Soil properties determine the elevational patterns of base cations and

micronutrients in plant-soil system up to the upper limits of trees and shrubs

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Abstract

To understand whether base cations and micronutrients in the plant-soil system change with elevation, we investigated the patterns of base cations and micronutrients

20   in both soils and plant tissues along three elevational gradients and three different climate zones in China. Base cations of Ca, Mg and K and micronutrients of Fe, Mn and Zn were determined in soils, trees and shrubs growing at lower and middle elevations as well as at their upper limits on Balang (subtropical, SW China), Qilian (dry-temperate, NW China) and Changbai (wet-temperate, NE China) mountains. No

25   consistent elevational patterns were found for base cation and micronutrient concentrations in both soils and plant tissues (leaves, roots, shoots and stem sapwood). Rather, soil pH, total soil nitrogen (TN), the soil organic carbon (SOC) to TN ratio (C:N), and total soil inorganic nitrogen (TIN) determined the elevational patterns of soil exchangeable Ca and Mg. Furthermore, multiple regression models showed that

30   soil pH and C:N were pivotal factors affecting soil Fe, Mn and Zn availabilities. In return, soil base cation and micronutrient availabilities played fundamental roles in determining the base cation and micronutrient concentrations in plant tissues. Our results highlight the importance of soil physicochemical properties (mainly SOC, C:N and pH) rather than elevation (i.e., canopy cover and environmental factors, especially

35   temperature), in determining base cation and micronutrient availabilities in soils and subsequently their concentrations in plant tissues.

Key words base cation, micronutrient, plant tissue, soil physicochemical property, shrubline, treeline

1 Introduction

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Base cations and micronutrients are essential for plant physioecological processes of

photosynthesis, metabolism, growth and productivity (Salisbury and Ross, 1992). For

instance, calcium (Ca) and magnesium (Mg) are fundamental for cell structure,

intracellular messaging and carbohydrate storage of plants (McLaughlin and Wimmer,

45   1999; Verbruggen and Hermans, 2013), although deficiency of these nutrients rarely

occurs (Berger et al., 2016; Cusack et al., 2016). Micronutrient deficiency, on the

other hand occurs more frequently, for instance when replenishment of micronutrients

via litter decomposition do not keep pace with output processes of plant uptake and

leaching (White and Zasoski, 1999; Hernandez-Apaolaza, 2014). High soil pH can

50   limit the availability of micronutrients, such as iron (Fe), inducing Fe deficiency

chlorosis in plants as a result of suppressed chlorophyll synthesis (Lucena, 2000),

while low soil pH can induce toxicities of Fe, manganese (Mn) and zinc (Zn)

constraining terrestrial net primary productivity (He et al., 2005; Reisenauer, 1988;

Tian et al., 2016). Both soil pH and soil organic matter (SOM) are fundamental

55   controllers over soil base cation and micronutrient availability (Martens and

Westermann, 1991; Wang et al., 2017) and subsequently their concentrations in plant

tissues. The concentrations of soil base cations and available micronutrients were

suggested to be positively and negatively correlated with soil pH, respectively, but

both positively correlated with SOM concentration (Reisenauer, 1988; Wang et al.,

60   2017). Quantifying base cation and micronutrient concentrations in soils and plant

tissues (leaves, roots, shoots, and stems) can help understand the nutritional status and

potential deficiencies of micronutrients during plant growth (Richardson, 2004).

However, little attention has been paid to base cation and micronutrient availabilities

as well as their inputs and outputs under changing environmental conditions (Rengel,

65   2007).

The plant distribution along elevational gradients reflects changes in

environmental conditions (Li et al., 2003, 2004, 2008a,b; Zhu et al., 2012a,b). Plants

growing at high elevation, especially close to their upper limits, are expected to be

highly sensitive to climate change, in particular to global warming (Noble, 1993).

70   Physiological studies of treeline trees have mainly focused on macronutrients (*e.g.*,

nitrogen (N), phosphorus (P), and Ca (Richardson, 2004; Liptzin et al., 2013; Mayor

et al., 2017), there are few data available for micronutrients in plant-soil systems

along elevational gradients.

Two hypotheses have been proposed to explain nutrient accumulation and/or

75   nutrient deficiency in plant tissues at high elevations (Oleksyn et al., 2002;

Richardson, 2004). First, the decrease in temperature with increasing elevation

declines soil microbial activity and plant metabolism, and thus constrains soil nutrient

cycling and plant uptake processes (Körner & Paulsen, 2004; Thébault et al., 2014).

At the alpine treeline, low temperature slows down microbial-mediated litter

80   decomposition and thus reduces nutrient supply to plants (van den Driessche, 1974;

Richardson, 2004). Second, another paradigm exists that plants retain higher nutrient

concentrations in their tissues to maintain metabolic capacity and to avoid cold injury

at higher elevations with cold growth conditions (Oleksyn et al., 2002). Whether

plants growing at high elevations have higher or lower base cation and micronutrient

85   concentrations is still unclear.

The change in environmental conditions, including temperature and growing

season length (Barry, 1981), provides a unique opportunity to examine the spatial

distribution of base cations and micronutrients in plant-soil systems. Uncertainties still

exists whether soil properties, plant cover, or environmental factors determine the

90   base cations and micronutrients in plant-soil systems. We, therefore, studied the base

cation (Ca, Mg, and K) and micronutrient (Fe, Mn, and Zn) concentrations in

plant-soil systems along elevational gradients up to the alpine treeline and shrubline in

sub-tropic, dry temperate and wet temperate climate zones in China. Soil base cation

and micronutrient concentrations can increase through soil weathering and

95   decomposition of organic matter, but can decrease with plant uptake and loss through

leaching. At low elevations, forests have closed canopies and become increasingly

more open with elevation. We therefore hypothesized that soil base cation and

micronutrient concentrations increase with increasing elevation because plant uptake

decreases more than the supply through weathering and decomposition with elevation.

100   We also expected that plants living at higher elevations would have greater base

cation and micronutrient concentrations in their tissues (leaves, roots, shoots, and

stem sapwood) to maintain physio-ecological processes in a colder environment. To

test these hypotheses, we collected soil and plant samples along three elevational

gradients from lower elevations up to the alpine treeline or shrubline in three different

105   climate zones in China, and studied the Ca, Mg, K, Fe, Mn, and Zn concentrations in

plant-soil systems.

2 Materials and methods

2.1 Site description and sample collection

110 Study sites were located in three climate zones (summarized in Table S1): Balang

mountains with a subtropical climate located in Wolong Nature Reserve (Balang,

102 °52′-103 °24′E, 30 °45′-31 °25′N) in southwestern China, Qilian mountains are

located in the dry-temperate climate zone (Qilian, 102 °58′-103 °01′E, 37 °14′-37 °20′N)

located in northwestern China, and Changbai mountain with a wet-temperate climate

115 (Changbai, 126 °55′-129 °00′E, 41 °23′-42°36 ′N) located in northeastern China (see Fig.

S1). The Wolong Natural Reserve is influenced by warm-wet monsoon masses in

summer and continental air masses in winter (Li et al., 2012). The mean annual

precipitation (MAP) of the Balang mountains is about 846 mm monitored by

Dengsheng Meteorological Station at 2730 m (Li et al., 2012). For the Qilian

120 mountains, the MAP is 435 mm, which is monitored by the Qilian weather station at

2787 m altitude (Qiang et al., 2003). The Changbai mountain is located in a typical

continental temperate monsoon climate zone with MAP increasing from 632 to 1154

mm along the elevational gradient from 530 to 2200 m (Shen et al., 2013).

In this study, the alpine treeline and shrubline are defined as the upper limit of

125 obvious trees and shrubs, respectively. The trees that were investigated are *Abies*

faxoniana (elevation range 2860-3670 m) for Balang, *Picea crassifolia* (elevation

range 2540-3250 m) for Qilian, and *Betula ermanii* (elevation range 1700-2030 m) for

Changbai. The shrubs are *Quercus aquifolioides* (elevation range 2840-3590 m), *Salix gilashanica* (elevation range 3020-3540 m), and *Vaccinium uliginosum* (elevation

130 range 1430-2380 m) for Balang, Qilian and Changbai, respectively. The soils from the

three sampling sites of Balang, Qilian, and Changbai were classified as Umbric Cryic

Cambisols, Calcaric Ustic Cambisols and Andic Gelic Cambisols, respectively (IUSS

Working Group WRB, 2014).

Plant tissue samples of current-year mature leaves, roots (< 2 mm), stem sapwood,

135 and shoots (twigs) from trees and shrubs were collected at lower and middle

elevations, as well as at the upper limits. At each elevation, 6 plots (10 m $\times$ 10 m)

were selected on southern slopes. Within each plot, 6-10 trees and shrubs of similar

height were randomly selected for tissue sampling. Soils (0-10 cm) were directly

collected under the canopy of trees or shrubs sampled for each plot using a 3-cm

140 diameter corer. Samples were collected at the middle of July for Balang, at the

beginning of August for Qilian, and at end of August for Changbai in 2014.

2.2 Chemical analysis

The soil samples were air-dried to constant weight for further analyses. For Balang

and Changbai, soil organic carbon (SOC) and total nitrogen (TN) was determined on

145 ground soils using an elemental analyzer (Vario MACRO Cube, Elementar, Germany).

For Qilian, the ground soil samples were treated with 12 M HCl according to Wang et

al. (2015) to remove inorganic C before organic C determination on the elemental

analyzer. Soil NO_3^--N and NH_4^+-N were extracted with a 2 M KCl solution and

measured using an AutoAnalyser III continuous Flow Analyzer (Bran & Luebbe,

150 Norderstedt, Germany). Soil total inorganic nitrogen (TIN) was the sum up of

extractable NO_3^--N and NH_4^+-N. Soil Olsen phosphorus (P) was quantified by

colorimetric analysis after extraction with a 0.5 M $NaHCO_3$ solution (Olsen et al.,

1954).

A subsample of 5 g soil was used to determine soil pH in a 1:5 (w/v) soil-to-water

155 extract. Soil exchangeable base cations were extracted with a 1 M ammonium acetate

solution (Wang et al., 2017). Soil available micronutrients were extracted by

diethylenetriamine pentaacetic acid (DTPA) according to Lü et al. (2016). Briefly, 10

g of soil was extracted by 20 ml 0.005 M DTPA + 0.01 M $CaCl_2$ + 0.1 M TEA

(triethanolamine) (pH 7.0). The slurry was shaken for 2 h at 180 rpm and then filtered

160 through ash-free filter paper. The concentrations of base cations and micronutrients

were determined using an atomic absorption spectrometer (AAS, Shimadzu, Japan).

Plant samples of leaves, roots, shoots and stem sapwood were oven-dried and

ground for base cation and micronutrient analyses. Root samples were washed prior to

being oven-dried. To determine total base cation and trace element concentrations, 0.2

165 g plant samples were digested with a mixture of acids of HNO_3 and $HClO_4$ (5:1, v/v)

on a hot plate. After the mixture turned into clear solution, the digests were decanted

into a 50 ml volumetric flasks and the volume was adjusted into 50 ml. The

concentrations of Ca, Mg, K, Fe, Mn, and Zn were determined by the AAS (Shimadzu,

Japan).

170 **2.3 Statistical analyses**

Normality of data was determined using the Kolmogorov-Smirnov test, and

homogeneity of variances using Levene's test. Two-way ANOVAs were executed to

determine the effects of plant life form (tree or shrub), elevation position and their

interactions on soil pH, SOC, soil exchangeable base cations and available

175   micronutrients, and total base cations and micronutrients in plant tissues. We assigned

sampling site as a random factor in the statistics, as this study aimed to test the general

elevational patterns instead of site-specific heterogeneity of base cations and

micronutrients in plant-soil system across three sites. Within each site, the effect of

elevation on measured parameters was determined by multiple comparisons with a

180   Tukey design for soils and each plant species. Pearson correlation analysis was used

to determine the relationships between measured parameters. All statistical analyses

were performed in SPSS 16.0 (SPSS, Inc., Chicago, IL, USA) and statistical

significance was accepted at $P < 0.05$.

185   **3 Results**

3.1 Soil pH and SOC

Soil pH was significantly different among elevational positions (Table 1). For both

Balang and Qilian, soil pH decreased with increasing elevation under tree canopy,

while it was the opposite trend under shrub canopy (Fig. 1a). For Changbai, the upper

190   limit of shrubs had significantly higher soil pH (Fig. 1a).

For all three sites, SOC concentration showed a hump-shaped trend with the

highest value at the middle elevation under tree canopy (Fig. 1b). Under shrubs, SOC

concentration significantly increased with increasing elevation for Balang and

Changbai, while it was the lowest at the upper limit of shrubs for Qilian (Fig. 1b).

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3.2 Changes in soil base cations and available micronutrients

Soil exchangeable Ca and Mg decreased with increasing elevation under tree canopy
of Balang and Changbai and under shrubs of Qilian (not for Mg) (Fig. 2a,b). However,
they showed the opposite trend under shrubs of Balang (not for Mg) and Changbai

200 and under trees of Qilian (Fig. 2a,b). Soil exchangeable K decreased with increasing
elevation under tree and shrub canopies at Balang and under trees at Qilian (Fig. 2c).

Soil available Fe was significantly affected by elevation position (Table 2, Fig.
2d). The upper limit had the lowest concentration under both tree and shrub canopies
for Balang and under shrub canopy for Changbai (Fig. 2d). For Qilian, soil available

205 Fe significantly increased with increasing elevation under both tree and shrub
canopies (Fig. 2a). For Balang, soil available Mn was significantly higher at the
middle elevation under tree canopies. Soil available Mn decreased with increasing
elevation under shrub and tree canopies for Balang and Qilian, respectively, while it
showed the opposite trend under both tree and shrub canopies of Qilian and under

210 shrubs of Changbai (Fig. 2e). Soil available Zn was significantly affected by plant life
form and the interactive effect between life form and elevation position (Table 2).
Specifically, soils at the upper limit had the highest available Zn under shrubs at
Changbai.

215 ## 3.3 Base cations in plants

For Balang, a significant decrease of Ca concentration was detected in the leaves of trees and shrubs (Fig. 3a), roots and shoots of trees (Fig. 3b,c), and stem sapwood of shrubs (Fig. 3d). For Qilian, Ca concentration decreased with increasing elevation in roots, shoots and stem sapwood of trees (Fig. 3b,c,d), and in shoots and stem sapwood

220   of shrubs (Fig. 3c,d). For Changbai, shoot Ca concentration decreased with increasing elevation for trees (Fig. 3c). Along with increasing elevation, a significant decrease of Mg was found in shrub leaves, tree roots, shrub shoots and stem sapwood at Balang (Fig. 3e,f,g,h), and in roots, shoots and stem sapwood of trees at Qilian (Fig. 3f,g,h), and in leaves and shoots of both trees and shrubs at Changbai (Fig. 3e,g). With the

225   increase in elevation, K concentration significantly decreased in leaves of trees, roots and stem sapwood of both trees and shrubs at Balang (Fig. 3i,j,l), in tree shoots of Qilian (Fig. 3k), and in leaves of both trees and shrubs at Changbai (Fig. 3i).

3.4 Micronutrients in plants

230   For Balang, Fe concentrations in leaves (Fig. 4a) and roots (Fig. 4b) showed a similar trend with soil available Fe, with the highest values at the middle elevation for both trees and shrubs. For Qilian, the highest Fe concentrations were found at the lower elevation in leaves (Fig. 4a), roots (Fig. 4b), shoots (Fig. 4c) and stem sapwood (Fig. 4d) for trees and in shoots (Fig. 4c) and stem sapwood (Fig. 4d) for shrubs. For

235   Changbai, Fe concentration was the highest in tree shoots at the middle elevation (Fig. 4c), in shrub leaves at lower elevation (Fig. 4a), and in roots, shoots and stem sapwood of shrubs at the upper limit of trees (Fig. 4b,c,d).

The Mn concentration decreased with increasing elevation in leaves and shoots of both trees and shrubs at Balang (Fig. 4e,g), in stem sapwood of shrubs at both Balang and Qilian (Fig. 4h). The Mn concentration increased with increasing elevation in leaves of trees at Qilian (Fig. 4e), in roots of both trees and shrubs at Changbai (Fig. 4f), in shoots of shrubs and stem sapwood of trees and shrubs at Changbai (Fig. 4g,h).

The Zn concentration was the highest at middle elevation for trees in leaves at Changbai (Fig. 4i), in roots at Qilian (Fig. 4j), in shoots at Changbai (Fig. 4k) and in stem sapwood at Balang (Fig. 4l). With the increase in elevation, a decrease of Zn concentration was found in roots of trees at Balang (Fig. 4j) and in stem sapwood of shrubs at Qilian (Fig. 4l); however, an increase of Zn was found in shrub roots at Changbai, in shoots of trees at Qilian and shrubs at Changbai (Fig. 4k), and in stem sapwood of trees at Qilian and shrubs at Changbai (Fig. 4l).

3.5 Correlations

Across all sampling sites and plant life forms, both soil exchangeable Ca and Mg were positively correlated with soil pH (Fig. S2a,b) and TN (Table 3), while they were negatively correlated with soil C:N, NO_3^-, NH_4^+ and TIN (Table 3). According to the multiple regression analyses (stepwise removal), soil pH and SOC explained 92% of the variance in exchangeable Ca (Table 3). Soil pH, SOC and NO_3^- explained 86% of the variance in exchangeable Mg (Table 3).

Soil available Fe, Mn and Zn negatively correlated with soil pH ($p < 0.01$; Table 3, Fig. S2c,d,e), and soil available Fe and Zn positively correlated with SOC, C:N and

260   NH$_4^+$ ($p < 0.01$; Table 3). According to the stepwise regression models, soil pH, TN,

C:N, and NO$_3^-$ explained 59% of the variance in soil available Fe (Table 3), and soil

pH and C:N explained 18% of the variance in available Mn (Table 3). For soil

available Zn, 72% of its variation was explained by pH, SOC, and NH$_4^+$ (Table 3).

Positive correlations were found between soil exchangeable Ca and Ca

265   concentrations in plant tissues ($p < 0.01$), between soil exchangeable Mg and Mg

concentrations in leaves and shoots ($p < 0.01$), and between soil exchangeable K and

K concentration in roots, shoots and stem sapwood (Table 4).

Negative correlations were found between soil available Fe and Fe concentrations

in both shoots and stem sapwood ($p < 0.01$), and between soil available Mn

270   concentrations and Mn concentrations in leaves, roots, shoots and stem sapwood

(Table 4). Soil available Zn positively correlated with Zn concentrations in leaves,

roots, shoots and stem sapwood (Table 4). For each micronutrient, significant and

positive correlations were found with its concentrations among plant tissues, except

for Fe in root *vs.* stem sapwood and Zn in leaf vs. stem sapwood (Table 4).

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4 Discussion

4.1 Elevational patterns of base cations and available micronutrients in soils and relationships with pH and SOC

Contrary to our first hypothesis, no consistent elevational patterns were detected for

280   soil exchangeable base cations and available micronutrients under either trees or

shrubs. Inconsistent elevational patterns of soil base cations and available

micronutrients indicated that plant uptake of these nutrients did not necessarily

decrease more than nutrient supply at higher elevation due to more open canopies.

Our results suggest that soil physiochemical parameters were the dominant

285 contributors and more important than environmental gradients affecting elevational

patterns of soil exchangeable base cations and available micronutrients (Fig. S2, Table

3). For instance, soil available Fe, Mn and Zn followed patterns of SOC under trees

along the elevational gradient at Balang (Table S2), while for shrubs at Balang, soil

pH, instead of SOC, regulated elevational patterns of soil available Fe, Mn and Zn

290 (Table S2). Our findings are consistent with a vast amount of previous studies

confirming the pivotal role of soil pH and SOC concentration in determining soil base

cation and micronutrient availabilities (Sharma et al., 2004; Lü et al., 2016; Wang et

al., 2017). However, the fundamental roles of SOC and soil pH in controlling soil base

cation and micronutrient availabilities, was not universal as suggested by the

295 relatively weak relationships of soil pH and SOC with soil base cations under tree

canopies at Changbai and with micronutrients under both tree and shrub canopies at

Qilian (Table S2).

Other soil parameters, such as C:N and extractable NO_3^- and NH_4^+ also

influenced the availability of base cations (Table 3). Soil C:N ratio serves as an

300 indicator of SOM decomposition status where more decomposed SOM possesses a

lower C:N ratio (Sollins et al., 2009) and a higher content of negatively charged

functional groups (i.e. phenolic, carboxyl, and hydroxyl groups) (Laudicina et al.,

2015). In this study, negative correlations between soil C:N and base cations (Table 3)

suggest that more decomposed SOM is beneficial for the retention of soil base cations.

305 Furthermore, soil with a higher level of extractable NO_3^- predisposes cations to leach

accompanied by loss of NO_3^- (Cremer and Prietzel, 2017). Therefore, significant

negative correlations were detected between soil NO_3^- and base cations in this study

(Table 3). Soil extractable NH_4^+ was also negatively correlated to exchange with Ca

and Mg, possibly because NH_4^+ can exchange with base cations on surface soil

310 colloids into soil solution thereby enhancing their loss (Wang et al., 2015; Cusack et

al., 2016).

A negative correlation between soil pH and soil available micronutrients (Table 3)

might be due to precipitation of micronutrient cations at higher soil pH (Rengel, 2007).

Indeed, solubility of micronutrients was suggested to decrease from 100-fold (for Mn

315 and Zn) to 1000-fold (for Fe) with one-unit increase of soil pH (Rengel, 2001). Soil

organic matter plays an important role in micronutrient retention due to its negative

charge (He et al., 2005; Wang et al., 2015, 2017). This may be a reason for the

positive relationships between SOC and micronutrients (although not always

significant, Table 3). While no general patterns were found for distribution of

320 micronutrients under both tree and shrub canopies with elevation, our results suggest

that the determinants of soil micronutrient availabilities were soil pH and SOC

concentration, which are reflections of long-term climatic conditions, plant-soil

interactions, and biogeochemical processes (Sinsabaugh et al., 2008).

325 **4.2 Elevational patterns of base cations and micronutrients in plants and**

plant-soil system

In contrast to our second hypothesis, both trees and shrubs at higher elevation did not

necessarily contain higher base cation and micronutrient concentrations in their

tissues. No general patterns were found for base cations and micronutrients in both

330   trees and shrubs along elevational gradients across the three sites (Fig. 3,4). Even

normalizing the data to per unit concentration of soil available nutrients, there were

still no consistent elevational patterns for both base cations and micronutrients in

plant tissues (Fig. S3). This suggests that base cation and micronutrient concentrations

in plants are influenced by other factors besides elevation-induced changes in

335   temperature, precipitation, specific nutrient absorption characteristics of different

tissues, soil base cation and micronutrient availabilities and other edaphic properties

(Richardson, 2004). Rather, soil base cation and micronutrient availabilities were an

important factor influencing their concentrations in plant tissues across all plant

species and sampling sites (Table 4). Similar results were found for macronutrients

340   (i.e. nitrogen and phosphorus) suggesting that "plants are what they root in" (Elser et

al., 2010; Han et al., 2014). However, plant nutrients did not covary with soil nutrients

along a 2200 km-long climatic gradient in grasslands of northern China (Luo et al.,

2015, 2016). The discrepancy of our study with Luo et al. (2015, 2016) might be

driven by different ecosystem types (forest vs. grassland), dominant climatic factor

345   gradients (temperature vs. precipitation), and different soil properties. The studies of

Luo et al. (2015, 2016) were conducted in grassland ecosystems where precipitation

played an essential role in nutrient concentrations in plant-soil systems. Moreover,

base cation and micronutrient cycling processes are likely to be different between

high-organic and fine-grained forest soils in our study versus low-organic and sandy

350   grassland soils in Luo et al. (2016). Our results suggest that individual plant species

reinforced patterns of soil nutrient availabilities in their vicinity causing a positive

feedback between plant and soil (Hobbie, 1992).

Very limited progress has been made toward base cation and micronutrient

translocation among plant tissues (Kochian, 1991). The topic of base cation and

355   micronutrient translocation in intact plant is important as it deals with the movement

of micronutrients from root to the leaves for physiological activities, such as

photosynthesis (Welch and Shuman, 1995). Also, it is an important process in

determining plant chemical composition and subsequently litter quality, litter

decomposition and nutrient release (Sun et al., 2016). Given earlier findings that

360   transport of base cations from roots to the leaves in woody plants is slow (van der

Heijden et al., 2015), we found no significant correlation for both Mg and K between

roots and leaves (Table 4). However, negative relationships of stem Mg vs. leaf Mg

and stem K vs. leaf K suggest that the plant internal pools of base cations could act as

sources of base cation supply for leaves (Weatherall et al., 2006). Translocation of

365   base cations within plant tissues is one of main physiological mechanisms buffering

low nutrient availabilities in soils (van der Heijden et al., 2015). For instance,

supplementation of Mg is a critical process to maintain photosynthesis in forests

growing on acid and cation poor soils (Verbruggen and Hermans, 2013). In support of

this, we found significantly positive correlations between Mg and soluble sugar

370   concentrations (one of the main photosynthate) in leaves across the three sites (Fig.

S4a), while relationships were more pronounced at Changbai (Fig.S4b) where soil pH

and exchangeable Mg was the lowest (Fig. 1a, 2b).

Unlike Ca, Mg, Mn and Zn, the concentrations of K and Fe in plant leaves and

shoots decoupled with their availabilities in the soil (Table 4), which may suggest that

375   not only availability of these nutrients in soils affect their leaf concentrations, but that

also other environmental factors (*e.g.*, temperature) played more important roles in

affecting plant nutrition (van den Driessche, 1974). We do not know why this

decoupling only occurred for K and Fe, but possibly factors such as temperature

constrained soil microbial activity and plant metabolism (Körner and Paulsen, 2004)

380   and subsequently uptake of these nutrients by plants. On the other hand, plants often

increase nutrient uptake to compensate for decreased metabolism at low temperature

(Reich and Oleksyn, 2004). Thus, these opposite effects of temperature on K and Fe

concentrations in plant tissues may have obscured their relationships with K and Fe

availability in the soil along the elevational gradients. While plant nutrient

385   concentrations were mainly influenced by nutrient availabilities in the soil and by

plant-internal translocation processes, we found no consistent evidence that plants

accumulate more base cations and micronutrients in their tissues to better adapt to

cold environments at higher elevation.

390   **5 Conclusions**

We did not find consistent elevational patterns of base cations and micronutrients in

plant-soil systems along three different elevation transects up to the alpine treeline

and shrubline in different regions of China. Rather, our results highlight the essential

roles of specific edaphic properties of soil pH, SOC and extractable nitrate and

395   ammonium in regulating soil base cation and micronutrient availabilities among

sampling sites. Soil available base cations and micronutrients were mostly positively

correlated to concentrations of base cations and micronutrients in plant tissues, except

for K and Fe. Our results suggest that base cation and micronutrient concentrations in

plants located in upper limits of the tree- and shrublines are largely controlled by their

400   availabilities in the soil, rather than by plant adaptations to avoid cold injury at higher

elevations.

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Data Availability

Data sets for this paper can be obtained via personal communication.

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Author contributions

Mai-He Li designed the study; Xue Wang, Heyong Liu, Jinfei Yin and Zhan Shi did

the plant and soil measurements; Ruzhen Wang and Xue Wang analyzed the data;

Ruzhen Wang wrote the manuscript; Mai-He Li, Feike A. Dijkstra and Artemi Cerdà

415 revised the manuscript; Mai-He Li and Yong Jiang provided funding and laboratory

facilities for this study.

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Tables

Table 1 Two-way ANOVAs (*F* values) of the effect of plant life form (L, tree or

shrub), elevation position (E), and their interactions on soil pH, soil organic carbon

595   (SOC), base cations in soils (exchangeable form) and plants (total) across sampling

sites.

	Soil pH	SOC	Soil Ca	Soil Mg	Soil K	Leaf Ca	Root Ca	Shoot Ca	Stem Ca	Leaf Mg	Root Mg	Shoot Mg	Stem Mg	Leaf K	Root K	shoot K	stem K
L	0.18	5.75*	1.02	8.15**	24.64**	9.74*	1.69	10.85*	39.36**	93.41*	8.35**	15.82**	118.58**	12.57**	6.41*	63.56**	87.00**
E	3.16*	10.12**	1.22	1.71	15.21**	7.82*	3.85*	8.36**	1.17	0.83	5.85**	2.42	10.47*	9.30*	0.22	0.48	0.85
L×E	15.57**	3.34*	2.40	0.55	8.61*	2.24	8.55**	6.61**	1.11	1.82	7.20**	5.23**	0.37	0.96	1.01	2.20	2.84

* and ** indicate significant level at P < 0.05 and 0.01, respectively.

600 **Table 2** Two-way ANOVAs (*F* values) of the effect of plant life form (L, tree or

shrub), elevation position (E), and their interactions on soil micronutrients in both

soils (available form) and plants (total) across sampling sites.

	Soil Fe	Soil Mn	Soil Zn	Leaf Fe	Root Fe	Shoot Fe	Stem Fe	Leaf Mn	Root Mn	Shoot Mn	Stem Mn	Leaf Zn	Root Zn	Shoot Zn	Stem Zn
L	8.72**	2.60	6.89**	64.67**	0.72	0.12	8.54**	0.03	27.05**	40.67**	25.17**	11.83**	2.01	4.40*	80.60**
E	5.75**	1.54	0.01	0.02	1.80	0.50	2.40	7.13**	2.63	1.54	0.53	0.67	0.71	1.67	3.61*
L×E	0.10	1.69	4.42*	0.36	3.40*	3.73*	0.61	0.15	2.81	1.22	2.37	0.90	1.93	1.34	2.12

* and ** indicate significant level at P < 0.05 and 0.01, respectively.

605

Table 3 Regression statistics relating soil base cations and micronutrients to other soil physicochemical parameters under all trees and shrubs across three sampling sites. The TN, C:N, TIN, and Olsen P represent soil total nitrogen, SOC to TN ratio, total inorganic nitrogen, and Olsen phosphorus.

	Ca	Mg	K	Fe	Mn	Zn
pH	**0.94****	**0.87****	-0.06	**-0.64****	**-0.36****	**-0.73****
SOC	0.12	0.24*	0.18	0.30**	0.07	**0.37****
TN	**0.39****	**0.51****	0.18	**-0.01**	0.03	0.11
C:N	-0.45**	-0.44**	-0.11	**0.60****	**0.02**	0.44**
NO$_3^-$	-0.24*	**-0.29****	**0.28****	**-0.05**	0.02	0.08
NH$_4^+$	-0.38**	-0.33**	-0.10	0.46**	0.15	**0.63****
TIN	-0.38**	-0.39**	0.19*	0.17	0.08	0.36**
Olsen P	0.10	0.18	**0.49****	-0.05	0.04	0.03
Multiple	0.96**	0.93**	0.53**	0.77**	0.43**	0.85**

610

For both linear and multiple regression, R values are labeled with * and ** indicating significant level at $P < 0.05$ and 0.01, respectively. For multiple regressions (Multiple), R values of soil parameters with significant contributions are presented in bold type.

Table 4 Correlation analyses for base cations and available micronutrients in soil and

615 plant tissues of leaf, root, shoot and stem sapwood across sampling sites, plant life

form and elevation position.

Base cations and micronutrients	Correlation analyses				
Ca		Soil Ca	Leaf Ca	Root Ca	Shoot Ca
	Leaf Ca	0.60**			
	Root Ca	0.56**	0.37**		
	Shoot Ca	0.56**	0.37**	0.54**	
	Stem Ca	0.56**	-0.01	0.24*	0.43**
Mg		Soil Mg	Leaf Mg	Root Mg	Shoot Mg
	Leaf Mg	0.66**			
	Root Mg	0.10	-0.09		
	Shoot Mg	0.44**	0.44**	0.21*	
	Stem Mg	0.10	-0.41**	0.17	-0.09
K		Soil K	Leaf K	Root K	Shoot K
	Leaf K	-0.06			
	Root K	0.34**	-0.08		
	Shoot K	0.32**	0.07	0.44**	
	Stem K	0.21*	-0.46**	0.55**	0.20*
Fe		Soil Fe	Leaf Fe	Root Fe	Shoot Fe
	Leaf Fe	-0.17			
	Root Fe	-0.07	0.37**		
	Shoot Fe	-0.43**	0.38**	0.27**	
	Stem Fe	-0.39**	0.35**	0.13	0.53**
Mn		Soil Mn	Leaf Mn	Root Mn	Shoot Mn
	Leaf Mn	0.30**			
	Root Mn	0.28**	0.67**		
	Shoot Mn	0.35**	0.61**	0.89**	
	Stem Mn	0.32**	0.46**	0.19*	0.22*
Zn		Soil Zn	Leaf Zn	Root Zn	Shoot Zn
	Leaf Zn	0.52**			
	Root Zn	0.57**	0.69**		
	Shoot Zn	0.62**	0.86**	0.88**	
	Stem Zn	0.44**	0.11	0.53**	0.48**

* and ** indicate significant level at $P < 0.05$ and 0.01, respectively.

Figures

620

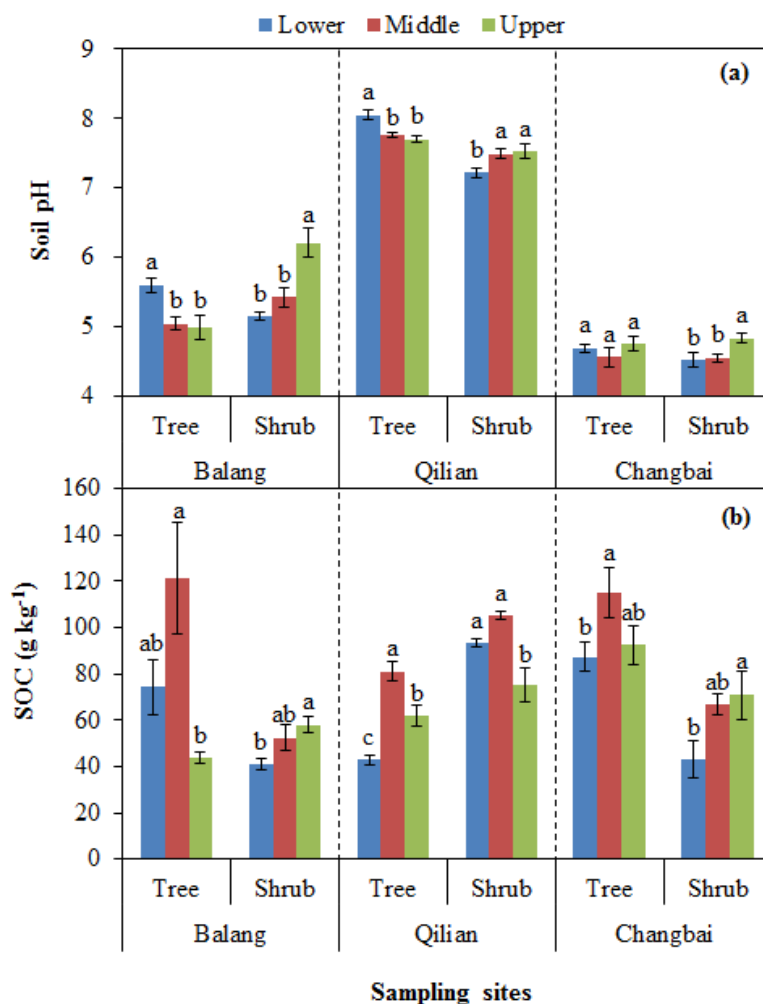



Fig. 1 Soil pH values (a) and soil organic carbon (SOC) concentration (b) at lower

and middle elevations as well as at the upper limit of treelines or shrublines for each

of the three sites. Different letters indicate significant differences among three

625   elevations within treeline or shrubline for each site.

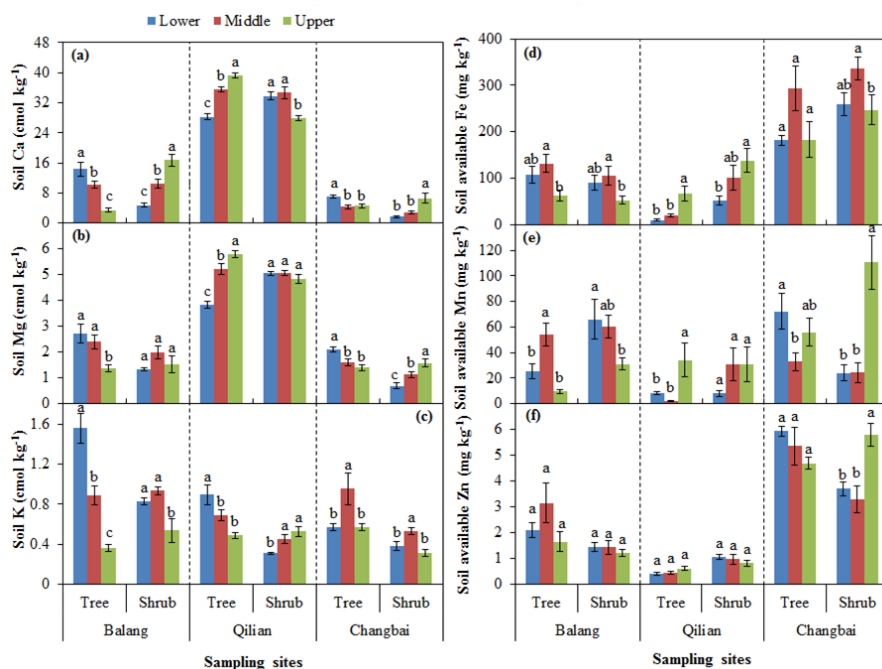
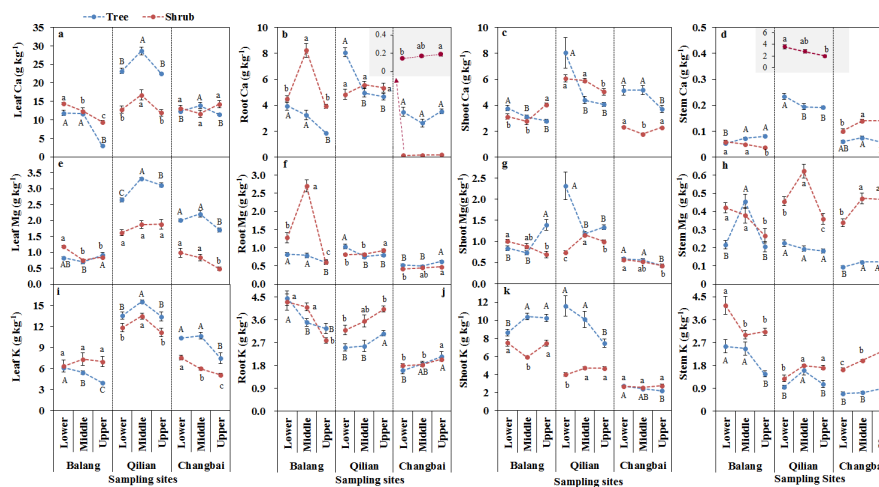



Fig. 2 Concentrations of soil exchangeable base cations of Ca (a), Mg (b) and K (c)

and available micronutrients of Fe (d), Mn (e) and Zn (f) at lower and middle

630   elevations as well as at the upper limit of trees or shrubs for each of the three sites.

Different letters indicate significant differences among three elevations within treeline

or shrubline for each site.

635   **Fig. 3** Base cation concentrations of Ca (a, b, c, d), Mg (e, f, g, h) and K (I, j, k, l) in

plant tissues of leaf, root, shoot and stem sapwood at lower and middle elevations as

well as at the upper limit of trees or shrubs for each of the three sites. Different letters

indicate significant differences among three elevations within treeline or shrubline for

each site.

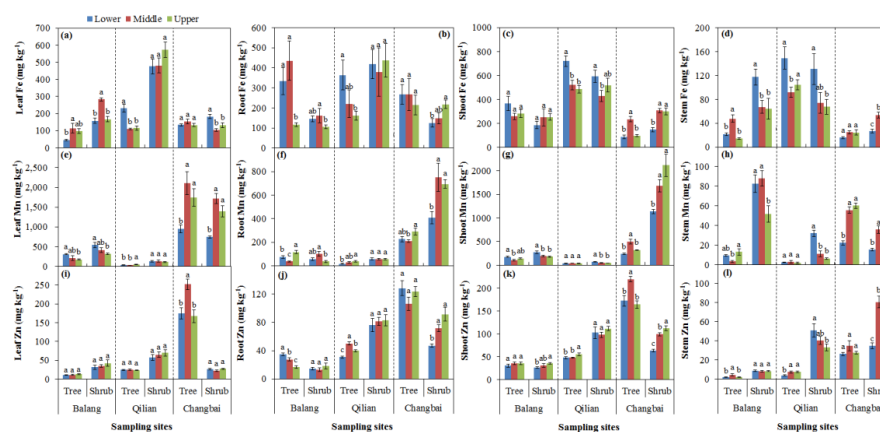



Fig. 4 Micronutrient concentrations of Fe (a, b, c, d), Mn (e, f, g, h) and Zn (I, j, k, l)

in plant tissues of leaf, root, shoot and stem sapwood at lower and middle elevations

as well as at the upper limit of trees or shrubs for each of the three sites. Different

letters indicate significant differences among three elevations within treeline or

shrubline for each site.