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The Effects of Long-Term Precipitation Exclusion on Leaf Photosynthetic Traits, Stomatal Conductance, and Water Use Efficiency in *Phyllostachys edulis*

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Abstract: Ongoing climate change is projected to intensify drought stress globally. Understanding the response mechanisms of *Phyllostachys edulis* (Carrière) J. Houz. (moso bamboo) to long-term drought is crucial, given its significance as a carbon sequestration resource. In this study, precipitation exclusion was implemented to simulate drought stress and we investigated the effects of long-term drought on the photosynthetic parameters, stomatal conductance, and water use efficiency of moso bamboo. The results showed that throughout all growth seasons, the maximum net photosynthetic rates (P_{max}) of bamboo at all ages under long-term drought conditions (after 8 years of precipitation exclusion treatment) were significantly lower than those of the control ($p < 0.05$). It can be concluded that long-term drought reduced the maximum photosynthetic capacity of the bamboo at all ages. Under long-term drought conditions, there were many seasons where the light saturation point (LSP) of first-degree (1–2 years old) bamboo and third-degree (5–6 years old) bamboo under drought was significantly lower than those of the control, while the LSP value of second-degree (3–4 years old) bamboo under drought was significantly higher than that of the control. This suggests that long-term drought reduced the ability of first-degree and third-degree bamboo to utilize strong light, while improving the ability of second-degree bamboo to utilize strong light in summer, autumn, and winter. Under long-term drought conditions, the light compensation point (LCP) and the apparent quantum efficiency (AQY) of the bamboo decreased. It can be concluded that long-term drought reduced the ability of first-degree bamboo to utilize weak light in all seasons, as well as the ability of second-degree bamboo to utilize weak light in spring and autumn; meanwhile, it improved the ability of second-degree bamboo to utilize weak light in summer and winter, and the ability of third-degree bamboo to utilize weak light in spring, summer, and autumn. In the high light range (PAR*i* > 1000 $\mu\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$), there were significant differences in stomatal conductance (g_s) among different the different treatments of bamboo, which were influenced by both the growing season and the forest age. Compared to the control, under drought conditions, the stomatal conductance of third-degree bamboo increased in spring and that of the second-degree bamboo increased in autumn. The correlation analysis showed that the relationship between the stomatal conductance and vapor pressure deficit (VPDL) of bamboo under long-term drought conditions showed a significant polynomial relationship in both high and low light ranges. The correlation between the instantaneous water use efficiency (*iWUE*) and VPDL for the drought and control treatments of bamboo also showed a significant polynomial relationship in high light ranges. It was found that long-term drought changed the photosynthetic parameters of the bamboo, reflecting its ability to tolerate and adapt to drought in different seasons. Age-related differences in photosynthetic parameters should be fully considered in forest age structure adjustments and forest thinning procedures to strengthen the light intensity and maintain the opening of the stoma. These results provide a theoretical basis for the efficient and sustainable cultivation of bamboo under global climate change.

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1. Introduction

Low water availability has been considered the main environmental factor limiting plant growth and yield worldwide, and global climate change will likely increase drought stress and further limit plant productivity across a growing fraction of land area [1,2]. The plant water availability is decreased during drought, primarily due to the reduced osmotic potential, which limits the ability of plants to absorb water [3]. The performance of plants will be reduced during prolonged and severe drought events, the consequences of which include lower productivity [4] and an increased mortality rate [5]. It is well documented that one of the primary physiological impacts of drought is on photosynthesis [6–9]. Drought stress results in stomatal closure and reduced transpiration rates, decreased water potential of the plant tissues, decreased photosynthesis and growth, and the accumulation of the plant hormone abscisic acid (ABA) [6]. At the leaf level, the instantaneous water-use efficiency (*iWUE*), which quantifies the rate of carbon uptake per unit of water lost, represents a key characteristic of the ecosystem's functioning that is central to the global cycles of water, energy, and carbon [4,6,10–12]. Improving the plant *iWUE* and its capacity to tolerate reduced water availability has been a significant focus of scientific research [4,6,10–14]. A number of studies have already been conducted to determine the impact of drought stress (DS) on plant photosynthetic conditions [4,15–17]. These studies usually use gas exchange and the instantaneous water use efficiency as key metrics to evaluate the potential plant productivity [4,10,12,17,18] and adaptation to changing environmental conditions [12,19–22]. Instantaneous water use efficiency is a reliable indicator for determining how terrestrial ecosystems respond to climate change [12,14,23]. Given its importance in determining the relationship between forest productivity and the climate, accurately representing the relationship between stomatal conductance (g_s) and *iWUE* is crucial [12]. This can be estimated in several ways, but it is currently unclear how different measures of *iWUE* relate, and how well they each capture variation in *iWUE* with soil moisture availability [18,23].

Bamboo is widely distributed in Southeast Asia, Africa, and Latin America, playing a crucial role in ecosystem services and carbon cycling within terrestrial ecosystems. China is one of the countries with the largest distribution area of bamboo forests and the richest variety of bamboo resources, with a long history in bamboo production and utilization [24]. There are about 500 bamboo species in China, and in terms of bamboo distribution, bamboo value, and other economic values, moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz.) is the most important bamboo species [25]. Moso bamboo has the advantages of fast growth, early maturity, high yield, versatility, and high income, making it a vital plant whose plantation area is expanding at a rate of 3%, establishing bamboo forests as continuously growing carbon sinks [26–28]. However, in the context of global climate change, the frequency and intensity of extreme weather and climate events are increasing, posing an unprecedented threat to the structure and function of ecosystems. Water, as an important condition for plant growth, is closely related to the productivity of bamboo. Therefore, droughts have a significant potential impact on the productivity of bamboo forests [29,30]. The terrain of bamboo forests is complex and irrigation is difficult. Therefore, seasonal droughts in autumn and winter can hinder the growth of bamboo. Under limited water resources, enhancing the water use efficiency in bamboo forests is the key to improving productivity levels.

The research on bamboo has covered rich content [31], but there has been relatively little research on the dynamic changes in photosynthetic parameters, stomatal conductance, and instantaneous water use efficiency of bamboo with growth season and age, as well as its adaptability to long-term drought [31]. Therefore, this study conducted a precipitation exclusion experiment on bamboo in the field, and systematically studied and elucidated the temporal dynamic changes in photosynthetic parameters, stomatal conductance, and instantaneous water use efficiency of bamboo plants, as well as their response to simulated drought. This study indirectly revealed the regulatory strategies of leaf stomatal conductance and instantaneous water use efficiency in bamboo's adaptation to light and water environments.

In particular, water stress is a major environmental factor that negatively affects photosynthesis and causes water loss to carbon fixation in plants [18]. Such an increased scarcity of water resources is of great concern for cultivated trees like *Phyllostachys edulis*. It is thus of major importance to identify *Phyllostachys edulis* individuals with a high leaf instantaneous water use efficiency (*iWUE*, defined as the ratio of carbon assimilation (A) to transpiration (E), A/E [6,32]) to enhance the sustainability of future plantations. To improve the *iWUE* in cultivated plants, experts have proposed either decreasing the stomatal conductance (g_s) under well-watered conditions or increasing the responsiveness of stomata during the early stages of water stress [33]. Bamboo is a cloned plant with physiological integration characteristics [34], and the age-related structure of adult shoots is an important factor influencing the productivity of bamboo groves [34]. One study indicated that there are differences in the photosynthetic capacity of individuals of different ages in naturally growing moso bamboo [31]. Therefore, it is necessary to study the age-related differences in photosynthetic capacity for moso bamboo under long-term drought conditions. How the coupled effects between the drought and the light conditions on the g_s and the *iWUE* may vary among *P. edulis* plants of different ages during the different seasons has also not been examined.

Regulation of the g_s is an efficient means of optimizing the relationship between water loss and carbon uptake in plants [4,11,12,35]. The representation of stomatal regulation of transpiration and CO_2 assimilation is key to forecasting terrestrial ecosystem responses to global change [12]. Many studies have pointed toward stomatal control as a way to avoid or attenuate the negative impacts of droughts [3,4,18,35]. Under well-watered conditions, drought-sensitive individuals often exhibit higher g_s values than tolerant individuals, but tend to close their stomata at the early stages of the drought, thus avoiding soil water deficits [36]. However, the responses of the g_s and the *iWUE* of *P. edulis* to drought and their variation in individuals of different ages across the seasons are unknown. In this study, we compare the dynamic changes in photosynthetic properties, the g_s and leaf water use efficiency, under DS conditions for different ages of *P. edulis* during different seasons. The objective of this *P. edulis* cultivation was to establish a differentiation based on the g_s and the *iWUE* to examine the relationship between the g_s and the *iWUE* for bamboo plants of different ages, as well as their drought tolerance. The purpose of this study was to investigate the sensitivity of photosynthesis, stomatal conductance, and water use efficiency responses to soil water availability after long-term drought for *P. edulis*. We aimed to study how the stomatal control of *P. edulis* at different ages under different water conditions responds to and avoids or alleviates the negative effects of drought, and how it relates to synchronous changes in the water use efficiency. And our goal was to finally provide a theoretical basis for the efficient and sustainable cultivation of *P. edulis* under global climate change.

2. Materials and Methods

2.1. Study Site

The experiment was conducted at the Miaoshanwu Auxiliary Station of the Qianjiangyuan Forest Ecosystem Positioning Observation and Research Station of the State Forestry and Grassland Administration of China, located in the western suburbs of Fuyang District, Hangzhou (30°05′59″ N, 120°00′33″ E). The terrain of this area belongs to the Tianmu Mountains in the low-mountain and hilly area of western Zhejiang, and belongs to the subtropical monsoon climate zone. The annual average temperature is 16.1 °C, the highest temperature is 40.2 °C, the lowest temperature is −14.4 °C, and the average annual precipitation is 1441.9 mm. During the experimental period (2014–2023), the average annual precipitation in the sample plot was 1461.8 mm. The soil is classed as acidic red soil. The bamboo forest in the experimental area was planted in the 1960s and is a natural regeneration forest under extensive management. The physical and chemical properties of the soil were determined synchronously at this study site before our experiment. The soil organic carbon content of the Miaoshanwu bamboo forest is 38.44 $g \cdot kg^{-1}$, the soil nitrogen content is 2.85 $g \cdot kg^{-1}$, and the soil available phosphorus content is 6.03 $mg \cdot kg^{-1}$. Specific determination standards and test methods referred to forestry industry standards of the People's Republic of China (LY/T 1228-2015 [37], LY/T 1232-2015 [38], LY/T 1237-1999 [39], and so on), and all of the standards drafted by the Research Institute of Forestry, Chinese Academy of Forestry and issued by the State Forestry and Grassland Administration. Among them, this study's determination of the soil total nitrogen and available nitrogen was based on the standard of LY/T 1228-2015; the determination of the soil total phosphorus and available phosphorus was based on the standard of LY/T 1232-2015; and the determinations of the studied soil's total organic matter content was based on the standard of LY/T 1237-1999.

2.2. Method

2.2.1. Experimental Materials and Sample Site Setup

The experimental bamboo forest has on-years (years when many new shoots are produced) and off-years (years when no or few new shoots are produced) [40] (e.g., 2014 was an off-year, 2015 was an on-year, and so on). Six standard plots of 20 m $\times$ 20 m were established, with a slope of approximately 20°, facing due south, and an elevation of 169 m. The diameter at breast height and the height of bamboo plants within the sample plot were measured using a per wood detection method. The density of the bamboo forest in the sample plot was 3875 plants $\cdot$ hm^{-2}, with a canopy closure degree of 0.95. The diameters of the bamboo plants at breast height were 4.0–13.6 cm, with an average diameter of 9.8 cm and an average height of 13.2 m. There were almost no shrubs or herbs under the forest, but the surface was covered with a certain amount of litter, with an average thickness of about 2.0 cm. We thinned the mountain plants once every 2 years, without fertilizing or plowing, and only picked and dug spring bamboo shoots.

2.2.2. Design of Precipitation Exclusion Experiments

In late July 2014 (after achieving the growth of tall bamboo), six representative plots with a size of 10 m $\times$ 10 m were selected and set up among six standard plots (20 m $\times$ 20 m), including three natural growth (control) plots and three precipitation exclusion plots. The control and drought plots appeared in pairs and were separately surveyed for their background. The sparse shrubs were removed from three representative plots and the "ceiling method" was used to simulate the precipitation exclusion. A greenhouse for rainfall interception (with an area of 11 m $\times$ 11 m) was built by using a PVC waterproof board at a height of 1.5 m above the ground, and glue was used to bond the gaps between a plastic cloth and the bamboo joint. To ensure that the slope, terrain, and forest conditions in the drought plots were as consistent as possible with those in the control plots, one side of the greenhouse was aligned parallel to the contour line. A trench about 50 cm deep and 20 cm wide was excavated around the sample site, and a white iron sheet about 50 cm deep was buried along the trench. At the same time, a plastic film was laid inside the trench to prevent water from seeping in from the side and provide better drainage. After simulating precipitation exclusion using the ceiling method, the rainfall in the sample plot was reduced by 80% relative to the control. We only excavated similar trenches around the same site without any other treatment. This artificial precipitation exclusion drought experiment is still ongoing, with the bamboo still surviving in the precipitation exclusion plots, but the number of new bamboo has decreased compared to the control treatment each year.

2.2.3. Determination of Soil Moisture Content

During the experiment, when sampling and measuring the nitrogen content, four soil profiles were collected as representatives in the field test sample area. Soil samples at a depth of 0–20 cm were collected from each profile and brought back to measure the soil moisture content. In this experiment, the soil moisture content of the bamboo control plot was significantly higher than that of the rainfall drought control plot in each growth season. The average soil moisture content of the 0–20 cm soil in the control plot was 23.42 ± 1.09% to 30.15 ± 0.94% across each season, while the average soil moisture content of the 0–20 cm soil in the rainfall drought control plot for 1 year was 4.44 ± 0.87% to 4.92 ± 0.53% across each season.

2.2.4. Photosynthesis and Changes in Light Response Parameters

After 8 years of natural growth and precipitation exclusion treatment experiments, days with clear and cloudless weather were selected in October 2022 (autumn), December 2022 (winter), April 2023 (spring), and August 2023 (summer). With the help of temporary ladders and operating platforms in the field, photosynthesis was measured using a portable photosynthesis system (LI-6400, Li-Cor Inc., Lincoln, NE, USA) to analyze the light response curves of bamboo leaves from the different treatment groups (control and precipitation exclusion) in situ from 9:00 to 12:00 each morning. Moso bamboo forests have a biennial growth cycle: more than 90% of their new shoots are produced during the on-year, during which leaves of the old bamboo turn yellow; in the off-year, the leaves remain green [40]. Moso bamboo leaves are usually replaced with new leaves every 2 years. So, moso bamboo usually grows by one degree every two years, hence 1–2-year-old bamboo plants were named first-degree bamboo, and 3–4-year-old bamboo plants were named second-degree bamboo, and so on. Bamboo plants of different degrees (1–2-year-old individuals representing one degree of bamboo, and so on) were selected from the precipitation exclusion and control plots, and one bamboo plant for each different degree of growth was selected from each plot, ensuring they showed consistent growth and similar diameters at breast height, and 1–2 mature leaves were selected from the middle canopy for in situ measurements. So, a total of 18 bamboo plants were selected and tested from 6 sample plots. We utilized an open-air path with an air flow rate of 500 $\mu mol \cdot s^{-1}$, a leaf chamber temperature of 25 °C, an atmospheric CO_2 concentration of 400 $\mu mol \cdot mol^{-1}$, and a relative humidity of 60 ± 4%. Using the system's red and blue light sources, we set, from large to small, 1800, 1500, 1200, 1000, 800, 500, 200, 150, 120, 80, 50, 20, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation, after the instrument was calibrated and entered the working state; we recorded the measurement data, repeating the reading three times for each gradient. The instrument automatically recorded values such as the net photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (g_s), leaf-to-air vapor pressure deficit (VPDL), etc. According to the measured data, the classic model of Ye [40] was used to fit and calculate photosynthetic parameters such as the dark respiration rate (R_d), light compensation point (LCP), maximum net photosynthetic rate (P_n), and light saturation point (LSP). Finally, the average value of each fitted photosynthetic parameter was taken as the measured value for each degree. Then, we used P_n/T_r to calculate the instantaneous water use efficiency (*iWUE*) [32].

2.2.5. Data Analysis

Statistical analyses were conducted by using Microsoft Excel 2003 (11.0, Microsoft Corporation, Seattle, Washington state, USA) and SPSS16.0 (SPSS Corporation, Chicago, IL, USA). A one-way analysis of variance (ANOVA) ($p < 0.05$) was conducted to compare the effect of the drought stress on the photosynthetic parameters according to different ages by using the SPSS16.0 statistical software. For each bamboo plant, the average of three readings taken during the measurement of each photosynthetic index was taken as the final measurement value, which was used for the one-way analysis of variance. The least significant difference (LSD) method was used to determine significant differences between the means and multivariate groups of all parameters. The "non-linear" regression between the g_s and the *iWUE* was also analyzed for the two drought treatments according to the light range.

3. Results

3.1. Effects of Drought Stress on Photosynthetic Properties of P. edulis at Different Ages

The photosynthetic parameters showed variations between the long-term drought and control groups for the different ages of bamboo during different seasons (Figures 1–4). The maximum net photosynthetic rate (P_{max}) refers to the maximum absolute value of photosynthesis of plant leaves under optimal environmental conditions [41,42].

The results showed that in all growth seasons of the year, the maximum net photosynthetic rates (P_{max}) of bamboo at all ages under long-term drought conditions (after 8 years of the precipitation exclusion treatment) were significantly lower than those of the control ($p < 0.05$). In spring and summer, these values were higher for third-degree (5–6 years old) bamboo than they were for second-degree (3–4 years old) bamboo; in autumn, these values were higher for second-degree bamboo than they were for first-degree (1–2 years old) bamboo; in winter, these values were higher for third-degree bamboo than they were for first-degree bamboo. In the control treatment, the P_{max} value showed significant differences among the different ages in spring, summer, and autumn, and the order of P_{max} values according to their size for each age was the same as that for the drought plants. It can be concluded that long-term drought reduced the P_{max} of the bamboo at all ages. There were significant differences ($p < 0.05$) in the P_{max} of *Phyllostachys edulis* among different ages under long-term drought conditions.

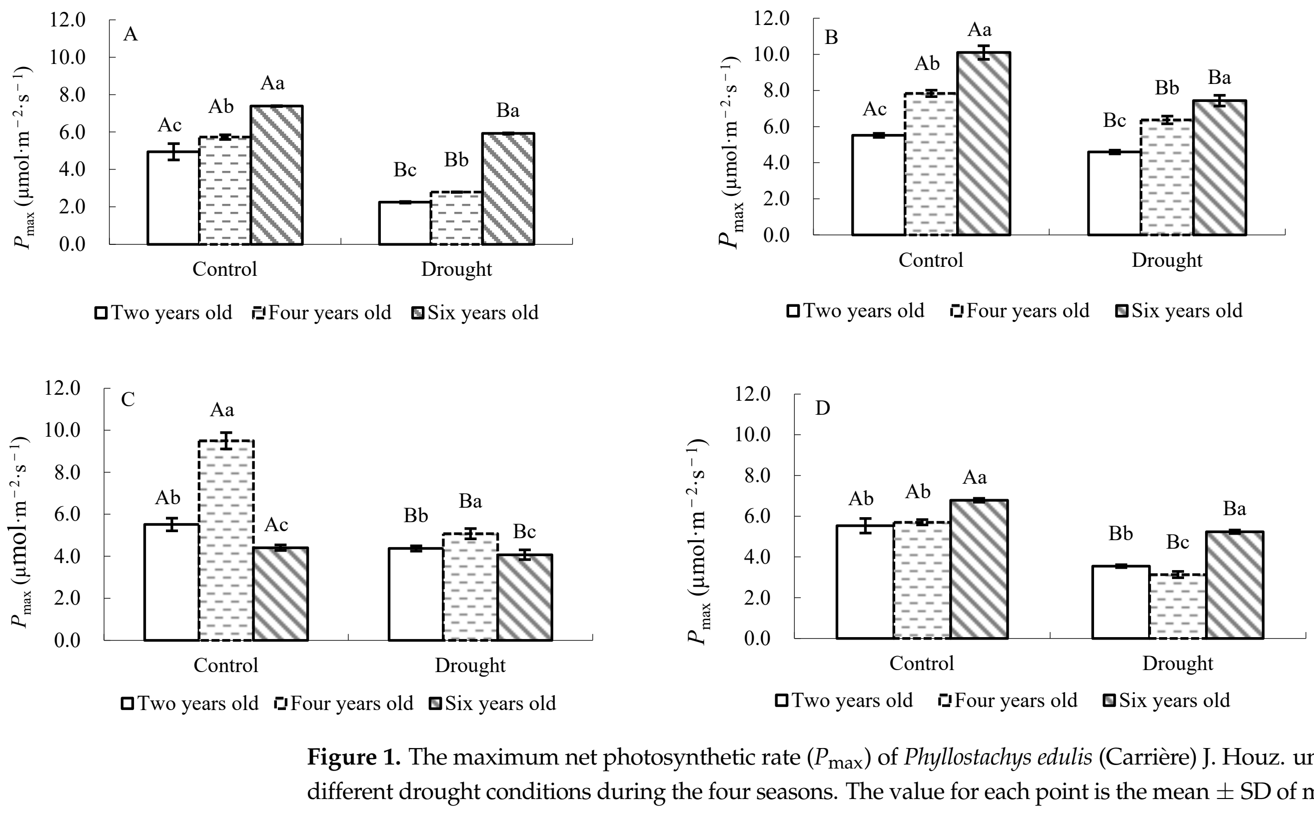

Figure 1. The maximum net photosynthetic rate (P_{max}) of *Phyllostachys edulis* (Carrière) J. Houz. under different drought conditions during the four seasons. The value for each point is the mean ± SD of more than eighteen measurements taken on the leaves from nine individuals (n = 9). Figures (**A**–**D**) denote spring, summer, autumn, and winter, respectively. The different capital letters (such as A, B, etc.) listed on each bar chart indicate significant differences among the drought treatments for individuals of the same ages ($p < 0.05$), and the different lowercase letters (such as a, b, c, etc.) listed on each bar chart indicate significant differences among individuals of different ages under the same drought treatment ($p < 0.05$). P_{max}—maximum net photosynthetic rate.

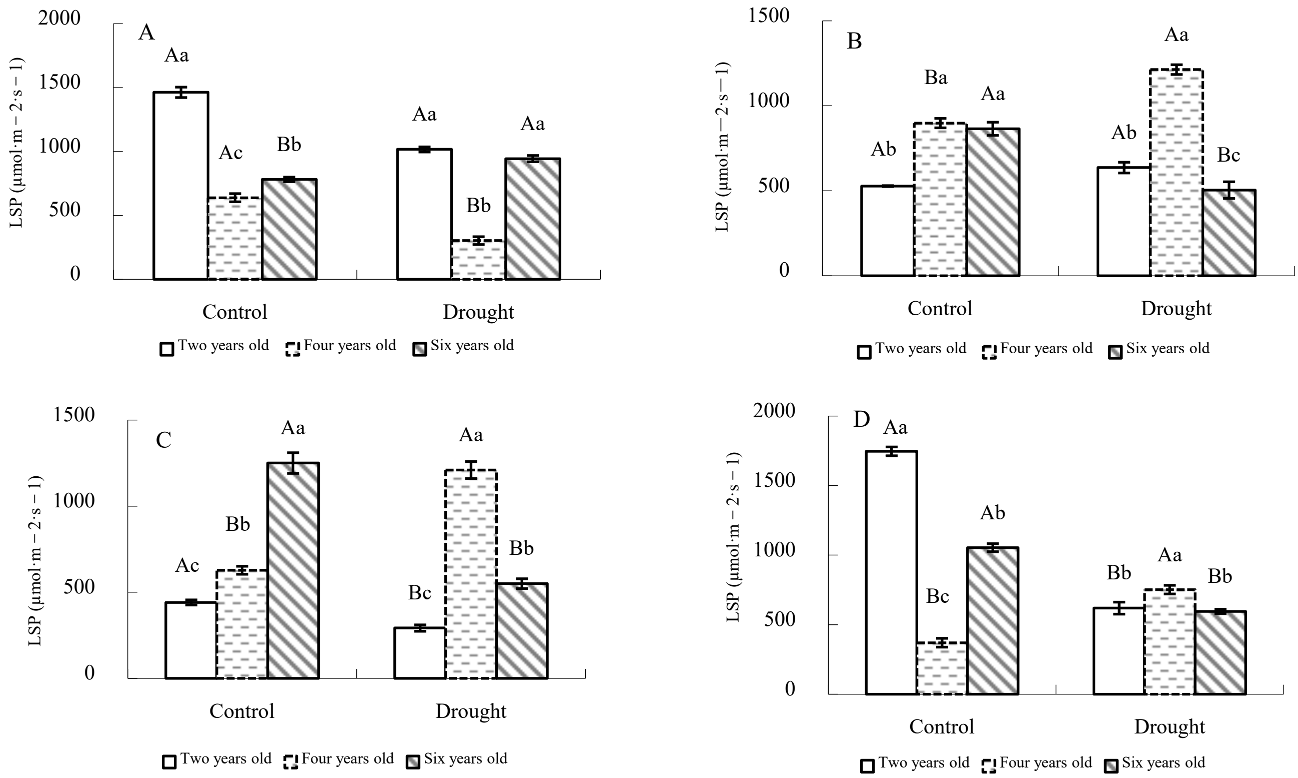

Figure 2. The light saturation point of *P. edulis* under different drought conditions during the four seasons. The value for each point is the mean ± SD of more than eighteen measurements taken on the leaves from nine individuals (n = 9). Figures (**A**–**D**) denote spring, summer, autumn, and winter, respectively. The different capital letters (such as A, B, etc.) listed on each bar chart indicate significant differences among the drought treatments for individuals of the same ages ($p < 0.05$), and the different lowercase letters (such as a, b, c, etc.) listed on each bar chart indicate significant differences among individuals of different ages under the same drought treatment ($p < 0.05$). LSP—light saturation point.

In our study, under long-term drought conditions, except for in the summer, the light saturation point (LSP) was significantly lower than that under the control conditions in all seasons for first-degree bamboo. Except for significantly lower LSP values in spring compared to the control, the LSP value of the second-degree bamboo under drought conditions was significantly higher than that of the control. Except for significantly higher LSP values in spring compared to the control, the LSP of the third-degree bamboo under drought conditions was significantly lower than of the control. Under long-term drought conditions, there were many seasons when the LSPs of the first-degree and third-degree bamboo were significantly lower than those of the control, and the LSP value of the second-degree bamboo under drought conditions was significantly higher than that of the control. It can be concluded that long-term drought reduced the ability of the first-degree and third-degree bamboo to utilize strong light, while improving the ability of the second-degree bamboo to utilize strong light in the summer, autumn, and winter.

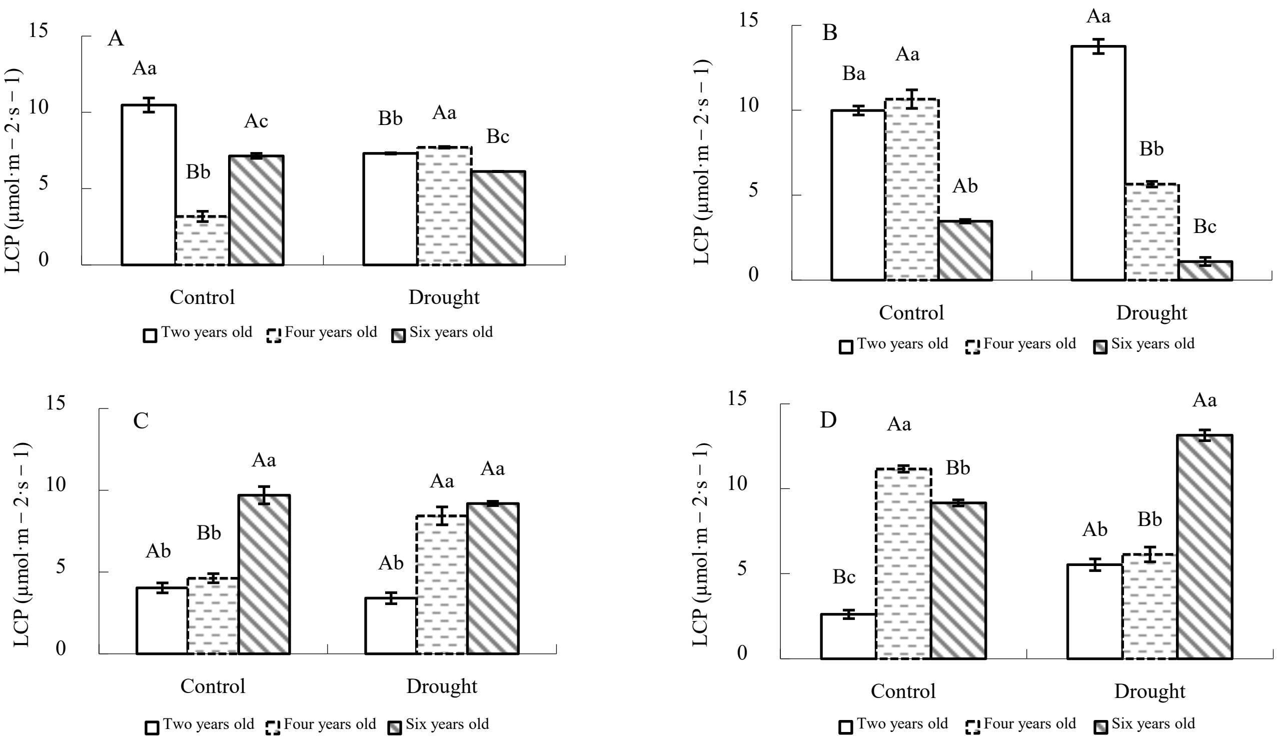

Figure 3. The light compensation points of *P. edulis* under different drought conditions during the four seasons. The value for each point is the mean ± SD of more than eighteen measurements taken on the leaves from nine individuals ($n = 9$). Figures (**A**–**D**) denote spring, summer, autumn, and winter, respectively. The different capital letters (such as A, B, etc.) listed on each bar chart indicate significant differences among the drought treatments for individuals of the same ages ($p < 0.05$), and the different lowercase letters (such as a, b, c, etc.) listed on each bar chart indicate significant differences among individuals of different ages under the same drought treatment ($p < 0.05$). LCP—light compensation point.

The light compensation point (LCP) refers to the light intensity at which the rate of carbon dioxide absorption via photosynthesis is equal to the rate of carbon dioxide released via respiration under certain conditions, causing an equilibrium state to be reached [43]. In this study, in spring, the LCP of the second-degree drought bamboo was significantly higher than of the control, while the LCPs of the bamboo of other degrees was significantly lower than that of the control. In summer, under drought conditions, the LCP of the first-degree bamboo was significantly higher than that of the control, while in other degrees, the LCP of this bamboo was significantly lower than that of the control. In autumn, under drought conditions, only the second-degree bamboo had a significantly higher LCP than that of the control. In winter, under drought conditions, the LCPs of the first- and third-degree bamboo were significantly higher than those of the control, while the LCP of the second-degree bamboo was significantly lower than that of the control.

Under long-term drought conditions, the light compensation points (LCPs) of bamboo in the spring and summer showed significant differences among the different ages ($p < 0.05$). It can be concluded that long-term drought conditions reduced the minimum level of light required for the zero net photosynthesis of first-degree bamboo in all seasons, and that of second-degree bamboo in spring and autumn, while these conditions improved the minimum level of light required for the zero net photosynthesis of second-degree bamboo in summer and winter, and that of third-degree bamboo in spring, summer, and autumn.

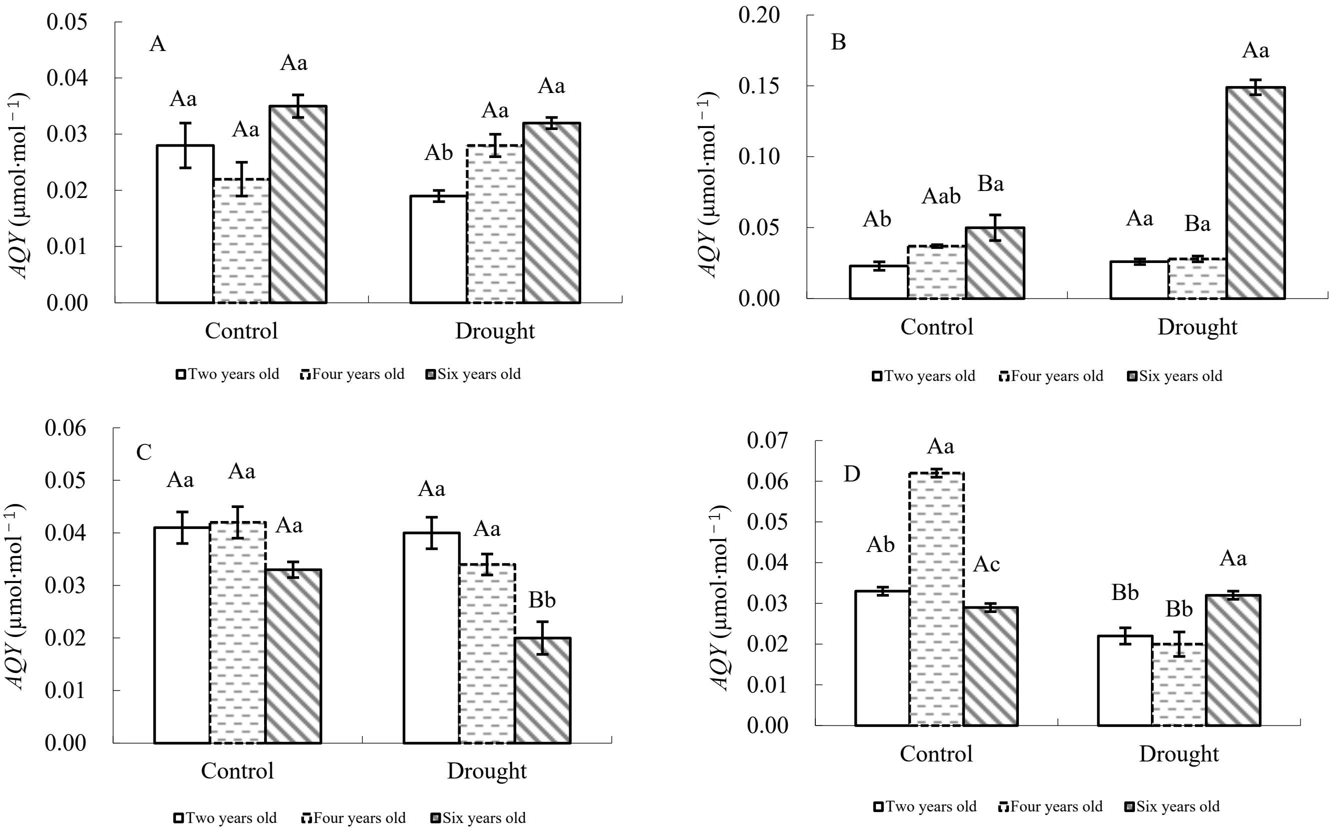

Figure 4. The apparent photon quantum efficiency of *P. edulis* under different drought conditions during the four seasons. The value for each point is the mean ± SD of more than eighteen measurements taken on the leaves from nine individuals (n = 9). Figures (**A**–**D**) denote spring, summer, autumn, and winter, respectively. The different capital letters (such as A, B, etc.) listed on each bar chart indicate significant differences among the drought treatments for individuals of the same ages (p < 0.05), and the different lowercase letters (such as a, b, c, etc.) listed on each bar chart indicate significant differences among individuals of different ages under the same drought treatment (p < 0.05). AQY—apparent photon quantum efficiency.

Under weak light, the photosynthetic rate increases sharply with the increase in light intensity, and the relationship between the two is linear, indicating that light is the only limiting factor of photosynthesis, and the slope of this line is the apparent photon quantum efficiency (AQY) [44]. This reflects the photosynthetic capacity of plants to absorb, convert, and utilize light energy under weak light [44]. It can be seen that under long-term drought conditions, the overall AQY of the bamboo decreased, indicating that the drought reduced the ability of the bamboo to utilize weak light.

3.2. Effect of Drought Stress on the Stomatal Conductance of P. edulis

Within the high light range (PARi > 1000 μmol · m^{-2} · s^{-1}), there were significant differences in stomatal conductance (g_s) among the different treatments of bamboo, which were influenced by both the growing season and the forest age (Figure 5). Compared to the control, under drought conditions, the g_s of the third-degree bamboo increased in spring and that of the second-degree bamboo increased in autumn, while that of all ages of bamboo under drought stress in the summer was lower than that of the control. During each growing season, the g_s of first-degree bamboo under drought conditions was significantly lower than that of the control. It can be concluded that under long-term drought conditions, the dynamic changes in g_s of bamboo at different ages were significantly influenced by the growing season.

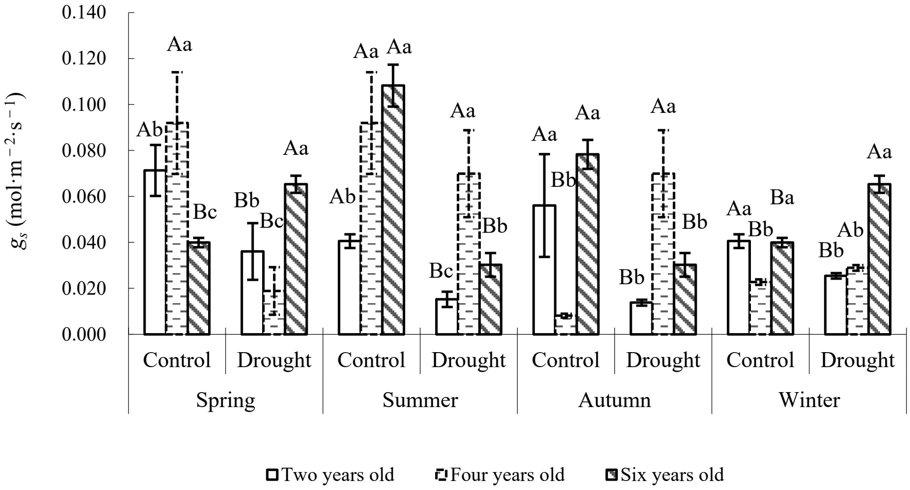

Figure 5. The variation in averages of the stomatal conductance (g_s) under photosynthetic active radiation (PAR*i*) of more than 1000 μmol·m^{-2}·s^{-1} for *P. edulis* plants of different ages under different drought conditions during the four seasons. The value for each point is the mean ± SD of more than eighteen measurements taken on the leaves from nine individuals (n = 9). The different capital letters (such as A, B, etc.) listed on each bar chart indicate significant differences among the drought treatments for individuals of the same ages ($p < 0.05$), and the different lowercase letters (such as a, b, c, etc.) listed on each bar chart indicate significant differences among individuals of different ages under the same drought treatment ($p < 0.05$). g_s—stomatal conductance.

3.3. Effect of Drought Stress on the Water Use Efficiency of *P. edulis*

The results showed that within the high light range, except for there being no significant difference in spring, the instantaneous water use efficiency (*iWUE*) of first-degree bamboo leaves was significantly lower than that of the control under drought conditions (Figure 6). The *iWUE* of third-degree bamboo leaves was significantly lower than that of the control under drought conditions. Except for significantly lower values being observed in autumn compared to the control, the *iWUE* values of second-degree bamboo leaves were significantly higher than those of the control under drought conditions. Under long-term drought conditions, the instantaneous water use efficiency of the bamboo varied among the different forest ages and was influenced by the seasons. In spring and winter, the *iWUE* value of the first-degree bamboo was significantly higher than that of the second-degree bamboo; in summer and autumn, the *iWUE* value of the second-degree bamboo was significantly higher than that of the first-degree and third-degree bamboo.

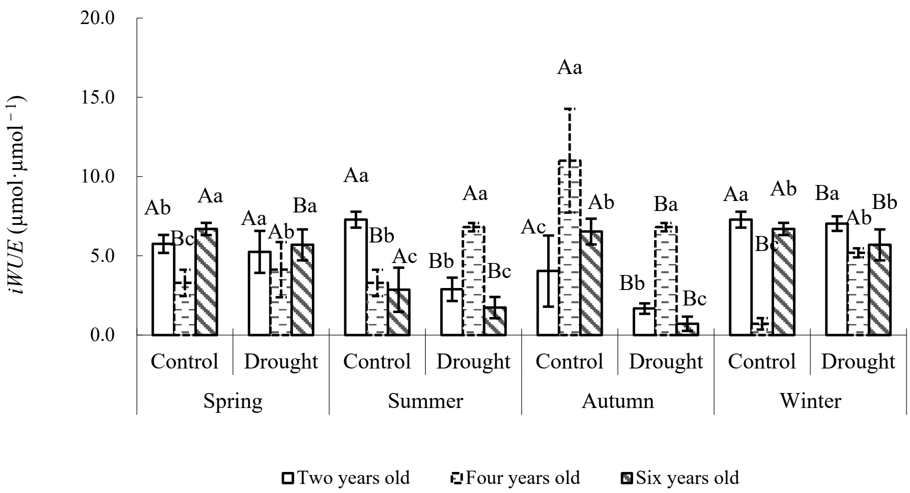

Figure 6. The variation in averages of the instantaneous water use efficiency (*iWUE*) under photosynthetic active radiation (PAR*i*) of more than 1000 μmol·m^{-2}·s^{-1} for *P. edulis* plants of different ages under different

drought conditions during the four seasons. The value for each point is the mean ± SD of more than eighteen measurements taken on the leaves from nine individuals (n = 9). The different capital letters (such as A, B, etc.) listed on each bar chart indicate significant differences among the drought treatments for individuals of the same ages ($p < 0.05$), and the different lowercase letters (such as a, b, c, etc.) listed on each bar chart indicate significant differences among individuals of different ages under the same drought treatment ($p < 0.05$). *iWUE*—instantaneous water use efficiency.

3.4. Relationship between Vapor Pressure Deficit, Stomatal Conductance, and Water Use Efficiency

Our "non-linear" regression analysis showed that the non-linear relationships between the stomatal conductance and vapor pressure deficit of bamboo leaves under the control treatment showed significant polynomiality in both high and low light ranges: that is, as the vapor pressure deficit of the leaves increased, the stomatal conductance first increased and then decreased (Figure 7a). The "non-linear" regression analysis showed that the relationship between the stomatal conductance and vapor pressure deficit of bamboo leaves under long-term drought stress was also a significant polynomial relationship, but only in the high light ranges (Figure 7b). In this case, as the vapor pressure deficit of the leaves increased, the stomatal conductance first decreased and then increased, which was opposite to the control treatment. A significant polynomial relationship between the stomatal conductance and the leaf-to-air vapor pressure deficit meant that there was a turning point during the process of the change.

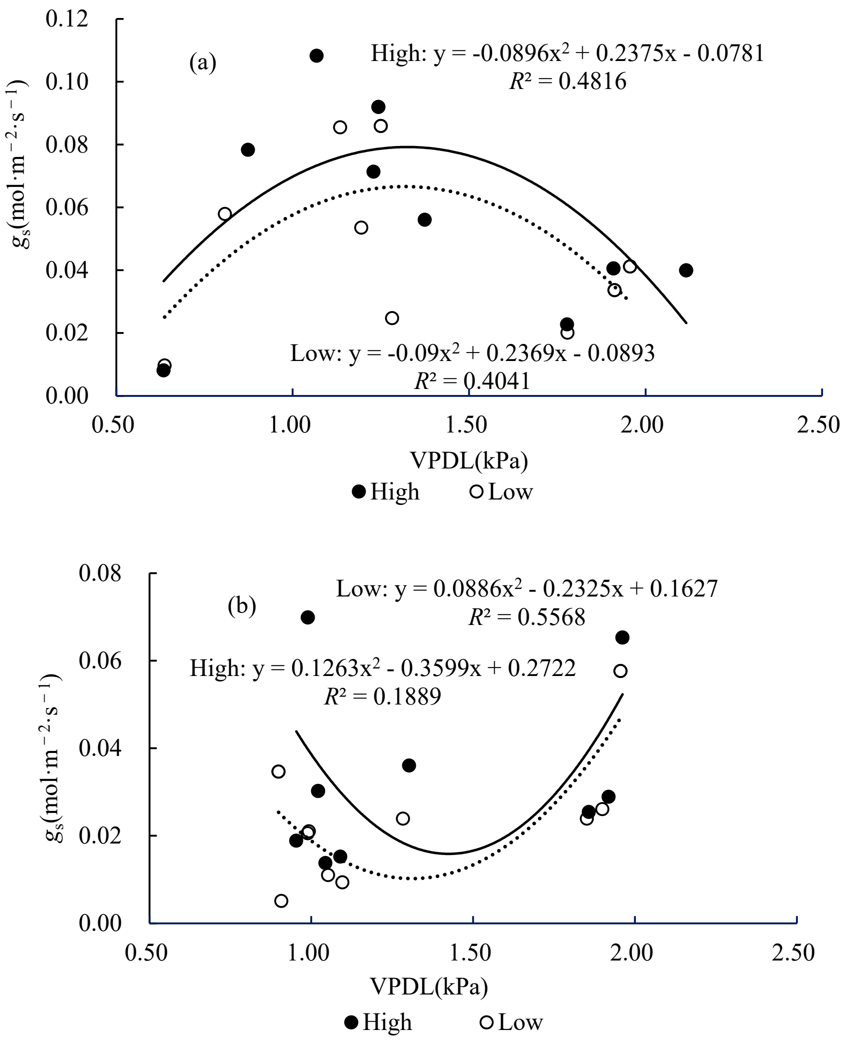

Figure 7. Relationship between the vapor pressure deficit (VPDL) and the average stomatal conductance (g_s) measured under photosynthetic active radiation (PAR*i*) of more than 1000 μmol·m^{-2}·s^{-1}

(High) or under PAR*i* of 500–1000 μmol·m^{-2}·s^{-1} (Low) for *P. edulis* plants of all ages across the seasons under different drought stress treatments. (**a**) Control; (**b**) drought. Solid circles represent points in the high light range, while hollow circles represent points in the low light range. The solid line represents the fitting of the high light range, and the dashed line represents the fitting of the low light range.

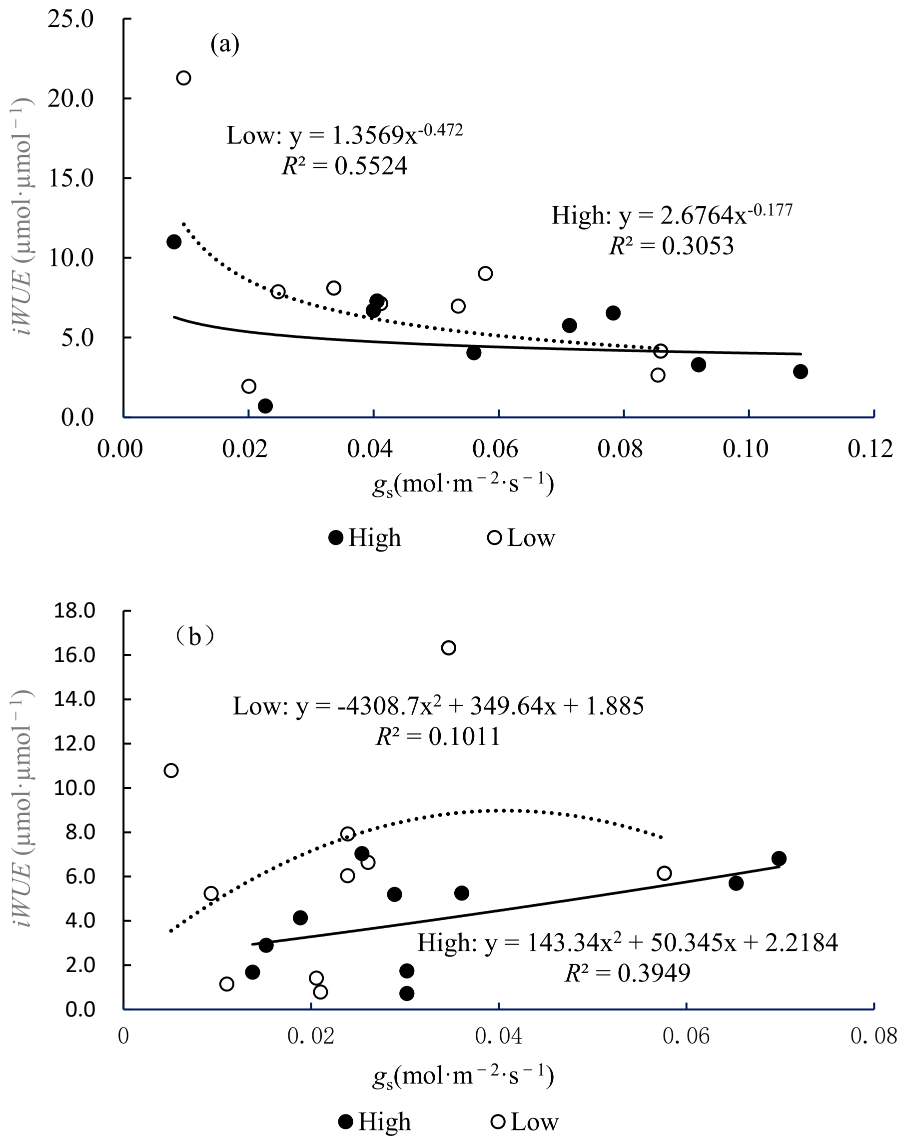

Figure 8. Relationship between the average stomatal conductance (g_s) and the average instantaneous water use efficiency (*iWUE*) measured under photosynthetic active radiation (PAR*i*) of more than 1000 μmol·m^{-2}·s^{-1} (High) or under PAR*i* of 500–1000 μmol·m^{-2}·s^{-1} (Low) for *P. edulis* plants of all ages across the seasons under different drought stress treatments. (**a**) Control; (**b**) drought. Solid circles represent points in the high light range, while hollow circles represent points in the low light range. The solid line represents the fitting of the high light range, and the dashed line represents the fitting of the low light range.

The regression analysis showed that the stomatal conductance and water use efficiency of bamboo leaves of different ages during the growing seasons was a power function relationship under high- and low-light conditions (Figure 8a); under drought conditions, they had a polynomial relationship(Figure 8b).

The non-linear regression analysis showed that the correlation between the instantaneous water use efficiency and vapor pressure deficit in the control group of bamboo showed a significant polynomial relationship in both the high and low light ranges. This means that as the vapor pressure deficit of the leaves increased, the instantaneous water use efficiency first decreased and then increased (Figure 9a). The non-linear regression analysis showed that under long-term drought stress, the correlation between the instantaneous water use efficiency and vapor pressure deficit of the bamboo also showed a significant polynomial relationship in both high and low light ranges: that is, as the vapor pressure deficit of the leaves increased, the instantaneous water use efficiency first decreased and then increased (Figure 9b).

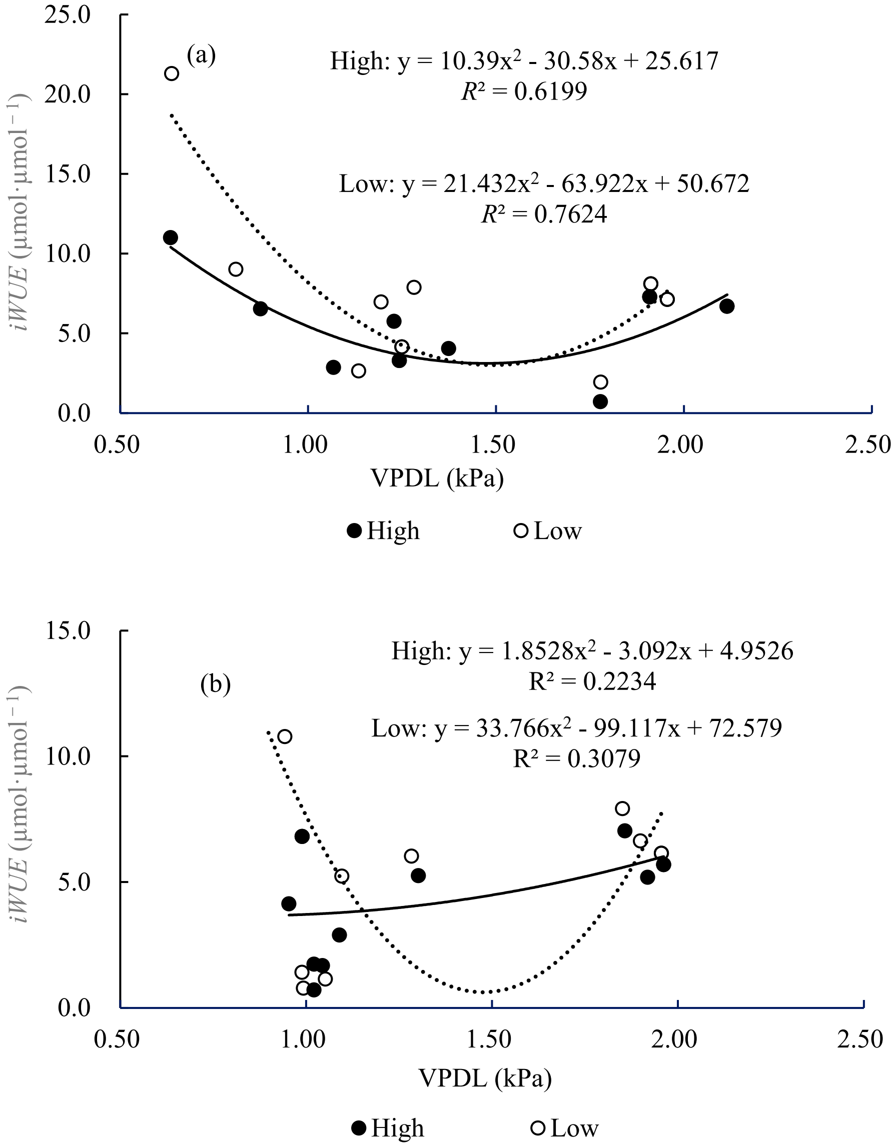

Figure 9. Regression analysis between the water use efficiency (*iWUE*) and vapor pressure deficit (VPDL) in high and low light ranges for different drought treatments. (**a**) Control; (**b**) drought. Solid circles represent points in the high light range, while hollow circles represent points in the low light range. The solid line represents the fitting of the high light range, and the dashed line represents the fitting of the low light range.

4. Discussion

4.1. Responses of P. edulis Photosynthetic Parameters to Drought Stress

With global warming and ecological damages, extreme drought events and water shortages have become increasingly serious ecological problems and critical environmental factors affecting plant production, their functional integrity, and the substantial ecological and economic transition of forests [35,45,46]. Identifying critical thresholds of drought impact intensity and duration is of high interest for assessing the potential abilities of tree species to adapt to the changing climate in their native environments [2,8,35]. More and more scholars are applying extreme drought stress to observe the responses of leaf physiological characteristics, their potential to recover from the imposed stress, and the desiccation and mortality processes among different populations [35,46,47]. Soil water content is a major environmental factor affecting plant growth, and drought stress often restricts plant growth and development, especially photosynthesis [8,48,49]. The soil's response to drought stress can influence the photosynthetic activity through reduced stomata conductance or by causing damage to the mesophyll cells [35,46,47]. For example, the $P_{\max}$ of mango plants (*Mangifera indica* Linn.) significantly decreased with the decrease in soil water content [8]. It was shown that the decrease in soil water content can lead to a decrease in the plant's ability to utilize strong light, and the optimal range of relative soil water content for the normal photosynthesis of mango plants was 45.1%–77.3% [8]. In accordance with Li et al. (2019)'s study [8], our study showed that the maximum net photosynthetic rates ($P_{\max}$) of bamboo of all ages after 8 years of precipitation exclusion treatment were significantly lower than those of the control ($p < 0.05$). In agreement with Li et al. (2019)'s study [8], in our research, the results revealed a sequence of leaf photo-physiological changes that gradually developed in response to severe drought conditions (Figures 1–4). Under long-term drought stress, the $P_{\max}$ of older bamboo was greater than that of younger bamboo in any season, and the size order of $P_{\max}$ across the age groups was consistent with that found for the control, which may reflect the physiological integration characteristics of bamboo. Compared with the young bamboo, the old bamboo experienced longer periods of drought, while its $P_{\max}$ remained higher than that of the young bamboo, reflecting its ability to tolerate drought as the bamboo forest age increases.

The light saturation point (LSP) and light compensation point (LCP) reflect the plant's ability to utilize light at high and low light intensities [40]. These were very useful primary indicators for measuring the relationship between light use and photosynthesis [40]. The LSP refers to the light intensity when the rate of photosynthesis absorption of carbon dioxide reaches the upper value and no longer increases under certain conditions [40]. Plants with a low LCP and a high LSP usually have high adaptability to the light environment, so selecting and cultivating plants that adapt to wide ranges of light conditions is important for better plant survival and growth under an extreme climate [48,50]. In this study, compared with the control, after long-term drought, the ability of the second-degree bamboo to utilize strong light increased in summer, autumn, and winter, while the ability of the first-degree and third-degree bamboo to utilize strong light decreased; in autumn and winter, an increase in the light compensation points for these bamboo indicated that the minimum level of light required for zero net photosynthesis increased under drought stress. The decrease in AQY further indicates that long-term drought led to a decrease in the ability of the bamboo to utilize weak light. This indicates that the photosynthetic activities of the *P. edulis* plants were suppressed when the soil water content was reduced to a threshold level, which was associated with the seasons and bamboo ages. This conclusion can provide a good basis for determining the optimum water conditions for the artificial cultivation of *P. edulis* or determining the threshold level of soil water content needed for drought tolerance. In this study, we found that there were significant differences in photosynthetic capacity among bamboo individuals of different ages under long-term drought conditions, and this was influenced by the growing season. This means that as the frequency of drought events increases, bamboo management needs to pay more attention to the regulation of stand structure, especially considering the age of the structure, and fully utilize the ability of bamboo individuals of different ages to adapt to drought conditions by utilizing strong and weak light.

4.2. Stomatal Conductance and Water Use Efficiency's Response to Light under Drought Stress

Plants' stomatal control of the gaseous exchange between leaves and the bulk atmosphere governs their CO_2 uptake for photosynthesis and transpiration, as well as their productivity and water use efficiency [11,12,14,23,35,51–53]. Recent research has mostly been related to g_s and the *iWUE* on a leaf level, and has revealed plants' inner water consumption mechanisms, providing a scientific basis for supplying plants with reasonable amounts of water [6,12–14,35,47,54]. Plants regulate stomatal conductance to optimize their carbon uptake with respect to water loss [6,14,55].

Zhou et al. (2013) have indicated that the rate of decline in g_s with drought varied considerably among species, with the g_s remaining nearly constant in some species while declining rapidly with drought in others [56]. In our study, compared to the control, the g_s of third-degree bamboo under drought conditions increased in spring and that of second-degree bamboo increased in autumn, while that of all bamboo age groups under drought stress decreased in the summer. During each growing season, the g_s of first-degree bamboo under drought conditions reduced significantly. It can be concluded that under long-term drought conditions, the dynamic changes in the g_s of the bamboo varied according to the different ages. This indicates that the stomatal behavior of bamboo individuals varies with their age.

Klein et al. (2013) have indicated that during summer, Corean pine (*Pinus halepensis*) individuals avoided drought stress by reducing their stomatal conductance [13]. Aranda et al. (2015) have also found that water constraints significantly decreased the photosynthetic rate and the stomatal conductance to prevent plant dehydration [57]. Compared with non-stressed conditions, drought stress decreased the g_s for all three functional plant groups significantly [54]. Drought-stressed experiments were carried out under diverse environmental conditions for one-year-old seedlings from four to seven European beech (*Fagus sylvatica* L.) populations, and it was found that the drought stress mainly affected gas exchange, and there were different responses to this water stress among the beech populations [47].

In our study, the regression analysis of the three indicators showed that long-term drought stress significantly changes the relationship between stomatal conductance, water use efficiency, and vapor pressure deficit in bamboo. This study found that in the lower vapor pressure deficit range, whether in the high or low light range, the stomatal conductivity of bamboo decreases with the increase in vapor pressure deficit, indicating that stomatal closure behavior occurs at this time; as the vapor pressure deficit continues to increase, the stomatal conductance will gradually increase. Compared with that in the high light range, the stomatal conductance increases earlier in the low light range. Under a control treatment, the stomatal conductance of bamboo increases first and then continues to decrease with the increase in vapor pressure deficit.

The regression analysis trend between the stomatal conductance and instantaneous water use efficiency shows that an increase in the stomatal conductance of bamboo under long-term drought stress will lead to a slow increase in its water use efficiency, which may be beneficial for improving bamboo productivity under drought conditions. In contrast, as the stomatal conductance increases, the water use efficiency actually decreases. It can be concluded that maintaining normal stomatal opening behavior and maintaining a certain degree of stomatal conductance is crucial for maintaining the water use efficiency of bamboo under drought conditions. We conclude that maintaining a certain vapor pressure deficit under drought stress for bamboo is very important, and this will be helpful in maintaining the stomatal conductance and ensuring efficient water use during the growth stage when faced with drought. In production and operation processes, these conclusions can be used as theoretical guidance.

Assuming a unique linear response function implies that the g_s of all of the leaves in the crown will be affected in the same way when drought develops [58]. There is a significant positive correlation between the soil relative water content and the stomatal conductance [59]. In our study, the correlation between the stomatal conductance and vapor pressure deficit in bamboo under long-term drought conditions showed a significant polynomial relationship in both high and low light ranges (Figure 7b). Under drought stress, there was a polynomial relationship between the stomatal conductance and water use efficiency of bamboo leaves of different ages in each growing season, regardless of there being high- or low-light conditions.

Therefore, we suggest that when the soil water supply becomes poor, the light intensity for *P. edulis* growth should be strengthened by thinning the forest, thus reducing the negative impacts on plant growth, and we even suggest that its *iWUE* will be improved under drought and high-light conditions.

The latest research indicates that when combined with the natural low levels of nitrogen availability in the summer and during intensified droughts, the impact of increased carbon dioxide content on carbon absorption in temperate coniferous forests is limited [60]. In the future, with climate change, the concentration of atmospheric CO_2 will increase. It is necessary to further study how individual photosynthesis parameters and the stomatal conductance of bamboo respond to drought and increased CO_2 concentrations during long-term drought stress [60].

5. Conclusions

Global climate change will likely make drought stress an even greater threat to plant growth and yield worldwide. This study has described the differences in photosynthesis parameters, the stomatal conductance, and the water use efficiency of *P. edulis* plants of different ages in response to long-term drought stress. The maximum net photosynthetic rate ($P_{\max}$) of bamboo at all ages under long-term drought conditions (after 8 years of precipitation exclusion treatment) was significantly lower than that of the control. After long-term drought stress, bamboo individuals of different ages showed different abilities to utilize strong and weak light in different seasons. All in all, it can be concluded that long-term drought stress activated the ability to utilize high-intensity light for second-degree bamboo plants during the summer, autumn, and winter, and reduced their utilization of low-intensity light. This study also provides important information regarding growth light conditions, showing that improved artificial cultivation techniques for *P. edulis* under drought conditions can be realized by adjusting the stand structure and increasing the distribution and absorption of intense light. In practice, for plant growth, age-related differences in photosynthetic responses should be fully utilized. It can be concluded that maintaining normal stomatal opening behavior and maintaining a certain degree of stomatal conductance are crucial for maintaining the water use efficiency of bamboo under drought conditions. It can also be concluded that maintaining a certain saturation of vapor pressure difference in bamboo under drought conditions is a very important measure to maintain stomatal conductance and ensure water use efficiency. In production and operation processes, these findings can serve as theoretical guidance.

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