

Variations in leaf and stem traits across two elevations in subtropical forests

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ABSTRACT

Understanding the variations in plant traits across elevations may provide valuable insights into the species structure and function of forests and their responses to climate change. To explore the patterns of trait variation across elevations, we analysed 14 leaf and stem traits associated with resource acquisition and stress tolerance in *Schima superba* Gardner & Champion, *Castanopsis chinensis* (Sprengel) Hance, and *Pinus massoniana* Lambert trees at two elevations in a subtropical forest in southern China. Wood density increased, whereas crown width, leaf water potential at 0700 hours (Ψ_{L-0700}), and leaf $\delta^{18}\text{O}$ decreased in high-elevation plants. Vessel diameter, daily maximum sap flux density, leaf $\delta^{13}\text{C}$, and leaf C and N concentrations per unit mass were comparable across elevations. We found species-specific variations in specific leaf area, midday leaf water potential, and leaf P concentration across elevations. Decreasing crown width with increasing elevation was associated with decreasing leaf $\delta^{18}\text{O}$ and Ψ_{L-0700} , suggesting that higher stomatal conductance may moderate the loss of carbon assimilation. We elucidated the adaptive strategies of plants in response to environmental change, and showed that physiological traits varied in coordination with structural traits. Future studies incorporating multi-dimensional trait analyses can improve our understanding of the responses of forest ecosystems to climate change and global warming.

Keywords: elevational gradient, leaf $\delta^{13}\text{C}$, leaf $\delta^{18}\text{O}$, leaf water potential, sap flux density, southern China, specific leaf area, wood density.

Introduction

According to the IPCC special report (IPCC 2018), in 2017, anthropogenic activities had led to an increase in global average air temperature to 1°C above the pre-industrial levels. Global climate warming is expected to continue during the 21st century, and the strongest warming of ocean waters is projected to occur in tropical and subtropical regions (IPCC 2014). Plants in different climatic regions are known to exhibit differing levels of temperature sensitivity, and tropical tree species generally have narrower thermal tolerance than temperate species (Cunningham and Read 2002). In the last five decades, the annual air temperature in the Dinghushan Biosphere Reserve, China, has increased by approximately 1°C. This area, where our study site is located, has a subtropical climate (Zhou *et al.* 2011). Reports on the effects of warming on plant growth and survival are inconsistent. However, warming is generally expected to enhance plant growth in cold regions, but reduce biomass productivity in subtropical areas. This discrepancy is ascribed to the differences in plant physiological responses in different geographical regions (van Mantgem *et al.* 2009; Liu *et al.* 2013; León-Sánchez *et al.* 2016; Li *et al.* 2016; Wang *et al.* 2017; Wu *et al.* 2019; Lie *et al.* 2021). Therefore, understanding the functional responses of plants to environmental gradients is important for accurately predicting forest dynamics under climate change.

The gradual changes in temperature along altitudinal gradients offer an excellent natural laboratory to investigate the impacts of climate warming on the structuring and functioning of forest ecosystems (Körner 2007; Thomas 2011; De Frenne *et al.* 2013). Functional traits can indicate plant fitness and influence organismal performance across differing

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environmental conditions (McGill *et al.* 2006; Westoby and Wright 2006). Spatial variations in plant traits across elevations may show similar trends associated with the effects of climate warming (Dunne *et al.* 2004; Fukami and Wardle 2005). Previous studies have reported that plants tend to exhibit acquisitive resource use strategies (higher specific leaf area, SLA; and lower wood density, WD) in favourable environments and more conservative strategies (higher WD, lower SLA, and lower maximum tree height) under stressful conditions (Poorter *et al.* 2008; Muscarella *et al.* 2016). Compared to lower elevations, higher elevations generally offer more stressful conditions including decreasing atmospheric pressure and temperature, increasing radiation, and shallow soils due to high precipitation and runoff that restrict plant growth (Tateno *et al.* 2004; Körner 2007; Thomas 2011; De Bello *et al.* 2012; Ding *et al.* 2019; Umaña and Swenson 2019). Leaf mass per unit area (LMA, the inverse of SLA) and leaf N concentration on an area basis (N_{area}) increase with elevation. These responses indicate the stress tolerance strategies of plants that accumulate more resources (such as carbon investments) on a per-leaf basis under abiotic constraints (Cordell *et al.* 1999; Hulshof *et al.* 2013; Read *et al.* 2014). Species at higher elevations have a smaller leaf area and higher WD and water use efficiency, which were associated with increased longevity in response to resource limitation (Huxman *et al.* 2008; Hernández-Calderón *et al.* 2014). Apart from the aforementioned spectrum of leaf and stem economics associated with carbon and nutrient use, leaf water economy is also an essential factor for assessing the diversity of resource use strategies (Prieto *et al.* 2018). Moreover, carbon and oxygen isotope ratios related to water use economy can also reflect more direct physiological responses to the environment. Of these, the former is correlated with photosynthesis and stomatal conductance, whereas the latter is inversely proportional to stomatal conductance (Cernusak *et al.* 2002, 2007; Weigt *et al.* 2018). Analysing the $\delta^{18}\text{O}$ levels in organic matter can help us understand the stomatal control of leaf water loss (Flanagan and Farquhar 2014; Sánchez-Bragado *et al.* 2016). Carbon assimilation and stomatal conductance have been shown to increase with elevation due to greater water availability (Richardson and Berlyn 2002; Van de Water *et al.* 2002; Adams and Kolb 2004; McDowell *et al.* 2008; Bresson *et al.* 2011). The increase in $\delta^{13}\text{C}$ with elevation is explained by increasing stomatal conductance and more photosynthetic discrimination due to decreasing temperatures and increasing light intensity and soil moisture (Körner *et al.* 1991; Beerling *et al.* 1996; Sun *et al.* 1996; Pan *et al.* 2016). However, Wang *et al.* (2010) reported that $\delta^{13}\text{C}$ levels do not always increase with elevation. Moreover, Reed and Loik (2016) reported an increase in plant water potential with elevation due to increasing soil moisture. Thus, plant morphological traits (such as SLA and WD) tend to reflect conservative resource use strategies, whereas their

physiological traits (such as stomatal conductance and water potential) reflect acquisitive resource use strategies as a response to high elevation. Using field experimental studies to investigate these contrasting responses to environmental changes in plant morphological and physiological traits can help uncover the adaptive mechanisms of plants under changing environmental conditions.

Exploring the changes in correlations among plant traits along elevational gradients is an important task in ecology, and could help elucidate the mechanisms of resource exploitation by plants, which are currently unclear (Sterck *et al.* 2011; Umaña and Swenson 2019; Dusenage *et al.* 2021; Mujawamariya *et al.* 2021). Few studies have investigated intraspecific trait variations across environmental gradients; however, the results may have significant implications in predicting community structure and function under environmental changes (Violle *et al.* 2012; Siefert *et al.* 2015; Des Roches *et al.* 2018). Recently, Umaña and Swenson (2019) have emphasised the importance of defining intraspecific variations in functional traits along elevational gradients for improving our understanding of species dynamics and responses to environmental changes. Therefore, in the present study, we asked the following questions: (1) how do the morphological and physiological traits of trees vary across elevations in subtropical forests? and (2) what are the underlying factors governing traits shifts across elevations? To answer these questions, we measured 14 leaf and stem traits related to resource acquisition and construction cost in trees at two elevations in a subtropical forest in south China. We analysed these data to elucidate the major ecophysiological strategies of trees at two elevations.

Materials and methods

Study site

This study was conducted in the Dinghushan Biosphere Reserve located in the Guangdong Province of southern China (23°10'N, 112°10'E). This region has a monsoonal climate with a mean annual rainfall and mean annual air temperature of 1927 mm and 21°C, respectively. Approximately 75% of the annual rainfall occurs during March–August (Lu *et al.* 2010). We conducted our research in two 80-year-old coniferous and broad-leaved mixed forests (70 m and 360 m above sea level, respectively). These forests are at a mid-succession stage, and are dominated by broadleaf tree species (such as *Schima superba* and *Castanopsis chinensis*) and coniferous tree species (such as *Pinus massoniana*) (Zheng *et al.* 2020). The understorey layer has high species diversity and contains tree seedlings, shrubs, and herbaceous plants of various species *Litsea rotundifolia* var. *oblongifolia* (Nees) Allen, *Psychotria rubra* (Lour.) Poir, *Cratoxylum cochinchinense* (Lour.) Blume, *Ficus variolosa* Lindl. ex Benth., *Rhodomyrtus tomentosa* (Ait.) Hassk., *Ardisia*

Table 1. Soil pH, soil organic matter content (SOM), total N concentration (N), total P concentration (P) and soil water content (θ) at a depth of 20 cm at the two elevations in our study site.

Soil characteristic	70 m	360 m
pH	3.93a (± 0.10)	3.81a (± 0.04)
SOM (g kg ⁻¹)	19.15a (± 2.77)	24.52a (± 2.19)
N (g kg ⁻¹)	0.94a (± 0.11)	1.03a (± 0.06)
P (g kg ⁻¹)	0.23a (± 0.01)	0.13b (± 0.01)
θ (m ³ m ⁻³)	0.34a (± 0.05)	0.36a (± 0.02)

$n = 3$. Data are shown as the mean \pm s.e. Different letters indicate significant differences in soil characteristics between the two elevations at $P < 0.05$.

quinquegona Blume, *Lophatherum gracile* Brongn., *Gahnia tristis* Nees, *Dicranopteris pedata* (Houttuyn) Nakaike and *Adiantum capillus-veneris* L. The soil is a loam soil, and its characteristics are in Table 1. To avoid the effects of differences in water content, the field experiment was conducted in June 2019, when both elevations received sufficient rainfall.

Measurement of environmental variables

Soil water content (θ , m³ m⁻³) was measured at seven randomly selected locations at each elevation using a TDR 300 sensor (Spectrum Technologies, Inc., Illinois, USA). Three soil samples at a depth of 20 cm were collected at each sampling point and stored in sealed bags for the measurement of soil physiochemical properties. Soil organic matter (SOM) levels were measured using the potassium dichromate volumetric method. Total nitrogen (N) and total phosphorus (P) levels in the soil were measured with the Kjeldahl method, and soil pH was measured using a pH meter (HANNA, pH211, Italy). Solar radiation, air temperature (T) and air relative humidity (RH) were automatically monitored using the WatchDog 2700 station (Spectrum Technologies, Inc., Illinois, USA). Vapour pressure deficit (VPD, KPa) was calculated according to the following empirical formula (Campbell and Norman 1998):

$$\text{VPD} = a \times e^{[bT/(T+c)]} \times (1 - \text{RH})$$

where a , b and c are constants with values of 0.611, 17.502 and 240.97, respectively; T is the air temperature; and RH is the air relative humidity.

Measurement of plant morphological and physiological traits

We selected five individuals per species for trait measurements. The diameter at breast height (DBH) and tree height (H) were measured using a tape and a VERTEX IV dendrometer (Haglöf Inc., Langsele, Sweden), respectively. Crown width (C_w) was calculated as the mean of four perpendicular crown radii measured in each cardinal

direction. We collected 2 cm long cores from the stem of each sample tree at a height of 1.3 m above the ground using an increment borer (Haglöf Inc., Langsele, Sweden). The barks of the cores were removed, and the cores were dried at 65°C to a constant weight. Core volumes were calculated as the volumes of cylinders with 2 cm in length and 0.515 cm in diameter. Wood density (WD) was calculated as the dry mass divided by the respective core volume. Additionally, stem cores (~1 cm in length) were collected at a height of 1.3 m using the increment borer. The bark was removed and the cores were immediately placed in glass bottles with 50% ethanol. These were embedded in paraffin and radial sections were prepared for further structural observation. Each sample was photographed at 50 \times magnification using a digital microscopy, and vessel diameters were measured using the CaseViewer 2.4 software (3DHISTECH Ltd., Budapest, Hungary). Several vessels were randomly selected from 3–5 samples of each species for the measurement of vessel diameter (VD, μm). Several fully expanded sun-exposed leaves were used for leaf area measurements using a leaf area meter (LI-3000C, LI-COR, Inc., Nebraska, USA), and the leaves were mixed and dried for dry mass determination. SLA was calculated by dividing the leaf area by leaf dry mass. Total C concentrations in leaves were measured through the oxidation of potassium dichromate and titration with an Fe²⁺ solution using an isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., Bremen, Germany). Total N (N_{mass}) and P concentrations of leaves were measured by micro-Kjeldahl digestion followed by indophenol blue and Mo-Sb colorimetric methods using a UV-8000 spectrophotometer (Metash Instruments Corp., Shanghai, China). Carbon and oxygen isotope ratios in leaf organic matter were determined using the DELTA V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc.) and Finnigan Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., MA, USA), respectively. The isotopic values are reported using the delta notation and are relative to PDB standard for carbon and the VSMOW standard for oxygen ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively).

Monitoring of stem sap flux density

A pair of Granier thermal dissipation probes (length, 20 mm) were vertically installed into the stem xylem at 1.3 m above the ground for each sample tree (Granier 1987) according to the methods of Zhu *et al.* (2016). The temperature differences between the two probes were recorded using a data logger (Delta-T Devices Ltd., Cambridge, UK). Sap flux density per unit sapwood area (J_s , g m⁻² s⁻¹) was calculated according to the Granier equation. The normalised J_s was calculated by dividing the instantaneous J_s by the daily maximal J_s . For each tree species, the normalised J_s was used to compare the sensitivity of sap flux to VPD in trees at the two elevations.

Measurement of leaf water potential

From each sample tree, we collected 3–5 branches with several leaves exposed to the sun using a 20 m long pole pruner. Leaf water potential was measured at 0700 hours (when sap flux started, Ψ_{L-0700}) and at midday (1200 hours) (Ψ_{L-mid}) on 28 and 30 June 2019 using a pressure chamber (1000, PMS Instrument Co., Corvallis, OR, USA). The lowest Ψ_{L-mid} was used as a proxy of drought tolerance.

Statistical analyses

Statistical analyses were performed using the SPSS 25 software (IBM, Inc., New York, USA). The environmental variables at the two elevations were compared using paired-samples *t*-tests at a significance level of $P < 0.05$. Differences in soil properties and the leaf and stem traits of each tree species between the two elevations were analysed by independent-sample *t*-tests at $P < 0.05$. The responses of normalised J_s to VPD were compared between the two elevations using a UNIANOVA analysis. Multivariate associations between leaf and stem traits were analysed with a principal component analysis (PCA) across two elevations.

Results

Environmental variables

We compared the means of environmental variables in June 2019. Solar radiation was higher but T and VPD were lower at 360 m (high elevation) than at 70 m (low elevation) (Fig. 1; $P < 0.05$). The mean T was $26.84 \pm 0.04^\circ\text{C}$ and $25.66 \pm 0.04^\circ\text{C}$ at the 70 m and 360 m sites, respectively (Sheet 1 in Supplementary Information). Soil pH, SOM, N and θ were not significantly different between the two elevations; however, soil P was lower at 360 m than at 70 m (Table 1, $P < 0.05$).

Variations in leaf and stem traits with increasing elevation

When the morphological trait data were collated for three tree species, DBH and H were not significantly different between the two elevations, but C_w was lower at 360 m than at 70 m (Table 2, $n = 15$, $P < 0.05$). The daily maximal sap flux density per unit sapwood area (J_{\max}) of each tree species did not differ significantly between the two elevations (Table 3, $P > 0.05$). Based on the J_s values at $\text{VPD} > 1$ kPa, the slope of the linear regression between normalised J_s and VPD values was higher at 360 m than at 70 m for both *S. superba* and *C. chinensis*. For *P. massoniana*, the normalised J_s was not related to VPD at 70 m (Fig. 2). These results indicate the higher sensitivity of water transport rate to VPD in plants at a higher elevation.

Leaf $\delta^{13}\text{C}$, leaf C and N_{mass} values for the three tree species did not differ significantly between the two elevations

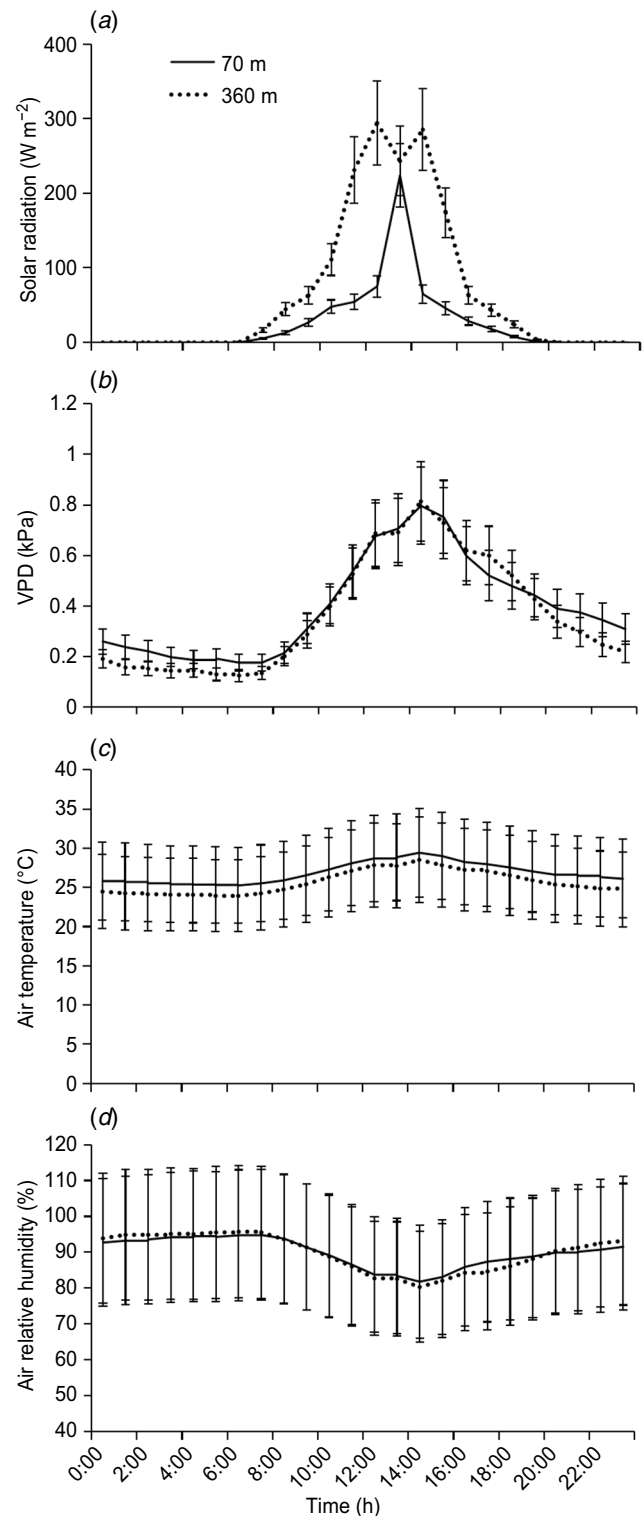


Fig. 1. Diurnal patterns of (a) mean solar radiation, (b) vapour pressure deficit (VPD), (c) air temperature, and (d) air relative humidity in June 2019 at two elevations. Vertical lines in the figure indicate the s.e.

(Table 3; $P > 0.05$). In *C. chinensis*, the SLA was lower at 360 m than at 70 m. The SLA of the other two tree species

Table 2. Diameter at the breast height (DBH), tree height (H), and crown width (C_w) of the sample trees of three tree species at the two elevations.

Species	n	DBH (cm)		H (m)		C_w (m)	
		70 m	360 m	70 m	360 m	70 m	360 m
<i>S. superba</i>	5	22.61a (± 0.60)	19.89a (± 1.73)	11.16a (± 0.38)	11.46a (± 0.41)	3.15a (± 0.25)	2.27b (± 0.20)
<i>C. chinensis</i>	5	24.15b (± 1.86)	29.55a (± 1.24)	12.84a (± 0.44)	11.90a (± 0.79)	3.50a (± 0.31)	3.19a (± 0.30)
<i>P. massoniana</i>	5	31.29a (± 4.51)	22.59a (± 1.05)	13.64a (± 1.24)	13.28a (± 0.63)	3.31a (± 0.63)	1.70a (± 0.30)
Mean	15	26.01a (± 1.83)	24.01a (± 1.31)	12.55a (± 0.51)	12.21a (± 0.40)	3.32a (± 0.23)	2.38b (± 0.22)

Data are shown as the mean \pm s.e. Different letters indicate significant differences in traits between two elevations at $P < 0.05$.

Table 3. Variations in leaf and stem traits of three tree species at the two elevations.

	<i>S. superba</i>		<i>C. chinensis</i>		<i>P. massoniana</i>	
	70 m	360 m	70 m	360 m	70 m	360 m
WD (g cm^{-3})	0.51b (± 0.01)	0.58a (± 0.01)	0.59b (± 0.02)	0.67a (± 0.01)	0.62b (± 0.02)	0.66a (± 0.03)
SLA ($\text{cm}^2 \text{g}^{-1}$)	101.29a (± 2.99)	95.10a (± 4.96)	123.80a (± 6.34)	92.10b (± 5.68)	58.98a (± 4.52)	52.35a (± 2.22)
VD (μm)	13.70 a (± 3.11)	9.96 a (± 1.93)	11.14 a (± 2.17)	9.80 a (± 0.70)	13.17 a (± 1.97)	12.22 a (± 0.88)
J_{max} ($\text{g m}^{-2} \text{s}^{-1}$)	46.21a (± 7.89)	65.95a (± 5.71)	44.56a (± 5.00)	62.49a (± 19.95)	51.56a (± 9.80)	33.54a (± 7.49)
$\delta^{13}\text{C}$ (‰)	-31.69a (± 0.41)	-31.14a (± 0.33)	-31.14a (± 0.26)	-30.46a (± 0.25)	-29.15a (± 0.37)	-29.09a (± 0.07)
$\delta^{18}\text{O}$ (‰)	24.93a (± 0.20)	24.05b (± 0.26)	26.23a (± 0.16)	24.79b (± 0.18)	21.60a (± 0.26)	20.78b (± 0.11)
$\Psi_{\text{L-0700}}$ (MPa)	-0.21a (± 0.01)	-0.46b (± 0.05)	-0.14a (± 0.04)	-0.32b (± 0.06)	-0.58a (± 0.05)	-0.79b (± 0.07)
$\Psi_{\text{L-mid}}$ (MPa)	-1.20a (± 0.02)	-1.69a (± 0.31)	-1.37a (± 0.15)	-1.61a (± 0.16)	-1.17a (± 0.09)	-1.42b (± 0.06)
C (%)	44.90a (± 0.58)	45.01a (± 0.58)	45.26a (± 0.62)	45.71a (± 0.57)	45.96a (± 0.63)	46.54a (± 0.70)
N_{mass} (g kg^{-1})	12.72a (± 0.45)	12.7a (± 0.35)	13.40a (± 1.27)	14.92a (± 1.97)	12.22a (± 1.44)	10.04a (± 1.31)
P (g kg^{-1})	0.59a (± 0.22)	0.54a (± 0.04)	1.05a (± 0.15)	0.46b (± 0.02)	1.44a (± 0.13)	0.44b (± 0.15)

The traits include wood density (WD), specific leaf area (SLA), vessel diameter (VD), maximum of daily sap flux density per unit sapwood area (J_{max}), water potential at 0700 hours ($\Psi_{\text{L-0700}}$, when sap flux started) and at midday ($\Psi_{\text{L-mid}}$), $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, leaf C (C), N (N_{mass}), and P concentration (P). $n = 5$. Data are shown as the mean \pm s.e. Different letters indicate significant differences in the traits of each tree species between two elevations at $P < 0.05$.

did not differ significantly between elevations; however, their mean SLA was relatively low at 360 m, indicating high leaf construction costs at high elevations. Leaf P levels were lower at 360 m than at 70 m for *C. chinensis* and *P. massoniana*, but were similar between elevations for *S. superba*. Stem WD was higher at high elevation for all three tree species, indicating higher stem construction costs. Although VD was smaller at 360 m than at 70 m for all three species, the differences were not statistically significant. Both leaf $\delta^{18}\text{O}$ and $\Psi_{\text{L-0700}}$ values were lower at 360 m than at 70 m for all three tree species ($P < 0.05$). Only *P. massoniana*, a gymnosperm, exhibited lower $\Psi_{\text{L-mid}}$ values at high elevation, which likely indicates its higher drought tolerance.

In the PCA, the first two principal components explained 77.4% of the total variation (Fig. 3). The first axis explained 51.6% of the variation and mainly separated species according to traits associated with resources acquisition; that is, species with high leaf $\delta^{18}\text{O}$, $\Psi_{\text{L-0700}}$, and SLA were placed at high axis values and those with high leaf $\delta^{13}\text{C}$ and C were placed at low axis values. The second axis explained an additional 25.8% of the variation. Species separation along the second axis was determined by traits associated

with drought resistance; that is, species with high VD and $\Psi_{\text{L-mid}}$ were at high axis values and those with high WD were at low axis values. Leaf-specific traits (including SLA, N_{mass} , $\delta^{18}\text{O}$, $\Psi_{\text{L-0700}}$, $\delta^{13}\text{C}$, and C) characterised the first PCA axis, where SLA, N_{mass} , and $\delta^{18}\text{O}$ had an opposite influence compared to the other two traits. The second PCA axis was determined by wood-specific traits (including VD, $\Psi_{\text{L-mid}}$ and WD), where WD seemed to have a trade-off relationship with VD.

Leaf and stem traits in relation to crown width across elevations

C_w was positively related to leaf $\delta^{18}\text{O}$ and $\Psi_{\text{L-0700}}$ (Fig. 4), indicating that the decrease in C_w across elevations was mainly caused by decreasing leaf $\delta^{18}\text{O}$ and $\Psi_{\text{L-0700}}$.

Discussion

PCA results revealed that the first and second axes represented the major ecological strategies of trees related to resource

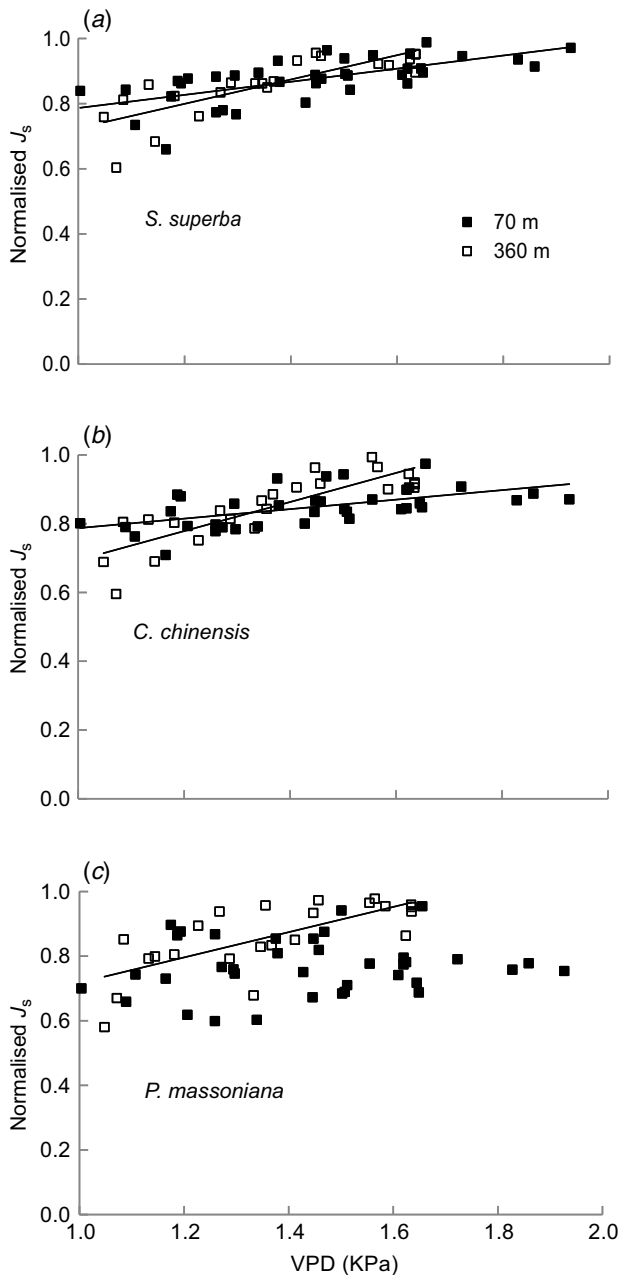


Fig. 2. Relationship between the normalised sap flux density per unit sapwood area (J_s) and vapour pressure deficit (VPD) for three tree species at the two elevations. The normalised J_s was calculated as the instantaneous J_s divided by the daily maximal J_s . Each dot represents the normalised J_s at VPD > 1 kPa for one sample tree. The lines are linear regressions fitted to the data: $y = 0.2015x + 0.5852$, $R^2 = 0.4338$, $P < 0.01$ at 70 m site and $y = 0.3733x + 0.3515$, $R^2 = 0.6612$, $P < 0.01$ at 360 m site for (a); $y = 0.1381x + 0.649$, $R^2 = 0.3103$, $P < 0.01$ at 70 m site and $y = 0.4227x + 0.2713$, $R^2 = 0.7139$, $P < 0.01$ at 360 m site for (b); and no relationship at 70 m site and $y = 0.03909x + 0.3269$, $R^2 = 0.512$, $P < 0.01$ at 360 m site for (c).

acquisition and stress resistance, respectively. In the present study, changes in leaf and stem traits with increasing elevation reflected an ability to resist drought. The

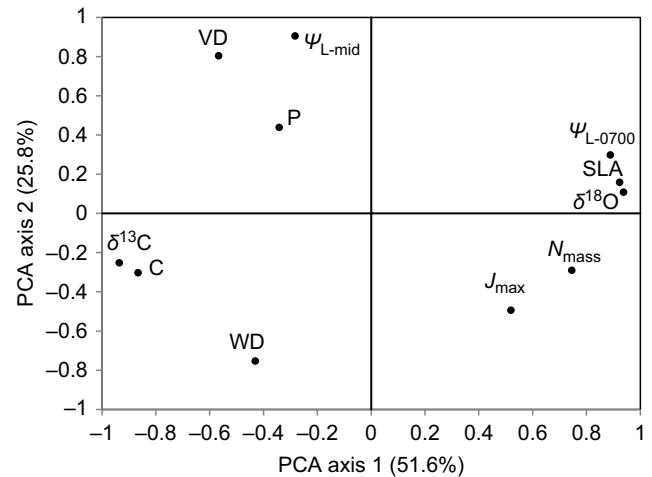


Fig. 3. Principal component analysis (PCA) of leaf and stem traits for three tree species across two elevations. The traits include wood density (WD), specific leaf area (SLA), vessel diameter (VD), maximum of daily sap flux density per unit sapwood area (J_{\max}), water potential at 0700 hours (Ψ_{L-0700} , when sap flux started) and at midday (Ψ_{L-mid}), $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, leaf C (C), N (N_{mass}), and P concentration (P).

decreases in leaf $\delta^{18}\text{O}$ (indicating increased stomatal conductance) and Ψ_{L-0700} were associated with a decrease in crown width at high elevation. Although WD increased at high elevation, it could not account for the variations in structural parameters. In the following sections, we discuss our results in more detail and explore their implications in trait-based ecology.

Variations in leaf and stem traits across two elevations

SLA decreased significantly at high elevation only in *C. chinensis*, and did not vary significantly in *S. superba* and *P. massoniana*. The statistically non-significant variation in SLA across elevations was inconsistent with the results from previous studies showing that SLA is more variable than other traits (Messier et al. 2010; Fajardo and Piper 2011; Umaña and Swenson 2019). SLA is a highly plastic trait, and can adjust to a range of environmental conditions during plant growth (Sultan 2000; Poorter et al. 2009). Trees exhibit a more conservative resource use strategy at high elevations. This is typically characterised by a lower SLA and thicker leaves with lower light-capturing area per unit biomass investment, indicating an adaptation to high radiation and low CO_2 concentrations (Kao and Chang 2001; Körner 2007; Poorter et al. 2009; Homeier et al. 2010; Hernández-Calderón et al. 2014; Read et al. 2014; Ding et al. 2019; Umaña and Swenson 2019). In *Metrosideros polymorpha* Gaud., SLA varies approximately four-fold along elevation gradients, and the decrease in SLA with increasing elevation is mainly ascribed to decreasing temperatures and changes in water availability at high elevation (Milla et al. 2009; Poorter et al. 2009; Scheepens et al. 2010).

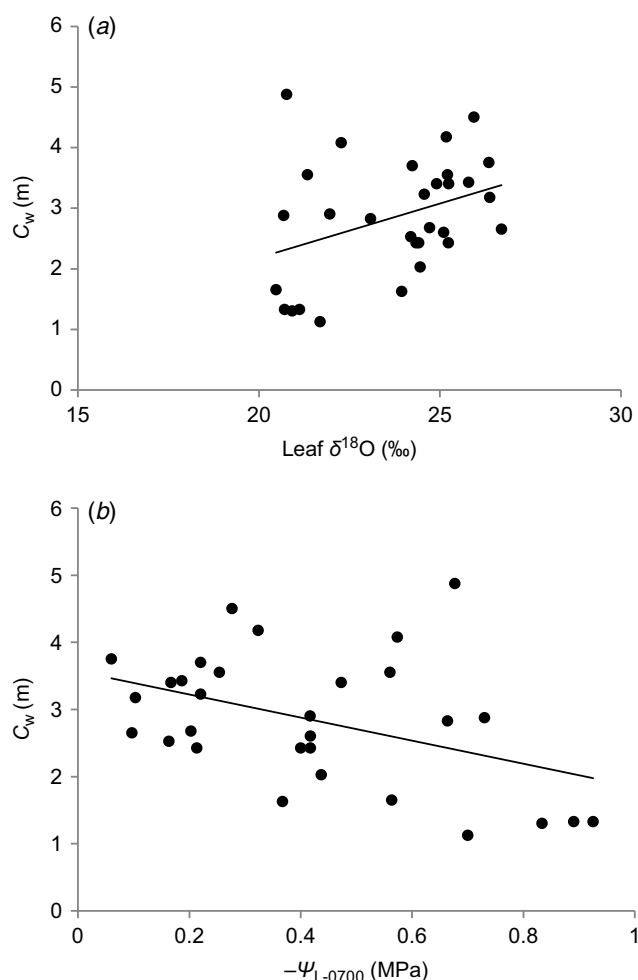


Fig. 4. Crown width (C_w) in relation to (a) leaf oxygen isotope composition $\delta^{18}\text{O}$ and (b) leaf water potential at 0700 hours (Ψ_{L-0700}) for three tree species at the two elevations. Each dot represents the trait value of one sample tree. The regression equations are included in the figure. r is the Pearson correlation coefficient. The lines are linear regressions fitted to the data: $y = 0.1789x - 1.3941$, $r = 0.362$, $P = 0.049$ for (a); and $y = -1.7238x + 3.57$, $r = 0.431$, $P = 0.017$ for (b).

Multiple abiotic factors are known to covary with elevation, which may complicate the patterns of variation in plant traits (Körner 2007; Umaña and Swenson 2019). The strong association between SLA and leaf nutrient concentrations (Wright *et al.* 2004; Fyllas *et al.* 2009; Baraloto *et al.* 2010) suggested that the change in SLA across elevations may have been caused by environmental variables other than soil fertility conditions in this study. This is indicated by the fact that SLA did not decrease with lower leaf P concentrations at high elevation. Moreover, limited water availability can positively or negatively influence SLA, and this can be quantified by decreasing growth and leaf structure investments (Silva *et al.* 2004; Aspelmeier and Leuschner 2006). Therefore, when investigating the impacts of warming on

vegetation, it is important to avoid the confounding effects of soil water availability on plant traits along an elevation gradient (Mujawamariya *et al.* 2018, 2021). The reduced abiotic differences between elevations during the rainy season may also lead to the lack of a clear relationship between SLA and elevation (Swenson *et al.* 2006; Gotsch *et al.* 2010). We found that soil moisture was comparable between the two elevations during the study period, which could partly explain the weak relationship between SLA and elevation in the present study. However, a wider range of elevation gradients needs to be considered when investigating the specific reasons for variations in SLA across elevations.

Leaf chemical traits have been recognised to be mainly mediated by soil fertility (Asner and Martin 2016). In the present study, soil P concentration decreased significantly at high elevation, and leaf P levels were correspondingly lower in *C. chinensis* and *P. massoniana*. Leaf P increases with elevation in fertile sites, but does not vary in infertile sites (Asner and Martin 2016). This suggests that the high elevation site in this study may have been P-limited, which is also supported by the leaf N:P being >14 at this site (data not shown). Suppressed foliar P levels in low-fertility soil are correlated with increased investment in leaf structure and defence (such as the increased LMA) and decreased photosynthetic pigment (Asner *et al.* 2014). Ding *et al.* (2019) found that leaf N and P concentrations per unit mass decreased with increasing elevations, and ascribed this to the conservative resource use strategies of evergreen trees at high elevation. In this study, we did not find any changes in N_{mass} with elevation. This is congruent with the results of Read *et al.* (2014), who ascribed the lack of responses in N_{mass} to the other constraints varying independently of elevation. For instance, soil N availability, which is strongly associated with leaf N, showed no global variation with elevation (Körner 2007). Acquisitive species tend to show higher SLA and N_{mass} but lower N_{area} (Shipley *et al.* 2006). In this study, we found an increase in N_{area} and a decrease in SLA with increasing elevation only for *C. chinensis* (Sheet 2 in Supplementary Information). This partially corroborates the notion that dominant tree species exhibit conservative strategies at high elevations. Alternatively, the increase in leaf N content at high elevation may have resulted from the lower temperature at higher elevations (Körner 1999; Weih and Karlsson 2001). Leaf N content is more concentrated under cold conditions due to reduced growth (Körner and Larcher 1988; Morecroft *et al.* 1992), and high elevation plants typically show restricted growth due to low temperatures and a shorter growing season. Moreover, N uptake by the roots of these plants is not as limited, resulting in higher leaf N content (Hultine and Marshall 2000; Pop *et al.* 2000). However, the air temperature was $>20^\circ\text{C}$ at the high elevation site in our study, which may not have been low enough to influence leaf N content. Decreased leaf size may also cause an increase in leaf N with altitude (Cordell *et al.* 1998, 1999). This, combined with the

relatively stable SLA across elevations, may explain the lack of variation in leaf N in our study.

High WD and low SLA values indicate a trade-off between resource allocation to metabolic production and growth rate (Sterck *et al.* 2006). Tree species with high LMA and WD dominated the high elevations. These traits are associated with increased longevity and improved carbon acquisition via more efficient photosynthesis (due to a higher capacity for RuBP (primary acceptor of CO₂ in the Calvin cycle RuBP) regeneration at low temperatures) (Huxman *et al.* 2008; Hernández-Calderón *et al.* 2014), therefore compensating for a decreased growth rate. A high WD is typically associated with higher conductive safety and greater mechanical support, and may confer increased resistance to stem breakage by wind and other extrinsic forces (Stratton *et al.* 2000; ter Steege and Hammond 2001; Chave *et al.* 2009). However, some studies have reported a lack of change in WD along elevational gradients. This could be due to the conflicting effects of mechanical support and hydraulic functions caused by multiple abiotic factors across elevations (Fajardo and Piper 2011; Siefert *et al.* 2015; Fajardo 2016; Umaña and Swenson 2019). For instance, some studies have attributed the low intraspecific variation in WD across elevations to the mixed impacts of variation in precipitation and canopy height along elevational gradients (Siefert *et al.* 2015; Fajardo 2016; Umaña and Swenson 2019). This inconsistency with our results may be partly due to the comparable tree heights across elevations in our study. A higher sapwood density at high elevations is associated with a reduction in conduit number and size (Gričar *et al.* 2005; Hoch and Körner 2005; Rossi *et al.* 2008). A decrease in VD with increasing elevation is generally considered to confer increased safety from embolism caused by freeze–thaw cycles (Noshiro and Suzuki 1995; Fisher *et al.* 2007; Jiménez-Noriega *et al.* 2017; Pandey *et al.* 2021). WD is also affected by the thickness and width of conduit wall and fibre structures (Hacke *et al.* 2001, 2005). In the present study, the conduit diameter did not significantly differ across elevations. However, the increase in WD may have resulted from changes in conduit wall or fibre traits, which can maintain efficient water transport within the xylem system while offering biotic and abiotic safety. In this study, Ψ_{L-0700} was found to be related to other plant traits. Ψ_{L-0700} may indicate the amount of water stored within the plants for use in transpiration, which have not been reported by any studies to date. This was demonstrated by the higher WD at high elevations in the present study, suggesting lower water content of the xylem. Several studies have reported the correlations between minimum leaf water potential (Ψ_{L-mid}) and other plant functional traits (Bucci *et al.* 2004; Santiago *et al.* 2004; Chave *et al.* 2009), as Ψ_{L-mid} is strongly linked with plant rooting depth. In this study, the soil moisture was comparable between the two elevations, which suggested an unlimited water supply at both sites. This may

explain the decoupling of the relationship between plant traits and root depth (and therefore, Ψ_{L-mid}). Furthermore, we observed that Ψ_{L-0700} (associated with tree height) was correlated with plant traits (leaf $\delta^{18}\text{O}$ and WD; Sheet 3 in Supplementary Information). This suggests that Ψ_{L-0700} is an important trait with potentially profound ecological implications in the intraspecific responses to environmental change, and deserves thorough investigation in future studies.

Since an increase of leaf $\delta^{18}\text{O}$ is associated with a decrease in stomatal conductance (Sheshshayee *et al.* 2005; Barbour 2007; Cernusak *et al.* 2009; Cabrera-Bosquet *et al.* 2011), we propose that a smaller leaf $\delta^{18}\text{O}$ indicates higher stomatal conductance at high elevation in this study. The elevation-related intraspecific variations in leaf $\delta^{18}\text{O}$ were also reflected in the responses of the normalised J_s to VPD, which was more sensitive to water demand at high elevation. Similarly, a higher stomatal sensitivity to VPD at high elevation has been reported in temperate mountain forests (Jung *et al.* 2014). An increase in maximum stomatal conductance with elevation facilitates more carbon assimilation under lower CO₂ partial pressure (Bresson *et al.* 2011). Apart from stomatal behaviour, changes in the ratio of leaf area to sapwood area ($A_L:A_S$) can also regulate the efficiency of water transpiration in trees (Fischer *et al.* 2002; Franks *et al.* 2007; Martínez-Vilalta and García-Forner 2017). A decrease in $A_L:A_S$ may increase water supply to leaves and prevent a decline in canopy conductance (Monserud and Marshall 2001; Fischer *et al.* 2002). Moreover, the decreased crown width and invariant DBH in this study may indicate a larger sapwood area per unit leaf area at the high elevation site. This further suggests an improved capacity for water supply through stem to leaves in the high elevation plants. Denser wood is known to be associated with low leaf area per stem area (Ackerly 2004; Wright *et al.* 2006). This finding supports our aforementioned suggestion, as we found an increase in WD at the high elevation site. Comparable sap flux densities per unit sapwood area and smaller $A_L:A_S$ values may also lead to a higher transpiration rate per unit leaf area, which is implied by the higher stomatal conductance of plants at high elevation. Previous studies have confirmed that an increase in leaf $\delta^{13}\text{C}$ with increasing elevation is attributable to the decrease in stomatal conductance, an increase in carboxylation efficiency (caused by a higher N content or leaf mass per area), and higher internal resistance (Morecroft *et al.* 1992; Hultine and Marshall 2000). The decrease in leaf $\delta^{18}\text{O}$ (that is, higher stomatal conductance) at high elevation was expected to result in a decrease in leaf $\delta^{13}\text{C}$. However, the leaf $\delta^{13}\text{C}$ remained constant across the two elevations in the present study. In addition, we found a negative correlation between leaf $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (data not shown; Pearson correlation coefficient, -0.727 , $P < 0.01$), indicating that photosynthetic capacity drives variations in leaf $\delta^{13}\text{C}$ (Flanagan and Farquhar 2014). Therefore, we suggest that increased photosynthetic

capacity, rather than stomatal conductance, likely played a crucial role in maintaining constant leaf $\delta^{13}\text{C}$ across the two elevations in the present study.

Several studies have reported that photosynthetic capacity increases along elevational gradients (Girardin *et al.* 2010; Bresson *et al.* 2011; Fan *et al.* 2011; Huasco *et al.* 2014). Environmental factors such as temperature and solar radiation, rather than soil properties, regulate photosynthetic capacity and elevated CO_2 concentrations can reduce photosynthesis capacity (Ainsworth and Rogers 2007; Smith *et al.* 2019). Thus, in our experiment, the increased solar radiation and the reduced atmospheric CO_2 concentration likely contributed to the enhanced photosynthetic capacity of plants at higher elevation. Woodruff *et al.* (2007) reported that high photosynthetic rates were associated with increasing transpiration rates in the tree canopy. In our study, the sap flux density per unit sapwood area did not change at high elevation, and the crown width decreased in plants at the high elevation site. Furthermore, an increased transpiration rate per unit leaf area may be associated with the high photosynthetic capacity in high elevation plants. As CO_2 concentrations decrease with elevation, the sensitivity of photosynthesis to stomatal conductance increases (Zhang *et al.* 1993; Niinemets 2002; Premoli and Brewer 2007; Reed and Loik 2016). Consequently, an increase in stomatal conductance with elevation may improve photosynthetic capacity by favouring CO_2 diffusion, thus counterbalancing the diffusive limitations caused by morphological adaptations (such as an increase in LMA) (Niinemets 2002; Gago *et al.* 2019). Therefore, we suggest that a trade-off between CO_2 uptake and hydraulic risk (associated with WD) due to stomatal apertures may have profound implications for the functional fitness of plants to environmental changes.

Plant life history theory suggests that species that exhibit rapid resource exploitation can be characterised by high SLA, hydraulic conductance, photosynthetic rates, and stomatal conductance, and low wood density (Reich *et al.* 1997; Wright *et al.* 2004; Díaz *et al.* 2016). However, Augustine and Reinhardt (2019) found differing levels of plasticity among morphological and physiological traits in first-year conifer seedlings exposed to water stress. In this study, we found evidence for conservative resource use strategies (including high WD and low leaf P) as well as acquisitive resource-use strategies (including improved leaf-level stomatal conductance, indicated by variations in leaf $\delta^{18}\text{O}$) in plants at high elevation. Grady *et al.* (2013) indicated that the relationships among leaf economic traits may not apply to adaptive variation at the intraspecific level. They suggested that a higher leaf area to sapwood area ratio could increase whole-canopy photosynthesis, thus compensating for low leaf-level photosynthesis. This is consistent with our findings; that is, the decrease in leaf-level photosynthetic capacity in low elevation plants does not necessarily indicate a low whole-tree carbon assimilation

rate. This is because a larger canopy width as a surrogate of leaf area may compensate for the loss of leaf-level photosynthetic capacity. Moreover, a decrease in respiration coupled with the photosynthetic capacity at low elevation likely favoured carbon fixation within plants (Dusenge *et al.* 2021; Mujawamariya *et al.* 2021). Therefore, it is necessary to investigate these traits at different plant tissue levels in order to thoroughly elucidate the intraspecific adaptive mechanisms to changing environments.

Responses of the canopy width to trait variations across elevations

Umaña and Swenson (2019) proposed a structural spectrum at the canopy level, ranging from 'cheap' leaves (high SLA, low construction cost) comprising a bigger crown to leaves with low SLA comprising smaller crowns. Consistent with this, we observed a smaller crown width at high elevation, although the differences in SLA across elevations were species-specific. Normand *et al.* (2008) proposed two main hypotheses to explain the changes in tree canopy structure with elevation. (1) First, the hydraulic limitation theory suggests that water-related environmental stress along elevational gradients would affect canopy expansion. The plant canopy has high water demand; therefore, changes in its structure and function could moderate water transport through the stems from the roots under adverse conditions (McDowell *et al.* 2002; Martínez-Vilalta *et al.* 2009; Gebrekirstos *et al.* 2011; Rosas *et al.* 2019). The height and total leaf area of plants were constrained as a response to the stressful climate at high elevation (Dierig *et al.* 2006; Ahmad *et al.* 2016, 2018; Leitold *et al.* 2018). Smith *et al.* (2019) reported that over the dry season, leaf area decreased in low canopy surfaces due to low soil water availability. In the present study, the lower water potential in the morning in high elevation plants likely indicated higher daily levels of water tension within the xylem. Therefore, the increased stomatal conductance and decreased crown width likely ensured sufficient water supply to leaves. (2) Second, the demand for mechanical support with changing environments modifies tree allometry (Henry and Aarssen 1999; Osunkoya *et al.* 2007; Normand *et al.* 2008). The climate features at high elevation include high wind exposure, which damages the upright plants (Premoli and Brewer 2007; Poorter *et al.* 2009; Wang *et al.* 2010). Species with lighter wood grow faster and reach the canopy faster in order to acquire more light resources (Enquist *et al.* 1999); however, this is not necessary for plants at high elevations that receive high solar radiation. Therefore, a high wood density, combined with a small canopy width, can promote whole-plant mechanical support and resistance to stem breakage from extrinsic forces such as wind (ter Steege and Hammond 2001).

Conclusions

Some physiological traits of leaves and stems such as leaf $\delta^{18}\text{O}$ and water potential showed plasticity across two elevations in response to environmental stresses. A decrease in leaf $\delta^{18}\text{O}$ resulted in an increase in stomatal conductance, thus assuring water transport efficiency within the xylem. Combined with a larger WD, this likely helped protect the xylem from cavitation under the more negative water potentials at high elevations. The leaf $\delta^{13}\text{C}$ remained constant and stomatal conductance increased, which probably helped maintain net carbon assimilation for the high tissue construction cost (high LMA and WD) at high elevation. Thereby, stomatal activity could play a central role in regulating the ecophysiological responses of plants to changing environments. In addition to the widely studied leaf and stem economics spectrum, measurements of other physiological traits such as leaf water potential, stomatal conductance, and transpiration rate should also be investigated along environmental gradients in future studies. Such investigations can improve our understanding of resource use strategies in forest ecosystems under changing environmental conditions.

Supplementary material

Supplementary material is available [online](#).

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