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Changes in Growth Parameters, C:N:P Stoichiometry and Non-Structural Carbohydrate Contents of *Zanthoxylum armatum* Seedling in Response to Five Soil Types

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Abstract: *Zanthoxylum armatum* (*Z. armatum*) is an economic crop widely planted for both spice and medicinal purposes in Southwest China. Soil is a key environmental condition that affects seedling growth and development, and screening suitable soil types is of great significance for the large-scale cultivation of crops. This study designed growth experiments of *Z. armatum* seedlings in red soil (RS), yellow soil (YS), acidic purple soil (ACPS), alkaline purple soil (ALPS), and alluvial soil (AS) to screen for more suitable soil types. The growth traits of *Z. armatum* seedlings and the carbon (C), nitrogen (N), phosphorus (P), C:N:P stoichiometry, and non-structural carbohydrate (NSC) content of different organs were comparatively analyzed. The results showed that the morphological indexes of *Z. armatum* seedlings cultured in AS were better than those in the other four soils. AS and RS may be beneficial for the culture of *Z. armatum* seedlings due to higher nutrient levels in three organs. Two-factor ANOVA and PCA analysis showed that C, N, and P and their proportions would affect the uptake and distribution of NSC in various organs of *Z. armatum* seedlings. These results showed that soil types and plant organs significantly affected the accumulation and distribution of N, P, and NSC in *Z. armatum* seedlings. These results are conducive to screening soil types suitable for the growth and development of *Z. armatum* and provide data support for further large-scale cultivation of *Z. armatum* in suitable areas.

Keywords: *Zanthoxylum armatum*; soil type; organs; growth parameters; stoichiometry; non-structural carbohydrates

1. Introduction

Soil is the basic substrate for plant growth and development, and its physicochemical properties are important external influencing factors for plant growth and development [1,2]. Different types of soil represent different physical and chemical characteristics due to differences in their formation processes, nutritional conditions, etc., which will lead to differences in water absorption efficiency, nutrient absorption, and transportation efficiency during plant growth and development [3,4]. In plants, the responses of physiology and biochemicals, such as photosynthesis, mineral metabolism, etc., are closely related to the growth environment, especially soil types [1,5,6]. Variations in plant growth status and chemical composition content are evidence that plants could be

affected by environmental conditions such as soil. Significant differences in plant growth parameters and oil yield per plant are observed between *Mentha arvensis* grown in different soil types [7]. Different soil textures influence the phytochemical contents and antioxidant properties of *Solanum nigrum* L. cultivated in variable soil types [8]. These reports suggested that different soil types do have an impact on plant growth and development.

Carbon (C), nitrogen (N), and phosphorus (P) are considered essential elements in the processes of plant growth [9]. C can form the basic structure of plants and accounts for about 50% of their biomass [10]. N and P play vital roles in protein and nucleic acid formation and are also prominent mineral nutrients affecting plant biomass production [10,11]. Thus, the levels of C, N, and P serve as indicators for assessing nutrient absorption efficiency, utilization effectiveness, and adaptability to environmental stress in plants. C, N, and P are strongly coupled in plant biochemical functions, and their balance and interaction relationship usually alter physiological activity and growth rates [12]. C:N:P chemometrics has turned into the most explored factor in the interactional mechanism between plant growth and the eco-environment [13,14]. Some studies have found that plant N:P is related to growth rate, which means that N:P can be used as an index to predict plant growth rate [11,15]. Previous studies have shown that both N and P are key limiting elements controlling plant development and primary production, and N:P helps to understand the limiting types of ecosystems, which is crucial for screening and modifying soil conditions [16]. The external supply rate of C, N, and P limits the uptake of nutrients, and the functional divergence of plant tissues leads to internal differences in plant organs [17]. The nutrient distribution and their stoichiometry in plants represent the choices that plants make when acquiring and distributing above-ground and subsurface resources [18]. Plants can be curtailed due to insufficient soil nutrition, and they will constantly adjust the physiological and ecological processes of vegetative organs to ensure their normal growth and development [19]. Soil types, representing changes in the soil environment, will directly affect the adaptation strategies of plants and change the stoichiometric ratio of plants [20]. As a consequence, it is very necessary to broaden our knowledge about C, N, and P and their ecological stoichiometric characteristics in plants.

Non-structural carbohydrates (NSC), generally including glucose, fructose, sucrose, and starch, are prominent energy sources for plant growth and metabolism and play a crucial role in plant resistance to external adverse environmental stresses [21,22]. NSC is the product of plant photosynthesis. When the amount of carbon obtained by the plant is greater than the amount of carbon required for growth, its photosynthates are deposited in the form of NSC, and these NSCs can play specific roles at the appropriate time for the survival, growth, and/or other physiological functions of plants [23,24]. In plant organs, the quantity of NSCs commonly reflects C supply as well as the balance between C acquisition and consumption [25]. Higher NSC concentrations can improve the drought resistance and cold stress resistance of plants, which is beneficial for the survival and growth of plants in adverse environments [26,27]. Plants may adjust their biomass, nutrient content distribution, and photosynthetic characteristics to meet their own growth and development needs in response to different soil environments, which is an adaptation strategy to variable environments [21,28]. Therefore, studying the changes in plant nutrient content and stoichiometry in different soils provides a basis for exploring the relationship between plant functions and environmental adaptation mechanisms and is of great significance for analyzing and evaluating the soil type most suitable for plant growth.

Zanthoxylum armatum DC. (*Z. armatum*) is a small deciduous tree of *Zanthoxylum*, belonging to the Rutaceae family, and has enormous value for development, utilization, and long-term cultivation in Southwest China, Pakistan, India, etc. [29]. In Southwest China, the fruit of *Z. armatum* is usually harvested in its immature state, and the pericarp of *Z. armatum* is green, so it is called Qinghuajiao or Tengjiao, etc. The pericarp of its

fruits can be used directly as traditional seasoning condiments or ground into powder for cooking in Sichuan cuisine, offering a unique, numb taste [30]. Moreover, different parts of *Z. armatum* include amides, essential oils, alkaloids, lignans, flavonoids, polyphenols, etc., which show antiviral, anti-tumor, antibacterial, anti-inflammatory, analgesic, antioxidant, and other pharmacological activities [31,32]. Thus, *Z. armatum* is also used in traditional Chinese medicine in China and can be used for the treatment of fever, toothache, stomachache, bruises, rheumatoid arthritis, etc. [32–34]. Due to its higher yield, stronger adaptability, and higher economic values, people have started to commercially cultivate this plant for rural livelihood improvement in Southwest China. Recently, the planting area of *Z. armatum* in China has been expanded and increased, and there is a wide range of soil types in these cultivation areas [29,35]. Although *Z. armatum* can grow on a variety of soil types, its production and quality vary significantly between different geographical locations. The seedling stage is the most critical life-history stage in plants, while the demands of different seedlings have diversified demands for a suitable soil environment [6,36]. The growth status of seedlings is important for large-scale cultivation of *Z. armatum* under different soil conditions, which directly and indirectly affects the growth cycle and the potential yield of *Z. armatum*. Thus, it is particularly important to evaluate and analyze the adaptability of *Z. armatum* seedling cultivation to different soil types in order to get the maximum yield of this plant. Here, the current study was designed to analyze growth parameters, nutrient content, and NSC content of *Z. armatum* seedlings in response to five soil types. These findings may offer an effective way to screen for suitable soil type and nutrient management during seedling cultivation.

2. Materials and Methods

2.1. Experimental Site

The experimental site lies at Sichuan Agricultural University in Chengdu, China, with geographical coordinates of 103°52' E, 30°42' N. It belongs to a subtropical monsoon climate with four distinct seasons, a mild climate, and abundant rainfall. The annual rainfall varied from 801.4 to 1445.5 mm. The rainy season lasts from June to September, with an average annual relative humidity of 84%. The annual average temperature is 17.5 °C, the monthly average highest temperature is 27.0 °C (July), the monthly average lowest temperature is 6.0 °C (January), and the annual average Sunshine duration is 1104.5 h.

2.2. Soil Basic Information

The RS, YS, ALPS, ACPS, and AS were obtained from Sanxing Village, Fengle Township, Shimian County, Ya'an, China (N 29°32', E 102°54', H 878 m), Baisheng Village, Baolin Town, Qionglai, Chengdu, China (N 30°21', E 103°30', H 552 m), Jifeng Town, Zhongjiang County, Deyang, China (N 31°03', E 104°68', H 900 m), Laobanshan Reading Park (N 29°58', E 102°58') in District Yucheng, Ya'an, China, and the Village Jing-shan, Town Yongan, District Shuangliu, Chengdu, China (30°36'59.54" N, 104°00'41.14" W, H 425 m), respectively. These soils were classified, crushed, sieved, and air-dried in the sun for further use. Soil pH was measured via an electrode pH meter in a suspension of soil and water (1:2). The TN content was measured using the Kjeldahl method [37]. The organic matter content was measured by potassium dichromate oxidation—the external heating method [37]. TP content was measured by the Mo-Sb colorimetric method [37]. The main physico-chemical properties of five soils are displayed in Table 1.

Table 1. Main physico-chemical properties of five types of soil.

Soil Type	pH	Organic Matter (g·kg ⁻¹)	Total Nitrogen (g·kg ⁻¹)	Total Phosphorus (g·kg ⁻¹)
Red soil (RS)	4.9	16.64	1.14	0.067
Yellow soil (YS)	4.8	33.50	1.89	0.080
Acidic purple soil (ACPS)	4.3	42.53	2.33	0.235
Alkaline purple soil (ALPS)	8.7	20.99	1.65	0.301
Alluvial soil (AS)	8.1	38.38	2.35	0.300

2.3. Seedling Culture

Mature *Z. armatum* fruits (red) were collected in October 2021 from Lezhi County, Ziyang, China, and were dried in the shade at room temperature. The seeds were separated from the pericarps and deposited in damp sand until used. In February 2022, 500 seeds were sown in a box with nutrient soil in a green house. After 25–30 days, the seeds began to sprout, and the seedlings grew up to fully extended cotyledons (Stage BBCH10, about 2 cm high). One hundred seedlings were selected and planted in pots containing 10 kg of different soils (diameter and height, 28 × 22 cm, and the soil layer height, 20 cm). These pots were placed in the greenhouse of Sichuan Agricultural University from March 2022 to August 2022. During the seedling cultivation, the relative water moisture of the soils was checked and maintained at 60–80%, and weed and pest management were performed uniformly.

2.4. Sample Collection and Growth Parameter Measurement

After cultivation, the basic growth parameters of 10 seedlings in each group, such as plant height and ground diameter, were measured and recorded. Five seedlings were randomly collected from each group and sectioned into roots, stems, and leaves. Three parts were cleaned with deionized water, and the fresh weight (FW) was measured. They were first dried at 105 °C for 30 min, and then dried the second time for 12 h at 70 °C until they reached constant weight. The dry weight (DW) of each sample was recorded, and the relative water content (RWC) was calculated.

2.5. Determination of Nutrient Element Content

The dried samples of leaves, stems, and roots were grinded and sieved using a 60-mesh sieve, and then the content of C, N, P, and NSC was measured. The total C content was measured using the potassium dichromate sulfuric acid oxidation method. The total N and total P were measured by the semi-micro Kjeldahl method, and the total P was measured using molybdenum antimony anti-colorimetry [37].

2.6. Measurement of NSC Content

NSC content was measured using the anthrone colorimetric method. In brief, 100 mg of sample was added to 10 mL of 80% ethanol and heated in a boiling water bath for 10 min. The extracts were centrifuged at 4000 rpm for 10 min at room temperature, and the supernatant was collected. These steps were repeated three times, and the supernatants were combined and diluted with deionized water to 50 mL. The precipitate was suspended in 10 mL of 30% perchloric acid, and the mixtures sat overnight. The suspension was extracted in a water bath at 80 °C for 10 min and centrifuged at 4000 rpm for 10 min at 4 °C. The supernatants were harvested and diluted with deionized water to 50 mL for starch extraction. For glucose determination, 0.1 mL of extract was blended with 5 mL of anthrone solution. After 15 min in a water bath at 90 °C, the reaction solutions were measured at a wavelength of 620nm when they were cooled. For sucrose determination, 0.1 mL of 7.6 M KOH and 0.1 mL of sugar extraction were mixed and placed for

10 min in boiling water, and then 5 mL of anthrone solution was added. The reaction mixtures were placed for 15 min in 90 °C water. After cooling, the absorbance was measured at a wavelength of 620 nm. For fructose determination, 0.1 mL of extract was blended with 5 mL of anthrone solution and placed in a water bath at 25 °C for 90 min. The absorbance was recorded at a wavelength of 620 nm. For starch determination, the test steps were the same as for glucose. The contents of glucose, fructose, sucrose, and starch were estimated based on the standard curves of glucose, sucrose, fructose, and starch, respectively. The data were shown as µg/mg dry matter.

2.7. Statistical Analysis

Data analyses were processed using Excel and SPSS 27.0, and the significant differences in *Z. armatum* seedling growth parameters, non-structural sugar, and nutrient element content in different soil types were examined by one-way ANOVA and Duncan methods. A correlation heatmap was established using the Pearson correlation coefficient to study the correlation among C content, N content, P content, C:N:P stoichiometry, and NSC content. A two-factor analysis of variance was adopted to examine the effects of different soil types and organs and their interactions on C, N, P, its stoichiometric ratio, and NSC in leaf, stem, and root. The above significance levels are set as $\alpha = 0.05$. The drawings were drawn using Origin 2021. To get a good idea of the relationships between tested parameters and treatments, principal component analysis (PCA) was performed using OriginPro 2021.

3. Results

3.1. Influences of Soil Types on the Growth Parameters

As exhibited in Table 2, the plant height of seedlings cultured in different types of soil is AS > ALPS > RS > ACPS > YS. There were no significant differences in seedling height among ACPS, RS, and YS ($p > 0.05$), but there was a significant difference compared to seedlings in other soil types ($p < 0.05$). The ground diameter showed a similar trend compared to the plant height. When seedlings were cultured in ALPS and RS, there was no significant difference in ground diameter ($p > 0.05$), while there was a significant difference in other soil types ($p < 0.05$). These results showed that plant height and ground diameter are related to soil types. The fresh weight of leaves, stems, and roots in the AS remarkably exceeds that in the other soil types ($p < 0.05$), but there were no obvious differences when seedlings were cultured in RS, ACPS, and ALPS ($p > 0.05$). Moreover, the fresh weight of three organs cultured in YS had the lowest levels. The highest fresh biomass of roots was observed when seedlings were cultured in the AS, and there were no significant differences between cultures in other soil types ($p > 0.05$). The dry biomass of leaves, stems, and roots cultured in AS was remarkably higher than that of other soil types, but there were no obvious differences among ALPS, RS, and ACPS (Table 2).

Table 2. Effects of five soil types on growth indexes of *Z. armatum* seedlings.

Soil Type		RS	YS	ACPS	ALPS	AS
Plant height (cm)		56.1 ± 10.78 ^c	44.72 ± 7.3 ^d	54.14 ± 5.01 ^{cd}	66.46 ± 4.56 ^b	77.22 ± 9 ^a
Ground diameter (mm)		8.56 ± 0.64 ^b	6.82 ± 0.53 ^d	7.76 ± 0.19 ^c	9.09 ± 0.69 ^b	10.62 ± 0.7 ^a
Fresh weight (g)	Leaf	28.47 ± 8.64 ^b	16.25 ± 2.35 ^c	26.91 ± 1.22 ^b	31.25 ± 5.08 ^b	48.25 ± 3.93 ^a
	Stem	16.26 ± 5.01 ^b	8.92 ± 0.95 ^c	12.94 ± 0.66 ^{bc}	18.09 ± 1.25 ^b	27.64 ± 4.15 ^a
	Root	36.3 ± 9.04 ^{ab}	22.42 ± 0.74 ^b	26.25 ± 6.76 ^b	24.63 ± 10.19 ^b	54.28 ± 19.21 ^a
Dry weight (g)	Leaf	9.21 ± 2.83 ^b	5.53 ± 0.92 ^c	8.79 ± 0.52 ^{bc}	10.66 ± 1.65 ^b	32.17 ± 2.62 ^a
	Stem	6.94 ± 2.1 ^b	3.98 ± 0.56 ^c	5.59 ± 0.22 ^{bc}	8.05 ± 0.43 ^b	12.44 ± 2.18 ^a
	Root	8.17 ± 2.03 ^b	5.08 ± 0.78 ^b	6.93 ± 0.86 ^b	7.05 ± 2.52 ^b	14.91 ± 3.5 ^a
RWC (%)		67.69 ± 0.27	66.06 ± 0.8	67.35 ± 0.43	65.86 ± 0.46	66.66 ± 2.2

Stem	57.28 ± 0.55	55.42 ± 2.4	56.73 ± 2.42	55.44 ± 1.09	55.11 ± 1.13
Root	77.39 ± 2.15	77.33 ± 3.6	72.86 ± 4.48	70.96 ± 1.73	71.47 ± 4.8

Different lowercase letters represent the obvious differences of various indicators in different soil types ($p < 0.05$).

3.2. Influences of Soil Type on C, N, and P Contents

From Figure 1 and Table 3, it can be concluded that soil types and the interaction of soil type and organs had no significant impact on the C content in the different organs of *Z. armatum* seedlings, while soil type, organs, and their interaction had a remarkable impact on N and P contents ($p < 0.01$). As exhibited in Figure 1A, the C content in the organs of the seedlings planted under five soil types was the stem, root, and leaf. From the highest to the lowest, the C contents of the leaves, stems, and roots ranged from 350.33 to 406.28 g/kg, from 449.71 to 458.61 g/kg, and from 387.62 to 430.58 g/kg (Figure 1A), respectively. As shown in Figure 1B, the N contents in the different organs have great differences, and the N content of leaves was variably and considerably greater than that of the roots and stems. The N content of the leaves, stems, and roots ranged from 18.65 to 24.61 g/kg, from 6.02 to 12.76 g/kg, and from 11.89 to 17.72 g/kg, respectively. Moreover, the highest N content in seedlings was observed in RS, and the lowest value was found in AS. The N contents of roots, stems, and leaves in RS were 17.72 g/kg, 12.76 g/kg, and 24.61 g/kg, respectively, and the contents of roots, stems, and leaves in AS were 11.89 g/kg, 6.02 g/kg, and 18.65 g/kg, separately. These results showed significant differences in the N content of different organs cultured in the two soil types. As exhibited in Figure 1C, the P content of the leaves, roots, and stems ranged from 0.35 to 0.44 g/kg, 0.34 to 0.42 g/kg, and 0.28 to 0.34 g/kg, respectively. Among the five soil types, ACPS seedlings had the highest P content in their roots, stems, and leaves; the contents were 0.42 g/kg, 0.34 g/kg, and 0.44 g/kg, respectively. Moreover, when these seedlings were cultured in AS, the P content in their leaves and roots was the lowest, and the contents were 0.35 g/kg and 0.34 g/kg, respectively.

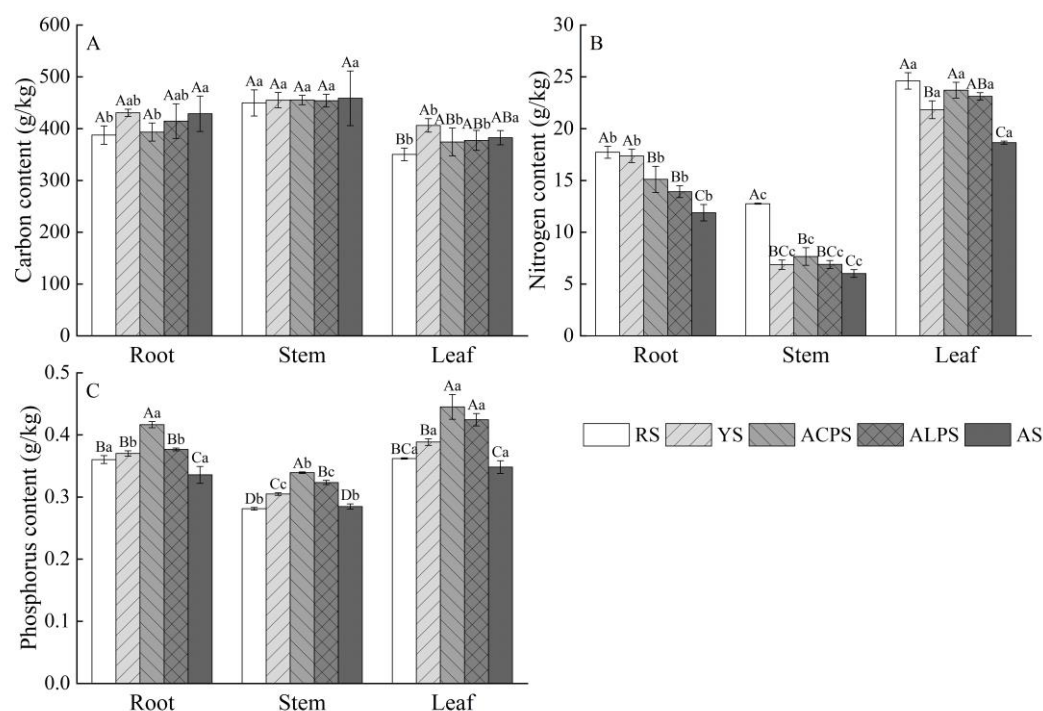


Figure 1. Influences of five soil types on the C (A), N (B), and P (C) contents in leaves, stems, and roots of *Z. armatum* seedlings. The data are shown as means ± SE ($n = 3$). Different capital letters

represented the differences among five soil types in the same tissues, and different lower-case letters represented the differences among different tissues in the same soil type ($p < 0.05$).

Table 3. Two-factor variance analysis of C, N, and P content, stoichiometric ratio, and non-structural sugar in leaves, stems, and roots of *Z. armatum* seedlings in five soil types.

Target	Source of Variation		
	Soil Type	Organ	Soil Type × Organ
C content	1.947	26.113 **	0.452
N content	66.641 **	1172.280 **	9.021 **
P content	92.034 **	321.649 **	4.104 **
C/N	27.251 **	425.359 **	8.883 **
C/P	13.862 **	133.170 **	0.796
N/P	79.003 **	562.228 **	6.687 **
Glucose content	4.829 **	21.706 **	5.362 **
Fructose content	10.346 **	55.789 **	5.927 **
Sucrose content	49.574 **	68.128 **	14.443 **
Starch content	9.454 **	70.579 **	2.376 *

Note: The value is the F-value of the analysis of variance. * indicates significant ($p < 0.05$); ** indicates highly significant ($p < 0.01$).

3.3. Influences of Soil Types on the Accumulation of C, N, and P

As exhibited in Figure 2, the total accumulation of C, N, and P showed a similar trend cultured in five soil types, and the total accumulation of C, N, and P in *Z. armatum* seedlings reached the maximum of 24.4 g/plant, 852.04 g/plant, and 19.75 mg/plant cultured in AS, respectively. Moreover, the values reached the significance level with other soils ($p < 0.05$). However, the minimum accumulation of C, N, and P was observed when these seedlings were cultured in YS, and the values represented 6.25 g/plants, 236.15 mg/plant, and 5.24 mg/plant, respectively. Moreover, the total accumulations of C in roots and stems were little different, and were generally lower than those in leaves (Figure 2A). As shown in Figure 2B, in most soil types, the accumulation of N in various organs showed a significant difference ($p < 0.05$), with leaves > roots > stems. In various soil types, the trend of P accumulation in various organs is the same as that of N accumulation (Figure 2C). These results show that the accumulation of C, N, and P is related to soil types and tissues, which may be due to the differences in nutrient requirements in *Z. armatum* seedlings.

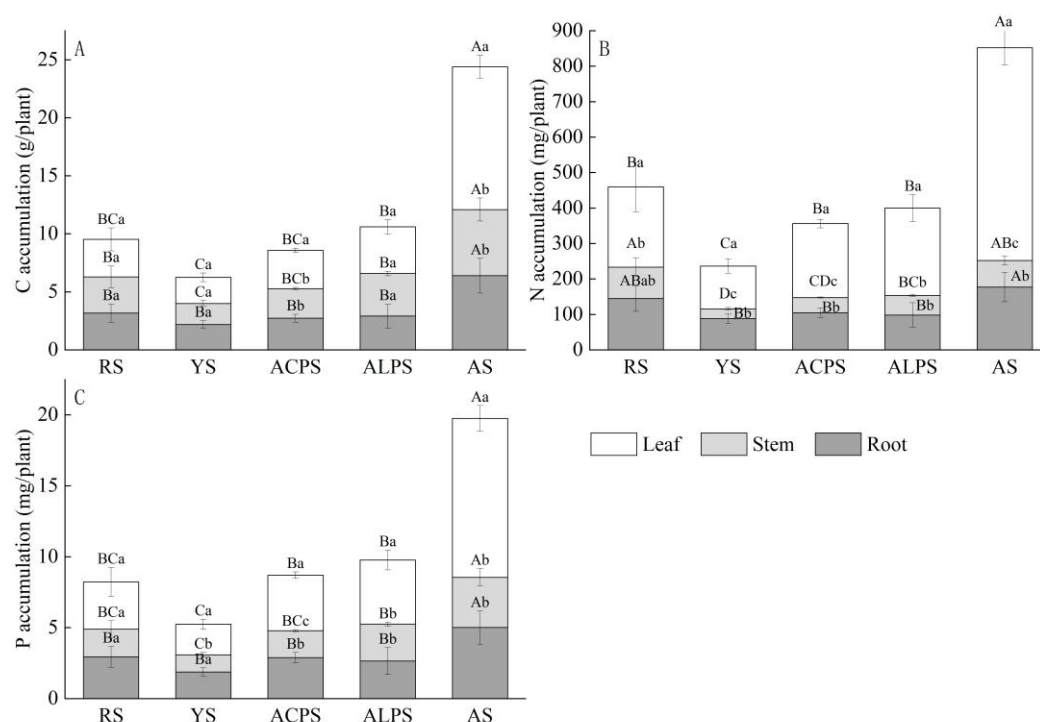


Figure 2. Influences of five soil types on the accumulation of C (A), N (B), and P (C) in *Z. armatum* seedlings. The data are shown as means \pm SE ($n = 3$). Different capital letters represented the differences among five soil types in the same tissues, and different lower-case letters represented the differences among different tissues in the same soil type ($p < 0.05$).

3.4. Influences of Five Soil Types on Stoichiometry

As shown in Figure 3 and Table 3, soil types and organs have extremely significant influences on the C/N, C/P, and N/P ratios in *Z. armatum* seedlings ($p < 0.01$), and their interaction has an extremely noticeable impact on the ratios of C/N and N/P ($p < 0.01$). However, the interaction of soil types and organs has no obvious effects on the C/P ratios. The mean C/N and C/P of seedlings cultured in five soil types showed significant differences in each organ, with stems significantly higher than roots and roots significantly higher than leaves ($p < 0.05$). However, mean N/P ratios showed the opposite trend. Moreover, the C/N ratios of leaves, stems, and roots cultured in the RS are the smallest, but the N/P ratios are the largest. The leaves, stems, and roots cultured with AS have the highest C/N and C/P. The C/P of the leaves, stems, and roots cultured in the ACPS are the smallest. The N/P ratios of leaves and stems do not show significant differences in YS, ACPS, ALPS, and AS, while the N/P ratios of roots do not show significant differences in ACPS, ALPS, and AS.

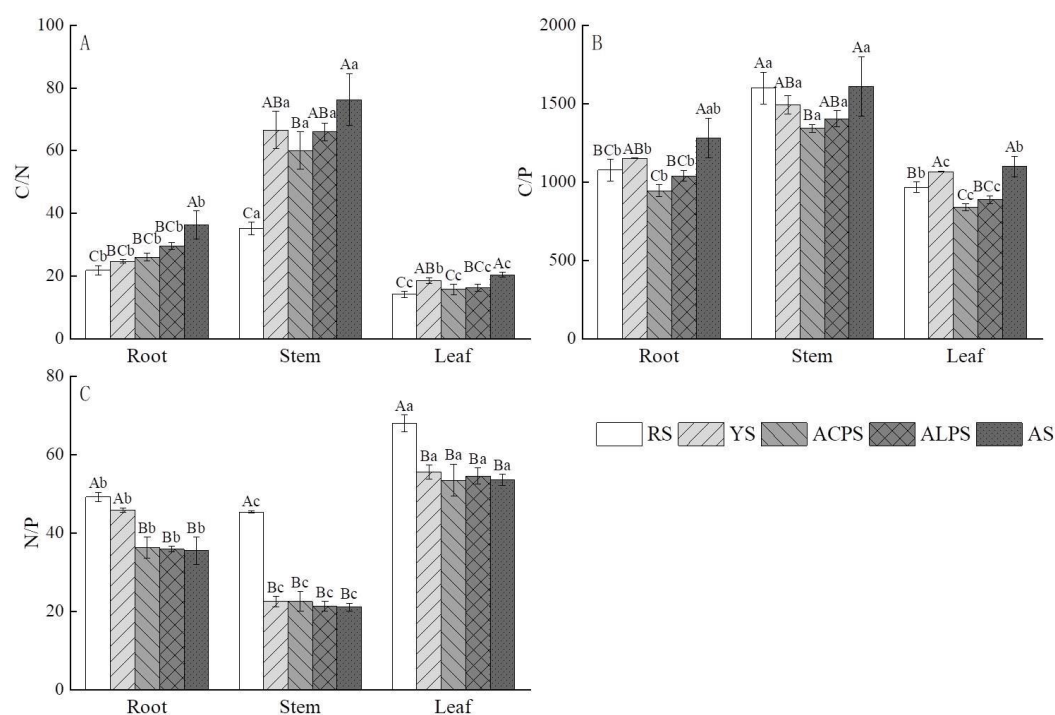


Figure 3. Effects of five soil types on C:N (A), C:P (B), and N:P (C) of leaves, stems, and roots in *Z. armatum* seedlings. The data are shown as means ± SE (n = 3). Different capital letters represented the differences among five soil types in the same tissues, and different lower-case letters represented the differences among different tissues in the same soil type (p < 0.05).

3.5. Effects of Five Soil Types on Non-Structural Carbohydrates (NSC)

As shown in Figure 4 and Table 3, soil type and organ have extremely significant effects on non-structural sugar (p < 0.01). Their interaction has extremely significant effects on soluble sugar (p < 0.01) and significant effects on starch (p < 0.05). Among the five soil types, the seedlings in ACPS have the lowest glucose content in their roots and leaves, while the seedlings in YS have the highest glucose content in their leaves. In addition, only seedlings planted on YS and AS show significantly higher glucose content in leaves compared to roots and stems (Figure 4A). Among the five soil types, the fructose content of seedlings planted on ACPS is the lowest in stems and leaves, and the fructose content in the roots is the lowest in ALPS. In most soil types, the fructose content of seedlings is shown as leaf > stem > root in each organ (Figure 4B). The sucrose contents of leaves and stems cultured in the AS were significantly higher than those in other soil types. However, the values in two purple soils were significantly lower than those in other soil types. Similarly, the sucrose contents in the roots cultured with AS were remarkable higher than those of in other soil types. However, the sucrose content of seedlings planted in two purple soils was markedly greater than that of those cultured in YS and RS (Figure 4C). The starch contents of leaves, stems, and roots cultured in the YS were relatively higher than those in the other soil types. The starch content of leaves cultured in the RS was the lowest, the starch content of stems cultured in the AS was the lowest, and the starch content of roots cultured in the RS, ACPS, and ALPS was relatively lower than those of the other soil types (Figure 4D).

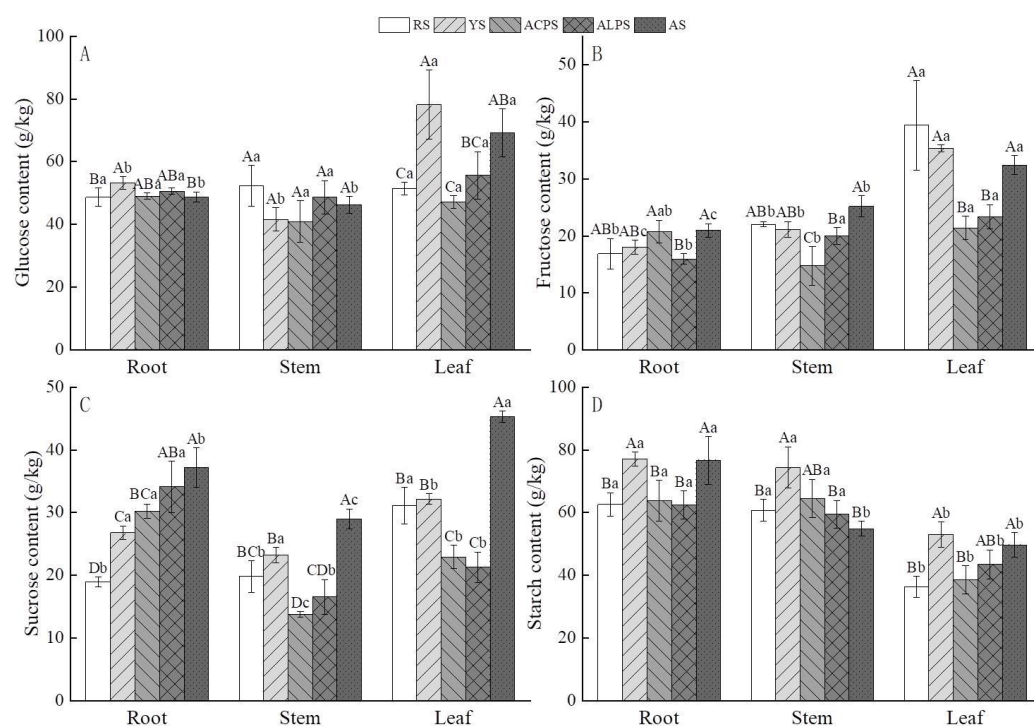


Figure 4. Effects of five soil types on non-structural carbohydrates (NSC) contents in *Z. armatum* seedlings. The data are shown as means \pm SE ($n = 3$). (A), glucose content. (B), fructose content. (C), sucrose content. (D), starch content. Different capital letters represented the differences among five soil types in the same tissues, and different lower-case letters represented the differences among different tissues in the same soil type ($p < 0.05$).

As shown in Figure 5, in five soil types, the total accumulation of glucose, fructose, sucrose, and starch showed a different trend, and the total accumulation of glucose, fructose, sucrose, and starch in *Z. armatum* seedlings reached the maximum of 3531.66, 1668.85, 2372.08, and 3424.59 mg/plant cultured in AS, respectively. These values reached the significance level with other soils ($p < 0.05$). However, the minimum accumulation of glucose, fructose, sucrose, and starch was observed when these seedlings were cultured in YS, and the values represented 868.07, 371.19, 406.41, and 980.57 mg/plant, respectively. These results show that the accumulation of glucose, fructose, sucrose, and starch is related to soil types and tissues in *Z. armatum* seedlings.

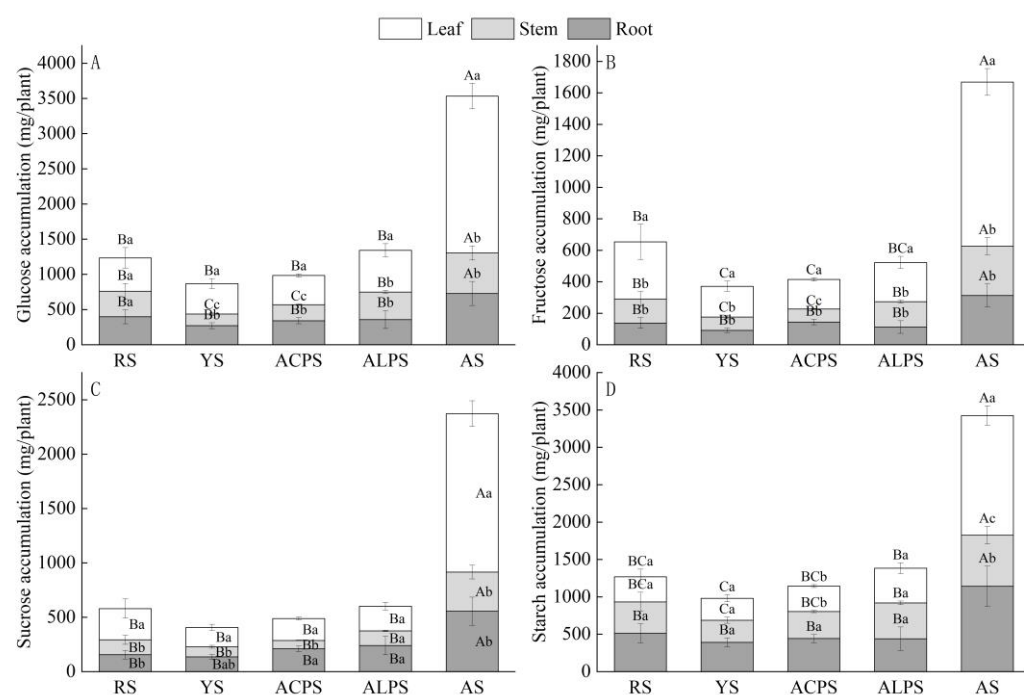


Figure 5. Effects of five soil types on the accumulation of glucose (A), fructose (B), sucrose (C), and starch (D) in *Z. armatum* seedlings. The data are shown as means \pm SE ($n = 3$). Different capital letters represented the differences among five soil types in the same tissues, and different lower-case letters represented the differences among different tissues in the same soil type ($p < 0.05$).

3.6. Correlation Analysis

Figure 6 reveals the correlation between various measurement results of *Z. armatum* seedlings. C content had significant positive correlations with C:N ($r = 0.86$, $p < 0.05$), C:P ($r = 0.89$, $p < 0.05$), and starch ($r = 0.67$, $p < 0.05$), and noticeable negative associations with N content ($r = -0.91$, $p < 0.05$), P content ($r = -0.73$, $p < 0.05$), N:P ($r = -0.86$, $p < 0.05$), fructose ($r = -0.49$, $p > 0.05$), glucose ($r = -0.37$, $p > 0.05$), and sucrose ($r = -0.35$, $p > 0.05$), respectively. N content was positively related to P content ($r = 0.74$, $p < 0.05$), N:P ($r = 0.96$, $p < 0.05$), glucose ($r = 0.53$, $p < 0.05$), fructose ($r = 0.51$, $p > 0.05$), and sucrose ($r = 0.27$, $p > 0.05$), and negatively related to C:N ($r = -0.94$, $p < 0.05$), C:P ($r = -0.84$, $p < 0.05$), and starch ($r = -0.64$, $p < 0.05$), respectively. P content showed a certain degree of positive correlation with N:P ($r = 0.53$, $p < 0.05$), glucose ($r = 0.24$, $p > 0.05$), fructose ($r = 0.045$, $p > 0.05$), and sucrose ($r = 0.095$, $p > 0.05$), and a negative correlation with C:N ($r = -0.72$, $p < 0.05$), C:P ($r = -0.95$, $p < 0.05$), and starch content ($r = -0.41$, $p > 0.05$), respectively. C:N showed positive correlation with C:P ($r = 0.83$, $p < 0.05$) and starch ($r = 0.42$, $p > 0.05$), and negative correlation with N:P ($r = -0.92$, $p < 0.05$), glucose ($r = -0.53$, $p < 0.05$), fructose ($r = -0.35$, $p > 0.05$), and sucrose ($r = -0.35$, $p > 0.05$). C:P showed a positive correlation with starch ($r = 0.48$, $p > 0.05$) and a negative correlation with N:P ($r = -0.69$, $p < 0.05$), glucose ($r = -0.32$, $p > 0.05$), fructose ($r = -0.20$, $p > 0.05$), and sucrose ($r = -0.25$, $p > 0.05$). N:P showed a positive correlation with glucose ($r = 0.57$, $p < 0.05$), fructose ($r = 0.61$, $p < 0.05$), and sucrose ($r = 0.32$, $p > 0.05$), but was negatively related to starch ($r = -0.61$, $p < 0.05$). Glucose was positively related to fructose ($r = 0.64$, $p < 0.05$) and sucrose ($r = 0.54$, $p < 0.05$), but was negatively related to starch content ($r = -0.30$, $p > 0.05$). Fructose was positively related to sucrose ($r = 0.51$, $p < 0.05$), but negatively related to starch ($r = -0.61$, $p < 0.05$). As shown in Table 3, soil type showed statistical significance for the tested parameters, except for C contents. There were significant organs for all tested parameters. Significant interactions of soil type \times organ were observed for the N, P, C:N, N:P, glucose, fructose, sucrose, and starch content.

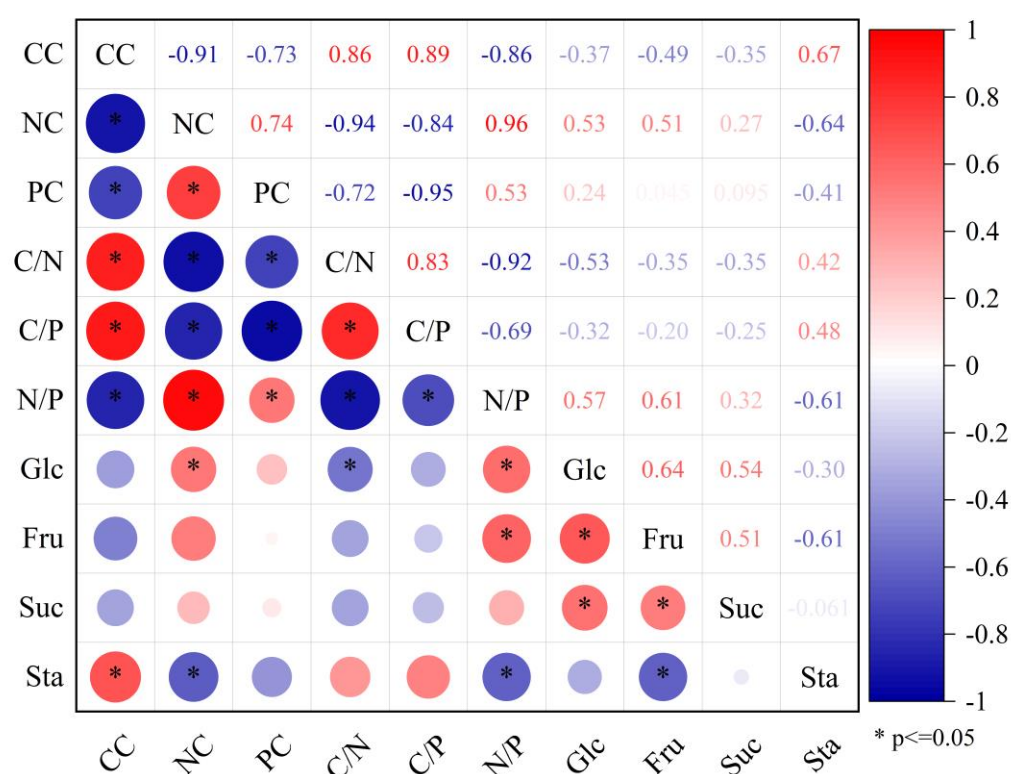


Figure 6. Correlation analysis among different tested parameters in *Z. armatum* seedlings. * Indicated significant ($p \leq 0.05$). The red area indicated positive correlations. The blue area represented negative correlations. CC, carbon content. NC, nitrogen content. PC, phosphorus content. C/N, C/P, and N/P. Glu, glucose content. Fru, fructose content. Suc, sucrose content. Sta, starch content.

3.7. Principal Component Analysis (PCA)

As shown in Figure 7, significant differences were observed when *Z. armatum* seedlings were cultured in five soil types. The contribution rate of the principal component 1 (PC1) is 62.0%, with the highest weight. The contribution rate of the principal component 2 (PC2) is 16.9%, and the two principal components account for a cumulative 78.9% of the data variation. Between various chemical components and stoichiometric ratios, NC, PC, and N/P will have a strong positive response to PC1, while CC, C/N, and C/P will have a strong negative response to PC1. Glc, Fru, and Suc have a strong positive response to PC2, while PC will have a strong negative response to PC2. Analysis shows that there is a positive correlation between CC, C/N, C/P, and Sta, while there is also a positive correlation between Glc, Fru, Suc, NC, and N/P. Meanwhile, there is a negative correlation between CC, C/N, C/P, and Sta, and NC, PC, and N/P. These results indicated that the variations of C, N, P, and NSC contents, C/N, C/P, and N/P, can be used to explain and better understand the growth and nutrient uptake in *Z. armatum* seedlings in response to five soil types.

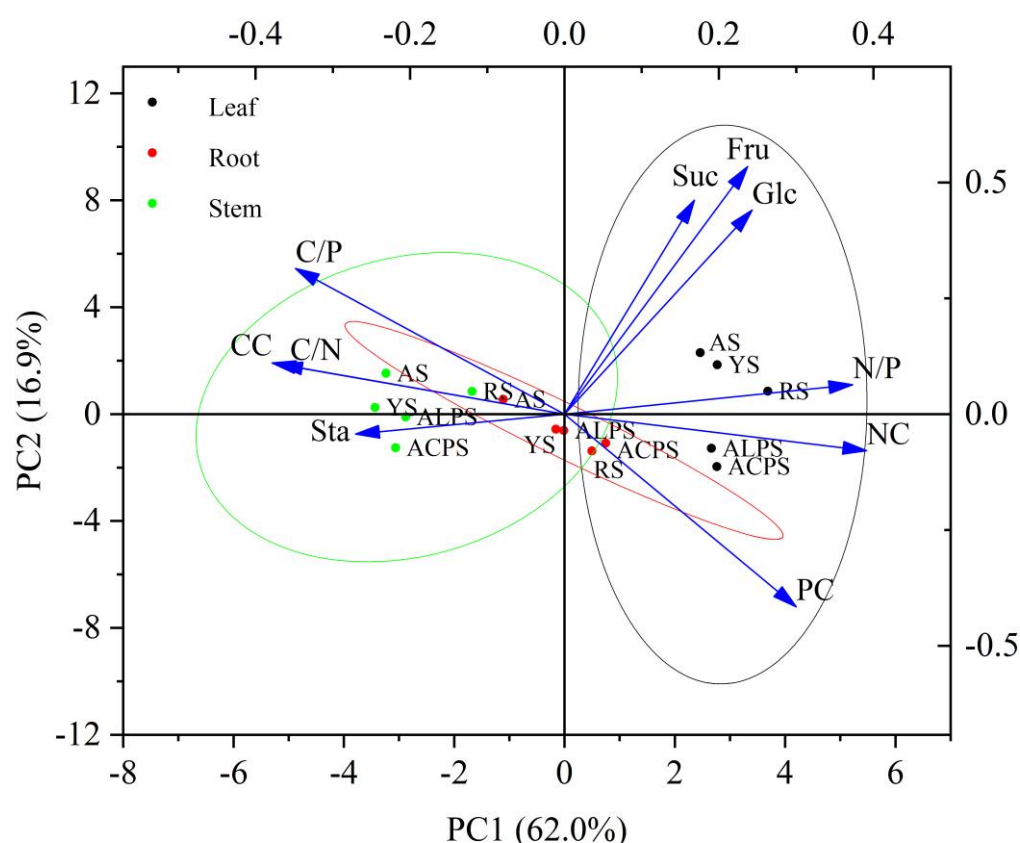


Figure 7. PCA of chemical constituents of *Z. armatum* seedlings in different organs under five soil types. CC, carbon content. NC, nitrogen content. PC, phosphorus content. C/N, C/P, and N/P. Glu, glucose content. Fru, fructose content. Suc, sucrose content. Sta, starch content. The percentage change described for each component is given next to the axis. Location of a trait in the diagram closest to the intersection of 0 on the x-axis (PC1) and y-axis (PC2).

4. Discussion

Soil, as a basic condition for agricultural production, has a significant impact on plant growth, yield, and biochemical contents [6,8]. Growth parameters, like seedling height, ground diameter, and biomass, can reflect the growth status of plants in response to various environmental conditions, like soil [6,7]. Previous reports showed that plant height, base diameter, and biomass of *Jatropha curcas* plants are related to soil types, and the growth status of different species varies significantly in different types of soils [37]. Previous studies also suggested that *Phellodendron chinense*, *Ricinus communis*, and *Firmiana simplex* seedlings show significant differences in seedling height, basal diameter, and total biomass when they are cultured in RS, YS, ALPS, and ACPS [6,38,39]. These variations are due to different soil types with different physical, chemical, and microbial community structures. The content of various nutrients provided by soil, soil texture, water holding capacity, and changes in microbial and soil enzyme activities can all have a certain impact on the nutrient absorption and utilization efficiency of plant growth and development. Therefore, different plants adapt to different soil types.

Z. armatum plant is a perennial and economic crop that is widely distributed in Southwest China and has strong adaptability to variable growth conditions [40]. Studies have shown that its chemical composition varies with changes in climate and soil conditions and is significantly affected by the species and geographical variation of *Zanthoxylum* [32,41,42]. Although *Z. armatum* may adapt to a variety of soil types, the soil can offer the foundation of nutrition for better seedling growth, maximum fruit yield, and optimal quality, which will be considered the optimal soil type. As shown in Table 2, the

AS displays the best comprehensive performances in terms of the agronomic and nutrient characteristics, like seedling height, base diameter, and biomass, as well as the nutrient contents of *Z. armatum*, followed by those of ALPS, ACPS, RS, and YS in the order from high to low. The reason may be that *Z. armatum* prefers to grow and proliferate in clay or loamy soil enriched with high organic matter [43]. AS possesses the above conditions, and the pH of AS is alkaline and contains a higher level of organic matter, total nitrogen, and total phosphorus. Moreover, its texture is loose, and its air permeability is good (Table 1). Thus, this type of AS is suitable for seedling cultivation of *Z. armatum*. The results show that YS has good organic matter content, but its growth is still poor. This may be due to its poor water permeability, poor air permeability, and heavy clay texture. The soil properties, like organic matter, water-holding capacity, texture, water permeability, air permeability, etc., had significant influences on plant growth and development [1,8,44]. Soil pH is also a limiting factor, implying that an appropriate pH value is more conducive to plant growth [29]. Good soil structure, loose soil, good ventilation performance, and high organic matter content are conducive to the growth and development of seedlings (Table 2). Table 2 shows that *Z. armatum* growing in different soil types has certain differences in growth status and nutrient composition. Therefore, screening the appropriate soils is a useful way to expand the suitable planting area of *Z. armatum*, cultivate high-quality seedlings, and improve fruit yield.

Mineral elements, such as C, N, and P, play an indispensable role in the life of plants. C is the structural foundation in different organs of plants, while N and P are the necessary components for the metabolism of nucleotides, proteins, sugars, and lipids [13,45]. In plants, C:N and C:P ratios may reflect the utilization capacity of C assimilation in the process of nutrient uptake. The N:P ratio is widely regarded as an effective index of nutrient supply in plant systems, suggesting that plant growth is limited by N and/or P [17]. Thus, we know that the changes in C, N, and P contents and their stoichiometric ratios in *Z. armatum* seedlings cultured in five soil types are of great significance for screening suitable soil for further widespread cultivation in Southwest China.

The present study shows that significant differences among the N and P contents of *Z. armatum* were observed in response to five soil types, and organ types have significant effects on the content of C, N, and P in *Z. armatum* seedlings (Figure 1, Table 3). Moreover, our report also suggests that the soil type-organs interactions have remarkable impacts on the N and P contents of *Z. armatum* seedlings (Figure 1, Table 3). The N content in different organs of *Z. armatum* cultured in RS is significantly higher than that in other soils, and the P contents cultured in ACPS and ALPS are greater than those in other soils (Figure 1). The contents of N and P of seedlings in AS soil are lower in the five soil types. One of the reasons for this may be that the diversity of physico-chemical properties in the five soil types and the higher values of P are observed in ACPS and ALPS (Table 1), which might result in differences in the content absorbed by *Z. armatum* seedlings. It may also be because the different growth rates of *Z. armatum* seedlings lead to inconsistent stages, and the elements absorbed and utilized are different [11]. Since the biomass of *Z. armatum* planted on different soil types showed obvious trends, the C, N, and P of the whole seedlings also showed the same trends (Figure 2). Many studies have found that the nutrient stoichiometry varies in different organs in response to various environmental conditions, including soil types. Some reports indicated that the N and P contents and N:P ratios in the leaves are significantly greater than those of stems and roots, while the C content and C:N and C:P ratios of stems are significantly higher than those of leaves and roots [14,46,47]. Our results are consistent with these above-mentioned studies (Figure 2). In most cases, leaves had the lowest C:N ratio and stems had the highest C:N ratio, which might be connected with the sugar transfer from photosynthetic tissues to structural tissues. As an important organ of photosynthesis, leaves need higher nutrient concentrations to improve their photosynthetic and metabolic capacity. This also indicates that leaves preferentially distribute nutrients relative to stems and roots, and the nutrient content of stems decreases with individual devel-

opment. As a supporting structure, the stem has a higher content of C-rich structural compounds such as lignin and cellulose, so the values of C:N, C:P, and N:P exceed those of leaves [21,23,47,48]. Based on the above results, this clearly shows that the C:N:P stoichiometry of different organs varies depending on their function. The present results showed that the relationships of C, N, and P contents and ratios among the three organs responded to different soil types. Among the five soils, the values of C:N and C:P in seedlings cultivated in AS were greater than those of other soil types, which meant that the support structure of *Z. armatum* was better in AS, which was conducive to the early growth of seedlings. The maximum N:P of seedlings growing in RS indicated that *Z. armatum* had a higher nutrient concentration in RS. Therefore, AS and RS are more suitable for the cultivation of *Z. armatum* seedlings.

NSC, which mainly includes glucose, fructose, sucrose, and starch, are products of plant photosynthesis, and its levels in plant organs can reflect the correction of C uptake. Moreover, NSC levels are also necessary for transport metabolism and osmotic regulation, which can be used to resist adverse external environments in plants [22,27]. Soil, as one of the environmental factors, will affect the normal physiological metabolism of trees and then change the storage of carbohydrates in trees and their distribution in various organs [27]. Therefore, NSC can be used as one of the indexes to evaluate whether a certain soil is suitable for the cultivation of *Z. armatum* [49]. NSC is stored in different organs in the form of mobile carbon and participates in physiological metabolic processes such as material transport, energy metabolism, osmotic regulation, and stress adaptation [49]. The present study indicated that soluble sugars, such as glucose, fructose, and sucrose, have higher content in leaves, while starch has a lower content in leaves than in stems and roots (Figure 4), which was similar to the results of previous studies and reflected the performance of plants adapting to the environment by adjusting NSC usage strategies [50]. In addition, the C contents, N contents, C:N, and N:P were apparently associated with the NSC contents in *Z. armatum* seedlings (Figures 6 and 7). Notably, the C, N, and P contents in the leaves are the key factors affecting the changes in NSC storage (Figures 6 and 7). This may be due to the fact that photosynthesis and NSC accumulation in leaves are closely related to N concentration and P concentration. With increasing N contents in leaves, the photosynthesis of plants significantly increases. In addition, increasing nitrogen can improve the fixation and assimilation abilities of CO₂, as well as the production of NSC [20,21]. In this study, N:P was remarkably positively related to glucose and fructose and negatively correlated with the concentrations of starch. This indicated that changes in N:P can affect the reciprocal conversion of soluble sugars and starch, playing a vital role in the fluctuation of NSC contents. Our results are consistent with those of other plants [51]. Among the five soil types, the NSC content of *Z. armatum* seedlings cultured in ACPS and ALPS is lower, indicating that these two soil types had fewer stress effects.

5. Conclusions

In summary, this study selected the soil type that is more suitable for the growth and cultivation of *Z. armatum* seedlings in five different soils and measuring their growth and nutrient absorption. Research has shown that the changes in experimental parameters of *Z. armatum* seedlings are related to soil types with different physical and chemical properties. Although there are certain differences in growth parameters, nutrient accumulation and distribution, and NSC content among seedlings, *Z. armatum* seedlings can grow well in all five soil types. Among the five representative soil types, the seedlings cultured in AS had higher C/P and C/N, while those cultured in RS had higher N/P. AS and RS were beneficial for cultivating *Z. armatum* seedlings through higher nutrient levels. Two-factor ANOVA and PCA analysis showed that C and N contents and their proportions would affect the accumulation and distribution of NSC in *Z. armatum* plants, reflecting the adaptation of *Z. armatum* plants to different soil types. The results showed that ACPS and ALPS had less stress effect, while YS and AS had more

NSC accumulation. These findings will help us understand how this plant develops different nutrient acquisition strategies under different soil conditions and provide directions for finding effective ways for farmers to choose suitable soil types for planting *Z. armatum* seedlings before these plants are widely planted.

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