

Article

Functional Traits of *Quercus aliena* var. *acuteserrata* in Qinling Huangguan Forest Dynamics Plot: The Relative Importance of Plant Size and Habitat

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Abstract: Variation in intraspecific functional traits is one of the important components of community variation, and has drawn the attention of researchers. Studying the variation of traits under different plant sizes and habitats helps to reveal the adaptation mechanism of plants. We explored intraspecific trait variations by focusing on the widespread species *Quercus aliena* var. *acuteserrata* in a 25 ha warm, temperate, deciduous broadleaved forest plot in the Qinling Mountains. We measured nine morphological and chemical traits for 90 individuals from different plant sizes and habitats. In addition, we evaluated the relative impact of plant size and environment on *Q. aliena* var. *acuteserrata* with multiple regression models. We found that plant size explained the most variance of traits. As plant size increased, the trees tended to have lower leaf nitrogen concentrations, lower leaf phosphorus concentrations, higher leaf carbon concentrations, higher leaf dry matter content (LDMC), and thinner leaves, indicating the transformation from rapid resource acquisition strategy to conservative resource-use strategy. Habitats could only explain the changes in chemical traits. Leaf carbon concentration was principally affected by topographical factors and was significant different among habitats. Leaf nitrogen concentration and LPC were significantly limited by soil N and P. In conclusion, shifts in size-dependent traits met the growth requirements of *Q. aliena* var. *acuteserrata*; the high tolerance traits associated with this tree species might elucidate important mechanisms for coping with changing environments.

Keywords: functional traits; plant size; habitat filtering; adaptive mechanisms



Citation: Qiu, J.; Han, A.; He, C.; Dai, X.; Jia, S.; Luo, Y.; Hao, Z.; Yin, Q. Functional Traits of *Quercus aliena* var. *acuteserrata* in Qinling Huangguan Forest Dynamics Plot: The Relative Importance of Plant Size and Habitat. *Forests* **2022**, *13*, 899. <https://doi.org/10.3390/f13060899>

Academic Editor: Eustaquio Gil-Pelegrín

Received: 5 May 2022

Accepted: 8 June 2022

Published: 9 June 2022

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1. Introduction

Plant functional traits are defined as morpho-physio-phenological traits of plants which impact fitness (growth, reproduction and survival), and thus provide a mechanistic understanding of how traits influence plant performance [1,2]. They are important indicators of plants' ecological functions, and facilitate the understanding of plant adaptation mechanisms in changing environments [3,4]. LDMC and specific leaf area (SLA) are key traits to shaping plants' functional strategies [5]. High LDMC often endows plants with the ability of structure construction and allows them survive in adverse environments, such as low temperature [6]. SLA is related to light utilization and the resource allocation strategies of plants [7,8]. Leaf nutrient concentration also participates in plant tissue construction and photosynthesis [9]. Changes in plant morphological and physiological traits may greatly reduce the adverse effects of environments and reveal adaptive mechanisms under a given constraint [10,11].

Recent studies have suggested that abiotic factors have a significant effect on functional traits, particularly topography and soil conditions, which play an important role in shaping plants' functional strategies [8,12]. Altitude and slope are the two most important

topographic factors and influence the functional traits of plants through the redistribution of light, soil moisture, and nutrients [13]. Plants in high altitude and slope tend to have higher SLA and leaf area (LA), and lower leaf phosphorus concentration and leaf nitrogen concentration [14,15]. Soil nutrient content also influences the physiological process of plants [16,17]. Soil phosphorus stress could affect N uptake and distribution in leaves, limiting the photosynthesis of plants [18]. Generally, plants with long-lived leaves, thick leaves, low leaf nitrogen concentration, and high LDMC tend to grow in resource-limited environments, while high LA, SLA and LTN allow plants to grow in resource-rich environments [19]. Since functional traits can reflect the ecological adaptability of plants, studies on relationships between functional traits and environmental conditions help us to better understand the adaptive mechanism of plants in forests [20].

Although the filtering effect of the environment is important, effects of plant size on plant resource utilization strategies and adaptive mechanisms cannot be ignored. With increasing plant size, the variation in physiological processes has important consequences for metabolism, architecture and functionality, which can affect the response of plants to the environment [21]. Recent studies have revealed that life stage is an important determinant of most leaf traits [22]. Generally, small trees with low LDMC, high SLA, LA, leaf nitrogen concentration and leaf phosphorus concentration tend to obtain resources to meet quick growth. Inversely, adults tend to utilize more resources to complete high construction costs [23,24]. This shift in resource strategy may occur at the reproductive onset [25]. Leaf thickness (LT) and leaf tissue density (TD) are related to the protecting mechanism. As they grow, plants tend to have thicker leaves and lower TD, which slows the diffusion rates of water vapor and CO₂ through the leaves [26]. In addition, wood density (WD) is a key functional trait strongly related to plant size, regulating plants' mechanical stability and hydraulic conductance [27–29]. However, it is unclear how plant size and environment jointly shape intraspecific leaf trait shifts. Additionally, we need more studies to test the relative importance of plant size and environment on plant traits.

The Qinling Mountains form an important geographical boundary between North and South China, and are an important natural geographic barrier in East Asia. Their complex topography and heterogeneous micro-environments create distinctive biodiversity [30]. *Q. aliena* var. *acutiserrata* is one of the most important dominant and widespread species in the Qinling Mountains, and plays an irreplaceable role in maintaining the biodiversity and stability of ecosystem [31,32]. Thus, it provides an excellent model for us to test the effects of environmental factors and plant size on plant functional traits.

Here, we tested the relative importance of plant size and habitats on the functional traits of *Q. aliena* var. *acutiserrata* in a 25 ha warm, temperate, deciduous broadleaved forest plot in the Qinling Mountains. We measured nine traits belonging to small, medium and large trees from six different habitats. Specially, we selected three chemical traits including leaf carbon concentration, leaf nitrogen concentration, and leaf phosphorus concentration, and six morphological traits including SLA, LDMC, LA, LT, TD, and WD. We addressed the following two questions: (1) What are the differences in functional traits among different plant sizes and habitats? (2) What is the relative contribution of plant size and environment (topography and soil condition) to trait variation? Based on the wide distribution of *Q. aliena* var. *acutiserrata* in the plot, we hypothesized that environment would not conclusively influence growth and distribution. In contrast, we hypothesized that the effects of plant size would drive trait divergence, particularly for leaf morphological traits.

2. Materials and Methods

2.1. Study Site and Soil Sampling

The study was conducted in Changqing National Nature Reserve (33°32'21" N, 108°22'26" E) in the middle of the Qinling Mountains, China. In this area, the climate is transitional between northern subtropical and warm temperate, with a mean annual temperature of 12.3 °C. The mean annual precipitation is 908.0 mm, which is concentrated from July to September. The soil is brown soil with a pH of 5.96. The reserve area is

characterized by more stone than soil with an elevation ranging from 880 m to 2430 m. The large elevation difference and characteristics of climate transition have led to the obvious vertical distribution of vegetation along the elevation gradient.

A permanent forest dynamic plot with an area of 25 ha (500 m × 500 m) was established in the deciduous broadleaved forest in Changqing National Nature Reserve in 2019. The elevation of the plot ranged from 1280.3 m to 1581.8 m. The plot was divided into 625 sub-plots of 20 m × 20 m, and each sub-plot was subdivided into 16 quadrats of 5 m × 5 m. Within each quadrat, all trees with a diameter at breast height (DBH) ≥ 1 cm were mapped, identified, measured, and tagged.

Habitat classification was performed by multiple regression trees (MRT) based on three main topographic variables (elevation, slope, and convexity) [33,34]. The 625 plots were assigned to six habitat types: low flat, low ridge, low slope, high gully, high ridge, and high slope. The attributes of each habitat type are summarized in Table 1.

Table 1. Six habitats classified in this study.

Habitat Types	Mean Elevation ± SE	Mean Slope ± SE	Mean Convexity ± SE
Low flat	1322.3 ± 3.44	10.9 ± 0.73	−2.1 ± 0.63
Low ridge	1360.8 ± 2.41	24.8 ± 0.54	1.0 ± 0.28
Low slope	1374.9 ± 4.12	27.1 ± 0.45	−1 ± 0.17
High gully	1442.1 ± 3.63	36.2 ± 0.4	−0.9 ± 0.19
High ridge	1503.8 ± 4.38	31.7 ± 4.38	1.1 ± 0.24
High slope	1526.1 ± 2.87	26 ± 0.56	2.4 ± 0.37

Soil samples were collected in the grid of 30 m × 30 m, and a total of 957 points were sampled. The depth of the soil sample collection was 10 cm. Soil samples were air-dried and passed through a 2 mm mesh to remove gravel and coarse plant debris. Soil samples were then ground. Total N and total P were tested. Total N was measured using a kjeldahl nitrogen determination apparatus. Total P was determined by the H₂SO₄-HClO₄ digestion method.

2.2. Plant Sampling and Measurements of Plant Functional Traits

We collected leaf samples from 90 individuals of *Q. aliena* var. *acutiserrata* from six habitats. Considering the life history characteristics of *Q. aliena* var. *acutiserrata* and the overall quantity distribution of DBH in the plot, we divided the individuals into small trees (1 cm < DBH ≤ 5 cm), medium trees (5 cm < DBH ≤ 20 cm), and large trees (DBH > 20 cm) [35]. For each growth stage, 3–5 individuals were sampled in each habitat. Then, leaves and branches were collected with a long-reach pruner from the upper sunny part of the canopy of each individual [36]. For each individual, 30–50 leaves and three branches were preserved in plastic bags for the analyses of morphological and chemical traits (Table 2).

Table 2. Plant functional traits measured in this study.

Trait	Abbreviation	Unit	Organ	Type
Specific leaf area	SLA	cm ² g ^{−1}	Leaf	Morphological
Leaf dry matter content	LDMC	g/g	Leaf	Morphological
Leaf area	LA	cm ²	Leaf	Morphological
Leaf thickness	LT	mm	Leaf	Morphological
Leaf tissue density	TD	g cm ^{−3}	Leaf	Morphological
Leaf carbon concentration per unit leaf mass	LCC	mg g ^{−1}	Leaf	Chemical
Leaf nitrogen concentration per unit leaf mass	LNC	mg g ^{−1}	Leaf	Chemical
Leaf phosphorus concentration per unit leaf mass	LPC	mg g ^{−1}	Leaf	Chemical
Wood density	WD	g cm ^{−3}	branch	Morphological

Leaf area (LA, cm²) was measured by a picture of each fresh leaf surface with a digital camera and Motic Images Plus 2.0 (Motic China, Xiamen, China) software. The leaves were placed in a drying oven for 72 h at 60 °C to determine the dry mass. Specific leaf area (SLA, cm² g^{−1}) was calculated as the ratio of LA to the dry mass. Leaf fresh mass and leaf thickness (LT, mm) were measured immediately on harvest day. LT was measured three times on different parts of the leaf with a slide gauge, avoiding the influence of the veins. Leaf dry mass content (LDMC, g/g) was calculated as the ratio of leaf dry mass to leaf fresh mass. Leaf tissue density (TD, g cm^{−3}) was calculated as the ratio of reciprocal SLA to LT. The wood density of the branches (WD, g cm^{−3}) was calculated as the ratio of dry weight to the volume of the branches. Leaves were ground into a fine power, and leaf carbon concentration (mg g^{−1}), leaf phosphorus concentration (mg g^{−1}), and leaf nitrogen concentration (mg g^{−1}) were determined with an elemental analyzer (Euro Vector EA3000, Milan, Italy).

2.3. Statistical Analysis

Differences in leaf traits among different habitats and plant sizes were tested with one-way analysis of variance (ANOVA), and the Tukey HSD test was used for post hoc analysis. We used Pearson's correlation to analyze the relationships between pairwise traits and carried out the significance tests with the 'psych' package [37]. The relationships between traits and soil factors were tested with linear regression analyses. The multiple regressions were used to evaluate the explanatory power of plant sizes and environmental factors on functional traits. R² was used to estimate the explanatory power of the regression models. The best models were selected by Akaike information (AIC) from different combinations of plant sizes and different environmental factors. The model with the lowest AIC was selected as the best one. All analyses were based on data satisfying normality assumptions. All statistical analyses were conducted in R software v.3.6.1 [37].

3. Results

As for the differences in plant functional traits between the three plant sizes, LDMC and LT significantly increased with the growth of *Q. aliena* var. *acutiserrata* (Figure 1b–d). LA, SLA and TD had no significant differences among the different plant sizes (Figure 1a,c,e). WD was significantly different among plant sizes. With increasing DBH, there was a lower WD in old trees (Figure 1i). In addition, there were also significant differences in chemical traits among different plant sizes (Figure 1f–h). Small trees had greater leaf nitrogen concentrations, greater leaf phosphorus concentrations, and smaller leaf carbon concentrations than large trees. As for the differences in the plant functional traits among the six habitats, no significant differences were found except for leaf carbon concentration.

As for habitats, we found soil N and P influenced plant functional traits significantly. LT and leaf carbon concentrations increased, and leaf nitrogen concentration and leaf phosphorus concentration decreased with increasing soil N (Figure 2d,f–h). While leaf nitrogen concentration and leaf phosphorus concentration were positively correlated with soil P (Figure 3g,h), WD was positively correlated with soil P (Figure 3i). With respect to the topographical factors' effects on plant functional traits, we found that *Q. aliena* var. *acutiserrata* individuals had lower leaf carbon concentrations in the habitat with a steeper slope and higher altitude (Table 3). Through the selection of the best model and variance decomposition, we found that plant size could better explain the changes in morphological traits than environmental factors (Table 4), while soil P could better explain the variance in leaf nutrition content (Table 4). Overall, no explanation was found for SLA changes (Table 4).

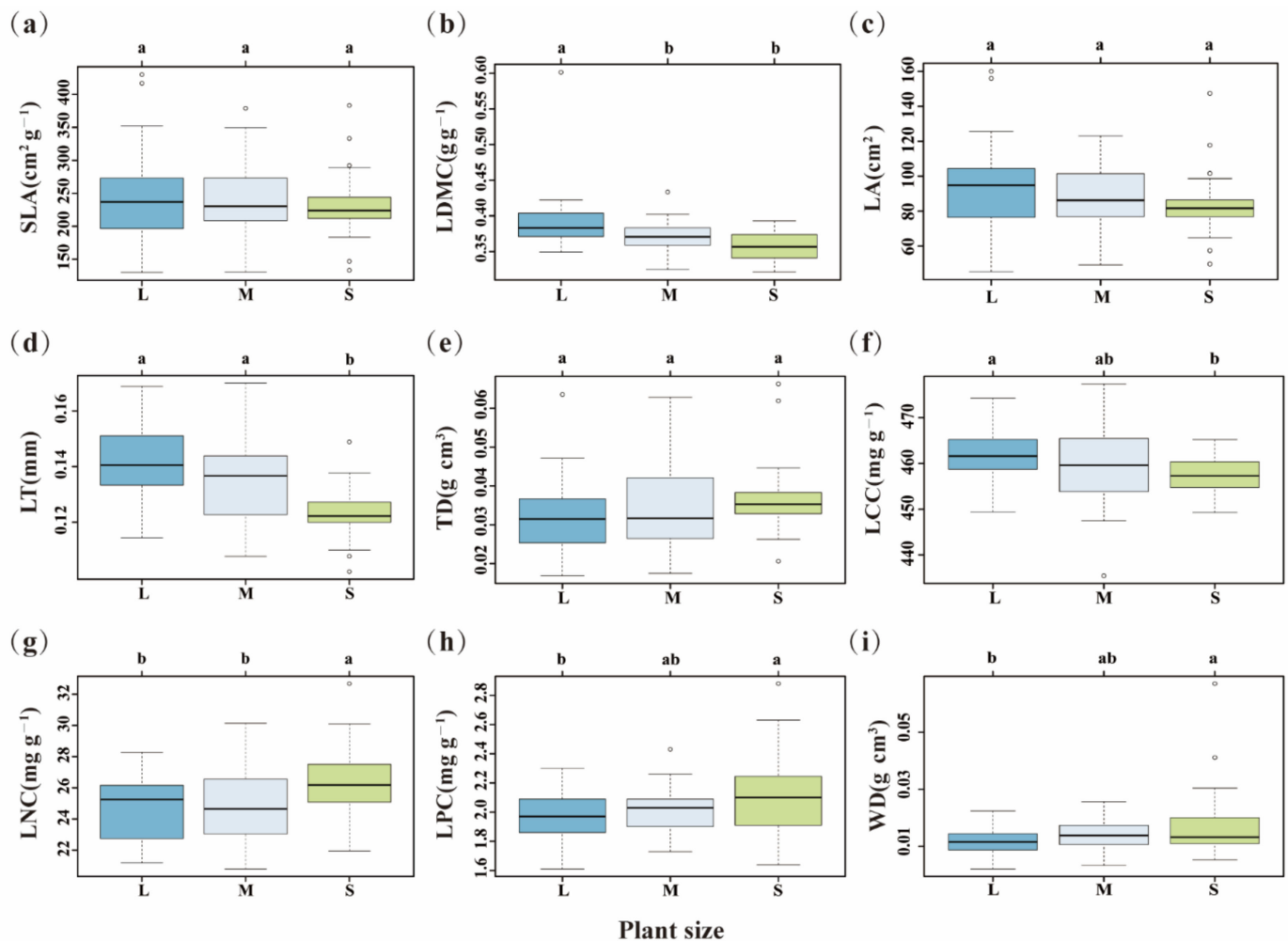


Figure 1. Differences in the functional traits (a–i) of *Q. aliena* var. *acutiserrata* among three plant sizes. Abbreviations of plant size: L (large tree); M (medium tree); S (small tree). Trait abbreviations: SLA (specific leaf area); LDMC (leaf dry matter content); LA (leaf area); LT (leaf thickness); TD (leaf tissue density); LCC (leaf carbon concentration per unit leaf mass); LNC (leaf nitrogen concentration per unit leaf mass); LPC (leaf phosphorus concentration per unit leaf mass); and WD (wood density).

Table 3. Differences in the functional traits of *Quercus aliena* var. *acutiserrata* among six habitats.

Trait	Habitats						
	<i>p</i> Value	Low Flat	Low Ridge	Low Slope	High Gully	High Ridge	High Slope
LA	0.957	89.135 ± 25.56 a	85.165 ± 21.97 a	86.748 ± 13.28 a	86.259 ± 27.79 a	90.736 ± 17.98 a	91.25 ± 19.05 a
SLA	0.915	240.269 ± 68.46 a	238.165 ± 66.02 a	226.748 ± 37.33 a	228.52 ± 74.91 a	248.052 ± 54.19 a	244.032 ± 54.63 a
LDMC	0.369	0.371 ± 0.02 a	0.359 ± 0.02 a	0.383 ± 0.02 a	0.380 ± 0.03 a	0.368 ± 0.02 a	0.379 ± 0.07 a
LT	0.272	0.138 ± 0.01 a	0.132 ± 0.02 a	0.138 ± 0.01 a	0.128 ± 0.01 a	0.129 ± 0.01 a	0.135 ± 0.01 a
TD	0.867	0.330 ± 0.01 a	0.352 ± 0.01 a	0.334 ± 0.01 a	0.369 ± 0.01 a	0.333 ± 0.01 a	0.329 ± 0.01 a
WD	0.864	0.013 ± 0.01 a	0.016 ± 0.02 a	0.012 ± 0 a	0.015 ± 0 a	0.014 ± 0 a	0.014 ± 0 a
LCC	<0.05	463.529 ± 5.44 a	460.063 ± 4.48 ab	460.773 ± 9.63 ab	456.01 ± 5 b	458.332 ± 6.84 ab	459.659 ± 5.24 ab
LNC	0.267	24.987 ± 1.74 a	25.859 ± 1.41 a	24.412 ± 1.99 a	25.940 ± 3.11 a	25.788 ± 2.77 a	24.590 ± 2.41 a
LPC	0.0684	2.025 ± 0.15 a	2.104 ± 0.26 a	1.909 ± 0.12 a	2.044 ± 0.26 a	2.113 ± 0.2 a	1.975 ± 0.18 a

p values indicate the significance, and different letters represent significant difference in different habitats. Trait abbreviations: SLA (specific leaf area); LDMC (leaf dry matter content); LA (leaf area); LT (leaf thickness); TD (leaf tissue density); LCC (leaf carbon concentration per unit leaf mass); LNC (leaf nitrogen concentration per unit leaf mass); LPC (leaf phosphorus concentration per unit leaf mass); and WD (wood density).

Table 4. Summary of the multiple regression models for the impact of plant size and environmental factors on functional traits.

Hypotheses	Predictors (Standardized Coefficient)	Adjusted R ²	p-Value	AIC
SLA				
Plant size	Size	−0.04101	0.9213	762
Topographical factors	Altitude, Slope,			
Soil factors	Soil N, Soil P			
LDMC				
Plant size	Size (+0.387)	0.157	<0.001	−624.89
Topographical factors	Slope (0.144)	0.031	0.141	−637.86
LA				
Plant size	Size (+0.212)	0.034	<0.05	562.46
LT				
Plant size	Size (+0.27)	0.224	<0.01	−787.08
Soil factors	Soil N(+0.45)	0.098	<0.001	−801.32
TD				
Plant size	Size (−0.193)	0.0264	0.0657	−841.62
LCC				
Plant size	Size (+0.325)	0.095	<0.01	338.98
Topographical factors	Altitude (−0.219), Slope (−0.23)	0.136	<0.05	332.58
Leaf nitrogen concentration				
Plant size	Size (−0.178)	0.046	0.084	149.23
Soil factors	Soil P (+0.283)	0.091	<0.01	153.76
LPC				
Plant size	Size (−0.172)	0.047	0.094	−295.37
Topographical factors	Slope (−0.199)	0.051	<0.05	−294.15
Soil factors	Soil P (+0.239)	0.073	<0.05	−292.63
WD				
Plant size	Size (−0.247)	0.072	<0.05	−263.25
Soil factors	Soil P (−0.174)	0.086	<0.01	−261.76

The model with lowest AIC (Akaike information criterion corrected for spatial autocorrelation) was selected as the best one. The variable selection was performed within each trait separately. The directions of the relationships are shown in brackets for the significant terms. + represents positive correlation; − represents negative correlation. Trait abbreviations: SLA (specific leaf area); LDMC (leaf dry matter content); LA (leaf area); LT (leaf thickness); TD (leaf tissue density); LCC (leaf carbon concentration per unit leaf mass); LNC (leaf nitrogen concentration per unit leaf mass); LPC (leaf phosphorus concentration per unit leaf mass); and WD (wood density).

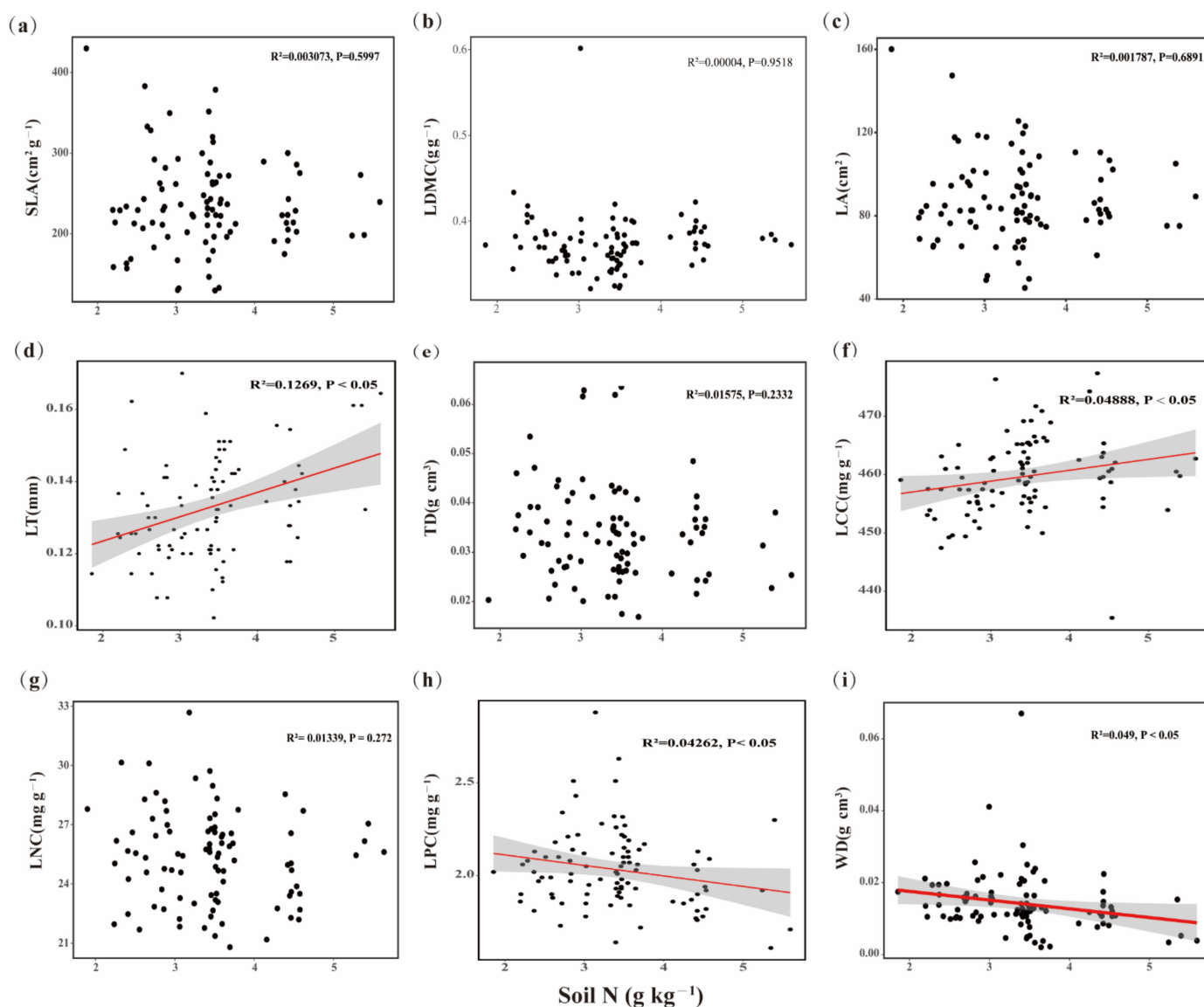


Figure 2. The effects of soil N on functional traits (a–i). The shaded regions indicate 95% confidence intervals of the predicted values. Trait abbreviations: SLA (specific leaf area); LDMC (leaf dry matter content); LA (leaf area); LT (leaf thickness); TD (leaf tissue density); LCC (leaf carbon concentration per unit leaf mass); LNC (leaf nitrogen concentration per unit leaf mass); LPC (leaf phosphorus concentration per unit leaf mass); and WD (wood density).

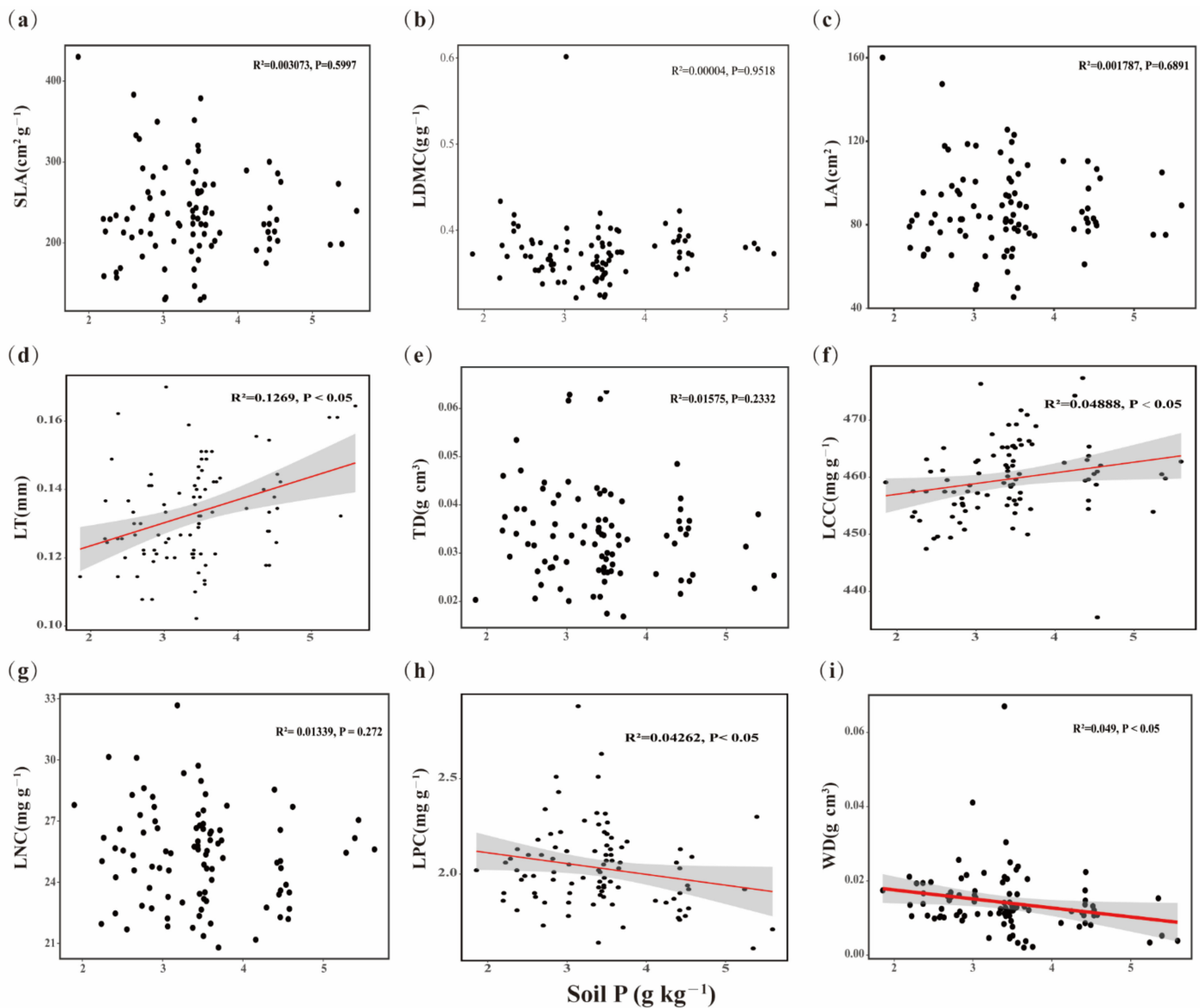


Figure 3. The effects of soil P on functional traits (a–i). The shaded regions indicate 95% confidence intervals of the predicted values. Trait abbreviations: SLA (specific leaf area); LDMC (leaf dry matter content); LA (leaf area); LT (leaf thickness); TD (leaf tissue density); LCC (leaf carbon concentration per unit leaf mass); LNC (leaf nitrogen concentration per unit leaf mass); LPC (leaf phosphorus concentration per unit leaf mass); and WD (wood density).

According to the analysis of correlations between traits, we found LT and SLA were positively related to LDMC, LA and TD. LDMC had a significantly negative correlation with SLA. For the morphological and chemical traits, LDMC was negatively related to both leaf nitrogen concentration and leaf phosphorus concentration. LA was negatively related to leaf carbon concentration and leaf nitrogen concentration. LT was related to all chemical traits. In addition, leaf nitrogen concentration was strongly related to leaf phosphorus concentration (Table 5).

Table 5. Correlation coefficients among leaf functional traits of *Quercus aliena* var. *acutiserrata*.

	LT	LDMC	LA	SLA	TD	WD	LNC	LCC
LDMC	0.23 *							
LA	0.23 *	0.03						
SLA	0.14	−0.28 **	0.95 ***					
TD	−0.52 ***	0.17	−0.84 ***	−0.85 ***				
WD	−0.15	−0.09	−0.03 *	0.007 **	0.07			
LNC	−0.27 **	−0.38 ***	−0.03 *	0.09	−0.003 **	0.12		
LCC	0.26 *	0.09	−0.02 *	−0.054	−0.054	−0.11	0.06	
LPC	−0.22 *	−0.42 ***	−0.07	0.08	−0.05 *	0.09	0.46 ***	−0.1

Significant correlations (in bold) are denoted by asterisks: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Trait abbreviations: SLA (specific leaf area); LDMC (leaf dry matter content); LA (leaf area); LT (leaf thickness); TD (leaf tissue density); LCC (leaf carbon concentration per unit leaf mass); LNC (leaf nitrogen concentration per unit leaf mass); LPC (leaf phosphorus concentration per unit leaf mass); and WD (wood density).

4. Discussion

4.1. Differences in Functional Traits among Plant Sizes

Due to the considerable longevity and complex structure within the tree species, the functional traits of different individual sizes presented significant differences [38]. In this study, differences in SLA, LA and TD were not found among different plant sizes. LA reflected the leaf size and shifts, representing the adaptive strategies of plants to the surrounding environment. Chang et al. found a positive relationship between LA and plant size, improving photosynthetic capacity and promoting the growth of large trees [26]. In the study of Zheng et al., a contrary trend was found [39]. According to most studies, there are no consistent conclusions about size-dependent changes in LA [40]. In our study, there were no significant changes in the LA of different sized plants, which might be ascribed to an adaptation of *Q. aliena* var. *acutiserrata* to changing light environments. This is conducive to strengthening the competitive ability of small trees to find light. In addition, TD is negatively related to LA according to some studies [41]. When larger parts of the leaf materials were used to construct a protective structure or increase TD, there were no additional resources to increase LA. We found SLA was positively related to LA and negatively related to TD. Therefore, the lack of a significant difference in SLA among different plant sizes might be a comprehensive reflection of LA and TD.

Our results indicated that large trees had higher LDMC and thicker leaves than small trees. LDMC was an effective indicator for plants to adapt to resource-limited environment, indicating the ability of plants to obtain resources, balance growth, and resist environment stress [41]. Higher LDMC and thicker leaves increased leaf biomass and kept water in plant leaves, but also enhanced the ability of plants to resist strong light [42]. This is in line with the conservative resource utilization strategy to meet the higher demand of construction costs in large trees [43]. The observed positive relationship of LDMC and LT to plant size might be linked to the relationship between leaf nutrient content and resource utilization strategy. Our results showed that small trees had lower leaf carbon concentrations and higher leaf nitrogen concentrations and leaf phosphorus concentrations, while large trees had lower leaf nitrogen and leaf phosphorus concentrations and higher leaf carbon concentrations, which was consistent with the results of Gao et al. [9]. Leaf carbon concentration forms the basis of plant structure and is an important energy source for biochemical reactions [44]. As the growth of plants, individuals optimize their survival and growth by different investments of nutrients in different organs [45]. Small trees devote more nutrients to growth, but ignore leaf development, leading to lower LDMC and LT. Meanwhile, more leaf nitrogen concentrations and leaf phosphorus concentrations also meet higher photosynthetic demand and improve the rate of photosynthetic carbon assimilation in small trees [46]. Medium and large trees have a greater ability to compete for resources such as light and nutrients, and this strategy could be advantageous for meeting the needs of all plant parts [47].

4.2. Effects of Environmental Factors on Leaf Functional Traits

In this study, no significant differences of traits were found among different habitats—except leaf carbon concentrations (Table 4)—which is consistent with the results of Raquel et al. [48]. We suggest that the shortage of trait differences among habitats may be common to dominant species. They all had common tolerance mechanisms to changing environments, and this might be why they are widely distributed [49]. Otherwise, the small sampling range could also have affected our judgment of plant adaptation mechanisms. For example, functional traits such as LA and LMA (inverted SLA) did not change significantly at lower altitudes. At the altitude of 3100 m, the relationship between plant traits and altitude show a turning point, according to the study of Zhao et al. [50]. This fact encourages us to appropriately increase the research range in our functional trait studies. In this study, the change in leaf carbon concentration was better explained by topographical factors. Leaf carbon concentration was higher in low-altitude areas due to good hydraulic conditions and soil nutrient enrichment. Meanwhile, low temperature and strong radiation in high-altitude areas might restrict carbon investment and break the carbon balance of *Q. aliena* var. *acutiserrata*, resulting in lower leaf carbon concentrations. Otherwise, steeper terrain of the high gully reduced the availability of water and nutrients, which led to the lowest leaf carbon concentrations among the six habitats [51].

Following the effects of habitat on functional traits, we further analyzed the effects of soil N and P on functional traits in order to better understand the adaptability of *Q. aliena* var. *acutiserrata*. Our study showed that the variance in leaf nitrogen concentration and leaf phosphorus concentration was mainly explained by soil P, and increased with soil P. In this study, the average soil P content was 0.26 g/kg, which was lower than national average soil P level (0.65 g/kg) [52]. P limitation was common in the forests of this study, which limited the development of plants [53,54]. In addition, nitrogen (N) deposition has occurred in recent years and caused the N saturation of forests, which also increases leaf N:P ratio and P limitations [55]. When soil N is increased, the soil acidification seriously affects the absorption of various nutrient elements in soil by plants, according to the study of B. et al., inducing low leaf nitrogen concentrations and leaf phosphorus concentrations [56]. It also breaks the balance of soil nutrient uptake in plants. However, we suggest that constant leaf morphological traits in response to different soil N and P contents might be an important adaptive mechanism to low soil P availability [57]. In the study of Chai et al., *Q. aliena* var. *acutiserrata* could not adapt to adverse living conditions (e.g., higher altitude), which was consistent with our results [26]. *Q. aliena* var. *acutiserrata* might occupy a niche in which other tree species cannot invade without the aid of physiological adjustment [58]. Whether this is due to competitive ability or physiological tolerance, the adaptive mechanisms of *Q. aliena* var. *acutiserrata* are worth further exploration.

5. Conclusions

In this research, we aimed to identify variations in traits under different plant sizes and habitats to reveal the adaptation mechanisms of *Q. aliena* var. *acutiserrata*. We found that plant size explained more variances in functional traits than environmental factors, especially morphological traits. Soil N and P content constrained changes in leaf nitrogen concentration, leaf phosphorus concentration, and WD. However, we did not detect correlations between topographical factors and most traits, except leaf carbon concentration. This suggests that some individuals of *Q. aliena* var. *acutiserrata* have not completely adapted to severe environments at a very small spatial scale. In conclusion, shifts in traits met the growth requirements of individuals of different plant sizes, such as the construction costs of large trees and the growth costs of small trees. Traits associated with the high tolerance of *Q. aliena* var. *acutiserrata* might comprise important mechanisms for coping with changing environments, which is worth further exploration.

Author Contributions: Conceptualization, J.Q. and Q.Y.; methodology, J.Q. and A.H.; software, J.Q. and Q.Y.; validation, J.Q., C.H. and X.D.; formal analysis, J.Q.; investigation, J.Q. and A.H.; resources, J.Q.; writing—original draft preparation, J.Q.; writing—review and editing, J.Q., C.H. and X.D.; visualization, J.Q.; supervision, S.J. and Y.L.; project administration, Q.Y.; funding acquisition, Q.Y. and Z.H. All authors have read and agreed to the published version of the manuscript.

Funding: This study was financially supported by the National Natural Science Foundation of China (32001171, 32001120) and the Fundamental Research Funds for the Central Universities.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: The data in this study can be obtained by contacting the author by email.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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