Response of Specific Leaf Area to a Large-Scale Environmental Gradient in Five Forest Types in China

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ABSTRACT: Understanding the response of plant traits to environmental change is critical. Specific leaf area (SLA) is an important plant functional trait, correlating with environmental conditions and indicating certain ecophysiological traits. Although the SLA-environment relationship has been extensively studied, SLA response at the regional scale is limited. In order to study how SLA changes with environment at the regional scale, SLA and abiotic data were collected from five forest types distributed across 746 sites. These data were collected from studies examining the effect on SLA to temperature, precipitation and altitudinal variation. The mean SLA was 149 ± 18 , 100 ± 7 , 151 ± 17 , 154 ± 22 and 113 ± 25 $\text{cm}^2 \text{g}^{-1}$ in Boreal/temperate *Larix* forest (TLF), boreal/alpine *Picea-Abies* forest (APAF), temperate/subtropical montane *Populus-Betula* deciduous forest (MPBF), temperate deciduous broadleaf forest (TDBF) and subtropical evergreen broadleaf forest (SEBF), respectively. With increasing mean annual temperature (MAT), SLA increased significantly in TLF and SEBF, but decreased significantly in APAF and MPBF. As mean annual precipitation (MAP) increased, SLA significantly increased in TLF and significantly decreased in TDBF. A significant negative correlation occurred between SLA and altitude in APAF, TDBF and SEBF. These results indicated that SLA may predict tree response to environmental change in some forest types.

KEYWORD: altitude; environmental change; precipitation; phenotypic plasticity; SLA; temperature.

1 INSTRUCTION

Earth has recently experienced profound environmental change from rising mean global temperatures and changes in precipitation patterns (IPCC 2007; Wu et al. 2011) potentially affecting plants. Plants can adapt and tolerate relatively large environmental changes (Knight & Ackerly 2003), their phenotypic plasticity tolerates rapid and flexible adjustment to environmental change (Sultan 2000). Understanding the effects of environmental factors on phenotypic expression is crucial for predicting plant response in real time to environmental change (Hudson et al. 2011).

One strategy for plants to adjust to changes in environmental conditions is to modify their leaf morphology (Niinemets 2001, Wright et al. 2004). A key leaf trait is specific leaf area (SLA, leaf area per unit dry mass), which quantifies light capture and CO_2 assimilation capacity (Wei et al. 2011). Substantial intraspecific variation in SLA is common, often correlating with temperature and water availability (Poorter et al. 2009). The phenotypic plasticity of SLA has important implications for the

survival probability of plant populations under changing environmental conditions (Scheepens et al. 2010). SLA has become increasingly popular for characterizing vegetation responses to environmental variation (e.g. Warren et al. 2006, Milla et al. 2008, Martin & Asner 2009, Scheepens et al. 2010, Wei et al. 2011). Previous work indicated that SLA usually decreases with increasing altitude (Milla 2009), probably responding to decreasing temperature (Körner 2003a), or changes in water availability (Poorter et al. 2009). Plant species occurring in more stressful environments have smaller, thicker leaves and exhibit lower SLA (Knight & Ackerly 2003). The SLA-environment relationship has been studied extensively (e.g. Scheepens et al. 2010, Wei et al. 2011), but the response of SLA at the regional scale is unclear (Milla et al. 2008). Uncertainty exists if the strategy shift in SLA is caused by environmental change as both these factors vary within and across plant species (Garnier et al. 2004, Li et al. 2005, Luo et al. 2005, Wei et al. 2011). Elucidating this relationship is required to advance our understanding of ecosystem function and environmental change.

In China forests cover a large geographic area. The forest environments are characterized by steep temperature, precipitation and altitudinal gradients, providing ideal conditions to examine shifts in SLA across environmental gradients. To investigate a forest-level shift in plant SLA across different environments, we tested if the SLA in five different forest types shifted relative to changes in temperature, precipitation and altitude.

2 MATERIALS AND METHODS

2.1 Dataset

We compiled an SLA dataset ($n = 746$) from Luo's (1996) database ($n = 685$). These data included five

major forest types in China: Boreal/temperate *Larix* forest (TLF), boreal/alpine *Picea-Abies* forest (APAF), temperate/subtropical montane *Populus-Betula* deciduous forest (MPBF), temperate deciduous broadleaf forest (TDBF) and subtropical evergreen broadleaf forest (SEBF).

These are typical forest types that occur from northern to southern China (Luo 1996). For each selected data point we collected data on: latitude, longitude, altitude, mean annual temperature (MAT), precipitation (MAP) and biome type. We recorded the geographic range and climate for each forest type (Table 1).

Table 1. Geographic and climatic ranges for the five forest types in data

Forest type	Latitude (°N)	Longitude (°E)	Altitude (m)	Mean annual temperature (°C)	Mean annual potential evapotranspiration (mm)	Mean annual precipitation (mm)
TLF	28.62-52.60	86.40-131.80	441-4240	-6.2-12.9	340-522	357-1274
APAF	26.14-52.60	81.10-131.80	410-4200	-6.6-13.9	329-739	370-1937
MPBF	25.75-52.50	85.20-134.00	150-3640	-5.5-16.0	358-940	241-1283
TDBF	28.25-51.70	103.00-134.00	177-2600	-3.3-18.6	429-926	410-1142
SEBF	20.70-30.25	85.20-120.17	80-4160	3.5-25.4	386-1132	637-2323

2.2 Data analysis

The slope and intercept of the regressions, SLA-MAT, SLA-MAP and SLA-altitude relationships were estimated using the standardized major axis regression of the data (SMATR software Version 2.0, Falster et al., 2006, Warton et al. 2006).

3 RESULTS

The mean SLA values in the five forest types ranged from 129–188, 89–116, 125–172, 112–239 and 74–268 $\text{cm}^2 \text{g}^{-1}$ (TLF, APAF, MPBF, TDBF and SEBF, respectively). The differences within-forest type was relatively small in TLF (1.5 times), APAF (1.3 times) and MPBF (1.4 times) and relatively large in TDBF

(2.1 times) and SEBF (3.6 times). The mean SLA was high in TLF, MPBF and TDBF (149 ± 18 , 151 ± 17 and $154 \pm 22 \text{ cm}^2 \text{g}^{-1}$, respectively) and low in APAF and SEBF (100 ± 7 and $113 \pm 25 \text{ cm}^2 \text{g}^{-1}$, respectively).

The relationship between SLA and MAT was significantly positive in TLF and SEBF and significantly negative in APAF and MPBF ($P \leq 0.041$, Table 2). SLA showed a significant positive correlation with MAP in TLF and a significant negative correlation with MAP in TDBF ($P \leq 0.008$). SLA significantly decreased in APAF, TDBF and SEBF with increasing altitude ($P \leq 0.001$). There was no correlation with SLA in TLF and MPBF.

Table 2. Standardized major axis regression (SMA) slopes and y-intercepts (β_{SMA} and α_{SMA} , respectively) for data of SLA ($\text{cm}^2 \text{g}^{-1}$) and mean annual temperature (MAT) ($^{\circ}\text{C}$), mean annual precipitation (MAP) (mm) and altitude (m). Data, grouped according to forest types, taken from Luo (1996).

Forest type	Environmental factor	β_{SMA} (95% CI)	α_{SMA} (95% CI)	<i>n</i>	R^2	<i>P</i>
TLF	MAT	6.2820 (4.9570, 7.9630)	158.5 (153.3, 163.6)	48	0.350	<0.001
	MAP	0.1011 (0.0755, 0.1354)	88.6 (69.3, 108.0)		0.003	0.721
	altitude	0.0198 (0.0154, 0.0254)	121.5 (112.8, 130.1)		0.030	0.106
APAF	MAT	-2.1450 (-2.4870, -1.8510)	108 (106.4, 109.7)	168	0.063	0.001
	MAP	-0.0253 (-0.0289, -0.0220)	121.0 (118.0, 124.0)		0.207	<0.001
	altitude	-0.0085 (-0.0097, -0.0074)	126.3 (122.6, 130.0)		0.189	<0.001
MPBF	MAT	-5.003 (-5.943, -4.212)	170.7 (165.6, 175.8)	127	0.045	0.017
	MAP	-0.0965 (-0.1150, -0.0810)	214.6 (202.7, 226.5)		0.014	0.188
	altitude	0.0204 (0.0172, 0.0244)	118.7 (111.8, 125.7)		0.009	0.279
TDBF	MAT	-9.1180 (-10.6310, -7.820)	207.6 (198.1, 217.2)	165	0.007	0.301
	MAP	0.2355 (0.2025, 0.2738)	1.7 (-21.7, 25.1)		0.042	0.008
	altitude	-0.0453 (-0.0520, -0.0395)	213.8 (204.7, 222.9)		0.200	<0.001
SEBF	MAT	8.5250 (7.5100, 9.6780)	-13.9 (-30.6, 2.7)	238	0.018	0.041
	MAP	0.0834 (0.0735, 0.0948)	-4.5 (-20.1, 11.1)		0.009	0.136
	altitude	-0.0318 (-0.0361, -0.028)	149.7 (143.6, 155.8)		0.048	0.001

4 DISCUSSION

Temperature is a key driver to variation in SLA in TLF, SEBF, APAF and MPBF. SLA showed a significant positive association increases with increasing MAT in TLF and SEBF, suggesting temperature regulation (Scheepens et al. 2010). Increasing SLA is probably a response to increasing temperatures among and within plant species (Körner 2003b). The increase in SLA can be realized through a decrease in leaf density and thickness (Atkin et al. 2006, Poorter et al. 2009). The decrease in leaf density occurs when expanding cell expansion, which leads to larger cells and less cells per unit leaf volume, while the decrease in thickness occurs from a reduction in the number of palisade parenchyma layers (Poorter et al. 2009). However, APAF and MPBF SLA showed the opposite response, i.e., their SLA significantly decreased with increasing temperature. This response is because leaves with lower SLA can better withstand and recover their photosynthetic capacity following exposure to high temperatures compared with species having higher SLA. Moreover, temperature and precipitation are often negatively correlated, with lower precipitation in warmer environments (Knight & Ackerly 2003). The negative correlation between temperature and

precipitation may explain why SLA decreased in APAF and MPBF.

SLA significantly increased with increasing MAP in TDBF, supporting other studies (e.g., Raich et al. 1997, Wang & Gao 2004, Wright et al. 2005). Plants may produce leaves with higher SLA in environments with greater water availability because enhanced water use efficiency is associated with increased photosynthetic tissue relative to transpiration area (Fonseca et al., 2000, Wright et al., 2001), suggesting a link between SLA and photosynthetic performance (Knight & Ackerly 2003).

SLA commonly decreases with reduced rainfall (Schulze et al. 2006, Warren et al. 2006). Under drought stress, lower SLA indicates thicker or more dense leaves, conferring drought tolerance as those leaves have a higher proportion of their mass in cell wall tissue, with the ability to withstand lower water potentials (Martinez et al. 2007, Cano et al. 2008, Mitchell et al. 2008, Walls 2010). Plants in TDBF appeared to respond to drought using similar mechanisms, with lower SLA reducing water loss (Fernández & Reynolds 2000), enabling the trees to overcome prolonged drought. In contrast, SLA was significantly higher with increasing MAP in APAF. Some researchers (e.g., Chabot & Hicks 1982) found that sclerophylly with low SLA, occurred in some high-rainfall environments (e.g. wetlands), possibly

an adaptation to infertile-soil because soil is an important factor controlling leaf traits (Ordoñez et al. 2009). APAF occur at relatively high altitudes, resulting in poor soil fertility where low nutrient levels may be important in favoring a low SLA (Turner 1994, Fonseca et al. 2000). Moreover, high precipitation often accompanies low temperature in mountain forests, potentially reducing SLA.

SLA evolved between plants and their environment to minimize the negative influence of harsh conditions (Meng et al. 2007). Altitude broadly influences plant species and environmental factors (Ma et al. 2010). Cordell et al. (1998) found that SLA of *Metrosideros polymorpha* decreased significantly with increasing elevation. Körner (2003b) found a decrease in SLA with increasing elevation resulting from leaf/needle size becoming smaller but thicker (Pan et al. 2009). Similarly, our study found that SLA significantly decreased with altitude in APAF, TDBF and SEBF. Ma et al. (2010) demonstrated that SLA was closely associated with photosynthetic capacity. Decreasing SLA with increasing altitude was realized through an increase in leaf density and thickness (Atkin et al. 2006, Poorter et al. 2009). We suggest that these changes are an investment in photosynthetically active tissue, promoting leaf efficiency in light capture (Körner 2003b, Scheepens et al. 2010). Moreover, increasing photon flux density from reduced cloud cover during the growing season at higher altitude could be a complementary mechanism of low SLA of trees at high altitudes (Milla 2009).

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