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Competition and Niche Differentiation of Water and Nutrients between *Broussonetia papyrifera* and *Platycladus orientalis* under Prolonged Drought Stress

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Abstract: Little is known about the competition between and niche differentiation of water and nutrients between angiosperm and gymnosperm tree species under prolonged drought stress, especially in fragile environments. We imposed 21 d drought and competition treatments on *Broussonetia papyrifera* and *Platycladus orientalis* and measured water, N, and P contents, the isotopic composition of N and C, the activity of P assimilation enzymes, and stomatal conductance under solo planting and mixed planting to characterize resource diversity and competition in response to treatments. The N content, δ^{13}C, δ^{15}N, phosphomonoesterase, phosphodiesterase, g_s, and foliage water content were significantly affected by the soil water content. The δ^{15}N content in young leaves showed that N competition between these two plants could be alleviated through niche differentiation, but the changes in the PDE: PME ratio for these two plants indicated that they lost the niche differentiation of the P source under drought stress. Additionally, it was observed that foliage water content, WUE, N contents, and N and P sources were significantly affected by interspecific competition, and *Broussonetia papyrifera* benefited from water competition under moderate drought. Our results indicate that plants have different competition and niche differentiation modes to different nutrients under drought stress, and the effect of interspecific water competition should be seriously considered in mixed forests in semiarid areas.

Keywords: angiosperm; gymnosperm; interspecific competition; water stress; stable isotopic

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1. Introduction

Global warming may lead to an increase in the duration, intensity, and frequency of drought worldwide [1]. Long-term or extreme drought will lead to plant death or change the composition, structure, and function of plant communities. When studying the impact of environmental change, interspecific relationships and the effects of species competition have been viewed as dominant factors influencing community structure in ecological research. It is generally believed that niche differentiation can mitigate the negative effects of drought stress on plants, but Kunstler et al. [2] found that the degree of trait dissimilarity between species had little influence on reducing competition. Competition determines the interspecific or intraspecific distribution pattern of net available resources [3]. Dominant, highly competitive species in the community can alleviate the risk of drought stress by "plundering resources", but interspecific competition also makes the position of the lowly competitive species deteriorate more. Although a broad body of literature exists regarding the study of plant performance responses to drought combined with competition, less is known about the underlying variation in physiology [4]. Many studies have reported the water source niche differentiation and competition of mixed-species stands under water deficiency, but their results are inconsistent. [5–7]. The fact that resources competition and niche differentiation occur in mixed-species stands can be obtained from in situ studies, but the results are often formed by many ecological factors [8] and species-specific functional traits of plants, so confusing results are easily obtained. To study the interspecific competition more accurately under drought conditions, artificial simulation experiments under controllable laboratory conditions and in situ experiments are both indispensable.

Drought not only affects the water characteristics of plants but also affects their nutrient absorption [9,10]. Soil water deficit significantly directly inhibited the absorption of soil elements with transpiration flow and reduced ion mobility in the soil [11] and limited the decomposition, mineralization, and nutrient cycling of soil elements [12]. Therefore, under drought conditions, the water competition of plants in a community will also affect the nutritional status of plants. Among all the nutrient elements required for plant growth, nitrogen (N) and phosphorus (P) are undoubtedly the most important and widely considered. The N: P ratio can determine the main characteristics and structure of plant communities and reflect the relationship between supply and demand and the circulation of nutrition [13–15], especially in nutrient-limited systems. Inorganic N, which includes nitrate and ammonium, may nonetheless be generally thought to be the dominant source of N for plants [16]. The nitrogen source composition of plants has always been an issue that has received much attention. P is an essential nutrient taken up by plants as the orthophosphate anion (Pi). Phosphate monoesters are the main phosphorus sources for plants, and phosphate diesters also can be absorbed by plants in cold or damp environments [17–19]. Phosphomonoesterase (PME, EC 3.1.3.2) and phosphodiesterase (PDE, EC 3.1.4.1) are rate-limiting enzymes in the assimilation processes of phosphate monoesters and phosphate diesters, respectively [20]; therefore, the PDE: PME ratio can be used for the qualitative analysis of plant P source changes [21].

B. papyrifera and *P. orientalis* are native to eastern Asia [22,23] and frequently coexist in mixed forests. With the main objective of studying the variations in water, nitrogen, and phosphorus nutritional status between *B. papyrifera* and *P. orientalis* under the combined effects of drought and competition, we conducted a simulation experiment in an artificial climate chamber and focused on the following specific questions:

(1) Does the niche differentiation of nitrogen and phosphorus occur between *B. papyrifera* and *P. orientalis* under drought stress?
(2) Does interspecific competition affect the status of the water, nitrogen, and phosphorus nutrition of *B. papyrifera* and *P. orientalis* under drought stress, and who is the winner?

2. Materials and Methods

2.1. Plant Material and Drought Treatment

The angiosperm specie—*Broussonetia papyrifera* L. Vent. and gymnosperm specie—*Platycladus orientalis* L. Franco were selected as the experimental materials. *B. papyrifera* belongs to the Moraceae family and is a large, fast-growing, shallow-root-system, deciduous broad-leaved woody species. *P. orientalis* from the Cupressaceae family is an evergreen tree species with a well-developed root system and a long lifespan. Seeds were sown in wet perlite and germinated at 25 °C in a greenhouse. On the 15th day after seed germination, vigorous seedlings were transplanted into humus soil. The environmental conditions for seedling growth were as follows: a 12 h photoperiod with a day/night temperature of 25/16 °C and a photosynthetic photon flux density of 400 μmol m^{-2} s^{-1} with 60–65% relative humidity. To eliminate individual size differences as much as possible, an experiment was started when the seedlings grew to 30 cm tall (approximately 2.5 months old for *B. papyrifera* and 10 months old for *P. orientalis*).

To study the effect of soil water competition in these two plant species under drought stress, plants were planted alone in a 40 cm × 30 cm box with 18 cm of nutrient soil, and they were also planted with two species together in a 40 cm × 60 cm box with the same thickness of nutrient soil. Figure 1 shows the planting modes and soil sampling points. In order to supplement the water consumed via evapotranspiration, and according to the results of the pre-experiment, 75 mL and 55 mL of water was added to the control group of *B. papyrifera* and *P. orientalis* every day to maintain soil moisture, respectively. The prolonged drought treatment group stopped adding water until the end of the experiment (21 days) to simulate long-term drought without rainfall. Following treatment, soils were sampled once every ten days at the positions shown in Figure 1 to analyze the water content of plants; the parameters of leaf gas exchange were measured once every five days; and the leaves and roots were sampled to determine the water content, carbon, phosphorus, and nitrogen contents and $\delta^{13}C$, $\delta^{15}N$, and PME and PDE activities. Plant tissue was stored at −80 °C until further analysis was performed.

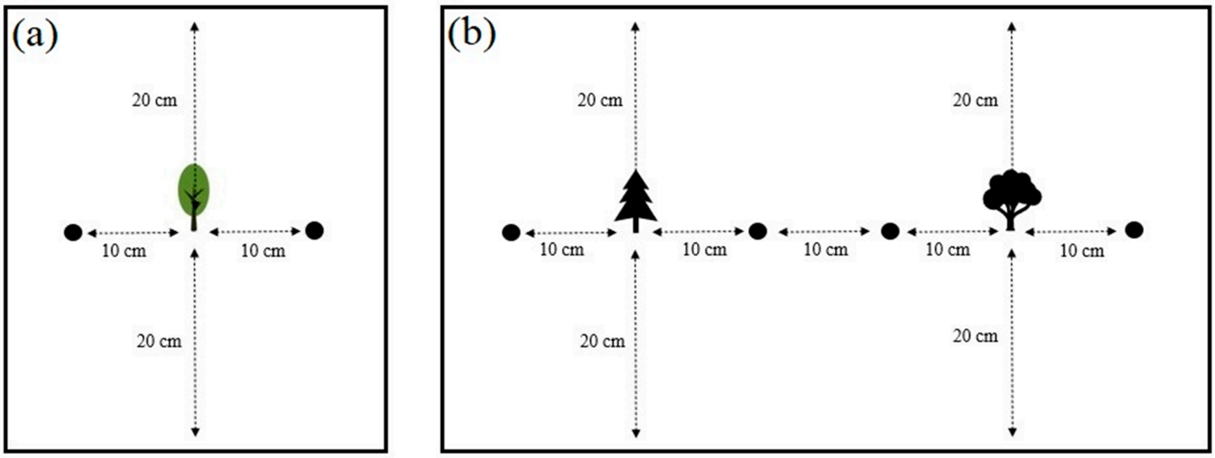

Figure 1. Planting modes and soil sampling points. (**a**) Solo planting; (**b**) mixed planting; • are the soil sampling points.

2.2. Measurement of Leaf Gas Exchange

The latest fully developed leaves in the middle and upper parts of the plant were selected for the determination of leaf gas exchange. The stomatal conductance (g_s) was measured using a Li-6400 portable photosynthesis measurement system (Li-6400, Li-Cor, Lincoln, NE, USA) from 10: 00 to 11: 00 am. The PPFD was 400 µmol m^{-2} s^{-1}, and the temperature was 25 °C. Here, the leaf area of *P. orientalis* was converted from its leaf dry weight using the following formula [24]:

$$S_{ori} = 161 \times M_{ori} \quad (1)$$

where S_{ori} is the leaf area of *P. orientalis* and M_{ori} is the leaf dry weight of *P. orientalis*.

2.3. Nitrogen and Phosphorus Contents

Fresh plant samples were dried at 65 °C for 3 days and ground for N and P content testing, and a 0.3 g sample was added to 10 mL of H_2SO_4. Then, a graphite digestion instrument (SH420, Hanon, Dezhou, China) was used. A total P assay kit was used for sample P content determination, and the test was carried out with a microplate reader (Synergy H1, BioTek, Winooski, VT, USA) according to the instructions. A Kjeldahl apparatus (K1100, Hanon, Dezhou, China) was used for N content determination.

2.4. Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) Isotope Compositions

The fresh samples were soaked in 1 mol L^{-1} HCl for 1 h to remove exogenous inorganic carbon. Then, the samples were dried at 65 °C for 3 days and ground to a fine powder. A 2.0 mg fine-powder sample was wrapped in a tin capsule (5 × 8 mm), and the $\delta^{13}C$ and $\delta^{15}N$ values were determined using a continuous-flow isotope ratio mass spectrometer (MAT 253; Thermo Fisher Scientific, Waltham, MA, USA).

2.5. Root PME and PDE Activities

PME activity was assayed according to the method of Tabatabai and Bremmer [25] with some modifications. The reaction mixture containing 0.2 g of fresh root sample was incubated for 10 min at 37 °C with 4 mL of modified universal buffer (MUB), pH 8, and 1 mL of 5 mmol L^{-1} para-nitrophenyl phosphate (pNPP; MFCD00284586, Sigma–Aldrich, St Louis, MO, USA). The reaction was stopped by adding 1 mL of 0.5 mol L^{-1} $CaCl_2$ and 4 mL of 0.5 mol L^{-1} NaOH and immediately centrifuging the mixture for 2 min at 12,000 g. The amount of p-nitrophenol released was measured in the supernatant at 412 nm.

PDE activity was assayed according to the method of Eivazi and Tabatabai [26] with some modifications. The reaction mixture containing 0.2 g of fresh root sample was incubated for 10 min at 37 °C with 4 mL of modified universal buffer (MUB; 0.1 mol L^{-1}) pH 8.0 and 1 mL of 5 mmol L^{-1} bis para-nitrophenyl phosphate (bis-pNPP; CAS645-15-8, Aladdin, Shanghai, China). The reaction was stopped by adding 1 mL of 0.5 mol L^{-1} $CaCl_2$ and 4 mL of 0.5 M NaOH and immediately centrifuging the mixture for 2 min at 12,000 g. The amount of p-nitrophenol released was measured in the supernatant at 412 nm.

2.6. Data Analysis

Five replicates were used for soil and leaf water contents measurement, and three replicates were used for physiology and biochemistry parameter measurement. One-way ANOVA followed by Duncan's multiple range test was performed to explore the differences among the plant parameters under separate treatments. A general linear model was used to explore the interspecific competition effect, with the planting pattern (sole or mixed) as a fixed effect and the plant parameters at every sampling time as dependent variables. If there were significant differences ($p < 0.05$) between the two groups, we judged that a competition effect definitely existed. To explore the difference in the water control strategy between *B. papyrifera* and *P. orientalis*, ANOVA and a general linear model were performed using SPSS 25.0 (SPSS Inc., Chicago, IL, USA). Linear regression analysis was performed to calculate Pearson's correlations between soil water content and N content, P content, $\delta^{13}C$, $\delta^{15}N$, PME, PDE, g_s, and foliage water content, and this test was performed using ORIGIN 95 (OriginLab Inc., Northampton, MA, USA).

3. Results

3.1. Soil Water Content

To study the water competition between B. papyrifera and *P. orientalis* under mixed planting conditions, the change in soil water content was continuously monitored. As shown in Figure 2, at 11 d, soil water contents in the rhizosphere of B. papyrifera were not significantly different between the solo planting and mixed planting conditions within the 3 cm deep soil layer via Duncan's test ($p < 0.05$). Within the 9 cm deep soil layer, the water content was significantly different between the mixed planting inside (MPI) and mixed planting outside (MPO) conditions, but the difference was not significant compared with the solo planting (SP) condition and MPO or MPI, and MPO < SP < MPI. The differences among the three simple points disappeared within the 15 cm deep soil layer. At 21 d, the water content in the SP condition was significantly lower than in the MPI and MPO conditions, and there no significant differences between the MPI and MPO conditions within the 3 cm deep soil layer. Within 9 cm deep soil layers, the water content was significantly different between the MPI and SP conditions, but the difference was not significant compared with the MPO and MPI or SP conditions, and SP < MPO < MPI, and there were no significant differences among the three sample points at the 15 cm depth.

At 11 d, the water contents in the rhizospheres of *P. orientalis* displayed significant differences between the solo planting (SO) and mixed planting inside (MOI) conditions, and MOI < MOO (mixed planting outside) < SO within the 3 cm and 9 cm deep soil layer, and the water content in the MOI condition was significantly lower than that in the MOO and SO conditions, and there no significant differences between the MOO and SO conditions within the 15 cm deep soil layer. At 21 d, the water content in the MOI condition was significantly lower than that in the MOO and SO conditions, and there no significant differences between the MOO and SO conditions within the 3 cm and 15 cm deep soil layer; the water content in the MOI condition was significantly lower than that in the SO condition within the 9 cm deep soil layer.

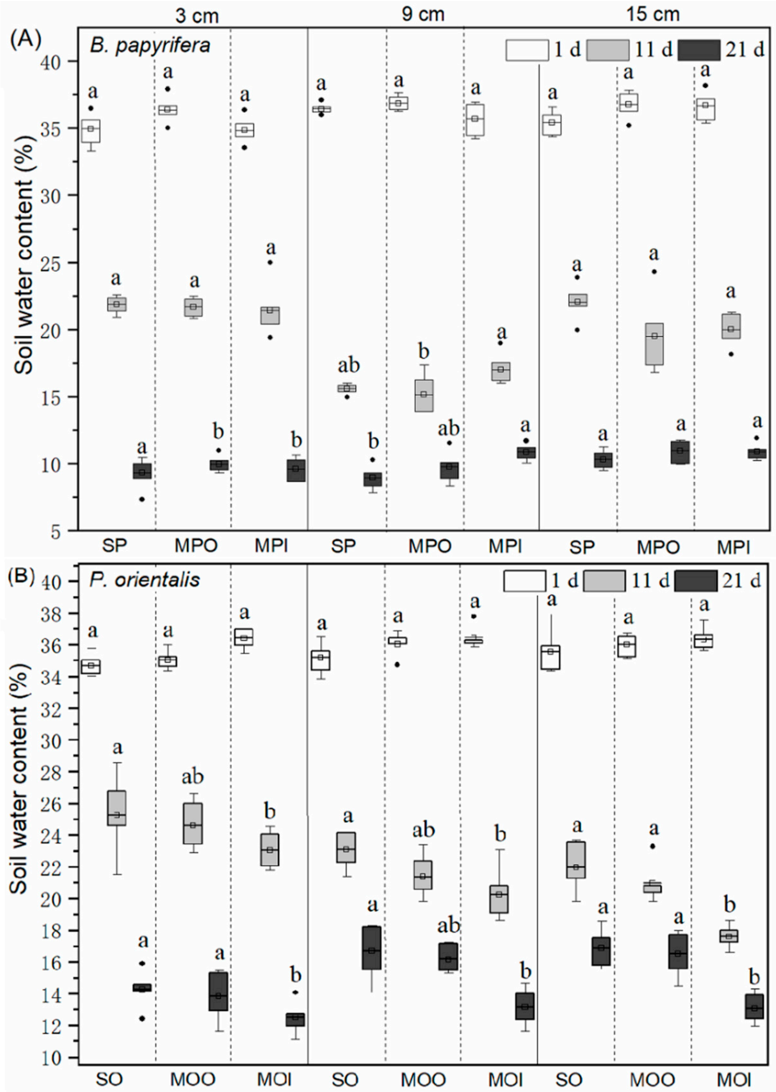

Figure 2. Soil water contents in the rhizosphere of *B. papyrifera* (**A**) and *P. orientalis* (**B**). Letters denote significant differences among soil sampling points ($p < 0.05$). SP—*B. papyrifera* under solo planting, MPO—outside of *B. papyrifera* under mixed planting, MPI—inside of *B. papyrifera* under mixed planting, SO—*P. orientalis* under mixed planting, MOO—outside of *P. orientalis* under mixed planting, MOI—inside of *P. orientalis* under mixed planting.

3.2. Leaf Water Contents, δ^{13}C Value, and g_s

As shown in Figure 3, the water contents in both plant leaves steadily dropped under prolonged drought conditions. Using Duncan's test ($p < 0.05$), significant differences existed between the solo planting and mixed planting conditions at 11 d and 16 d for *B. papyrifera* and 11 d for *P. orientalis.* Under prolonged drought conditions, the δ^{13}C values in both plants increased at 11 d.

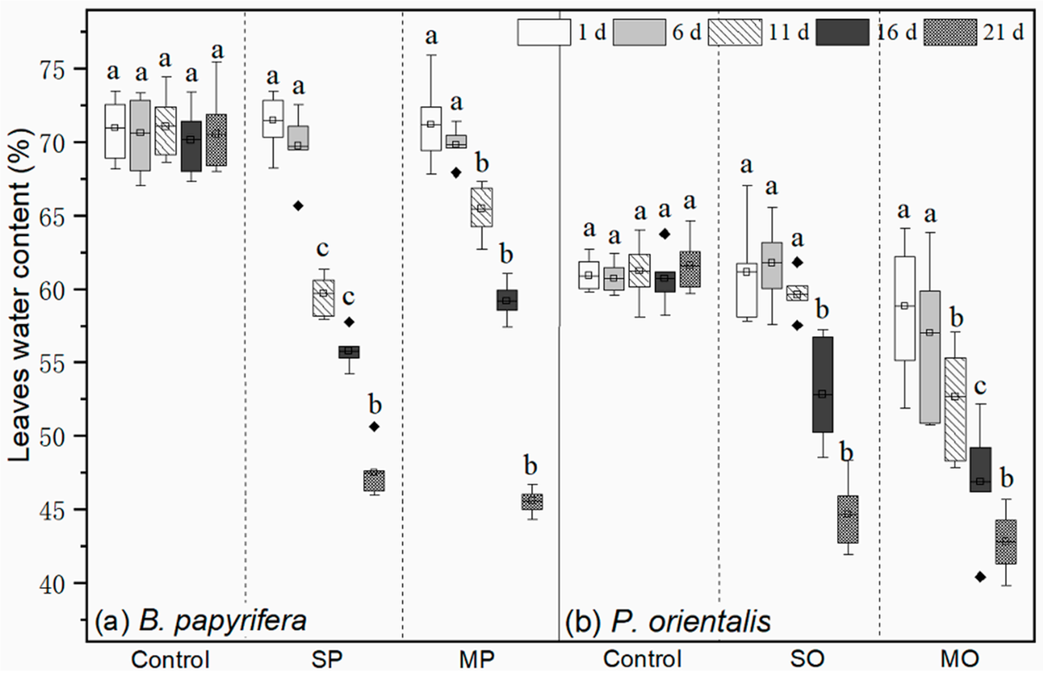

Figure 3. Leaf water contents in *B. papyrifera* and *P. orientalis*. Letters denote significant differences among different planting and treatment modes ($p < 0.05$). SP—*B. papyrifera* under solo planting, MP—*B. papyrifera* under mixed planting, SO—*P. orientalis* under mixed planting, MO—*P. orientalis* under mixed planting.

After 11 d, the δ^{13}C value in *B. papyrifera* continued to increase, but the δ^{13}C value in *P. orientalis* was almost maintained at the same level. Significant differences ($p < 0.05$) existed between the solo planting and mixed planting conditions and only occurred on day 16 for *B. papyrifera* (Figure 4A,B). As shown in Figure 4C,D, under prolonged drought conditions, the g_s in *B. papyrifera* under the two planting modes both decreased with the extension of processing time after 6 d. The g_s in *P. orientalis* decreased sharply at 11 d and then declined slightly.

3.3. N Contents and δ^{15}N Values

The N contents relative to water contents of leaves are represented in Figure 5A,B. Using linear regression analysis, the nitrogen content and water content in *B. papyrifera* leaves showed a significant positive relation under the solo planting and mixed planting conditions (solo: $r = 0.7229$, $p < 0.01$; mixed: $r = 0.7702$, $p < 0.01$), On the contrary, there were significant negative correlations between the nitrogen content and water content in *P. orientalis* leaves under the solo planting and mixed planting conditions (solo: $r = -0.6459$, $p < 0.01$; mixed: $r = -0.7976$, $p < 0.01$).

Under prolonged drought conditions, the δ^{15}N value in *B. papyrifera* leaves began to decrease sharply from the 11th d, and there was a significant difference ($p < 0.05$) between the mixed planting and solo planting conditions. The δ^{15}N value in *P. orientalis* leaves decreased slightly from the 16th d, and a significant difference between the two planting modes only existed at 16 d (Figure 5C,D).

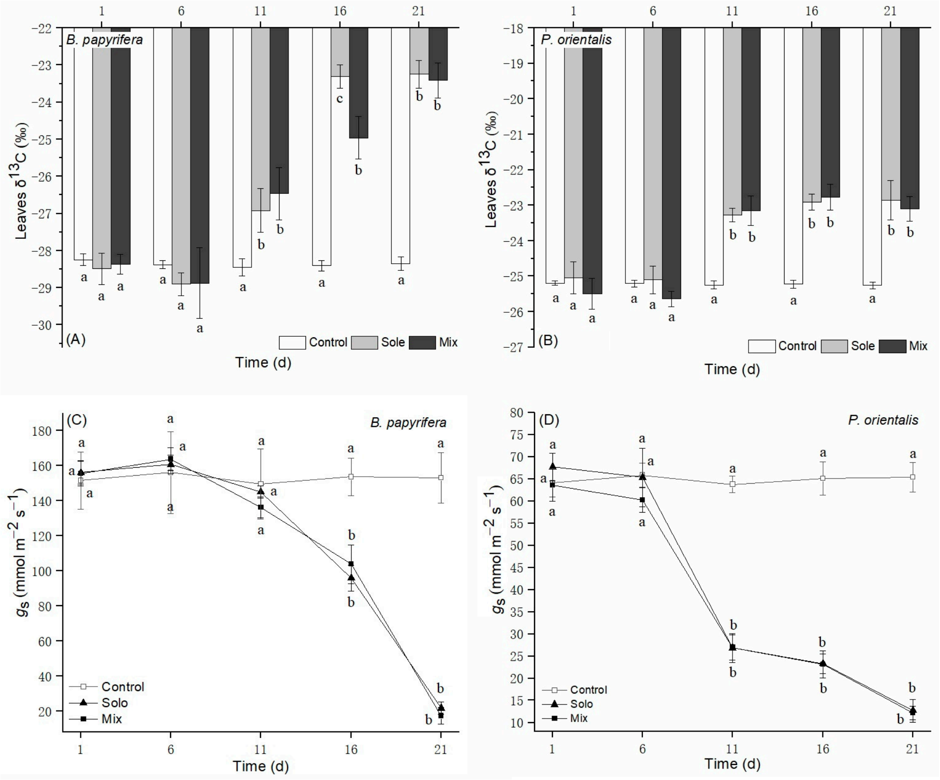

Figure 4. The leaves' δ^{13}C value in *B. papyrifera* (**A**) and *P. orientalis* (**B**). Leaves' g_s value in *B. papyrifera* (**C**) and *P. orientalis* (**D**). Letters denote significant differences among different planting and treatment modes ($p < 0.05$).

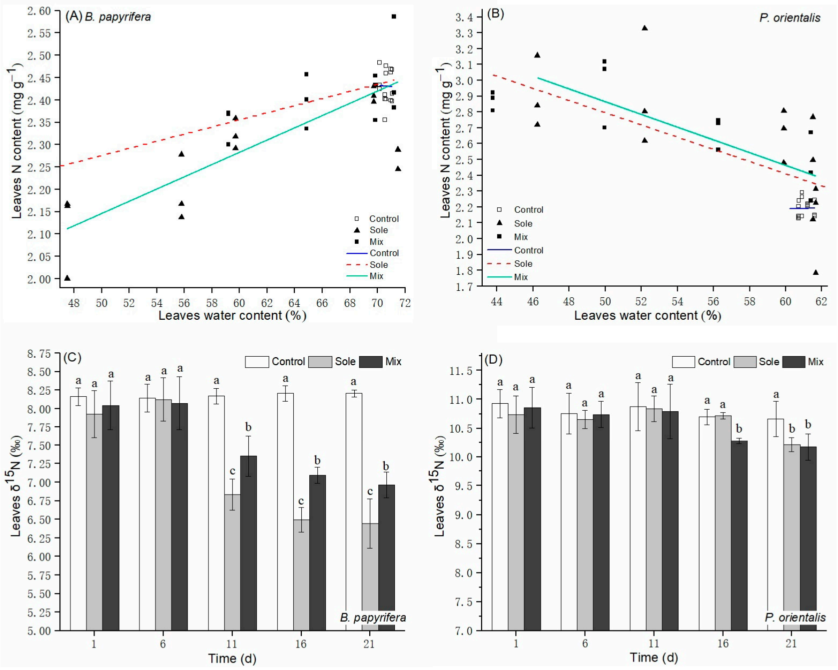

Figure 5. The leaves' N content relative to water content in *B. papyrifera* (**A**) and *P. orientalis* (**B**). Curve fits in the graphs are separate linear regressions. Leaves' δ^{15}N value in *B. papyrifera* (**C**) and *P. orientalis* (**D**). Letters denote significant differences among different planting and treatment modes ($p < 0.05$).

3.4. P Contents and PDE: PME Ratio

The P contents relative to the water contents in leaves are represented in Figure 6A,B. There was no correlation between the phosphorus content and water content in *B. papyrifera* leaves under the solo and mixed planting conditions (solo: $p = 0.7652$; mixed: $p = 0.1913$), and the same was true for *P. orientalis* (solo: $p = 0.7652$; mixed: $p = 0.1913$). Under prolonged drought, the PDE: PME ratio in *B. papyrifera* roots decreased from 0. 56 on day 1 to 0.24 at 11 d under the solo planting condition, and from 0.54 at 1 d to 0.30 at 11 d under the mixed planting condition. Then, this ratio increased at 21 d and was 0.33 under the solo and mixed planting conditions. The PDE: PME ratio in *P. orientalis* roots decreased from 1.39 at 1d to 0.39 at 11 d under the solo planting condition and from 1.31 at 1 d to 0.43 at 11 d under the mixed planting condition. Then, this ratio increased at 21 d and was 0.78 under the solo and mixed planting conditions. (Figure 6C,D).

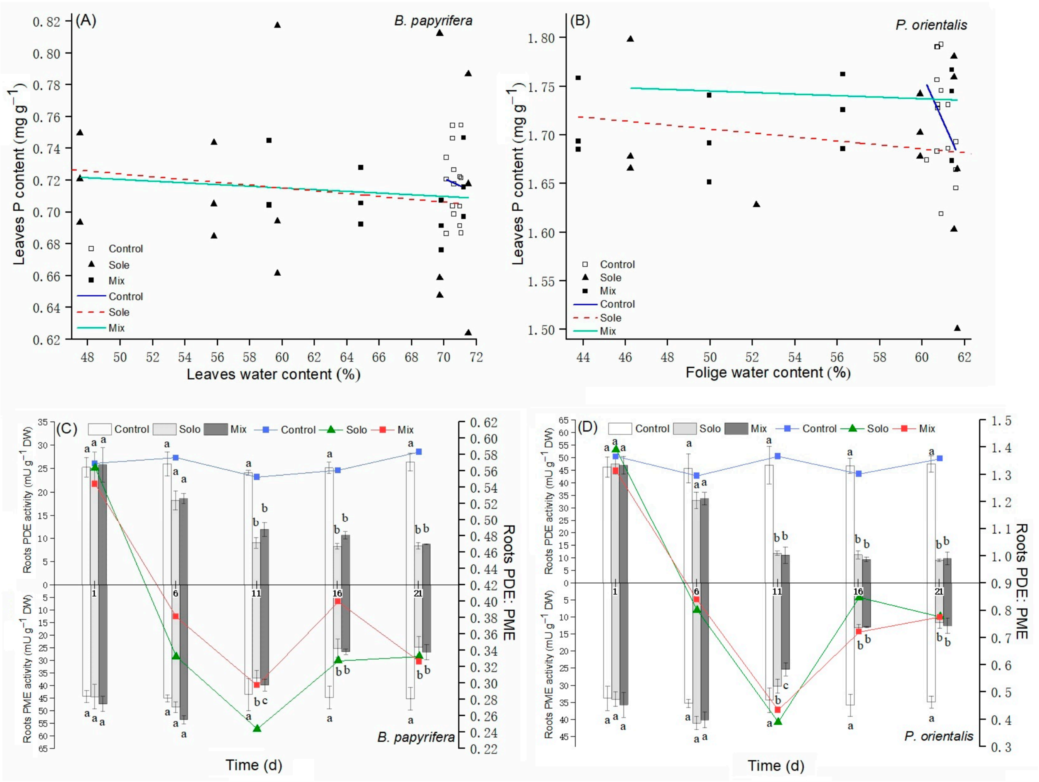

Figure 6. The leaves' P content relative to water content in *B. papyrifera* (**A**) and *P. orientalis* (**B**). Curve fits in the graphs are separate linear regressions. The roots' PDE: PME ratio in *B. papyrifera* (**C**) and *P. orientalis* (**D**). Letters denote significant differences among different planting and treatment modes ($p < 0.05$).

3.5. Correlation and Difference Analysis

As shown in Table 1, linear regression analysis was performed to calculate Pearson's correlations between the soil water content and N content, P content, δ^{13}C, δ^{15}N, PME, PDE, g_s, and foliage water content. For *B. papyrifera*, there was no correlation between soil water contents and P contents; there was a significant positive correlation between soil water contents and N contents; and there was an extremely significant positive correlation between soil water contents and δ^{13}C, δ^{15}N, PME, PDE, g_s, and leaf water contents. For *P. orientalis*, there was no correlation between soil water contents and P contents; a significant positive correlation between soil water contents and δ^{15}N; an extremely significant positive correlation between soil water contents and δ^{13}C, PME, PDE, g_s, and leaves' water contents; and an extremely significant negative correlation between soil water contents and N contents.

Table 1. *p*-value and Pearson's r between soil water content and N content, P content, δ^{13}C, δ^{15}N, PME, PDE, g_s, and leaf water content.

	B. papyrifera ***p*-Value**	**Pearson's r**	***P. orientalis*** ***p*-Value**	**Pearson's r**
δ^{13}C	3.65×10^{-6} ***	0.8648	2.20×10^{-7} ***	0.9064
N content	0.0206 *	0.5405	2.30×10^{-7} ***	−0.9059
δ^{15}N	2.28×10^{-4} ***	0.7634	0.0128 *	0.5739
P content	0. 8149	−0.0594	0.6883	−0.1016
PME	6.24×10^{-5} ***	0.8021	2.50×10^{-7} ***	0.9048
PDE	2.54×10^{-7} ***	0.9046	6.07×10^{-9} ***	0.9411
g_s	2.79×10^{-4} ***	0.7567	3.61×10^{-13} ***	0.9828
Leaf water content	1.89×10^{-5} ***	0.8316	4.71×10^{-7} ***	0.8967

Soil water content is the average value of soil layers and sampling points. *p*-value and Pearson's r were calculated with linear regression analysis (* $p < 0.05$ and *** $p < 0.001$).

As shown in Table 2, a general linear model was used to analyse the difference between solo planting and mixed planting. For *B. Papyrifera*, a significant difference between the two planting methods in leaf water contents emerged at 11 d, and in δ^{15}N, δ^{13}C, N content, PDE and leaf water content emerged at 16 d. For *P. orientalis*, a significant difference between the two planting methods in PME and leaf water contents emerged at 11 d, in δ^{15}N, δ^{13}C and PDE at 16 d.

Table 2. *p*-values in solo planting and mixed planting conditions in *B. papyrifera* and *P. orientalis*.

	***p*-Value**									
	B. papyrifera					***P. orientalis***				
	1 d	**6 d**	**11 d**	**16 d**	**21 d**	**1 d**	**6 d**	**11 d**	**16 d**	**21 d**
δ^{13}C	0.689	0.964	0.440	**0.012**	0.655	0.689	0.964	0.440	**0.012**	0.655
N content	0.870	0.959	0.136	**0.035**	0.157	0.911	0.935	0.874	0.861	0.822
δ^{15}N	0.675	0.865	0.059	**0.006**	0.072	0.676	0.619	0.878	**0.001**	0.800
P content	0.845	0.799	0.761	0.779	0.791	0.490	0.833	0.588	0.299	0.977
PME	0.426	0.091	0.264	0.568	0.587	0.542	0.611	**0.036**	0.710	0.617
PDE	0.815	0.817	0.058	**0.013**	0.334	0.815	0.817	0.058	**0.013**	0.334
g_s	0.938	0.567	0.340	0.659	0.658	0.205	0.286	0.980	0.954	0.758
Leaf water content	0.873	0.930	**0.010**	**0.040**	0.073	0.585	0.951	**0.010**	0.212	0.695

p-values were calculated with general linear model.

4. Discussion

4.1. Plants' Water Status and Water Source Competition

How much water plants can get from soil is not only related to the distribution and absorption capacity of their roots but is also affected by the water competitiveness of neighboring plants [27]. In this study, the variation in water distribution in rhizosphere soil between the two planting modes was caused by water competition under mixed planting conditions, and *B. papyrifera* benefited from water competition, as shown by Duncan's test. The δ^{13}C was positively related to WUE under drought stress [28]. The competition effect emerged in *B. papyrifera* at 16 d, and plants under the mixed planting condition had lower WUEs (Figure 4A), which would imply that they were in a better water available environment. There was no difference in the δ^{13}C value of *P. orientalis* between the two planting modes (Figure 4B), and the slow growth rate and rigid stomatal regulation strategy of *P. orientalis* may have weakened the effect of interspecific competition. Conifers and broad-leaved plants have different strategies in water and nutrition regulation in arid environments because of their significant differences in morphological structures and physiological mechanisms [29,30]. Stomatal behavior can respond to environmental changes and interspecific competition [31]. Under prolonged drought conditions, the g_s values in *P. orientalis* showed that this plant took more rigid stomatal regulation and tried to reduce water loss, but *B. papyrifera* still maintained stomatal conductance before extreme drought occurred (Figure 4C,D). Previous studies observed that seedlings employed a riskier strategy when planted with a high-water-use competitor, and seedlings employed a more conservative strategy when planted with a low-water-use competitor [31]. However, in the current study, there were no significant differences in plants' stomatal behavior between the solo planting and mixed planting conditions. This competitive advantage is related to the two species exhibiting significant differences in their root morphology. *B. papyrifera* has more root branches and fine roots, which is beneficial for enhancing the absorption of soil water; the main root of the *P. orientalis* root is wider and has fewer branches, which is better for the expansion of roots to further ranges and deeper soil layers. Additionally, there is a difference in the xylem structure between angiosperms and gymnosperms [32]. Due to the low hydraulic conductivity of tracheids relative to vessels, the absorption and transportation of water are limited in gymnosperms [33].

4.2. Plants N Status and N Sources Change

B. papyrifera and *P. orientalis* displayed opposite change patterns in the relationship between leaf water and nitrogen content (Figure 5A,B). Under solo planting and mixed planting conditions, there was a significant positive correlation between the leaf nitrogen content and water content in *B. papyrifera*, which was similar to the results of many studies [34–36]; however, there was a significant negative correlation between the leaf nitrogen content and water content of *P. orientalis*. It is speculated that the young leaves of *P. orientalis* obtain N from old leaves to synthesize abundant N-containing osmoregulation substances to maintain osmotic pressure during stomatal closure under water deficiency conditions. Under prolonged drought conditions, the change in $\delta^{15}N$ value in *B. papyrifera* leaves was greater than that in *P. orientalis* leaves (Figure 5C,D), which also implied that *B. papyrifera* obtain more N from the environment and have more flexible N sources, while N in *P. orientalis* was transported from old tissues. In addition, because NO_3^- must be reduced to NH_4^+ before it can be used for plant metabolism, the assimilation event of nitrate is more complex, as mentioned by Evans et al. [37]; if plants use NO_3^- as a nitrogen source, the leaves have relatively high $\delta^{15}N$. From this view, *B. papyrifera* used more ammonium as a nitrogen source under drought stress in this study. The differences in the N source composition and the N pool in young leaves may show that the N competition pressure between these two plants could be alleviated under drought stress.

4.3. Plants P Status and P Sources Change

The availability of N and P is affected by drought in soil through different mechanisms. There was no correlation between the leaf P contents and water contents in *B. papyrifera* and *P. orientalis* (Figure 6A,B), which suggests that there was enough P stored in the plants to supply the growth of young leaves. P stored in roots could be used by plants for growth at times when availability is low [38]. The P content in young *P. orientalis* leaves was much higher than that in *B. papyrifera*, which should be because the growth time of *P. orientalis* of the same size is much longer than that of *B. papyrifera*, so more P accumulates in the P body. A large number of nutrient reserves obtained before drought events would make *P. orientalis* acquire a stronger recovery ability after rainfall [39–41]. Under the control treatment, the PME activity in *B. papyrifera* was higher than that in *P. orientalis*, but the PDE activity in *P. orientalis* was higher than that in *B. papyrifera* (Figure 6C,D), which should be related to the fact that angiosperms are more suitable for mesophytic habits and gymnosperms are more suitable for hydrophytic habits [42] and enable niche differentiation between these two plants in P resource utilization. Under drought stress, the PDE: PME ratio in both plants decreased sharply under prolonged drought, showing that the activity of PDE is heavily dependent on soil moisture; this may be because phosphate diesters are usually degraded rapidly in dry environments and the enzyme activity is driven by relative resource availability [43,44]. The PDE: PME ratio in these two plants underwent almost the same changes under prolonged drought, which indicated that they might have lost the niche differentiation of the P source and that P competition was exacerbated under drought stress.

4.4. Interspecific Competition Analysis

The competition mode of trees is driven by environmental factors and controlled by the dominant limiting factor [45]. In this study, except for the P content in leaves, the physiological and biochemical parameters of plants were significantly affected by soil water contents under prolonged drought conditions (Table 1). This shows that water competition was a decisive factor in interspecific nutritional competition between *B. papyrifera* and *P. orientalis*. Meanwhile, a general linear model was used to analyze the interspecific competition effect (the difference between the solo planting and mixed planting conditions) (Table 2). The results showed that water characteristics, N and P characteristics, and resources were significantly affected by interspecific competition under moderate drought conditions, but the interspecific competition effect did not exist under heavy drought conditions. In the current study, *B. papyrifera* benefited from interspecific competition. Previous studies also indicated that broad-leaved species competition dominates interspecific interactions in growth and water and nutrition utilization in mixed stands [46,47]. However, Liu et al. found that the level of N uptake in *Pinus massoniana* and *Pinus elliottii* were inhibited by the presence of *Michelia maudiae* and *Schima superba*, respectively, but almost no inhibitions occurred when *M. maudiae* was grown together with *P. elliottii* or *S. superba* was grown together with *P. massoniana* [48]. This indicates that angiosperms do not always have the advantage when competing with gymnosperms.

5. Conclusions

The present study indicated that *B. papyrifera* benefits from water and nutrient competition under moderate drought, and the competition mode of *B. papyrifera* and *P. orientalis* is controlled by the dominant limiting factor—soil water content. The N competition between these two plants could be alleviated through niche differentiation, but they lose the niche differentiation of the P source under drought stress conditions. This study illustrated that when coexisting with *B. papyrifera* in mixed stands, the effect of drought stress on *P. orientalis* will be amplified through interspecific competition; this means that the effect of interspecific water competition on mixed forests should be seriously considered in semiarid areas.

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