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Effect of Wind on the Relation of Leaf N, P Stoichiometry with Leaf Morphology in *Quercus* Species

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Abstract: Leaf nitrogen (N) and phosphorus (P) stoichiometry correlates closely to leaf morphology, which is strongly impacted by wind at multiple scales. However, it is not clear how leaf N, P stoichiometry and its relationship to leaf morphology changes with wind load. We determined the leaf N and P concentrations and leaf morphology—including specific leaf area (SLA) and leaf dissection index (LDI)—for eight *Quercus* species under a simulated wind load for seven months. Leaf N and P concentrations increased significantly under these conditions for *Quercus acutissima*, *Quercus rubra*, *Quercus texana*, and *Quercus palustris*—which have elliptic leaves—due to their higher N, P requirements and a resultant leaf biomass decrease, which is a tolerance strategy for *Quercus* species under a wind load. Leaf N:P was relatively stable under wind for all species, which supports stoichiometric homeostasis. Leaf N concentrations showed a positive correlation to SLA, leaf N and P concentrations showed positive correlations to LDI under each wind treatment, and the slope of correlations was not affected by wind, which indicates synchronous variations between leaf stoichiometry and leaf morphology under wind. However, the intercept of correlations was affected by wind, and leaf N and P use efficiency decreased under the wind load, which suggests that the *Quercus* species changes from “fast investment-return” in the control to “slow investment-return” under windy conditions. These results will be valuable to understanding functional strategies for plants under varying wind loads, especially synchronous variations in leaf traits along a wind gradient.

Keywords: leaf N; P stoichiometry; leaf morphology; synchronous variations; wind load; *Quercus* species

1. Introduction

The leaf economics spectrum (LES) is a general concept describing coordinated variations in leaf traits across environmental gradients [1], which can reflect the adaptation strategy of plants under diverse environmental stresses [2]. It is known that LES refers to leaf life and physiology, and includes two strategies of resource utilization. At the quick-return end, leaves have a high photosynthetic rate, high respiration rate, high nutrient content, short leaf lifespan, and low-cost dry-mass investment; at the slow-return end, leaves present the reverse trend, exhibiting a long leaf lifespan [3,4]. Leaf nitrogen (N), phosphorus (P) stoichiometry is correlated to leaf morphology [1,2,5,6]. For example, leaf N and P concentrations will vary based on the specific leaf area (SLA) [7–9], and leaf stoichiometry shows covariations with leaf morphology [6]. Moreover, leaf N, P stoichiometry is closely related to

environment. For example, leaf N, P concentrations differ along latitudinal gradients [10]. Less is known, however, about the responses to wind environmental gradients of leaf N, P stoichiometry and its relationship to morphology.

Previous studies have mostly focused on investigating leaf morphology, structure, and physiology in a windy environment, exhibiting synchronous variations [11–13]. To adapt to wind, leaf area and SLA decreased [13–15], leaf thickness increased [16], and photosynthetic rate decreased due to the long CO₂ diffusion path for thick leaves [17]. Therefore, N and P need to be more preferentially allocated to non-photosynthetic functions, such as increasing cell wall thickness to strengthen the leaf's mechanical toughness [18–20]. In a limited number of previous studies, only the leaf N concentration was found to be higher under wind when compared to wind-protected leaves [13,21,22]; leaf P concentrations and N:P were not studied under wind. Leaf P concentrations should exhibit similar trends to N concentrations [10,23,24], and leaf N:P should remain stable along environmental gradients [7,25], due to similar biochemical pathways for N and P [7]. Therefore, two hypotheses are proposed based on the previous studies: 1) leaf N, P concentrations will increase, and leaf N:P will remain stable under a wind load; 2) leaf N, P stoichiometry and leaf morphology will display synchronous variation under a wind load.

Eight *Quercus* species with diverse leaf shapes—including elliptic and lanceolate leaves—were selected to be tested for their responses to a wind load. Leaf morphological (width, length, SLA, and leaf dissection index (LDI)) and photosynthetic physiological (photosynthesis, transpiration, and stomatal conductance) responses were found in our previous studies, the results of which demonstrated that species with lanceolate leaves or deeply lobed elliptic leaves (higher LDI) exhibited better adaptation to windy conditions [13,17,26]. In this study, leaf N, P concentrations, N:P, and their relations with leaf morphology (SLA, LDI) were determined to test the two hypotheses, which may be valuable to understanding the adaptation strategy for plants in windy environments.

2. Materials and Methods

2.1. Materials and Growing Conditions

Eight *Quercus* species were collected from the nursery at Research Institute of Subtropical Forestry in Hangzhou: *Quercus acutissima* Carruth., with elliptic leaves; *Quercus rubra* L. and *Quercus falcata* Michx., with shallowly lobed elliptic leaves; *Quercus texana* Buckl, *Quercus palustris* Muenchh., and *Quercus coccinea* Muenchh., with deeply lobed elliptic leaves; and *Quercus virginiana* Mill. and *Quercus phellos* L., with lanceolate leaves. Seedlings, 100 individuals for each species, were transplanted to 25 cm deep pots with a 20 cm diameter in January 2013. All transplanted seedlings were acclimated for one month in a greenhouse. Fifty-four average-sized seedlings, of average base diameter and height, per species were then selected for the study.

2.2. Experimental Design

Nine rooms were constructed from glass with a size of 2 m × 2 m × 2 m and were housed within a greenhouse with air temperature between 20 and 35 °C for the entirety of the experiment. Three treatments were designed: control (CK); about 4 m s⁻¹ wind speed (T1); and about 6 m s⁻¹ wind speed (T2). Here, 6 m s⁻¹ was used because it is the annual average wind speed in the open area of our coastal station in Shanghai, and 4 m s⁻¹ is the annual average wind speed on the leeward side of forest windbreaks [27]. Each treatment had three replicates that were randomly assigned to each of the nine rooms. In each room, eight *Quercus* species, with six seedlings of each species, were randomly placed in each row. The wind load was produced by electric-powered fans for two one-hour durations at 0:00 and 12:00 from 1 March to 7 October, following the procedure developed by Murren and Pigliucci [15]. Each day, each species was moved one row from left to right, and individual trees were moved within the row, to ensure that each species and individual were subjected to similar

wind exposure in each treatment room. All trees were watered equally every day with tap water to compensate for evaporative loss. All treatments were identical except for wind load.

2.3. Leaf Morphology and Leaf N and P Concentrations Measurements

After the experiment, healthy and mature fresh leaves were sampled for determining leaf morphology. Thirty leaves were selected from six plants of each species from each room, and scanned to produce digitized images. Leaf perimeter and area were analyzed by Wseen Leaf Area Analysis Systems (Wseen Co., Ltd., Hangzhou, China). Leaves were dried to their constant weight, then weighed to the nearest 0.001 g using an electronic balance (JA12002, Jinghai Instruments Co., Ltd., Shanghai, China). SLA was calculated as leaf area/mass. LDI was calculated by perimeter/square root of area [28].

Each dried sample was ground using a mill and sieved through a 1 mm mesh screen. Leaf N concentration was determined for each sample using an autoanalyser (Kjeltec 2300 Analyzer Unit, Foss, Sweden), and leaf P concentration was determined by inductively coupled plasma atomic emission spectrometry (ICP-OES, Thermo scientific optima 7000 series, Agilent Technologies Inc., Santa Clara, CA, USA) at wave length of 177.4 nm [29]. Leaf N and P data are expressed as dry mass for direct comparison with previous studies.

2.4. Statistical Analysis

The data obtained for leaf N and P concentrations and N:P exhibited significant heteroscedasticity and non-normal distributions using One-Sample Kolmogorov-Smirnov test (Appendix A Table A1). Thus, these variables were transformed using the natural logarithm prior to analysis to eliminate major departures from normality or homogeneity of variances [26].

Scatter plots were then used to visualize the relationships among leaf traits. Standardized major axis slope (SMAs) described bivariate line-fitting scaling relationships among leaf traits. One-way ANOVA was used to test the differences in leaf stoichiometry among wind treatments. All statistics were analyzed by SPSS 15.0 (SPSS, Chicago, IL, USA), and the DOS-based computer package (S) MATR (Version 3.3.3, 2017, Vienna University of Economics and Business, Vienna, Austria) and Excel 2007 (Microsoft Corporation, Redmond, WA, USA).

3. Results

3.1. Effects of Wind on Leaf N, P Stoichiometry for *Quercus* Species

Both leaf N and P concentrations increased under wind treatments for *Q. acutissima*, *Q. rubra*, *Q. texana*, and *Q. palustris*, all having elliptic leaves (Figure 1a,b). Only leaf P concentrations increased under wind treatments for *Q. virginiana* with lanceolate leaves. Leaf N:P was not affected by wind for all species ($p > 0.05$) (Figure 1c). Leaf N and P concentrations showed positive correlations under each treatment, and SMAs fitted among treatments did not show significant differences in slope (test for SMA heterogeneity, 95% CIS, $p = 0.26$) and in intercept ($p = 0.79$) (Figure 2).

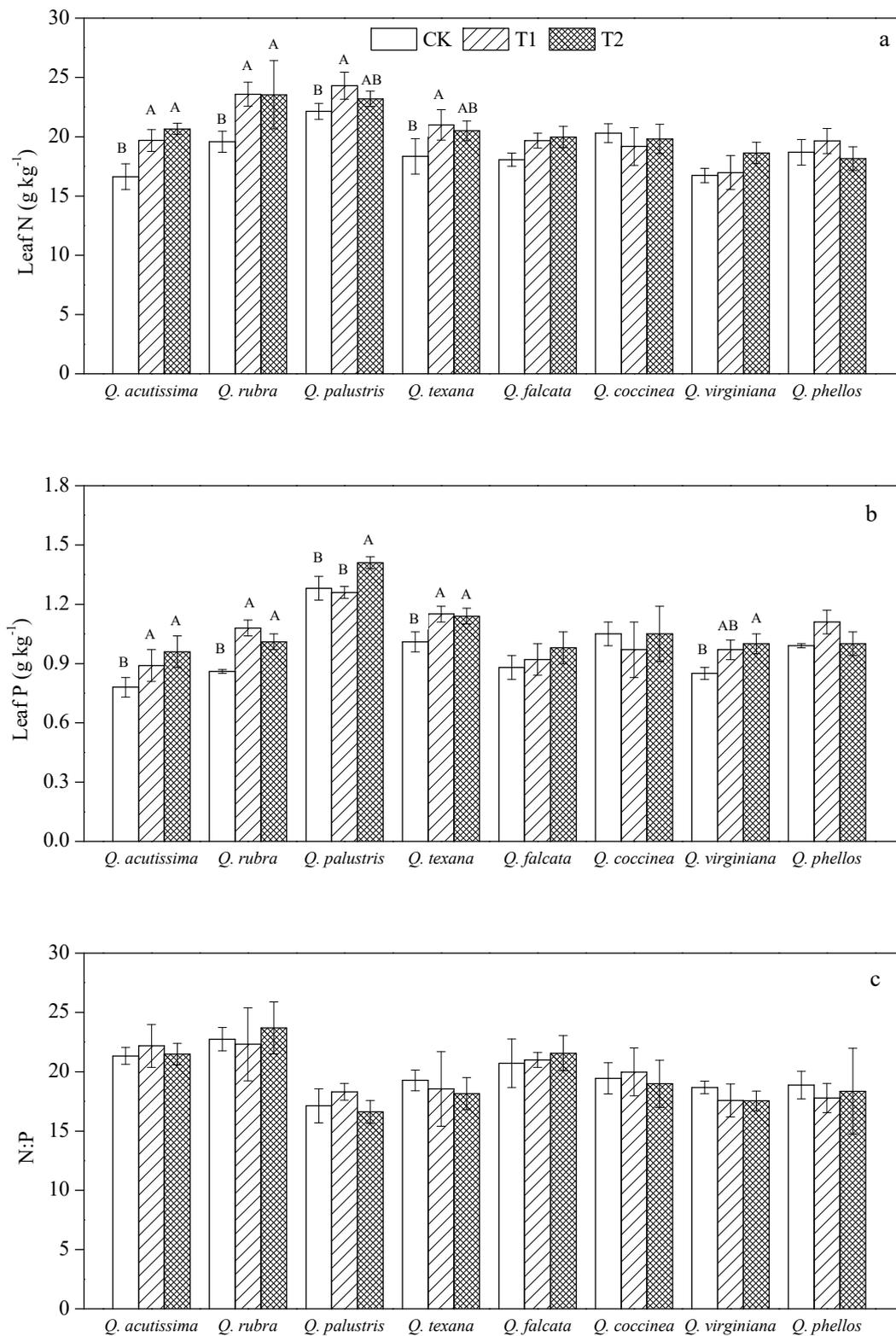


Figure 1. Effects of wind on leaf N, P stoichiometry (means \pm standard deviation) for *Quercus* species. (a) Leaf N concentration; (b) Leaf P concentration; (c) Leaf N:P. For each species, different capital letters on the bars indicate significant differences among treatments ($p < 0.05$). CK: control, T1: about 4 m s⁻¹ wind speed, T2: about 6 m s⁻¹ wind speed.

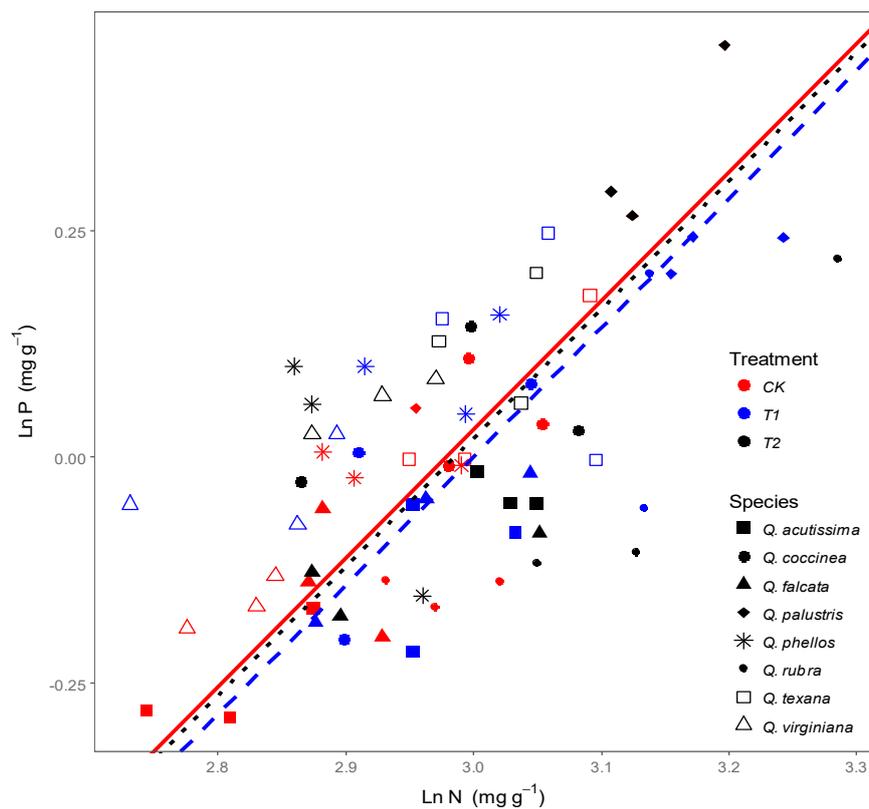


Figure 2. Relationships between leaf N and P concentrations for *Quercus* species under wind load. Ln N and Ln P: leaf N and P concentrations were transformed using the natural logarithm prior to analysis. CK: control, T1: about 4 m s^{-1} wind speed, T2: about 6 m s^{-1} wind speed. CK: $y = 1.02x - 3.04$, $R^2 = 0.56$, $p < 0.01$; T1: $y = 0.67x - 1.98$, $R^2 = 0.35$, $p < 0.01$; T2: $y = 0.81x - 2.37$, $R^2 = 0.217$, $p = 0.01$. SMAs fitted among treatments did not show significant differences in slope (test for SMA (Standardized major axis) heterogeneity, 95% CIS (Confidence intervals), $p = 0.26$) and in intercept ($p = 0.79$).

3.2. Effects of Wind on Relationships between Leaf N, P Stoichiometry and Leaf Morphology

Leaf N concentration and SLA showed positive correlations under each treatment (Figure 3a), and the slope of correlations was not affected by wind ($p = 0.96$); the intercept, however, decreased significantly under wind treatments ($p < 0.01$). Leaf P concentration and SLA showed no correlations under each treatment (Figure 3b). Leaf N, P concentrations and LDI showed positive correlations (Figure 4), and the slope of correlations was not affected by wind (leaf N concentration and LDI: $p = 0.55$, leaf P concentration and LDI: $p = 0.83$, respectively). The intercept, though, decreased significantly under wind treatments ($p < 0.01$, $p = 0.03$, respectively).

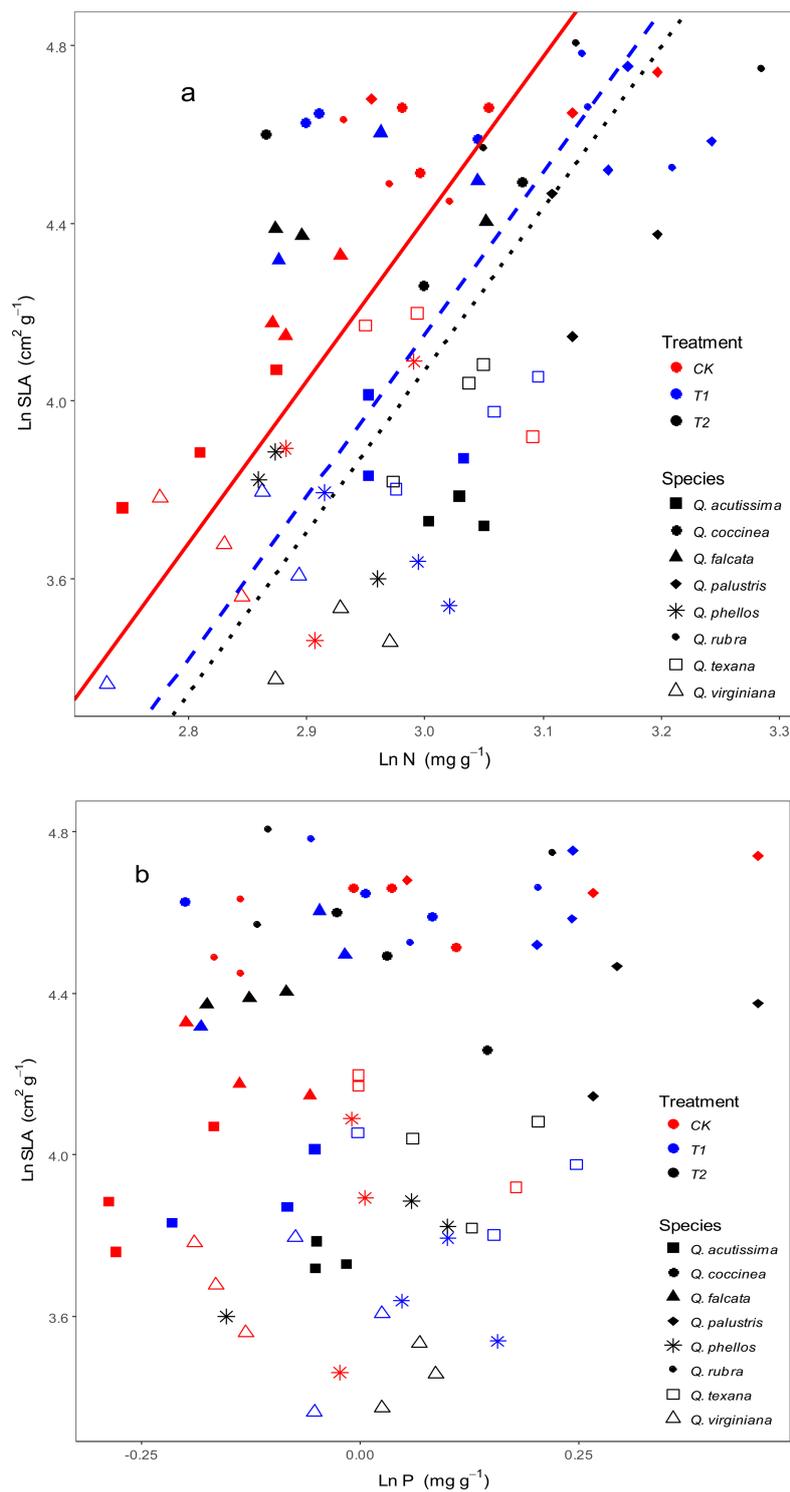


Figure 3. Relationships between leaf N, P concentrations and SLA (Specific leaf area) for *Quercus* species under wind load. Ln N, Ln P and Ln SLA: leaf N, P concentrations and SLA were transformed using the natural logarithm prior to analysis. CK: control, T1: about 4 m s^{-1} wind speed, T2: about 6 m s^{-1} wind speed. (a) Leaf N concentration and SLA. CK: $y = 1.78x - 0.99$, $R^2 = 0.17$, $p = 0.04$; T1: $y = 2.06x - 2.01$, $R^2 = 0.33$, $p < 0.01$; T2: $y = 1.83x - 1.41$, $R^2 = 0.18$, $p = 0.04$. SMAs fitted among treatments did not show significant differences in slope ($p = 0.96$), but apparent in intercept ($p < 0.01$); (b) Leaf P concentration and SLA.

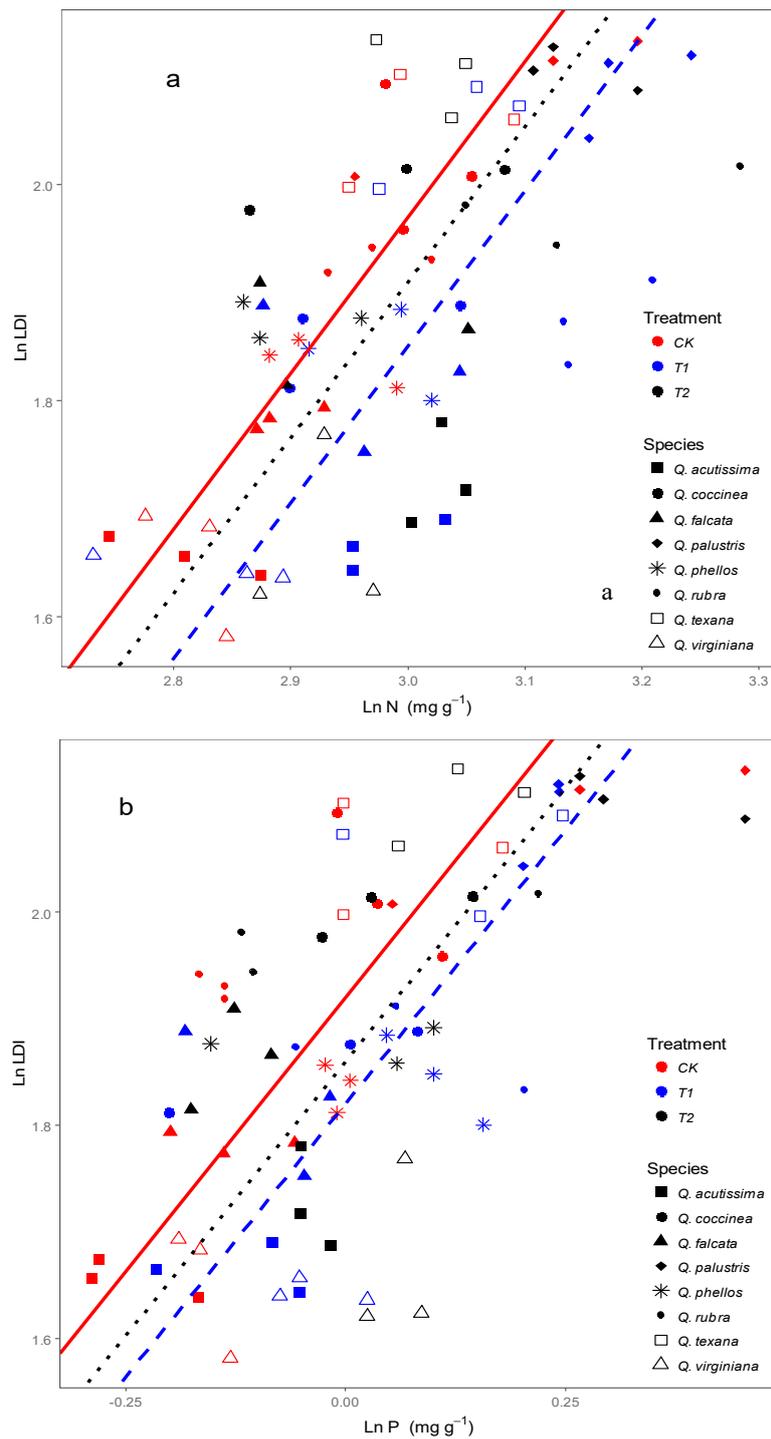


Figure 4. Relationships between leaf N, P concentrations and LDI (Leaf dissection index) for *Quercus* species under wind load. Ln N, Ln P and Ln LDI: leaf N, P concentrations and LDI were transformed using the natural logarithm prior to analysis. CK: control, T1: about 4 m s⁻¹ wind speed, T2: about 6 m s⁻¹ wind speed. (a) Leaf N concentration and LDI. CK: $y = 1.19x - 1.58$, $R^2 = 0.41$, $p < 0.01$; T1: $y = 0.83x - 0.67$, $R^2 = 0.45$, $p < 0.01$; T2: $y = 0.78x - 0.44$, $R^2 = 0.23$, $p = 0.02$. SMAs fitted among treatments did not show significant differences in slope ($p = 0.55$), but apparent in intercept ($p < 0.01$); (b) Leaf P concentration and LDI. CK: $y = 0.90x + 1.95$, $R^2 = 0.436$, $p < 0.01$; T1: $y = 0.73x + 1.83$, $R^2 = 0.43$, $p < 0.01$; T2: $y = 0.48x + 1.89$, $R^2 = 0.22$, $p = 0.02$. SMAs fitted among treatments did not show significant differences in slope ($p = 0.83$), but apparent in intercept ($p = 0.03$).

4. Discussion

4.1. Response of Leaf N, P Stoichiometry to Wind

Leaf N, P concentrations were significantly impacted by wind for most *Quercus* species with elliptic leaves, which were similar to leaf morphology and photosynthesis in our previous studies [13,17,30]. The leaf N, P concentrations of *Quercus* species with lanceolate leaves, except for leaf P concentration of *Q. virginiana*, were not significantly impacted by wind, likely due to leaf shapes having reduced drag from wind as described previously [13].

Leaf N, P concentrations were found to increase with wind load, which is consistent with previous studies in which leaf N concentration under a wind regime was found to be higher than those under a no wind environment [11,21,22]. One reason for this is that plants must allocate more N and P to leaf cell walls under windy conditions in order to increase cell wall thickness to strengthen the leaf's mechanical toughness [18–20]. Previous studies suggest that the N found in cell walls probably represented structural proteins such as hydroxyproline-rich glycoproteins [31,32]. Another reason is that more biomass was allocated to the organs that are only slightly or not at all affected by mechanical stimuli from wind loads, such as the roots [11,33,34], and leaf biomass was found to decrease under wind load for *Quercus* species with elliptic leaves [13]. It is possible that leaf N, P concentrations increased due to the decrease in leaf biomass under the wind load since there was a dilution effect caused by high leaf area and biomass growth under no wind load [21]. In addition, wind can increase the movement of water from the leaf surface by removing the boundary layer where water vapor hugs the surface of leaves, thus creating a shorter path for water to reach the atmosphere [35,36]. Therefore, more nutrition—such as calcium, nitrogen, and phosphorus—would be transported from the roots and stems to leaves, accompanied by an increase in leaf water evaporation [37]. We also found that leaf transpiration rate increased under wind load for *Q. texana*, *Q. palustris*, and *Q. virginiana* in a previous study [30]. This may be another reason for higher leaf N, P concentrations under wind load.

Leaf stoichiometric relationships vary among plant life form [10], sizes [38], ages [39,40], and environmental gradients [41]. But stoichiometric relationships are not found to differ along soil nutrient gradients or latitudinal gradients [42,43]. In this study, our findings supported the claim that stoichiometric relationships remain stable under different wind conditions, with a synchronous variation between leaf N and P concentrations. Responses of N and P biochemical pathways were similar [7]: both leaf N and P concentrations increased for *Quercus* species, and thus leaf N:P did not vary under the wind load. These results bolster support for our first hypothesis, and provide additional evidence for stoichiometric homeostasis.

4.2. Response of Relationships between Leaf Stoichiometry and Morphology to Wind

Leaf N, P stoichiometry, which plays a vital role among leaf traits, has been closely linked to leaf morphology in previous studies [1,6]. For example, leaf N and P concentrations have been correlated to SLA at a large spatial scale [7,44,45]. Here, we also found positive correlations between leaf N concentration and SLA under each treatment; meanwhile, SMAs fitted for leaf N concentration and SLA did not shift in slope among treatments. This indicates that wind load significantly impacted leaf N, P concentrations and SLA, but did not change the relationship between leaf N concentration and SLA, suggesting relative stability of the leaf N-SLA relationship for a given *Quercus* species. This is consistent with our previous study on the leaf stoichiometry-morphology relationship [6].

Some studies have found that species with higher SLA are likely to be toothed [46] and have a higher photosynthetic rate [28,47,48]. Therefore, higher leaf N and P concentrations may be needed to support photosynthesis. In our study, LDI was positively correlated to leaf N and P concentrations. SMAs fitted for leaf N and P concentrations and LDI did not shift in slope among treatments, which indicates that relationships between leaf N and P concentrations and LDI kept a synchronous variation, demonstrating that stoichiometry-morphology relationships do not vary under

wind load. This supports our second hypothesis that leaf N, P stoichiometry and leaf morphology display synchronous variations under wind load.

LES holds that plant traits do not vary independently but rather form groups of co-varying traits, which can explain the trade-off strategy for plants under environmental stresses [1,49]. Here, leaf N, P concentrations increased to support leaf structural components under a wind load, with leaf thickness increasing and leaf size decreasing [13], inducing lower SLA and LDI. These are stress tolerance strategies for *Quercus* species under a wind load. For this reason, leaf N, P stoichiometry and leaf morphology showed synchronous variations under the wind load.

However, intercepts of SMAs changed significantly among treatments, with lower intercepts under the wind load (Figures 3 and 4). This suggests that lower values of SLA and LDI were found under wind treatments than in control conditions for a given value of leaf N or leaf P concentrations because the N and P use efficiency decreased due to the wind load. For example, both leaf photosynthetic nitrogen-use efficiency (PNUE) and photosynthetic phosphorus-use efficiency (PPUE) significantly decreased under wind (Appendix A Table A2). This indicates that the *Quercus* species changed from “fast investment-return” in the wind-protected environment to “slow investment-return” in windy conditions, which is consistent with previous studies along soil moisture, soil nutrients, and temperature gradients [8,50,51]. We believe this study is the first to reveal synchronous variations between leaf N, P stoichiometry and leaf morphology under a wind load, which will be of value in understanding functional strategies for plants under a wind load, and be supplemental for LES along a wind gradient.

5. Conclusions

Leaf N and P concentrations increased significantly for most *Quercus* species with elliptic leaves under wind, while leaf N:P was stable for all species. *Quercus* species changed from “fast investment-return” in a wind-protected environment to “slow investment-return” in windy conditions. Specifically, leaf N and P concentrations increased, use efficiency (PNUE and PPUE) and SLA decreased, and leaf N, P concentrations and leaf morphology showed synchronous variations to adapt to wind. These results will be of value in understanding the functional strategies for plants under wind stress and in the construction of shelterbelts to ensure plant growth in windy areas.

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

Appendix

Table A1. One-Sample Kolmogorov-Smirnov Test.

		N (g kg ⁻¹)	P (g kg ⁻¹)	N:P
N		72	72	72
Normal Parameters ^{a,b}	Mean	19.984	1.029	19.741
	Std. Deviation	2.4026	0.1729	2.390
Asymp. Sig. (2-tailed)		0.039	0.002	0.013

^a Test distribution is Normal; ^b Calculated from data.

Table A2. Variance analysis of leaf PNUE and PPUE for eight *Quercus* species under wind load.

	DF	PNUE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			PPUE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		
		MS	F	P	MS	F	P
Tree species	7	179410.515	39.239	0.000	57420784.71	25.746	0.000
Treatment	2	25103.133	5.490	0.007	12724003.31	5.705	0.006

PNUE = Pn/leaf N concentration; PPUE = Pn/leaf P concentrations.

The methods of PNUE and PPUE were cited in “Guo, R., Sun, S., Liu, B. Difference in leaf water use efficiency/photosynthetic nitrogen use efficiency of Bt-cotton and its conventional peer. Scientific Reports, 2016, 6: 33539”

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