

## Article

# The Impact of Long-Term Dry-Season Irrigation on *Eucalyptus* Tree Height Growth: Insights from Leaf Photosynthesis and Water Conduction

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**Abstract:** Tree height is a crucial characteristic of plant ecological strategies and plantation productivity. Investigating the influence of dry-season irrigation on the tree height growth in *Eucalyptus* plantations contributes to a deeper understanding of precise improvement and sustainable development in such plantations. We conducted a field experiment in a *Eucalyptus* plantation with three-year fertilization and five-year dry-season irrigation to compare their effects on height growth rate during wet vs. dry seasons. Our findings revealed that long-term dry-season irrigation significantly increased the height growth rate of *Eucalyptus urophylla* × *E. grandis* by improving leaf hydraulic conductivity and photosynthetic rate during the dry season. However, in the wet season, the tree height growth rate in the fertilization treatment outperformed the other treatments significantly. Interestingly, we also found that leaf photosynthetic capacity contributed more to accelerating height growth than water conduction within the leaves. By examining the differences in leaf structural and functional traits, our results shed light on the impact of long-term dry-season irrigation on the height growth of *E. urophylla* × *E. grandis* plantations. Furthermore, this research provides both theoretical and empirical evidence supporting the application of dry-season irrigation and the potential for further enhancing plantation productivity in seasonally arid areas.

**Keywords:** height growth rate; photosynthetic rate; leaf hydraulic conductivity; *Eucalyptus* plantation



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## 1. Introduction

The *Eucalyptus* tree, widely known for its economic and ecological significance, plays a crucial role in various industries, including timber, paper, and biomass production [1]. *Eucalyptus* plantations are widely cultivated in the southern region of China, which is characterized by a subtropical monsoon climate featuring distinct dry and wet seasons. Specifically, the dry season spans from October to March of the subsequent year, during which the annual precipitation accounts for less than 20% of the total rainfall [2]. Relevant studies have demonstrated that the growth of *Eucalyptus* is adversely affected during the dry season due to water scarcity [3–5]. Hence, delving into the physiological mechanisms by which *Eucalyptus* plantations adapt to dry-season irrigation becomes essential in driving their growth and productivity to new heights.

The growth of trees requires plants to synthesize organic matter through photosynthesis and obtain sufficient water to maintain the normal metabolism of canopy organs. *Eucalyptus* trees are highly dependent on water availability for their physiological processes, including photosynthesis and water conduction [6]. Photosynthesis, the primary

process responsible for converting solar energy into chemical energy, directly influences the growth and development of trees [7,8]. Studies have shown that water scarcity significantly reduces photosynthetic activity [9,10], leading to decreased growth rates in *Eucalyptus* trees. Additionally, water conduction, the process through which water is transported from roots to leaves, plays a crucial role in maintaining water balance and facilitating tree growth [11–13]. Previous studies have commonly examined the effects of water availability on *Eucalyptus* growth by analyzing traits associated with photosynthesis and water conduction separately [3,14,15]. However, there is a lack of research examining the extent to which leaf photosynthesis and water transport contribute to the growth of *Eucalyptus* tree height under dry-season irrigation in seasonal arid regions.

Structural traits have significant effects on regulating both leaf photosynthesis and hydraulic functions in plants [16–18]. Among these, leaf thickness and vein density play critical roles in regulating leaf photosynthetic rate and hydraulic conductivity. Leaf water conductivity refers to the ability of leaves to effectively transport water to chloroplasts and has an impact on the accumulation of carbon in leaves [19]. Leaf thickness is a key factor in regulating the diffusion distance for CO<sub>2</sub> to reach the chloroplasts. Furthermore, it can impact the movement of water to the photosynthetic site and its subsequent transpiration from the leaf [20,21]. Additionally, leaf veins serve as the pathway of least resistance for water transport within leaf blades, and their abundance also determines the speed of transport [22]. Increased vein density and reduced leaf thickness can effectively reduce the transportation distance for CO<sub>2</sub> and H<sub>2</sub>O, thereby enhancing the photosynthetic rate and leaf hydraulic conductivity [21,23].

Furthermore, fertilization practices are commonly employed in *Eucalyptus* plantations to enhance growth and productivity, but the productivity of *Eucalyptus* plantations in China lags behind that of countries such as Brazil [24]. Therefore, by modifying traditional planting practices, we aim to optimize the productivity of *Eucalyptus* plantations by implementing drip irrigation during the dry season, aiming to alleviate the growth limitations imposed by seasonal drought on plantations. Previous studies have suggested that fertilization can improve photosynthetic efficiency and water uptake capacity in trees [25,26]. However, the impact of long-term dry-season irrigation after fertilization on leaf photosynthesis and water conductivity capacity during both wet and dry seasons still lacks research.

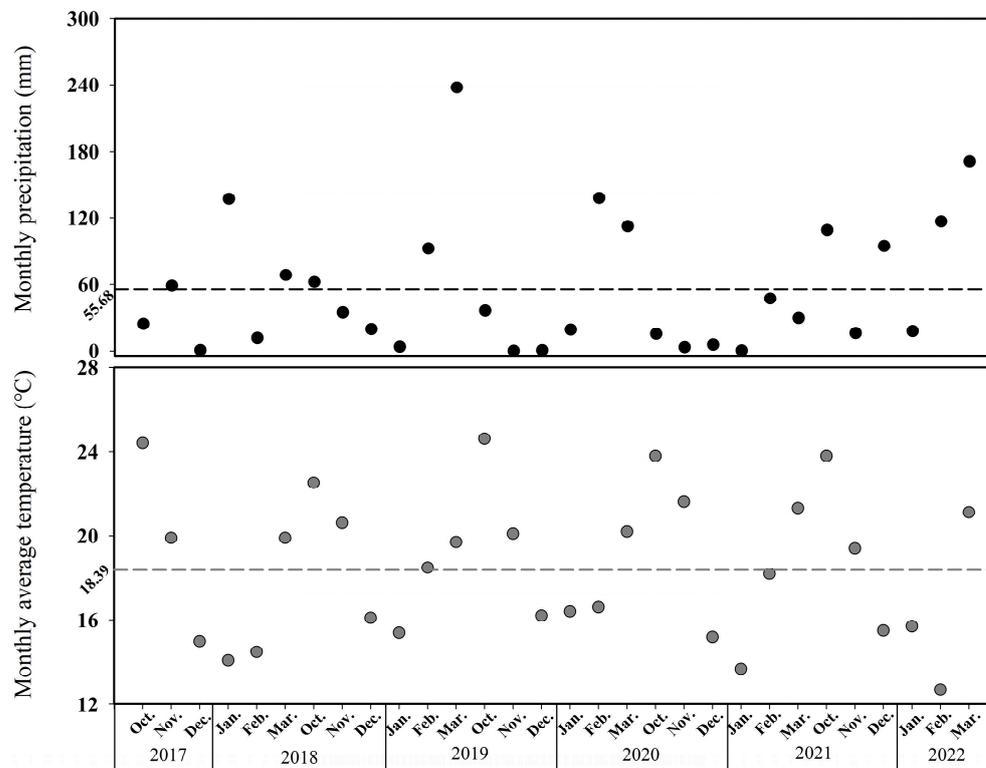
In this study, various dry-season irrigation and fertilization treatments were implemented for the *E. urophylla* × *E. grandis* plantations. Height growth rate, leaf functional traits, and structural traits were determined among the four different treatments. We aim to investigate the following inquiries: (1) How does dry-season irrigation affect the leaf structural and functional traits of *E. urophylla* × *E. grandis* plantations during both wet and dry seasons? (2) How do these alterations affect the plant height growth rate under dry-season irrigation?

## 2. Materials and Methods

### 2.1. Study Site and Plant Material

The experimental forest site was situated at the Teaching & Research Base of South China Agricultural University (SCAU) in Zengcheng District, Guangzhou (23°14'48" N, 113°38'20" E). This region has a typical subtropical monsoon climate with an average annual precipitation of approximately 1900 mm, with the majority occurring during the wet season from April to September. The average annual temperature is 21.6 °C. Analysis of meteorological data for Guangzhou City reveals that during the dry season from 2017 to 2022, Zengcheng District experienced an average monthly precipitation of only 55.68 mm (Figure 1). Additionally, the average monthly temperature of 18.39 °C during the dry season falls within the temperature range associated with maximum growth of *Eucalyptus* trees, as studies have shown that temperatures above 18 °C are conducive to their growth [27]. The soil is the common red soil in South China. The initial experimental soil conditions were as follows: pH: 4.92, organic matter: 7.03 g/kg, total nitrogen: 0.35 g/kg, total phosphorus: 0.15 g/kg, and total potassium: 8.83 g/kg. The field water holding capacity of the soil was

20.41%, with a bulk density of 1.55 g/cm<sup>3</sup>. In April 2017, healthy *E. urophylla* × *E. grandis* seedlings, measuring approximately 20–35 cm in height and free from any signs of disease or mechanical damage, were planted under optimal conditions. The planting density was 1667 plants per hectare.

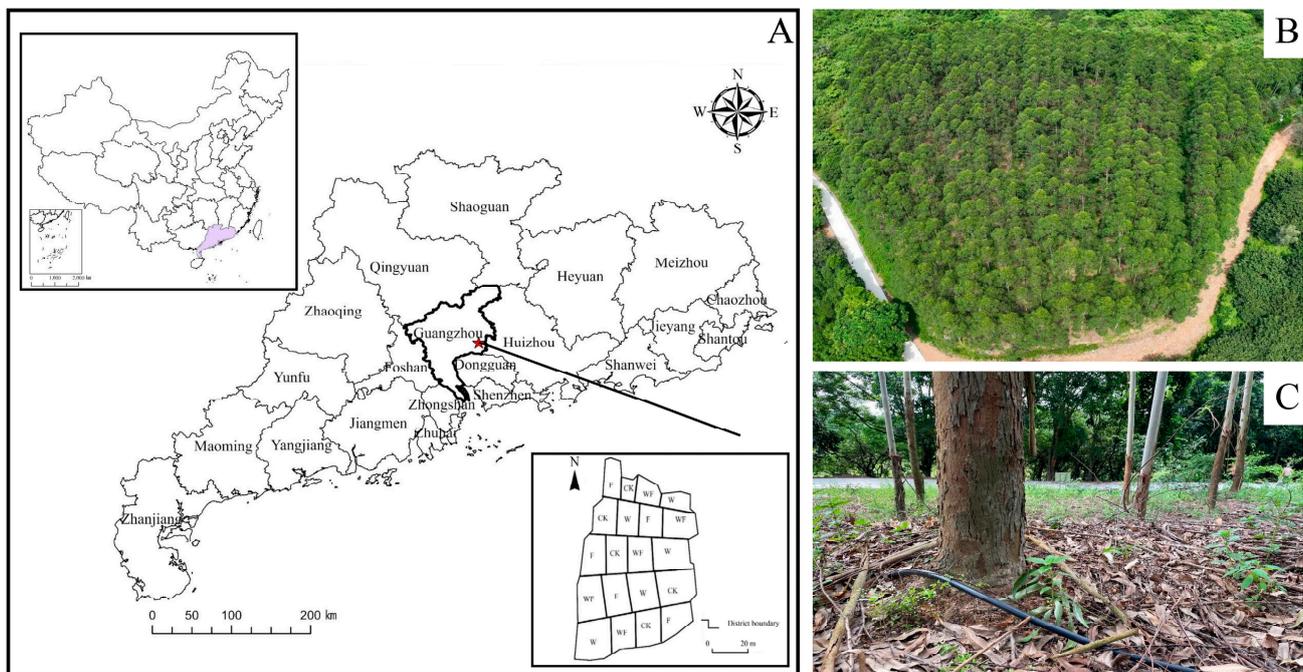


**Figure 1.** The monthly precipitations and average temperatures in the dry seasons of Zengcheng District, Guangzhou, from 2017 to 2022. Dash lines indicate the average monthly precipitation (55.68 mm) and the average monthly temperature (18.39 °C), respectively.

## 2.2. Experimental Design

The experiment utilized an orthogonal design, incorporating irrigation and fertilizer treatments [5]. During the dry season of each year, water was provided exclusively through drip irrigation equipment. The forestland was partitioned into five terraces, with each terrace housing four distinct treatments, as illustrated in Figure 2. The plots varied in size from 20 to 92 trees and were arranged randomly. The treatments for each terrace consisted of (1) a blank control group (CK); (2) dry-season irrigation only (W); (3) conventional fertilization only (F); and (4) both dry-season irrigation and fertilization (WF). To minimize interference from neighboring treatments, the measured trees were positioned in the center of each treated plot. Dry-season irrigation involved a 4 h duration, maintaining the soil's relative water content (measured at a depth of 40 cm and 40 cm away from the trees) above 80% for three days following irrigation. Drip irrigation was applied for a total of 8 h per week at a rate of 4 L/h, amounting to 32 L/week per tree. The irrigation period spanned from 1 October 2017 to 31 March 2022, covering five consecutive dry seasons. The collected precipitation in the wet season and some groundwater were used for irrigation. A waterproof and anti-corrosion partition, 50 cm in depth, was buried between each treatment plot. According to Yang et al. [28], although the soil water content fluctuated, the treatments with dry-season irrigation (W and WF) were almost always higher than those without water supply (CK and F). Fertilizer application rates matched those typically used for *Eucalyptus* production in China and were sourced from Guangdong Dayi Agroforestry Ecological Technology Co. The foundation fertilizer was added in March 2017 with 400 g per tree, with a total of 24 g N, 72 g P<sub>2</sub>O<sub>5</sub>, and 24 g K<sub>2</sub>O. For the F and WF treatments, the first superficial

fertilizer was provided in July with 300 g per tree and contained 45 g N, 21 g P<sub>2</sub>O<sub>5</sub>, and 24 g K<sub>2</sub>O. The second and third topdressings, with 400 g per tree containing 60 g N, 28 g P<sub>2</sub>O<sub>5</sub>, and 32 g K<sub>2</sub>O, were applied in July 2018 and July 2019, respectively. Fertilization was carried out continuously for three years (F and WF), consistent with prevailing practices in *Eucalyptus* plantations across China. Following five years of treatment, data collection was conducted in August and October of 2021, as well as January of 2022. Each plot was replicated three times, resulting in a total of 15 samples per treatment group.



**Figure 2.** The information on experimental plots (A), overview of the site (B), and the dry-season irrigation facilities (C). CK, W, F, and WF represent control conditions, 5 years of dry-season irrigation, only conventional fertilization (only fertilizer in the first three years), and both dry-season irrigation and fertilization.

### 2.3. Measurement of Height Growth Rate

The tree height was measured using a comparative method with a special carbon fiber tall tree pruner (net length of 20 m). Tree height measurements were taken for all trees of the four treatments in August and October of 2021 and January of 2022 (a total of 745 trees). By calculating the difference in tree height between two months and dividing it by the number of days elapsed, we determined the height growth rate ( $H_T$ ) of the wet and dry seasons, respectively, for each treatment.

### 2.4. Measurement of Leaf Functional Traits

Leaf gas exchange measurements were performed on cloudless days in August 2021 and January 2022, between 9:00 am and 11:00 am, with the Li6800 photosynthetic instrument (Li-Cor, Lincoln, NE, USA). For each treatment, three measurements were carried out, whereby the photosynthetic rate ( $A_n$ ) was measured in five fully developed leaves per plant. Therefore, a total of 225 values of the photosynthetic rate were measured for each treatment in each season. The photosynthetic photon flux density was set at 1500 mol m<sup>-2</sup> s<sup>-1</sup> to ensure consistent light-saturated photosynthetic rates among all treatments. Furthermore, we kept the ambient CO<sub>2</sub> levels at 400 μmol mol<sup>-1</sup> and temperature at 26 °C throughout all the measurements. To minimize the effects of vapor pressure deficit (VPD), the chamber's relative humidity was controlled within the range of 70% to 90%. Before measurement, the leaves were allowed to stand for 5–10 min under the above conditions to stabilize photosynthetic parameters.

Leaf hydraulic conductance ( $K_{\text{leaf}}$ ) was measured following the methods from Brodribb and Holbrook [29]. Branches with leaves were selected and cut at predawn and quickly put into black bags along with damp towels for 1 h. The initial water potential ( $\psi_{\text{leaf}}$ ) of leaves was measured with the pressure chamber (PMS Instruments, Albany, OR, USA). The adjacent leaves were then cut in water and rehydrated for 10 s. The water potential of the rehydrated leaves was immediately measured. Leaf hydraulic conductance was calculated using the following formula:

$$K_{\text{leaf}} = C \times \ln(\psi_0/\psi_f)/t$$

where  $C$  represents the leaf capacitance,  $\psi_0$  denotes the initial water potential,  $\psi_f$  represents the leaf water potential after rehydration, and  $t$  is the duration of rehydration (10 s). The values of  $C$  before and after turgor loss were determined by leaf pressure–volume relationships and normalized by leaf area, as follows:

$$C = \Delta\text{RWC}/\Delta\psi_1 \times (\text{DM}/\text{LA}) \times (\text{WM}/\text{DM})/M$$

where RWC indicates the relative water content, DM represents leaf dry mass (g), LA means leaf area ( $\text{m}^2$ ), WM represents the mass of leaf water at 100% RWC (g), and  $M$  is the molar mass of water ( $\text{g mol}^{-1}$ ). One branch per tree was sampled, and three values were measured for each branch, resulting in a total of 45 measurements for each treatment in each season.

### 2.5. Measurement of Leaf Structural Traits

Vein density was determined following the method described by Sack and Scoffoni [22]. Five leaves were sampled from each tree, and from each leaf, three rectangles (with an area of at least  $1 \text{ cm}^2$ ) were obtained from the top, middle, and bottom sections. These sections were then soaked in a 5%  $w/v$  NaOH/ $\text{H}_2\text{O}$  solution for a period of five days. Subsequently, the leaves were rinsed with water and immersed in a commercial bleach solution (6%  $w/v$  NaClO/ $\text{H}_2\text{O}$ ) for approximately 15 min. After a second rinse with water, the leaves were stained with a 1%  $w/v$  safranin/ethanol solution for 10 min. Following this, the leaves were kept in 100% ethanol for 20 min before being transferred back to water for imaging. Photos of each section were taken using an optical microscope equipped with a digital camera (Leica ICC50 W). The length of all veins in each image was measured using ImageJ software (version 1.53t) [30]. Leaf vein density ( $VD$ ) was calculated as the sum of vein length divided by the leaf area.

To obtain cross-sections, the top, middle, and bottom of each leaf were carefully cut. These sections were then photographed using the aforementioned light microscope. Furthermore, the leaf thickness ( $LT$ ) was measured using ImageJ software (version 1.53t). For  $VD$  and  $LT$ , a total of 225 values were measured for each treatment in each season, respectively.

### 2.6. Statistical Analysis

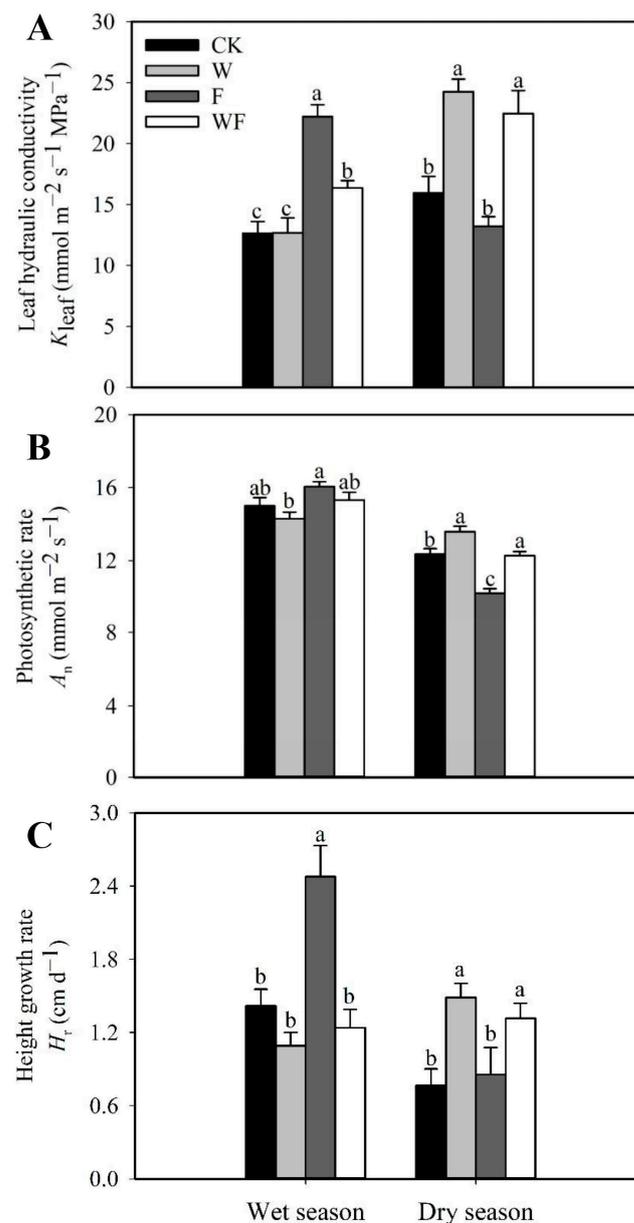
The ANOVA analysis was employed to compare trait values across the four treatments. Associations between measured traits were analyzed separately for the wet and dry seasons using Pearson correlation in SPSS (Chicago, IL, USA). To analyze all data together, standard major axis (SMA) regression was conducted using the SMATR software (version 2.0) [31]. Additionally, the “varpart” in the R package *vegan* v.2.5–6 [32] was utilized to estimate the unique contributions of  $K_{\text{leaf}}$ ,  $A_n$ , and leaf structural traits (including  $LT$  and  $VD$ ) to  $H_r$ .

## 3. Results

### 3.1. Response of Functional Traits to Five-Year Dry-Season Irrigation

The height growth rate ( $H_r$ ) and the leaf functional traits differed among treatments in the wet and dry seasons (Figure 3). For leaf hydraulic conductivity ( $K_{\text{leaf}}$ ), during the wet season, the trees subjected to fertilization (F and WF) exhibited a significantly higher

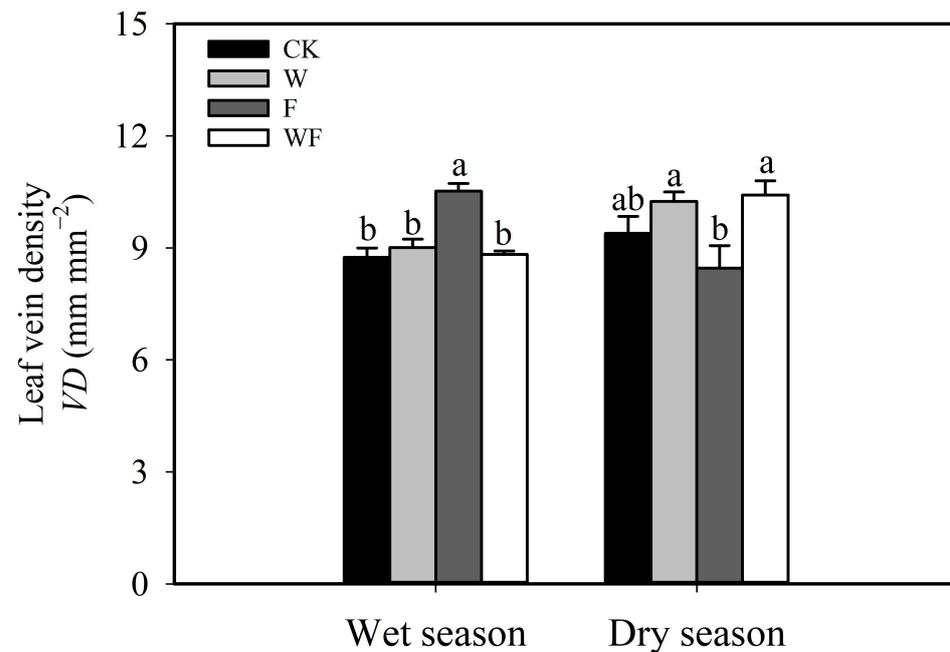
$K_{\text{leaf}}$  compared to the non-fertilized trees (CK and W); however, during the dry season, the  $K_{\text{leaf}}$  of the dry-season irrigation treatments (W and WF) was significantly higher than that of the non-irrigated treatment (CK and F) (Figure 3A). Regarding the photosynthetic rate ( $A_n$ ), during the wet season, there was no significant difference among the CK, F, and WF treatments, but the  $A_n$  of W was significantly lower than that of the F treatment. During the dry season, the  $A_n$  of the dry-season irrigation treatments (W and WF) was significantly higher than that of the non-irrigated treatment (CK and F) (Figure 3B). As for the height growth rate ( $H_r$ ), during the rainy season, there was no significant difference among the CK, W, and WF treatments, but they were all significantly lower than the F treatment. During the dry season, the  $H_r$  of the dry-season irrigation treatments (W and WF) was also significantly higher than that of the non-irrigated treatment (CK and F) (Figure 3C).



**Figure 3.** Leaf hydraulic conductivity (A), photosynthetic rate (B), and height growth rate (C) of *Eucalyptus urophylla* × *grandis* under control conditions (CK), dry-season irrigation (W), fertilization (F), and both dry-season irrigation and fertilization (WF) in wet season and dry season. Lowercase letters indicate significant differences ( $p < 0.05$ ). The total values for analysis were 360 (A), 1800 (B), and 1490 (C), respectively.

### 3.2. Response of Structural Traits to Five-Year Dry-Season Irrigation

Different treatments did not have a significant effect on leaf thickness (*LT*), but they significantly affected leaf vein density (Figures 4 and S1). During the wet season, the F treatment exhibited significantly higher leaf vein density (*VD*) compared to the other treatments, while during the dry season, the F treatment had the lowest *VD*. The *VD* of the dry-season irrigation treatments (W and WF) was significantly higher than that of the non-irrigation treatments (CK and F) during the dry season (Figure 4).



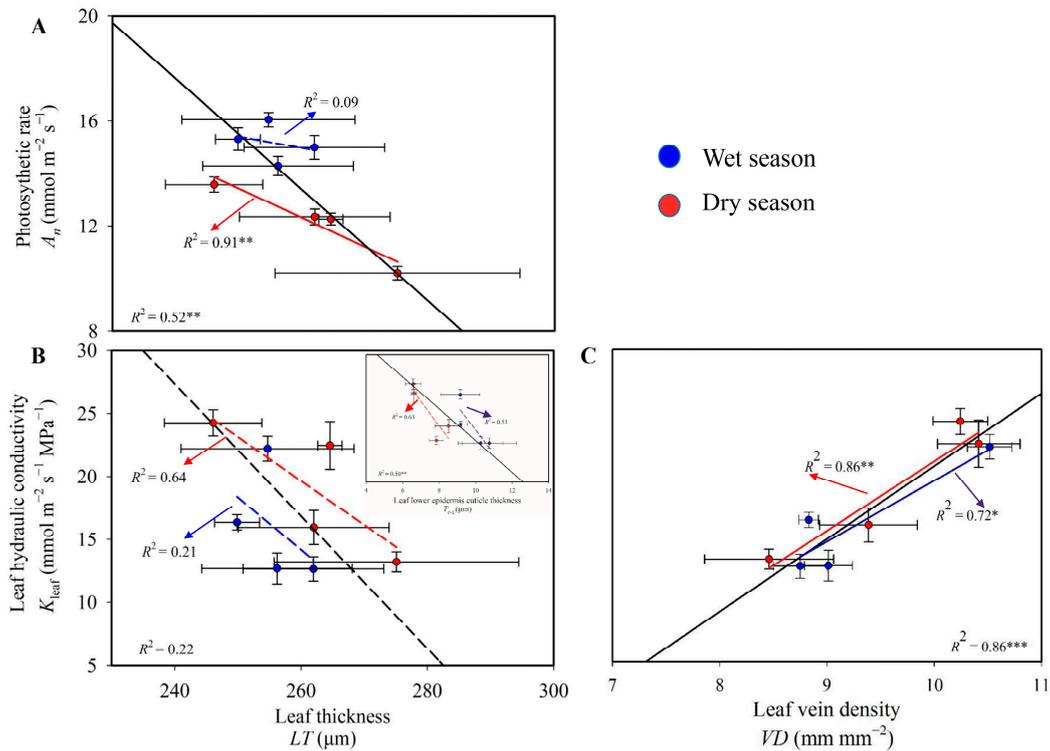
**Figure 4.** Leaf vein density of *Eucalyptus urophylla* × *grandis* under control conditions (CK), dry-season irrigation (W), fertilization (F), and both dry-season irrigation and fertilization (WF) in wet season and dry season. Lowercase letters represent significant differences ( $p < 0.05$ ). The total value for analysis was 1800.

### 3.3. Associations between Functional Traits and Structural Traits

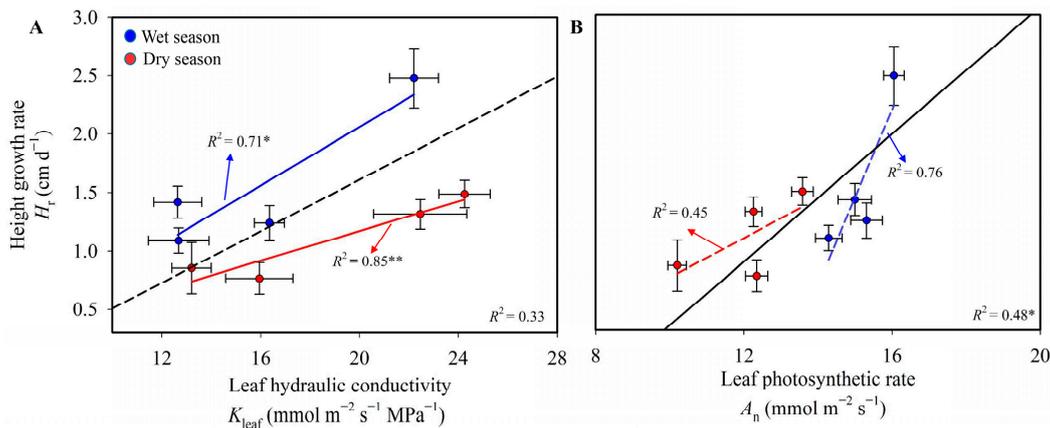
Overall, the *LT* showed a negative correlation with both  $A_n$  and  $K_{leaf}$  (Figure 5A,B). However, their relationships differed in the wet and dry seasons: in the dry season, the *LT* was significantly negatively correlated with  $A_n$ , but this relationship was not significant in the wet season. While the *LT* did not have a significant relationship with  $K_{leaf}$  in both the wet and dry seasons, the thickness of the leaf lower epidermis cuticle layer ( $T_{c-L}$ ) was significantly negatively correlated with  $K_{leaf}$ . Moreover, regardless of the season, there was a significantly positive correlation between *VD* and  $K_{leaf}$  (Figure 5C).

Both  $A_n$  and  $K_{leaf}$  had an impact on the  $H_r$  (Figure 6). The  $H_r$  and  $K_{leaf}$  were significantly correlated in both wet and dry seasons. Additionally, the  $H_r$  of different treatments was higher in the wet season than in the dry season (Figure 6A). The  $A_n$  was also significantly positively correlated with  $H_r$ , but their relationships were not significant in both wet and dry seasons (Figure 6B).

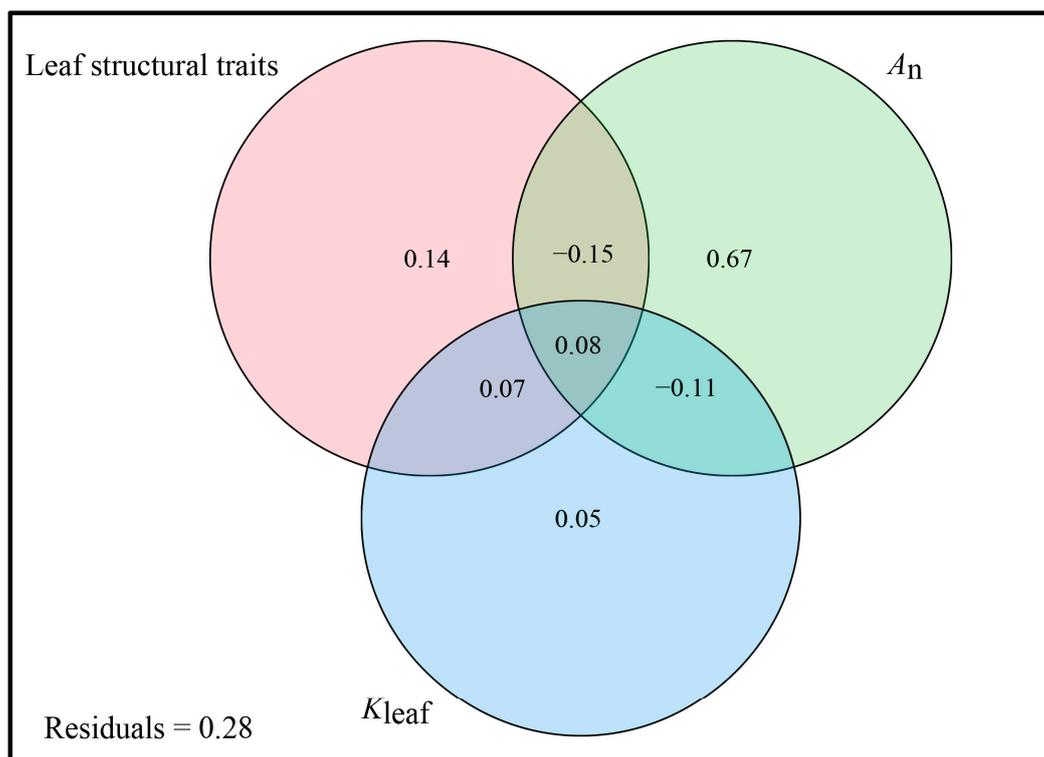
In order to determine the leaf traits that strongly influenced the height growth rate of *E. urophylla* × *grandis*, we assessed the individual impacts of  $A_n$ ,  $K_{leaf}$ , and leaf structural traits (*LT* and *VD*) on  $H_r$ . The unique effect of  $A_n$  and leaf structural traits on  $H_r$  were 67% and 14%, respectively, whereas that of  $K_{leaf}$  was only 5% (Figure 7).



**Figure 5.** Relationship between leaf structural traits and leaf functional traits. (A) Leaf thickness ( $LT$ ) and photosynthetic rate ( $A_n$ ); (B) leaf thickness ( $LT$ ) and leaf hydraulic conductivity ( $K_{leaf}$ ); (C) leaf vein density ( $VD$ ) and leaf hydraulic conductivity ( $K_{leaf}$ ). Blue and red circles with blue and red lines represent wet season and dry season, respectively. Standardized major axis (SMA) slopes (black lines) are indicated for all data together. Straight lines represent significant correlations: \*,  $p < 0.1$ ; \*\*,  $p < 0.05$ ; and \*\*\*,  $p < 0.01$ . Dash lines indicate no significant correlations. The values of  $A_n$ ,  $LT$ , and  $VD$  for each treatment in each season were averaged from 225 measurements, while  $K_{leaf}$  was obtained by averaging 45 measurements.



**Figure 6.** Relationship among functional traits. (A) Leaf hydraulic conductivity ( $K_{leaf}$ ) and height growth rate ( $H_r$ ); (B) photosynthetic rate ( $A_n$ ) and height growth rate ( $H_r$ ). Blue and red circles with blue and red lines represent wet season and dry season, respectively. Standardized major axis (SMA) slopes (black lines) are indicated for all data together. Straight lines represent significant correlations: \*,  $p < 0.1$ ; \*\*,  $p < 0.05$ . Dash lines indicate no significant correlations. The values of  $A_n$  and  $K_{leaf}$  for each treatment in each season were obtained by averaging 225 and 45 measurements, respectively. The values of  $H_r$  for each season were obtained by averaging 169 (CK), 212 (W), 178 (F), and 186 (WF) measurements, respectively.



**Figure 7.** The variance partitioning results of a comprehensive model of height growth rate ( $H_r$ ), incorporating leaf hydraulic conductivity ( $K_{leaf}$ ), photosynthetic rate ( $A_n$ ), and leaf structural traits, including leaf thickness ( $LT$ ) and leaf vein density ( $VD$ ) as explanatory variables. The results are presented as a percentage, representing the explained variance.

#### 4. Discussion

##### 4.1. Effect of Long-Term Dry-Season Irrigation on Plant Height Growth

Consistent with previous studies [33–35], we found that under well-hydrated conditions (during the wet season), the tree height growth rate was primarily influenced by fertilizer treatments. However, there were no significant differences between the WF treatment and the treatments without fertilizer (CK and W). During the dry season, the tree height growth of the W and WF treatments was not limited by drought due to sufficient water supply through drip irrigation, resulting in rapid growth, but there was no significant difference between them. This can be explained by two reasons. First, the external cause for the differential performance of tree height growth rates among different treatments during the wet and dry seasons in this study may be attributed to variations in soil nutrient availability (Table S1). Through five years of water supplementation, the nutrients increased by fertilization in the WF treatment were also utilized more in the previous dry seasons, which was consistent with previous studies where WF's growth was significantly higher than other treatments [4], resulting in no significant difference in tree height growth rates between the WF and W treatments during the dry season in this study. Similarly, in the F treatment, the fertilization nutrients were not fully utilized during the previous five years' dry seasons. Therefore, in well-watered conditions during the wet season, the F treatment exhibited significantly higher nutrient availability, leading to remarkable tree height growth. Second, a larger leaf vein density of the F treatment in the wet season and the W and WF treatments in the dry season can reduce leaf hydraulic resistance, thereby enhancing leaf water transport efficiency and promoting photosynthetic rates [19,21,36], ultimately promoting tree height growth. Moreover, although there were no significant differences in functional traits ( $K_{leaf}$ ,  $A_n$ , and  $H_r$ ) between the WF and W treatments during the dry season, the functional traits of the W treatment were consistently higher than those of the WF treatment. This may be due to the initial rapid growth of the

WF treatment, facilitated by sufficient water and nutrient conditions [4]. As tree height increases, the resistance to water transport to the canopy leaves increases [37], and the pathway for downward transport of organic matter becomes longer, requiring more energy consumption [38]. Therefore, compared to the shorter trees of the W treatment, the trees of the WF treatment may experience greater growth resistance, resulting in smaller functional traits during the dry season despite both treatments receiving supplemental irrigation.

Somewhat unexpectedly, the leaf thickness of all treatments did not change significantly during the wet or dry season. One possible explanation is that trees subjected to drought stress tend to increase leaf thickness, thereby elongating the water transport distance within the leaves and improving water use efficiency [21,39]. Additionally, taller trees tend to develop thicker and smaller leaves to reduce moisture evaporation [7,40]. Following three years of fertilization and five years of dry-season irrigation, the trees of the W and WF treatments displayed greater tree height. However, the trees of the F and CK treatments experienced more severe drought stress during the dry season. Therefore, all four treatments showed an increase in leaf thickness, resulting in no significant differences in leaf thickness among the treatments during the dry season. During the wet season, leaf thickness variations may be influenced more by genetic factors, as the differences in leaf thickness among the treatments were relatively small, given that they belong to the same tree species.

#### 4.2. Effect of Leaf Structural and Functional Traits on Plant Height Growth

In all four treatments during both wet and dry seasons, the height growth rate was significantly affected by leaf hydraulic conductivity and photosynthetic rate. This illustrates that the adaptations of H<sub>2</sub>O transport capacity and carbon assimilation capacity due to dry-season irrigation can enhance plant growth rate. Leaf resistance contributes to approximately 80% of the total resistance in plant water transport [41–44]. Research by Nardini and Salleo [45] revealed that *Laurus nobilis* had 92% of its water transport resistance located in its leaves. Leaves account for a significant proportion of the entire plant hydraulic pathway and are usually more susceptible to water stress compared to other plant organs [41,46], thus affecting leaf photosynthetic carbon assimilation [36]. Therefore, leaves may play a disproportionately important role in plant adaptation to drought [47]. In this study, the hydraulic conductivity of *E. urophylla* × *grandis* leaves significantly influenced tree height growth rates. *E. urophylla* × *grandis* trees that received dry-season irrigation maintained higher leaf hydraulic conductivity, allowing their height growth to remain unrestricted.

Notably, our findings revealed that carbon assimilation capacity had a significantly greater and distinct impact on the increase in height growth rate under prolonged dry-season irrigation when compared to leaf hydraulic conductivity and leaf structural traits. In Ochnaceae species, Schneider et al. [48] reported that enhancing stomatal anatomy to reduce the distance of CO<sub>2</sub> transport proved to be a more efficient strategy, as compared to modifying water transport structures such as increasing leaf vein density. In light of our discoveries, a plausible explanation could be that for plants, modifying water transport-related traits is a more resource-intensive process compared to altering CO<sub>2</sub> transport-related traits. This could lead to inadequate adjustments in leaf hydraulic conductivity and structural traits (*LT* and *VD*). Therefore, under dry-season irrigation, leaves of *E. urophylla* × *grandis* are more inclined to invest in other, more “cost-effective” traits to enhance photosynthetic carbon assimilation efficiency, thereby increasing tree height growth rates. We also found that leaf traits in our study cannot explain the 28% variation in tree height growth rates. As previously indicated by studies [49–52], other traits, such as root system characteristics and wood traits, may have additional effects on tree height growth rates. Therefore, future research should consider including more plant traits as variables in order to further investigate their impact.

However, our results also come with limitations. Our findings are based on *Eucalyptus* plantations in Guangzhou City and may not fully represent all seasonally dry regions, as differences in geographical location, climate, and soil can also influence *Eucalyptus* growth.

Furthermore, this experiment did not include additional treatments regarding the frequency and intensity of irrigation and the amount and type of fertilizer, which makes it difficult to accurately determine the optimal strategies for dry-season irrigation and fertilization.

## 5. Conclusions

We conducted a field experiment in a *Eucalyptus* plantation with three-year fertilization and five-year dry-season irrigation to compare their effects on height growth rate. Our results indicate that long-term dry-season irrigation has contrasting effects on the tree height growth rate of an *E. urophylla* × *grandis* plantation in southern China. During the dry season, long-term dry-season irrigation significantly enhanced the tree height growth rate of *E. urophylla* × *grandis* by improving leaf water transport efficiency and photosynthetic carbon assimilation efficiency. After 5 years of dry-season irrigation, the height growth rate of *Eucalyptus* trees was increased by 73% compared to non-irrigated conditions in the dry season. However, during the wet season, only the trees with fertilization treatment exhibited a higher height growth rate. Furthermore, our findings indicate that leaf photosynthetic capacity plays a more prominent role in accelerating the height growth rate compared to water conduction in leaves. These results provide valuable insights into the divergent impacts of long-term dry-season irrigation on tree height growth rate and also offer empirical evidence supporting the implementation of dry-season irrigation and the potential for enhancing plantation productivity in regions with seasonal aridity.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14102017/s1>, Figure S1: Leaf thickness of *Eucalyptus urophylla* × *grandis* under control conditions (CK), dry-season irrigation (W), fertilization (F) and both dry-season irrigation and fertilization (WF) in wet season and dry season; Table S1: The total nitrogen, total phosphorus, total potassium of the soil under control conditions (CK), dry-season irrigation (W), fertilization (F) and both dry-season irrigation and fertilization (WF).

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