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Leaf Functional Traits and Relationships with Soil Properties of *Zanthoxylum planispinum* 'dintanensis' in Plantations of Different Ages

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Abstract: To explore the changes of leaf functional traits of *Zanthoxylum planispinum* 'dintanensis' with growth and development and its relationship with soil properties, which can clarify the response of the plantation to soil properties and suitable strategy. The research results can provide a scientific basis for plantations management. We explored the response of leaf functional traits to soil by using redundancy analysis in 5–7-, 10–12-, 20–22-, and 28–32-year *Z. planispinum* 'dintanensis' plantations. The results showed that: (1) The coefficients of variation of leaf traits ranged from 0.41% to 39.51%, with mostly medium and low variation, with the lowest variability in leaf water content (0.51–0.85%); The 5–7, 10–12, 20–22-year-old plantations were laid at the "slow investment-return" end of the economic spectrum while 28–32-year plantations were close to "fast investment-return" end. (2) The *Z. planispinum* 'dintanensis' tended to suit the environment via making trade-off and coordination of leaf functional traits. Leaf dry matter content decreased with an increase in leaf carbon/leaf nitrogen ratio, which is the trade-off between nitrogen usage efficiency and nutrient fixation capacity in *Z. planispinum* 'dintanensis'. (3) Redundancy analysis suggested that soil carbon/nitrogen ratio, soil total calcium, soil water content, soil available phosphorus, soil carbon/calcium ratio were highly correlated with leaf functional traits, while soil elemental stoichiometry had a greater reflection on leaf functional traits than their own content.

Keywords: karst; plantation age; stoichiometry; redundancy analysis; suitable strategy

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1. Introduction

Plant functional traits are morphological, physiological, and phenological characteristics that affect the growth, reproduction, and survival of plants [1,2]. They function as indicators of the mutual feedback between plants and their environments [3]. Plants are composed of organs, such as roots, stems, and leaves of which leaves are both the main site of photosynthesis and an important organ for maintaining hydrological security. Leaf functional traits can reflect the efficiency of resource use, such as light, temperature, and soil [4], and the combination of a series of trade-offs and synergistic relationships among leaf traits is called the leaf economic spectrum, which integrally characterizes the plant's suitability to habitats and resource use strategies [5]. Therefore, exploring leaf functional traits can better elucidate the dynamics of plant growth suitability with the environment.

There is a substantial body of research on the functional traits of mixed-age plantations and the formulation of suitable strategies. Chen et al. found that fine root carbon/nitrogen/phosphorus ratio *Pinus tabulaeformis* and *Robinia pseudoacacia* plantations was inconsistent with increasing plantation age [6]. Wang et al. showed that the stoichiometry of different organs in a *Metasequoia glyptostroboides* plantation was different in mixed-age plantations, and the growth of young and mature trees were limited by nitrogen and phosphorus, respectively [7]. Chang et al. showed that the nutrient content of leaf nitrogen, phosphorus, and potassium in a larch plantation in the Qinling mountain area did not change consistently with plantation age [8]. Fan et al. suggested that there is a close coupling relationship between soil and plant nutrients in a *Eucalyptus* sp. plantation [9]. Lin et al. studied the effects of soil nutrients and water content on leaf nutrients and stoichiometry in a *Leucaena leucocephala* forest at different ages, and they reached the conclusion that available soil nutrients and soil water content were the main factors limiting plant growth [10]. Nelson et al. concluded that leaf functional traits are influenced by the plantation age and habitat characteristics [11]. He et al. found that *Pinus massoniana* showed strong plasticity in its adaptation to the environment as indicated by coupled, coordinated, or combined traits [12]. These studies indicate that the responses of leaf functional traits to plantation ages are different and they have elucidated the level of environmental influence on plantations at different developmental stages. However, the change of the suitable strategy of *Z. planispinum* 'dintanensis' plantation with age is not clear, which is not conducive to the dynamic adjustment of plantation management measures.

Z. planispinum 'dintanensis' is a variety of *Z. planispinum* [13,14], in the family Rutaceae, which is a deciduous shrub or dungarunga. As a valued ecological and economic plant in Guizhou karst area, *Z. planispinum* 'dintanensis' is lithophytic and has the characteristics of calcium preference and drought tolerance, helping to conserve water and soil, and it plays a significant role in mitigating rocky desertification [15]. The pericarp is well known for its strong aroma, strong hemp flavor, and high yield, which makes it a protected geographical trademark, with high development potential for functional products [16,17]. Research has mainly focused on soil nutrients, functional traits, and stoichiometry [14,18,19], leaving the interactions between growth and environment unclear. Moreover, the fruit harvesting reduces nutrient levels, which leads to differences in available nutrients in plantations of different ages. Thus, the driving effect of soil on leaf functional traits in different ages needs to be further investigated. Since the soil background values in this study are approximate, the leaf functional traits are considered to be mainly influenced by the growth and developmental processes of the *Z. planispinum* 'dintanensis', so the leaf trait change drivers are mainly discussed in relation to the soil. This study selected 5–7-, 10–12-, 20–22-, and 28–32-year-old plantations in Bashan village, Huajiang Town, Guanling County, Anshun City, and Guizhou Province as the experimental sites, and adopted redundancy analysis to investigate the relationships between soil factors and leaf functional traits in *Z. planispinum* 'dintanensis'. The aim was to investigate: (1) how the leaf economic spectrum and suitable strategy vary with plantation age; (2) the connections among leaf functional traits, and (3) how the soil water content, soil elements status, and stoichiometry regulate leaf functional traits. The purpose is to reveal the response and suitable strategy of the *Z. planispinum* 'dintanensis' plantation to the environment and to provide a theoretical basis for plantation management.

2. Materials and Methods

2.1. Overview of the Study Area

The study area has a subtropical, humid, monsoon climate, with an average annual precipitation of 1100 mm. The rainfall is abundant but unevenly distributed throughout the year. The altitude is 530–1473 m, with a relative elevation difference of 943 m, and the terrain fluctuates between largely severe and moderate rock desertification [14]. The area is mainly covered by calcareous soil, rich in calcium and magnesium elements. The soil layer is shallow and discontinuous, resulting in a low water and nutrient holding capacity. The carbonate rocks in the study area are typically developed and can represent the characteristics of the regional habitat. Additionally, the research results can provide a reference for similar areas (Figure 1).

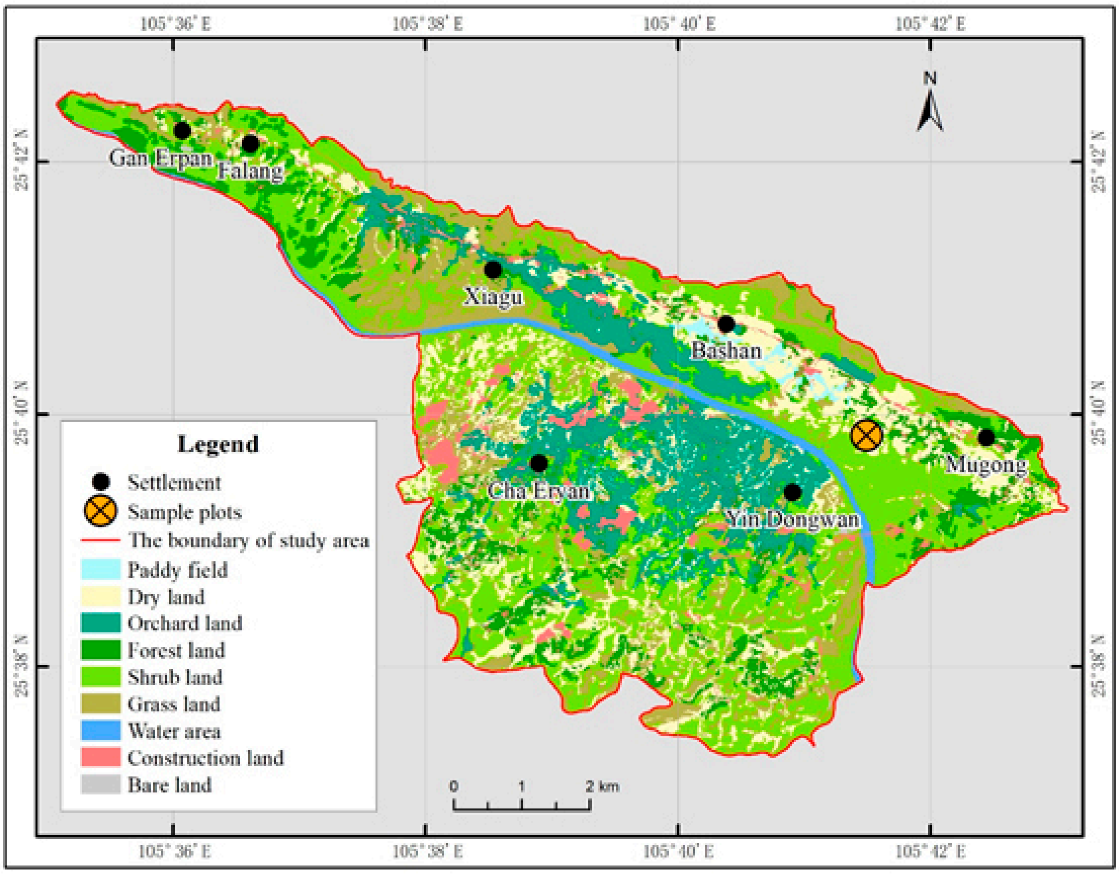

Figure 1. The sample plot distribution map.

Z. planispinum 'dintanensis' is planted mainly in the low-lying soil accumulation area below 700 m. Plantations are established by transplanting seedlings into the field. Management techniques have resulted in relatively stable plantations. *Z. planispinum* 'dintanensis' has been planted in this area for more than 30 years, extending over more than 1000 hectares. The benefits include the control of rocky desertification and sustainable economic growth in the area.

2.2. Sample Plot Setting

The study areas were located in Bashan village, Huajiang Town, Guanling County, Anshun City, and Guizhou Province. During the vigorous growth period in July 2020, *Z. planispinum* 'dintanensis' plantations at sites with similar conditions (middle and lower slope, sunny slope, 5–10° slope, limestone soil, and immediate soil temperature of 25–26.5 °C) were selected in the area centered around 35°39′49.64″ N, 105°41′30.09″ E, with an elevation of 621 m. According to the planting layout, the plantations were divided into 5–7, 10–12, 20–22, and 28–32-year-old groups using space instead of time. Since re-planting may happen in the process of stand cultivation, the plantation age is presented as an interval value rather than a specific value. The stands were mainly pure plantations, and there were no other cultivated crops interspersed within the *Z. planispinum* plantation. Due to the fragmentation and high heterogeneity of habitats in karst areas, three 10 m × 10 m sample plots were set up as three replications in plantations of different ages. In total, 12 sample plots were set up with a buffer zone of more than 5 m wide between each sample plot. The height, density, crown width, vegetation coverage, and yield of the trees in each sample plot were measured (Table 1).

Table 1. Basic characteristics of plots.

Age	Tree Height (m)	Density (Plant/ha)	Crown (m)	Coverage (%)	Yield (Plant/kg)
5–7	3.0	1150	3 × 3	100	6–7
10–12	3.0	1150	3 × 3	100	7–8
20–22	3.5	1000	3.5 × 3.5	90	4–5
28–32	4.2	650	4 × 5	70	1–1.5

2.3. Plant Description and Identification

Z. planispinum 'dintanensis' are evergreen shrubs, 2–4.5 m high. The stems and branches have sharp, reddish-brown thorns, and the base of the thorns is wide and flat; Branchlets, shoots, and leaves are glabrous or occasionally pilose. Leaves are pinnately compound. Lobules are usually lanceolate or lanceolate elliptic, opposite or alternate, 4–9 cm long, 1.5–2.5 cm wide, smooth, and glabrous. Cymose panicles axillary or concurrent at the top of lateral branches, with a length of 2–7 cm. The ripe pericarp is mostly olive green, with a number of conspicuously raised round punctured oil glands [20].

Changsheng Wei, the Senior Engineer of Zhenfeng County Forestry Bureau, and Dr. Yanghua Yu, one of the authors of this paper, jointly undertook the formal identification of the plant materials. The voucher specimens were deposited in the publicly available School of Life Sciences, Guizhou Normal University. Deposition code numbers are 990010, 200012, and 200055.

2.4. Sample Collection

Five plants with good growth and consistent tree height and crown width were selected from each sample plot. Four to six mature leaves were selected from each plant along the four directions of east, south, west, and north of each plant. Selected leaves exposed to full sunlight, consistent in size, fully unfolded, and free from obvious symptoms of pathogens, were then placed in cool and dark conditions until further processing in the laboratory. In addition, a mixed sample of 200 g leaves were collected for determining the leaf carbon, nitrogen, and phosphorus contents.

Five soil samples were collected after removing litter and avoiding fertilized areas from each sample plot at a depth from 0 up to 20 cm according to the S-shaped point sampling method [21]. The soil collected from each sample plot was mixed thoroughly after removing plant and animal residues and gravels, and a total of 12 soil samples were obtained. The soil samples were dried naturally in a lab, ground, and passed through 1.0 and 0.25 sieves, respectively.

2.5. Selection of Leaf Functional Traits and Soil Properties Parameters

The fragmented and shallow soil cover in karst regions lead to poor water retention capacity. Leaf thickness can reflect the suitability strategy of plants to water, and leaf water content, leaf water use efficiency, and leaf stable carbon isotope is related to soil water conditions. Carbon, nitrogen, and phosphorus, as important biogenic elements in soil, affect carbon, nitrogen, and phosphorus in leaves, specific leaf area, and leaf dry matter content, then they further affect the photosynthetic capacity of leaves. The process of the soil nitrogen cycle also affects the leaf stable nitrogen isotope. In addition, *Z. planispinum* 'dintanensis' is a calcicole plant, so soil calcium also plays a regulatory role in its growth and development. Therefore, the selected soil factors were soil water content, soil organic carbon, soil total nitrogen, soil total phosphorus, soil total calcium, soil available nitrogen, soil available phosphorus, soil available calcium, soil carbon/nitrogen ratio, soil nitrogen/phosphorus ratio, soil carbon/calcium ratio, and soil calcium/phosphorus ratio—12 in total; leaf table carbon isotope and leaf water use efficiency both indicate the water usage efficiency of plants and the latter was selected as the leaf factor. Thus, the selected leaf factors were leaf thickness, specific leaf area, leaf dry matter content, leaf water content, leaf nitrogen, leaf phosphorus, leaf carbon, leaf stable nitrogen isotope, and leaf water use efficiency. The selected leaf factors and soil factors can further clarify the regulation effects of soil moisture content, element forms, and stoichiometry on leaf functional traits of *Z. planispinum* 'dintanensis'.

2.6. Index Determination Method

2.6.1. Leaf Traits Determination

The leaf thickness was measured with Vernier calipers (SF2000, Guilin, China), with an accuracy of 0.01 mm, by taking three measurements from the upper middle and lower leaf regions (avoiding the main leaf veins) and using the average value as the leaf thickness. The leaf area was measured using a leaf area meter (LI-COR 3100C Area Meter, LI-COR, Lincoln, NE, USA). Leaf fresh weight was measured using a balance (JJ124BC, Changshu, China) with an accuracy of 0.0001 g. The leaves were immersed in water for 12 h without light; then, after removing them, the water on the leaf surface was quickly absorbed with absorbent paper, and the leaf saturated fresh weight was obtained. To obtain leaf dry weight, the leaves were dried in an oven for 30 min at 105 °C and then at 70 °C to a constant mass. Leaf nitrogen was determined by Kjeldahl's method; leaf phosphorus was determined by molybdenum antimony anti colorimetry; leaf carbon/nitrogen ratio, leaf carbon/phosphorus ratio, and leaf nitrogen/phosphorus ratio were measured as element mass ratio.

In 2019, the team studied leaf carbon, leaf nitrogen, leaf phosphorus, and their stoichiometric characteristics in the early stage, and the results showed that it could better indicate the nutrient limitation. Therefore, these indicators were still adopted in the more systematic study of leaf functional traits in 2020, but their ages are different, and they can clarify the law of nutrient limitation from a longer time scale. The combination of leaf chemometrics and leaf functional traits is helpful to reflect the process of plant suitability to the environment; leaf stable carbon isotope and leaf stable nitrogen isotope were determined by a stable isotope mass spectrometer (Thermo Scientific MAT253, Bremen, Germany). Specific leaf area, leaf dry matter content, leaf water content, leaf tissue density, and leaf water use efficiency [22] were calculated according to the following formula:

$$\text{Specific leaf area} = \text{Leaf area}/\text{Leaf dry weight} \tag{1}$$

$$\text{Leaf dry matter content} = \text{Leaf dry weight}/\text{Leaf saturated fresh weight} \tag{2}$$

$$\text{Leaf water content} = (\text{Leaf fresh weight} - \text{Leaf dry weight})/\text{Leaf fresh weight} \times 100\% \tag{3}$$

$$\text{Leaf tissue density} = \text{Leaf dry weight}/(\text{Leaf area} \times \text{leaf thickness}) \tag{4}$$

$$\text{Leaf water use efficiency} = C_a/1.6(\delta^{13}C_p - \delta^{13}C_a + b)/(b - a) \tag{5}$$

$$\delta^{13}C_a = -6.429 - 0.006 \exp\,[0.0217(t - 1740)] \tag{6}$$

In Formulas (5) and (6), C_a stands for the CO_2 concentration (approximately 0.038%) in atmosphere; $\delta^{13}C_p$ is the abundance of stable carbon isotope in sample leaves; $\delta^{13}C_a$ is the abundance of stable carbon isotopes in the atmosphere (‰); a is the stable carbon isotope fractionation value produced by diffusion (approximately 4.4‰); b is the stable carbon isotope fractionation value produced by carboxylation reaction (approximately 27‰); t is the year when the sample was taken. In this study, the sample was taken in 2020, and t = 2020 was substituted into Formula (6) to calculate $\delta^{13}C_a$, which was −9.04.

2.6.2. Determination of Soil Physical and Chemical Properties

Soil water content was determined by an electrode method, referring to Bao et al. to determine the soil chemical properties [23] in which soil organic carbon was determined by the potassium dichromate oxidation external heating method; soil total nitrogen and soil available nitrogen were determined by the Kjeldahl method and alkaline hydrolysis diffusion method, respectively. Soil total phosphorus and soil available phosphorus were determined by the acid melting method and hydrochloric acid sulfuric acid extraction, respectively. Soil total calcium and soil available calcium were determined by the diethylenetriamine penta-acetic acid extraction method. Soil carbon/total nitrogen ratio, soil nitrogen/phosphorus ratio, soil carbon/calcium ratio, and soil calcium/phosphorus ratio were measured as the element mass ratio (Table 2).

Table 2. Descriptive statistics of soil factors.

Age (a)	Soil Water Content (%)	Soil Total Nitrogen (g/kg)	Soil Organic Carbon (g/kg)	Soil Total Phosphorus (g/kg)	Soil Total Calcium (g/kg)	Soil Available Nitrogen (mg/kg)
5–7	22.47 ± 0.85 a	2.62 ± 0.34 a	23.65 ± 4.31 a	0.43 ± 0.11 b	8.3 ± 2.69 ab	175 ± 14.14 a
10–12	26.23 ± 1.09 a	2.50 ± 0.30 a	15.3 ± 0.85 b	0.80 ± 0.20 ab	12.75 ± 6.33 a	162 ± 5.66 a
20–22	24.97 ± 4.01 a	2.00 ± 0.52 a	15.05 ± 2.47 b	1.11 ± 0.24 a	2.5 ± 1.20 b	222.5 ± 110.71 a
28–32	23.23 ± 4.81 a	2.12 ± 0.43 a	16.5 ± 2.26 ab	0.77 ± 0.18 ab	3.9 ± 1.27 ab	145 ± 29.70 a
Age (a)	**Soil Available Phosphorus (mg/kg)**	**Soil Available Calcium (mg/kg)**	**Soil Carbon/ Nitrogen Ratio**	**Soil Nitrogen/Phosphorus Ratio**	**Soil Carbon/ Calcium Ratio**	**Soil Calcium/Phosphorus Ratio**
5–7	32.70 ± 5.80 a	1109.00 ± 185.26 a	9.00 ± 0.48 a	6.37 ± 2.35 a	2.92 ± 0.42 ab	20.65 ± 11.31 a
10–12	20.2 ± 5.37 a	989.50 ± 156.27 a	6.16 ± 0.41 b	3.27 ± 1.19 ab	1.36 ± 0.62 b	17.50 ± 12.38 a
20–22	36.65 ± 9.55 a	1018.50 ± 412.24 a	7.625 ± 0.76 ab	1.80 ± 0.08 b	7.39 ± 4.02 a	2.14 ± 1.07 a
28–32	33.65 ± 7.28 a	1145.00 ± 35.36 a	7.86 ± 0.53 a	2.76 ± 0.10 ab	4.37 ± 0.85 ab	5.02 ± 0.47 a

Different letters indicate significant differences among plantation ages at the 0.05 significance level.

2.7. Data Processing

Preliminary data sorting was done in Microsoft Excel 2013. The Kolmogorov–Smirnov method in SPSS 20.0 was used to test the normality of the leaf and soil data. For data that were normally distributed, one-way ANOVA and least significant difference was applied. For non-normally distributed data, Dunett's T_3 method was used. Data were presented in the form of mean ± standard deviation and mean and standard deviation of leaf traits based on plot level. Pearson correlation analysis was performed on the functional traits of each leaf using the "corrplot" packages in R software. Canoco 4.5 was used for redundancy analysis of leaf functional traits and soil factors to investigate the magnitude of the effect of soil factors on leaf functional traits [24]. Coefficients of variation of leaf functional traits = standard deviation/mean × 100%. Sample sizes of three were used to determine the mean, standard deviation, and coefficient of variation. The sample sizes to determine Pearson correlation and redundant analysis was 12.

3. Results

3.1. The Variation Characteristics of Z. planispinum 'dintanensis' Suitability Strategy and Its Economic Spectrum at Different Plantation Ages

As shown in Table 3, the coefficients of variation of leaf functional characters of *Z. planispinum* 'dintanensis' at different ages was 0.41–39.51%, with mainly medium and low coefficients of variation, indicating that the leaf traits had stable variation characteristics during plant development. The coefficients of variation of leaf dry matter content (2.18–4.56%), leaf water content (0.51–0.85%), leaf carbon (2.65–7.61%), and leaf stable carbon isotope (0.41–3.14%) was low. Specific leaf area, leaf water content, and leaf stable nitrogen isotope showed significant differences at different plantation ages. Specific leaf area reached the highest level in the 28–32-year plantation (132.22 cm^2/g), which was significantly higher than that of other three plantation age groups. Leaf water content was 63.46–66.00% and significantly lower in the 5–7- and 10–12-year groups than in the other two age groups. Leaf stable nitrogen isotope reached the highest in the 10–12-year group (3.20‰), suggesting a more open soil nitrogen cycle. Leaf thickness, leaf dry matter content, leaf tissue density, leaf nitrogen, leaf phosphorus, leaf carbon, leaf carbon/nitrogen ratio, leaf carbon/phosphorus ratio, leaf nitrogen/phosphorus ratio, and leaf stable carbon isotope showed no significant differences in all age groups, among which leaf thickness was 0.34–0.37 mm, leaf dry matter content was 31.00–33.00%, and did not change significantly with age. There was no obvious change pattern found in leaf tissue density with age.

Leaf nitrogen, leaf phosphorus, and leaf carbon increased first and then decreased with plantation age. Leaf carbon/phosphorus and leaf nitrogen/phosphorus ratios were rank ordered as 10–12 > 5–7 > 28–32 > 20–22-year group, while leaf carbon/nitrogen ratio was rank ordered as 20–22 > 28–32 > 5–7 > 10–12-year group. Leaf stable carbon isotope and leaf water use efficiency were higher in the late stage of growth, indicating a higher water usage efficiency at this stage.

Table 3. Mean, standard deviation, and coefficient of variation of leaf functional traits of Z. *planispinum* 'dintanensis' at different plantation ages.

Indicator	5–7 a	10–12 a	20–22 a	28–32 a
Leaf thickness (mm)	0.38 ± 0.01 a (3.17%)	0.37 ± 0.03 a (7.65%)	0.36 ± 0.05 a (13.94%)	0.34 ± 0.09 a (27.43%)
Specific leaf area (cm^2/g)	87.37 ± 1.31 b (1.50%)	89.70 ± 6.29 b (7.02%)	91.88 ± 20.65 b (22.47%)	132.22 ± 2.81 a (2.12%)
Leaf dry matter content (%)	32.50 ± 0.71 a (2.18%)	33.00 ± 1.41 a (4.29%)	32.00 ± 1.41 a (4.42%)	31.00 ± 1.41 a (4.56%)
Leaf water content (%)	64.59 ± 0.35 b (0.55%)	63.46 ± 0.54 b (0.85%)	66.00 ± 0.45 a (0.69%)	65.95 ± 0.33 a (0.51%)
Leaf tissue density (g/cm^3)	0.33 ± 0.01 a (2.18%)	0.33 ± 0.03 a (8.58%)	0.32 ± 0.02 a (6.73%)	0.31 ± 0.03 a (9.13%)
Leaf nitrogen (g/kg)	23.70 ± 0.57 a (2.39)	22.25 ± 0.50 a (2.22%)	21.00 ± 1.98 a (9.43%)	22.10 ± 2.97 a (13.44%)
Leaf phosphorus (g/kg)	1.64 ± 0.35 a (21.19%)	1.02 ± 0.23 a (22.19%)	1.67 ± 0.40 a (24.21%)	1.63 ± 0.25 a (15.62%)
Leaf carbon (g/kg)	419.00 ± 18.38 a (4.39%)	373.00 ± 9.90 a (2.65%)	399.50 ± 30.41 a (7.61%)	415.00 ± 12.73 a (3.07%)
Leaf carbon/nitrogen ratio	17.70 ± 1.20 a (6.75%)	16.76 ± 0.07 a (0.42%)	19.04 ± 0.35 a (1.86%)	18.99 ± 3.13 a (16.46%)
Leaf carbon/phosphorus ratio	263.38 ± 67.05 a (25.46%)	373.81 ± 73.22 a (19.59%)	244.91 ± 41.02 a (16.75%)	257.13 ± 32.35 a (12.58%)
Leaf nitrogen/phosphorus ratio	14.79 ± 2.79 a (18.84%)	22.31 ± 4.47 a (20.03%)	12.85 ± 1.92 a (14.92%)	13.87 ± 3.99 a (28.75%)
Leaf stable nitrogen isotope (‰)	0.86 ± 0.02 b (2.17%)	3.20 ± 0.15 a (4.80%)	2.17 ± 0.86 ab (39.51%)	1.80 ± 0.72 ab (39.82%)
Leaf stable carbon (‰)	−28.31 ± 0.30 a (1.07%)	−28.10 ± 0.12 a (0.41%)	−27.84 ± 1.12 a (4.03%)	−27.90 ± 0.88 a (3.14%)
Leaf water use efficiency (umol/mol)	81.21 ± 3.18 a (3.92%)	83.48 ± 1.22 a (1.46%)	86.15 ± 11.81 a (13.71%)	85.54 ± 9.20 a (10.76%)

Different letters indicate significant differences among plantation ages at the 0.05 significance level; Values in brackets indicate the coefficients of variation.

Among many functional traits, specific leaf area, leaf thickness, leaf tissue density, and leaf tissue density are the best variables in the classification axis of plant resource utilization [25,26]. Based on these results, considering that the habitat characteristics of plantations are changing rapidly and that the plantation age in this study varies greatly, we attempted to elucidate the changes in ecological resource strategies of *Z. planispinum* 'dintanensis' to obtain light, temperature, water, air, heat, and soil with plantation age by using leaf economic spectrum. Our analyses demonstrated a lower specific leaf area and a higher leaf tissue density, leaf thickness, and leaf dry matter content, in 5–7, 10–12, and 20–22-year-old plantations, which puts them at the "slow investment-return" end of the leaf economic spectrum, while the lower leaf tissue density, leaf thickness, and leaf dry matter content, and higher specific leaf area, put the 28–32-year-old plantation at the "fast investment-return" end of the same spectrum (Figure 2).

3.2. Trade-Off and Synergistic Relationship between Leaf Functional Traits of Z. planispinum 'dintanensis'

Figure 3 shows the relationship among leaf functional traits. Leaf phosphorus showed a significant positive correlation with leaf carbon and leaf water content. Leaf dry matter content decreased with an increase in leaf carbon/nitrogen ratio, which is the trade-off between plant nitrogen usage efficiency and nutrient fixation capacity. Leaf carbon/phosphorus ratio showed a very significant positive correlation with leaf nitrogen/phosphorus ratio, and they both decreased with increasing leaf water content. Leaf stable nitrogen isotope had a reverse effect with leaf phosphorus and leaf carbon, indicating that the nitrogen cycle was affected by the contents of carbon and phosphorus in leaves. There were no significant correlations found among other leaf functional traits. Correlation analysis indicated that *Z. planispinum* 'dintanensis' suits its environment through trade-off and coordination of leaf functional traits.

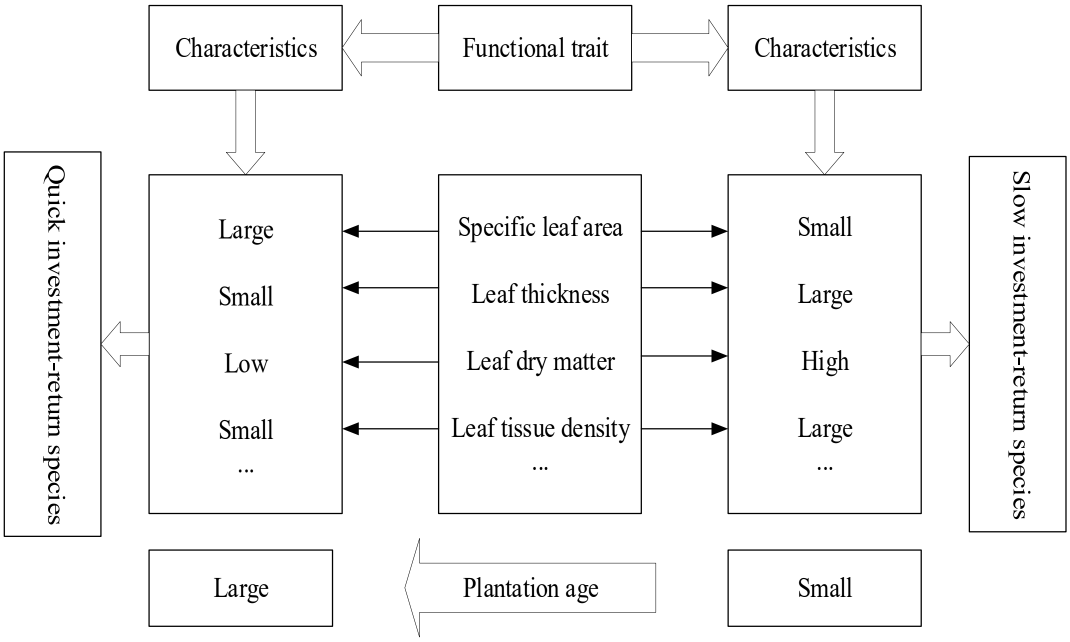

Figure 2. Conceptual illustration of leaf economics spectrum [27,28].

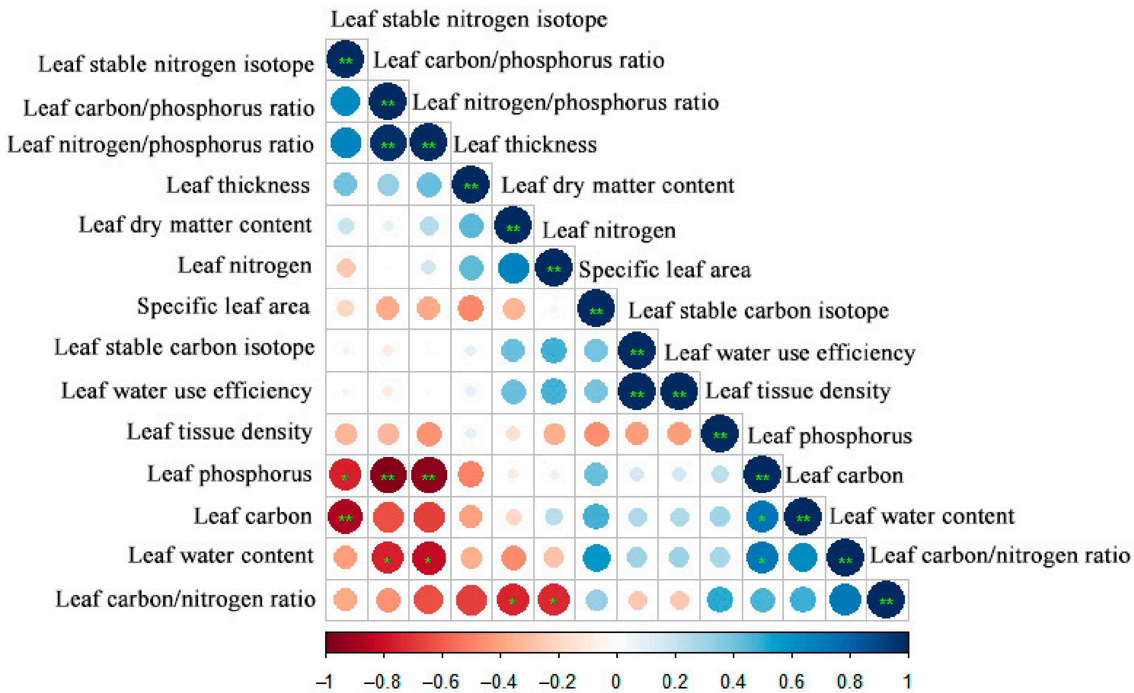

Figure 3. Correlation among leaf functional traits of *Z. planispinum* 'dintanensis' at different plantation ages. Circles with asterisks indicate significant correlations at the 0.05 level (*) and the 0.01 level (**).

3.3. The Relationships between Soil Factors and Leaf Functional Traits of *Z. planispinum* 'dintanensis'

In our previous study, based on the principle of collinearity, the minimum data set was adopted to reduce the soil indicators from 25 to 12, based on which redundancy analysis was performed for leaf functional traits and soil factors. From Table 4, it can be seen that the eigenvalues of redundancy analysis on the first and second axis were 0.434 and 0.240, the accumulated explanation rate was 67.4%, and the total explanation rate was 90.9% on the first four axes. The variation fell mainly on the first and second axis, suggesting a good connection between soil factors and leaf functional traits.

Table 4. Eigenvalues of the ordination axes and the cumulative percentage variance of functional trait–environment relation explained by ordination axes.

Item	Ordination Axes of RDA				
	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Sum of All Canonical**
Eigenvalues	0.434	0.240	0.161	0.075	1
Cumulative percentage variance of functional traits/%	43.4	67.4	83.4	90.9	_

"_" indicates that there is no data.

In Figure 4, taking soil factors as explanatory variables (blue arrows), and leaf functional traits as response variables to soil factors (red arrows), the relationship between leaf functional traits and soil factors were analyzed by linear constrained redundancy analysis sorting. The length of the line connecting the soil factor arrows represents the magnitude of its effect on leaf functional traits, and the size of the angle between the line connecting the soil and leaf functional traits arrows indicates the level of correlation between them. Smaller acute angles indicate greater positive correlations. While the larger obtuse angles indicate negative correlations, an angle close to 90° indicates the lack of significant correlation.

According to Table 5 and Figure 4, the effects of soil factors on the leaf traits of *Z. planispinum* 'dintanensis' showed a significant effect of soil carbon/nitrogen ratio > soil total calcium > soil organic carbon > soil available phosphorus > soil carbon/calcium ratio, while the other soil factors had less of an effect. The soil carbon/nitrogen ratio was more positively correlated with leaf water use efficiency, leaf nitrogen, leaf carbon, and leaf phosphorus, and negatively correlated with leaf thickness and leaf stable nitrogen isotope. Soil total calcium positively correlated with leaf thickness and leaf dry matter content, and was significantly negatively correlated with leaf carbon. All leaf traits were negatively correlated with soil water content except leaf stable nitrogen isotope, which showed a positively correlation. Leaf water content, specific leaf area, and leaf phosphorus more positively correlated to soil available phosphorus. Soil carbon/calcium ratio was positively correlated with leaf water content, specific leaf area, leaf phosphorus, leaf carbon, and leaf water use efficiency, and negatively correlated with leaf dry matter content, leaf thickness, and leaf stable nitrogen isotope. These results suggested soil carbon/nitrogen ratio, soil total calcium, soil water content, soil available phosphorus, and soil carbon/calcium ratio were highly correlated with leaf functional traits, while soil elemental stoichiometry had a greater correlation on leaf functional traits than their own contents.

Table 5. Soil factor explained variance and significance test.

Soil Factor	Explained Variance (%)	*p*
Soil carbon/nitrogen ratio	12.06	0.004
Soil total calcium	11.04	0.008
Soil water content	10.52	0.012
Soil available phosphorus	10.27	0.024
Soil carbon/calcium ratio	9.20	0.038

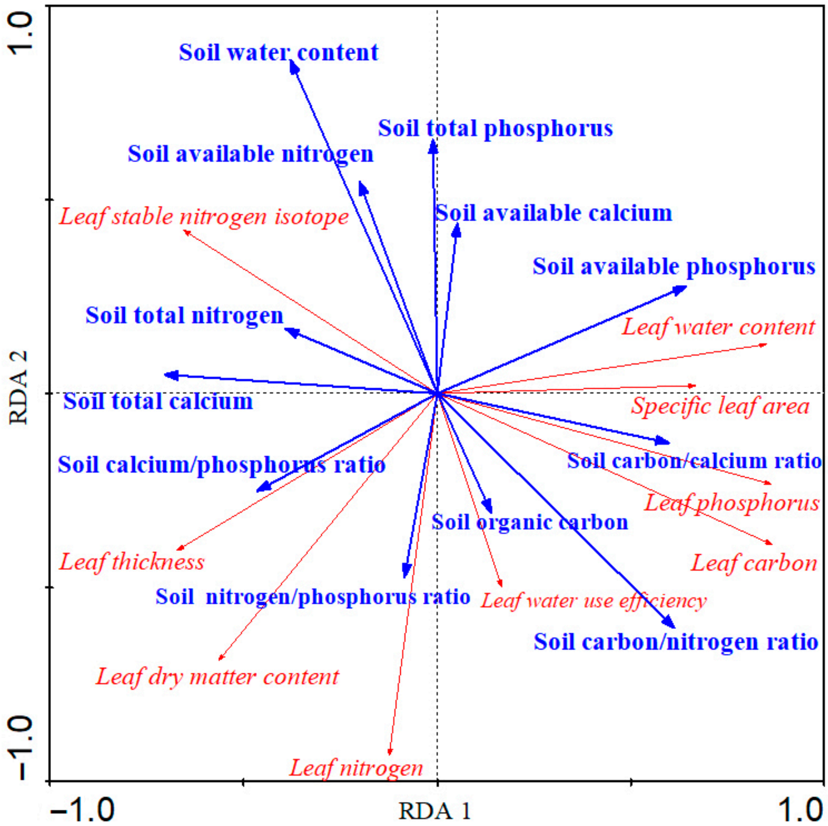

Figure 4. Redundancy analysis of the relationship between leaf functional traits of *Z. planispinum* 'dintanensis' and soil factors.

4. Discussion

4.1. The Leaf Economic Spectrum and Suitability Strategy of Z. planispinum 'dintanensis' Varies with Plantation Age

Soil nitrogen, phosphorus, and other biogenic elements in the study area are deficient [29]. Coupled with the challenges of geological and seasonal drought [30], karst areas gradually degenerate into arid and barren habitats. This study found that most leaf traits did not differ significantly with plantation age and that coefficients of variation were low, indicating that *Z. planispinum* 'dintanensis' plantation gradually develop stable functional traits to suit the habitat during growth. The low coefficient of variation may be a result of the formation of specific traits into which plants devote their resources during long-term suitability for unfavorable habitats [31,32]. The arid and barren habitat in the study area leads to a preference for species with lower trait variability, and thus *Z. planispinum* 'dintanensis' plantations are highly suitable in this area, which is basically consistent with the research results of He et al. [33] in the karst mountains of Guilin. Although the *Z. planispinum* 'dintanensis' is planted artificially, its age is long, and it has formed a long-term coupling relationship with the habitat, which provides strong support for studying its suitability. Some studies have shown that leaf dry matter content is a relatively stable variable on the resource acquisition axis [34], which is similar to the results of this study (the coefficient of variation was 2.18–4.56%). However, this study found that the coefficient of variation of leaf water content (0.51–0.85%) is lower than that of leaf dry matter content. This is because plants growing in arid environments are easily limited by water availability. Their water content is relatively low [35], so the fluctuation of leaf water content is small. Specific leaf area was strongly correlated with photosynthetic capacity and was significantly higher in 28–32 year-old plantations than that of the other three plantation age groups, which was attributed to the reduced density of the stand (Table 1), which allowed the leaves to receive more light and thus enhanced photosynthetic capacity [4,36]. This paper only explores the change of leaf traits with plantation age, and future studies will investigate the change of phenotypic trait plasticity by using plantation age and environment as dual factors to isolate their contribution to phenotypic trait plasticity.

This paper focuses on selecting typical phenotypic traits to characterize the economics of leaf utilization of ecological resources, which is the scientific basis for screening key agronomic traits. The current study showed that the 5–7-, 10–12-, and 20–22-year-old groups stood at the "slow investment-return" end of the leaf economic spectrum, with a tendency toward weak photosynthesis, small specific leaf area, and a longer life. When the specific leaf area is low, the products of photosynthesis are mostly invested to increase the length or resistance of the water diffusion pathway [37]. In addition, the leaf dry matter content, leaf thickness, and leaf tissue density increased correspondingly for the purpose of reducing water loss induced by transpiration, thus increasing the water usage efficiency and the plant suitability to drought and aridity [38,39]. The plantation at the slow end is a conservative strategy, which usually includes a low respiration rate and low leaf turnover rate to prevent carbon loss, with enhancement of the plant resistance to adversity [40]. In the 28–32-year group with growth decline, the assimilation efficiency of leaf carbon by increasing specific leaf area, while leaf tissue density, leaf thickness and leaf dry matter content are reduced, the ecological strategy of "fast investment-return" is adopted to prioritize the nutritional growth. This stage has high productivity and water transport efficiency and a large capacity to obtain and utilize nutrients and fix carbon. However, the ability of the tissue to tolerate drought stress is weak, resulting in poor suitability to a low resource environment [35]. It may be that the growth decline observed in the 28–32-year group resulted in a weaker capacity to use limited environmental resources. In this study, indirect traits, such as chemical traits, were not included in the construction of the leaf economic spectrum. However, in the future, traits, such as metrological and physiological traits, will be included to comprehensively assess the economics of utilizing the resources of *Z. planispinum* 'dintanensis'.

4.2. The Trade-Off and Synergic Relationship among Leaf Functional Traits of Z. planispinum 'dintanensis'

In the process of suitability the environment, plants are comprehensively affected by physiological, phylogenetic, environmental, and other factors, resulting in correlation between plant functional traits [27]. Leaf traits manifest a trade-off or synergistic relationship. In this study, leaf carbon was significantly and positively correlated with leaf phosphorus due to the fact that leaf phosphorus characterizes the ability of plants to assimilate carbon dioxide, leaf phosphorus participates in the photosynthetic process of leaves by affecting chlorophyll and protein content in plants [41], and leaf carbon, the main product of photosynthesis, increases with the increase of leaf phosphorus. This study also found that leaf nitrogen/phosphorus ratio had a very significant negative correlation with leaf phosphorus but not with leaf nitrogen, indicating that phosphorus might impose more restrictions to plant growth than nitrogen, which was consistent with the study of Güsewell et al. [42]. Moreover, plants need phosphorus-rich RNA to support protein synthesis during rapid growth, resulting in a faster increase in phosphorus than nitrogen [43], and creating a very significant negative correlation between leaf nitrogen/phosphorus ratio and leaf phosphorus. The leaf dry matter content was observed to decrease with a leaf carbon/nitrogen ratio increase, which indicated the trade-off relationship between plant nitrogen usage efficiency and nutrient fixation (the plant's ability to fix nutrients in the body and use them through growth, physiological and other processes) in our study, because leaf dry matter content is an indicator of nutrient fixation capacity [44], and the leaf carbon/nitrogen ratio is an indicator token of nitrogen utilization efficiency, a higher value indicates a higher nitrogen utilization. In our research, leaf stable nitrogen isotope was negatively correlated with leaf phosphorus and leaf carbon. At present, the mechanism of leaf nutrient elements affecting leaf stable nitrogen isotope is unclear. However, it may be that these elements have a direct or an indirect influence on nitrogen physiological metabolism.

4.3. The Regulation Effect of Soil Factors on the Leaf Functional Traits of Z. planispinum 'dintanensis'

Redundancy analysis showed that leaf functional traits were correlated with multiple soil factors, among which soil carbon/nitrogen ratio, soil total calcium, soil water content, soil available phosphorus, and soil carbon/calcium ratio were most significant. The soil carbon/nitrogen ratio influences the available nutrient supply capacity by affecting the nutrient mineralization rate, thus acting on leaf functional traits [45]. Water supply to plants was dependent on precipitation and soil moisture storage. In spite of the rich precipitation in the karst area, water easily leaks through cracks, resulting in poor soil water retention, and water deficit will inhibit photosynthesis and plant growth [46]. In the research area, soil water content and leaf nitrogen were negatively correlated, which was inconsistent with Cao's research [47]. This is because water deficiency in plants increases the nitrogen allocation to leaves, increases the osmotic pressure in cells, and reduces water loss by reducing stomatal conductance, thus reinforcing water loss protection mechanisms [48]. Calcium can improve the suitability of calcicole plants to arid habitats, yet, it may cause adverse impacts on normal plant growth and development when it exceeds a threshold. In the research area, soil total calcium was positively correlated with leaf thickness and leaf dry matter content, and negatively correlated to leaf carbon, indicating that increased calcium can enhance a plant's capacity to resist adversity. However, in excess it can cause reduced carbon storage, thus reducing plant primary productivity. Zhang et al. [49] indicated that the accumulation of Ca^{2+} in a rocky desertification area led to high soil alkalinity, thus promoting leaf nitrogen content and net photosynthesis rate. The content of phosphorus-related nutrients in soil directly affects the leaf phosphorus absorption capacity. The available soil phosphorus and leaf phosphorus in *Z. planispinum* 'dintanensis' plantations were significantly positively correlated, which is consistent with the conclusion of Fu et al. that plant leaf phosphorus in karst areas is restricted by the availability of soil phosphorus [50], and it also supports the view that soil phosphorus is an important driving factor of leaf phosphorus [51]. Phosphorus is a major element for protein and amino acid synthesis, and phosphorus limitation leads to lower photosynthetic rates and carbon fixation capacity of plants. The leaf nitrogen/phosphorus ratio was less than 14 in the 28–32-year-old plantation, which is limited by nitrogen [52] but not by phosphorus; therefore, soil available phosphorus positively correlated to specific leaf area and leaf carbon, with a relatively high value.

5. Conclusions

(1) The coefficients of variation of leaf functional traits of *Z. planispinum* 'dintanensis' ranged from 0.41% to 39.51%, mostly with medium and low variation. The 5–7, 10–12, and 20–22-year-old plantations were laid at the "slow investment-return" end of the economic spectrum while 28–32-year plantations were close to the "fast investment-return" end.
(2) Z. *planispinum* 'dintanensis' tended to suit the karst environment via making trade-off and coordinating leaf functional traits.
(3) Soil carbon/nitrogen ratio, soil total calcium, soil water content, soil available phosphorus, soil carbon/calcium ratio were highly correlated with leaf functional traits, while soil elemental stoichiometry had a greater reflection on leaf functional traits than their own content.

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