elevation, suggesting that P may become a limiting element for plant growth at high elevation. The present study suggests that the upper limit of *Q. aquifolioides* on Balang Mountain may be co-determined by winter root NSC storage and P availability. Our results contribute to better understanding of the mechanisms for plants' upper limit formation.

1. Introduction

Global warming is altering soil biogeochemistry in mountain systems around the world (Mayor et al., 2017), and there is increasing evidence that mountains are highly responsive to global climate change (Pauli et al., 2012). The global occurrence of mountains across all latitudes and the influential effect of declining temperature with increasing elevation, leading to the formation of treelines (Körner, 2012), offer unique opportunities to examine warming-induced phenomena in a natural context. As many environmental factors, such as temperature, precipitation, soil chemical and physical properties and growing season length, change simultaneously with elevation (White et al., 1999; Hughes, 2000; Körner, 2007), elevation can be used as a proxy for variation in biotic and abiotic characteristics to study and better understand how changes in climate may affect the growth and physiology of plants (Davis et al., 1991).

Environmental variation along elevational gradients may influence the functional and structural features of plants (Cordell et al., 1998; Peterson, 1998; Sexton et al., 2009), thus determining their growth (Lica(c)24.5(r)14.b(i)0(o-14.n(-v7820.4(g)14.a(e)0(i513.7(-v7820..1(2302.(ho)27.1(t)1

edge of Qinghai-Tibetan Plateau in southwestern China. The study area has a subtropical inland mountain climate with sunny, dry winter (November to April) and warm, humid summer (June to September). According to long-term climate data collected at 1920 m a.s.l. (Wolong Nature Reserve Authority), the annual mean precipitation is 995 mm, with rainfall mainly occurring from May to September, and the annual mean temperature is 12.8 °C, with the monthly mean temperature of 17.0 °C in July and −1.7 °C in January. Soil on the study slope is mountain brown soil with a depth of <50 cm.

Along the elevational gradient on the sunny slope of the Balang Mt., three climate stations were established at 2800, 3200 and 3500 m a.s.l., respectively. Climate data were collected for 2012 and 2013.

2.2. Study species and sampling protocol

Quercus aquifolioides occupies a wide range of habitats and occurs at altitudes from 2000 to 4500 m a.s.l. (Zhou, 1992; Zhu et al., 2012a, 2012b). It is a dominant, late-successional and climax species of the sclerophyllous evergreen broad-leaved forests on sunny, south-facing slopes in the region of the Hengduan Mountains (93°18′–104°43′ E, 26°33′–31°55′ N), southwestern China. On the sunny (south) slope of the Balang Mt. pure *Q. aquifolioides* stand ranged from 2800 m to 3600 m a.s.l. (upper limit). This naturally generated shrub stand is 30–35 years old, and comprises multi-stemmed clumps. Since the nature reserve was established in 1976, the *Q. aquifolioides* stands had not been disturbed.

We randomly selected six plots (5–10 m × 10 m) within the *Q. aquifolioides* stands at each of six elevations along the elevational gradient, i.e., 2843, 2978, 3159, 3327, 3441, and 3589 (±5) m a.s.l. The distance between any two plots at the same elevation was at least 50 m apart. We recorded the environmental conditions of each plot, and measured the mean height (H), mean diameter at breast height (DBH) and number of main stems of *Q. aquifolioides* clumps in each plot. Growth characteristics of *Q. aquifolioides* are summarized in Table 1. Samples were taken on 18–19 July 2014 (hereafter referred to as summer, i.e., at the time of peak growth) and on 6–7 November 2014 (winter, at the dormant season), when the plots at the lowest elevation (2843 m) were already covered by a thin layer of snow.

In each plot, four types of *Q. aquifolioides* tissues (2-year old leaves, 2-year old shoots, stem sapwood, and fine roots with a diameter of <0.5 cm) were sampled from >5 randomly selected individuals on each of the two sampling dates (summer, winter). Samples of leaves and shoots were taken from non-shaded branches on the upslope side of plants, between 10:30 and 16:00, when all plots received direct sunshine (Graham et al., 2003). To collect fine roots, we first found coarse roots originating from each selected *Q. aquifolioides* plant, and then fine roots (<0.5 cm in diameter) attached to those coarse roots were manually excavated using mini-spade, mini-pick, and trowel. Only fine roots that were located within the 0–20 cm soil layer around the stump (<50 cm) and covered by soil were collected, i.e., we did not collect any deep roots from parent materials (soil depth was <20 cm on the study slope) and roots exposed to air or sunlight. Leaves, shoots and fine roots collected from all trees within a plot were pooled and mixed to get a sample for each tissue for each plot ($n = 6$ plots), respectively. All samples were immediately stored in a cool box in the field, killed in a microwave oven in the evening (40 s at 600 W), and dried to a constant weight at 65 °C in Wolong Forest Ecosystem Research Station located at 2800 m a.s.l., and kept dry until laboratory treatments.

On 18–19 July 2014, mineral soils (0–10 cm depth) were also taken, after removing soil organic matter, from 4 to 6 locations in each plot and then mixed homogeneously to get a composite soil sample for each plot ($n = 6$ plots). Soils were taken from the 0–10 cm layer only because soil depth was <20 cm on that slope and the majority of fine root biomass in forest stands occurs in the top 0–20 cm soil layer (Jackson et al., 1996; Meinen et al., 2009). For each soil sample, a subsample was restored in 4 °C to test the quick-acting N, and the other subsample was dried for the measurement of P and other elements.

Table 1
Growth (mean ± 1SE, $n = 6$) of the sampling trees of *Quercus aquifoliodes* along the elevation gradient on the sunny slope of the Balang Mt.

	Elevation (m a.s.l.)	No. of stems per clump	Mean height (m)	Mean diameter at breast height (cm)
1	3589	2.3 ± 1.2	1.8 ± 0.6	5.5 ± 1.0
2	3441	7.5 ± 2.9	2.8 ± 0.5	7.4 ± 1.0
3	3327	7.4 ± 2.9	2.8 ± 0.9	5.1 ± 1.7
4	3159	6.1 ± 4.5	2.8 ± 0.9	5.6 ± 2.0
5	2978	3.5 ± 1.6	3.1 ± 0.7	7.1 ± 2.8
6	2843	7.0 ± 1.8	3.7 ± 0.3	8.2 ± 2.0

2.3. Non-structural carbohydrate (NSC) analysis

Dried plant material was shattered through a ball mill instrument. The powdered material (0.1 g) was put into a 15 mL centrifuge tube, where 5 mL of 80% ethanol was added. The mixture was incubated at 80 °C in a water bath shaker for 30 min, and then centrifuged at 4000 rpm for 5 min. The pellets were extracted two more times with 80% ethanol. Supernatants were retained for soluble sugar determinations, and the ethanol-insoluble pellet was used for starch extraction. Concentrations of NSC for a sample was defined as soluble sugar concentration plus starch concentration.

Soluble sugars in the supernatants were determined using the anthrone method (Seifter et al., 1950). An aliquot of the extract was hydrolysed in 5 mL of 0.4% anthrone solution (4 g anthrone in 1000 mL 95% H_2SO_4) in a boiling water bath for 10 min. After cooling, the sugar concentration was determined spectrophotometrically (ultraviolet-visible spectrophotometer 752S; Cany Precision Instruments Co., Ltd., Shanghai, China) at 620 nm. Glucose was used as a standard. The sugar concentration was calculated on a dry mass basis (% d.m.) and also on a leaf area basis (g/m^2, for leaves only).

Ethanol in the ethanol-insoluble pellet was removed by evaporation. Starch in the residue was released in 2 mL distilled water for 15 min in a boiling water bath. After cooling to room temperature, 2 mL of 9.2 mol L^{-1} $HClO_4$ was added. Starch was hydrolysed for 15 min. Distilled water (4 mL) was added to the samples. The samples were then centrifuged at 4000 rpm for 10 min. The pellets were extracted one more time with 2 mL of 4.6 mol L^{-1} $HClO_4$. Supernatants were retained, combined and filled to 25 mL, to measure the glucose concentration spectrophotometrically (ultraviolet-visible spectrophotometer 752S) at 620 nm using anthrone reagent, and the starch concentration was then calculated by multiplying glucose concentration by the conversion factor of 0.9 (Osaki et al., 1991). The starch concentration was described on a dry mass basis (% d.m.) and also on a leaf area basis (g/m^2, for leaves only).

2.4. Nitrogen and phosphorus analysis

Concentrations of total N of tissues were analyzed using a C/N analyzer (Vario Micro cube, Germany). Concentrations of total P were determined following ammonium molybdate method after nitric acid and perchloric acid (2:1) digestion (Sparks et al., 1996).

The availability of soil N (nitrate and ammonium) was determined colorimetrically from 1 M KCL soil extracts from fresh soil samples using an Auto Continuous Flow Analyzer (Bran & Luebbe, Norderstedt, Germany). The availability of soil P was determined by the molybdenum blue colorimetric method (Murphy and Riley, 1962) after extraction by 0.5 M $NaHCO_3$ (Olsen, 1954).

2.5. Statistical analysis

Data were tested for normality and homogeneity of variance, and transformed to logarithm when normality and homogeneity of variance

Table 2
The effects of elevation, sampling season (summer and winter), tissue type, and their interactions on concentrations of non-structural carbohydrates (NSC), total nitrogTf1.94238.8(gi(,)-262(N)0()27.8(,)-188.9(t)17.2(o)19.6(-)TJT(ta)-24.1(l)-358.1(p)-11.6(h)-1.9o)-16(sp)-19.2(h)-1.
aquifoliodes plants, tested with three-way ANOVAs.

Effects	df	NSCN	P	N:P
Season gi(,S))-2312.7(1,)-257.1(24026.75108(3.09)TJ4.7818004.25126.481967				
S × E	5, 240	10.77***	3.73*** 7.19*** 4.42***	3.92***
S × T × E	15, 240	***	1.52	
		2971***	1.31	2972***

F values are given. Note, degree of freedom (df) and significance levels ($^{ns}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$).

could not be met. First, we tested the effects of sampling season (summer, winter), tissue type (4 types), elevation (6 levels), and their interactions on tissue NSC, N, P, NSC:N, and N:P, and found that tissue type interacted with elevation to affect the parameters studied (Table 2). We, therefore, analyzed the effects of sampling date and elevation on each parameter for each tissue type separately (Table 3). To explore the dynamic pattern along the elevational gradient, we tested the relationship between physiological indexes (NSC, N, P, NSC:N, and N:P) and altitude with regression analysis (Figs. 1–6), as well as the correlation analysis between soil and each tissue (Table 4). All the statistical analyses were done using SPSS (v. 20.0, SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Climatic factors and soil N and P along the elevational gradient

The climatic pattern along the elevational gradient showed almost the same trend for the two years, and annual and growing season patterns differed only in the numeric value (Fig. 1). Air temperature (Fig. 1A, B) decreased linearly with elevation, but soil temperature did not (Fig. 1C, D). Temperature lapse rate was 0.46 °C per 100 m. Growing season air humidity (Fig. 1H) increased linearly with elevation, but annual air humidity did not (Fig. 1G). The precipitation was significantly less at lower elevations than at the highest elevation (Fig. 1E, F). Available soil N increased linearly with increasing elevation, but available soil P decreased linearly with elevation (Fig. 1I, J).

3.2. Plant tissue N and P along the elevational gradient

Plant tissue N and P concentration varied significantly with sampling season, tissue type, and elevation (Table 2). Total N and P level in different plant tissues changed significantly with sampling season, except for N in shoots (Table 3). In summer, tissue N concentration did not show any clear elevational trends (Fig. 2A, C, E, G). In winter, N concentration in leaves and fine roots decreased linearly with increasing elevation (Fig. 2B, H). In summer, P level in all plant tissues decreased linearly with increasing elevation (Fig. 3A, C, E, G). In winter, P levels in leaves and fine roots reased linearly with increasing elevation (Fig. 3B, H).

3.3. Plant tissue NSC along the elevational gradient

There was no season effect on tissue NSC concentrations (Table 2), but NSC levels varied significantly with both sampling season and tissu type (Tables). In summer, the NSC concentrations in leaves n and 3 creased significantly linearly with increasing elevation (Fig. 4A), but NSC levels in other tissues did not show any elevational trends (Fig. 4C, E, G). In winter, the NSC concentrations in fine roots significantly de creased with increasing elevation (Fig. 4H).

3.4. Plant tissue NSC:N and N:P along the enilelevational gradient

Plant NSC and N:P ratio were signi

							ns
	S × E		**	1.30ns	0.92ns	1.72ns	ns
Shoots	Season (S)	1, 60	0.18ns	1.08ns	***	0.09ns	
					ns	4.89***	7.17***
	S × E		ns	2.21ns	3.04*	1.55ns	
			ns	3.46**	5.61***	3.32*	6.60***
	S × E		ns	0.98ns	8.32***	0.53ns	
						ns	
				ns	3.24**	3.77**	4.79***

F values are given. Note, degree of freedom (df) and significance levels ($^{ns}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$).

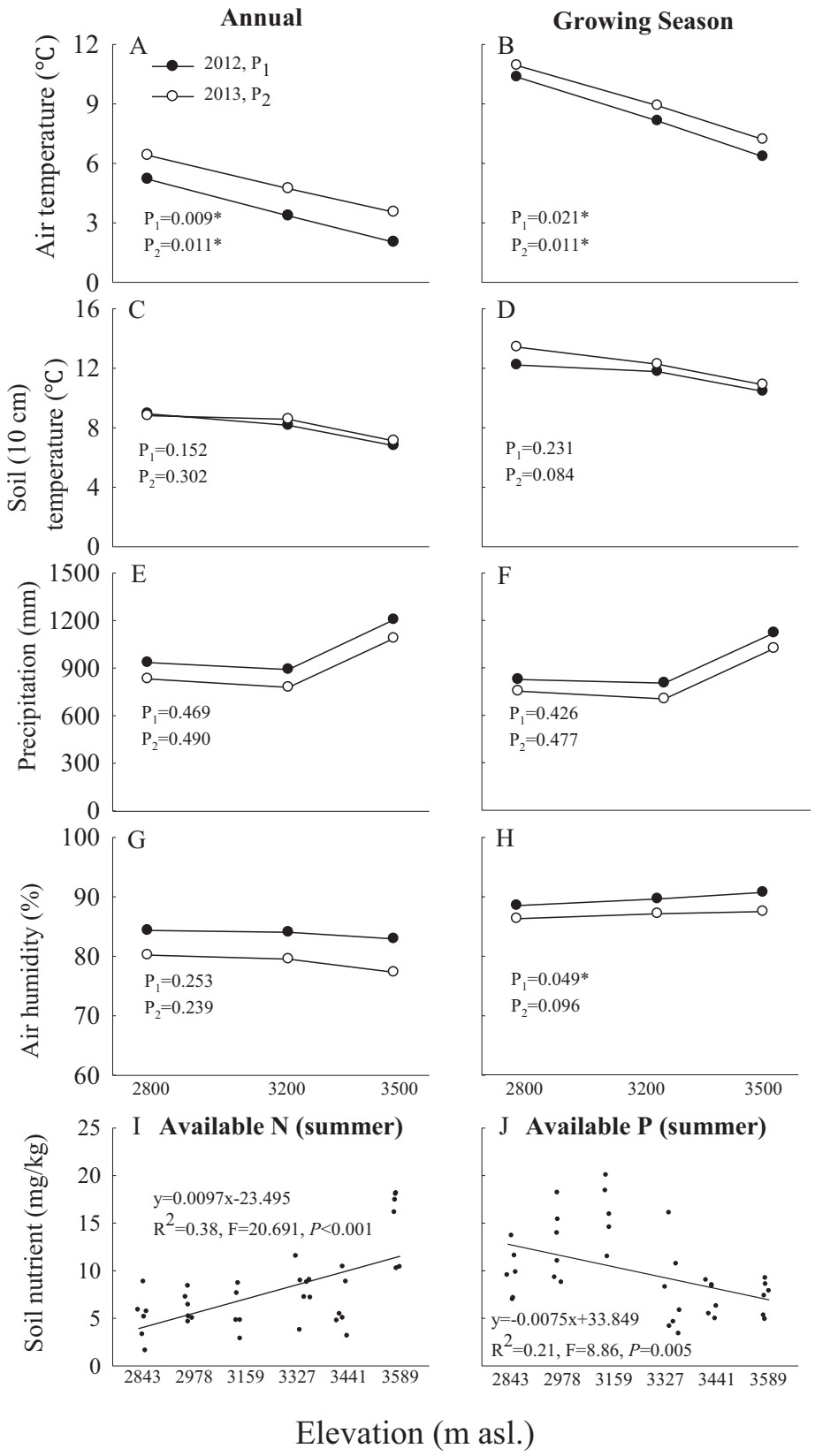


Fig. 1. Annual average and growing season meteorological conditions in relation to elevation in 2012 and 2013 (A–H) and soil available nutrient (I and J) conditions in growing season in 2014. P_1 means value of 2012; P_2 means value of 2013.

the end of the growing season may influence winter survival and early spring re-growth, playing an important role in the persistence and development of *Q. aquifoliodes* at its upper distributional elevations. The root NSC concentrations decreased significantly with increasing elevation in winter, this phenomenon, indeed, did not imply fully depletion of mobile carbohydrates in plants growing at their elevational limit

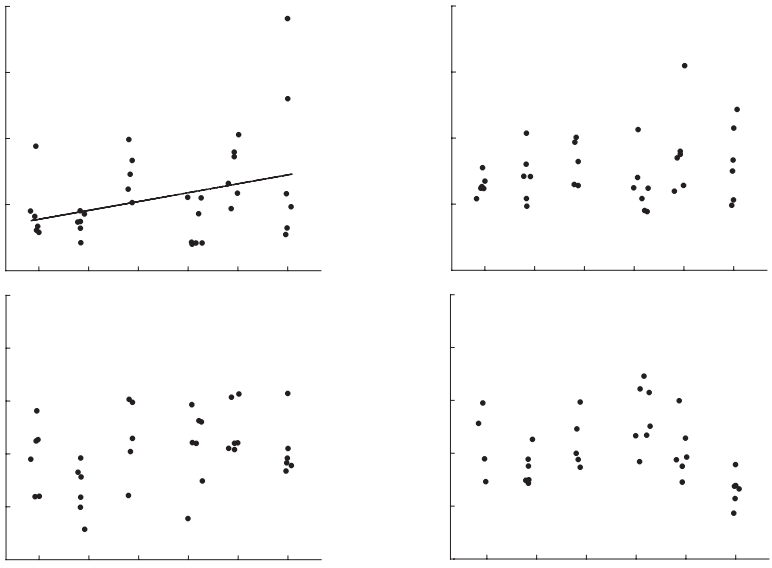
(Fig. 4H). Moreover, increasing root biomass with increasing elevation (Leuschner et al., 2007; Graefe et al., 2008; Moser et al., 2011; Zhu et al., 2012a, 2012b) may compensate for the decreasing NSC concentration when considering the root NSC pool size.

We found that soil available N increased significantly with increasing elevation (Fig. 1I), which may be a result of decreasing mineralization (Kitayama et al., 1998; Soethe et al., 2008) and increasing organic matter (Dieleman et al., 2013; Du et al., 2014) and thus increasing organic N content in soils with altitude. In general, N cycling rates (e.g., nitrification and denitrification) tend to be more active at lower elevations than higher elevations in subtropical and tropical mountain forests (Vitousek, 1994; Pendry and Proctor, 1996; Leuschner et al., 2007), which may lead to decreasing N availability with increasing elevation (Sjögersten and Wookey, 2005), and thus, alpine ecosystems are often thought to be N limited (Vitousek and Howarth, 19[illegible]

study, high frequency of thunderstorm and snowfall may provide sufficient available N in soils at high elevations (Fig. 1I). However, plant tissue N concentrations (Fig. 2A–H) did not positively respond to increases in soil N availability with increasing elevation (Fig. 1I). At higher elevations, lower temperature and shorter growing season may restrict plants' N uptake and use (Vitousek, 1994; Liptzin et al., 2013; Sundqvist et al., 2014), leading to a decoupling between soil N availability (Fig. 1I) and plant tissue N (Fig. 2A–H) concentrations (Table 4). Some studies described an increase in N accumulation and conservation with increasing elevation as adaptive responses to low temperature in alpine ecosystems, to enhance or maintain the metabolic capacity of plants in cold environment (Richardson et al., 2001; Shi et al., 2006). Our result showed a stable pattern of N in different tissues along the elevational gradient in summer, suggesting that N resource does not

oth plant tissue P (Fig. 3) and
g elevation. Consequently, there
on between plant tissue P and soil
4), suggesting that P is more limited
me studies have also provided evidence
importance of P versus N limitation with in-
de Weg et al., 2009). Low P availability in soils
nutrient absorption and utilization, and indirectly
d physiological processes in plants, which further
decrease in total P levels in different tissues at high el-
. 3). However, Chen et al. (2013) measured leaf N and P
tions of 386 woody species in 14 forest sites across eastern
nd found that both leaf N and P concentrations were negatively
elated with mean annual temperature but positively correlated
th soil N and P contents. Other studies showed that leaf N and P concentrations first increased and then decreased with increasing elevation (Van de Weg et al., 2009; Fisher et al., 2013). Previous studies demonstrated that changes in leaf N and P concentrations reflected environmental conditions more than plant intrinsic characteristics, such as genotype (Ågren and Weih, 2012) and taxonomy (Zhang et al., 2012).

Plant N and P contents often influence each other during the growing season, especially in leaves (Kang et al., 2011; Yuan and Chen, 2012). Our results showed an increasing pattern of N:P in leaves in summer, which is consistent with previous studies (Yuan and Chen, 2012; Fisher et al., 2013). Several studies found that tissue N:P ratio increased with increasing elevation (Kang et al., 2011; Yuan and Chen, 2012; Chen et al., 2013; Zhao et al., 2016). However, based on data gained from 386 woody species across eastern China, Chen et al. (2013) reported that growing season leaf N:P ratio was positively correlated with mean annual temperature, i.e. N:P ratio decreases with increasing elevation.



immobilization with increasing elevation (Rinnan et al., 2007; Nadelhoffer et al., 1991).

4.2. Seasonal variation of NSC and nutrients in different tissues

Seasonal variation of NSC indicated a season-dependent carbon balance between carbon acquisition (photosynthesis) and carbon investment (growth and respiration), which is consistent with previous studies (Shibata and Nishida, 1993; Palacio et al., 2008; Zhu et al., 2012a, 2012b). In summer, tissue NSC concentration did not decrease with increasing elevation (Fig. 4A, C, E, G), whereas in winter, root NSC concentration significantly linearly decreased with elevation (Fig. 4H). NSC may transfer among different tissues depending on the relative activity between tissues or between sources and sinks (Finn and Brun, 1982), or at the expenses of growth during the growing season to guarantee the survival of plants in winter, because high tissue NSC concentrations help to avoid intra- and intercellular ice formation and thus freezing damage. Moreover, tissue NSC levels may also be either passively (source-to-sink flow) or actively (gene expression) controlled (Wiley and Helliker, 2012). For example, when irradiance or source activity is insufficient, biomass of stems and roots decreases, NSC can be transferred from roots to leaves (Lee et al., 2007). Variations of environmental conditions at higher elevations may, therefore, cause resource remobilization among different tissues, which is also a strategy of plants to face the harsh habitat (Gaucher et al., 2005; Kilpeläinen et al., 2005) such as low temperature.

Available soil N increased with increasing elevation (Fig. 1I), indicating that soil N resources were sufficient to support *Q. aquifolioides* growth along the elevational gradient, even at the upper limit. A worldwide comparison revealed that trees at their upper limits did not have any disadvantages in N supply compared to plants at lower elevations (Körner, 1989). Unlike N in soil and plant tissues, both soil available P (Fig. 1J) and plant tissue P (both in summer and winter) decreased with increasing elevation (Fig. 3A–H), which may, as mentioned

availability of soil N, associated with increasing elevation, suggests that increasing temperature with global warming may lead to a decrease in the relative importance of P versus N limitation for *Q. aquifolioides*.

NSC:N in shoots and fine roots was similar between winter and summer, suggesting that the pattern of carbon and N balance was relatively stable (Figs. 2 and 4). Carbon and N levels in plants generally reflect the difference between uptake (photosynthesis; source activity) and demand (metabolism, growth and export; sink activity) (Körner, 2003). Increasing NSC:N with altitude indicated that carbon source did not limit tree growth and development along this elevational gradient. Other factors can be more limiting for plant growth and distribution in this study area. A linear increase in the NSC:N with altitude may indicate relative increases in N limitation with altitude (He et al., 2006). In the current study, however, variation in NSC:N was caused more by increasing NSC levels rather than by decreasing N concentrations. Nevertheless, nutritional constraints at high elevation may still hamper the conversion of carbohydrates into N- and/or P-based compounds (e.g., amino acids, proteins), as well as the transport of these compounds from leaves to other plant organs (Körner, 2003).

The ratio of N to P can be regulated by soil nutrient availability, tree growth rates and plant needs (Tessier and Raynal, 2003; Elser et al., 2003; Reich and Oleksyn, 2004; Hogan et al., 2010) and, as such, is regarded as an important index to explain nutrient limitation pattern (Wardle et al., 2004; He et al., 2006). A review of 40 fertilization studies revealed that an N:$P > 16$ indicated P limitation, while an N:$P < 14$ is indicative of N limitation. At N:P between 14 and 16, either N or P can be limiting or plant growth is co-limited by N and P together (Koerselman and Meuleman, 1996). In summer, N:P in leaves increased significantly with elevation, and much more than in other tissues. N:P was higher than 16 in leaves but lower than 14 in other tissues in summer. In both summer and winter, we found a tendency for increasing N:P with altitude in all tissues. We suggest that P limitation plays a more important role than N limitation on *Q. aquifolioides* growth at higher elevations. Zhao et al. (2014) found that tree leaf N:P ratios increased, while leaf N and P concentrations decreased with elevation (500–2300 m a.s.l.) in northeastern China. Conversely, N:P ratios decreased significantly as elevation increased, especially at the transition from krummholz to the alpine tundra in a Himalayan treeeline ecotone (Müller et al., 2017). He et al. (2016) found that plant and soil nutrient properties did not change linearly with elevation from 50 to 950 m a.s.l. in subtropical China.

5. Conclusions

Our results fully supported our 1st and 2nd hypotheses but are only partly in line with our 3rd hypothesis (see Introduction). Plant NSC levels depend on tissue type, elevation, season, and tissue P, but it was not correlated with tissue N. This study showed that the availability of soil N significantly increased with increasing elevation, probably because of the slowing organic matter cycling under low temperature and N deposition from snow at high elevations. Conversely, the availability of soil P decreased progressively with increasing elevation, which implies increasing P limitation with increasing elevation. Soil nutrient availability influenced by climate (temperature and precipitation), soil (leaching and weathering) and biotic factors (litter quality

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