will grow, and to  
77 determine the degree of plasticity for each species.

## 78 **Materials and methods**

### 79 **Species selection**

80 Six *Eucalyptus* species were selected from both dry and wet sclerophyll forest types located  
81 in the temperate region of Victoria, south-east Australia. The co-occurring species *E.*  
82 *microcarpa* (grey box), *E. polyanthemos* (red box) and *E. tricarpa* (red ironbark) represent  
83 the dry open "box-ironbark" sclerophyll forest of the warm temperate region of Victoria  
84 (Newman 1961; Orscheg et al. 2011). Annual rainfall in this region ranges from 400 to 970  
85 mm and the maximum/minimum temperature ranges from 23 to 33°C / -1 to 4°C respectively  
86 (Boland et al. 2006). *Eucalyptus obliqua* (messmate stringybark), *E. radiata* (narrow-leaved  
87 peppermint) and *E. sieberi* (silvertop ash) represent the wet sclerophyll forest. These forests  
88 are classified as "ash forests" and occur within the wet and cool temperate regions of  
89 Australia with an annual rainfall of 500 to 2400 mm and maximum/minimum temperature  
90 ranges from 19 to 29°C / -2 to 8°C, respectively (Boland et al. 2006). For the purpose of this  
91 study the "ash forest" species will be referred as cool-moist species and the "box-ironbark  
92 forest" species will be referred as warm-dry species (Appendix1).

93 Seeds from four provenances (Prov 1–4) of each species were selected to represent different  
94 geographic locations and elevations. One provenance from *E. microcarpa*, *E. tricarpa*, and *E.*

95 *radiata* failed to germinate and were not used in the trials. Species and provenance details,  
96 and the number of seedlings used in the experiment are further summarised in Appendix 1  
97 and abbreviations, units and calculations are provided in Table 1.

## 98 Seedling propagation

99 Seeds were germinated on plastic trays with a mixture of pine bark, mined sand, sieved coir  
100 peat, dolomite and Saturaid 1500 g m<sup>-3</sup> (wetting agent). Trays were placed in a glasshouse  
101 under ambient conditions and were watered everyday with an automatic sprinkler system.

102 Seedlings were transferred to 1 L seedling pots with general potting mix with pinebark and  
103 coarse mined sand and slow release fertilizers Debco green jacket (N: P: K 16.5:4.1:9.6) 4000  
104 g m<sup>-3</sup>, Saturaid 1500 g m<sup>-3</sup> and dolomite upon reaching the three-leaf stage (in January, 2011).  
105 Seedling pots were placed under 50% mesh shade cloth to protect them from direct sun and  
106 heat, and watered daily. After 6 months (July 2011) seedlings were transferred to 25 L pots  
107 (one seedling per pot) with the same general potting mix and fertilizers and kept outside at  
108 ambient conditions with daily irrigation for another two months until the commencement of  
109 the experiment in September, 2011.

## 110 **Experimental design**

111 The experiment conformed to a randomised factorial design with four climatic conditions that  
112 incorporated three climate mediated and one ambient climate glasshouses (G1–G4) with two  
113 soil moisture regimes (M). Three to seven replicates per provenance for each species  
114 (according to seedling availability) for a total of 948 seedlings were used in the experiment  
115 (Appendix 1). The experiment was carried out for one year (September 1, 2011 – August 31,  
116 2012) at the Burnley campus of the University of Melbourne, Australia.

117 Glasshouse treatments (G1–G4): To identify the growth response under different  
118 environmental conditions, climatic conditions in three glasshouses were mediated and in one  
119 glasshouse unmediated to achieve variability in  $T_{\max}$ ,  $T_{\min}$  and  $H_{\text{mean}}$ . To account for the  
120 fluctuation in climate conditions that resulted from the mediation of climate versus the use of  
121 a controlled climate treatment (which was not possible given the size of the experiment and  
122 lack of infrastructure), HOBO weather stations were installed in each glasshouse to record  
123 hourly temperature, and air humidity from the beginning of the experiment (Table 1,  
124 Appendix 2). Photoperiod length (daily sunlight hours) was computed from sunset and

sunrise time for Melbourne (Table 1). Soil moisture availability (M) was characterised by well-watered (WW) and water-stressed (WS) treatments to represent conditions of perennial moist availability and chronic soil moisture deficits (Table 1).

#### Plant measurements

Height and diameter of the seedlings were measured to calculate above ground relative growth rate in height ( $RGR_H$ , mm days<sup>-1</sup>) and diameter ( $RGR_D$ , mm days<sup>-1</sup>), and height growth cessation (Table 1) for the first time 10 days after the beginning of the experiment and every 20 days thereafter following Green (2005; 2007).

#### Data analysis

The effects of temperature, air humidity, photoperiod length, soil moisture availability and species and provenance (ranging from 2–4 depending on species, see Appendix 1) on height and diameter growth within the glasshouse treatments (G1–G4) were tested for within and between the two groups of species using a Mixed Linear Model (MLM). Strong correlations were found between mean maximum temperature ( $T_{max}$ ), minimum temperature ( $T_{min}$ ) and Photoperiod ( $Ph_{mean}$ ) ( $r = 0.71$  to  $0.85$ ,  $P \leq 0.001$ ) and between mean temperature ( $T_{mean}$ ) and  $T_{max}$ ,  $T_{min}$  and  $Ph_{mean}$  ( $r = 0.85$  to  $0.95$ ,  $P \leq 0.001$ ). Due to these high correlations, three individual models were developed separately for  $T_{max}$ ,  $T_{min}$ , and  $Ph_{mean}$  in combination with species provenance (Prov), species (Sp) and soil moisture regime (M) as factors, with mean air humidity ( $H_{mean}$ ) as covariate and measurement time as a random effect. Bonferroni multiple comparison tests were then used to determine pairwise differences between the provenances within the species.

Height growth cessation functions were analysed following Kaplan and Meier (1958) to find the proportion of species that exhibit height growth cessation in respective treatments over time. Cox's proportional hazard regression non-parametric test (Cox 1976) was used to see which climate factor was the most influential on the growth cessation for each species. To identify the most influential factor for growth cessation, similar models were developed as used in the MLM analysis taking  $Ph_{mean}$ ,  $T_{max}$  and  $T_{min}$  in combination with M, Prov and  $H_{mean}$ . Each of these analyses were performed with SPSS Ver. 20 (2011).

A Generalised Additive Model (GAM, Hastie and Tibshirani 1990) was used to model both  $RGR_H$  and  $RGR_D$  of each species as a function of the  $T_{mean}$  under the two moisture regimes

(WW, WS; within G1–G4).  $T_{\text{mean}}$  was used as it had highest correlation with  $T_{\text{max}}$  and  $T_{\text{min}}$  ( $r = 0.85$  to  $0.95$ ,  $P \leq 0.001$ ).  $\text{RGR}_H$  and  $\text{RGR}_D$  were used as response variables and  $T_{\text{mean}}$  as predictor for the modeling with a quasi-poisson distribution using the GAM mgcv package (Wood 2006) in R (R Development Core team 2008).

## Results

### Climatic conditions

The treatment conditions provided suitable amounts of environmental variability to observe changes in growth. Generally, variations in climate were significantly different during summer (Dec–Feb). Specifically,  $T_{\text{max}}$  within G2 was significantly greater ( $P \leq 0.001$ ) than G1 during summer. During summer,  $T_{\text{min}}$  within G2 was significantly lower ( $P \leq 0.001$ ) than that in G4.  $H_{\text{mean}}$  in G2 was significantly greater ( $P \leq 0.001$ ) than in G3 during spring and summer. Highest mean  $T_{\text{max}}$  recorded was  $34.7^\circ\text{C}$  with highest maximum temperature of  $52.0^\circ\text{C}$  recorded in summer in G2 (Appendix 2).

### Height and diameter growth

All species: Moisture generally had a significant positive effect on height and diameter growth, exceptions to this pattern were exhibited by *E. microcarpa* (for  $\text{Ph}_{\text{mean}}$ ), *E. polyanthemos* ( $T_{\text{min}}$ ), *E. obliqua* ( $T_{\text{max}}$ ) and *E. radiata* ( $T_{\text{max}}$ ) (Table 2). Moisture also typically had a greater effect on diameter and height growth for warm-dry species under  $T_{\text{min}}$  and  $T_{\text{max}}$  than cool-moist species (Table 2). Increasing  $\text{Ph}_{\text{mean}}$  typically affected diameter more than height growth and for diameter, a significant positive interaction with M was found for all species except *E. microcarpa* indicating a greater sensitivity to soil moisture under longer  $\text{Ph}_{\text{mean}}$  (Table 2). There was a significant decline in height and diameter growth with increasing  $T_{\text{max}}$  for all species except *E. microcarpa* and *E. polyanthemos* and also a significant decline in diameter growth with increasing  $T_{\text{min}}$  for all species except *E. sieberi* (Table 2).

### Between Species Groups

Cool-moist species exhibited greater height and diameter growth ( $P \leq 0.001$ ) than warm-dry species (Fig. 1). Growth response varied between the two groups of species with height growth of warm-dry species more tolerant to higher  $T_{\text{max}}$ ,  $T_{\text{min}}$  and lower  $H_{\text{mean}}$  conditions



while, diameter growth was found sensitive to decreasing  $Ph_{mean}$  and  $H_{mean}$  and increasing  $T_{max}$  and  $T_{min}$  conditions. Increasing  $T_{min}$  had more of a negative effect on cool-moist species than warm-dry species (Table 3).

#### Within Species Groups

Warm-dry species: Within this group increasing  $Ph_{mean}$ ,  $T_{max}$ ,  $T_{min}$  affected the diameter growth with significant differences between species detected. These differences were not detected for height growth. The effect of  $H_{mean}$  and its interaction with  $Ph_{mean}$ ,  $T_{max}$ ,  $T_{min}$  suggests that diameter growth is positively affected by increasing  $H_{mean}$  but height growth is not (Table 3).

Between the species: In contrast to *E. microcarpa* and *E. polyanthemos*, height and diameter growth of *E. tricarpa* decreased with increasing  $T_{max}$  similar to the response of cool-moist species (Table 2). Height and diameter growth of *E. tricarpa* increased with increasing  $H_{mean}$  under  $T_{max}$ , similar to the response of cool-moist species. Diameter, but not height growth decreased with increasing  $T_{min}$  for all three species.  $H_{mean}$  did not affect the height or diameter growth of *E. microcarpa* under the  $T_{max}$  model, and neither the height growth under the  $T_{min}$  model (Table 2). The non-significant or positive response to the interaction between M and either  $T_{max}$  or  $T_{min}$  suggest *E. microcarpa* and *E. polyanthemos* have the capacity to maintain growth under moisture limited conditions, while there was a significant decrease in both height and diameter growth of *E. tricarpa* for both of these interactions (Table 2). An increase in  $Ph_{mean}$  facilitated height growth in *E. microcarpa* and *E. polyanthemos* and also diameter growth for all three warm-dry species (Table 2). Significant positive interactions between  $H_{mean}$  and  $Ph_{mean}$  and negative interactions between  $H_{mean}$  and  $T_{min}$ , suggest that diameter growth is sensitive to lower  $Ph_{mean}$  and higher  $T_{min}$  in combination with lower  $H_{mean}$  conditions (Table 2). Moisture availability did not affect the growth of *E. microcarpa* under increasing  $Ph_{mean}$ , while there was a significant increase in height and diameter growth of both *E. polyanthemos* and *E. tricarpa* with increasing soil moisture availability.

Cool-moist species: Relative to warm-dry species, increasing  $T_{max}$  and  $T_{min}$  had a negative effect on height growth indicating that growth of cool-moist species is sensitive to high temperatures. Significant effects of  $H_{mean}$  and its interactions suggest that the cool-moist species are reliant on high  $H_{mean}$  for height and diameter growth. Height growth differed

significantly among all cool-moist species, while the diameter growth of *E. radiata* was significantly different to *E. obliqua* and *E. sieberi* (Table 3).

Height and diameter growth decreased with increasing  $T_{\max}$  for all cool-moist species and also with increasing  $T_{\min}$  for *E. obliqua*. Height and diameter growth of all cool-moist species increased with  $H_{\text{mean}}$  under  $T_{\max}$ , and the significant negative interaction of  $H_{\text{mean}} \times T_{\max}$  suggest these species require higher  $H_{\text{mean}}$  to maximise growth under higher  $T_{\max}$ .  $H_{\text{mean}}$  effects on growth under  $T_{\min}$  were limited to height growth in *E. sieberi* and diameter growth of *E. obliqua* and *E. radiata*. The significant negative interaction of  $H_{\text{mean}} \times T_{\min}$  for *E. obliqua* and *E. radiata* suggests diameter growth in these species is sensitive to lower  $H_{\text{mean}}$  under higher  $T_{\min}$  conditions. The non significant effect of M under  $T_{\max}$  indicates *E. obliqua* and *E. radiata* have a higher capacity to withstand moisture limitations than *E. sieberi*. Both height and diameter growth of *E. obliqua* and *E. radiata* increased with  $Ph_{\text{mean}}$ . For all three species there was a significant increase in diameter growth with  $H_{\text{mean}}$  and M under  $Ph_{\text{mean}}$  and significant interactions for  $H_{\text{mean}} \times Ph_{\text{mean}}$  and  $M \times Ph_{\text{mean}}$  indicating that higher  $Ph_{\text{mean}}$ ,  $H_{\text{mean}}$  and M were required to maximise diameter growth.

Provenance effects: Provenance had a significant effect on height and diameter growth of *E. microcarpa* and *E. polyanthemos* across all three models and for *E. tricarpa* under  $T_{\max}$  (Table 2). The interaction of  $\text{Prov} \times M$  had a significant effect on both height and diameter growth of all warm-dry species across all three models, with the same trend for  $\text{Prov} \times H_{\text{mean}}$  with the exception of *E. tricarpa* under  $Ph_{\text{mean}}$  and  $T_{\min}$  (Table 2). Provenance had a more limited effect on the growth of cool-moist species and across all three models included a significant  $\text{Prov} \times M$  effect on growth of *E. obliqua* (height), *E. radiata* (height and diameter) and *E. sieberi* (diameter) and a significant  $\text{Prov} \times H_{\text{mean}}$  effect on diameter growth of *E. sieberi* (Table 2).

Clinal variation for growth was found between the species provenances with provenances exhibiting growth changes across their distributional ranges that correlated with elevation. Strong clinal trends were found for *E. microcarpa* and *E. obliqua* (Appendix 1) with lower elevation provenances exhibiting greater height and diameter growth than higher elevation provenances. However, for *E. polyanthemos*, *E. tricarpa* and *E. radiata*, higher elevation provenances exhibited greater height and diameter growth than lower elevation provenances. These latter results suggest that a conservative growth strategy has been adopted by these

provenances from warmer and drier climates, which may be an adaption to help reduce drought induced mortality.

#### Relative Growth Rate

A significant relationship was found between  $RGR_H$  and  $RGR_D$  with  $T_{mean}$ . Mean threshold temperatures were also detected for all the species (Fig. 1). The cool-moist species had a greater  $RGR_H$  than warm-dry species under the well-watered regime.  $RGR_H$  decreased under the water-stressed regime and the response was more pronounced for the cool-moist species (Fig. 1).

Under the well-watered regime, the  $RGR_H$  optimal  $T_{mean}$  was 21°C for all species. However, under the water-stressed regime, the  $RGR_H$  optimal  $T_{mean}$  for *E. microcarpa* and *E. polyanthemos* (21°C) was higher than the four other species (20°C). For all species, optimum  $T_{mean}$  for  $RGR_D$  was lower than for  $RGR_H$ . Under the well-watered regime, optimal  $T_{mean}$  for  $RGR_D$  was 18–19°C. However, the  $RGR_D$  optima decreased under the water-stressed regime for all the species (16–17°C). Optimum  $RGR_H$  for all species corresponded with the  $T_{mean}$  recorded for late spring to midsummer and end of summer to mid autumn (Appendix 2). A lower optimum for  $RGR_D$  under the water-stressed regime corresponded with the  $T_{mean}$  of early spring and early winter (Appendix 2).

#### Growth cessation (height)

A consistent and significant effects of  $T_{max}$ ,  $T_{min}$ ,  $Ph_{mean}$  and  $H_{mean}$  (under  $T_{max}$  model) across all species clearly indicated that hot and dry days resulted in height cessation (Table 4). Height cessation was greater in cool-moist than warm-dry species with *E. microcarpa* exhibiting the lowest response (60%) followed by *E. polyanthemos* (65%) which indicates that these species have a high degree of phenotypic plasticity. For the other species, the response rate was greater than 70% with highest cessation for *E. obliqua* (83%). Overall, warm-dry species exhibited a greater capacity to withstand higher  $T_{mean}$  conditions than cool-moist species (Fig. 1). Significant provenance and moisture availability differences were limited to *E. obliqua* (Table 4).

Temperature thresholds for the cessation of height growth were found for both high and low mean temperatures. *Eucalyptus microcarpa* was found to display the greatest tolerance to high temperatures with growth cessation occurring at 47°C, while for *E. polyanthemos* and *E.*

*tricarpa* the height growth cessation temperatures were 43°C and 45°C, respectively under the water-stressed treatment (Fig. 1e). Within the cool-moist species, growth cessation temperature was 34°C for all for the species under the watered-stressed treatment (Fig. 1f). The water-stressed conditions truly distinguished the temperature thresholds that exist between the two species-groups and highlight the competitive advantage the warm-dry species have in warmer and drier climates.

The growth initiation threshold for *E. microcarpa* and *E. polyanthemos* was 9°C while for *E. tricarpa* the lower temperature threshold for growth initiation was 8°C (Fig. 1a). For the cool-moist species, *E. radiata* initiated growth from 5°C and the other two species from 7°C (Fig. 1b).

## **Discussion**

### **Growth and Phylogenetic response**

Marked differences in growth responses were found between the two groups of forest species, which may be explained by their phylogenetic difference. The warm-dry species are in the *Symphyomyrtus* subgenera while the cool-moist species are in the *Monocalyptus*. The two subgenera tend to exploit the environment in different ways (Davidson and Reid 1980) hence; variations in growth rate are likely to be found in response to environmental variation (Noble 1989). *Monocalyptus* have higher growth rates on mesic sites while *Symphyomyrtus* species are better adapted to dry conditions (Davidson and Reid 1980; Florence 1996) and a similar response was found in our study as cool-moist species had greater height and diameter growth and warm-dry species displayed lower growth but greater tolerance to high temperatures and lower air humidity. Trait selection may favour one strategy over the other depending upon the environmental stressors (Loehle 1998, Green 2005) and in our case, *Symphyomyrtus* species seemingly favour traits that enhance drought tolerance.

### **Environmental effects and growth traits – Height and diameter**

Moisture regime was found to be one of the most influential factors that controlled height and diameter growth with greater growth occurring when moisture was not limiting. Our finding is supported by the studies highlighting the significance of moisture for seedling growth (Ladiges and Ashton 1974; Cannell et al. 1978; Myers and Landsberg 1989; Battaglia and Reid 1993; Tomlinson and Anderson 1998; Pinto et al. 2011). *Eucalyptus microcarpa*, *E.*

*polyanthemos*, *E. radiata* and *E. obliqua*, however, exhibited phenotypic plasticity to water limitation that may help these species tolerate drier climatic/ edaphic conditions. Our findings are supported by Myers and Neales (1984) who found that *E. microcarpa* and *E. polyanthemos* (Merchant et al. 2006) are adapted to xeric conditions, have a wide temperature niche and are more drought tolerant than *E. tricarpa* (Boland et al. 2006). The plastic response exhibited by *E. microcarpa* to variability in soil moisture availability is likely due to the species drought response traits particularly with low transpiration rates, high sap wood density, and low water potential of -5.0 MPa for turgor loss (Yunusa et al. 2010). *Eucalyptus radiata* was found to be more drought tolerant than *E. sieberi*, which suggests it will grow better on drier sites than *E. sieberi*, which is supported by Ellis (1971) and Florence (1996). Bachelard (1986) showed that compared to other *Eucalyptus* species like *E. maculata* and *E. pilularis*, *E. sieberi* has reduced capacity to withstand water-stressed conditions with water potentials of -1.5 MPa decreasing the osmotic potential for this species. In contrast, *E. obliqua* can maintain gas exchange down to water potentials of -2.48 MPa (Sinclair 1980), which would infer a greater ability for *E. obliqua* to maintain growth as water becomes limiting compared to *E. sieberi* (Bachelard 1986). Our findings suggest that the ecophysiological traits of the studied species have a large influence on the growth phenology as water becomes increasingly limited.

In our study,  $T_{max}$  in combination with moisture and air humidity was the best predictor for height growth for cool-moist species, which suggests that height growth is more of a function of temperature (Korner 2006) and response to temperature and moisture is typically reflected in height growth versus other growth traits (Kozlowski and Pallardy 1997). Sensitivity of cool-moist species to high temperature and low air humidity may increase transpiration leading to growth reduction (Leonardi 2000; Mortensen 2000). High temperature and lower air humidity leading to high vapour pressure deficits (VPD) in summer reduces growth which suggests that growth is sensitive to high VPD (Leonardi 2000) and for this study, the cool-moist species seemingly displayed a growth phenology that is sensitive to VPD. Growth was not sensitive to temperature for the drought tolerant species *E. microcarpa* and *E. polyanthemos* but the growth of *E. tricarpa* was temperature sensitive suggesting that its growth phenology is intermediate between other warm-dry and the cool-moist species.

Temperature dependence on growth was displayed by most of the species; however, the response of *E. sieberi* was limited to  $T_{max}$  suggesting that growth occurs when temperature

thresholds are met irrelevant of photoperiod length. *Eucalyptus microcarpa*, *E. polyanthemos*, *E. obliqua* and *E. radiata* displayed growth responses that were dependent upon photoperiod length. The largest photoperiodic responses were displayed by *E. obliqua* and *E. radiata* suggesting that these species require a minimum base temperature in interaction with a critical day length for growth to occur. The photoperiodic response of *E. obliqua* and *E. radiata* indicates that the species displayed highly temperature dependent photoperiodic response for their growth phenology (Vaartja 1959). Interestingly, *E. tricarpa* demonstrated such a response only for diameter growth. Photoperiodic responses varied according to species despite their coexistence. A similar response was found between coexisting species *E. salmonopholia* and *E. torquata* with the former responding positively to photoperiod and the latter not showing any response (Vaartaja 1963). The varying expression of temperature dependence for growth by some of the studied species may help them adapt to new environments (Vaartaja 1963) and can be regarded as a positive plastic trait (Green 2005).

The predictors for diameter growth,  $T_{min}$  and  $Ph_{mean}$ , were strongly correlated suggesting a high reliance on photoperiod length and a minimum temperature threshold for diameter growth to occur. A similar response was found for *E. regnans* where photoperiod alone did not limit growth (Ashton 1956, 1975a; Cremer 1960), but the interaction between day length and temperature did (Ashton 1975a). For eucalypts, increasing day length typically results in increased growth if temperatures are adequate (Scurfield 1961), which suggests an interaction between temperature and photoperiod exists for some species. Vaartaja (1963) found that most tree species from warm climates within the southern hemisphere exhibit a temperature and moisture dependent photoperiodic response and photoperiodic ecotypes occur within eucalypts, which is consistent with our findings. Our findings suggest that photoperiod is an important factor in growth phenology and all of the studied species exhibited a temperature dependent photoperiodic response in relation to diameter growth (Paton 1980) while some species exhibited this response in relation to height growth.

#### Environmental effects and growth traits - Growth Rates

This study was successful in identifying the sensitivity of growth to multiple factors and species optimum  $RGR_H/RGR_D$  as a function of  $T_{mean}$ . The  $RGR_H$  of the warm-dry species were consistently higher than the cool-moist species under drought conditions, which likely reflects the drought tolerance of these species (Ellis 1971; Florence 1996; Merchant et al. 2007) and correlates with the wider temperature niche condition found for these dry

sclerophyll forest species (Appendix 1). When moisture was not limiting, however, the cool-moist species exhibited higher  $RGR_H$  and  $RGR_D$ , which is consistent with the subgeneric response of *Monocalyptus* having higher growth rates than the slower growing *Symphyomyrtus* species (Myers and Neales 1984; Noble 1989). The sharp decline in  $RGR_D$  for cool-moist species under increasing temperature suggests that warm-dry species have a higher degree of phenotypic plasticity for  $RGR_D$ . This allows them to tolerate moisture limitations and higher temperatures than that occur within their current climatic envelopes (Cochrane et al. 2011). Difference in RGR found during the study can also be explained by the tree size traits of the species in their habitat; for example, *E. obliqua* can grow to be very tall (45–90 m) while *E. microcarpa* grows to 15–25 m (Boland et al. 2006).

#### Future climate and RGR

Present mean annual temperature (MAT) range observed for Victoria is 15–18°C (March 2012–Feb 2013, [www.bom.gov.au](http://www.bom.gov.au)) and temperatures are predicted to increase by 4°C with decreases in water availability and more drought events expected to occur by the 2080s (CSIRO and the Bureau of Meteorology 2007). Among the warm-dry species, the  $RGR_H$  of *E. tricarpa* suggests it may benefit in locations where MAT increases to 22°C but increases beyond this may result in reductions in height growth. When compared with all studied species, increase in MAT and decreases in water availability may benefit *E. polyanthemus*. The  $RGR_H$  of *E. sieberi* suggests that this species has the capacity to maintain growth to a threshold of temperature increase of 2°C under drought stress, but further increases will lead to declines in growth. However, the growth phenology of *E. obliqua* suggests greater flexibility in response to changes in MAT and soil moisture availability.  $RGR_D$  profiles suggest that current temperature conditions are suitable for growth, but if water limitations increase then  $RGR_D$  will decline for most of the species. Water limited conditions may facilitate increased  $RGR_D$  for *E. polyanthemus* compared to *E. tricarpa*. For cool-moist species, water limited conditions may facilitate increased  $RGR_D$  for *E. radiata* and *E. obliqua* relative to *E. sieberi*.

#### Height Growth Cessation

Generally longer days accompanied by high  $T_{max}$  and low  $H_{mean}$  resulted in height growth cessation for all the studied species. The lower height growth initiation temperature found for cool-moist species may be explained by the species' higher frost resistance (Layton and

Parsons 1972) and growth ability at lower temperatures. The growth temperature range for warm-dry species, *E. microcarpa* and *E. polyanthemos*, were greater than for cool-moist species but their basal temperatures were also greater which explains the higher growth rates for cool-moist species under cooler temperatures.

#### Phenotypic Plasticity and Clinal Variation

Cochrane et al. (2010) suggested that the temperature tolerance of species may be wider than the climatic envelop that they are occupying and they may exhibit phenotypic plasticity enabling them to adapt to climatic warming. During this study, species exhibited a range of phenotypic plastic traits that may help in combating the impacts of climate variability and change (Aitken et al. 2008). *Eucalyptus microcarpa*, *E. polyanthemos*, *E. obliqua* and *E. radiata* demonstrated phenotypic plastic behaviour to moisture limitation for height/diameter growth. Additionally, *E. microcarpa* and *E. polyanthemos* also demonstrated plasticity to high temperatures and low air humidity. *Eucalyptus microcarpa* exhibited greater plasticity than other species for higher temperature conditions. Phenotypic plasticity and local adaptation traits have also been found in provenances of *Abies pinsapo* in response to contrasting temperature and water availability (Linares et al. 2012). Green (2005) found that two of three co-occurring species varied in their plasticity with *Pinus contorta* and *Picea glauca* exhibiting only temperature dependency while *Abies lasiocarpa* exhibiting strong photoperiodic responses for growth. In the study by Green (2005), it was concluded that the temperature dependent species exhibited higher plasticity and would have a competitive advantage over photoperiodic species under climate change, as they would be able to take advantage of warmer temperatures during shorter days while photoperiodic species will continue to curtail growth in response to the photoperiod. In our study, temperature dependence but non photoperiodic responses were detected for *E. tricarpa* and *E. sieberi*. This may aid in their growth responses to climate change, which in turn may give them a competitive advantage over co-occurring species. We also detected strong clinal variation in our study for most of the species for height/diameter growth. Similar trait responses have also been shown for *E. camaldulensis* with provenances from tropical origins only suitable for growing in dry, tropical environments (Sun and Dickinson 1997). Vaartaja (1963) also found clinal variation in *E. dives* in relation to growth responses to photoperiod length. Likewise, height growth rate declined for six woody species in France as altitude of the provenance site increased showing strong clinal trends that suggests genetic variation may be the underlying



cause behind varying phenological growth traits under different environmental conditions (Vitasse et al. 2009). The clinal variability shown by some species in our study suggests that not all provenances have the ability to adapt to warmer conditions *in situ* via phenotypic plasticity but instead may need to rely on genetic adaptation (Rehfeldt et al. 2001).

#### Future climate and species vulnerability

For the co-occurring dry species, greater tolerance traits and plasticity displayed by *E. microcarpa* suggests its productivity may increase under climate change. Growth of *E. tricarpa* may benefit under a defined range of temperature increase but if drier conditions arise then the species may be outcompeted by *E. polyanthemos*. The recruitment of *E. tricarpa* in Victorian “box ironbark” forests has recently been found to be highly restricted (Orscheg et al. 2011). Combining this with the species limited growth under increasing temperatures, decreased moisture availability and lower air humidity (all predicted to occur due to climate change), suggests that *E. tricarpa* is at risk of being out competed by its current co-occurring species due to their divergent growth phenologies.

For the co-occurring cool-moist species, the flexible RGR and tolerance to moisture limitation exhibited by *E. obliqua* may help it maintain its productivity across a wider range of climate conditions compared to the other species, but climate change will likely have negative effects on growth for all cool-moist species. Non-photoperiodic, but temperature dependent growth response of *E. sieberi* suggests that it may gain a growth advantage over *E. radiata* and *E. obliqua* during warmer winter days, which could have impacts on species competition for resources. High summer temperatures will reduce growth of all the species, particularly *E. radiata* and *E. obliqua*. Across all species our results show that if soil moisture availability is unlimited, then beneficial effects on the height growth may occur even if temperature increases by 4°C. Temperature induced declines in growth will likely require ‘climate change’ temperatures 6 to 7°C higher than the current mean temperatures. However, the diameter growth will likely be negatively affected by 3 to 4°C rise in mean annual temperature. Height growth is important for competing with neighbours while diameter growth is necessary to mechanically and physiologically support the development of a crown (Sumida et al. 1997). For this reason, achieving greater height growth rates at the cost of reduced diameter growth under increased temperatures, as observed in our study, suggests that species’ growth phenology is related to the partitioning of resources to other organs in response to change in temperature. The long-term ecological and physiological consequences

of this phenological driven trade-off between height and diameter growth, particularly under the context of climate change, requires further investigation.

## Conclusion

This study was able to identify thresholds for growth for six species and the trade-off strategies they may be using to respond to environmental variation. Temperature, soil moisture availability, air humidity and photoperiod length were all found to be important variables controlling the growth phenology of the studied species. Four species were found to exhibit significant photoperiodic responses to height and diameter growth while only one species exhibited temperature dependency. Within species variation was detected, which suggests that phenological ecotypes exist, which lead to different growth responses. Plasticity and clinal variation were identified, which suggests that species may be able to respond to certain degrees of climate change. Phenological growth response models were able to provide insights into how species may respond to a changing climate and highlighted that co-occurring species will likely respond differently to climate change. This divergent response in species phenology suggests that species-specific growth will likely interact with the warming and drying conditions under climate change, which in turn is likely to result in changes in forest composition through interspecific competition.

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**Table 1** Variables, associated measurement techniques and formulas used throughout the study.

Variable	Description, Reference	Measurement technique	Formula and/or unit
<b>Climate</b>			
$T_{\text{mean}}$	Mean temperature	HOBO micro station data logger H21-002, $\pm 0.2^{\circ}\text{C}$ , measured hourly. Calculated as the mean of mean daily temperature over two consecutive time intervals (= 20 days)	$^{\circ}\text{C}$
$T_{\text{max}}$	Mean maximum temperature	HOBO micro station data logger H21-002, $\pm 0.2^{\circ}\text{C}$ , measured hourly. Calculated as the mean of daily maximum temperature over two consecutive time intervals (= 20 days)	$^{\circ}\text{C}$
$T_{\text{min}}$	Mean minimum temperature	HOBO micro station data logger H21-002, $\pm 0.2^{\circ}\text{C}$ , measured hourly. Calculated as the mean of daily minimum temperature over two consecutive time intervals (= 20 days)	$^{\circ}\text{C}$
$H_{\text{mean}}$	Mean Air Humidity	HOBO micro station data logger H21-002, measured hourly. Calculated as the mean of daily mean air humidity over two consecutive time intervals (= 20 days)	%
M	Soil moisture	HOBO micro station data logger H21-002, measured hourly. In one pot under each watering regime (WW, WS) per experimental treatment.	$\text{m}^3 \text{ m}^{-3}$
$Ph_{\text{mean}}$	Mean Photoperiod	Mean number of daylight hours computed from sunrise and sunset times for Melbourne ( $37.60^{\circ}\text{S}$ $145.00^{\circ}\text{E}$ ) by Geoscience Australia, Australian Government. Calculated as the mean of daily light hours over two consecutive measurement intervals (= 20 days)	hours
<b>Experimental treatments</b>			
WW	Well-watered Elfeel et al. (2011)	$G1 \square G4 = 0.42 \text{ m}^3 \text{ m}^{-3}$ (soil moisture availability under saturation). Seedlings received water to saturation daily	$\text{m}^3 \text{ m}^{-3}$
WS	Water-stressed Elfeel et al. (2011) Quraishi and Kramer 1970	$G1 \square G4 = 0.22 \text{ m}^3 \text{ m}^{-3}$ (soil moisture availability from September $\square$ February). Plants received water to saturation on a plant-by-plant basis following the first signs of wilting.	$\text{m}^3 \text{ m}^{-3}$
<b>Plant</b>			
H	Height	Height Pole	nearest cm
D	Diameter	Electronic digital calipers just above the first inter node at the same point in each measurement	nearest mm ( $\pm 0.01$ )
$RGR_H$	Relative Growth Rate in height Ashton (1975a)	Calculated for each seedling and time interval between two consecutive measurements where $H_1$ and $H_2$ are seedling height at the beginning and end of each time interval ( $t_1$ and $t_2$ ), respectively	$RGR_H = (H_2 - H_1) / (t_2 - t_1)$ Given $t_2 - t_1 = 20$ $RGR_H = (H_2 - H_1) / 20$ $\text{cm day}^{-1}$
$RGR_D$	Relative Growth Rate in diameter Ashton (1975a)	Calculated for each seedling and time interval between two consecutive measurements where $D_1$ and $D_2$ are seedling diameter at the beginning and end of each time interval ( $t_1$ and $t_2$ ), respectively	$RGR_D = (D_2 - D_1) / (t_2 - t_1)$ Given $t_2 - t_1 = 20$ $RGR_D = (D_2 - D_1) / 20$ $\text{mm day}^{-1}$
	Height growth cessation	Recorded when no difference in height between two consecutive measurements.	$H_2 - H_1 = 0$



Green 2005

Plants with completely dry leaves and brittle stems without visible growth were recorded as dead.

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**Table 2** Significance of effect of the mixed linear model of  $Ph_{mean}$ ,  $T_{max}$  and  $T_{min}$  in combination with Provenance (Prov), M, and  $H_{mean}$  for height and diameter growth. Symbols indicate a significant ( $P \leq 0.05$ ) positive (+) or negative (□) effect when there is rise in  $Ph_{mean}$ ,  $T_{max}$ ,  $T_{min}$ , M and  $H_{mean}$ . Abbreviations follow Table 1, *ns* not significant.

Variable	<i>E. microcarpa</i>			<i>E. polyanthemos</i>			<i>E. tricarpa</i>			<i>E. obliqua</i>			<i>E. radiata</i>			<i>E. sieberi</i>		
	$Ph_{mean}$	$T_{max}$	$T_{min}$	$Ph_{mean}$	$T_{max}$	$T_{min}$	$Ph_{mean}$	$T_{max}$	$T_{min}$	$Ph_{mean}$	$T_{max}$	$T_{min}$	$Ph_{mean}$	$T_{max}$	$T_{min}$	$Ph_{mean}$	$T_{max}$	$T_{min}$
<b>Height</b>																		
$Ph_{mean}/T_{max}/T_{min}^a$	+	<i>ns</i>	<i>ns</i>	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	-	<i>ns</i>	+	-	-	+	-	<i>ns</i>	<i>ns</i>	-	<i>ns</i>
Prov	-	-	-	+	+	+	<i>ns</i>	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	-	<i>ns</i>	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
M	<i>ns</i>	+	+	+	+	<i>ns</i>	+	+	+	<i>ns</i>	<i>ns</i>	+	+	<i>ns</i>	+	<i>ns</i>	+	+
$H_{mean}$	+	<i>ns</i>	<i>ns</i>	+	+	+	+	+	<i>ns</i>	+	+	<i>ns</i>	+	+	<i>ns</i>	<i>ns</i>	+	+
Prov × M	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	<i>ns</i>	<i>ns</i>	<i>ns</i>
Prov × $Ph_{mean}/T_{max}/T_{min}$	+	+	+	+	+	+	<i>ns</i>	-	<i>ns</i>	+	-	<i>ns</i>	<i>ns</i>	-	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Prov × $H_{mean}$	+	+	+	+	+	-	<i>ns</i>	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	+	<i>ns</i>
M × $Ph_{mean}/T_{max}/T_{min}$	<i>ns</i>	+	<i>ns</i>	+	<i>ns</i>	<i>ns</i>	+	-	-	<i>ns</i>	-	-	<i>ns</i>	-	-	<i>ns</i>	-	-
M × $H_{mean}$	<i>ns</i>	+	+	+	<i>ns</i>	<i>ns</i>	+	+	+	+	+	+	+	+	+	+	+	+
$H_{mean} \times Ph_{mean}/T_{max}/T_{min}$	+	<i>ns</i>	<i>ns</i>	+	<i>ns</i>	+	+	-	<i>ns</i>	+	-	+	+	-	+	+	-	<i>ns</i>
Prov difference <sup>b</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	2 <sup>a</sup> 3 <sup>b</sup> 4 <sup>a</sup>	2 <sup>a</sup> 3 <sup>b</sup> 4 <sup>a</sup>	2 <sup>a</sup> 3 <sup>b</sup> 4 <sup>a</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	2 <sup>a</sup> 3 <sup>a</sup> 4 <sup>b</sup>	2 <sup>a</sup> 3 <sup>a</sup> 4 <sup>b</sup>	2 <sup>a</sup> 3 <sup>a</sup> 4 <sup>b</sup>			
<b>Diameter</b>																		
$Ph_{mean}/T_{max}/T_{min}$	+	<i>ns</i>	-	+	<i>ns</i>	-	+	-	-	+	-	-	+	-	-	<i>ns</i>	-	<i>ns</i>
Prov	-	-	-	+	+	+	<i>ns</i>	+	<i>ns</i>	-	-	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	+	+
M	<i>ns</i>	+	+	+	+	<i>ns</i>	+	+	+	+	<i>ns</i>	<i>ns</i>	+	<i>ns</i>	<i>ns</i>	+	+	<i>ns</i>
$H_{mean}$	+	<i>ns</i>	+	+	<i>ns</i>	+	+	+	+	+	+	+	+	+	+	+	+	<i>ns</i>
Prov × M	+	+	+	+	+	+	+	+	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	+	+	+	+	+	+
Prov × $Ph_{mean}/T_{max}/T_{min}$	+	+	-	+	+	<i>ns</i>	<i>ns</i>	-	<i>ns</i>	+	-	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Prov × $H_{mean}$	+	+	+	+	+	+	+	+	+	+	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	+	+	+
M × $Ph_{mean}/T_{max}/T_{min}$	<i>ns</i>	+	<i>ns</i>	+	+	<i>ns</i>	+	-	-	+	-	-	+	<i>ns</i>	<i>ns</i>	+	<i>ns</i>	<i>ns</i>
M × $H_{mean}$	<i>ns</i>	+	+	+	<i>ns</i>	<i>ns</i>	+	+	+	<i>ns</i>	+	+	<i>ns</i>	+	+	<i>ns</i>	+	+
$H_{mean} \times Ph_{mean}/T_{max}/T_{min}$	+	<i>ns</i>	-	+	<i>ns</i>	-	+	-	-	+	-	-	+	-	-	+	-	<i>ns</i>
Prov difference	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup> 4 <sup>c</sup>	2 <sup>a</sup> 3 <sup>b</sup> 4 <sup>a</sup>	2 <sup>a</sup> 3 <sup>b</sup> 4 <sup>a</sup>	2 <sup>a</sup> 3 <sup>b</sup> 4 <sup>a</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>b</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>b</sup> 4 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>b</sup> 4 <sup>c</sup>	2 <sup>a</sup> 3 <sup>a</sup> 4 <sup>b</sup>	2 <sup>a</sup> 3 <sup>a</sup> 4 <sup>b</sup>	2 <sup>a</sup> 3 <sup>a</sup> 4 <sup>b</sup>			

<sup>a</sup>Where ' $Ph_{mean}/T_{max}/T_{min}$ ' appears, the variable is either  $Ph_{mean}$ ,  $T_{max}$  or  $T_{min}$  depending the model tested as indicated by the column header. <sup>b</sup>Significance of differences among provenances are indicated by means followed by different superscripts. See Appendix 1 for provenance details.

**Table 3** Significance of effect of the mixed linear model of  $Ph_{mean}$ ,  $T_{max}$  and  $T_{min}$  in combination with Species (Sp), M, and  $H_{mean}$  for height and diameter growth. Symbols indicate a significant ( $P \leq 0.05$ ) positive (+) or negative (□) effect when there is rise in  $Ph_{mean}$ ,  $T_{max}$ ,  $T_{min}$ , M and  $H_{mean}$ . Individual species belonging to the ‘warm-dry’ or ‘cool-moist’ groups are indicated in Appendix 1. Abbreviations follow Table 1, *ns* not significant.

Variable	Warm-dry species			Cool-moist species		
	$Ph_{mean}$	$T_{max}$	$T_{min}$	$Ph_{mean}$	$T_{max}$	$T_{min}$
<b>Height</b>						
$Ph_{mean}/T_{max}/T_{min}^a$	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	-	-
Sp	<i>ns</i>	-	<i>ns</i>	+	<i>ns</i>	<i>ns</i>
M	+	+	+	+	+	+
$H_{mean}$	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	+	+
Sp × M	+	+	+	+	+	+
Sp × $Ph_{mean}/T_{max}/T_{min}$	<i>ns</i>	-	<i>ns</i>	+	-	-
Sp × $H_{mean}$	+	+	+	+	<i>ns</i>	<i>ns</i>
M × $Ph_{mean}/T_{max}/T_{min}$	+	+	<i>ns</i>	+	+	+
M × $H_{mean}$	+	+	<i>ns</i>	+	+	+
$H_{mean} \times Ph_{mean}/T_{max}/T_{min}$	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	-	<i>ns</i>
Sp difference <sup>b</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	4 <sup>a</sup> 5 <sup>b</sup> 6 <sup>c</sup>	4 <sup>a</sup> 5 <sup>b</sup> 6 <sup>c</sup>	4 <sup>a</sup> 5 <sup>b</sup> 6 <sup>c</sup>
<b>Diameter</b>						
$Ph_{mean}/T_{max}/T_{min}^a$	+	-	-	+	-	-
Sp	+	+	+	+	+	<i>ns</i>
M	+	+	<i>ns</i>	+	<i>ns</i>	+
$H_{mean}$	+	+	+	+	+	+
Sp × M	+	+	+	+	+	+
Sp × $Ph_{mean}/T_{max}/T_{min}$	+	-	<i>ns</i>	+	-	-
Sp × $H_{mean}$	+	+	+	<i>ns</i>	<i>ns</i>	<i>ns</i>
M × $Ph_{mean}/T_{max}/T_{min}$	+	+	<i>ns</i>	+	+	+
M × $H_{mean}$	+	<i>ns</i>	<i>ns</i>	<i>ns</i>	+	+
$H_{mean} \times Ph_{mean}/T_{max}/T_{min}$	+	-	-	+	-	-
Sp difference <sup>b</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	1 <sup>a</sup> 2 <sup>b</sup> 3 <sup>c</sup>	4 <sup>a</sup> 5 <sup>b</sup> 6 <sup>a</sup>	4 <sup>a</sup> 5 <sup>b</sup> 6 <sup>a</sup>	4 <sup>a</sup> 5 <sup>b</sup> 6 <sup>a</sup>

<sup>a</sup>Where ‘ $Ph_{mean}/T_{max}/T_{min}$ ’ appears, the variable is either  $Ph_{mean}$ ,  $T_{max}$  or  $T_{min}$  depending the model tested as indicated by the column header. <sup>b</sup>Significance of differences among species within ‘warm-dry’ or ‘cool-moist’ groups are indicated by means followed by different superscripts. See Appendix 1 for species details.

**Table 4** Cox's proportional hazard regression analysis on height cessation indicating the significance of  $Ph_{mean}$ ,  $T_{max}$  and  $T_{min}$  models. \*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.0001$ ; *ns* not significant. Abbreviations follow Table 1.

	$Ph_{mean}$	$Ph_{mean}$			$T_{max}$	$T_{max}$			$T_{min}$	$T_{min}$		
		Prov	M	$H_{mean}$		Prov	M	$H_{mean}$		Prov	M	$H_{mean}$
<i>E. microcarpa</i>	***	<i>ns</i>	<i>ns</i>	<i>ns</i>	***	<i>ns</i>	<i>ns</i>	***	***	<i>ns</i>	<i>ns</i>	<i>ns</i>
<i>E. polyanthemos</i>	***	<i>ns</i>	<i>ns</i>	***	***	<i>ns</i>	<i>ns</i>	***	***	<i>ns</i>	<i>ns</i>	<i>ns</i>
<i>E. tricarpa</i>	***	<i>ns</i>	<i>ns</i>	<i>ns</i>	***	<i>ns</i>	<i>ns</i>	***	***	<i>ns</i>	<i>ns</i>	<i>ns</i>
<i>E. obliqua</i>	***	*	<i>ns</i>	<i>ns</i>	***	*	<i>ns</i>	*	***	*	*	*
<i>E. radiata</i>	***	<i>ns</i>	<i>ns</i>	<i>ns</i>	***	<i>ns</i>	<i>ns</i>	***	***	<i>ns</i>	<i>ns</i>	<i>ns</i>
<i>E. sieberi</i>	***	<i>ns</i>	<i>ns</i>	<i>ns</i>	***	<i>ns</i>	<i>ns</i>	***	***	<i>ns</i>	<i>ns</i>	<i>ns</i>

# **Appendix 1** Description of selected eucalypts, seed source information and number of seedlings per treatment

	Geographical range	Temperature range (°C)	Rainfall range (mm year <sup>-1</sup> )	Altitude range (m)	Provenance (seed lot number)	Altitude (m asl)	Geographical position	<i>n</i> <sup>g</sup>
Warm-dry species								
1. <i>E. microcarpa</i> <sup>bcd</sup> (Grey Box)	24.8–37.5°S	1–7/25–33	400–760	40–800	Em 1 (Seeding Vic. 9273)	249	37°05’S; 143°74’E	14 (G1□G4)
					Em 2 (Seeding Vic. 6540)	118	37°68’S 144°44’E	14 (G1□G4)
					Em 3 (CSIRO 16036)	280	37°06’S; 143°32’00’’E	6 (G1□G4)
					Em 4 (CSIRO 17419)	340	36°58’S; 144°03’E	NA
2. <i>E. polyanthemos</i> <sup>bce</sup> (Red Box)	32.5–38°S	-1–4/23–30	450–970	120–780	Ep 1 (CSIRO 17222)	120	37°39’S; 147°50’ E	10 (G1)
					Ep 2 (CSIRO 15342)	240	36°51’S; 144°24’E	14 (G1□G4)
					Ep 3 (CSIRO 15337)	420	36°28’S; 146°41’E	14 (G1□G4)
					Ep 4 (Greening Aus. MIS 950764)	509	37°14’ S; 144°27’ E	6 (G1□G3)
3. <i>E. tricarpa</i> <sup>bcf</sup> (Red Ironbark)	25–38.3°S	2–4/24–28	550–1000	20–360	Et 1 (Seeding Vic. 4414)	300	36°43’S; 144°25’E	NA
					Et 2 (Seeding Vic. 2506)	174	36°45’S; 144°21’E	14 (G1□G4)
					Et 3 (CSIRO 20450)	120	37°56’S; 146°43’E	14 (G1□G4)
					Et 4 (CSIRO 20453)	0	37°28’S; 148°33’E	14 (G1□G4)
Cool- moist species								

4. <i>E. obliqua</i> <sup>abc</sup> (Messmate Stringybark)	28–43.5°S	-4–8/19–29	500–2400	0–750	Eo 1 (CSIRO 15901)	270	38°51'S; 143°30'E	14 (G1□G4)
					Eo 2 (CSIRO 15902)	616	37°26' S; 144°12' E	14 (G1□G4)
					Eo 3 (CSIRO 15914)	194	37°20'S; 145°05' E	14 (G1□G4)
					Eo 4 (Seeding Vic. 1578)	560	37°47' S; 144°31'S	14 (G1□G4)
5. <i>E. radiata</i> <sup>bce</sup> (Narrow leaved Peppermint)	28–39°S	-4–2/23–30	650–1100	50–1200	Er 1 (CSIRO 17311)	300	37°26'S; 145°27'E	NA
					Er 2 (Greening Aus. 970312)	174	37°44'S; 145°27'E	14 (G1-G4)
					Er 3 (Seeding Vic. 1715)	170	38°30'59"S; 143°41'40"E	14 (G1□G4)
					Er 4 (Seeding Vic. 3263)	380	37°48'13"S; 143°54'33"E	14 (G1-G4)
6. <i>E. sieberi</i> <sup>abc</sup> (Silvertop Ash)	33–42°S	-2–5/22□27	700–1400	0–100	Es 1	140	37°41'S; 148°45'E	14 (G1□G4)
					Es 2 (CSIRO 20043)	800	34°20'S; 150°12' E	14 (G1□G4)

Source: <sup>a</sup>Australian Forest Profiles (2002); <sup>b</sup>Boland *et al.* (2006); <sup>c</sup>[www.ersa.edu.au](http://www.ersa.edu.au); <sup>d</sup>[www.environment.gov.au](http://www.environment.gov.au); <sup>e</sup>[www.metrotrees.com.au](http://www.metrotrees.com.au);

<sup>f</sup>[www.florabank.org.au/](http://www.florabank.org.au/); <sup>g</sup>*n* = Number of seedlings per treatment (equal number of seedlings under WW and WS/EWS soil moisture regime), NA = not germinated and excluded from the analysis, G1□G4 Glasshouse treatment (see Table 1).

1 **Appendix 2** Mean (standard errors in brackets) climatic conditions within each of the  
2 experimental treatments (glasshouses, G1–G4). Significance of differences among treatments  
3 are indicated by means followed by different superscripts. \*  $P \leq 0.05$ , \*\*  $P \leq 0.001$ , *ns* non  
4 significant.

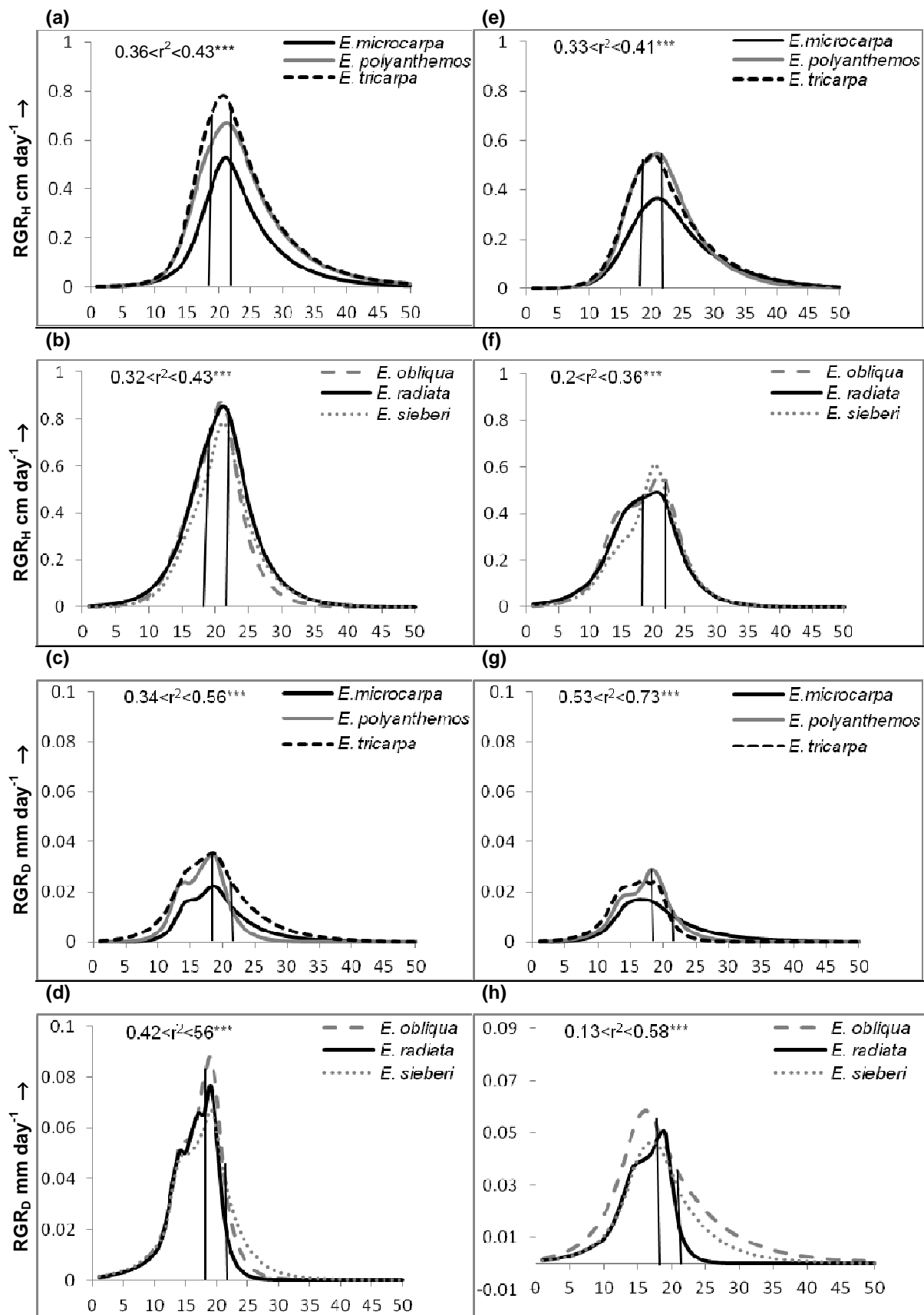
	G1		G2		G3		G4		P
Mean Temperature (°C)									
Spring	18.1	(1.8)	19.2	(1.16)	18.8	(0.7)	19.7	(0.9)	ns
Summer	21.5	(0.5)	23.0	(0.72)	22.1	(0.8)	23.7	(0.5)	ns
Autumn	16.0	(1.4)	17.2	(1.66)	16.9	(1.5)	17.5	(1.4)	ns
Winter	10.4	(0.5)	11.7	(0.34)	11.7	(0.5)	11.4	(0.4)	ns
Annual	17.1	(1.2)	18.4	(1.19)	18.0	(1.1)	18.8	(1.2)	ns
Maximum Temperature (°C)									
Spring	25.0	(2.3)	29.6	(1.14)	26.0	(1.1)	28.6	(1.1)	ns
Summer	27.4 <sup>a</sup>	(0.5)	34.7 <sup>b</sup>	(1.20)	31.4 <sup>ab</sup>	(1.1)	33.5 <sup>b</sup>	(0.9)	**
Autumn	22.3 <sup>ab</sup>	(1.8)	31.0 <sup>b</sup>	(2.23)	29.7 <sup>ab</sup>	(2.8)	26.0 <sup>ab</sup>	(2.0)	*
Winter	15.0 <sup>ab</sup>	(0.6)	25.5 <sup>b</sup>	(1.16)	23.2 <sup>ab</sup>	(1.6)	17.8 <sup>ab</sup>	(0.7)	***
Annual	23.1 <sup>a</sup>	(1.3)	30.8 <sup>b</sup>	(1.13)	28.2 <sup>ab</sup>	(1.2)	27.4 <sup>ab</sup>	(1.6)	**
Minimum Temperature (°C)									
Spring	10.6	(0.4)	12.1	(0.78)	13.6	(0.2)	12.5	(0.7)	ns
Summer	15.3 <sup>ab</sup>	(0.5)	14.6 <sup>a</sup>	(0.37)	15.3 <sup>ab</sup>	(0.6)	16.5 <sup>b</sup>	(0.3)	**
Autumn	11.3	(0.9)	10.6	(1.17)	10.6	(1.2)	12.4	(1.0)	ns
Winter	7.2	(0.4)	6.6	(0.95)	6.5	(0.5)	7.4	(0.4)	ns
Annual	11.7	(0.8)	11.4	(0.85)	12.0	(0.9)	12.8	(0.9)	ns
Mean Humidity (%)									
Spring	68.6 <sup>a</sup>	(1.2)	75.5 <sup>a</sup>	(0.69)	76.5 <sup>b</sup>	(2.2)	65.2 <sup>ab</sup>	(2.5)	**
Summer	64.2 <sup>ac</sup>	(1.8)	73.3 <sup>a</sup>	(3.10)	77.8 <sup>b</sup>	(1.3)	61.2 <sup>bc</sup>	(1.7)	**
Autumn	73.1	(2.7)	82.8	(1.84)	84.0	(1.3)	78.3	(4.8)	ns
Winter	83.6	(0.9)	88.2	(1.51)	90.1	(1.1)	86.7	(2.1)	ns
Annual	71.3 <sup>a</sup>	(2.1)	79.3 <sup>ab</sup>	(1.90)	81.7 <sup>b</sup>	(1.5)	71.7 <sup>a</sup>	(3.0)	**

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7 **Figure 1** GAM model prediction of relative growth rate in height ( $RGR_H$ ) and diameter  
8 ( $RGR_D$ ) in relation to mean temperature ( $T_{mean}$ ). The first vertical line indicates the average  
9 daily mean annual temperature of Victoria (March 2012–February 2013) and the second  
10 vertical line indicates the 4°C rise projection for Victoria by the year 2080. Well-watered  
11 treatments (a-d) and water-stressed treatments (e-h). \*\*\*  $P \leq 0.0001$ .  
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$T_{\text{mean}} (^{\circ}\text{C}) \rightarrow$

$T_{\text{mean}} (^{\circ}\text{C}) \rightarrow$

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