



Effects of ontogenetic stage and leaf age on leaf functional traits and the relationships between traits in *Pinus koraiensis*

Meng Ji^{1,2} · Guangze Jin^{1,2} · Zhili Liu^{1,2}

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Abstract Investigating the effects of ontogenetic stage and leaf age on leaf traits is important for understanding the utilization and distribution of resources in the process of plant growth. However, few studies have been conducted to show how traits and trait-trait relationships change across a range of ontogenetic stage and leaf age for evergreen coniferous species. We divided 67 *Pinus koraiensis* Sieb. et Zucc. of various sizes (0.3–100 cm diameter at breast height, DBH) into four ontogenetic stages, i.e., young trees, middle-aged trees, mature trees and over-mature trees, and measured the leaf mass per area (LMA), leaf dry matter content (LDMC), and mass-based leaf nitrogen content (N) and phosphorus content (P) of each leaf age group for each sampled tree. One-way analysis of variance (ANOVA) was used to describe the variation in leaf traits by ontogenetic stage and leaf age. The standardized major axis method was used to explore the effects of ontogenetic stage and leaf age on trait-trait relationships. We found that LMA and LDMC increased significantly and N and P decreased significantly

with increases in the ontogenetic stage and leaf age. Most trait-trait relationships were consistent with the leaf economic spectrum (LES) at a global scale. Among them, leaf N content and LDMC showed a significant negative correlation, leaf N and P contents showed a significant positive correlation, and the absolute value of the slopes of the trait-trait relationships showed a gradually increasing trend with an increasing ontogenetic stage. LMA and LDMC showed a significant positive correlation, and the slopes of the trait-trait relationships showed a gradually decreasing trend with leaf age. Additionally, there were no significant relationships between leaf N content and LMA in most groups, which is contrary to the expectation of the LES. Overall, in the early ontogenetic stages and leaf ages, the leaf traits tend to be related to a "low investment-quick returns" resource strategy. In contrast, in the late ontogenetic stages and leaf ages, they tend to be related to a "high investment-slow returns" resource strategy. Our results reflect the optimal allocation of resources in *Pinus koraiensis* according to its functional needs during tree and leaf ontogeny.

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✉ Zhili Liu
liuzl2093@126.com

¹ Center for Ecological Research, Northeast Forestry University, Harbin 150040, People's Republic of China

² Key Laboratory of Sustainable Forest Ecosystem Management—Ministry of Education, Northeast Forestry University, Harbin 150040, People's Republic of China

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Introduction

Trees, as long-lived organisms, increase in size and structural complexity during ontogeny. Increasing tree age may result in changes in leaf mechanical strength, hormonal regulation, vegetative/reproductive allocation, the ability to absorb nutrients, and adaptation to environmental conditions, all of which may induce associated changes in tree structure and function (Thomas 2011; Martin and Thomas

2013; Damián et al. 2018; Song et al. 2019). Thus, tree age or ontogenetic stage may be an important cause of trait variation (Steppe et al. 2011; Kuusk et al. 2018). Leaves, as the main organs of photosynthesis in plants, serve as energy converters for primary producers in ecosystems. The growth development and trait characteristics of leaves directly influence the basic behavior and functioning of a plant (Poorter et al. 2008; Falster et al. 2018). Previous studies have suggested that the expression of leaf traits, i.e., leaf thickness, leaf mass per area (LMA), mass-based leaf nitrogen (N) content, and phosphorus (P) content, may vary by ontogenetic stage (England and Attiwill 2005; Juárez-López et al. 2008; Palow and Kitajima 2012; Liu et al. 2020;). However, previous studies on functional traits have generally focused on a certain ontogenetic stage (Azuma et al. 2019) or comparisons based on young and mature individuals (i.e., young trees and canopy trees) (Greenwood et al. 2008; Mediavilla and Escudero 2009; Palow and Kitajima 2012; Kuusk et al. 2018), with fewer studies based on all ontogenetic stages. The trait variation in the early and middle stages of ontogeny may differ from that in the later stages of ontogeny (Thomas and Winner 2002; Thomas 2010). Revealing variations in traits throughout ontogenetic stages will advance our understanding of the causes of intraspecific trait variation.

For evergreen coniferous trees with long leaf longevity, resource investment, allocation patterns, and trait characteristics vary with leaf age (Reich et al. 1991; Pantin et al. 2012; Mediavilla et al. 2014; Liu et al. 2020). For example, studies have shown that LMA and leaf dry matter content (LDMC) increase and N decreases with leaf age (Niinemets and Lukjanova 2003; Niinemets et al. 2006; Han et al. 2008; Liu et al. 2020). Details of the various patterns of leaf functional traits by leaf age are helpful for better understanding the adaptive strategies used by plants to maximize carbon-gain, which is the basis for explaining the mechanisms that maintain community structure and optimize productivity (Kikuzawa and Lechowicz 2011).

Recently, the study of plant functional traits has not been limited to single or grouped traits, but the interconnections and trade-offs between traits have received more attention (Wright et al. 2004, 2005; Osnas et al. 2013; Cui et al. 2020). The leaf economic spectrum (LES) describes the coordinated variation in leaf structural, chemical and physiological traits over a resource gradient, reflecting the trade-off between cost in leaf structure and resource return time for leaf economic traits (Wright et al. 2004). However, the LES is based on multivariate analyses of cross-species data and does not distinguish interspecific and intraspecific trait-trait relationships. Additionally, the application of the LES is mainly focused on the adaptation of leaf traits to abiotic factors, i.e., precipitation, temperature, elevated CO₂ and soil fertility (Wright et al. 2005; Ordoñez et al. 2009; Kikuzawa et al. 2013; Cui et al. 2020;). However, several studies have

shown that the plant ontogenetic stages are a nonnegligible factor in the LES (Niinemets 2015; Siefert et al. 2015; He and Yan 2018; He et al. 2019; Liu et al. 2019). Therefore, understanding the connections and trade-offs between functional traits in different ontogenetic stages is essential to improve the predictive ability of the LES.

Pinus koraiensis Sieb. et Zucc. is the keystone species of the zonal climax vegetation (mixed broadleaved-Korean pine (*Pinus koraiensis*) forest) in northeastern China. Revealing the variation in leaf traits during tree ontogeny and leaf ontogeny is important for understanding plant trade-off strategies and species coexistence mechanisms. In this study, we collected leaf samples from 67 *P. koraiensis* trees across a wide range of tree sizes (0.3–100 cm diameter at breast height (DBH)). We determined the age of each tree and divided them into four groups, i.e., young trees, middle-aged trees, mature trees and over-mature trees, based on the characteristics of the different ontogenetic stages of *P. koraiensis* (Zu 1987). We measured four leaf functional traits, including two leaf morphological traits (i.e., LMA and LDMC) and two leaf chemical traits (i.e., N and P), in the different ontogenetic stages and leaf ages. Our aim was to explore the effects of ontogenetic stage and leaf age on leaf traits and to reveal whether and how ontogenetic stage and leaf age modulates the leaf trait-trait relationships.

Materials and methods

Study site

The field work was conducted at the Liangshui National Natural Reserve (47°10'50" N, 128°53'20" E) in northeastern China. The reserve is the most typical and complete mixed coniferous and broad-leaved forest system in the northern temperate zone remaining in China. The reserve has a total forested area of 1.88 million m³. It is situated 280–707 m above sea level and has an average slope of 10°–15°. The region has a temperate continental monsoon climate regime, characterized by cold, dry winters and warm, wet summers. The mean annual temperature is –0.3 °C, the mean maximum temperature is 7.5 °C, and the mean minimum temperature is –6.6 °C. The mean annual precipitation is 676 mm, and the average number of days of precipitation is 120–150 d. The annual snow accumulation period is 130–150 d.

Experimental design

Here, we aimed to systematically reveal the effects of ontogenetic stage and leaf age on leaf traits and trait-trait relationships. In mid-October 2018, when the elongation of the current-year shoots was complete, we selected 67 *P.*

koraiensis across a wide range of tree sizes (0.3–100 cm DBH) in the mixed broadleaved-Korean pine forest. There were 2 individuals with $DBH < 1.0$ cm (measured with a Vernier caliper, and base diameter was used instead of DBH), 29 individuals with $1.0 \leq DBH < 30$ cm (the difference in the DBH between the closest individuals was ca. 1 cm), and 36 individuals with $30 \leq DBH \leq 100$ cm (the difference in the DBH between the closest individuals was ca. 2 cm). We also measured tree height and tree age based on the relationship between DBH and the age of each sampled *P. koraiensis* (Hu et al. 2009). Then, we divided the 67 *P. koraiensis* into four tree age groups, i.e., age group I: young trees (1–80 years), age group II: middle-aged trees (81–140 years), age group III: mature trees (141–200 years), and age group IV: over-mature trees (> 201 years) (Zu 1987). The basic information for the *P. koraiensis* individuals in the different tree age groups is summarized in Table 1.

One sample branch (containing all leaf age classes) was collected from the south side of the upper one-third of the exposed canopy for each individual by a professional climber. All the sample branches from the 67 individuals were collected within three consecutive days. We determined the needle age class based on the possible presence of polycyclic shoots and the relative darkness and hardness of the leaves (Eimil-Fraga et al. 2015). The current-year leaves were defined as 0 years old. The leaves formed the previous year were the 1-year-old leaves and so on. All the existing leaves of different leaf ages were collected from each sample branch. To prevent the leaves from losing water, the collected sample leaves were immediately sealed in plastic bags and transported to the laboratory for the determination of morphological and chemical traits.

Leaf trait measurements

Four functional traits, i.e., LMA (g m^{-2}), LDMC (mg g^{-1}), N (mg g^{-1}), and P (mg g^{-1}), were determined for each leaf age class. LMA is closely related to investment in leaf construction and is an important indicator reflecting plant ecological strategies (Westoby et al. 2002). LDMC indicates the leaf water content, storage capacity and strategies for distributing nutrients and substances (Hodgson et al. 2011). N and P are important elements that affect plant metabolism,

energy transmission and ecological processes (Abdala-Roberts et al. 2018; Guo et al. 2020).

We counted the total needle number and measured the average needle length using a ruler (0.1 cm) and the leaf fresh mass (LFM, g) with an electronic balance (0.0001 g). The total needle volume was determined by the volume displacement method (Chen et al. 1997) for each leaf age group. The total needle area for each leaf age group was calculated using the equation from Liu et al. (2020). The sample needles were then dried at 65 °C for 72 h and weighed to obtain the leaf dry mass (LDM, g). The LMA and LDMC were calculated as:

$$\text{LMA} = \text{LDM}/\text{LA} \quad (1)$$

$$\text{LDMC} = \text{LDM}/\text{LFM} \quad (2)$$

The total N was measured by the indophenol blue colorimetric method and the total P was measured by the Mo-Sb colorimetric method using AQ2 automatic discontinuous chemical analyzer (SEAL Analytical, Inc., USA) after the dried sample needles had been digested with $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$.

Statistical analysis

All the statistical analyses were performed using R-3.2.5 (R Core Team 2016). One-way analysis of variance (ANOVA) and least significant difference (LSD) tests were used to test the significant differences in leaf traits among the different tree age groups and leaf ages. The leaf trait values were \log_{10} -transformed before analysis because log-transformation approximately normalized the data. The standardized major axis (SMA) estimation method (Warton et al. 2006) was used to calculate the slope and intercept of the growth equation of any two leaf traits in each tree age group and for each leaf age. A likelihood ratio test was used to test the heterogeneity of the regression slope (Warton and Weber 2002). If there was no significant difference in the slopes, a common slope was used. If there was heterogeneity among the groups, multiple post hoc comparisons were performed. We determined the significance of the difference between the slope and 1. If the slope was significantly different from 1, it indicated that there was an allometric growth relationship

Table 1 Statistical information for *Pinus koraiensis* in four tree age groups (mean \pm SE). Different letters indicate significant differences between tree age groups ($p < 0.05$, Tukey's HSD)

Tree age group	Tree age (year)	DBH (cm)	Height (m)	Number of individuals
Young trees	39 \pm 2 ^d	9.19 \pm 1.19 ^d	7.37 \pm 0.83 ^d	15
Middle-aged trees	119 \pm 2 ^c	25.89 \pm 1.55 ^c	17.18 \pm 0.78 ^c	17
Mature trees	173 \pm 1 ^b	51.15 \pm 2.63 ^b	22.07 \pm 0.67 ^b	21
Over mature trees	242 \pm 4 ^a	80.49 \pm 1.92 ^a	27.78 \pm 0.42 ^a	14

between the two variables; if the difference was not significant, it indicated that there was an isometric growth relationship (Warton et al. 2006). The abovementioned data analysis was performed by the ‘agricolae’ package and ‘smatr’ package in R software (R Core Team 2016).

Results

Leaf trait variations

Variation in leaf traits with ontogenetic stage

The ontogenetic stage had significant effects on the LMA, LDMC, N and P ($p < 0.05$) (Fig. 1). The LMA and LDMC of the young trees were significantly lower than those of the middle-aged trees, mature trees and over-mature trees. The overall trend was that the LMA and LDMC showed an upward trend with increasing ontogenetic stage. However, N and P showed a downward trend with increasing ontogenetic stage.

Variation in leaf traits with leaf age

There was a significant difference in the leaf traits (LMA, LDMC, N and P) of leaves of different ages in the same tree age group ($p < 0.05$) (Fig. 1). For all tree age groups, the LMA and LDMC of the current-year leaves were significantly smaller than those of the older leaves ($p < 0.05$), but there was less variation in the LMA and LDMC of the 1-year-old, 2-year-old and 3-year-old leaves. Overall, LMA and LDMC showed an upward trend with increasing leaf age. For all tree age groups, N and P showed a significant downward trend with leaf age ($p < 0.05$). Among them, the N of the 1-year-old leaves was the largest, but there was no significant difference between the current-year and 1-year-old leaves, and the N of the 3-year-old leaves showed a sharp decline.

Trait-trait relationships

Variations in trait-trait relationships with ontogenetic stage

N decreased with LDMC in age group II (middle-aged trees), age group III (mature trees) and age group IV (over-mature

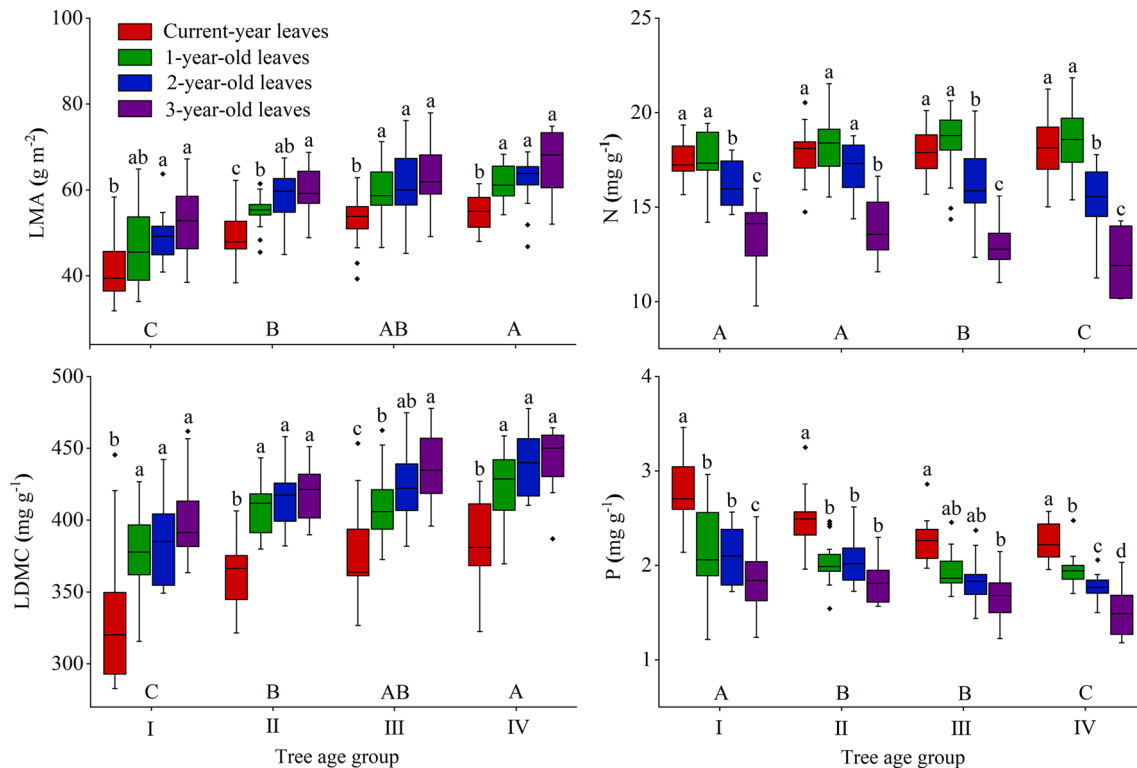


Fig. 1 Leaf mass per area (LMA), leaf dry matter content (LDMC) and mass-based leaf nitrogen content (N) and phosphorus content (P) of *Pinus koraiensis* in different tree age groups and with different leaf ages. I: young trees; II: middle-aged trees; III: mature trees; IV: over-mature trees. Different capital letters below the boxes indicate that the

leaf traits were significantly different among the four tree age groups. Different lowercase letters above the boxes indicate that the leaf traits were significantly different among a given leaf age for each tree age group ($p < 0.05$)

trees), and the slopes of the SMA regression exhibited the following pattern: age group II > age group III > age group IV. The relationship between the regression slopes was significant for age group II and age group IV ($p < 0.05$). The correlation between N and LDMC was not significant in age group I (young trees).

N increased with P in all tree age groups, and the slopes of the SMA regression exhibited the following pattern: age group I < age group II < age group III < age group IV. Additionally, among the regression slopes, there were significant relationships between age group I and the rest of the age groups as well as between age group II and age group IV ($p < 0.05$).

LDMC increased with LMA, and P decreased with LDMC in all tree age groups ($p < 0.05$). P decreased with LMA in age groups II, III and IV but was unrelated to LMA in age group I ($p < 0.05$). Additionally, there was no heterogeneity in the SMA slopes for LDMC-LMA, P-LMA, or P-LDMC among the age groups ($p > 0.05$), and the common slopes were significantly different from 1 ($p < 0.05$). However, N showed a decreasing trend with the increase in LMA in age group IV ($p < 0.05$) but was unrelated to LMA in age groups I, II and III ($p > 0.05$).

Variations in trait-trait relationships with leaf age

LDMC increased with LMA in all the leaf age groups ($p < 0.05$), and the SMA slopes showed a gradual increasing trend. There were significant relationships between the regression slopes of the current-year group and the rest of the leaf age groups ($p < 0.05$). P decreased with LDMC in the 1-year-old and 3-year-old leaves, and the relationship between the regression slopes of these groups was significant. N increased with P in the 2-year-old and 3-year-old leaves, but the relationship between the regression slopes was not significant. P decreased with LMA in the current-year and 2-year-old leaves, and there was no heterogeneity in the SMA slopes. N showed an increasing trend with the increase in LMA in the 1-year-old leaves ($p < 0.05$) but was unrelated to LMA in the rest of the leaf age groups.

Discussion

Leaf trait variations

Our results demonstrate that ontogenetic stages and leaf age had significant effects on the LMA, LDMC, N and P of *P. koraiensis* (Fig. 1), which may be due to genetic variation in trees and the response of plants to environmental factors, such as light intensity and soil nutrient availability (Scheepens et al. 2010; Wright et al. 2004).

Variation in leaf traits with ontogenetic stage

LMA and LDMC were lower and N and P were higher in the early ontogenetic stages, favoring a "low investment-quick returns" resource strategy, while the LMA and LDMC were higher and N and P were lower in the later ontogenetic stages, favoring a "high investment-slow returns" resource strategy (Wright et al. 2004; Reich and Cornelissen 2014; Reich and Flores-Moreno 2017).

LMA showed a significant increase with increasing ontogenetic stage, in agreement with the findings of previous studies (Greenwood et al. 2008; Kuusk et al. 2018). A lower LMA means a lower economic investment per leaf area, which contributes to higher resource-use efficiency and growth rates in young trees and may be a genetic ecological strategy in other plants (Wright et al. 2004; Steppe et al. 2011; He and Yan 2018). Additionally, the trees are increasing in size as they age. Tree size may have a greater effect than tree age on leaf structural and physiological traits (Ambrose et al. 2009; Mencuccini et al. 2017). In tall trees, light intensity and water-use efficiency change with the vertical gradient, which in turn leads to changes in leaf physiological characteristics (Ambrose et al. 2009; Coble and Cavaleri 2015; Chin and Sillett 2017). As tree height increases, increased evaporation requirements and restrictions on vertical water transport may limit the physiological function of upper canopy leaves (Woodruff and Meinzer 2011; Ishii et al. 2014), resulting in greater LMA in the leaves of tall trees. Because there is less evaporative surface area per leaf mass, increasing the LMA can effectively reduce the water loss from the leaves of tall trees (Richardson et al. 2000). Many studies have shown that hydraulic limitation is a key factor in the decline in the physiological functioning of trees (Kolb and Stone 2000; Koch et al. 2004). In addition, the greater LMA in the later ontogenetic stages may cause a higher electrical conductivity from the stomata to the chloroplast, which may limit photosynthesis (Niinemets 1997b; Cavaleri et al. 2010).

LMA and LDMC typically indicate a plant's ability to acquire nutrients and water. According to previous studies, LMA is sensitive to changes in light availability, and the higher the light availability, the higher the LMA (Niinemets and Kull 1995; Niinemets et al. 2001; Poorter et al. 2009), but LDMC does not change with the typical light environment (Hodgson et al. 2011). Therefore, compared with LMA, LDMC can better reflect the ability of plants to acquire resources (Roche et al. 2004; Hodgson et al. 2011). In this study, LDMC increased with increasing ontogenetic stage, which is consistent with the findings of some previous studies (Mason and Donovan 2014) but not all (He and Yan 2018). A smaller LDMC means a higher water content and a lower dry matter mass per volume (Wilson et al. 1999; Bill and Thi-Tam 2002; Pérez-Harguindeguy et al. 2013).

Overall, the smaller LMA and LDMC may reflect the tendency of young trees to allocate fewer resources to developing leaves, minimize investment and maximize returns, and achieve higher growth rates and biomass productivity, which benefits the competitive ability of young trees (Weiher et al. 1999; Saura-Mas and Lloret 2007).

N is the main component of chlorophyll and photosynthetic enzymes (Ordoñez et al. 2009). Therefore, the decline in N with ontogeny may reflect the reduction in the photosynthetic rate of leaves, which is consistent with previous studies (Gower et al. 1996; Niinemets 1997b; Merilo et al. 2009). However, N is also correlated with leaf tissue structure (Harrison et al. 2009; Takashima et al. 2004), and the increased investment in chemical defense substances by tall trees may also lead to an increase in N (Dominy et al. 2003; Boege 2005; Sendall and Reich 2013). Some studies have also found that N does not change with tree height or age (Day et al. 2001; Niinemets 2002).

P showed a significant downward trend with increasing ontogenetic stage; this finding is surprising because it seems to be inconsistent with previous observations (Palow and Kitajima 2012; Song et al. 2019). This may be the result of tree size altering the pattern of P allocation (Niinemets and Kull 2003). In general, shorter trees tend to allocate more P to their leaves to improve carbon acquisition efficiency, whereas taller trees may need to allocate more P to their roots (Niinemets and Kull 2003).

Variation in leaf traits with leaf age

Changes in leaf functional traits with leaf age can reflect plant life history strategies and the allocation of leaf resources (Niinemets et al. 2006; Han et al. 2008). LMA and LDMC increased and leaf N and P contents decreased significantly with increasing leaf age (Fig. 1), which is consistent with the widely observed patterns (Han et al. 2008; Liu et al. 2020). Furthermore, the various patterns of leaf functional traits with leaf age were similar in all the ontogenetic stages. The various patterns occur because, compared to old leaves, young leaves require more resources to optimize organ function and maximize light acclimation (Sultan 2000). Young leaves are at the "low investment-quick returns" end of the LES, which is helpful for seizing more resources as soon as possible and completing growth and reproduction quickly.

The LMA and LDMC of the current-year leaves were significantly lower than those of the older leaves in nearly all the tree age groups (Fig. 1), possibly because of the continuous accumulation and lignification of the cell wall during leaf aging (Mediavilla and Escudero 2003). Additionally, the current-year leaves have the lowest LDMC, which means that the leaves have sufficient water content to support a strong metabolic rate. This result confirms that younger leaves have greater photosynthetic potential

than older leaves (Escudero and Mediavilla 2003; Niinemets et al. 2006). Moreover, LMA and LDMC had less variation in the 1-year-old, 2-year-old and 3-year-old leaves. This may be because the structural traits of the older leaves are relatively stable. As trees grow, the longer-lived leaves retained on the older branches will be increasingly covered by the newly extended branches and leaves, so that older leaves usually exist in the shaded part of the canopy. According to previous studies, the light microenvironment can change the effects of needle aging on photosynthesis and coniferous structure (Robakowski and Bielinis 2017). However, some studies have shown that the structure of older needles is only slightly affected by changes in light intensity (Niinemets et al. 2006; Han et al. 2008). In addition, the ability of older leaves to adapt to different light conditions is usually less than that of younger leaves (Brooks et al. 1994; Oguchi et al. 2003). At the same time, needles usually do not change their anatomical structure (except for the secondary growth of vascular tissue) after full expansion in the first growing season (Ewers 1982). Therefore, needle structural traits vary less for older leaves.

In the shade canopy, older leaves may use different biochemical mechanisms to maximize carbon gains. For example, 1-year-old leaves may redistribute nitrogen to thylakoid proteins in a relatively short period of time to adapt to shaded environments (Brooks et al. 1994), which may increase the N in the leaves. This may be the reason why the N was higher in the 1-year-old leaves than in the current-year leaves in this study (Fig. 1). This result is in line with the study by Han et al. (2008). However, overall, N showed a downward trend with increasing leaf age, which is consistent with previous studies (Niinemets et al. 2006). Studies have shown that changes in N are mainly due to nitrogen dilution, which is attributable to the accumulation of nonstructural carbohydrates and an increase in needle carbon concentration with leaf aging (Niinemets 1997a; Niinemets et al. 2006; Han et al. 2008). It has also been shown that nutrients such as N and P can be transferred from senescent leaves and transported to other tissues to promote the growth of young leaves (Nambiar and Fife 1991; Killingbeck 1996;). In this study, there was no significant difference in the N between the current-year and 1-year-old leaves at different ontogenetic stages (Fig. 1). Even in the middle-aged trees, there was no significant difference in the N of the current-year, 1-year-old, and 2-year-old leaves. However, the N content of the 3-year-old leaves dropped sharply. The most likely reason for this is that the 3-year-old *P. koraiensis* leaves are close to the leaf life span, and senescent leaves begin to resorb N, which means that the leaves may be about to fall off. This result agrees with the findings of a study by Escudero and Mediavilla (2003).

Trait-trait relationships

The trait-trait relationships of *P. koraiensis* are generally consistent with the LES (Reich and Cornelissen 2014). For example, there were significant positive correlations between LDMC and LMA and between N and P and significant negative correlations between P and LMA, between N and LDMC, and between P and LDMC, with allometric growth relationships between the traits (Tables 2, 3 and Figs. 2, 3). Contrary to the expectation of the LES, leaf N content was significantly correlated with LMA in this study but only for the over-mature trees and 1-year-old leaves; the traits were negatively correlated for the former group and positively correlated for the latter group. However, there was no significant correlation between these traits for most groups. Niinemets (2015) also found that there was no significant correlation between N and LMA in *Quercus ilex*. This may be because the availability of forest nutrients in different soils and different geographic locations has a greater impact than tree age or leaf age on N (Niinemets 2002; Portsmouth et al. 2005; Portsmouth and Niinemets 2006; Juárez-López et al. 2008), while tree age or leaf age have greater impacts

on LMA. In addition, the relationship between N and LMA may vary among different species. Therefore, the relationship between N and LMA in the LES varies considerably at the intraspecies level (Siefert et al. 2015).

Variations in trait-trait relationships by ontogenetic stage

In our study, the SMA slope between N and LDMC and between N and P changed in different tree age groups, which is consistent with the findings of previous studies indicating that plant size may affect the patterns of some leaf trait-trait relationships (Liu et al. 2010; Niinemets 2015).

According to previous studies, more than half (up to 75%) of N is allocated to chloroplasts for photosynthesis (Warren and Adams 2002, 2006), and only 10–30% is allocated to the cell wall (Stitt and Schulze 1994), which can indirectly indicate leaf toughness. However, LDMC is generally considered an indicator of leaf toughness (Poorter et al. 2018), and a higher LDMC means that most of the tissue is composed of solid and heavy material. The negative correlation between N and LDMC reflects the differences of resource allocation and utilization by plants. In addition, the absolute

Table 2 Results of the standardized major axis (SMA) analysis of the correlations among the leaf mass per area (LMA), leaf dry matter content (LDMC) and mass-based leaf nitrogen content (N) and phosphorus content (P) of *Pinus koraiensis* in four tree age groups

y	x	Tree age group	Number of samples	R^2	Slope	Intercept	Common slope test (P)	Heterogeneity of slopes (P)
LDMC	LMA	I	58	0.562	0.689	1.421	0.526	<0.001
		II	66	0.529	0.618	1.525		
		III	80	0.615	0.626	1.506		
		IV	53	0.285	0.74	1.304		
N	LMA	I	56	0.07	–	–	–	<0.001
		II	66	0.043	–	–		
		III	67	0.044	–	–		
		IV	49	0.168	–1.666	4.18		
P	LMA	I	56	0.05	–	–	0.502	<0.001
		II	66	0.12	–1.296	2.575		
		III	67	0.404	–1.189	2.383		
		IV	49	0.306	–1.51	2.967		
N	LDMC	I	56	0.064	–	–	0.001	<0.001
		II	66	0.074	–1.789	5.878		
		III	76	0.108	–1.985	6.401		
		IV	49	0.251	–2.21	7.004		
P	LDMC	I	57	0.137	–1.849	5.092	0.905	<0.001
		II	66	0.167	–2.097	5.772		
		III	67	0.571	–1.964	5.405		
		IV	49	0.366	–2.003	5.527		
N	P	I	57	0.407	0.593	1.009	<0.001	<0.001
		II	66	0.18	0.853	0.952		
		III	67	0.273	0.996	0.939		
		IV	49	0.57	1.103	0.907		

I: young trees; II: middle-aged trees; III: mature trees; IV: over-mature trees. R^2 is the coefficient of determination of the SMA regression, with bold numbers indicating significant relationships ($p < 0.05$)

Table 3 Results of the standardized major axis (SMA) analysis of the correlation among the leaf mass per area (LMA), leaf dry matter content (LDMC), and mass-based leaf nitrogen content (N) and phosphorus content (P) of *Pinus koraiensis* at different leaf ages

y	x	Leaf age	Number of samples	R^2	Slope	Intercept	Common slope test (P)	Heterogeneity of slopes (P)	
LDMC	LMA	0	67	0.61	0.670	1.427	0.003	<0.001	
		1	67	0.524	0.455	1.814			
		2	67	0.627	0.499	1.741			
		3	56	0.342	0.459	1.811			
	N	LMA	0	67	0.032	–	–	–	<0.001
			1	67	0.146	0.571	0.265		
			2	67	0.003	–	–		
			3	47	0.025	–	–		
	P	LMA	0	64	0.265	–0.832	1.789	0.219	0.205
			1	64	0.103	–	–		
			2	64	0.068	–0.904	1.871		
			3	47	0.061	–	–		
N	LDMC	0	67	<0.001	–	–	–	–	
		1	67	0.012	–	–			
		2	67	0.026	–	–			
		3	47	0.022	–	–			
P	LDMC	0	64	0.191	–1.276	3.646	0.001	<0.001	
		1	64	0.036	–	–			
		2	64	0.149	–1.807	5.011			
		3	47	0.011	–	–			
N	P	0	64	<0.001	–	–	0.043	<0.001	
		1	64	0.053	–	–			
		2	64	0.173	0.827	0.979			
		3	47	0.301	0.783	0.939			

The leaf ages of 0, 1, 2 and 3 represent current-year leaves, 1-year-old leaves, 2-year-old leaves and 3-year-old leaves, respectively. R^2 is the coefficient of determination of the SMA regression, with bold numbers indicating significant relationships ($p < 0.05$)

values of the slopes of N and LDMC significantly increased with ontogenetic stage. This may be because the leaves of the later ontogenetic stages are exposed to higher light availability than the leaves of the early ontogenetic stages. Takashima et al. (2004) showed that oak plants grown under low light conditions (30% natural light) had higher chlorophyll content than those grown under high light conditions (90% natural light). Therefore, the leaves of the later ontogenetic stages have lower N and chlorophyll contents.

The significant positive correlation between N and P indicates that these elements exert a synergistic action to enhance the photosynthetic capacity of plants (Osaki et al. 1993). However, the slopes of the N–P relationships were steeper (more positive) with increasing ontogenetic stage in this study (Table 2 and Fig. 2), which reflects the difference in N and P utilization strategies during the ontogenetic stages of *P. koraiensis*. Liu et al. (2010) showed that P may be very limited in large trees rather than in small trees. However, light availability is greater for larger trees, and the leaves need more chlorophyll for photosynthesis to maintain growth in adulthood (Savage et al. 2016). Furthermore, tree

growth requires more N, which is used in mechanical support structures (Dean 2004).

Variations in trait-trait relationships with leaf age

Together, LMA and LDMC can indicate the growth strategies of plants in different ontogenetic stages. In this study, there were positive correlations between LDMC and LMA for the four leaf age groups; this is consistent with the results of previous studies of plants at different ontogenetic stages (Tables 2, 3 and Figs. 2, 3). However, with increasing leaf age, the SMA slopes of the LMA–LDMC relationship gradually flattened (the absolute value of the slope decreased). Among them, the slopes of the LMA–LDMC relationship between the leaves of the current year and those of the other age classes were significantly different. However, there were no significant differences in the slopes of the 1-year-old, 2-year-old or 3-year-old leaves, which indicated that the LDMC increased more with increasing LMA in the current-year leaves than in the previous-year leaves. This is possibly because the response

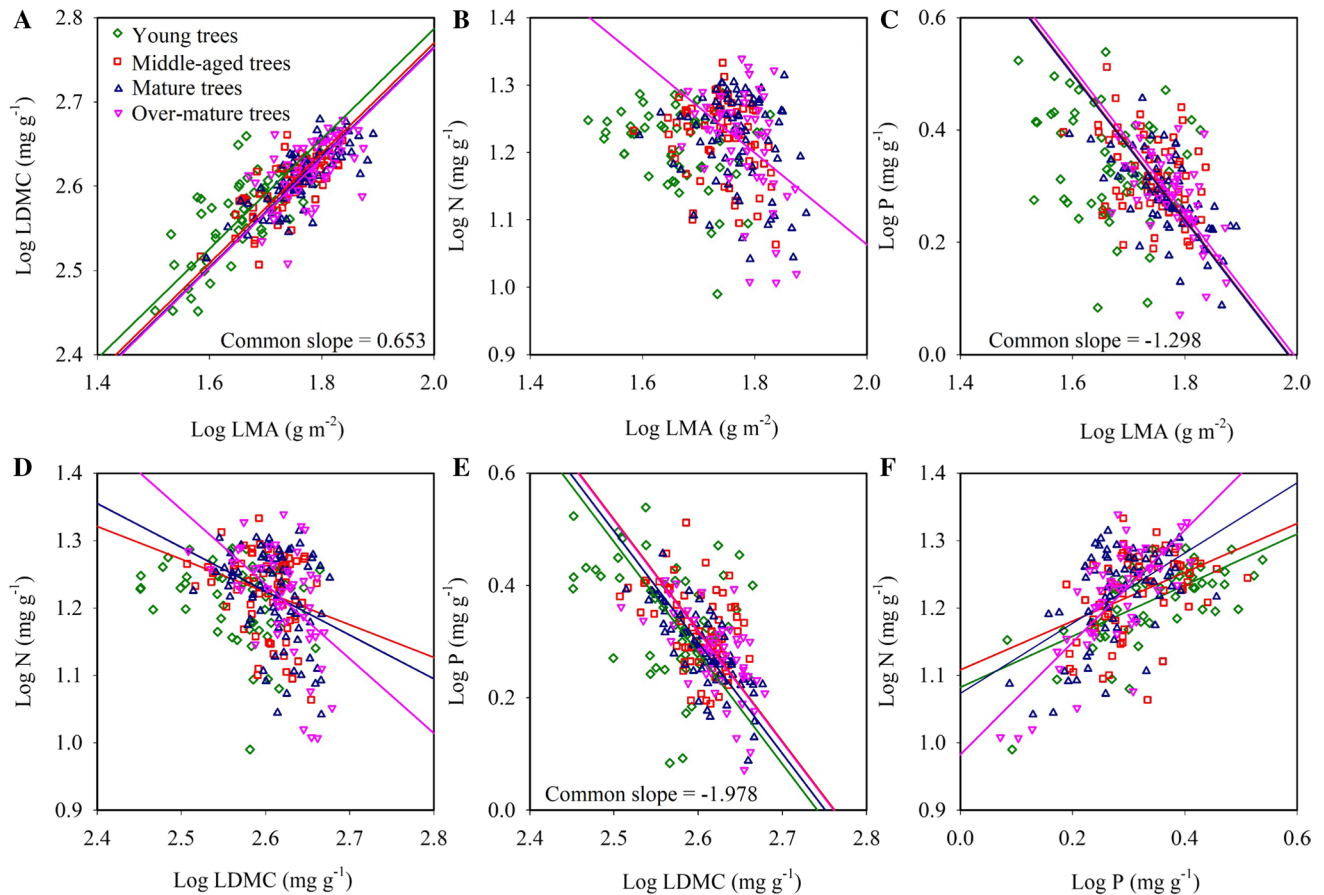


Fig. 2 Standardized major axis (SMA) relationships between the leaf mass per area (LMA) and leaf dry matter content (LDMC) (a), LMA and mass-based leaf nitrogen content (N) (b), LMA and mass-based leaf phosphorus content (P) (c), LDMC and N (d), LDMC and P (e)

and N and P (f) of *Pinus koraiensis* in four tree age groups. If there was no significant difference in the slopes of the regression lines, the common slope regression lines are shown. A line is not shown if there was not a significant correlation between the leaf traits

sensitivity between LMA and LDMC decreased with the accumulation of dry matter over the leaf life history.

Trait correlation is conducive to determining functional trade-offs and plant strategies; one functional trait can be used to infer another functional trait. Peng et al. (2018) constructed a model for estimating the specific leaf area based on LDMC and further separated the model by using the leaf age as the difference factor; the authors found that leaf age had an effect on the model, with older leaves having a lower model fit. This could be because changes in LDMC maintain a certain degree of relative independence (Garnier et al. 2001). In addition, in this study, N and LMA, P and LMA, N and LDMC, P and LDMC, and N and P were either significantly correlated in only a few leaf age classes or not correlated in any of the leaf age classes. This is probably because the structural traits (LMA and LDMC) and chemical traits (N and P) have different strategies for adapting to changes in leaf aging (Escudero and Mediavilla 2003; Niinemets et al. 2006).

Conclusion

In our study, ontogenetic stage and leaf age had positive effects on LMA and LDMC and negative effects on N and P, providing evidence that traits are affected by genetic variation and the response of plants to environmental factors. Our results also confirmed that most trait–trait relationships were consistent with the global leaf economic spectrum (LES). However, there were no significant relationships between N and LMA in most groups, which was contrary to the expectation of the LES. In addition, the absolute values of the slopes of the N–LDMC relationship and N–P relationship showed gradually increasing trends with ontogenetic stage, which suggests that the various patterns of some leaf trait–trait relationships could be modulated by ontogenetic stages. The absolute value of the slope of the LDMC–LMA relationship showed a gradually increasing trend with leaf age, but most pairwise–trait relationships were not significant, which suggests that leaf aging has different effects on

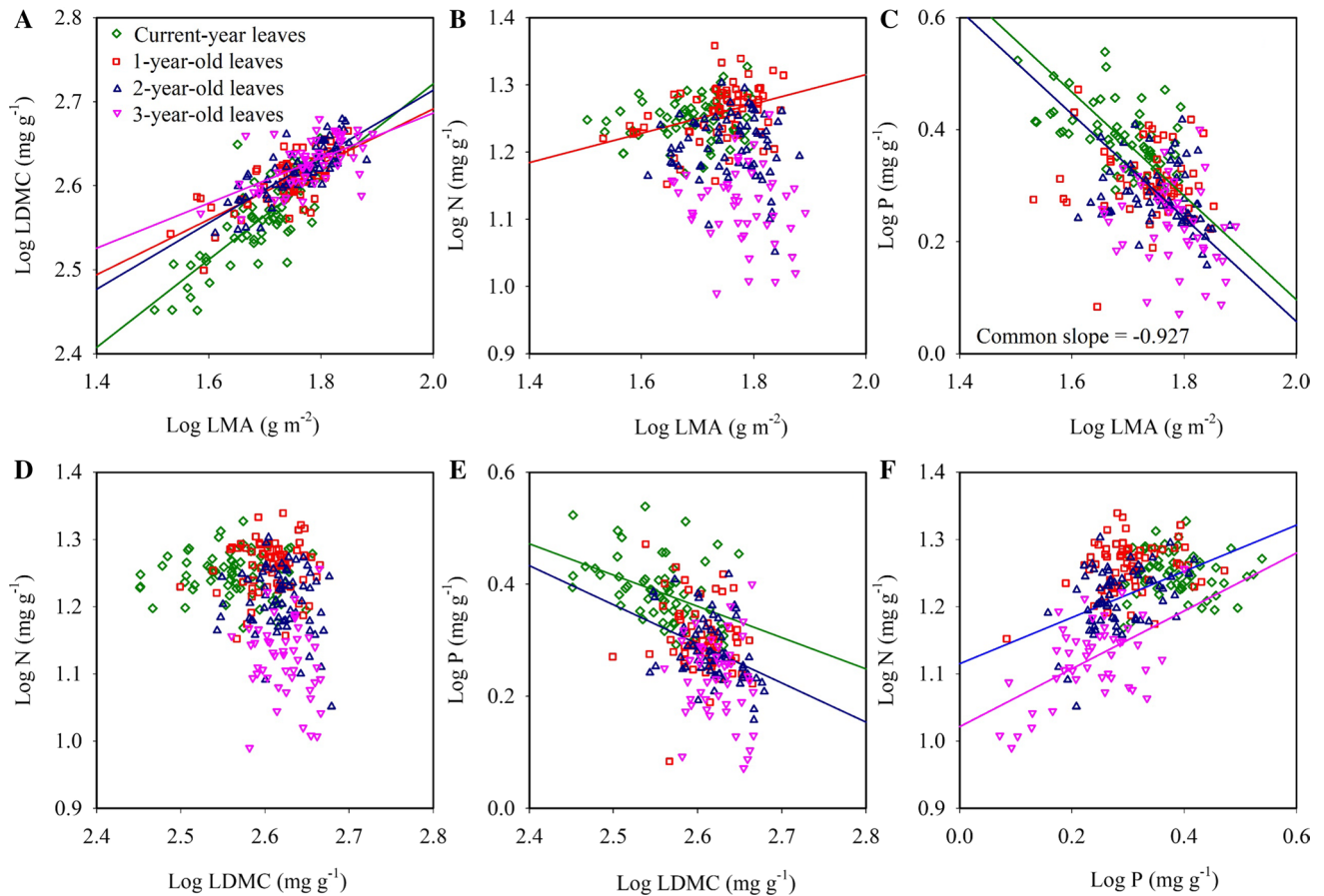


Fig. 3 Standardized major axis (SMA) relationships between the leaf mass per area (LMA) and leaf dry matter content (LDMC) (a), LMA and mass-based leaf nitrogen content (N) (b), LMA and mass-based leaf phosphorus content (P) (c), LDMC and N (d), LDMC and P (e)

and P and N (f) of *Pinus koraiensis* at different leaf ages. If there was no significant difference in the slopes of the regression lines, the common slope regression lines are shown. A line is not shown if the leaf traits were not significantly correlated

structural and chemical traits. Our study provides direct evidence for the coordination of LES traits within species and provides novel insights into understanding the LES at the intraspecific level.

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