

## Article

# Early Growth Characterization and C:N:P Stoichiometry in *Firmiana simplex* Seedlings in Response to Shade and Soil Types

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**Abstract:** Light and soil environments have extensive heterogeneity for many plants species affecting plant growth, reproduction, and distribution. However, the interaction effects of these two factors on the ecophysiological traits and adaptive strategy of plants remain largely unclear. In the present study, we set four shading levels and three soil types to investigate the effects of shade and soil type on seedlings growth, C:N:P stoichiometry responses, and nutrient use efficiency in *Firmiana simplex* (*F. simplex*). The maximum of total biomass was observed in acid purple soil under 75% shade, with a maximum difference of 3.6 times. With the increase in shading intensity, C content in the root, stem, and leaf reached maximum value under 75% shade. However, C content in the root and N content in the stem reached a maximum value of 420.6 g·kg<sup>-1</sup> and 13.7 g·kg<sup>-1</sup> in acid purple soil, respectively. With the increase in shading intensity, the total C and N accumulation showed a trend of progressive increase and then decrease, reaching the maximum value of 346.2 mg and 10.7 mg under 75% shade, respectively. The N:P ratios of various organ ranged from 3.1 to 11.9 in acid purple soil and red soil, indicating that the seedlings growth was restricted by nitrogen. We concluded that the interactions of shade and soil types might adjust the C:N:P stoichiometry and influence the dynamic balance between nutrients and organs in *F. simplex* seedlings.

**Keywords:** C:N:P stoichiometry; element accumulation; light intensity; nutrient limitation; plant-light-soil interaction; soil environment



**Citation:** Zhi, X.; Song, Y.; Yu, D.; Qian, W.; He, M.; Lin, X.; Zhang, D.; Gao, S. Early Growth Characterization and C:N:P Stoichiometry in *Firmiana simplex* Seedlings in Response to Shade and Soil Types. *Forests* **2023**, *14*, 1481. <https://doi.org/10.3390/f14071481>

Academic Editor: Adele Muscolo

Received: 7 May 2023

Revised: 15 July 2023

Accepted: 17 July 2023

Published: 19 July 2023



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## 1. Introduction

Light is crucial for the survival, growth, and development of plants. It is the mainly driving factor for photosynthesis and is also essential for plant growth and production [1–3]. Of all environmental factors, light usually show the heterogeneous in both space and time [4]. Distinct light environments can create different light intensities, which directly influence the photosynthetic activity, transpiration rate, nutrient elements, and water uptake, and change the chlorophyll content and affect seedlings growth and environmental adaptation [5]. Thus, plants growing in adverse light and environmental factors, especially during the early seedling stages, may develop the differences of morphological, nutrient, and metabolic adjustments as adaptations to various light environments [6–8]. Generally, deficient and/or excessive light intensities are harmful to plant growth and development, but moderate light intensity can enable them to increase growth and yield [9]. Studies showed that plants allocate more biomass to underground parts in order to improve the uptake of water and nutrients under high light intensity, whereas low light usually

reduces carbon accumulation and plant growth and increases the allocation proportion of leaves and stems biomass [10,11]. Moreover, plants maximized light interception for improved carbon gain in order to suit the needs of low-light environments. In some shade-adapted plants, leaves have less supporting tissue and number of mesophyll cells per unit area, and the specific leaf area (SLA) is generally higher under low-light conditions. Thus, the photosynthetic capacity is lower than those of in the leaves of sun-acclimated plants [3,12]. Moreover, previous studies indicated that different plant species have different utilization characterization of carbon, nitrogen, and phosphorus in response to various light intensity [4,13]. These results suggested that growth and nutrient accumulation characteristics of plants may indicate their adaptability and tolerance to light environments. However, it remains unknown to what extent the growth environment influences the variable nutrient uptake and distribution patterns in some plants.

Soil plays a key role in colonization, competition, growth, and development of plants, and provide water, nutrients, and other conditions [14]. Various soil types have different physical and chemical properties and can influence nutrient uptake and distribution characteristics during the growth process of plants [15]. Although plants may adapt to many soil types, the growth, biomass allocation, root architecture, nutrient absorption, and physiological characteristics are directly or indirectly affected by the differences in soil types [16,17]. Earlier studies showed that under low nitrogen (N) and low phosphorus (P) conditions, the ratios of C:N and C:P in leaves of plants are lower, resulting in more efficient nutrient utilization efficiency [18]. Moreover, nutrients are more easily absorbed in fertile, moist, and well-drained loam, which improves seedlings growth and development in some plants [19,20]. These studies can not only help to understand the growth characteristics and nutrient distribution of seedlings, but also promote seedling establishment and growth by the changes in soil nutrients under different soil types.

Ecological stoichiometry is a branch of ecology that combines stoichiometry with biology, chemistry, and physics [21]. It not only deals with the balance mechanism of nutrients and energy, but also reveals the balance of mineral elements in the interactions of natural ecosystems, which provide new insights to understand energy flow and mineral cycling [22,23]. C, N, and P are important essential elements, and are also components of RNA, DNA, protein, and other metabolisms during plant growth and development [24,25]. In plants, the contents of C, N, and P and C:N:P stoichiometry can reflect the nutrient demands and their dynamic balance of nutrient supply from the soil, and also reflect adaptive defense responses and growth status in response to external growth environments [26]. Moreover, the ratios of C:N and C:P represent the ability of mineral uptake and accumulation in plants, representing the status of nutrient utilization [27]. The ratio of N:P can represent the nutrient status in plants and indicate the limitation degree of N and/or P in the plant–soil system [28]. Numerous studies have evaluated that significant differences in the contents of C, N, and P and C:N:P stoichiometry are found, which are related to light intensity, soil types, N addition, and plant species, etc. [23,29,30]. In fact, seedlings growth and formation are significantly affected by a complicated environment, such as light, soil types, and other factors. Thus, the interaction effects of shade and soil types on seedling growth characteristics and C:N:P stoichiometry in plants, especially at early growth stages of seedling, are still needed.

*F. simplex*, belonging the family Sterculiaceae, is widely cultivated and grown throughout various regions in China. It can grow in plain, hilly, or gully areas [31,32]. *F. simplex* is today recognized as a woody oil crop, and its seeds have about 30% oil content. The main fatty acids from its seeds are linoleic acid (30.2%), oleic acid (22.2%), and palm acid (17.4%). Among them, the content of linoleic acid was 2.5–5 times higher than those of oils in rapeseed and peanut, etc. [33,34]. Some reports had showed that *F. simplex* is a potential and promising renewable resource for biodiesel production [31,32]. Moreover, *F. simplex* can absorb various harmful gases, for example sulfur dioxide and chlorine, and help clean the air, which plays an important role in city afforestation. Hence, with a renewing interest, the aim of this research will study the variations of shading and soil types on the early

growth parameters and C:N:P stoichiometry in *F. simplex* seedling. These results will help to better understand the dynamic balance of biomass allocation and C, N, and P components, as well as how environmental factors influences the nutrient uptake and distribution patterns, which will provide a scientific basis for the conservation and management of *F. simplex* seedlings.

## 2. Materials and Methods

### 2.1. Study Site

The study site was set up at the roof of the fifth teaching building of Sichuan Agricultural University in Chengdu, China, which lies between 30°42'16" N and 103°51'29" E at altitudes of 505 m. Climatically, this site belongs to the mid-latitude inland subtropical humid monsoon climate, and long-term climate data show mean annual temperature of 16.4 °C. The average annual rainfall is 896.1 mm; the rainy season is mainly from June to September with a mean relative humidity of 84.0%. The average annual sunshine hours are 1104.5 h, and the annual frost-free period is 282 days [35].

### 2.2. Experimental Material

In October 2021, mature and healthy seeds were collected from more than five individual trees in Wenjiang District, Chengdu City, China. Seeds were dried at 30 °C and selected and stored in plastic boxes (Labeled, No. 20211020) at room temperature. Acid purple soil, yellow soil, and red soil belong to the main soil types widely distributed and representative in Sichuan, China, and were collected in the campus of Sichuan Agricultural University, Yu-cheng District, Ya-an, China (29°58' N, 102°58' E, altitude 578 m), Bai-sheng Village, Bao-lin Town, Qiong-lai, China (30°21' N, 103°30' E, altitude 552 m), and San-xing Village, Feng-le Town, Shi-mian, Sichuan, China (29°32' N, 102°54' E, altitude 878 m), respectively. Three independent multiple plots of 12 m × 12 m were randomly designated for each sampling point, and five sub-plots of 1.5 m × 1.5 m were established at the center and diagonal of each plot for subsequent soil sampling. All selected sites have similar topography to ensure comparability of soil samples. Soil samples were collected from each plot, and the depth of the soil layer was 0–20 cm, which was used for seedling cultivation. These soils were air-dried, crushed, sieved, and homogenized under strong light for further analysis. Some physical and chemical properties of these soils were analyzed (Table 1).

**Table 1.** Physical and chemical properties of three types of soil.

| Soil Type      | pH            | SOC (g·kg <sup>−1</sup> ) | BD (g·cm <sup>−3</sup> ) | TN (g·kg <sup>−1</sup> ) | TP (g·kg <sup>−1</sup> ) | TK (g·kg <sup>−1</sup> ) |
|----------------|---------------|---------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| B <sub>1</sub> | 4.34 ± 0.13 b | 42.53 ± 1.31 a            | 1.24 ± 0.08 b            | 2.33 ± 0.18 a            | 0.24 ± 0.01 a            | 4.99 ± 0.13 a            |
| B <sub>2</sub> | 5.14 ± 0.16 a | 16.64 ± 0.66 c            | 1.30 ± 0.06 a            | 1.14 ± 0.07 b            | 0.07 ± 0.00 b            | 3.15 ± 0.08 b            |
| B <sub>3</sub> | 4.79 ± 0.12 a | 33.50 ± 0.64 b            | 1.32 ± 0.07 a            | 1.89 ± 0.11 a            | 0.08 ± 0.00 b            | 2.21 ± 0.09 c            |

Note: SOC: soil organic carbon, BD: bulk density, TN: total nitrogen, TP: total phosphorus, TK: total potassium, B<sub>1</sub>: acid purple soil, B<sub>2</sub>: red soil, B<sub>3</sub>: yellow soil. Data represent five replicates with mean ± SE (*n* = 5). Values with the same letter in the same column are not significantly different ( $\alpha$  = 0.05).

### 2.3. Seedling Culture and Experimental Design

Seeds were soaked in water at 40 °C for 24 h, and then evenly spread on a plastic plate with four layers of gauze. These seeds were placed in an incubator at 30 °C for 7 days, and then were planted in pots containing 10 kg of different soils (diameter 28 cm, height 22 cm, and the soil layer height 15 cm). Eight seeds were sown per pot, and 2 weeks after sowing, the seedlings were thinned to one plant per pot. It contained four shading levels: natural light (A<sub>1</sub>, 0% of shading rate), 50% shade (A<sub>2</sub>, 28% of shading rate), 75% shade (A<sub>3</sub>, 45% of shading rate), and 95% shade (A<sub>4</sub>, 72% of shading rate), and combined with three soil types: acid purple soil (B<sub>1</sub>), red soil (B<sub>2</sub>), and yellow soil (B<sub>3</sub>). The experiment consisted of a 4 × 3 factorial scheme with nine replicates per treatment and a total of 108 pots. An open ground with flat terrain and no cover was selected, and an arched steel canopy with length, width, and height of 3 m × 2.5 m × 2.5 m was built. During the experiment, the

relative shading rate was converted after measuring by a TES-1332A illuminance meter. The relative soil moisture was kept at about 60%–80% and weed control and pest control management were carried out uniformly.

#### 2.4. Measurement of Growth Parameters

After 45 days, five uniformly seedlings were randomly harvested from each group, and their sapling height (cm), basal diameter (cm), and leaf area (cm<sup>2</sup>) were measured. After cleaning with deionized water, the samples of leaves, stems, and roots were dried at 105 °C for 30 min and at 70 °C for 12 h.

#### 2.5. Analysis of Plant and Soil Physicochemical Properties

The dried soil samples (5.0 g) were added to 25 mL of distilled water in a stomacher to homogenize at 10,000 r/min and were kept for 30 min at room temperature to obtain clear supernatant for pH determination [36]. The soil samples were collected in five volumetric soil rings (volume 100 cm<sup>3</sup>) to determine the soil bulk density [36]. Soil organic carbon content was determined with K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub> oxidation and FeSO<sub>4</sub> titration methods [37]. Moreover, the dried roots, stems, and leaves were ground in a mill (FW80, Taisite, Tianjin, China), and passed through a 100-mesh standard sieve to obtain samples. Total nitrogen content of the plant and soil samples was measured using the semi-micro-Kjeldahl method after digestion with H<sub>2</sub>SO<sub>4</sub>-H<sub>2</sub>O<sub>2</sub> [37]. Total phosphorus content was determined using the Mo-Sb colorimetric method after digestion with H<sub>2</sub>SO<sub>4</sub>-HClO<sub>4</sub> [37]. Total potassium contents were quantified by flame photometry method [37].

#### 2.6. Statistical Analyses

Root–shoot ratio, specific leaf area, and robustness were calculated according to the biomass of roots, stems, and leaves, sapling height, basal diameter, and leaf area [35]. The calculation formula was as follows: root–shoot ratio = root biomass/stem biomass, specific leaf area = unifoliate area/total biomass, robustness = biomass of stem and leaf/sapling height. According to the difference of element contents of each organ, the element accumulation and distribution ratio in *F. simplex* seedlings were calculated. Nutrient utilization efficiency refers to the biomass produced by unit nutrient. According to the increment of biomass and the amount of element accumulation, the calculation formula was as follows [35]: element accumulation = organ element content × organ biomass, nutrient utilization efficiency = total biomass increase/total nutrient accumulation. Data were analyzed using SPSS 24.0 (SPSS, Inc., Chicago, IL, USA) with two-way ANOVA. LSD was used to test the significance difference between treatments ( $\alpha = 0.05$ ). Redundancy analysis (RDA) was conducted using the CANOCO 5.0 tool to evaluate the relationships between growth parameters, stoichiometric characteristics, and environmental factors.

### 3. Results

#### 3.1. Effects of Shading Treatments and Soil Types on Growth Parameters

Shading treatments had significant effects on sapling height ( $p < 0.05$ ), but soil types had no significant influences on sapling height ( $p > 0.05$ ). Moreover, the interactions of soil types and shading treatments showed significant difference ( $p < 0.05$ ). The sapling height increased with the rising shading intensity, and the overall trend was progressively increased, reaching the maximum value in the A<sub>4</sub>B<sub>2</sub> group, representing a 49.3% increment (Table 2). However, the overall trend of basal diameter was contrary to the sapling height. There was a certain difference in basal diameter under different treatments compared to the control, but the maximum value was observed under the interaction of natural light and red soil (Table 2). Based on two-way analysis of variance, shading treatments and soil types as well as their interactions had remarkable influences on basal diameter ( $p < 0.05$ ). Under 95% shading conditions, the basal diameter reached the minimum, and the maximum difference was 56.3% (Table 2). Shading treatments had significant impacts on root–shoot ratio, specific leaf area, and robustness ( $p < 0.05$ ). With the rising shading intensity, the

root–shoot ratio and robustness significantly decreased. The minimum of root–shoot ratio and robustness were observed under 95% shade, and the maximum difference was 60.9% and 76.5%, respectively. Moreover, the specific leaf area showed opposite trends compared to the root–shoot ratio and robustness. Under 95% shade, the specific leaf area reached the maximum, and the maximum difference was 1.99 times higher than those of the control. These findings suggested that soil types and the interactions of shade and soil types have remarkable influences on the specific leaf area and robustness, but no significant impacts were observed on the root–shoot ratio (Table 2,  $p > 0.05$ ).

**Table 2.** Effects of shading and soil types on growth parameters.

| Treatment                     | SH (cm)        | BLD (cm)         | SLA (cm <sup>2</sup> ·g <sup>−1</sup> ) | R/T             | Rob(g·cm <sup>−1</sup> ) |
|-------------------------------|----------------|------------------|-----------------------------------------|-----------------|--------------------------|
| A <sub>1</sub> B <sub>1</sub> | 7.10 ± 0.39 C  | 0.399 ± 0.025 Ab | 56.17 ± 3.07 Bb                         | 0.319 ± 0.016 A | 7.31 ± 0.32 Aa           |
| A <sub>1</sub> B <sub>2</sub> | 7.25 ± 0.32 C  | 0.411 ± 0.019 Aa | 59.53 ± 3.80 Ba                         | 0.313 ± 0.017 A | 6.90 ± 0.17 Ab           |
| A <sub>1</sub> B <sub>3</sub> | 7.08 ± 0.15 C  | 0.387 ± 0.023 Ac | 52.71 ± 3.71 Bb                         | 0.307 ± 0.119 A | 7.77 ± 0.38 Aa           |
| A <sub>2</sub> B <sub>1</sub> | 8.20 ± 0.18 B  | 0.385 ± 0.021 Aa | 71.71 ± 3.66 Bb                         | 0.160 ± 0.014 B | 6.23 ± 0.49 Ba           |
| A <sub>2</sub> B <sub>2</sub> | 8.83 ± 0.21 B  | 0.372 ± 0.014 Ab | 75.45 ± 2.64 Ba                         | 0.164 ± 0.008 B | 5.67 ± 0.36 Ba           |
| A <sub>2</sub> B <sub>3</sub> | 8.73 ± 0.26 B  | 0.367 ± 0.018 Ac | 63.68 ± 3.94 Bb                         | 0.162 ± 0.113 B | 6.24 ± 0.16 Ba           |
| A <sub>3</sub> B <sub>1</sub> | 9.50 ± 0.19 A  | 0.391 ± 0.022 Aa | 66.70 ± 1.94 Bb                         | 0.171 ± 0.016 B | 6.88 ± 0.24 Ba           |
| A <sub>3</sub> B <sub>2</sub> | 9.30 ± 0.17 B  | 0.401 ± 0.019 Aa | 71.57 ± 3.53 Ba                         | 0.167 ± 0.020 B | 6.77 ± 0.14 Ba           |
| A <sub>3</sub> B <sub>3</sub> | 9.33 ± 0.22 AB | 0.389 ± 0.017 Aa | 63.79 ± 2.61 Bb                         | 0.160 ± 0.117 B | 6.92 ± 0.06 Ba           |
| A <sub>4</sub> B <sub>1</sub> | 10.40 ± 0.25 A | 0.277 ± 0.013 Ba | 168.05 ± 3.84 Aa                        | 0.131 ± 0.009 B | 1.95 ± 0.10 Ca           |
| A <sub>4</sub> B <sub>2</sub> | 10.58 ± 0.20 A | 0.263 ± 0.009 Ba | 154.48 ± 3.04 Ab                        | 0.125 ± 0.015 B | 1.75 ± 0.12 Ca           |
| A <sub>4</sub> B <sub>3</sub> | 10.03 ± 0.17 A | 0.269 ± 0.011 Ba | 151.12 ± 3.44 Ab                        | 0.120 ± 0.116 B | 1.83 ± 0.07 Ca           |

Note: SH, saplings height; BLD, basal diameter; SLA, specific leaf area; R/T, root–shoot ratio; Rob, robustness; A<sub>1</sub>, natural light; A<sub>2</sub>, 50% shade; A<sub>3</sub>, 75% shade; A<sub>4</sub>, 95% shade; B<sub>1</sub>, acid purple soil; B<sub>2</sub>, red soil; B<sub>3</sub>, yellow soil. Results are shown as means ± SE ( $n = 5$ ). Different uppercase and lowercase letters represent significant difference among different shading conditions and three soil types, respectively ( $p < 0.05$ ).

### 3.2. Effects of Shading Treatments and Soil Types on Biomass and Its Distribution

As shown in Figure 1, the significant differences of the root, stem, leaf, and total biomass were observed in response to different shading treatment ( $p < 0.05$ ). The root, stem, and total biomass had similar trend, but the leaf biomass showed different trend. The maximum and minimum of total biomass were observed under 75% and 95% shading treatments, respectively. The values of seedlings under 75% shading treatments were 3.6 times higher than those of under 95% shading treatments (Figure 1). These results indicated that soil types and shading treatments as well as their interactions had no remarkable influences on the roots, stems, leaves, and total biomass ( $p > 0.05$ ), and the maximum values were observed when these seedlings were cultured in acid purple soil.

### 3.3. Effects of Shading Treatments and Soil Types on C, N, and P Contents

As shown in Figure 2, the significant changes in C, N, and P content were observed in response to shading treatments and soil types. Moreover, there were significant interactions ( $p < 0.05$ ). In leaves, the C and N contents were significantly higher than those of in the root and stem under different shading treatments. With the rising shading intensity, the C content of roots, stems, and leaves reached maximum value at 75% shade treatments, and then decreased. The maximum was 28.0% higher than those of other shading treatments (Figure 2a). The content of N and P had a similar trend at different tested groups. Compared to the control, the N and P content slowly increased under 50% and 75% shade treatment, and the increase were 1.7 times and 2.4 times higher than those of the control, respectively (Figure 2b,c). In addition, three soil types also had different effects on the C, N, and P content in different organs of *F. simplex* seedlings. When these seedlings were cultured in acid purple soil, the maximum value of the C content in the root and the N content in the stem were recorded. When these seedlings cultured in red soil, the maximum value of the N content in the root and the P content in the stem were observed. However, the maximum value of C,

N, and P content in the leaves were observed when these seedlings cultured in yellow soil. These significant differences suggested that the C, N, and P content in *F. simplex* seedlings are related to shading treatments, soil types, and organs as well as their interaction.

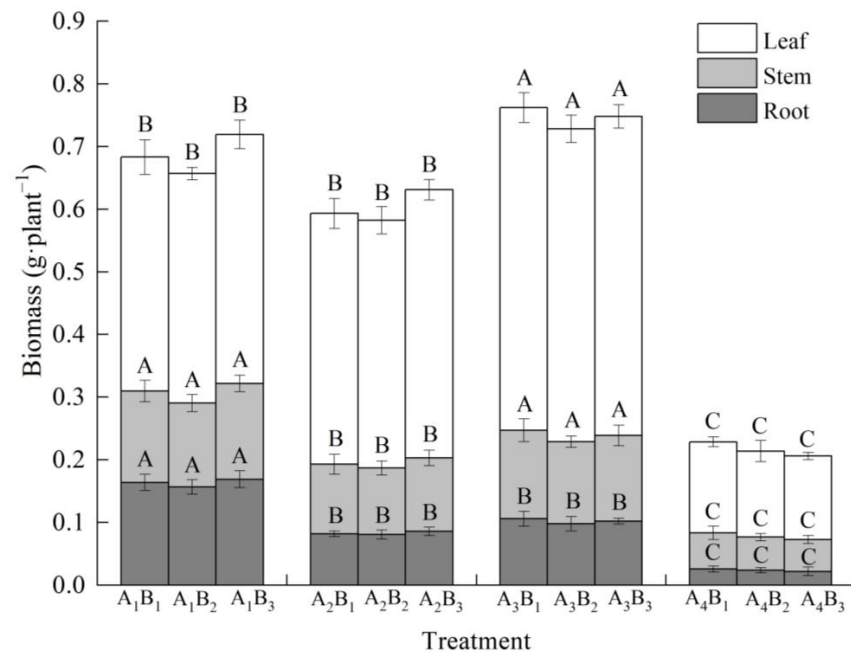


**Figure 1.** Effects of shading treatment and soil type on the biomass of different organs. A<sub>1</sub>: natural light, A<sub>2</sub>: 50% shade, A<sub>3</sub>: 75% shade, A<sub>4</sub>: 95% shade, B<sub>1</sub>: acid purple soil, B<sub>2</sub>: red soil, B<sub>3</sub>: yellow soil. Data are shown as means  $\pm$  SE ( $n = 5$ ). Different uppercase letters represent significant difference among different shading conditions and three soil types, respectively ( $p < 0.05$ ).

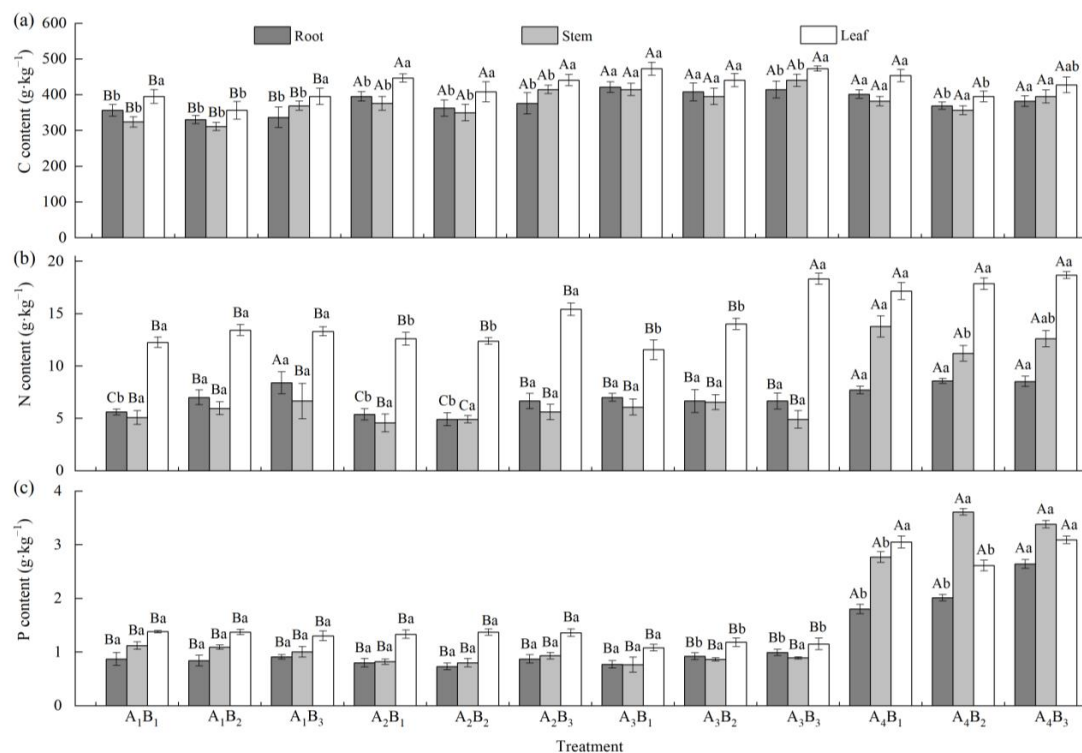


**Figure 2.** Effects of shading treatment and soil type on C content (a), N content (b), P content (c). Data are shown as means  $\pm$  SE ( $n = 5$ ). Different uppercase and lowercase letters represent significant difference among different shading conditions and three soil types, respectively ( $p < 0.05$ ).

### 3.4. Effects of Shading Treatments and Soil Types on C, N, and P Accumulation

As shown in Figure 3, the significant changes in C, N, and P accumulation were observed in response to shading treatments and soil types. Moreover, there were significant interactions of shading treatments and soil types ( $p < 0.05$ ). In general, the orders of total accumulation of C, N, and P were leaf > stem > root, and these values showed significant differences in response to shading treatments and soil types. With the rising shading intensity, the total accumulation of C and N of roots, stems, and leaves reached maximum value at 75% shading treatments, and then decreased at 95% shading treatments (Figure 3a,c). Similarly, the total N accumulation showed a similar trend compared to those of the C and P accumulation. These results indicated that excessive shading may limit the uptake of C, N, and P, and further inhibit their accumulation to a certain extent in *F. simplex* seedlings (Figure 3).

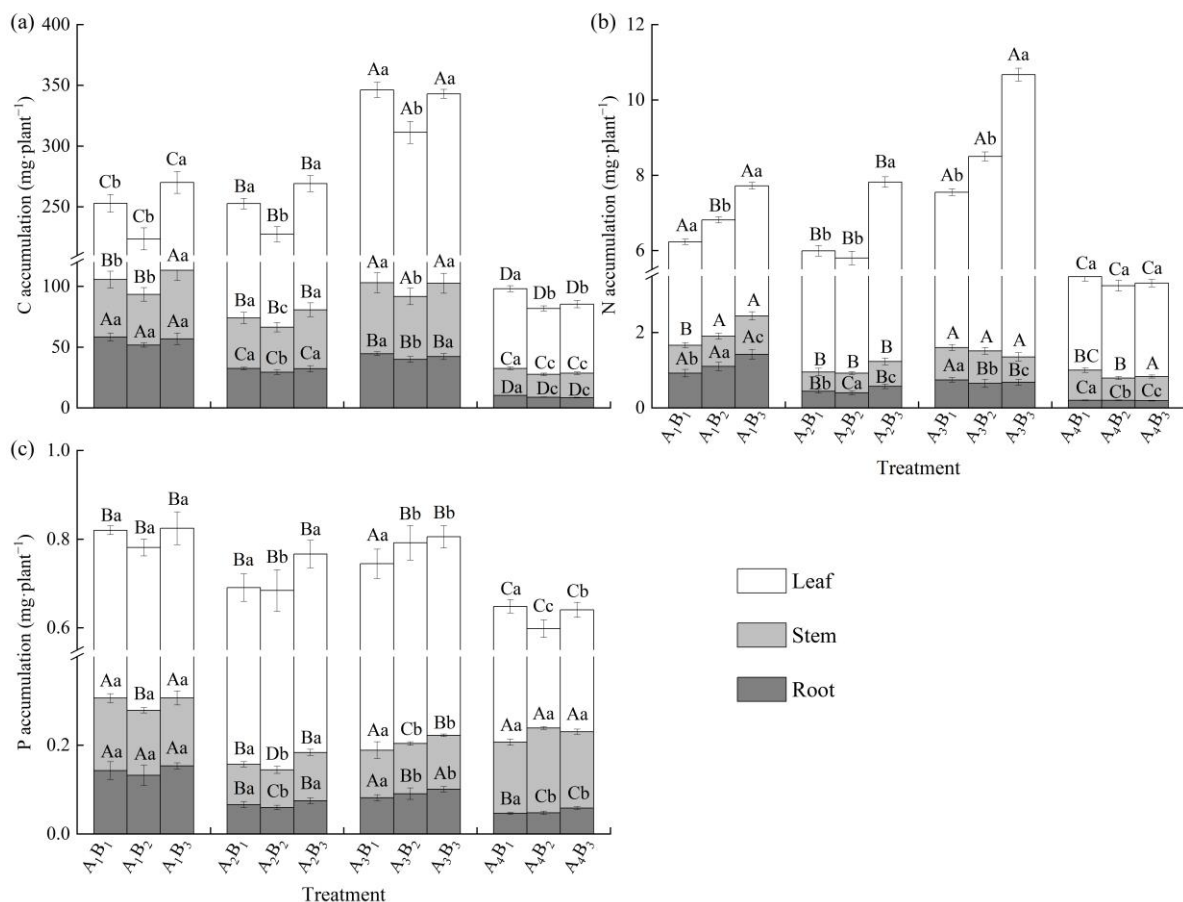


**Figure 3.** Effects of shading treatment and soil type on C accumulation (a), N accumulation (b), and P accumulation (c). Data are shown as means  $\pm$  SE ( $n = 5$ ). Different uppercase and lowercase letters represent significant difference among different shading conditions and three soil types, respectively ( $p < 0.05$ ).

### 3.5. Effects of Shading Treatments and Soil Types on C, N, and P Stoichiometric Ratio

As shown in Figure 4, the significant changes in C:N, C:P, and N:P ratios were observed in response to shading treatments. However, there was no significant change in C:N, C:P, and N:P ratios in the stem and N:P ratio in the root when these seedlings were cultured in three soil types ( $p < 0.05$ ). In general, the changes in C:N and C:P ratios in the roots and leaves were similar and showed a progressive increase and then rapid decrease. The maximum and minimum values were observed when these seedlings were cultured under 75% and 95% shading treatments, respectively (Figure 4a,c). The N:P ratio of roots, stems, and leaves had significant differences in response to shading treatments. The minimum

values of the N:P ratio of roots and leaves were observed when these seedlings cultured under 95% shading treatments, and the maximum values were 2.2 times higher than those of 95% shading treatments (Figure 4b). In addition, three soil types also had different effects on the C:N, C:P, and N:P ratios in different organs of *F. simplex* seedlings. The changes in C:N, C:P and N:P ratios showed similar trend when these seedlings were cultured in three soil types, which showed a progressive increase and then rapid decrease. These differences suggested that the C:N, C:P, and N:P ratios in *F. simplex* seedlings are related to shading treatments, soil types, and organs as well as their interactions.

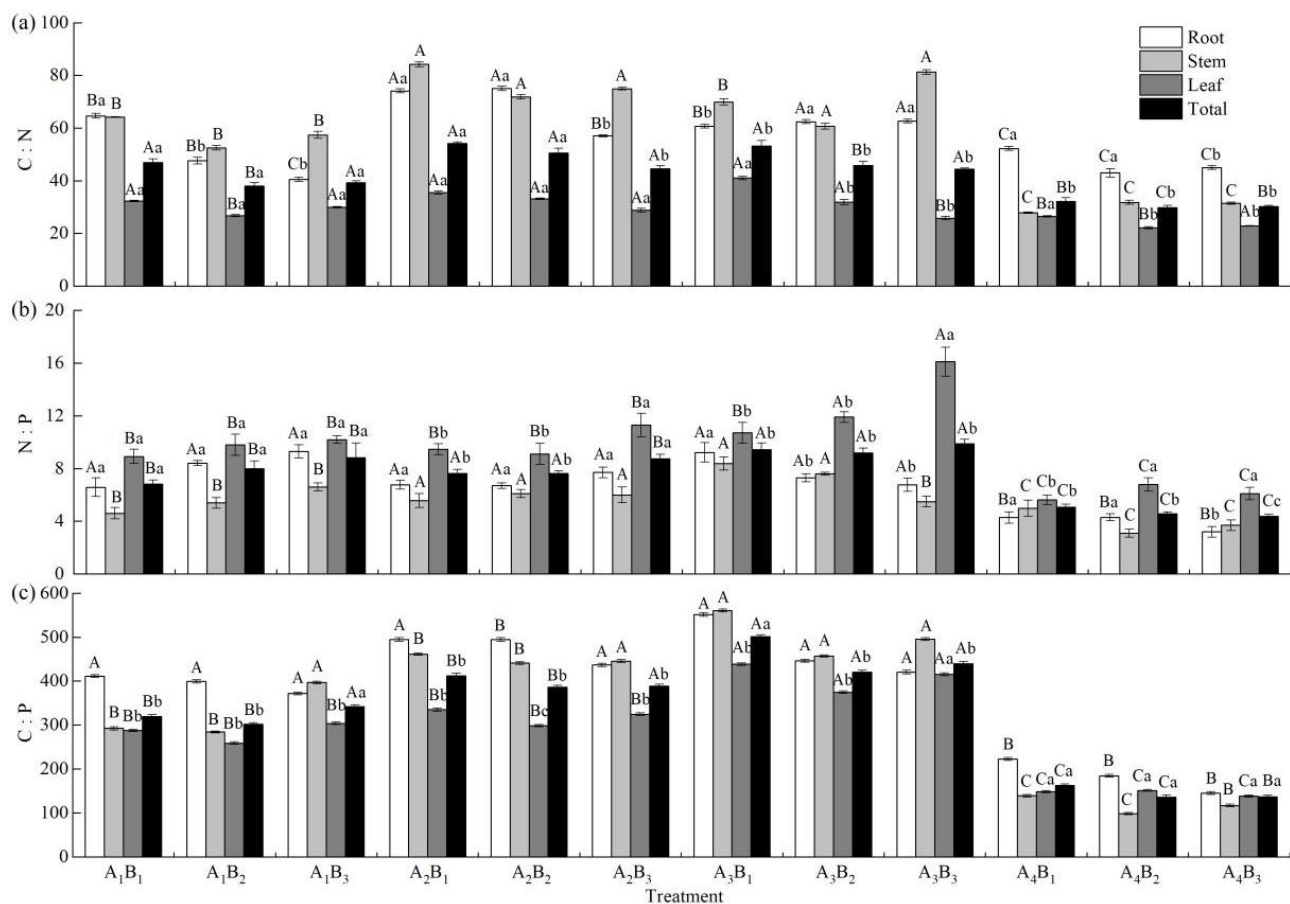


**Figure 4.** Effects of shading treatment and soil type on C:N (a), N:P (b), C:P (c). Data are shown as means  $\pm$  SE ( $n = 5$ ). Different uppercase and lowercase letters represent significant difference among different shading conditions and three soil types, respectively ( $p < 0.05$ ).

### 3.6. Effects of Shading Treatments and Soil Types on C, N, and P Use Efficiency

As shown in Figure 5, the significant changes in C, N, and P use efficiency were observed in response to shading treatments, soil types, and their interaction ( $p < 0.05$ ). In general, compared with the control, C use efficiency showed a reducing trend when these seedlings were cultured at different shading treatment. However, the N and P use efficiency showed little differences in response to shading treatments compared with the control, except for 95% shading treatments (Figure 5). In addition, three soil types also had different effects on the C, N, and P use efficiency in *F. simplex* seedlings. The changes in P use efficiency showed a progressive increase and then rapid decrease when these seedlings were cultured in three soil types. Moreover, the maximum values of C use efficiency were observed when these seedlings were cultured in yellow soil, and the maximum values of N and P use efficiency were recorded when these seedlings were cultured in acid purple soil. These differences showed that the C, N, and P use efficiency in *F. simplex* seedlings show a strong utilization ability in the interaction of 75% shading treatments and acid purple soil, which are related to shading treatments, soil types, and their interactions.

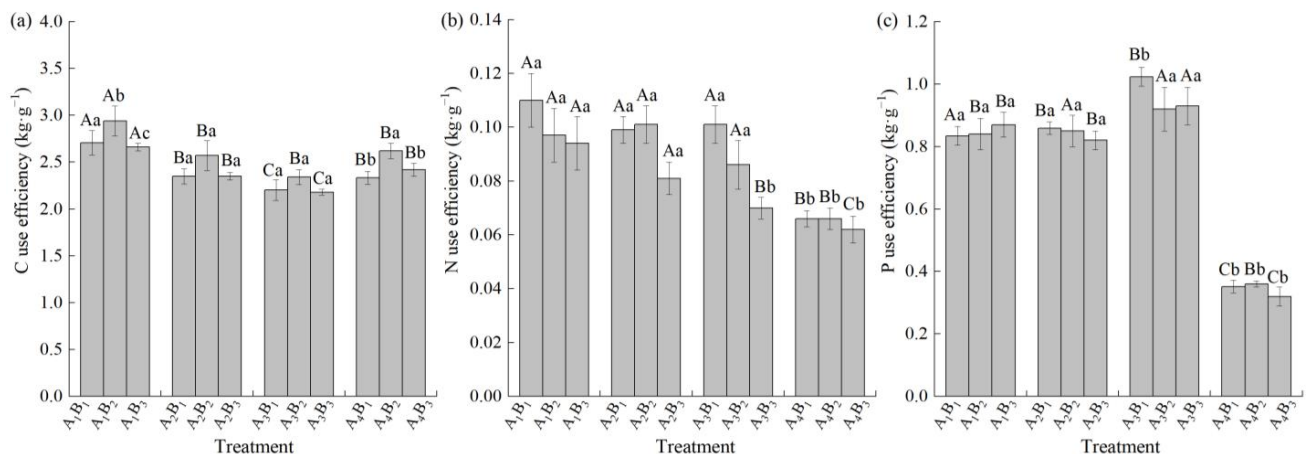


**Figure 5.** Effects of shading treatment and soil type on C use efficiency (a), N use efficiency (b), P use efficiency (c). Data are shown as means  $\pm$  SE ( $n = 5$ ). Different uppercase and lowercase letters represent significant difference among different shading conditions and three soil types, respectively ( $p < 0.05$ ).

### 3.7. Relationships among Growth Indices, Stoichiometric Characteristics, and Environmental Factors

RDA results showed that shading treatments and soil types can influence the growth parameters and stoichiometric characteristics to a certain extent. After correction, the value of  $R^2$  was 41.7%, and RDA1 axis and RDA2 axis jointly explained 50.4% of the total variance. Overall, 45.8% of the total variance was explained by RDA1 axis, and 4.6% of the total variance was explained by RDA2 axis. For these two factors, shading treatments significantly affected the growth parameters and stoichiometric characteristics ( $F = 27.2$ ,  $p = 0.002$ ). Shading treatments were positively related to sapling height, specific leaf area, C, N, and P content, and negatively correlated with basal diameter, robustness, root–shoot ratio, biomass, C, N, and P accumulation, and use efficiency (Figure 6). Organic carbon, total nitrogen, total phosphorus, and total potassium showed a positive correlation. Furthermore, it was found that organic carbon and total nitrogen were negatively correlated with C and N content, while bulk density was not significantly correlated with growth parameters and stoichiometric characteristics.

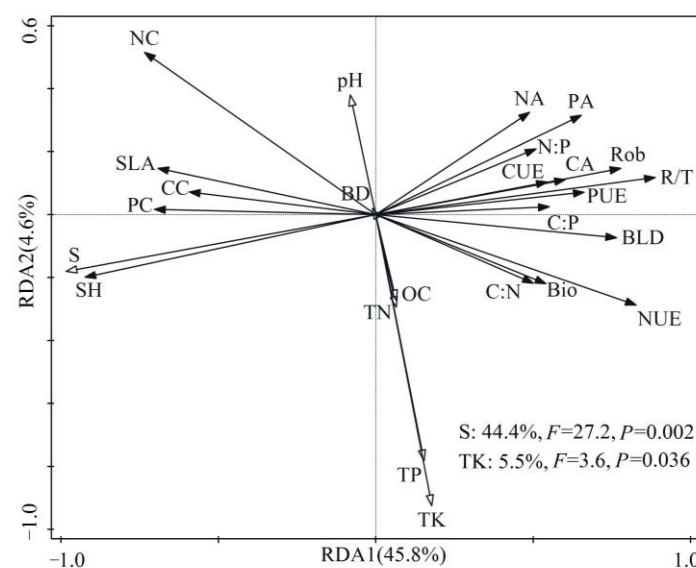


**Figure 6.** Relationship among growth parameters, stoichiometric characteristics, and environmental factors. Note: S, shading; OC, organic carbon; BD, bulk density; TN, total nitrogen; TP, total phosphorus;

TK, total potassium; SH, sapling height; BLD, basal diameter; SLA, specific leaf area; R/T, root–shoot ratio; Rob, robustness; Bio, biomass; CC, C content; NC, N content; PC, P content; CA, C accumulation; NA, N accumulation; PA, P accumulation; CUE, C use efficiency; NUE, N use efficiency; PUE, P use efficiency.

#### 4. Discussion

##### 4.1. Effects of Shading Treatments and Soil Types on Growth Performance

In the past few decades, many studies have shown that moderate shade is beneficial to plant height, ground diameter, SLA, and biomass accumulation, but high light intensity and excessive shadows will have significant inhibitory effects, which are not conducive to the normal growth and development of seedlings [10,38,39]. In our study, as the shading intensity increased, the plant height and SLA progressively increased, but basal diameter, root–shoot ratio, and robustness progressively decreased (Table 2). Nevertheless, it should be noted that the values of sapling height and SLA were the smallest under full-light condition. However, the values of basal diameter, root–shoot ratio, and robustness were the largest. By contrast, these morphological features were completely opposite under 95% shading treatments (Table 2). This might be due to overheating and high transpiration rates caused by excessive irradiance, which has an adverse effect on photosynthetic tissues, and plants had difficulty to maintain the nutrient balance under an extremely shaded environment. Ultimately, these changes resulted in poor growth and survival. Earlier studies have shown that plants, under shading treatments, show remarkable morphological changes, for example spindling, branch shortening, increased shoot–root ratio, and specific leaf area [1,40,41]. These changes allow plants to maximize light capture and utilization efficiency, and further decrease side effects when they are cultured under shading stress [9,12]. Thereby, these results reinforced the studies and showed that the morphological and structural changes in plants may be related to adaptive mechanisms in response to shading environment.

On the other hand, plants may adjust their biomass distribution in order to improve their ability to capture resources, and thereby alleviate the damage caused by environment conditions [42,43]. The present study revealed that *F. simplex* seedlings prioritize the shoots development over the root, and further reduce biomass allocation of roots and increase it to leaves when these seedlings are cultured under low-light conditions. Moreover, these changes in the leaves may be related to higher relative water content and nutrient absorption rates (Figure 1). Thus, these findings point to the high phenotypic plasticity of *F. simplex* seedlings in response to the interactions of different shading treatments and soil types, which plants achieve through a variety of regulatory mechanisms. Furthermore, the changes in morphology, growth, and nutrient content may be related to different physical and chemical properties of different soil types [15,44]. In this study, the total biomass of *F. simplex* seedlings was the largest when they were cultured in acid purple soil, which is similar to previously reported for *Ricinus communis* seedlings [20]. These findings show that the growth status of different species showed significant differences in response to different soil types, which may be related to their different adaptability.

##### 4.2. Effects of Shading Treatments and Soil Types on C, N, and P Contents and C:N:P Stoichiometric Characteristics

Nutrient uptake and stoichiometric depends on the interactions among plant species, soil types, and light environment [45]. In plants, different nutrients have showed different responses to light intensity and soil type, and the C, N, and P contents may reflect nutrient uptake, utilization efficiency, and the balance of mineral cycling [8,46]. Previous research has elucidated that leafy vegetables, lettuces, and four fern species exhibited higher mineral elements content under low light intensity [13,47]. Additionally, other reports also found that moderate shade supplies a more optimal light environment for photosynthesis in plants, which may lead to an increase in N and P contents in leaves [2,4,8]. In the present study, our results were in line with previous studies, showing that a higher C content was observed under 75% shading treatment, and higher P and N contents were observed under

95% shading treatment (Figure 2). This interesting variation could be caused by two reasons: One possible reason is that more N is expected to be allocated under shading conditions, and further lead to the N supply surpasses demand. The other reason may be due to the increased light intensity, which promotes photosynthesis in plants, and the increased fresh weight causes dilution of the mineral content. Interestingly, our findings did not agree with the results of Yang et al. and Puglielli et al. [48,49], who observed that reduced nitrogen and phosphorus levels in plants were recorded under low-light conditions. This reason was explained that higher light intensities have been shown to enhance photosynthesis and promote plant growth and development, and further lead to a significant increase in the N and P content in leaves.

The mineral accumulation and distribution in plants reflects the demand and absorption capacity for certain nutrient elements [45]. The present study suggests that the accumulation rate of nutrients in plants maintains a high synchronicity with the accumulation rate of dry matter, and this synchronicity is more obvious in plants during the seedling growth period. These findings were in line with our findings. Moreover, the total accumulation of C and P in seedlings on different soil types showed the same trend:  $B_1 > B_3 > B_2$ , which indicates that the demand of C and P in seedlings on different soil types had a high degree of synergy. In fact, this trend may be related to a higher SOC and TP content of soils. Previous studies have shown that moderate light conditions can increase nutrient and biomass accumulation in plants on different soil types, but excessive shade inhibits their accumulation [2,8]. Other reports also showed that appropriately increasing light intensity is beneficial to enhancing nutrient use efficiency [2]. Our findings were in line with earlier reports and supported that mineral accumulation and distribution in plants is related to the shading environment.

Plants exhibit varying elemental content and distribution characteristics, and ultimately display distinctive stoichiometric characteristics of elements through regulating the metabolism and circulation of C, N, and P [14]. Variations in the C:N, C:P, and N:P ratios among plants may reflect differences in their morphology, organs, and nutrient utilization efficiency in response to environment condition [26,29]. Previous examples of research have shown that the variations in leaf N:P ratios are an initial increase and then rapid decrease as the shading condition changes, and the appropriate shading intensity can increase the N:P ratio of the aboveground part in order to meet the physiological needs of metabolic processes [4,8,19]. Our results were consistent with earlier reports, and further supported our findings to some extent. Moreover, lower C:N and C:P ratios in stems and leaves showed that the lowest nutrient use efficiency and growth rate may occur under shading conditions [18]. The higher C:N and C:P ratios were observed in leaves under moderate shading conditions, indicating that a higher C:N or C:P ratio accumulated in seedlings [2]. In plants, the C, N, and P content and C:N:P stoichiometry exhibited significant variation across different plant organs and growth environment [30]. This might be because each organ has a distinct function on its growth and reproduction. On the other hand, previous studies showed that the nutrient limitation could be assessed by the N and P content as well as N:P ratio in plants. When the values of N:P was less than 14, plant growth was limited by N contents. When  $14 < \text{N:P} < 16$ , plant growth was limited by both N and P contents; however, when the values of N:P was higher than 16, their growth was limited by P content [50]. The present study showed that the N:P ratio of *F. simplex* seedlings was less than 14, indicating that the growth was significantly restricted by N contents. Moreover, the N:P ratio of each organ in *F. simplex* seedlings ranged from 3.1 to 11.9 in different type of soils, indicating that the N:P ratio was related to soil types (Figure 4). Collectively, from these results, it is speculated that N and P fertilizers were applied appropriately in the growth process of *F. simplex* seedlings according to different soil types and lighting environment, which can effectively promote the growth of *F. simplex* seedlings.

#### 4.3. Interrelationship between Environmental Factors and Growth Parameters, Stoichiometric Characteristics

Plant C:N:P stoichiometry played a crucial role in the regulation of nutrient limitation in response to the changes in growth environment [23]. In this study, environmental factors had a strong relationship with growth performance and stoichiometric characteristics (Figure 6). RDA results showed that shading conditions and soil types significantly affect the growth parameters and C:N:P stoichiometry (Figure 6). These results also verified that sapling height, specific leaf area, and C, N, and P content increased with the increase in shading intensity, while basal diameter, robustness, root–shoot ratio, biomass, C, N, and P accumulation, and use efficiency decreased with the increase in shading intensity (Figure 6). Our results were consistent with *R. communis* seedlings cultured in different soil types, which showed that the changes in N and P contents significantly affected the stoichiometric ratio of *F. simplex* seedlings [35]. Other studies also found that C:N and C:P ratios were proportional to the biomass and NUE and PUE in plant. These findings supported that the growth rate and nutrient conversion rate were relatively higher during the seedling stage [14]. Moreover, our results showed that the biomass has a significantly positive correlation with CA, NA, and PA, indicating that more nutrient accumulation leads to greater biomass. Previous reports showed the positive correlation between element content and the supply capacity of the element in the plant–soil system, which indicated that the growth of plant is significantly restricted by these elements [20]. Importantly, in our study, we also discovered that soil total nitrogen content had a significant positive correlation with the N:P ratio in *F. simplex* seedlings, indicating that the N content in *F. simplex* seedlings is obviously dependent on the soil N content.

#### 5. Conclusions

In summary, the present results supported that an increase in shading intensity and different soil types can adjust the growth conditions of *F. simplex* seedlings to a certain extent, and there were significant differences in growth parameters and C:N:P stoichiometry. This study also found that the C content and total C and N accumulation reached a maximum value under 75% shading treatments, whereas the maximum of total biomass, C content in the root, and N content in the stem were observed in acid purple soil. Furthermore, the early growth of *F. simplex* seedlings was restricted by nitrogen in acid purple soil and red soil, and was limited by nitrogen and phosphorus in yellow soil. Consequently, 75% shading conditions and acid purple soil were more suitable for the early cultivation of *F. simplex* seedlings. According to different soil types and lighting environment, nitrogen and phosphate fertilizers were applied appropriately at early growth stages in *F. simplex* seedlings. Further studies will investigate the fertilizer requirement characteristics at different growth stages of *F. simplex* seedlings and explain the nutrient–acquisition strategies and adjust nutrient utilization in response to N addition and soil types.

**Author Contributions:** Conceptualization, X.Z. and S.G.; methodology, S.G. and Y.S.; software, validation, investigation, X.Z. and Y.S.; data curation, X.Z., D.Y. and W.Q.; formal analysis, X.Z. and M.H.; writing—original draft preparation, X.Z. and S.G.; writing—review and editing, X.Z., Y.S., D.Y., W.Q., M.H., X.L., D.Z. and S.G. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was supported by the National Natural Science Foundation of China (Grant no. 32171775).

**Data Availability Statement:** The data that support the findings of this study are available from the corresponding author upon reasonable request.

**Acknowledgments:** The authors thank Yajuan Wang, Xiaobei Liu, and Zihan Guo from Faculty of Forestry, Sichuan Agricultural University, for their assistance during plant cultivation and harvesting.

**Conflicts of Interest:** The authors declare that there is no conflict of interest regarding the publication of this paper.

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