



Changes in leaf stomatal traits of different aged temperate forest stands

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Abstract Stomata control carbon and water vapor exchange between the leaves and the atmosphere, thus influencing photosynthesis and transpiration. Combinations of forest patches with different stand ages are common in nature, however, information of which stomatal traits vary among these stands and how, remains limited. Here, seven different aged forest stands (6, 14, 25, 36, 45, 55, and 100 years) were selected in typical temperate, mixed broadleaf-conifer forests of northeast China. Stomatal density, size and relative area of 624 species, including the same species in stands of different ages were selected. Stomatal density, size and relative area were distributed log-normally,

differing across all species and plant functional groups. Stomatal density ranged from 4.2 to 1276.7 stomata mm⁻², stomatal size ranged from 66.6 to 8315.7 μm², and stomatal relative area 0.1–93.3%. There was a significant negative relationship between density and size at the species and functional group levels, while the relative stomatal area was positively correlated with density and size. Stomatal traits of dominant species were relatively stable across different stand ages but were significantly different for herbs. The results suggest that stomatal traits remain relatively stable for dominant species in natural forests and therefore, spatial variation in stomatal traits across forest patches does not need to be incorporated in future ecological models.

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Introduction

Leaf stomata are composed of a pair of guard cells, the opening and closing of which are driven by moisture, temperature, light, and carbon dioxide (CO₂) in the short term

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(Casson and Gray 2008; Lau and Bergmann 2012). Stomata allow plants to exchange gas with the external environment, controlling photosynthesis and transpiration (Martin and Glover 2007; Franks and Beerling 2009), in addition to influencing net primary productivity and water use efficiency of the ecosystem (Kim and Lieth 2003; Miyashita et al. 2005). Therefore, ecological models and earth system models consider stomatal traits as important parameters for effectively simulating carbon, water, and energy cycles (Kelliher et al. 1995). Although the importance of stomata from the view of plant physiological ecology has been acknowledged, information about natural forests remains limited.

Plants respond quickly to short-term environmental changes by opening and closing their stomata, while morphological traits of stomata such as stomatal density (SD), stomatal size (SS), and stomatal relative area (SRA, %), are the result of long-term adaptations to the external environment. Several studies have shown how morphological traits vary for certain dominant species and common species in natural forest communities (Tian et al. 2016; Wang et al. 2016; He et al. 2018; Liu et al. 2018, 2019). However, most studies have demonstrated these variations in controlled experiments, while focusing on the short-term behavior of

stomatal opening and closing (Luomala et al. 2005; Fraser et al. 2009; Engineer et al. 2015). With increasing CO₂ concentrations, SD decreases, causing maximum stomatal conductance to decline and photosynthesis to increase (Hetherington and Woodward 2003). SD is generally negatively correlated with SS (Stenstrom et al. 2002; Martin and Glover 2007; He et al. 2018); however, this relationship is not sufficiently compensatory to equalize SRA (Liu et al. 2018). SRA represents an index of anatomical constraints on maximum stomatal gas exchange, where higher maximum stomatal gas exchange means higher productivity and competitiveness of plants (Bucher et al. 2018, 2019; Liu et al. 2018). Understanding how the morphological traits of leaf stomata vary could provide insights on the adaptation strategies of plants to changing external environments over the long term.

Natural forests are susceptible to natural and human disturbances (Xu et al. 2016) such as fire (Wang et al. 2013b), pests (Kurz et al. 2008), weather, grazing pressures, and land-use changes. In other words, most forests in the world are recovering from past disturbances and generally consist of patches containing stands of different ages (Fig. 1). Stand age is usually estimated as the time since the last

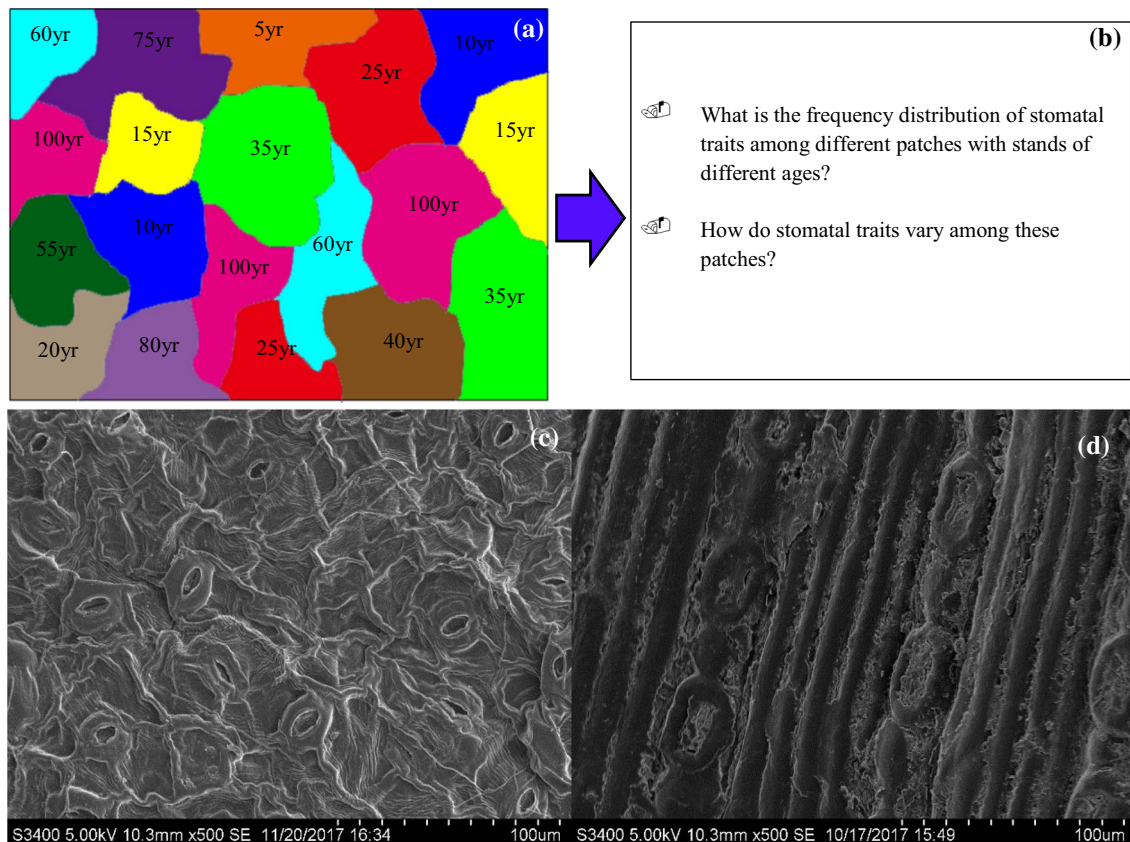


Fig. 1 Schematic of forest patches with stands of different ages. **a** Forest patches with stands of different ages; **b** questions of scientific importance; **c** stomata of the broad-leaved species *Acer tegmentosum* Maxim.; **d** stomata of the coniferous species *Pinus koraiensis* Sieb. et Zucc

major disturbance (Goulden et al. 2011; Pan et al. 2011; Poorter et al. 2016). How and/or which morphological stomatal traits (SD, SS, and SRA) vary among these patches remains unclear, even though such information is essential to optimize existing ecological models or to develop new ones.

In this study, seven adjacent temperate forest stands with different restoration times (6, 14, 25, 36, 45, 55, and 100 years) following selective cutting were selected. Three stomata morphological traits (SD, SS, and SRA) were measured in 624 plant species, including the same species in stands of different ages. The main objectives were to: (1) explore the distribution frequency of stomatal traits of typical north-temperate, mixed broadleaf-conifer forests as a whole; (2) demonstrate the relationships among different stomatal traits at the species level and for different plant functional groups (PFGs); and, (3) reveal how stomatal traits change with stand age. By delineating how forest age influences stomatal traits, we expected to reveal the importance of using stomatal traits as the main parameters in ecological models to predict ecological functions so as to optimize models.

Materials and methods

Site description

The field investigation was conducted in the Jiaohu Forestry Experimental Bureau (43°57' N, 127° 44' E) in Jilin Province, northeastern China. The site contains typical temperate, mixed broadleaf-conifer forests and has a continental monsoon climate, with short, mild summers and long, cold winters. The hottest and coldest months are July (21.7 °C) and January (−18.6 °C), respectively, and the average annual temperature is 3.8 °C. The average annual precipitation is approximately 695.9 mm. The soil type is brown forest soil (Zhang et al. 2017) and the dominant tree species are *Pinus koraiensis* Sieb. et Zucc., *Acer mono* Maxim., *Quercus mongolica* Fisch. ex Ledeb. and *Fraxinus mandshurica*

Rupr. The dominant shrub species are *Corylus mandshurica* Maxim. and *Rhamnus schneideri* Lévl. et Vant. The dominant herbaceous species are *Vitis amurensis* Rupr. and *Brachybotrys paridiformis* Maxim. ex Oliv.

Sampling and measurements

Field sampling

The field survey was conducted in August 2017. Due to long-term selective cutting as the main mode of forest management, patchy stands of different ages have formed along a restoration gradient (Fig. 1). Seven adjacent temperate stands on similar topography with different restoration ages (6, 14, 25, 36, 45, 55, and 100 years) were randomly selected after selective cutting.

Four 30 m × 40 m experimental plots were established in each stand, and two 5 m × 5 m quadrats and four 1 m × 1 m quadrats were located within each plot to measure shrub and herbaceous species (He et al. 2018; Liu et al. 2018). All plant species were present in the plots were collected. Latitude, longitude, and altitude and the composition of plant species were recorded for each plot. A total of 624 species of trees, shrubs, and herbs were collected (Table 1).

Measurement of stomatal traits

For each species within each plot, 20 or more mature leaves were collected from the top canopies of four healthy plants. The leaves were pooled, placed in sealed plastic bags, and immediately stored in a cooler box. Five to ten leaves from each sample were cut into 1.0 cm × 0.5 cm pieces and fixed in a 75% alcohol-formalin-glacial acetic acid-glycerin solution (90:5:5:5). Stomatal traits were observed using a scanning electron microscope (S-3400 N, Hitachi, Japan). Three pieces were selected from the pooled samples, and each photographed twice on the lower surface (Tian et al. 2016; Liu et al.

Table 1 Information on plots subjected to different restoration periods after selective cutting

Restoration duration (year)	Longitude (°N)	Latitude (°E)	Altitude (m)	No. of plant species			
				Tree	Shrub	Herb	Total
6	43°54'44"	127°39'47"	490.9	20 (16.5)	25 (20.7)	76 (62.8)	121
14	43°58'32"	127°41'11"	487.6	20 (25.3)	16 (20.2)	43 (54.4)	79
25	43°52'33"	127°34'0"	710.0	19 (22.6)	14 (16.7)	51 (60.7)	84
35	43°54'45"	127°40'01"	538.7	20 (25.3)	13 (16.4)	46 (58.2)	79
45	44°2'40"	127°45'28"	505.9	19 (20.2)	14 (14.9)	61 (64.9)	94
55	43°58'11"	127°44'18"	491.8	21 (28.4)	12 (16.2)	41 (55.4)	74
100	43°51'48"	127°49'11"	731.3	18 (23.4)	16 (20.8)	43 (55.8)	77

†Data in parentheses are the percentage of different growth types out of all plant species (%)

2018, 2019). The number of pores (N) and the area of the image (S_{Photo}) were recorded to obtain stomatal density (SD, stomata mm^{-2}). Five pores were randomly selected from each image to measure stomatal length (SL, μm) and hence, stomatal size (SS, μm^2). SD, SS, and SRA (%) were calculated as:

$$\text{SD} = N \div S_{\text{Photo}} \tag{1}$$

$$\text{SS} = \text{SL} \times \text{SL} \tag{2}$$

$$\text{SRA} = \text{SS} \times \text{SD} \times 10^{-4} \tag{3}$$

Dominant species

Height and diameter-at-breast-height (DBH) were recorded for each woody species with $\text{DBH} \geq 2$ cm. Biomass was calculated using species-specific allometric regressions with DBH and height. Dominant tree species are defined as the minimum number of species that, combined, account for 85% of the total biomass (Grime 1998; Avolio et al. 2019). Dominant shrub species are defined as the minimum number of species that, combined, account for 55% of the shrub biomass, and dominant herb species are defined as the top two of the importance-value = (the relative cover + the relative height + the relative frequency)/3 (Zhang et al. 2015).

Data analysis

Stomatal traits were log transformed to obtain the approximate normality for the analysis of frequency distributions. The Pearson correlation coefficient was calculated for the various stomatal traits. One-way ANOVAs were performed to compare differences in stomatal traits among different PFGs (trees, shrubs, herbs), as well as the variation in stomatal traits across stand ages. SD-SS relationships were tested using ordinary least squares (OLS) linear regressions, and differences in slope and intercept of SD-SS relationships among PFGs and stand ages were evaluated by standardized major axis (SMA) estimation using R-software. All data analyses and graphical presentations were performed using SPSS 13.0 (IBM Corp., Chicago, IL, USA) and SigmaPlot 10.5 software (Systat Software, Point Richmond, CA). Significance was set at $P=0.05$.

Results

Changes in stomatal traits

Across all 624 sampled plant species, the SD, SS, and SRA were distributed log-normally. The mean values of SD, SS, and SRA were 178.7 stomata mm^{-2} , 1064.2 μm^2 , and 12.7%, respectively, ranging from 4.2 to 1276.7 stomata mm^{-2} , 66.6 to 8315.7 μm^2 , and 0.1 to 93.2% (Fig. 2). The stomatal traits of dominant species did not significantly differ across different aged stands ($P > 0.05$, Table 2).

Fig. 2 Frequency distributions of stomatal density (a, SD), stomatal size (b, SS), and stomatal relative area (c, SRA) in temperate forests. N, number of species; Max, maximum; Min, minimum; CV, coefficient of variation. Data are the total of seven forests

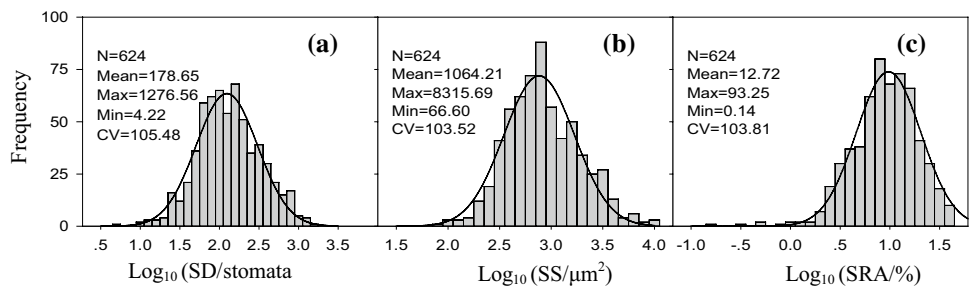


Table 2 Variance of stomatal traits along the stand ages

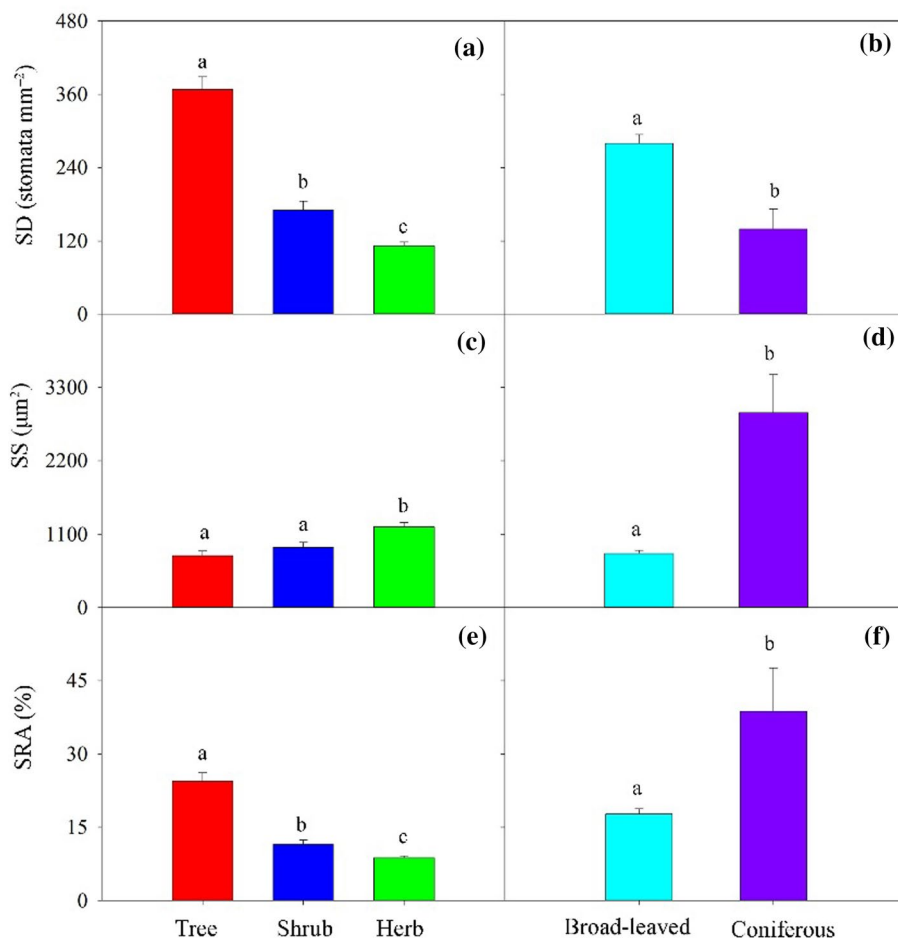
Level		Stomatal density (SD)		Stomatal size (SS)		Stomatal relative area (SRA)	
		F	P	F	P	F	P
Species		2.687	0.015	3.018	0.007	4.053	0.001
Dominant species		1.577	0.179	0.467	0.828	1.113	0.372
Plant functional groups	Tree	0.425	0.861	1.956	0.077	1.633	0.143
	Shrubs	2.810	0.014	1.058	0.393	6.654	<0.001
	Herbs	3.694	0.001	3.567	0.002	8.276	<0.001
	Broad-leaved	1.798	0.101	3.019	0.007	3.020	0.007
	Coniferous	0.786	0.609	1.614	0.332	4.817	0.076

SD, SS, and SRA differed significantly across different PFGs (trees, shrubs, and herbs, $P < 0.05$; Fig. 3). Trees had higher SD, smaller SS, and larger SRA than shrubs and herbs. There were significant differences in stomatal traits between coniferous and broadleaf species (Fig. 3). Broadleaf trees had higher SD and smaller SS than coniferous species. The distributions of stomatal traits for the seven different aged stands are shown in Fig. S1 and S2.

Changes in stomatal traits of different aged stand

Stomatal traits were distributed log-normally in the seven different aged stands (Fig. 4). SD and SRA were highest in 25-year-old stand and lowest in 36-year and 14-year-old stand, respectively. However, SS was largest in 55-year-old stand and smallest in the 14-year-old stand (Table S1). Coefficients of variation for SD, SS, and SRA were largest in the 14-year-old stand (Fig. 4). The stomatal traits of the different plant functional groups (PFGs) varied consistently for every stand age; however, trees tended to have higher SD, smaller SS, and larger SRA (Table S2).

Fig. 3 Changes in leaf stomatal traits across different plant functional groups. In each panel, data represent the mean \pm 1 SE. Data with the same lowercase letters represent no significant differences at $P = 0.05$. Woody species were divided into coniferous and broadleaved plants. SD: Stomatal density, SS: Stomatal size, SRA: Stomatal relative area



Relationships among stomatal traits

Strong negative relationships between stomatal density (SD) and stomatal size (SS) were found across species (Fig. 5a) and PFGs (Fig. 5b, Table S3), whereas SS decreased linearly with increasing SD (after log transformation). After standardized major axis (SMA) tests (Tables S5 and S6), there was a significant difference in the slope among PFGs ($P < 0.05$) where the slope of herbs was steeper than for trees and shrubs. For each stand age, SS tended to decrease linearly with increasing stomatal density (Fig. 5c, Table S4); however, the slopes differed significantly across stands of different ages. SD and SS were positively correlated with SRA at the species and PFG levels, irrespective of stand age.

Relationship between stomatal traits and stand age

Stomatal traits significantly differed among different aged stands at the species level ($P < 0.05$, Table 2) and between PFGs (Table S2). In the same plant functional groups, variations in stomatal traits differed between stand ages. For example, there was no significant difference in shrub SS

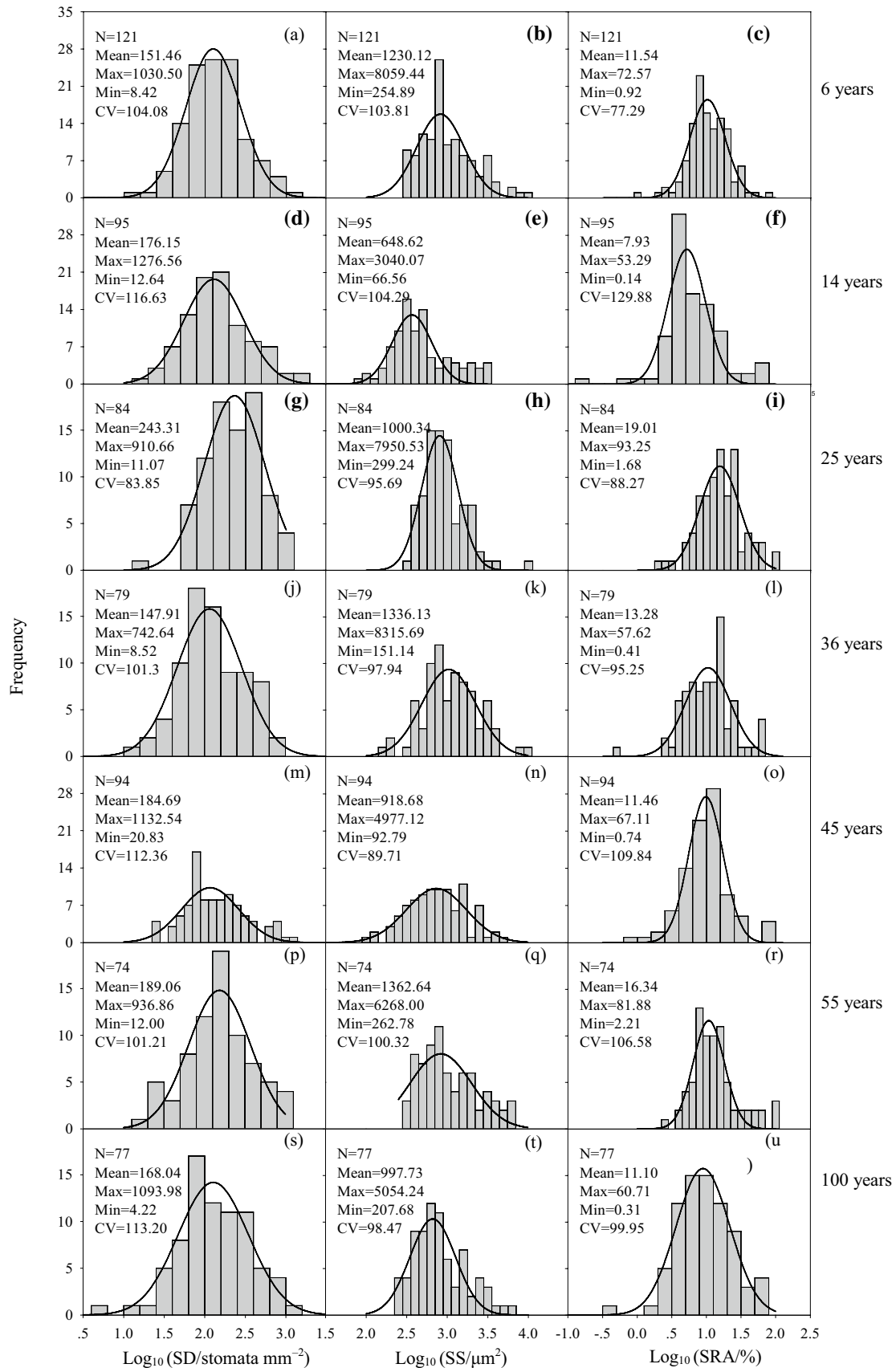


Fig. 4 Frequency distributions of stomatal density (SD), stomatal size (SS), and relative stomatal area (SRA) for temperate forests with different stand ages

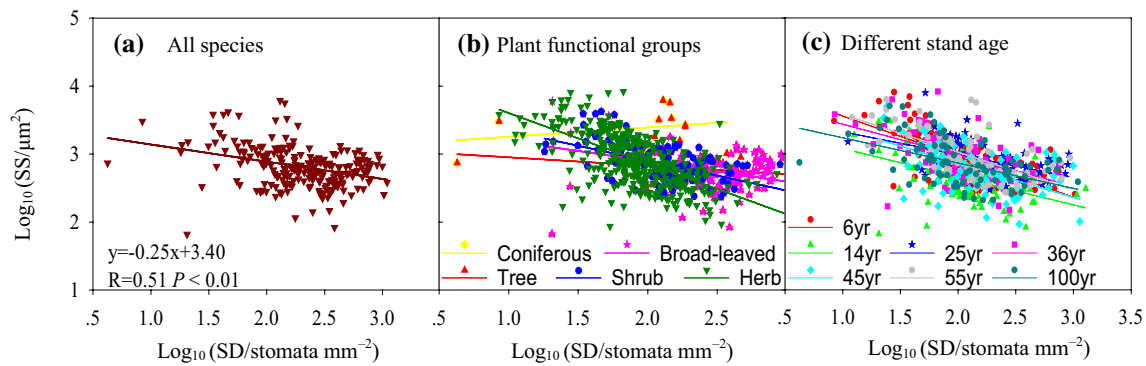


Fig. 5 Changes in the relationships between stomatal density (SD) and stomatal size (SS) at the species, plant functional group, and stand age levels

(stomatal size) among stands, whereas SD (stomatal density) significantly differed (Table 2). Variation in stomatal traits was irregular with increasing stand age ($P > 0.05$). Importantly, the stomatal traits of dominant species did not differ significantly across stand age ($P > 0.05$, Table 2).

Discussion

Variation in stomatal traits

Stomatal density, size and relative area for 624 plant species were used to quantify the distribution frequency of stomatal traits in these temperate forests, confirming and extending existing knowledge of the distribution of stomatal traits established by Hetherington and Woodward (2003). Previous reports on the stomatal traits of 90 woody and semi-woody plants showed that stomatal relative area ranged from 2.2 to 42.0%, while this study also provided information on herbaceous plants in which SRA ranged from 0.1 to 93.2%. This large variation in SRA among species could strongly influence the maximum stomatal conductance of plants, reflecting changes to maximum gas exchange under different environmental conditions.

Consistent with previous studies, stomatal traits differed significantly across plant functional groups (Fraser et al. 2009). This study showed that trees had the highest stomatal density and relative area, followed by shrubs and herbs, while the opposite pattern was found for stomatal size. These patterns reflect the different strategies of plant functional groups to adapt to their environment (Wang et al. 2016). For example, the larger stomatal relative size of trees allows them to adapt efficiently to dry environmental conditions. This combination of smaller stomatal size and greater stomatal density allows tree species to achieve maximum gas exchange when the environment is suitable (McDowell et al. 2008; Drake et al. 2013; Krober et al. 2015). In contrast,

large stomata are essential for herbs for optimal light capture when it is limited. Differences in stomatal traits between coniferous and broadleaf species reflect differences in vein structure (Lammertsma et al. 2011; Zhang et al. 2012). Stomatal size and relative area showed similar trends, being lower in broadleaf species and higher in coniferous plants, with the opposite pattern for stomatal density (Lammertsma et al. 2011). As coniferous species are often found in harsh, arid, or cold environments, lower stomatal density is beneficial to help maintain high water use efficiency (Yoo et al. 2010). The relative stomatal area of coniferous species is greater than for broadleaf species; consequently, the photosynthetic capacity of coniferous species per unit area is greater than for broadleaf species (Tian et al. 2016). Therefore, coniferous species likely have higher growth potential in our study area.

Trade-off between stomatal traits

Stomatal morphological traits can influence the balance of CO_2 uptake for photosynthesis against water loss by adjusting stomatal opening and closing. To some extent, stomatal relative area (SRA) is an index of how maximum stomatal gas exchange is constrained by anatomy (Tian et al. 2016; Bucher et al. 2018, 2019; Liu et al. 2018). This phenomenon is related to stomatal density and size which determine maximum anatomical stomatal conductance (Bucher et al. 2016; Sack and Buckley 2016), influencing the photosynthesis and transpiration of plants (Sack and Buckley 2016). Plants adapt to their environment by altering stomatal conductance, consequently stomatal relative area varies across environments (Fanourakis et al. 2015). For instance, under drought conditions, decreasing stomatal relative area minimizes water loss and improves water use efficiency, allowing plants to endure drought for longer periods (Drake et al. 2009; Franks and Beerling 2009; Taylor et al. 2012; Franks

et al. 2015). Higher stomatal relative area should benefit species exposed to low concentrations of CO₂, high irradiance and insufficient nutrients for higher productivity, than plants with smaller stomatal relative area (Franks and Beerling 2009; Taylor et al. 2012; Wang et al. 2016). Stomatal density and size allows researchers to estimate the theoretical, maximum anatomical stomatal conductance, indicating the extent to which plants are adapted to a given environment (Franks and Beerling 2009; Franks et al. 2009). Previous studies have shown that increasing stomatal density and decreasing stomatal size under water deficits help plants to adapt to drought conditions (Martinez et al. 2007). Through a trade-off between stomatal density and size, the relative stomatal area may be kept within an appropriate range to maximize ecological functions (Lawson and McElwain 2016). However, if the relative stomatal area increases due to increased stomatal density and constant stomatal size, or increased density and size, there would insufficient space to accommodate stomata, which in turn, would impact the other functions of leaves (Franks et al. 2009).

This study demonstrates a significant, negative correlation between stomatal density and size, here size decreased linearly with increasing density (Fig. 5). This supports Frank et al. (2009) studies on multiple species at various geological scales. This negative relationship between stomatal density and size represents a long-term adaptation (Hunt et al. 2003; Mott et al. 2008; Drake et al. 2013) that might be explained by physical and energetic constraints (Franks et al. 2009). The physical constraints mainly relate to the spatial limitations of embedding stomata with sufficient density and size into the leaf epidermis to optimize stomatal conductance. The energetic constraints relate to investment and return in terms of stomatal conductance, and thus photosynthesis and water use efficiency. The trade-off between stomatal traits might be an important strategy for adapting to the environment, independent of plant functional groups or stand age.

Stable stomatal traits of dominant species with stand age

The stomatal traits of the dominant species remained relatively stable across stands of different ages (Table 2), whereas the total stomatal traits (of all species) differed significantly between stand ages (Table 2). Changes in stomatal traits are mainly controlled by the external environment such as temperature, light intensity, CO₂ levels, and water supply (Casson and Gray 2008; Lau and Bergmann 2012; He et al. 2018). Consequently, plants can adapt to a given environment by adjusting their stomatal traits (Zhu et al. 2011; Wang et al. 2013a; Carlson et al. 2016). The stomatal traits of herbs were far more labile to change than those of trees and shrubs, with trees and shrubs being less affected

by the environment relative to herbs. Due to the influence of the herb component, total stomatal traits of all species differed significantly between different stand ages. However, in each stand, species in the upper layers, occupying favorable niches in terms of nutrient acquisition and water absorption. When the environment does not change drastically, dominant species retain their existing stomatal traits, exhibiting no variation (Delgado et al. 2011).

Conclusions

This study demonstrates how stomatal traits are distributed in typical temperate forests with different stand ages. Stomatal traits varied significantly across species and plant functional groups (Tables 2 and S2). This variation reflects the different strategies of plant functional groups to adapt to their environment. Stomatal traits of entire species were significantly different across different aged stands, whereas stomatal traits of dominant species remained relatively stable (Table 2). These findings indicate that variations of stomatal traits due to changing environments differed for all species, including dominant species. Considering the importance of dominant species in forests and the associated small variations in stomatal traits across forest patches, variations in stomatal traits between stands of different ages should not be incorporated in future ecological models.

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