



Toposequence variability in tree growth associated with leaf traits for *Larix gmelinii*



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ABSTRACT

Intraspecific variations in leaf traits and tree growth along environmental gradients are crucial for survival and distribution of the tree species, but they are substantially less quantified than interspecific counterparts. Here, we examined the intraspecific variations in leaf hydraulics and economics traits and growth of *Larix gmelinii* Rupr. – the predominant tree species in the Eurasian boreal forests with a toposequence approach. The toposequence included three replicated 1000-m transects of the larch plantation (31-year-old), each of which consisted of three plots located at the toe-, mid-, and top-slope, respectively. We found that the leaf hydraulics traits showed a “high-low-high” pattern along the toposequence, while the leaf economics traits, total biomass (TB) and TB increment (TBI) displayed an opposite trend, largely consistent with changes in site conditions especially soil nitrogen concentration. This suggests that the intraspecific variation in tree growth is coupled with leaf traits and site conditions. Leaf mass per area explained 21.9% of the variability in TB, while the ability of drought tolerance explained 22.5% of that in TBI; and the interactions of hydraulic and economic variables explained additional 23.1–26.2% of that in TB or TBI. This result indicates that leaf traits interactively affect TB and TBI, but the hydraulics and economics play major roles in the short-term growth rate and relatively long-term biomass stock, respectively. Together, our findings demonstrate that the larch trees acclimate the leaf traits and growth/biomass accumulation to site conditions, and provide insights into the mechanistic understanding of forest production.

1. Introduction

Leaf traits are commonly thought as predictors for tree growth (Poorter and Bongers, 2006; Poorter et al., 2012), and their responses to environmental changes are crucial for tree survival (McDowell et al., 2018) and competition (Kunstler et al., 2016). Interspecific variations in leaf traits and growth and their coordination have been well studied (e.g., Wright et al., 2004; Poorter and Bongers, 2006; Díaz et al., 2016), while intraspecific counterparts are much less investigated; and some recent studies showed contradictory results between them, mainly because of phenotypic modifications in response to environmental changes within a given species (Nicotra et al., 2010; Rosas et al., 2019; Asao et al., 2020). For example, Liu et al. (2018) reported that *Pinus sylvestris* var. *mongolica* with a lower growth rate showed a higher stem hydraulic conductivity, while Hoerber et al. (2014) reported a contradictory result for eight tropical tree species. Therefore, it is important to explore intraspecific variations in leaf traits and tree growth in response to environmental changes, extend the trait-based functional ecology,

and improve our prediction of forest production (Anderegg et al., 2018; Hayes et al., 2019).

Environmental changes modify leaf traits such as leaf nutrients (Ordoñez et al., 2009), photosynthesis (Maire et al., 2015), and hydraulics (Johnson et al., 2018), which determine the efficiency of carbon (C) sequestration and tree growth (Fan et al., 2012; López-Sampson et al., 2017). Increasing soil nutrients can shift leaf traits from resource-conservative to resource-acquisitive syndromes (Wright et al., 2004; Reich, 2014), e.g., increasing photosynthetic rate (Maire et al., 2015), leaf nitrogen (N) and phosphorus concentrations (Ordoñez et al., 2009), and leaf mass per area (LMA; Poorter et al., 2009); these phenomena, however, are largely found among species. Recently, Hayes et al. (2019) showed that *Glycine max* grown in sufficient light and high soil nutrients contents expressed more “resource-conservative” than those grown in shaded agroforestry systems. Grady et al. (2013) also reported that the fast-growing genotypes of riparian species showed conservative leaf traits. Thus, it is essential to know whether the well-established leaf economics spectrum (LES) is applicable within a species

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and how it is related to tree growth.

Plant hydraulics traits are suggested as the core of plant survival and growth (Sack et al., 2016), and thus crucial for the prediction of growth (Fan et al., 2012; Liu et al., 2018). Leaf hydraulics traits are vital for tree growth because leaves require sufficient water to sustain their photosynthesis and metabolism (Santiago et al., 2004; Brodribb et al., 2007; Nardini and Luglio, 2014). Xylem embolism substantially reduces photosynthesis by decreasing water transportation and inducing stomatal closure, and consequently leads to whole-plant growth decline and even tree death (Nardini et al., 2012; Choat et al., 2012). For example, Li et al. (2017) reported that tree growth rate was positively related to leaf stomatal conductance and leaf water potential in subtropical tree saplings. Eller et al. (2018) also found that the fast-growing trees possessed lower xylem safety margins and lower density wood but higher vulnerability to cavitation than the slow-growing trees in tropical forests. Reich (2014) proposed integrating hydraulics traits into LES as the “fast-slow spectrum.” However, some studies reported that leaf economics and hydraulics traits decoupled both intra- and inter-specifically (Li et al., 2015; Blackman et al., 2016); especially the intra-specific variations in leaf traits are unrelated with growth rate (Islam et al., 2018). Therefore, it is still inconclusive whether intraspecific leaf hydraulics traits can be combined into the LES.

Using plant functional traits to predict plant growth is important for evaluating vegetation life history strategies (Poorter and Bongers, 2006; Wright et al., 2010; Paine et al., 2015; Anderegg and Hillerislambers, 2015). There are multiple dimensions of tree traits (Li et al., 2015; Díaz et al., 2016), such as, tree height, seed size, leaf mass per area, and diameter at breast height (DBH), to represent light harvest, reproduction, leaf C investment, and growth, respectively (Poorter et al., 2008). However, these traits are interweaved and do not always well describe the underlying physiological processes. Direct relationships between physiological traits and tree growth are still scarce (Schuldt et al., 2016; Gleason et al., 2019) largely because of lacking detailed physiological traits (Paine et al., 2015). To improve modeling and management of forest production, it is essential to experimentally explore correlations between leaf traits and tree growth (Niinemets, 2015; Aranda et al., 2015; Blackman et al., 2017).

In this study, with an aim of understanding the mechanisms and improving the prediction of tree growth under different site conditions, we evaluated intraspecific variations in the leaf traits (hydraulics and economics) and growth and their correlations for Dahurian larch (*Larix gmelinii* Rupr.) trees in response to changes in soil conditions using a toposuccession approach. Dahurian larch is selected because it is the dominant tree species in the Eurasian boreal forests with extensive range and acclimation ability (Quan and Wang, 2018) and plays an important role in the regional C sequestration (Tang et al., 2018). We hypothesized that: (1) the larch trees on mid-slope grow faster than those on toe- and top-slopes because of less exposed stresses of soil N and moisture conditions; (2) leaf hydraulics and economics traits are strongly coupled within the larch, which extends the LES; and (3) leaf economics and hydraulics traits drive tree growth and biomass accumulation with distinct relative contributions.

2. Material and methods

2.1. Site description and experimental design

The study was conducted at the Maoershan Forest Ecosystem Research Station, northeastern China (45.4°N, 127.7°E, 400 m). The parent material is granite bedrock, and the soil is Hamplumbrepts or Eutroboralfs, with average slope is 10–15° (Wang, 2006). The typical climate is continental monsoon climate, with a warm and rainy summer, and dry and cold winter. The mean annual temperature is 3.1 °C, and the highest and lowest monthly temperatures are 22.0 °C (in July) and –18.5 °C (in January), respectively. The mean annual precipitation is 629 mm. The frost-free period is between 120 and 140 days

(Wang et al., 2013).

The Dahurian larch plantation was established by planting out 2-year-old seedlings from the same orchard in 1986. In the plantation, we randomly selected three replicate 1000-m toposuccession transects; and within each transect, we randomly established one 20 m × 3 m plot at the toe-slope, mid-slope, and top-slope, respectively. In each plot, four trees with their diameters at breast height (DBH, cm) close the mean DBH of the plot were randomly selected for measuring the tree growth and leaf traits between July and August in 2016.

2.2. Measurements of leaf economics traits

Leaf photosynthetic capacity was measured *in vitro* following the previous scheme (Tang and Wang, 2011) using LI-6400 portable photosynthesis system (Licor, Lincoln, NE, USA) between 07:30 and 11:30 local time. Briefly, branches were randomly sampled from the top-south canopy using a tree pruner, and the bottoms of the branches were kept in water during the *in vitro* measurements. The twig with needles on were put into the chamber to acclimate for ~10 min under the environmental settings (i.e., 400 ppmv of CO₂, 1500 μmol m⁻² s⁻¹ of irradiance (above the light-saturation point), 500 μmol s⁻¹ of flow rate, 20–25 °C of air temperature) before the measurement of photosynthesis started. After that, the twig was collected and put in a plastic bag in a cooler at 4 °C before being processed in the laboratory within 1 h. The twig in the chamber was marked in the field, on which all the needles were collected and scanned in the laboratory, and then calculated the pixel with an auto-calculating program to determine the projected leaf area and recalculated the area-based photosynthetic rate (A_{area} , μmol·m⁻²·s⁻¹). Finally, the needle samples were oven-dried at 65 °C for 72 h, and weighed the dry leaf mass for calculating leaf mass per area (LMA, kg·m⁻²). Meanwhile the needles adjacent to those for the A_{area} measurement were simultaneously sampled, oven-dried, and powered for measuring leaf N concentration (N_L , mg·g⁻¹, Kjeltac 8400, FOSS, Hillerod, Denmark).

2.3. Measurements leaf hydraulics traits

Predawn leaf water potential (Ψ_{pre} , MPa) was measured on fully sunlit twigs at 03:30–5:00 local time with a pressure chamber (Model 1505D, PMS Instruments, USA). The sampling was performed within one week without any rainfall event, so we assumed that soil moisture would not change much during this period. The shoots used for measuring pressure–volume (P–V) curves were clipped and immediately placed in black plastic bags, and brought back to the laboratory. The sampled shoot was re-clipped in water into ~10 cm long, and rehydrated until full hydration for ~1 h (leaf water potential (Ψ_l) > –0.1 MPa), from which the hydrated leaves were wiped off water and immediately weighed for the fresh leaf mass (S_w , g) before measuring Ψ_l with a pressure chamber, then air dried, reweighed for the mass (F_w , g), and measured Ψ_l again; repeated this process until Ψ_l was relatively constant. Finally, the leaves were scanned for the projected leaf area, then oven-dried at 65 °C for 72 h, and weighed for the leaf dry mass (D_w , g). Relative water content of the needles (RWC, %) was calculated as:

$$RWC = 100 \times (F_w - D_w) / (S_w - D_w) \quad (1)$$

The measurements of Ψ_l and RWC were used to construct the P–V curves. Leaf water potential at turgor loss point (TLP, MPa) was calculated from the P–V curve, and then the leaf water capacitance (C_{leaf}) was calculated as:

$$C_{leaf} = \frac{\Delta RWC}{\Delta \psi_l} \times \left(\frac{DW}{LA} \right) \times \left(\frac{WW}{DW} \right) / M \quad (2)$$

where WW is water mass in water saturation, and M is water molar mass (18 g·mol⁻¹).

The embolism vulnerability curve (VC) was developed with the

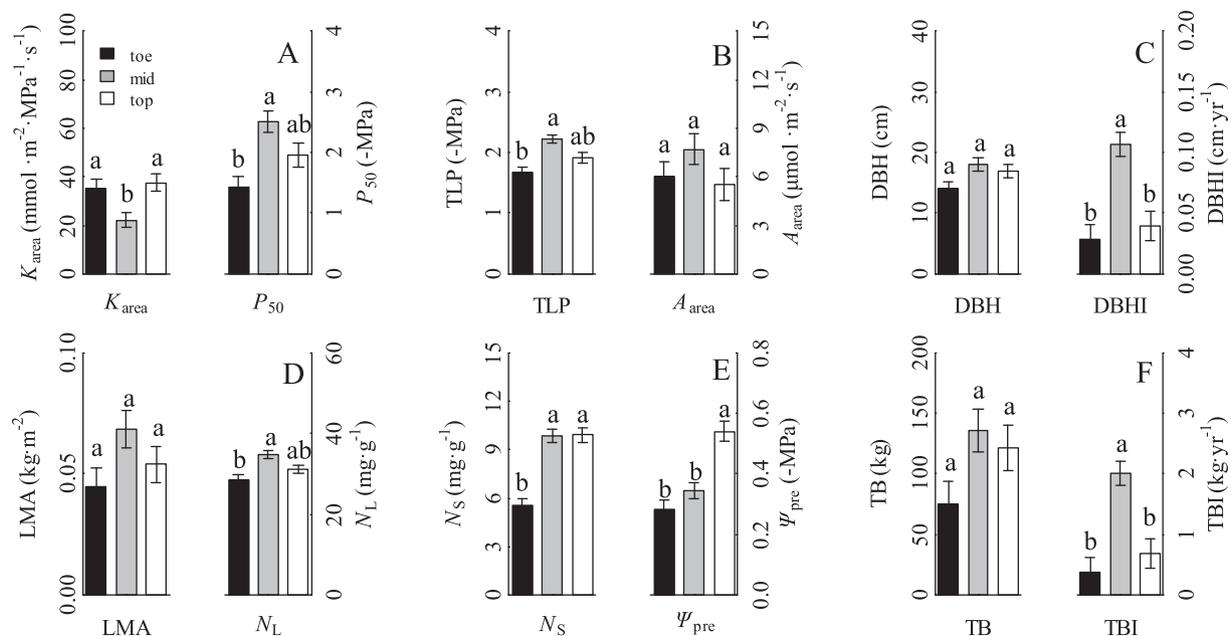


Fig. 1. Changes in leaf traits, growth, and soil properties along the toposequence. Different lowercase letters indicate significant differences among the slope locations ($p < 0.05$). K_{area} , leaf water conductance; P_{50} , leaf water potential at 50% loss of K_{area} ; TLP, turgor loss points potential; A_{area} , photosynthetic rate; LMA, leaf mass per area; N_L , leaf nitrogen concentration; N_S , soil nitrogen concentration; ψ_{pre} , predawn leaf water potential; DBH, diameter at breast height; DBHI, increment of DBH; TB, total biomass; TBI, increment of TB. $n = 29$ for all the variables except for N_S ($n = 45$).

rehydration method (Brodribb and Holbrook, 2003). The samples were collected with the same protocol as those for the P-V curves. In the laboratory, several shoots were set aside for different time periods to develop sequential initial leaf water potentials; they were then put into black plastic bags for equilibrium at least 30 min; after the balanced shoot water potential (Ψ_0) was determined, the shoot was recut in water and rehydrated for a few minutes (t), and re-measured for the shoot water potential (Ψ_f). Leaf water conductance (K_{area}) was calculated as

$$K_{area} = C_{leaf} \ln(\Psi_0/\Psi_f)/t \quad (3)$$

The VC was fitted by plot with the following function:

$$K_{area} = m/(1 + \exp(a * (\Psi_0 - b))) \quad (4)$$

where a and b are the coefficients, and m is a constant for each sample that depends on the maximum K_{area} . We first fitted the VCs for the mean Ψ values of -0.5 to 0 MPa and -1 to -0.5 MPa, respectively. The results showed that most of the K_{area} were higher when $\Psi > -0.5$ MPa, indicating that some unrealistically high values existed. Therefore, we removed the K_{area} within -0.5 to 0 MPa, and refitted the VCs by plot for toe-, mid-, and top-slope, respectively (Fig. S1). The maximum K_{area} ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$) was the mean of K_{area} when Ψ_0 between -0.5 and -1.0 MPa. The Ψ_1 that induced 50% loss of K_{area} was defined as P_{50} (MPa).

2.4. Measurements of soil nitrogen and tree growth characteristics

The 1000-m transects are rather gentle and vary in the elevation of 183 m (from 388 m at the toe to 571 m a.s.l. at the top) with changes in the mean annual temperature < 1.2 °C. However, the soil conditions vary substantially, especially the mean soil N concentration (N_S) changed by about 2-folds along the transects (5.53 – 9.89 $\text{mg}\cdot\text{g}^{-1}$). Since N is presumably the dominant limiting element to tree growth in temperate and boreal forests, we paid more attention to N_S by assuming that the transects are under similar climate conditions. Five topsoil (0–20 cm) samples per plot were randomly taken for determining N_S with the same protocol as that for N_L . The Ψ_{pre} was used as a proxy of the soil water potential (Ameglio et al., 1999).

Tree growth in DBH was measured with dendrometers that were

installed in May 2016. We re-measured DBH in November 2018 to obtain the increment of DBH (DBHI, $\text{cm}\cdot\text{yr}^{-1}$) in three growth periods. During the experiment, several sampled trees died and eventually the data contained 29 sample trees with at least two samples per plot. Total tree biomass (TB, kg, dry matter) and increment of TB (TBI, $\text{kg}\cdot\text{yr}^{-1}$) were calculated by the species-specific allometric equation developed previously at the same site [$\log_{10}(\text{TB}) = 2.021 + 2.474 \times (\log_{10}(\text{DBH}))$] (Wang, 2006).

2.5. Statistical analyses

We used the linear mixed effects model (lme4 and lmerTest packages in R) with a random intercept to evaluate the variations in leaf traits and tree growth among slope locations with the nested structure at the tree-level. The emmeans function (emmeans package) was used to calculate the mean values for each plot and conduct inter-plot comparisons at the tree-level. The lme model with a random intercept was also used to explore relationships between leaf traits and tree growth at the tree-level, and between leaf traits or tree growth and N_S or Ψ_{pre} at the plot-level (Figs. S2–S4). The Pearson's correlation analysis was used to explore correlations between leaf economics and hydraulics traits at the tree-level.

To avoiding potential overfittings in the exploration of the best predictor for TB and TBI, we performed the Principal Component Analysis (PCA) for the six leaf traits investigated at the tree-level. Based on the PCA results, we used the linear mixed effects models for TB or TBI and selected the best fitted model by the backward elimination procedure and Akaike information criterion (AICc function in MuMin package), which included K_{area} and LMA as the predictors for TB, and P_{50} and N_L for TBI. To quantify the relative contribution of each selected trait to TB or TBI, the variation partitioning in the vegan package was used. The data were 10-based log transformed if necessary. All the data analyses were performed with the R v4.0.2 (R Core Team, 2020).

Table 1
The Pearson's correlation coefficients between leaf traits.

	K_{area}	P_{50}	TLP	A_{area}	LMA
K_{area}					
P_{50}	-0.48**				
TLP	-0.41*	0.3			
A_{area}	-0.64***	0.37*	0.39*		
LMA	-0.55**	0.59***	0.51**	0.8***	
N_L	-0.4*	0.48**	0.54**	0.3	0.47**

Refer to Fig. 1 for the symbols and acronyms. The bold numbers denote statistical significant at $\alpha = 0.05$ level. ***, $p < 0.01$; **, $p < 0.01$; *, $p < 0.05$; $n = 29$.

3. Results

3.1. Intraspecific variations in leaf traits along the toposequence

The leaf hydraulics traits significantly varied along the transect ($p < 0.05$; Fig. 1). Specifically, the K_{area} on toe- and top-slope were greater ($36.5 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$) than that on mid-slope ($22.1 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$). The P_{50} on toe-slope was the greatest (-1.42 MPa), while that on mid-slope was the lowest (-2.50 MPa). Additionally, mid-slope had the lowest TLP (-2.22 MPa). K_{area} was negatively correlated with P_{50} and TLP (Table 1).

The leaf economics traits also changed with the slope locations (Fig. 1). The intraspecific variations in A_{area} and LMA were not significant, fluctuating between $5.55\text{--}7.68 \text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $0.045\text{--}0.068 \text{ kg}\cdot\text{m}^{-2}$, respectively. However, the N_L on mid-slope ($34.7 \text{ mg}\cdot\text{g}^{-1}$) was significantly ($p < 0.05$) greater than that on toe-slope ($28.6 \text{ mg}\cdot\text{g}^{-1}$). There was a significant ($p = 0.08$) correlation between N_L and LMA, but no significant ($p > 0.10$) correlation between A_{area} and N_L (Table 1). A_{area} , LMA, and N_L were significantly correlated negatively with K_{area} , but positively with P_{50} and TLP.

N_S and Ψ_{pre} varied significantly along the transect (Fig. 1). Top-slope had significantly higher N_S ($9.89 \text{ mg}\cdot\text{g}^{-1}$) but lower Ψ_{pre} (more negative, -0.54 MPa) than toe-slope (N_S , $5.53 \text{ mg}\cdot\text{g}^{-1}$; Ψ_{pre} , -0.28 MPa). P_{50} , TLP, LMA, and N_L were positively correlated with N_S (Fig. S2), but not significantly ($p > 0.05$) with Ψ_{pre} (Fig. S3).

3.2. Intraspecific variations in tree growth and associated with leaf traits

The tree growth and biomass accumulation were the greatest on mid-slope (Fig. 1), where the DBH, DBHI, TB and TBI were 116%, 312%, 138%, and 376%, respectively, greater than the mean values on toe- and top-slopes (15.6 cm , $0.034 \text{ cm}\cdot\text{yr}^{-1}$, 98.3 kg , and $0.53 \text{ kg}\cdot\text{yr}^{-1}$, respectively). Both TB and TBI were significantly and positively correlated with N_S , rather than Ψ_{pre} (Fig. S4).

The leaf economics and hydraulics traits were all positively correlated with TB and TBI except K_{area} that was negatively correlated (Figs. 2 and 3). The PCA analysis of the six leaf traits investigated (Fig. 4) showed that Axis 1 was mainly loaded by K_{area} , A_{area} and LMA (35% of the variation), Axis 2 by P_{50} and N_L (28% of the variation), and Axis 3 by TLP (20% of the variation). Based on the PCA results and the backward-elimination selection, the final model for TB included K_{area} and LMA as the predictors, while that for TBI included P_{50} and N_L . Further variation partitioning showed that K_{area} and LMA explained 2.5% and 21.9% of the variation in TB, and their interactions explained additional 26.2%; P_{50} and N_L explained 22.5% and 1.1% of the variation in TBI, and their interactions explained additional 23.1% (Fig. 5).

4. Discussion

4.1. Intraspecific variations in leaf traits and tree growth along the larch toposequence

We found significant intraspecific variations in leaf traits with contrasting trends of leaf economics (A_{area} , LMA and N_L) and hydraulics traits (K_{area} , P_{50} and TLP) in response to the changes in site conditions along the larch toposequence (Fig. 1); this indicates that trees adjusted their leaf traits to acclimate local site conditions (Anderegg and HilleRisLambers, 2015; Rosas et al., 2019). Compared with the top and toe-slope, the trees on mid-slope tended to have lower leaf hydraulic conductivity, and higher capacity of water-stress resistance (more negative P_{50} and TLP, Fig. 1), which were significantly correlated with N_S (Fig. S2). This result showed partly consistent with previous intraspecific results of negative correlations between hydraulic traits and soil N content (Faustino et al., 2013), but inconsistent with interspecific results of no correlations (Villagra et al., 2013). Conversely, relative to the top- and toe-slope, the trees on mid-slope tended to have a higher LMA and N_L (Fig. 1D) with positive correlations with N_S (Fig. S2). Therefore, the intraspecific variations in leaf hydraulics and economics traits are significantly affected by site conditions, especially by soil N content.

Coordination between leaf traits is crucial for trees to acclimate environmental changes (Poorter et al., 2009; Maire et al., 2015). Previous studies have widely verified the LES interspecifically, but less certain is whether the LES holds intraspecifically (Blackman et al., 2017), especially whether leaf hydraulics traits can be integrated into the LES (Reich, 2014; Blackman et al., 2017). We found that K_{area} , P_{50} and TLP were significantly correlated with A_{area} , LMA and N_L for the larch trees (Table 1), suggesting leaf hydraulics are coordinated with the economics traits within this species, i.e., stronger drought tolerance associated with more C and N investments at the price of lower leaf hydraulic conductance, supporting our second hypothesis. However, our results showed that A_{area} was negatively correlated with K_{area} (Table 1), which contradicted to the interspecific positive relationships reported previously (Brodrribb et al., 2007). A possible reason for this discrepancy is that the effect of leaf structure on the leaf hydraulics and economics among species may be different from that within species because of leaf longevity. The normal LES states that slow-growing species have thicker leaves with greater LMA and longevity, but less N_L , K_{area} and thus A_{area} than fast-growing species (Wright et al., 2004; Reich, 2014). In our case, the larch trees were reported to have no significant difference in leaf longevity with environmental changes (Quan and Wang, 2018). Nevertheless, A_{area} and N_L were positively correlated with LMA (Table 1), suggesting that the trees may modify the leaf structure and/or physiology in response to changes in site conditions. The positive correlation between LMA and P_{50} and negative between P_{50} and K_{area} (Table 1) also indicated the prominent role of leaf C economy in developing leaf hydraulic efficiency-safety trade-off. Thus, it is important to note that leaf traits correlations may differ between inter- and intra-specific, which need more investigations especially for tree species without leaf longevity changes.

Our results also showed that the trees on mid-slope with higher photosynthetic rate possessed greater tree growth (DBHI and TBI) and thus biomass accumulation (DBH and TB) than those on toe- and top-slope (Fig. 1), supporting our first hypothesis. The causes for this pattern are not certain because we did not survey all the associated abiotic factors. However, several pieces of evidence showed that soil conditions, especially soil N content play important roles in the tree growth. First, all the trees along the transects were planted in 1986 with the same aged seedlings from the same orchard, which minimized the potential biotic differences along the transects. Second, the 1000-m transects are rather gentle with changes in the mean annual temperature $< 1.2 \text{ }^\circ\text{C}$, and thereby with similar climate conditions. Third, substantial changes in N_S and Ψ_{pre} (a proxy of soil moisture (Ameglio

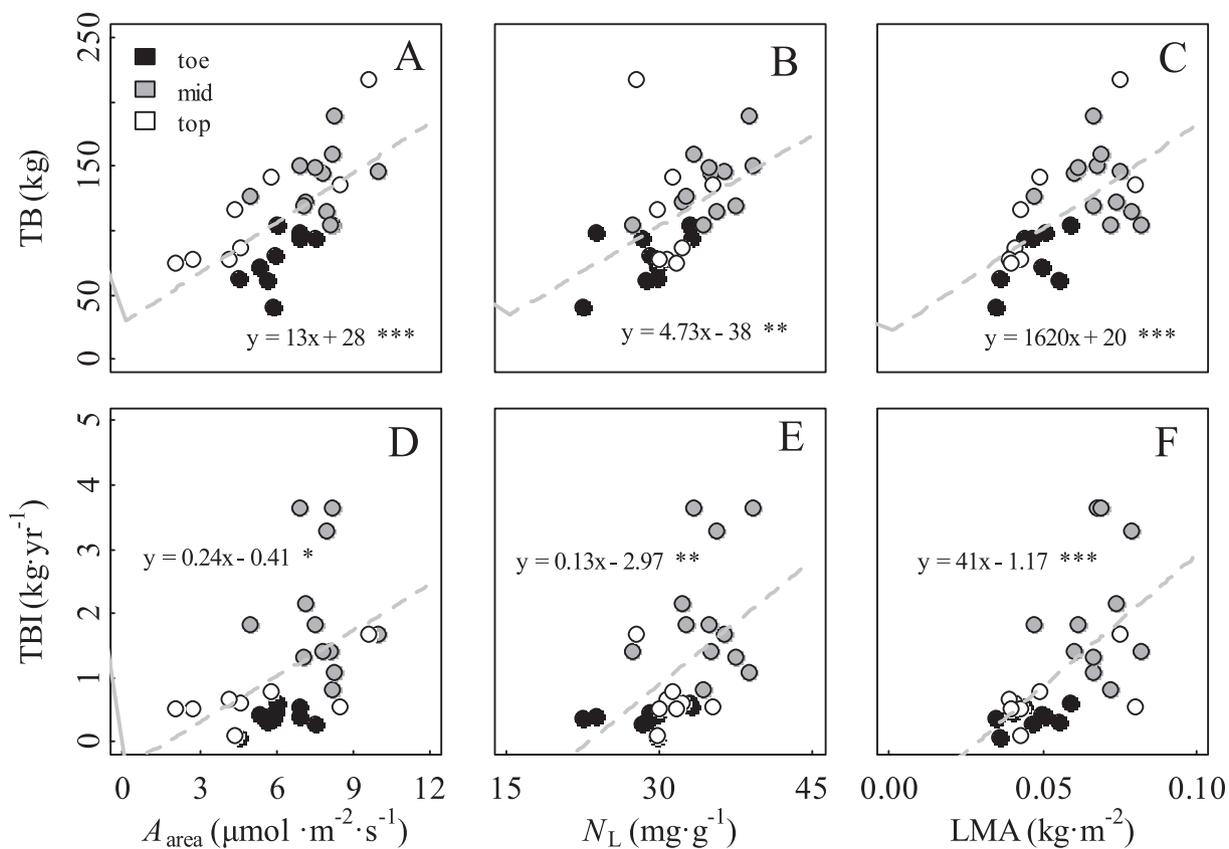


Fig. 2. Relationships between tree growth and leaf economics traits. The values were calculated from individual trees. $n = 29$, ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. Refer to Fig. 1 for the symbols and acronyms.

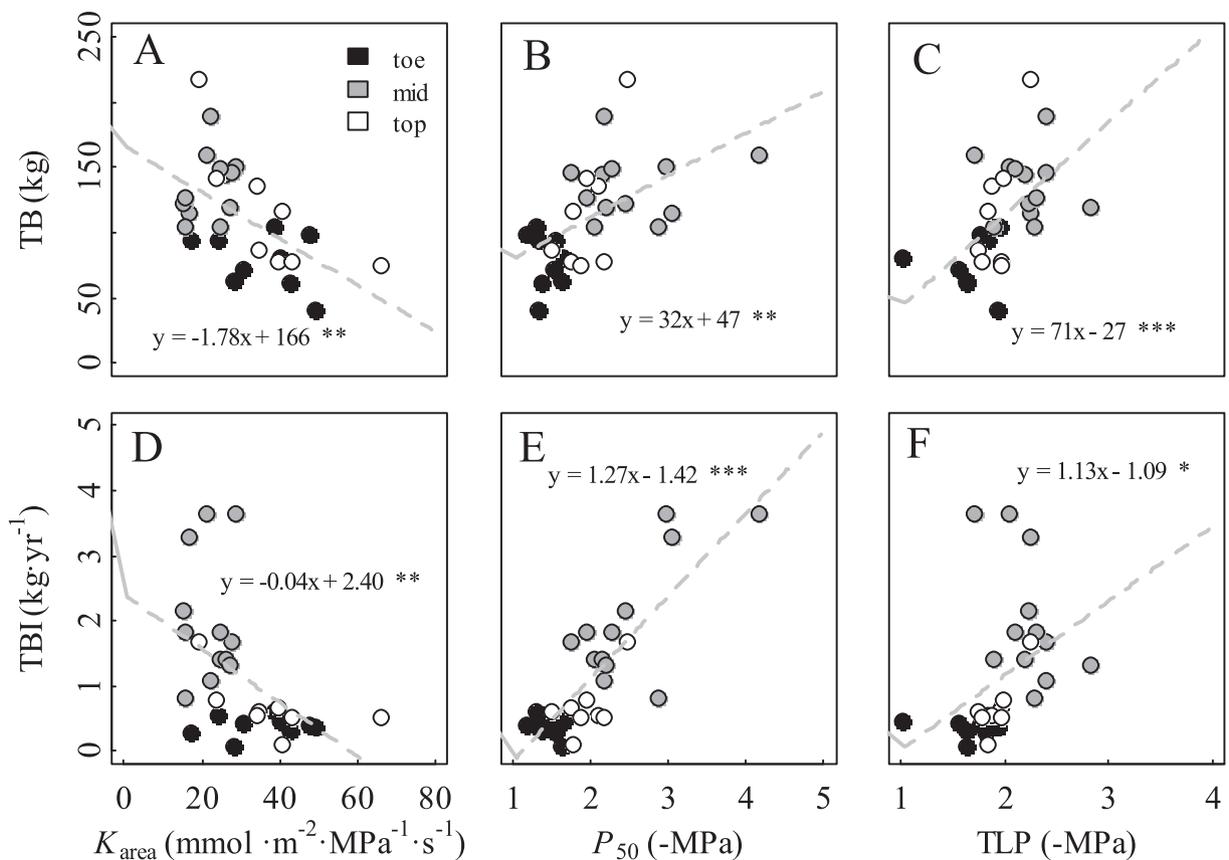


Fig. 3. Relationships between tree growth and leaf hydraulic traits. $n = 29$, ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. Refer to Fig. 1 for the symbols and acronyms.

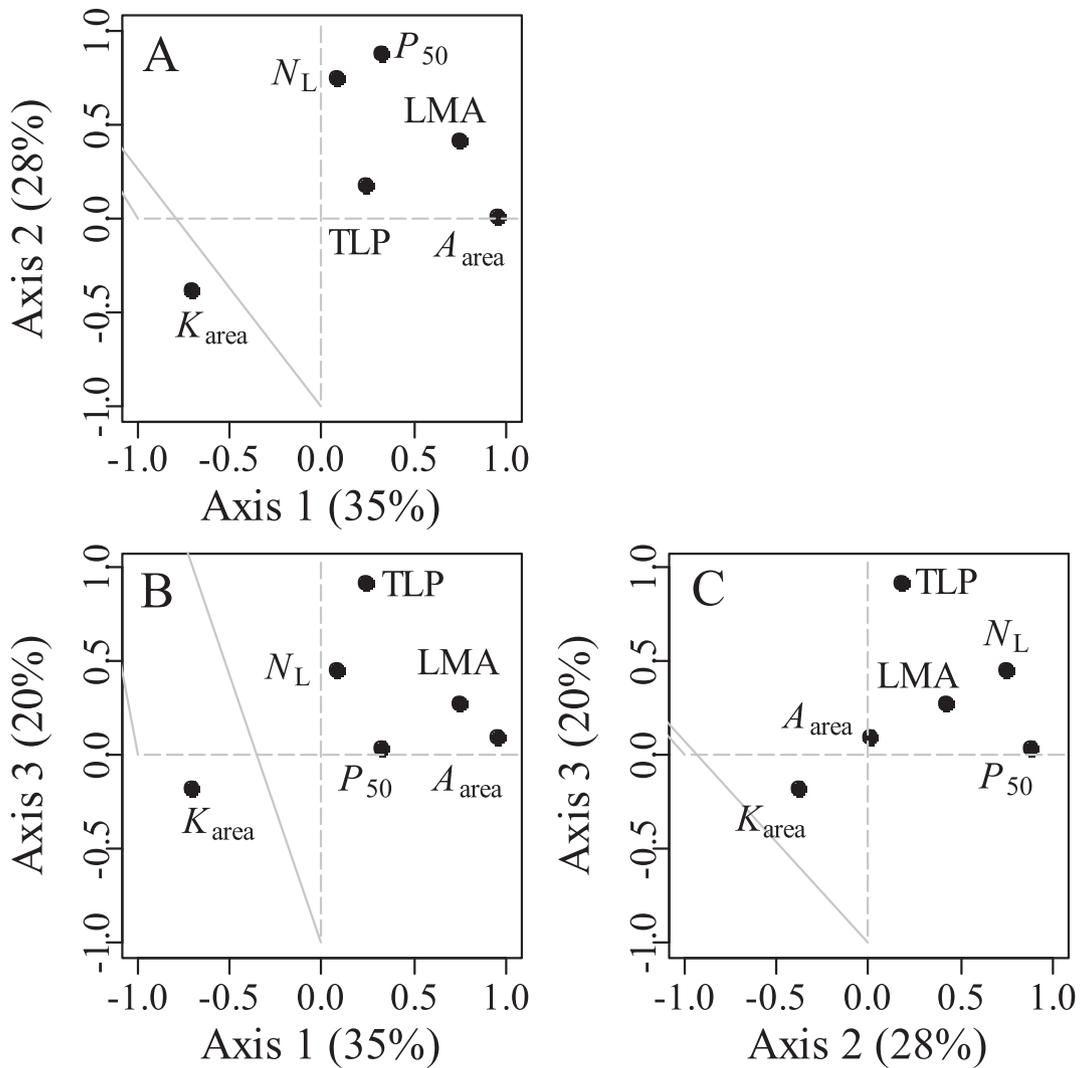


Fig. 4. The Principal component analysis of six leaf traits investigated. All traits are 10-based log transformed. Refer to Fig. 1 for the symbols and acronyms.

et al., 1999)) were detected along the transects (Fig. 1). Top-slope had higher N_S but lower Ψ_{pre} , while toe-slope had lower N_S but higher Ψ_{pre} , and mid-slope was in between; this suggests that the trees in mid-slope may be favorable for growth in both soil nutrition and moisture status. Further exploration showed that the growth was more significantly influenced by N_S than by Ψ_{pre} (Figs. S3 and S4). Soil N availability not only increases leaf N concentration (Fig. 2) for metabolic functions such

as photosynthesis and growth (Ordoñez et al., 2009; Palmroth et al., 2014; this study), but also indirectly affects tree growth rate via changing tree water transport systems (Goldstein et al., 2013, more discussion in Section 4.2). Collectively, soil N content is likely a major player in the tree growth along the toposequence.

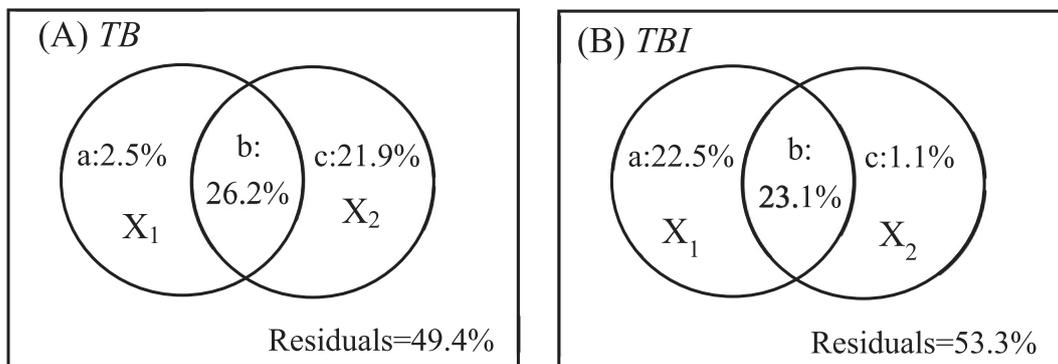


Fig. 5. Variations in biomass accumulation (TB) and growth rate (TBI) partitioned into two groups of explainable factors. Refer to Fig. 1 for the symbols and acronyms. K_{area} and LMA were the X1 and X2 for TB, respectively, and P_{50} and N_L were the X1 and X2 for TBI, respectively. The numbers in the circles represent percentages of the total variation in TB or TBI explained. a and c are unique effects, and b is the fraction of the joint effect.

4.2. Modelling larch tree growth with leaf traits

Leaf economics traits have been extensively used to predict tree growth (Poorter and Bongers, 2006; Grady et al., 2013; Reich, 2014). In this study, we found that the TBI and TB of the larch were significantly correlated with N_L (Fig. 2) and N_S (Fig. S2), supporting to some extent that interspecific relationships between leaf traits and tree growth can also be extended intraspecifically. However, such extensions may have some variants. Although the biomass accumulation in the larch increased with A_{area} and N_L , it accompanied with more investment into leaf structure (i.e., higher LMA). Possen et al. (2014) also found that the total biomass of *Betula pendula* was correlated with LMA. Grady et al (2013) reported that *Populus fremontii* with greater growth rate in the hot desert-riparian condition had higher LMA than that in other conditions, which might be caused by the limitation of leaf water loss through increasing water use efficiency under the hot-desert environment.

Hydraulics traits have been documented to have an important role on plant growth (Hoerber et al., 2014; Liu et al., 2018; Hernandez-Santana et al., 2019). Our results showed significant and negative relationships between K_{area} and tree growth or biomass accumulation (Fig. 3), suggesting leaf hydraulic efficiency decreased with tree size and growth rate. Such relationships may be attribute to a trade-off between relative growth rate and xylem safety given that tree growth rate and biomass accumulation were correlated negatively with K_{area} but positively with P_{50} and TLP (Table 1), in agreement with Fichot et al. (2011) who reported a negative correlation between the relative growth rate and the hydraulic efficiency for eight *Populus* hybrids.

The aforementioned results support our third hypothesis that leaf economics and hydraulics traits can predict the growth and biomass accumulation. To identify which traits were better predictors, we performed the variation partitioning and found that LMA (21.9%) contributed to TB much more than K_{area} (2.5%) (Fig. 5A), whereas P_{50} (22.5%) contributed to TBI much more than N_L (1.1%) (Fig. 5B); both TB and TBI were influenced by the interactions between hydraulic and economic variables. Collectively, these findings convey at least two implications. First, leaf hydraulics and economics play respective roles on the short-term C fluxes and relatively long-term C stocks of the larch trees. The ability of tolerance to hydraulic dysfunction is a more important driver of the tree growth than the leaf N content, whereas the capacity of C assimilation is a more important player in the biomass accumulation than the hydraulic conductivity. Second, leaf hydraulics and economics traits are strongly coupled with each other and interactively predict in the tree growth and biomass accumulation of the larch trees.

5. Conclusion

Our toposequence study of Dahurian larch from the same provenance showed that the leaf traits and tree growth varied significantly with slope position, but the variation patterns depended upon the metrics of traits. Along the toe-, mid- and top-slope with changing soil N concentration and moisture status, the hydraulics traits (K_{area} , P_{50} and TLP) showed a “high-low-high” pattern, while the economics traits (A_{area} , LMA and N_L) displayed an opposite trend, in accordance with those of tree growth and biomass accumulation (TBI and TB). These results suggested that the intraspecific variations in tree growth were coupled with those in leaf hydraulics and economics traits, which were mainly affected by soil N and moisture regimes. The variability in biomass accumulation was mainly explained by the capacity leaf C assimilation, while that in tree growth was mainly explained by the ability of leaf to tolerance drought. These findings extend the leaf economics spectrum intra-specifically and provide insights into tree growth associated with leaf traits in response to changes in site conditions, which have important implications in modeling and management of forest production.

CRedit authorship contribution statement

Zhimin Li: Investigation, Formal analysis, Methodology, Writing - original draft. **Chuanquan Wang:** Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing. **Dandan Luo:** Investigation, Writing - review & editing. **Quanzhi Zhang:** Investigation, Writing - review & editing. **Ying Jin:** Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118611>.

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