



Research paper

Soil water content and nitrogen differentially correlate with multidimensional leaf traits of two temperate broadleaf species

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ABSTRACT

The variation and correlation of leaf economics and vein traits are crucial for predicting plant ecological strategies under different environmental changes. However, correlations between these two suites of traits and abiotic factors such as soil water and nitrogen content remain ambiguous. We measured leaf economics and vein traits as well as soil water and nitrogen content for two different shade-tolerant species (*Betula platyphylla* and *Acer mono*) in four mixed broadleaved-Korean pine (*Pinus koraiensis*) forests along a latitudinal gradient in Northeast China. We found that leaf economics traits and vein traits were decoupled in shade-intolerant species, *Betula platyphylla*, but significantly coupled in a shade-tolerant species, *A. mono*. We found stronger correlations among leaf traits in the shade tolerant species than in the shade intolerant species. Furthermore, leaf economic traits were positively correlated with the soil water gradient for both species, whereas vein traits were positively correlated with soil water gradient for the shade intolerant species but negatively correlated in the shade tolerant species. Although economic traits were positively correlated with soil nitrogen gradient in shade intolerant species but not correlated in shade tolerant species, vein traits were negatively correlated with soil nitrogen gradient in shade tolerant species but not correlated in shade intolerant species. Our study provides evidence for distinct correlations between leaf economics and vein traits and local abiotic factors of species differing in light demands. We recommend that the ecological significance of shade tolerance be considered for species when evaluating ecosystem functions and predicting plant responses to environmental changes.

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1. Introduction

Leaves are the main organ of plant carbon assimilation, water transportation, and a wealth of other important ecological processes (Wright et al., 2004; Sack and Scoffoni, 2013; He et al., 2020). Leaf functional traits are of great significance for predicting ecosystem function and community assembly under future global change scenarios (e.g., drought and nitrogen deposition) (Wright et al., 2005; Domínguez et al., 2012; Jager et al., 2015). Variation in leaf functional traits in response to light conditions have been

shown to be closely related to plant ecological strategies and performance (Westoby et al., 2002; Blackman et al., 2016; Fajardo and Siefert, 2018). Thus, understanding how plant ecosystems function and communities are assembled requires investigation of trait variation in species with different shade tolerance. Recently, multidimensional traits (e.g., leaf economics or vein trait dimensions) have been shown to be closely related to plant adaptability (Laughlin and Wilson, 2014; Li et al., 2015; Liu et al., 2020a). Compared with covariant or simple dimensions, independent variation and diversified combinations of leaf traits play key roles in coping with complex environments. What is less clear, however, is whether leaf economics traits and leaf vein traits have independent responses to soil water content and soil total nitrogen in species with different shade tolerance strategies, e.g., shade-tolerant and shade-intolerant species.

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Trade-offs in plant functional traits, especially traits associated with resource uptake and transport, are hypothesized to drive variation in life history strategies among plants (Westoby et al., 2002; Fortunel et al., 2012; Liu et al., 2019a). One approach to understanding the trade-offs that leaves make between resource conservation and acquisition is through a leaf economics spectrum, which describes species with ‘fast’ leaves (e.g., leaves with higher specific leaf area and higher nitrogen content per mass) or ‘slow’ leaves (e.g., leaves with lower specific leaf areas and nitrogen contents) (Wright et al., 2004; Poorter et al., 2009; Reich and Cornelissen, 2014). Leaf vein traits are often decoupled from economics traits due to differences in structure, evolution and ecology (Sack and Scoffoni, 2013; Sack et al., 2014; Li et al., 2015). Leaf vein traits often indicate the efficiency of leaf water transport and the cost of leaf construction (Sack et al., 2005, 2013) as they are closely related to stomata density (Sack and Scoffoni, 2013), leaf size (Murphy et al., 2012, 2014), and leaf photosynthetic capacity (Brodribb et al., 2007; Brodribb and Field, 2010). Previous studies have demonstrated that at a community scale leaf economics traits and leaf vein traits are decoupled (Sack et al., 2014; Li et al., 2015; Blackman et al., 2016). An additional indicator of a tree species’ tolerance to low light environments is shade tolerance (Valladares and Niinemets, 2008). In a given environment, tree species with different shade tolerances can alter plant photosynthetic efficiency and water transport efficiency by adjusting their traits (Sack and Holbrook, 2006; Hallik et al., 2009). Therefore, analysis of plant adaptation strategies without considering shade tolerance of tree species may ignore important ecological processes. However, little is known about whether leaf economics traits and vein traits are similarly decoupled in shade-tolerant and shade-intolerant species.

The level of trait value is critical to species’ leaf adaptation strategy and may depend on species’ shade tolerance (Sack and Holbrook, 2006; Wright et al., 2010; Zhang et al., 2019). Shade-tolerant species generally adopt a conservative adaptation strategy. The specific leaf area (SLA) and chlorophyll content of these species is lower than in shade-intolerant species (Lusk and Warton, 2007; Wright et al., 2010). In contrast, shade-intolerant species use an acquisitive adaptation strategy. This strategy is characterized by having higher minor vein length per unit leaf area (VLA_{\min}) (Sack and Frole, 2006), which may contribute to higher gas exchange (Li et al., 2015), mesophyll light capture (Brodribb and Field, 2010), and greater transport efficiency (Russin and Evert, 1984). However, the relationship between leaf traits and shade tolerance in empirical studies (see Valladares and Niinemets, 2008; Niinemets, 2010 for a review) is contradictory, likely due, in part, to the confounding effect of environmental factors (e.g., soil factors) that are not explicitly considered (Sack et al., 2013; Yin et al., 2018). Shade tolerance is an integrative term that encompasses many aspects of life history far beyond light use efficiency (such as the ability to resist damage caused by excessive UV radiation, Valladares and Niinemets, 2008) and this issue still requires further exploration to understand variation and trait associations at species level.

Global drought and nitrogen deposition can play a role in filtering individuals in a community through variation in water and nutrient supply. Soil water content and soil total nitrogen strongly relate to plant adaptation strategies as they can significantly affect plant photosynthesis efficiency, water transport efficiency, and resource uptake (Ordoñez et al., 2009, 2010; Maire et al., 2015; Lin et al., 2020). Soil water content varies greatly in different environments and significantly affects soil microbial vitality and root development, thereby causing changes in plant nutrient and water absorption and utilization efficiency. Generally, plants in drier environments are characterized by higher VLA_{\min} (Yin et al., 2018) and the number of vein areoles per leaf area (VAA) (Sack and Scoffoni, 2013). Such a pattern of trait variation probably contributes to the

area and path of water exchange between the xylem and the surrounding mesophyll cells (Nardini et al., 2010), and further affects plant water use efficiency and photosynthetic efficiency (Murphy et al., 2014). Nutrient availability is often considered to be closely related to plant relative aboveground biomass (Zheng and Ma, 2018), thus causing a switch from nutrient limited competition in low soil total nitrogen to light limited competition in high soil total nitrogen (Hautier, 2009; DeMalach et al., 2017). Plants adapted to high soil total nitrogen tend to have higher SLAs (Maire et al., 2015) and a higher VLA_{\min} to underpin the greater light competitive capability (Sack and Scoffoni, 2013; Zheng and Ma, 2018). In recent years, studies have shown that differences in the shade tolerance of a plant species may affect the efficiency of its utilization of soil nutrients (Huang et al., 2012). Therefore, it is important to determine whether leaf economics traits and vein traits are correlated with abiotic factors such as soil water content and soil total nitrogen in shade-tolerant and shade-intolerant species.

In this study, we sought to determine whether the relationship between leaf economics traits and vein traits is constant between tree species. Because carbon assimilation and water transport differ between shade-tolerant and shade-intolerant species, we reasoned that in environments with low light conditions it may be more cost-effective for shade-tolerant species to couple leaf economics traits and vein traits. In contrast, shade-intolerant species may benefit more when economics traits and vein traits are decoupled, because this would provide a more diverse set of leaf strategies to adapt to complex environments. Thus, we first hypothesized that the shade tolerance of a species significantly alters the relationship between leaf economics traits and vein traits. Specifically, we predicted that leaf economics traits and vein traits would be coupled in shade-tolerant species and decoupled in shade-intolerant species. Second, we asked whether intraspecific leaf traits are correlated with local soil water and/or nutrient conditions. We hypothesized that intraspecific traits would have distinct responses to soil water content and soil total nitrogen. Specifically, traits related to leaf hydraulics (such as vein traits) would be more correlated with soil water content, and traits related to resource acquisition and utilization (such as leaf economics traits) would be more correlated with soil total nitrogen. To test these hypotheses, we measured eight leaf traits (four leaf economics traits and four vein traits), soil water content, and soil total nitrogen in one shade-tolerant and one shade-intolerant tree species. *Betula platyphylla* (Japanese white birch; hereafter birch) and *Acer mono* (painted maple; hereafter maple), which are common in broadleaved-Korean pine forests in Northeast China (Wang, 1994), show significant differences in their tolerance to shade (Niinemets and Valladares, 2006). The richness of these two species and the wide variety of soil factors in the study area provide an ideal setting for testing soil fertility–trait relationships at the intraspecific level.

2. Materials and methods

2.1. Sample design

The study area is situated in the broadleaved-Korean pine forests in Northeast China (Wang, 1994), which has a temperate continental monsoon climate (Table S1). We assessed variation in eight leaf traits in birch, *Betula platyphylla*, and maple, *Acer mono*, across five hierarchical ecological scales: (i) leaves in sun vs. leaves in shade; (ii) sunned leaves and shaded leaves within different canopy strata (upper; middle; lower canopy); (iii) leaves in different canopy strata within a tree; (iv) leaves of different trees within a site; (v) leaves from trees at different sites (Table 1). For each trait measured from each species, we collected 720 leaves from trees situated at four sites (Table S1), three trees per site, three

Table 1
Variation in four leaf economics traits and four vein traits of birch and maple.

Leaf traits	Abbreviation	Unit	Birch				Maple			
			Mean	Max	Min	SE	Mean	Max	Min	SE
Economics traits										
Specific leaf area	SLA	cm ² g ⁻¹	185.07b	305.39	128.79	3.824	242.69a	339.87	159.86	5.577
Leaf thickness	LT	mm	0.14a	0.20	0.08	0.003	0.12b	0.18	0.08	0.003
Leaf nitrogen content per mass	N _{mass}	mg g ⁻¹	31.90b	37.84	25.65	0.320	35.29a	42.37	27.44	0.363
Leaf nitrogen content per area	N _{area}	mg cm ⁻²	0.18a	0.23	0.11	0.003	0.15b	0.22	0.09	0.004
Vein traits										
Major veins length per unit leaf area	VLA _{maj}	mm mm ⁻²	0.19a	0.26	0.12	0.003	0.20a	0.25	0.15	0.003
Minor vein length per unit leaf area	VLA _{min}	mm mm ⁻²	7.61a	10.01	5.66	0.101	4.30b	5.68	3.03	0.077
Interveinal vein distance	IVD	mm	0.26b	0.35	0.17	0.006	0.33a	0.49	0.24	0.007
Number of vein areoles per leaf area	VAA	n mm ⁻²	11.90a	23.96	6.01	0.524	7.20b	11.96	2.89	0.285

Different letters indicate significant differences in economics or vein traits between birch and maple at the 0.05 level.

canopy strata per tree, two light exposures per canopy strata, 10 leaves per light exposure.

2.2. Sites and tree selection

We sampled leaves from mid-July to August 2017 within each study site. The birch tree, *B. platyphylla*, is shade intolerant; the maple tree, *A. mono*, is shade tolerant (Niinemets and Valladares, 2006). For each species, three individuals were selected with similar tree height (measured by clinometer, mean_{height} = 21.5 ± 1.1 m for birch; mean_{height} = 15.7 ± 1.1 m for maple) and diameter at breast height (DBH, mean_{DBH} = 38.1 ± 1.7 cm for birch; mean_{DBH} = 35.6 ± 2.3 cm for maple) on the south facing slope with similar slope angles. We divided the canopy of each sample tree into upper, middle and lower layers. The canopy height is the distance from the first living branch to the top of the tree. Within each canopy layer, sun and shade directions were divided, then one large sample branch was cut via tree climbing for each direction, 6 branches per tree in total. Within each branch, we selected 5 healthy and fully expanded leaves to measure leaf economics traits, 5 leaves to measure vein traits, and 10–20 leaves to measure leaf nitrogen content. Leaves were preserved in a mixture 90:5:5 of 70% ethanol, formalin, and glacial acetic acid.

We collected three soil subsamples after removing the leaf litter within one meter around each sample tree (soil corer, soil depth was 0–10 cm, and the sample angle was ~120°, Yang et al., 2019; Liu et al., 2020b). We then homogenized the three subsamples in a plastic bag and immediately transported them to the laboratory for soil water content and soil total nitrogen measurements.

2.3. Leaf trait measurements

We measured the leaf thickness of each leaf with a micrometer (avoiding the major veins, with an accuracy of 0.01 mm). Leaf fresh mass was measured with accuracy of 0.0001 g. A scanner (BenQ Corporation, China) was used to scan and measure leaf area (the accuracy is 0.01 cm²). We oven-dried the leaves until they achieved a constant mass (at 65 °C for at least 72 h) and then weighed (accuracy of 0.0001 g). SLA was calculated as leaf area divided by dry leaf mass (cm² g⁻¹).

After grinding and drying, 0.1 g leaf samples were subjected to a pre-digestion system for 40 min, followed by a double acid (H₂O₂ + H₂SO₄) digestion, then N_{mass} (mg g⁻¹) was determined with a Hanon K9840 auto-Kjeldahl analyzer (Jinan Hanon Instruments Co., Ltd., Jinan, China), N_{area} was calculated by dividing N_{mass} by SLA.

VLA_{maj} (Fig. 1) was calculated manually by using ImageJ software (NIH Image) after scanning leaf images with a scanner (BenQ Corporation, China). For VLA_{min}, we first softened the leaves in a 5%

sodium hydroxide solution, and then carefully removed the mesophyll to expose the minor veins. After bleaching to clear (5% sodium hypochlorite) and careful washing, the sample leaves were stained with 1% saffron (Sack et al., 2012). We then observed and photographed the samples under a light microscope (Olympus Electronics, Inc., Tsukuba, Japan) with electronic image analysis equipment. Interveinal vein distance (IVD), the number of vein areoles per leaf area (VAA) and minor veins were manually calculated by using ImageJ software (NIH Image). VLA_{min} was calculated as the total length of the minor veins per unit area (Blonder et al., 2011).

2.4. Soil water and nitrogen content

Soil water content (g g⁻¹) was determined using an oven drying method (Liu et al., 2020b). Soil total nitrogen (mg g⁻¹) was measured by Hanon K9840 auto Kjeldahl analyzer (Jinan Hanon Instruments Co., Ltd., China).

2.5. Statistical analysis

The mean, maximum, minimum and standard error for eight leaf traits of birch and maple leaves were calculated. Least significant differences (LSD) were used to test whether there was a significant difference in the mean of traits between birch and maple. Correlations among leaf traits were analyzed using Pearson correlation analysis, prior to analyses, in order to satisfy the criteria of linear statistical methods, logarithmic transformation was performed on all traits. For each species, we first used principal component analysis (PCA) to obtain PC1 scores of economic and vein traits, and then used Pearson correlation analysis to analyze the correlation between these two sets of traits (Li et al., 2015). We used the total principal component scores of birch and maple to analyze the correlation between economic traits and leaf vein traits and soil water content and soil total nitrogen. Pearson correlation analysis was used in this step.

3. Results

3.1. Correlations of economic and vein traits

PCA was employed to evaluate the correlations between leaf economics and vein traits (Fig. 2). The first two principal components accounted for most leaf trait variation for birch and maple (59.90% and 73.2%, respectively, Fig. 2). The first axis represents vein trait variation and the second axis represents leaf economics trait variation (Fig. 2 and Table S2). These two sets of traits were decoupled in birch ($p = 0.09$) but significantly coupled in maple ($p < 0.0001$) (Figs. 2 and S1).

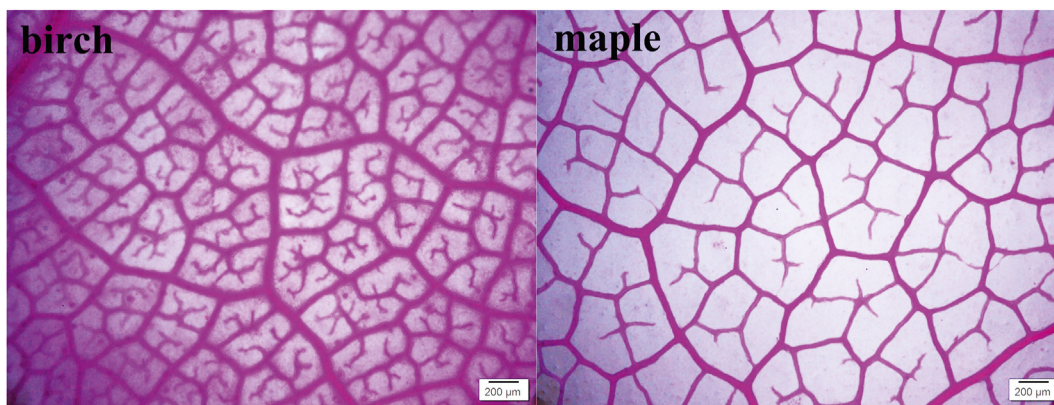


Fig. 1. The venation networks for birch and maple after clearing and staining.

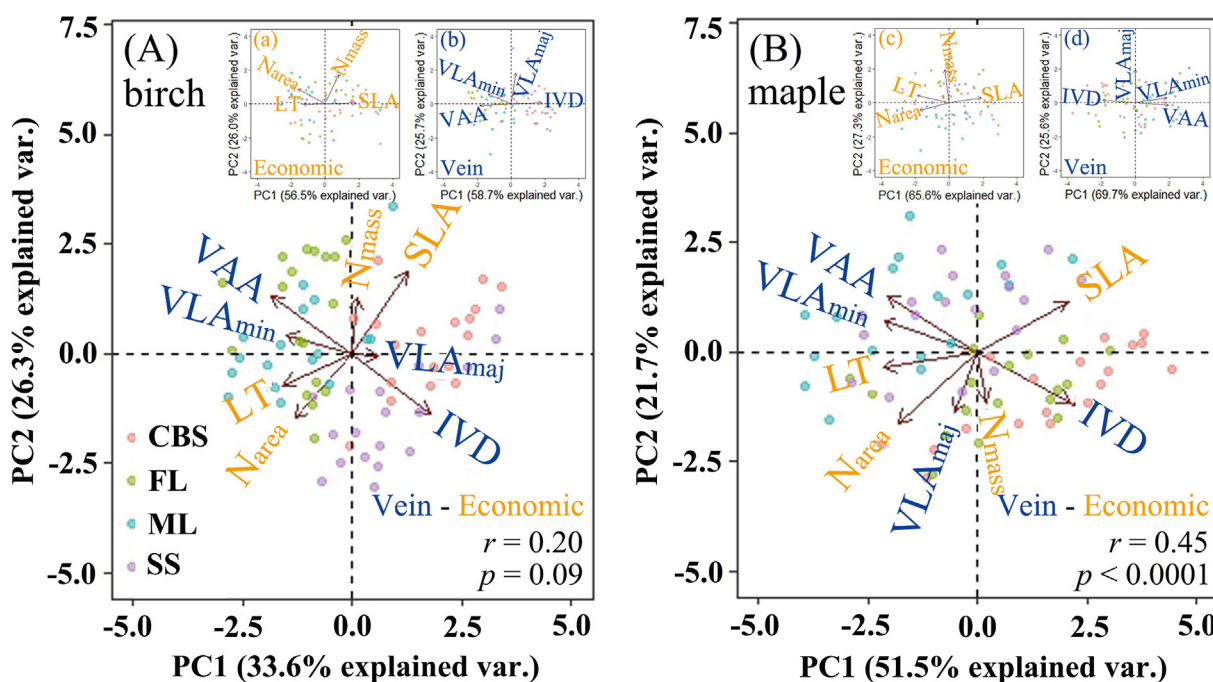


Fig. 2. Principal component analysis of eight leaf traits for (A) birch and (B) maple. The inset graph shows Principal component analysis of economics traits and vein traits (a–d). The arrows represent the principal component loadings associated with the leaf traits. The correlation between leaf economics traits and vein traits of birch and maple were analyzed by the first principal component scores of economics traits and vein traits. Leaf trait abbreviations are provided in Table 1. CB: Changbai mountain; ML: Muling; FL: Fenglin; SS: Shengshan.

Significant correlations between certain leaf traits were constant in birch and maple (Table 2). Among leaf economics traits, SLA was negatively correlated with leaf thickness and N_{area} , and leaf

Table 2
Bivariate relationships among eight leaf traits for birch (lower) and maple (upper; grey fill).

	SLA	LT	N_{mass}	N_{area}	VLA_{maj}	VLA_{min}	IVD	VAA
SLA		-0.79	0.05	-0.91	-0.38	-0.54	0.41	-0.38
LT	-0.49		-0.01	0.73	0.04	0.58	-0.64	0.61
N_{mass}	0.46	-0.20		0.36	-0.07	-0.08	0.17	-0.15
N_{area}	-0.86	0.44	0.06		0.33	0.47	-0.32	0.29
VLA_{maj}	0.00	-0.37	-0.14	-0.08		0.10	0.06	-0.09
VLA_{min}	-0.22	0.18	-0.15	0.16	0.04		-0.86	0.86
IVD	-0.07	-0.30	-0.21	-0.05	0.11	-0.50		-0.99
VAA	0.01	0.32	0.17	0.09	-0.13	0.56	-0.98	

thickness was positively correlated with N_{area} . Among vein traits, IVD was negatively correlated with VAA and VLA_{min} , and VLA_{min} was positively correlated with VAA (Table 2). In both shade-intolerant and shade-tolerant species, part trait–trait relationships were changed, such as SLA versus N_{mass} and N_{mass} versus N_{area} . Leaf economics traits were not correlated with vein traits in birch except leaf thickness versus VLA_{maj} , IVD, VAA (Table 2); but in maple, significant correlations were observed except for leaf thickness versus VLA_{maj} and N_{mass} versus VLA_{maj} , VLA_{min} , IVD, VAA (Table 2).

3.2. Soil water content and nitrogen differentially correlate with multidimensional leaf traits

For birch and maple, the principal component of economics traits indicates an axis from resource-conservative (lower SLA and

N_{mass}) to resource-acquisitive (higher SLA and N_{mass}) strategies. The principal component of vein traits indicates an axis from high leaf construction cost (higher VLA_{min} , VAA) to low leaf construction cost (lower VLA_{min} , VAA) (Figs. 2 and 3).

The correlation between the economics trait axis and soil water content was constant between tree species: the economics trait axis was positively correlated with soil water content (Fig. 3A and B). However, the relationship between the vein trait axis and soil water content changed from shade-intolerant to shade-tolerant species: the vein trait axis was positively correlated with soil water content in birch (Fig. 3A) but negatively correlated in maple (Fig. 3B).

The correlation between the leaf trait axis and soil total nitrogen was weaker. For birch, the economics trait axis was positively correlated with soil total nitrogen (Fig. 3C), but for maple, it was not correlated (Fig. 3D). The vein trait axis was negatively correlated with soil total nitrogen in maple (Fig. 3D), but not in birch (Fig. 3C).

4. Discussion

4.1. Adaptive mechanisms are distinct for shade-tolerant and shade-intolerant tree species

Our findings that leaf economics and vein traits are coupled in birch but uncoupled in maple trees supports the hypothesis that shade tolerance alters adaptive strategies between species. Furthermore, our results emphasize the multi-dimensionality of leaf trait adaptation to environmental change.

In shade-intolerant birch trees, we identified two independent leaf trait axes. The first axis describes the relationship between SLA

and N_{mass} . SLA reflects the efficiency of leaf dry-mass investment (Liu et al., 2019a, 2019b), while N_{mass} is integral to photosynthesis-related proteins. We discovered a negative relationship between these two traits, which is usually encountered in “fast-slow” species (Wright et al., 2004) and indicates a shift from resource-conservative (lower SLA and N_{mass}) to resource-acquisitive (higher SLA and N_{mass}) strategies. The second axis describes the variation in vein traits from high VLA_{min} , VAA and low IVD to low VLA_{min} , VAA and high IVD. This axis represents the trade-off between leaf construction cost and transportation distance (Sack and Scoffoni, 2013; Sack et al., 2013). Our finding that leaf economics and vein traits are decoupled (e.g., SLA and vein density) is consistent with previous studies (Sack and Frole, 2006; Dunbar-Co et al., 2009; Nardini et al., 2012; Blackman et al., 2016). One explanation for this decoupling of traits is that leaf economics and vein traits represent separate sub-systems (Li et al., 2015). For example, leaf economics traits are mainly located in palisade mesophyll tissues, whereas vein traits are mainly located in spongy mesophyll tissues. Consequently, these two sub-systems have likely undergone different evolutionary trajectories.

Our observation that leaf economics and vein traits are correlated in maple trees is similar to that of previous studies of woody species (Yin et al., 2018) and within eucalypt species (Blonder et al., 2013). The negative correlation between SLA and VAA, VAA, VLA_{min} and VLA_{maj} , and the positive correlation between SLA and IVD (Table 2) suggest that resource acquisitive species, such as maples, might improve resource use efficiency by reducing the cost of vein structure, while simultaneously improving leaf nutrient and water transport safety by increasing IVD (Sack et al., 2013). Furthermore, we found N_{mass} was not correlated with vein traits (Table 2), which

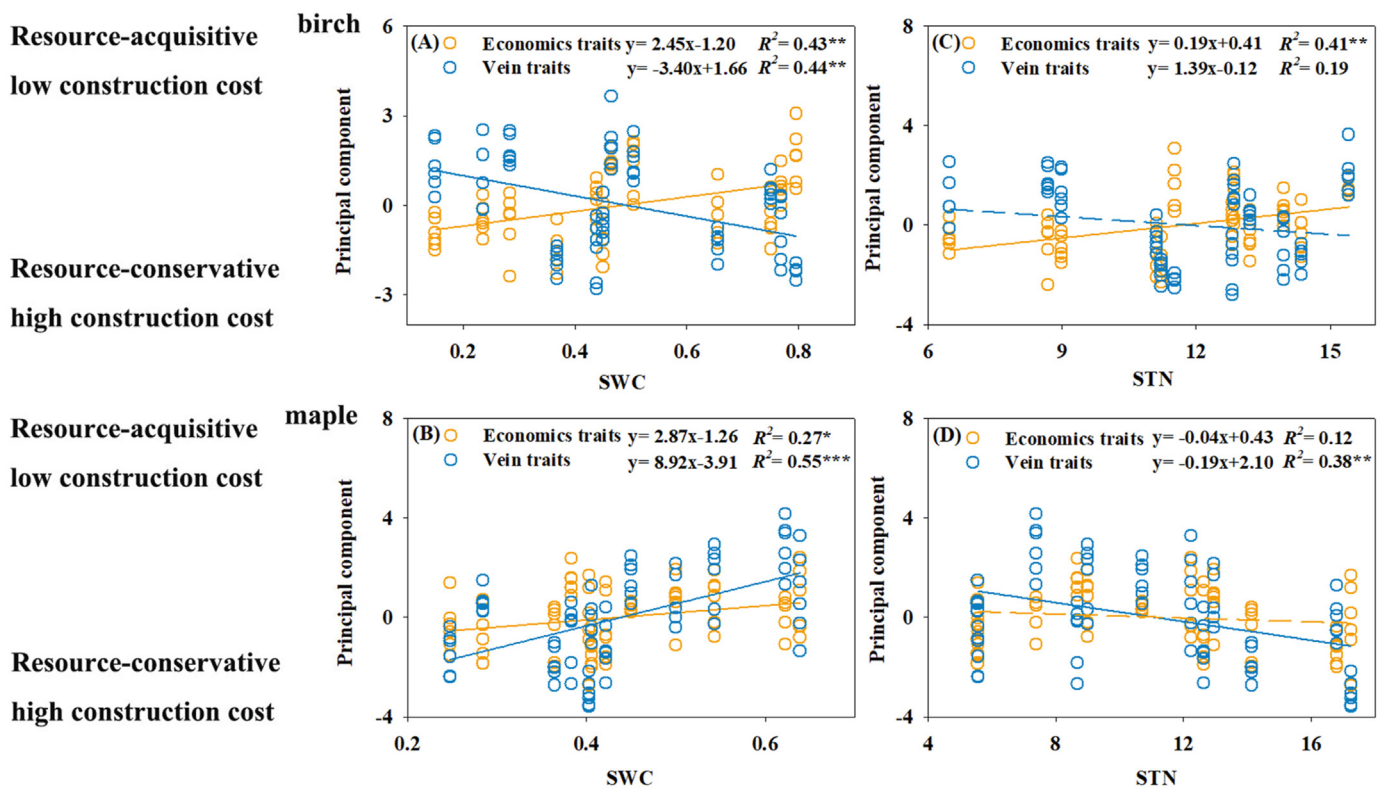


Fig. 3. Correlation between the first two principal component scores and soil water content and soil total nitrogen for birch (A, C) and maple (B, D). The first axis represents vein traits variation, from high leaf construction cost to low leaf construction cost; the second axis represents economics trait variation, from resource conservation to resource acquisition (See Fig. 2 for details). The solid line indicates that there is a significant correlation between the principal component scores and soil water content (SWC) or soil total nitrogen (STN), while the dashed line indicates that there is no significant correlation between the principal component value and SWC or STN. *, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$. Abbreviations of the leaf traits are given in Table 1. SWC, soil water content; STN, soil total nitrogen.

may be explained by the correlation between vein traits and palisade tissue (Yin et al., 2018), as they both play roles in gas exchange and water transpiration. In palisade tissue, most nitrogen is related to photosynthesis, whereas mass-based N may have both structural and functional roles (Osnas et al., 2013). Taken together, our findings suggest that leaf economics and vein traits may be coupled to increase resource use efficiency and plant survival in shade (Flores-Moreno et al., 2019; Liu et al., 2020a). Thus, observed variation in how economics traits and vein traits are coupled in various shade-tolerant species may be due to differences in potential trade-offs between leaf light capture and water conduction.

4.2. Soil water content and nitrogen differentially correlate with multidimensional leaf traits

The relationships of leaf economics and vein traits to soil water content and soil total nitrogen are distinct between birch and maple trees. We found that multidimensional leaf traits were significantly correlated with soil water content but weakly correlated with soil total nitrogen (Fig. 3). Along soil water content gradients, the economics axis of birch and maple trees shifted from resource-conservative strategies (lower SLA and N_{mass}) to resource-acquisitive strategies (higher SLA and N_{mass}) (Fig. 3A and B), which provides evidence that lower SLAs are generally distributed in relatively lower moisture areas (Niinemets, 2001; Wright et al., 2002; Stark et al., 2017; Luo et al., 2019). Lower SLAs in environments with low soil water content may be the result of thicker palisade tissue, which may contribute to maintaining high photosynthetic rate (He et al., 2017). Conversely, in environments with high soil water content, higher SLAs and larger surface areas may benefit plants with quick returns in leaves, e.g., investments in nutrients and dry mass (Wright et al., 2005).

Our results do not support the hypothesis that intraspecific traits have specific responses to soil water content and soil total nitrogen. The vein trait axis had species-specific responses to soil water content gradients (Fig. 3A and B). For maple, the vein trait axis shifted from less cost-effective (high VLA_{min}) to more cost-effective (low VLA_{min}) leaves (Fig. 3B). Higher VLA_{min} in environments with low soil water content (Table 2) enables higher leaf hydraulic conductance (Sack and Frole, 2006; Boyce et al., 2009), thus improving plant drought tolerance (Sack et al., 2013). VLA_{min} decreases with increasing soil water content, suggesting individuals with a conservative strategy actually require a lower leaf construction cost. The trade-off between leaf economics traits and vein traits along soil water content gradients is of great significance for improving the resource utilization efficiency of maple trees. For birch, the variation of the vein trait axis along soil water content gradients showed the opposite pattern: leaf economics traits with resource-conservative strategies correspond to more cost-effective vein traits in low soil water content conditions (Fig. 3A), which contrasts with the widespread observation of higher SLA being related to lower VLA_{min} . This is possible for birch because the weak correlation between economics traits and leaf vein traits may provide larger independent variation, however, this requires further investigation. Moreover, lower VLA_{min} reduces the cost of leaf construction and has been shown to make it possible for pioneer species to grow rapidly (Field et al., 2011).

The relationship between leaf economics and vein traits to soil total nitrogen was distinct between birch and maple trees (Fig. 3B and D). For birch, our study suggests that 'slow' leaf traits (low SLA) are favored in low soil total nitrogen environments. This is likely because a conservative resource strategy can minimize the sum of costs for acquiring and using nitrogen and water in photosynthesis (Shipley et al., 2006; Onoda et al., 2017). Forest aboveground

biomass and canopy cover increase significantly in high nitrogen soils; in addition, plants in low nitrogen soils tend to compete for nutrients, whereas plants in high nitrogen soils tend to compete for light (Hautier et al., 2009; DeMalach et al., 2017). 'Fast' leaf traits (high SLA) are at an advantage in soils with high total nitrogen because they may enhance plant resource acquisition efficiency through larger leaf area and shorter water transport paths. However, some studies have failed to find a significant correlation between SLA and soil nitrogen gradients (Ordoñez et al., 2009). In maple, leaf vein traits decreased with increasing soil total nitrogen. For example, higher VLA_{min} was favored in environments with low soil total nitrogen. This may be because tough leaves can better resist animal and wind damage, while lower VLA_{min} can enhance survival by reducing leaf carbon consumption. Furthermore, no significant correlation was found between economics traits and soil total nitrogen in birch, nor was any found between vein traits and soil total nitrogen in maple (Fig. 3B and D). This finding may indicate that the adaptation of plants to soil total nitrogen may differ depending on the shade tolerance of a species, which may promote coexistence between multiple species. Moreover, this suggests that adaptations to soil total nitrogen, e.g., changes in vein traits in birch or economic traits in maple, may not be as important as for other traits. In addition, these distinct correlations between species with different shade tolerances and soil total nitrogen may be related to the mycorrhizal type associated with these tree species. For example, arbuscular mycorrhizal (AM) fungi are commonly associated with shade-tolerant species, whereas ectomycorrhizal (ECM) fungi are often associated with shade-intolerant species. Previous studies have shown that AM-associated species usually grow in fertile areas with higher soil nitrogen content, whereas ECM-associated species grow in infertile areas with lower soil nitrogen content (Mao et al., 2019). Moreover, in plant nutrient economics strategies, ECM tree species tend to adopt resource-conservative strategies and AM tree species tend to adopt resource-acquisitive strategies (Valverde-Barrantes et al., 2018; Averill et al., 2019). These differences in habitat and nitrogen utilization strategies may be the reason why economics traits of birch and maple showed distinct correlations with soil total nitrogen.

5. Conclusion

Our study shows that trait correlations between economics and vein traits in species of different shade tolerances are not consistent. These two groups of traits were decoupled in birch but coupled in maple. Our results provide direct evidence for the differences in ecological strategies of different shade-tolerant species. Moreover, local abiotic factors differentially drove changes in multidimensional leaf traits. Specifically, soil water content dominated the variation in the multi-dimensional trait variation of two different shade tolerant tree species; in contrast, soil nitrogen primarily dominated the variation in economic traits of birch and vein traits of maple. Our results suggest that the multidimensionality of leaf traits of tree species may be shaped by local abiotic factors, and suggest that the relative abundance of species of different shade tolerances should be considered when quantifying ecosystem function and community assembly variation along soil gradients.

Author contributions

ZLL developed the idea; ZLL and MYJ carried out the experiment, MYJ analyzed the dataset; JDJ contributed to interpretation of data; and MYJ wrote the paper with substantial contributions from ZLL, JDJ, GZJ and QXG.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2023.03.001>.

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