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Leaf Functional Traits of *Zanthoxylum planispinum* 'Dintanensis' Plantations with Different Planting Combinations and Their Responses to Soil

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Abstract: Leaf structural and physiological traits, nutrients, and other functional properties reflect the ability of plants to self-regulate and adapt to the environment. Species diversity can positively affect plant growth by improving the habitat, and offers mutual interspecies benefits. Therefore, optimizing the types of plants grown in a specific area is conducive to achieving sustainable development goals for plant growth. In this study, companion planting of *Zanthoxylum planispinum* 'dintanensis' (hereafter *Z. planispinum*) with *Prunus salicina* Lindl., *Sophora tonkinensis* Gagnep., *Arachis hypogaea* L. and *Lonicera japonica* Thunb. was investigated, along with a monoculture *Z. planispinum* plantation. The effect of different planting combinations on the adaptive mechanisms of *Z. planispinum* and its response to the soil was explored. These results revealed that *Z. planispinum* preferred the slow growth strategy of small specific leaf area, high leaf water content, and high chlorophyll content after combination with *P. salicina*. Conversely, after combination with *S. tonkinensis*, *Z. planispinum* exhibited a fast growth strategy. Combination with *A. hypogaea* enabled *Z. planispinum* to adopt a transition from slow to fast growth. *Z. planispinum* regulated its economy of growth through multiple functional trait combinations, indicating that planting combinations impacted its adaptive strategies. The adaptability of *Z. planispinum* in combination with *P. salicina*, *L. japonica*, *A. hypogaea* and *S. tonkinensis* decreased in turn, with only the adaptability of *Z. planispinum* + *S. tonkinensis* lower than that of the pure forest. Leaf functional traits were jointly influenced by soil water content, microbial biomass carbon (MBC), MB nitrogen (N), MB phosphorus (P), available N, total P and available calcium (C:N:P). The main contributors were soil water content, the different component levels and stoichiometry of elements and the MB. The results demonstrated that companion planting can promote or inhibit the growth of *Z. planispinum* by adjusting its functional traits.

Keywords: planting combinations; investment strategy; plant adaptability; soil; response; karst

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1. Introduction

Plant functional traits are stable properties formed by their interaction with the external environment during growth and development, which can both respond to environmental changes and influence ecosystem functions [1]. The leaf is the main site of photosynthesis and a key organ for maintaining hydrological balance, sensitive to environmental changes and highly plasticity [2]. Leaf functional and structural traits such as leaf thickness (LT), specific leaf area (SLA), leaf dry-matter content (LDMC); and leaf physiological traits such as chlorophyll (Chl) content and leaf nutrient levels, can sensitively indicate the adaptive strategy, ability to adjust, and response patterns to resource competition in plants [3].

Strategic combinations of plant species according to their physiological and ecological characteristics and their spatial locations form efficient artificial composite ecosystems that promote each other. Mixed forests can change the properties of soil [4]. Variable inputs and decomposition rates of litter from configured species, as well as different types and quantities of root secretions, drive changes in the quality of soil fertility [5]. Nutrient reabsorption efficiency among the species present also changes the nutrient concentration of the soil [6]. In addition, plant type can indirectly affect the soil microbial community by changing the soil nutrient substrate [7]. Compared with pure forests, mixed forests can significantly improve the physical properties of soil, slow soil nutrient depletion and promote biomass recycling [8,9]. However, due to niche overlap between different species in mixed forest, water and nutrient competition and allelopathy can occur [10]. Therefore, clarifying the leaf functional traits and adaptability of *Zanthoxylum planispinum* 'dintanensis' (hereafter *Z. planispinum*) plantations in different planting combinations in the karst plateau canyon area in the middle of Guizhou Province, China, is beneficial for checking suitable planting patterns.

The response and adaptation strategies of plants to the environment have long been a central question in ecological research. At a small regional scale, soil is considered to be a key factor influencing leaf functional traits [11], due to its function in providing mechanical support and nutrient supply for plant growth [12]. In addition, the carbon (C): nitrogen (N): phosphorus (P) ratios can indicate the nutrient limitations of the ecosystem, reflecting the nutrient cycle and utilization efficiency within the plants [13]. It is, therefore, important to study the content and ratio of C, N, and P, as these nutrients affect the energy cycle and stability of ecosystems [14]. In recent years, many achievements have been made in exploring the synergy and trade-offs between leaf traits and soil factors on different latitudes [15], slopes [12], climates [16], community levels [17], etc. However, studies on the relationship between leaf functional traits and soil in different planting combinations are limited. Karst ecosystems are characterized by high habitat heterogeneity, fragile environment, low soil volume and weak nutrient supply capacity [18], but the adaptation mechanisms of native plants are still unclear [19]. Therefore, the study of the interactions between the karst plant *Z. planispinum* and soil is useful to conducting an in-depth analysis of its unique ecological strategies for adaptation to this habitat.

Z. planispinum is the oldest and most widely distributed pioneer tree species in the karst, dry hot valley of Guizhou Province, China [20]. During the process of long-term adaptation to the environment, the tree has formed excellent characteristics, such as calcium (Ca) preference, drought tolerance, and the ability to grow in stony areas. In recent years, the cultivation of pure forests on a large scale has led to the gradual degradation of soil fertility and productivity. The optimization of planting *Z. planispinum* in combination with other species is based on the biodiversity theory of restoring the terrestrial ecosystem. This is essential to prevent and control rocky desertification in karst areas and achieve sustainable development goals. However, the effect of planting combinations on the leaf functional traits of *Z. planispinum* and the relationship between the leaf functional traits and soil are unclear. Therefore, in this study, we selected four common planting combinations of *Z. planispinum* with *Prunus salicina* Lindl., *Sophora tonkinensis* Gagnep., *Arachis hypogaea* L. and *Lonicera japonica* Thunb., respectively, and compared them with pure forests. This study was conducted to explore the effects of planting combinations on the leaf functional traits of *Z. planispinum* and to analyze the response mechanisms of these traits to soil factors. We aimed to: (1) clarify the adaptation mechanism and resource utilization strategy of *Z. planispinum* in different planting combinations; (2) explore the adaptability of different planting combinations; and (3) extract the main factors from the soil that drive changes in the leaf functional traits of *Z. planispinum*. This study provides a scientific basis for diversity cultivation in plantations.

2. Materials and Methods

2.1. Study Sites

The research area was located in Zhenfeng County, Guizhou Province, China (105°38′35″E, 25°39′37″N), which has a mostly subtropical humid monsoon climate (Figure 1). The average annual rainfall is 1100 mm, with severe drought in winter, spring, and summer. The average annual temperature is 18.4 °C. It is a river valley terrain, with an elevation of 370~1,473 m [21]. The soil type is mainly lime soil, with limestone as the parent material.

Carbonate rock accounts for 78.45%, pH > 6.5, the soil layer is mostly <20 cm, and the soil cover is discontinuous. The soil is rich in Ca and Mg due to its high inheritance from the parent rock. The area exhibits rocky desertification, with low forest coverage and a bedrock exposure rate of 50~80% [21,22]. The types of microhabitats such as stone surfaces, stone ditches, stone cracks, stone grooves and stone caves are diverse, and the environmental heterogeneity is high. *Z. planispinum* has become a relatively stable ecological restoration tree species with the largest planting area in the study region. In addition, there are companion species such as *Zea mays*, *L. japonica*, *P. salicina*, *S. tonkinensis*, and *Arachis hypogaea*.

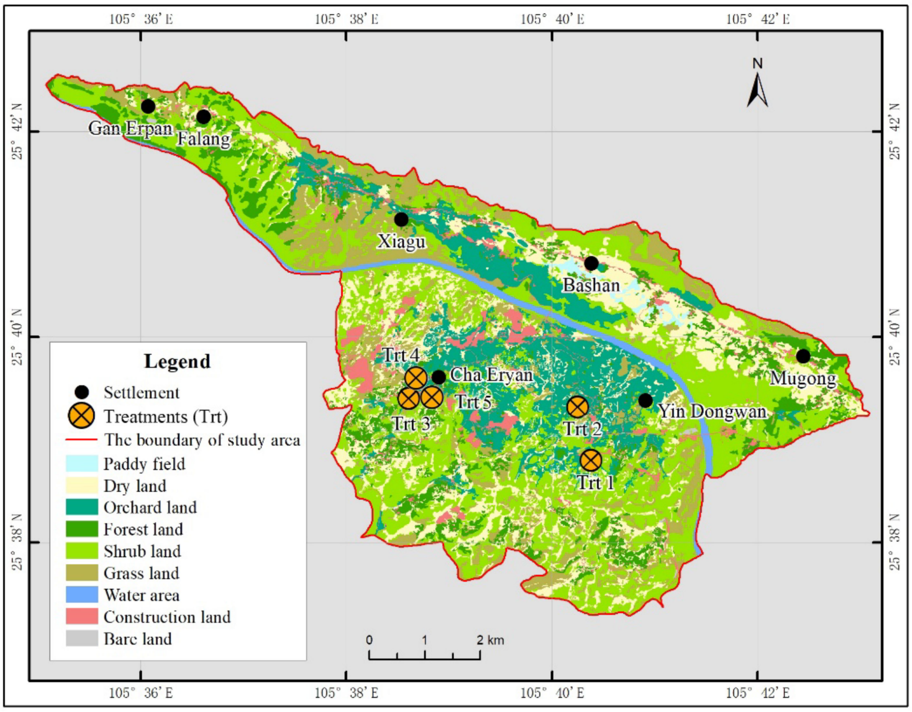

Figure 1. Distribution of treatments (Trt).

2.2. Treatment Setting

One treatment was set up for each of the five plantations (*Z. planispinum* + *P. salicina*, *Z. planispinum* + *S. tonkinensis*, *Z. planispinum* + *A. hypogaea*, *Z. planispinum* + *L. japonica*, and *Z. planispinum*) (Table 1). Before planting the experimental tree species, all treatments were planted mainly with *Z. mays*, with the same management measures and similar soil background values. In 2012, *Z. planispinum* was planted in five treatments. Since 2018, *P. salicina*, *S. tonkinensis*, *A. hypogaea*, and *L. japonica* have been planted around *Z. planispinum*. *A. hypogaea* has been planted continuously as an annual plant according to the phenology; other perennial plants are under community management. The age of the *Z. planispinum* individuals planted in the five treatments was 8 years, and the slope of all treatments was 10°. Detailed management practices for the five treatments can be found in the literature [23].

Table 1. Descriptions of plantation types.

Plantation Types	Species Combinations	Longitude	Latitude	Growing Area (ha)	Altitude (m asl)	Density (m)	Height (m)	Crown Width (m)	Coverage (%)
Trt 1	*Z. planispinum* + *P. salicina*	105°40′28.33″ E	25°37′57.41″ N	1.34	764	3 × 3	3.5	2 × 2.3	70
Trt 2	*Z. planispinum* + *S. tonkinensis*	105°40′19.79″ E	25°39′25.75″ N	0.67	728	2 × 2	2.0	1.2 × 1.8	60
Trt 3	*Z. planispinum* + *A. hypogaea*	105°38′36.32″ E	25°39′23.64″ N	0.67	791	2 × 2	2.5	2.5 × 2.8	85
Trt 4	*Z. planispinum* + *L. japonica*	105°38′36.35″ E	25°39′22.29″ N	6.67	814	3.5 × 3	2.5	1.5 × 2.5	70
Trt 5	*Z. planispinum*	105°38′35.64″ E	25°39′23.35″ N	33.35	788	3 × 4	2.2	2.5 × 2.3	65

The distance between plants was measured and expressed as "length × width", and the average value taken. Plant height was set as the distance from the root neck to the top of the main stem as measured by an altimeter. The width of the crown was measured with a tape measure, with the tree as the center. The measure was extended to the maximum value covered by the crown in the east-west and north-south directions, respectively. The average value of the two measurements was taken to obtain the width of the crown for each tree tested. For convenience in terms of operation and estimation, to measure coverage, a projected area approximately in the shape of a rectangle was measured using a tape measure. The maximum length and width of the lines corresponding to the upper part of the plant was used to estimate the projected rectangular area covered by the plant. All of the approximate projected areas of each plant in the area were added to calculate the total coverage. The calculation used to determine coverage was as follows:

$$\text{Coverage} = (S_1 + S_2 + \ldots + S_n)/S \times 100\% \tag{1}$$

2.3. Soil Sampling and Analysis

Between 19 and 21 November 2020, soil samples were collected, within a period of 15 or more consecutive sunny days. At this time, the soil material composition was relatively stable, and the degree of soil variability low. This ensured that fewer testing time-points could be used to characterize the component levels under long-term drought conditions, facilitating a better evaluation of the effect of the planting combinations on soil. Three sample squares (10 × 10 m) were set up in each treatment, with sufficient buffer strips left between the squares. Sampling points were laid along "S" lines in each sample square. We collected equal amounts of soil from the 0~10 and 10~20 cm soil layers (soil depth <20 cm) at each sample point. Samples from the same soil layer were fully mixed. The average value of the two soil layer values was taken for the final soil parameter calculation. Artificial fertilization areas (about 20 cm away from the tree trunks) were avoided as far as possible during sampling. The fresh soil samples were divided into two parts after removing gravel, root systems, and residues from animals and plants. One part was dried and passed through a 0.15 mm sieve to determine the soil nutrient contents. The other was sieved through a 2 mm sieve and stored at 4 °C to determine the microbial biomass as quickly as possible.

The soil water content (SWC) was measured with a TR-6 soil temperature and humidity meter. Soil pH was determined using the potentiometric method; soil organic carbon (SOC) with the potassium dichromate oxidation external heating method; total nitrogen (TN) through the Kjeldahl method; total phosphorus (TP) by using molybdenum antimony resistance colorimetry; total potassium (TK) with a sodium hydroxide melting flame photometer; and total calcium (TCa) by way of an atomic absorption spectrophotometer [24]. Available nitrogen (AN) was determined using the alkali hydrolysis diffusion method; available phosphorus (AP) using the HCl-H_2SO_4 extraction method; available potassium (AK) by flame photometry; and available calcium (ACa) content by atomic absorption spectrophotometry [25]. Soil microbial biomass carbon (MBC), nitrogen (MBN) and phosphorus (MBP) were determined with the chloroform fumigation K_2SO_4 extraction method [26]. Specific data are shown in Table 2. Relevant data have been previously analyzed [23]. This article uses existing data for in-depth analysis.

Table 2. Soil parameters in different planting combinations.

Soil Parameters	Trt 1	Trt 2	Trt 3	Trt 4	Trt 5
SWC	31.60 ± 6.29 ab	36.73 ± 2.65 a	25.05 ± 1.38 bc	28.69 ± 0.30 bc	21.15 ± 0.14 c
pH	6.70 ± 0.42 d	7.35 ± 0.33 bc	7.92 ± 0.05 ab	7.28 ± 0.05 cd	8.08 ± 0.05 a
SOC	37.73 ± 7.32 ab	29.40 ± 0.57 ab	28.68 ± 12.62 ab	50.83 ± 13.33 a	26.50 ± 2.19 b

Table 2. *Cont.*

Soil Parameters	Trt 1	Trt 2	Trt 3	Trt 4	Trt 5
TN	3.53 ± 0.46 ab	2.64 ± 0.07 b	2.78 ± 0.74 b	4.60 ± 0.44 a	2.76 ± 0.23 b
TP	1.37 ± 0.02 a	0.82 ± 0.03 b	1.10 ± 0.43 ab	1.52 ± 0.17 a	1.26 ± 0.04 ab
TK	6.95 ± 0.34 b	6.11 ± 1.51 b	12.33 ± 0.25 a	11.88 ± 0.53 a	10.88 ± 0.03 a
TCa	0.95 ± 0.28 b	1.48 ± 0.39 b	1.85 ± 0.71 b	1.88 ± 0.18 b	6.05 ± 0.21 a
AN	275.00 ± 74.25 ab	160.00 ± 5.66 b	161.75 ± 61.87 b	350.00 ± 55.15 a	153.75 ± 15.91 b
AP	45.80 ± 13.29 a	23.38 ± 11.63 a	26.55 ± 10.54 a	36.68 ± 10.01 a	20.08 ± 2.44 a
AK	393.00 ± 107.48 a	195.85 ± 32.03 b	172.75 ± 57.63 b	223.75 ± 98.64 ab	141.25 ± 2.47 b
ACa	317.50 ± 14.85 b	334.75 ± 0.35 b	347.75 ± 24.40 ab	371.00 ± 8.49 a	350.50 ± 7.07 ab
Soil C:N ratio	10.65 ± 0.70 a	11.13 ± 0.53 a	10.07 ± 1.85 a	10.97 ± 1.85 a	9.59 ± 0.00 a
Soil C:P ratio	27.68 ± 5.79 abc	35.83 ± 0.79 a	25.82 ± 1.33 bc	33.10 ± 4.99 ab	21.03 ± 2.38 c
Soil N:P ratio	2.59 ± 0.37 ab	3.22 ± 0.22 a	2.60 ± 0.34 ab	3.02 ± 0.05 a	2.19 ± 0.25 b
MBC	243.00 ± 4.95 a	254.75 ± 2.47 a	252.00 ± 2.83 a	262.75 ± 21.57 a	262.25 ± 26.52 a
MBN	12.40 ± 1.70 a	13.58 ± 1.31 a	14.38 ± 0.60 a	13.90 ± 1.06 a	14.08 ± 0.18 a
MBP	128.00 ± 23.33 a	144.50 ± 4.95 a	148.00 ± 8.49 a	154.50 ± 13.44 a	139.00 ± 3.54 a

Trts 1–5, five plantations, representing the research objectives of this article. SWC, soil water content; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; TCa, total calcium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; ACa, available calcium; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus. Means followed by the same lowercase letter are not significantly different ($p > 0.05$) among root types as determined by the least significance difference (LSD) test. Data are presented as mean ± standard deviation.

2.4. Leaf Sampling and Leaf Functional Trait Analysis

Z. planispinum leaves were collected in September 2021. At this time, the leaves had reached their full shape and were mature; new and old leaves could be distinguished easily. Because the treatments underwent the same nutrient management program in each growing season, the soil variations reflected the impact of the plants. In addition, as functional traits have a hysteresis effect on nutrient changes, soil and leaf samples were collected at different stages and selected at their most stable stages. Five *Z. planispinum* plants of good growth and uniform size were selected from each plot. We collected leaves of *Z. planispinum* from four directions (east, west, north, and south): 4–6 leaves from each direction. The collected leaves had good lighting conditions, were of similar size and shape, and were fully expanded and healthy. The collected leaves were wiped clean with gauze, numbered and marked, and then swiftly placed in a sealed bag for low temperature storage. Finally, they were taken back to the laboratory to determine their functional properties. In addition, about 200 g of leaves without disease and pests were collected from each plot. The samples were dried and crushed, and the contents of C, N, and P elements in the leaves were determined after passing through a 0.25 mm sieve.

On returning to the laboratory, we measured the leaf traits as soon as possible. The methods used to determine each trait specifically were as follows. Leaf fresh weight (LFW, g) of all numbered leaves was measured using a balance with an accuracy of ±0.0001 g. Leaf area (LA) was obtained by scanning the leaves using a Delta-T leaf area meter (Cambridge, UK). Electronic vernier calipers were used to measure the thickness at 0.25 cm on both sides of the main veins of the numbered leaves, and three points were selected uniformly for each leaf; the average value was taken as the leaf thickness of a single leaf. The Chl content (SPAD), as a typical physiological trait characterizing photosynthetic production capacity, was measured using a Minolta SPAD502 chlorophyll meter at three points on the main veins and leaf margins of the numbered leaves; the average value was taken to represent the Chl content of a single leaf. All numbered leaves were soaked in water for 12 h, and the water on the surface of the leaves was quickly dried with absorbent paper and weighed with an accuracy of ±0.0001 g on a balance to obtain the leaf saturated fresh weight (LSFW). After measuring the above functional trait indexes, the leaves were placed in an oven at 105 °C for 30 min and then baked at 70 °C until they achieved a constant weight to obtain the leaf dry weight (LDW). Specific leaf area (SLA), leaf tissue density (LTD), LDMC, and leaf water content (LWC) were calculated as follows:

$$SLA = LA/LDW \quad (2)$$

$$LTD = LDW/(LA \times LT/10) \quad (3)$$

$$LDMC = LDW/LSFW \times 100\% \quad (4)$$

$$LWC = (LSFW - LDW)/LFW \times 100\% \quad (5)$$

The leaf nutrient traits included leaf carbon (LC), leaf nitrogen (LN), and leaf phosphorous (LP) contents and their stoichiometric ratios. LC, LN, and LP contents were determined with the potassium dichromate external heating method, Kjeldahl nitrogen determination, and molybdenum antimony resistance colorimetry, respectively. The stoichiometric ratios were calculated according to the element: mass ratio. The leaf functional traits selected and their ecological implications are shown in Table 3.

Table 3. Leaf functional traits and their ecological implications [27,28].

Trait	Unit	Ecological Connotation
LT	mm	LT is closely related to the rate of light energy utilization and photosynthetic efficiency, affecting the water supply and storage of leaves and the process of material and energy exchange in photosynthesis; the larger the value, the more suitable the plant for resource-deficient habitats.
SLA	cm^2	SLA reflects the carbon acquisition strategies, growth strategies, and adaptation characteristics of plants to different habitats and affects their relative growth rates; the higher the photosynthetic rate, the higher the transpiration.
LDMC	$mg \cdot g^{-1}$	LDMC reflects the ability of plants to acquire and maintain environmental resources and the tissue construction of leaves. Higher values indicate that the leaves are better able to lock up nutrients in the body and reduce losses.
LWC	%	Leaf water content is important in breeding for drought tolerance and water retention traits of plants; higher values indicate higher drought resistance.
Chl	-	The higher the Chl content, the more photosynthetically active and shade-tolerant the plant.
LTD	$g \cdot cm^{-3}$	LTD is related to resource acquisition, indicating the ability of plants to store nutrients and water and resist external interference; the higher the value, the stronger the ability to resist interference.
LC	$g \cdot kg^{-1}$	The higher the LC value, the stronger the water supply capacity of the plant in a xerophytic environment.
LN	$g \cdot kg^{-1}$	The higher the LN value, the better the chlorophyll synthesis and photosynthetic efficiency.
LP	$g \cdot kg^{-1}$	LP promotes protein synthesis and physiological repair, and improves plant cold tolerance.
Leaf C:N ratio	-	C:N is proportional to the growth rate; the higher the value, the higher the carbon fixation advantage and nutrient utilization strategy, and the stronger the carbon assimilation ability.
Leaf C:P ratio	-	C:P represents the ability of plants to assimilate carbon when absorbing nutrients and the efficiency of carbon fixation in plants; the higher the value, the higher the carbon fixation advantage and nutrient utilization strategy, and the stronger the carbon assimilation ability.
Leaf N:P ratio	-	N:P indicates that plants are limited by nitrogen and phosphorus. If the value is >16, the plants are limited by phosphorus, if it is <14, the plants are limited by nitrogen, and between 14 and 16, both elements are limiting plant growth.

"-" indicates that the unit is dimensionless. LT, leaf thickness; SLA, specific leaf area; LDMC, leaf dry-matter content; LWC, leaf water content; Chl, chlorophyll; LTD, leaf tissue density; LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content.

2.5. Data Analysis

The Kolmogorov-Smirnov method was used to test the normality of each index. With a normal distribution, one-way analysis of variance (ANOVA) was performed using SPSS

20.0 (version 20.0, IBM SPSS, Armonk, NY, USA) to test the variability of the soil properties and leaf functional traits. The LSD test was used for post hoc multiple comparisons. Dunnett's T3 method was adopted when the distribution was not normal. The coefficient of variation (CV) is equal to the ratio of the standard deviation and mean value. Generally, CV $\leq$ 20% shows weak variation; 20% < CV $\leq$ 50% reflects moderate variation; and CV > 50% indicates strong variation [29]. The plasticity index (PI) indicates the degree of the response of traits to the planting combinations. The higher the value, the more sensitive the plant is to the external environment. For the calculation method, refer to Valladares et al. [30]:

$$\text{PI} = (\text{maximum} - \text{minimum})/\text{maximum} \tag{6}$$

The values used in the formula were all leaf functional traits. The nonlinear normal curve model was used to fit the relevant parameters of leaf functional traits. Pearson's method was used to analyze the correlation between leaf functional traits, and the "corrplot" program package in R4.1.2 software was used to plot the heatmap. Principal components (PC) analysis was used to screen out the main indexes that affected the variation in the leaf functional traits of *Z. planispinum*. Due to the different dimensions between the indicators, they were standardized and pretreated before evaluation. Then, the plant adaptability scores (PAS) of *Z. planispinum* with different planting combinations were calculated. The PAS calculation was combined with the weighted method, using the following formula:

$$\text{PAS} = \sum W_i \times F_i \tag{7}$$

where W_i is the contribution rate of each PC, and F_i is the PC score of each planting combination. By weighting the variance contribution rate (W_i) and factor score (F_i) of each PC factor, the PASs of different planting combinations are obtained.

Stepwise regression analysis was used to explore the effects of soil factors on the leaf functional traits of *Z. planispinum*. The data are expressed as mean ± standard value.

3. Results

3.1. Characteristics of Leaf Functional Traits of Z. planispinum in Different Planting Combinations

The change law of leaf functional traits of *Z. planispinum* in the five plantations are shown in Figure 2. The LT was highest in Trt 4 and was significantly greater than that in Trts 1 and 2; there was no significant difference between the other treatments. The SLA value in Trt 2 was the highest, significantly higher than that of other treatments, while that in Trt 4 was the smallest, significantly lower than that of Trts 2 and 3. The LDMC in Trt 1 was the highest, whereas that in Trt 2 was the lowest, but there was no significant difference among the five treatments. The LWC in Trt 1 was significantly lower than that in other treatments, and there was no significant difference among the other treatments. The LTD of Trt 1 was significantly higher than that of Trt 2. The Chl contents in Trts 1 and 5 were significantly higher than those in the other three treatments. The CV among different plantations was 5.8~26.9%, with the largest CV seen in Chl (26.9%), which indicated moderate variation, followed by LT (19.1%), LTD (18.0%), SLA (13.6%), and LDMC (9.1%); LWC had the lowest CV (5.8%).

The ANOVA results show that LC, LN, LP, leaf C:N, leaf C:P, and leaf N:P were not significantly different among the five plantations (Table 4). This indicated strong stability in the leaf nutrition index.

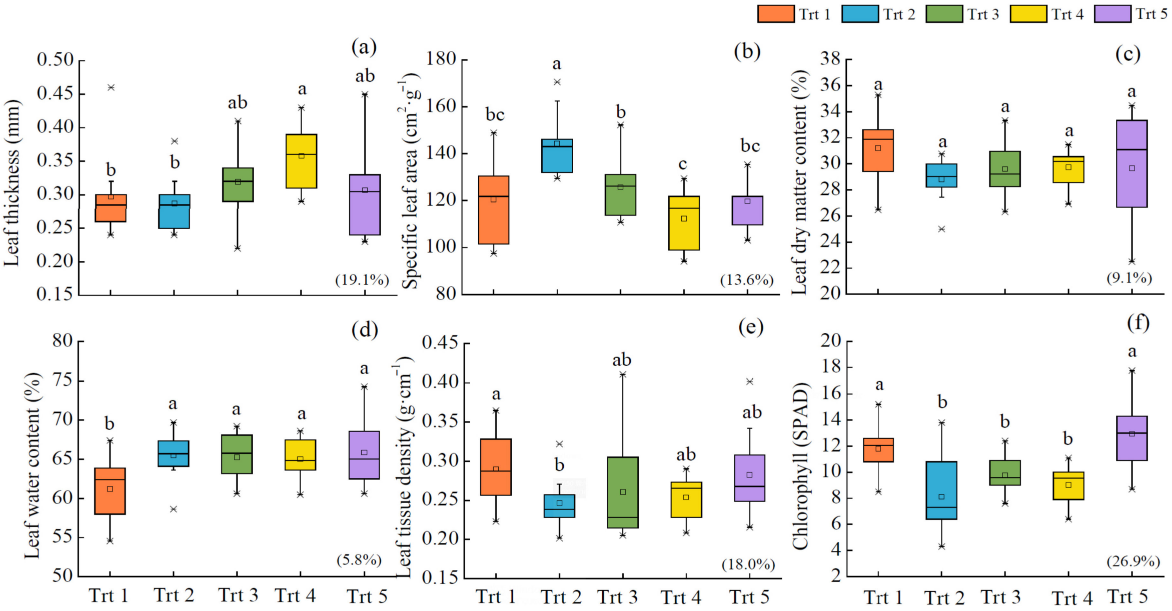

Figure 2. Leaf thickness (**a**), specific leaf area (**b**), leaf dry matter content (**c**), leaf water content (**d**), leaf tissue density (**e**) and chlorophyll (**f**) of *Z. planispinum* in different planting combinations. Trts 1–5, five plantations, representing the research objects of this article. Bars show mean ± standard deviation, n = 30. "□" in the box plot indicates the mean value of individual plant traits; different lowercase letters indicate significant differences between trait values ($p < 0.05$); percentages in parentheses are the CV.

Table 4. Carbon, nitrogen, and phosphorus contents and stoichiometric ratios of *Z. planispinum* leaves.

Plantation Type	LC (g·kg^{-1})	LN (g·kg^{-1})	LP (g·kg^{-1})	Leaf C:N Ratio	Leaf C:P Ratio	Leaf N:P Ratio
Trt 1	46.38 ± 1.43 a	2.79 ± 0.08 a	2.74 ± 0.34 a	16.60 ± 0.01 a	17.02 ± 1.58 a	1.03 ± 0.10 a
Trt 2	44.64 ± 4.21 a	2.93 ± 0.11 a	3.42 ± 0.72 a	15.23 ± 0.86 a	13.49 ± 4.07 a	0.88 ± 0.22 a
Trt 3	45.33 ± 4.39 a	3.11 ± 0.23 a	3.00 ± 0.16 a	14.58 ± 0.33 a	15.16 ± 2.27 a	1.04 ± 0.13 a
Trt 4	44.40 ± 2.83 a	3.20 ± 0.14 a	2.92 ± 0.42 a	13.88 ± 0.28 a	15.31 ± 1.21 a	1.10 ± 0.11 a
Trt 5	42.98 ± 0.90 a	2.85 ± 0.45 a	3.46 ± 0.51 a	15.28 ± 2.74 a	12.57 ± 2.12 a	0.82 ± 0.01 a
Coefficient variation/%	5.8	8.1	14.8	9.0	16.7	15.2

Trts 1–5, five plantations, representing the research objectives of this article. LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content. Means followed by the same lowercase letter are not significantly different ($p > 0.05$) among root types as determined by the LSD test. Data are presented as mean ± standard deviation.

3.2. Plasticity of Leaf Functional Traits of Z. planispinum in Different Planting Combinations

The PI values for Chl, LT, and LTD were higher than those for the other traits (PI > 0.50), indicating that they were sensitive to the planting combinations. In contrast, the plasticity change of LC was the least sensitive (PI < 0.20) and inert in response to the planting combination (Figure 3). These findings imply that the Chl content as a physiological trait, and LT and LTD as structural traits were more sensitive to the planting combinations.

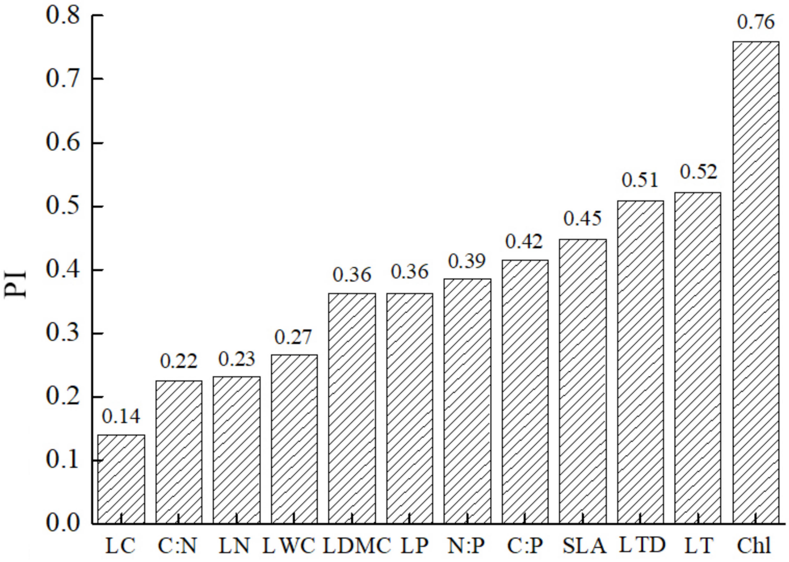

Figure 3. Plasticity index of the leaf functional traits of *Z. planispinum*. LT, leaf thickness; SLA, specific leaf area; LDMC, leaf dry-matter content; LWC, leaf water content; Chl, chlorophyll; LTD, leaf tissue density; LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content; C:N, leaf C:N ratio; C:P, leaf C:P ratio; N:P, leaf N:P ratio.

3.3. Correlation Analysis of the Leaf Functional Traits of Z. planispinum in Different Planting Combinations

Leaf thickness had significant negative correlations with SLA. Three pairs of traits were significantly positively correlated: Chl and LTD, LC and leaf C:P, and leaf N:P and C:P, respectively. Leaf water content was negatively and positively correlated with LDMC and LN, respectively. Leaf nitrogen content was significantly negatively correlated with leaf C:N, as was LP with leaf C:P and N:P. The correlations between LC, LN, and LP contents and their ratios were more significant than those between the other leaf functional traits (Figure 4).

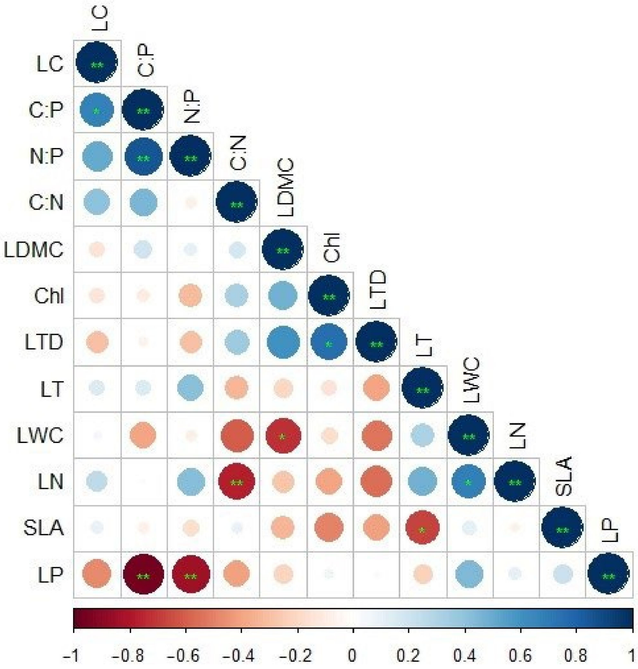

Figure 4. Correlation analysis of the leaf functional traits of *Z. planispinum*. LT, leaf thickness; SLA,

specific leaf area; LDMC, leaf dry-matter content; LWC, leaf water content; Chl, chlorophyll; LTD, leaf tissue density; LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content; C:N, leaf C:N ratio; C:P, leaf C:P ratio; N:P, leaf N:P ratio. Red indicates negative correlation, blue indicates positive correlation, and the darker the color, the stronger the significance. * Correlation is significant at the 0.05 level (2-tailed). ** Correlation is significant at the 0.01 level (2-tailed).

3.4. Analysis of the Adaptability of Z. planispinum in Different Planting Combinations

Following a PC analysis of the leaf functional traits of *Z. planispinum*, four principal components were extracted, which explained 88.41% of the cumulative variance. This finding indicated that these principal components could explain most of the information about the original variables (Table 5). Among them, the first was significantly positively correlated with LC, leaf C:P, and N:P, while it was significantly negatively correlated with LP. The second principal component was greatly affected by LN and had a positive effect on leaf C:N. The first and second principal components represented the LC, LN, and LP contents and their ratios. The third principal component had a significant negative correlation with LDMC and a significant positive correlation with LWC, representing the nutrients and water stored in the leaves. The fourth principal component was mainly controlled by SLA.

Table 5. Principal component analysis of leaf functional traits of *Z. planispinum*.

Factors	**Load Matrix of Principal Component**			
	PCA1	**PCA2**	**PCA3**	**PCA4**
LT	0.291	−0.508	0.309	0.625
SPAD	−0.235	0.534	−0.249	0.647
SLA	−0.097	0.114	0.210	**−0.943**
LDMC	0.104	0.115	**−0.873**	0.212
LWC	−0.305	−0.440	**0.769**	0.090
LTD	−0.217	0.520	−0.614	0.388
LC	**0.727**	0.196	0.452	−0.018
LN	0.107	**−0.823**	0.364	0.091
LP	**−0.928**	−0.076	0.220	−0.088
Leaf C:N ratio	0.366	**0.912**	−0.047	−0.055
Leaf C:P ratio	**0.979**	0.121	−0.107	−0.009
Leaf N:P ratio	**0.887**	−0.406	−0.076	0.052
Eigenvalue	3.905	3.586	2.068	1.050
Variance contribution rate/%	29.838	23.051	19.480	16.035
Cumulative variance contribution rate/%	29.838	52.889	72.370	88.405

LT, leaf thickness; SLA, specific leaf area; LDMC, leaf dry-matter content; LWC, leaf water content; Chl, chlorophyll; LTD, leaf tissue density; LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content. Bold font is the relatively large influence factor of each main component load factor.

The plant adaptability scores of *Z. planispinum* in different planting combinations were calculated (Table 6). The results showed that the *Z. planispinum* in Trt 1 had the strongest adaptability, followed by Trt 4, while Trt 2 had the lowest adaptability. The factor 3 score of Trt 1 was the lowest, indicating that it was mainly affected by the LDMC and LMC. The factor 4 score of Trt 2 was the lowest, and the SLA of Trt 2 was significantly higher than that of other treatments, which indicated that the SLA of *Z. planispinum* in Trt 2 was mainly affected by the high SLA. Trts 3 and 4 had the lowest factor 2 scores, indicating that they were highly restricted by LN and leaf C:N. The factor 1 score of Trt 5 was the lowest, indicating that it was mainly affected by LC, LP, and leaf C:P and N:P.

Table 6. Factor scores of leaf functional traits of *Z. planispinum*.

Sample Site	**Factor Score**				**Soil Quality Index**	**Rank**
	F_1	F_2	F_3	F_4		
Trt 1	1.409	1.934	**−2.516**	0.959	0.530	1
Trt 2	−0.93	−0.187	1.526	**−3.292**	−0.552	5
Trt 3	0.466	**−0.746**	0.631	−0.178	0.061	3
Trt 4	0.904	**−1.821**	0.731	1.303	0.201	2
Trt 5	**−1.844**	0.820	−0.373	1.208	−0.240	4

Trts 1–5, five plantations, representing the research objectives of this article. The bold font indicates the factor with the lowest score.

3.5. Effects of Soil Factors on Leaf Functional Traits

The Shapiro-Wilk normality test was performed for the 12 functional trait indicators (dependent variables). The data analysis revealed that the significance level of all indicators was greater than 0.05, indicating that the dependent variables obeyed a normal distribution, so the next step of the stepwise regression analysis was carried out.

The relationship between the leaf functional traits of *Z. planispinum* in response to soil factors was analyzed by stepwise regression (Table 7). The results showed that LT, Chl, SLA, LTD, and soil C:N were significantly correlated with the soil factor ($p < 0.05$), while the correlations between the remaining indicators and the soil factor were not ($p > 0.05$). LT was significantly correlated with MBP ($p < 0.05$). Chl was significantly correlated with soil N:P and MBN ($p < 0.01$), and in its regression equation, the standard regression coefficient of soil N:P (−0.937) was greater than that of MBN (−0.373), indicating that soil N:P was the main factor affecting Chl, while MBN was the secondary factor. SLA was highly significantly correlated with TP, SWC, and AN ($p < 0.01$), and the standardized coefficient of SWC (0.515) greater than that of TP (−0.412) and AN (−0.396), indicating that SWC was the main factor affecting SLA, followed by TP and AN. LTD was highly significantly correlated with soil N:P, soil C:P, MBC, SWC, and soil C:N ($p < 0.01$), where the standard regression coefficient was soil C:P (4.493) > soil N:P (−4.464) > soil C:N (−1.474) > MBC (−0.321) > SWC (0.21), indicating that LTD was mainly influenced by soil C:P and soil N:P. Leaf C:N had a significant correlation with ACa and MBC ($p < 0.05$), and the standardized coefficient of ACa (−0.908) was greater than that of MBC (0.564), indicating that the main factor affecting leaf C:N was ACa, with MBC a secondary factor. In summary, leaf functional traits were jointly influenced by SWC, MBC, MBN, MBP, AN, TP, ACa, soil C:N, C:P, and N:P.

Table 7. Stepwise regression analysis of leaf functional traits and soil quality.

Leaf Functional Traits	**Stepwise Regression Equation**	**Standardized Regression Coefficients**	**R-Square**	***P***
LT	LT = 0.071 + 0.002 × MBP	$B_{MBP} = 0.715$	0.449	0.020
Chl	Chl = 29.749 – 3.814 × N:P−0.65 × MBN	$B_{N:P} = -0.937$, $B_{MBN} = -0.373$	0.796	0.002
SLA	SLA = 127.27 – 17.515 × TP + 1.067 × SWC − 0.055 × AN	$B_{TP} = -0.412$, $B_{SWC} = 0.515$, $B_{AN} = -0.396$	0.960	0.000
LTD	LTD = 0.868–0.226 × N:P + 0.017 × C:P − 0.001 × MBC + 0.001 × SWC − 0.033 × C:N	$B_{N:P} = -4.464$, $B_{C:P} = 4.493$, $B_{MBC} = -0.321$, $B_{SWC} = 0.21$, $B_{C:N} = -1.474$	0.983	0.000
Leaf C:N ratio	C:N = 20.979 – 0.058 × ACa + 0.055 × MBC	$B_{ACa} = -0.908$, $B_{MBC} = 0.564$	0.628	0.013

P is significant. C:N, soil C:N ratio; C:P, soil C:P ratio; N:P, soil N:P ratio.

4. Discussion

4.1. Effect of Planting Combinations on the Leaf Functional Traits of *Z. planispinum*

Plants adapt to changes in the environment by adjusting their leaf morphology and internal physiological characteristics, resulting in a rich combination of traits [31,32]. After being combined with *P. salicina*, *Z. planispinum* improved nutrient acquisition by decreasing SLA to reduce water loss from the organism [33], which is a strategy for resisting water deficit stress. After planting with *L. japonica*, *Z. planispinum* formed a combination of drought-tolerant traits, with large LT values and a small SLA. It cooperatively resisted drought stress and adapted to the arid and barren living environment by reducing the SLA, strengthening defense tissues, storing nutrients, reducing water dissipation and improving drought tolerance and defense capabilities [34]. In general, the above two plantations had higher adaptive capacity than the other three plantations because, in addition to their stronger resource acquisition and defense functions, the former may also have more litter input to change the habitat quality. After planting with *S. tonkinensis*, *Z. planispinum* showed a rapid investment strategy of low LT, LDMC, and Chl, as well as high SLA and LWC, which met growth demands by reducing adaptability. The reasons are that the light supply to *Z. planispinum* was relatively stable after planting with *S. tonkinensis*, which is an understory crop. The thinner leaves lowered the required light intensity and CO_2 transmission distance and improved the photosynthetic capacity of the leaves [35]. It can be inferred that, in a habitat with abundant light, the *Z. planispinum* has less competitive pressure and mostly adopts a fast growth strategy. The results showed that there was a close relationship between the economic spectrum and the adaptive capacity of the leaves, but the mechanism of action needs to be studied in depth.

Apart from Chl, LT, and LTD, the overall plasticity of the leaf functional traits in *Z. planispinum* was relatively small. The reasons are as follows: (1) Due to the fragile habitat in karst areas (where the superposition of geological and seasonal drought causes a tendency for the environment to be xeric and there is a shallow soil layer and low soil reserves), *Z. planispinum* resists environmental stress by improving its stability; (2) In order to adapt to the nutrient poor environment, *Z. planispinum* adopts a conservative strategy of slow investment, which ultimately leads to a relatively low growth rate and low plasticity in the variation of traits. The structural traits of the leaves in this study were more plastic than the chemical traits, reflecting the different adaptation strategies adopted by *Z. planispinum* to cope with environmental changes [36]. The reason is that structural traits respond more sensitively and intuitively to changes in the external environment and adapt to dynamic changes in the resource environment through rapid adjustment. The LC, LN, and LP contents and their stoichiometric ratios in *Z. planispinum* in different planting combinations were not significantly different, and the CVs were all small, indicating that the biological organism was able to maintain the relative stability of its chemical composition [37]. This phenomenon showed that, as a suitable dominant species, *Z. planispinum* has higher internal stability and a more conservative approach to nutrient utilization, making it more suitable for water- and nutrient-deficient habitats [38,39]. In the future, the adaptation strategies and driving mechanisms of *Z. planispinum* need to be investigated further in conjunction with its internal stability mechanisms.

4.2. Coupling Relationship between the Leaf Functional Traits of Z. planispinum

Plants adapt to different environments through synergistic or trade-off relationships among leaf functional traits [40]. This study showed a significant negative correlation between LDMC and LWC, confirming that an increase in plant LDMC reduces LWC. This combination of traits is common in plant communities [41] because *Z. planispinum* can resist water stress by increasing its element retention capacity. Chlorophyll and SLA were negatively correlated with LTD and LT as the physical support structures, respectively, reflecting the resource balancing and allocation strategy of the leaves in terms of ecological function [41,42] and structure construction. *Z. planispinum*, therefore, improved the efficiency of resource allocation by adjusting the relationship between the photosynthetic capacity (fast growth) and material accumulation (slow growth), and thus alleviated habitat stress. There were strong correlations between LC, LN, LP, and their stoichiometry in *Z. planispinum*. This occurred because the plant's use of nutrients was influenced by the environment and its own demands. *Z. planispinum* adjusted its own leaf nutrient elements and stoichiometric ratio to adapt to the nutrient supply in the environment [43], which also verified the internal stability theory of ecological stoichiometry. Among the stoichiometric relationships, leaf C:P was significantly positively correlated and extremely significantly negatively correlated with LC and LP, respectively, indicating that the accumulation and consumption of C and P in *Z. planispinum* were not synchronized, and there was a trade-off effect, which may be related to the different cycling paths of C and P nutrient elements [44].

4.3. Response of Leaf Functional Traits to Soil Factors

This study found that leaf functional traits were affected mainly by the SWC, different forms of massive elements, element stoichiometric balance, and microbial biomass. Soil water affected the ecological adaptation strategy of *Z. planispinum*, and the reasons for this are as follows: (1) The characteristics of a dry and hot valley, shallow soils, and deeply burial groundwater in the study area made water the dominant factor, and the impact of the plantations on the water cycle of the micro-habitat may have aggravated the water restriction [45]; (2) Soil water is closely related to plant health [46], and drought stress makes trees more vulnerable to insect pests and pathogens [47]; shallow-rooted species such as *Z. planispinum* are particularly susceptible to water deficits; (3) Soil water and nutrients have a strong coupling relationship which, together, affect C fixation and microbial activity [48], as well as nutrient content and stoichiometry [49], which in turn have an impact on plant growth. This indicates that the effect of water on the adaptive capacity of plantations is worthy of further study.

Mineral nutrients affected the photosynthetic rate and plant composition of *Z. planispinum* [50], and there was also a strong synergistic effect between photosynthetic productivity and nutrients [51]. Therefore, the levels of mineral elements affected plant growth and adaptation. Both N and P are limiting elements that constitute the body and are important fertility indicators [52] which restrict the formation of ecosystem productivity and are therefore key factors that affect plant survival. However, C had no significant effect on plant adaptation, which is related to the fact that it is mainly derived from the atmosphere and can be conserved through photosynthetic fixation. In addition, the forms of N and P that affected plant growth were not the same, which may be due to the higher degree of N restriction in this area [53]. Furthermore, the relatively abundant P had a dilution effect on N [54], resulting in the limitation of AN. The P saturation caused an imbalance in the C:N:P ratios, leading to element deficiency and limiting ecosystem functions [55]. In addition, plants can absorb small molecular substances, such as free amino acids in the soil [56], and the degradation of soil organic structure in this area may also have been a reason for the lack of AN. Phosphorous is mainly derived from the geological environment and is less affected by soil structure and biological activity, and its main component forms are also different. Calcium is a characteristic element in karst areas, which is mainly inherited from the parent rock, and has both nutrient supply and signal transduction functions [57,58] with strong ecological regulation, so it has a significant effect on the growth of *Z. planispinum*, which is mainly composed of more active quick acting components.

Soil microbial biomass plays an important role in forest ecosystems by acting as a storage reservoir of biologically active nutrients [59]. It is a nutrient pool that is easy to decompose and turn over. It drives the biogeochemical cycle of biogenic elements [60], has a crucial impact on the terrestrial ecosystem, and plays an important role in the soil [61]. Moreover, ecological stoichiometry regulates the cycle of C, N, and other elements [62]; influences the balance of elements; determines the processes of nutrient mineralization, absorption, and utilization; and ultimately affects the productivity of the ecosystem [55]. Therefore, soil microbial biomass and element stoichiometry jointly affect plant growth and adaptation, and plant functional traits have synchronous responses to them. The comprehensive results of this study show that cultivating the organic structure of the soil is particularly important to improving the ecological adaptation traits of plants and is a key measure to improving their adaptive capacity. However, stoichiometry is dependent on water [63], and there is a strong coupling effect between soil components. Therefore, the comprehensive influence of soil action on leaf functional traits needs further study.

5. Conclusions

(1) *Z. planispinum* tended to have a slow investment strategy after planting with *P. salicina*. The combination with the *S. tonkinensi* showed a rapid growth strategy. Following combination with *L. japonica*, *Z. planispinum* tended to form a combination of traits that resisted drought and infertile environmental stress. The combination with *L. japonica* made the investment strategy of *Z. planispinum* adopt a transition from slow to fast. The results showed that species combination could affect the adaptive mechanism of *Z. planispinum*.

(2) *Z. planispinum* was relatively more adaptive when combined with *P. salicina* or *L. japonica*. However, the lowest adaptive capacity occurred when the *Z. planispinum* was planted in combination with *S. tonkinensis*. The results indicated that planting combinations can promote or inhibit the growth of *Z. planispinum*.

(3) The leaf functional traits of *Z. planispinum* were affected by SWC, MBC, MBN, MBP, AN, TP, ACa, C:N, C:P, and N:P, involving the effects of soil physical properties, soil elements, and their stoichiometry and microbial properties. In the future, it will be necessary to further study the comprehensive effect of soil action on leaf functional traits across a wider range of sites.

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