

# Temperature and Water Stress Integral Influence in Physiological Responses among Eucalyptus Genotypes <sup>†</sup>

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**Abstract:** Water stress is expected to reduce photosynthesis and leaf water potential to regulate plant water use efficiency. We hypothesized that higher summer temperatures increase photosynthesis and decrease water use, which are more pronounced in more stressed genotypes. This study investigated photosynthesis ( $A_n$ ), stomatal conductance ( $g_s$ ), and water stress integral (WSI) changes in the early development of *E. globulus*, *E. nitens*, and *E. nitens* × *E. globulus* hybrids during winter and summer.  $A_n$ ,  $g_s$ , and WSI showed a significant interaction ( $p > 0.001$ ) between genotype and season. Regardless of the season, *E. globulus* showed no significant changes in  $A_n$ , while higher increase was observed in *E. gloni* (50%) in summer. There was an increment in  $g_s$  between the seasons (167%), which was more pronounced in *E. nitens* (300%). This implied significant changes between species and seasons for  $iWUE$ . The lowest  $iWUE$  in summer was related to the lowest WSI, with *E. nitens* being different from other taxa ( $p = 0.01$ ). We observed a positive relationship between WSI and  $iWUE$  in summer, but negative in winter. The results suggest that WSI in winter helps to promote stomatal closure, which increases  $iWUE$ , since  $A_n$  presented small changes. Regardless of genotype, warm periods increased  $A_n$  and decreased  $iWUE$ , which imply different strategies of eucalyptus plantations in regions with water deficit.

**Keywords:** forest management; forest physiology; water use efficiency

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## 1. Introduction

Increased productivity of eucalyptus plantations has been achieved by the combination of silvicultural improvements and forest breeding, with selection of specific genotypes for adequate sites [1,2]. Selection of eucalyptus genotypes, such as Mediterranean eucalyptus species, requires knowledge on how they will be affected by the seasons (temperature and vapor pressure deficit (VPD)) or site availability throughout the year [3–5].

Breeding of trees that are tolerant of higher environmental changes may be a promising approach, but it requires knowledge on physiological mechanisms during plant development [6]. Short-term responses to avoid water and heat stress include higher water potential maintenance, carbon assimilation reduction, and stomatal closure [7]. Changes in photosynthesis and water use efficiency have been identified as key parameters for evaluating eucalyptus adaptation to

environmental constraints, such as water deficit and higher atmospheric demand [8]. However, researchers need to establish experiments in the field to determine the effects of physiological variables on plant development [9].

Our study investigated the genotype  $\times$  season physiological responses of 12 high productivity eucalyptus genotypes in two seasons in Chile. We evaluated that regardless of genotype, with the increase in temperature in summer, changes in photosynthetic rates will be greater than in winter; however, the increase in atmospheric demand (VPD) leads to a decrease in intrinsic water use efficiency, and genotypes that present the highest absolute water stress integral will be the least efficient in water use.

## 2. Experiments

### 2.1. Site Characteristics

The experiment was established 9.6 km east of Yumbel town in central South Chile (37° 8 0.01 S, 72°27'34.70" W). Soils are Entisols, formed by black volcanic sands of andesitic and basaltic origin with low water holding capacity. The Köppen classification is a warm-summer Mediterranean climate with winter rains (Csb). The average annual precipitation at the site was 1328 mm, occurring mainly in winter (600 mm), with 60 mm in summer. The mean annual temperature was 14.2 °C, with maximum temperature in January (38.9 °C) and minimum temperature in July (-1.7 °C). Solar radiation ranges from 10.4 MJ m<sup>-2</sup> day<sup>-1</sup> in July, during winter, to 29.3 MJ m<sup>-2</sup> day<sup>-1</sup> in January, during summer.

### 2.2. Experimental Design and Treatments

Considering 12 higher productivity eucalyptus genotypes, a completely randomized block design with three replicates was done in October 2017. Five genotypes were *Eucalyptus globulus* Labill (EG 17, EG 18, EG 21, EG 30, and EG 31), two were *E. nitens* H. Deane & Maiden (EN 13 and EN 14), and five were *E. nitens*  $\times$  *E. globulus* (*E. gloni*) hybrids (ENG 2, ENG 3, ENG 4, ENG 5, and ENG 8). In this study, seedlings with no visual disease symptoms or damage were selected. Experimental units were established by hand planting 16 plants (24 m<sup>2</sup>). Plant spacing was 1.5 m<sup>2</sup> (6667 trees ha<sup>-1</sup>) in order to accelerate any response of canopy closure and intraspecific competition. After one month, replanting was done to maintain homogeneous conditions across the experiment. Herbicides were used to keep the plants weed-free, and controlled-release fertilizer was used to keep plants without nutritional deficiency. To ensure survival, irrigation was applied from the planting time until March 2018 (first dry summer season), and from the end of November 2018 until mid-February 2019 (second dry summer season).

### 2.3. Physiological Measurements

Physiological variables were evaluated in four periods: early winter 2018 (12 June), mid-winter 2018 (8 August), early summer 2018 (14 December), and mid-summer 2019 (18 February). These dates coincided with different periods of temperature and VPD at the experiment site.

Predawn leaf water potential ( $\Psi_{pd}$ ) was measured using a Scholander pressure chamber (PMS Instruments, Corvallis, OR, USA). Measurements were made in one plant per plot, in mature, fully expanded, and sun-exposed leaves of the upper canopy between 4:00 and 6:00 h. Following Myers [10], we calculated the total water stress integral (WSI) as the cumulative integral of predawn leaf water potential ( $\Psi_{pd}$ ) over the entire period of mensuration:

$$WSI = \sum_{i=0}^t (\bar{\Psi}_{i,i+1} - c) * n \quad (1)$$

where  $\bar{\Psi}_{i,i+1}$  is the mean  $\Psi_{pd}$  for interval  $i,i+1$ , and  $c$  is the maximum value of  $\Psi_{pd}$  during the measurements, and  $n$  is the number of days at interval  $i,i+1$ .

Leaf gas exchange measurement included net CO<sub>2</sub> assimilation rate ( $A_n$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and stomatal conductance ( $g_s$ ,  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ). Measurements were done in one plant per plot, in mature, fully expanded, and sun-exposed leaves using a portable infrared gas analyzer LICOR-6400 (Li-Cor,

Inc., Lincoln, NE, USA). All measurements were done with reference CO<sub>2</sub> at 400  $\mu\text{mol}\cdot\text{mol}^{-1}$ , light intensity (PAR) in the leaf chamber at 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , constant flow rate of 500  $\mu\text{mol s}^{-1}$ , and leaf temperature ( $T_{\text{leaf}}$ ) of 20 °C. Intrinsic water use efficiency (iWUE,  $\mu\text{mol CO}_2 \text{mol}^{-1} \text{H}_2\text{O}$ ) was calculated using the ratio of  $A_n$  and  $g_s$ .

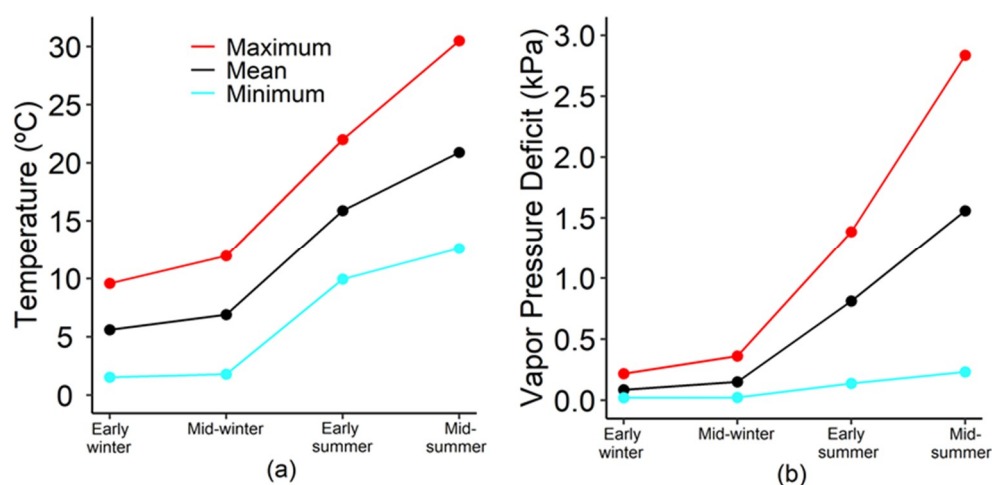
#### 2.4. Statistical Analysis

Analysis of variance (ANOVA) was used on the differences in WSI,  $A_n$ ,  $g_s$ , and iWUE in different seasons and genotypes. Seasons and genotypes were considered fixed effects, and blocks were considered random effects. All ANOVA analyses were performed using the MIXED procedure. Differences in WSI,  $A_n$ ,  $g_s$ , and iWUE were determined with the LSMEANS statement using the Tukey-Kramer adjustment ( $p < 0.05$ ). A Michalis-Menten model was fitted to evaluate the relationship between  $A_n$  and  $g_s$  throughout the seasons, considering all genotypes and individual taxa. Regression analysis was used in the GLM procedure to assess the relationship between iWUE and WSI at taxa level. Analyses were performed using SAS® Studio ([https://www.sas.com/en\\_us/software/studio.html](https://www.sas.com/en_us/software/studio.html)). All graphical analyses were performed in R software using the ggplot2 package [11].

### 3. Results

#### 3.1. Climate Data

Temperature presented a narrow range in winter periods, with a minimum close to 0 °C and maximum below 12 °C; a wider range was observed during summer, with a minimum below 10 °C and maximum above 20 °C (Figure 1a). VPD ranges from 0.02 to 0.30 kPa in winter periods. The minimum VPD remained constant throughout the year, but the maximum VPD was almost 3.00 kPa in mid-summer, increasing the VPD range in warm periods (Figure 1b).



**Figure 1.** (a) Air temperatures and (b) vapor pressure deficit during the measurement periods.

#### 3.2. Physiology

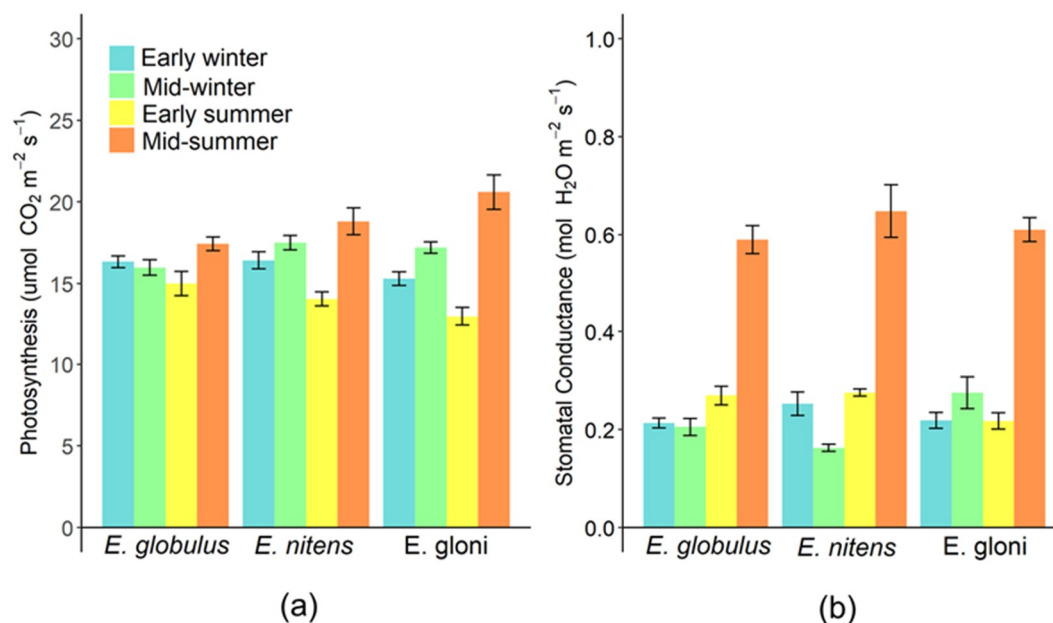
Season  $\times$  genotype had significant effects on all physiological variables ( $A_n$ ,  $g_s$ , iWUE, and WSI) ( $p < 0.001$ ) (Table 1). Across all genotypes in winter, small changes (>15%) were observed in the average values of  $A_n$  and iWUE, but the average WSI decreased by 31%. In summer, large changes in physiological variables were observed between early and mid-summer;  $A_n$  increased by 27%, while iWUE and WSI decreased by 85% and 27%, respectively.

**Table 1.** ANOVA *p*-values on season, genotype, and interaction effects on photosynthesis (An), stomatal conductance (gs), intrinsic water use efficiency (iWUE), and water stress integral (WSI).

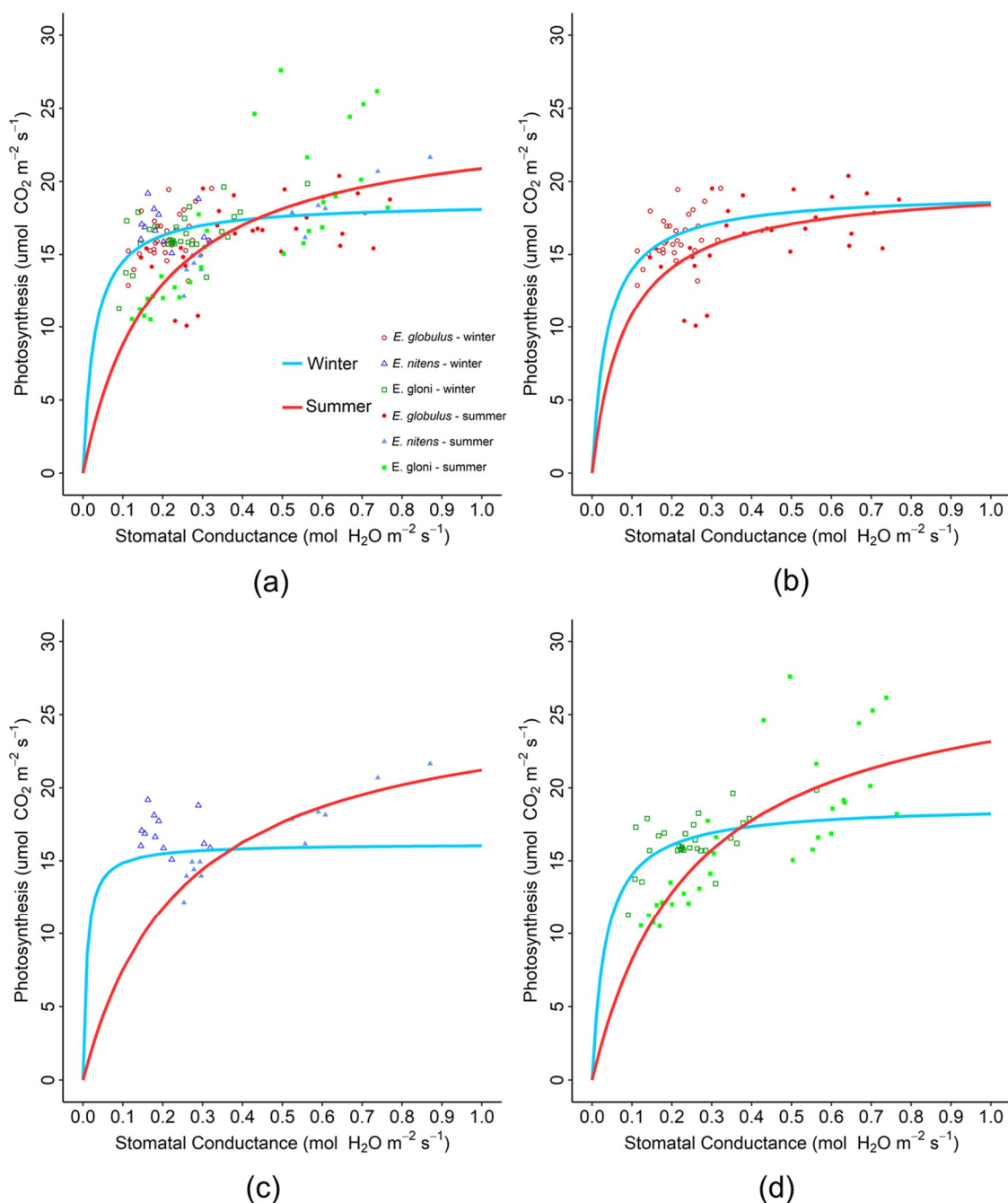
Effect	An	gs	iWUE	WSI
Seasons	<0.001	<0.001	<0.001	<0.001
Genotype	<0.001	<0.001	<0.001	<0.001
Seasons × Genotype	<0.001	<0.001	<0.001	<0.001

The lowest and highest average values of An were in similar periods among taxa. The lowest average An was in early-summer for *E. globulus* (14.99  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), for *E. nitens* (14.06  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), and for *E. gloni* (12.97  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). The highest average An was in mid-summer for *E. globulus* (17.43  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), *E. nitens* (18.81  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), and *E. gloni* (20.60  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Between early and mid-summer, the lowest changes in An was observed in *E. globulus* (+12%), and the largest changes in *E. nitens* (+26%) and *E. gloni* (+37%). The higher average gs was observed in mid-summer for *E. globulus* (0.59  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ), *E. nitens* (0.65  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ), and *E. gloni* (0.61  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ). Lower changes in gs were during winter (−7%), but in summer there was an increased in gs values for all genotypes, with average increment of 57%. We observed similar behavior in An and gs of eucalyptus genotypes throughout the seasons. Summer changes in gs were higher than summer changes in An, so we expect that lower values of iWUE in summer compare to winter.

We observed a positive relationship between An and gs, suggesting that An variation could be predicted by gs across seasons and taxa. The Michaelis Menten (MM) model was used to check this relationship (Figure 2). Full versus reduced model comparisons of MM for season effects showed that for all genotypes, season was significant ( $F = 25.52, p < 0.001$ ). Season comparison for individual taxa showed significant effects in *E. globulus* ( $F = 4.41, p < 0.017$ ), *E. nitens* ( $F = 28.02, p < 0.001$ ), and *E. gloni* ( $F = 11.29, p < 0.001$ ). The b parameters of the models represent the mean gs value, of which half of maximum An (a parameter) was attained (Table 2). In general, the models showed better fits for summer than winter. Only *E. nitens* and *E. gloni* in winter showed non-significance for the b parameter, which suggested that a maximum mean value was able to represent An in these taxa.



**Figure 2.** (a) Mean photosynthesis (An) and (b) mean stomatal conductance (gs) for eucalyptus taxa and seasons. Vertical bars correspond to standard error of taxa means.



**Figure 2.** MM models adjusted for  $g_s$  and  $A_n$  relationship for winter and summer for (a) all, (b) *E. globulus*, (c) *E. nitens*, and (d) *E. gloni* genotypes.

**Table 2.** MM models adjusted for  $g_s$  and  $A_n$  relationship for all genotypes and individual taxa (*E. globulus*, *E. nitens*, and *E. gloni*) that showed significant effects of seasons (winter and summer). MM models are represented by the expression  $A_n = a \cdot g_s / (b + g_s)$  and goodness of fit of models was evaluated by root mean square error (RMSE) and pseudo- $R^2$  values.

Model	Effects	Parameters		RMSE	R <sup>2</sup>
		a	b		
All genotypes	Winter & Summer	20.491 *	0.085 *	2.47	0.28
	Winter	18.597 *	0.028 *	1.44	0.21
	Summer	24.624 *	0.179 *	2.61	0.52
<i>E. globulus</i>	Winter & Summer	18.319 *	0.034 *	1.95	0.16

	Winter	19.251 *	0.038 *	1.4	0.21
	Summer	19.927 *	0.083 *	2.14	0.30
<i>E. nitens</i>	Winter & Summer	18.189 *	0.023 *	2.09	0.07
	Winter	16.181 *	0.009 ns	1.19	0.03
	Summer	26.580 *	0.253 *	0.93	0.89
<i>E. gloni</i>	Winter & Summer	23.818 *	0.119 *	2.75	0.45
	Winter	18.834 *	0.034 ns	1.41	0.32
	Summer	29.024 *	0.253 *	2.97	0.64

ns = not significant, \*  $p < 0.05$ .

Interestingly, summer showed higher  $g_s$  values to attain their maximum An for all taxa. Because of higher  $g_s$  values in winter, iWUE was lower than in summer. The ratio of a and b parameters represents the slope of iWUE relationship, ranked  $E. nitens > E. gloni > E. globulus$  in winter, and  $E. globulus > E. gloni > E. nitens$  in summer. *E. nitens* genotypes were that presented the highest reduction in average iWUE values (300%).

Full versus reduced model comparison of generalized linear model for season effects was significant ( $F = 35.14, p > 0.001, R^2 = 0.43$ ). We observed a significant interaction between absolute WSI and season ( $F = 9.98, p > 0.001$ ), because the direction of the relationship between these variables changed with seasons. In winter, we observed a positive correlation between absolute WSI and iWUE ( $iWUE = 67.742 + 0.268 * WSI$ ), where genotypes with higher absolute WSI had increased iWUE. On the other hand, in summer, we observed a negative correlation between absolute WSI and iWUE ( $iWUE = 62.708 - 0.178 * WSI$ ), indicating that more stressed genotypes were not able to use water efficiently. We also observed a significant effect of taxa level in winter ( $F = 3.45, p = 0.021, R^2 = 0.13$ ) and summer ( $F = 5.85, p = 0.001, R^2 = 0.21$ ). Only *E. nitens* was different at the slope coefficient, compared to *E. globulus* and *E. gloni*. In winter, we observed that the increase in iWUE with the increase in WSI was more pronounced in *E. nitens* (Figure 2a). The same was observed in summer, with a decrease in iWUE with an increase in WSI (Figure 2b).

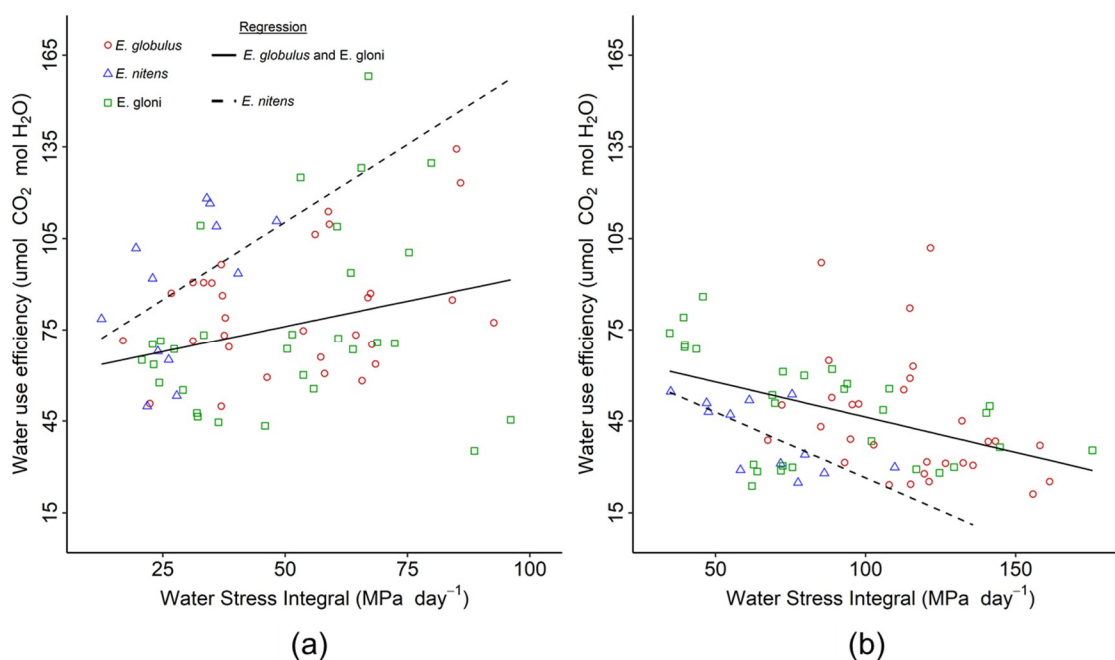


Figure 2. Adjusted regression lines for winter (a) and summer (b) periods for eucalyptus genotypes.

#### 4. Discussion

This study evaluated the changes in physiological variables in the early development of different eucalyptus genotypes during different seasons. A limited number of experiments have tested how genotypes physiological responses perform according to changes in temperature and atmospheric demand. This is very important considering that many studies have shown the importance of changes in temperature and atmospheric demand on forest development [12–14]. Similar to the study of Butnor et al. [15], small values of  $A_n$  were observed during winter (low temperatures), which suggested that cooler temperatures in winter affected plant metabolism.

Hikosaka et al. [16] observed that  $A_n$  and  $g_s$  may increase or decrease if temperatures are below or above the optimum, consequently affecting  $iWUE$ . At the study site, the average optimum temperature for eucalyptus growth was 16 °C [2], which was observed in summer periods. Considering that the plants were well-watered, this could be the reason for the higher maximum  $A_n$  values in summer compared to winter for all taxa. However,  $A_n$  declined with maximum temperatures above 30 °C [17], which suggested that maximum  $A_n$  is not stable during summer days. Negative relationship between temperature and  $A_n$  was observed by Aspinwall et al. [18], which suggested that eucalyptus responses reflect a common homeostatic constraint to seasonal changes in temperature.

The increase in  $g_s$  values was also observed in summer periods, mainly because  $g_s$  responded to the increase in photosynthetic active radiation (PAR), as always observed in summer months [19]. On the other hand, with an increase in  $g_s$ , we observed a decrease in  $iWUE$  in summer, with higher atmospheric demand mainly for *E. nitens* (300%). This was different from the results of other studies, which showed stomatal closure as the first physiological response to water stress [20]. This could be caused by lower soil water content or higher VPD. Lim et al. [21] highlighted that wet tropical eucalyptus plantations and well-watered experiments do not follow a pattern of strong VPD effect on  $g_s$  and  $A_n$  reduction; these could be the reason why high VPD in summer did not present a reduction in  $g_s$  values.

Larger values of WSI were observed among eucalyptus genotypes in winter periods, ranging from –12 to –96 MPa day<sup>-1</sup>, and between –34 and –181 MPa day<sup>-1</sup> in summer. Different relationships between WSI and  $iWUE$  among seasons were observed, indicating a possible interaction effect of temperature and WSI in response to  $iWUE$ . In winter, genotypes with higher absolute WSI also presented higher  $iWUE$ . Higher values of leaf water potential, which increased WSI, acclimated genotypes to maintain lower stomatal conductance [22]; this was more pronounced in *E. nitens*. In contrast, in summer, stressed genotypes had lower  $iWUE$ , indicating higher water loss from the leaf due to stomatal opening. Differences in regression lines indicated that *E. nitens* was more physiologically sensitive to changes in WSI in both seasons, presenting higher stomatal control to limit water loss when cumulative water conditions were less favorable, as observed in the study of Gauhier and Jacobs [23] on *Juglas nigra* L trees. Future studies may provide drought responses during summer periods to observe that physiological variables will respond in a similar way when compared with well-watered treatments.

#### 5. Conclusions

High incremental changes in photosynthesis were observed in summer months for almost all eucalyptus genotypes, showing its positive relationship with temperature in well-watered experiments. Because of irrigation during summer, soil water availability was not a constraint, and stomatal conductance followed photosynthesis behavior, decreasing intrinsic water use efficiency during periods of higher atmospheric demand when compared to winter. Significant relationships were observed between water stress integral and intrinsic water use efficiency in different seasons and taxa. We demonstrated that *E. nitens* was more sensitive to changes in water stress integral, and less tolerant to drought than *E. globulus* and *E. gloni*.

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