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Article in *Crop and Pasture Science* · January 2015

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# Across-trophic variation of potassium, calcium and magnesium stoichiometric traits in a parasitism food chain across temperate and subtropical biomes

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**Abstract.** Potassium (K), calcium (Ca) and magnesium (Mg) are three macro-elements essential for plants and animals. The ratios K : Mg or K : (Ca + Mg) are viewed as indices of physiological status in livestock animals. In plants, Ca, Mg and K concentrations can vary with climate in terrestrial ecosystems. Here, with a widespread tree species (Chinese cork oak, *Quercus variabilis* Blume) and an acorn predator (the weevil *Curculio davidi* Fairmaire), we investigate how K, Ca and Mg vary in soils, plant tissues (leaves and acorns) and a consumer (herbivore insects) with climatic variables induced by latitude (LAT) across the temperate–subtropical areas of eastern China. Concentrations of K, Ca and Mg in soils, leaves, acorns and weevil larvae showed different degrees of variation across the study area, but only Mg concentration increased significantly with rising LAT across all four trophic levels, albeit with varying slopes. With rising mean annual temperature (MAT) and precipitation (MAP), soil Ca significantly decreased, as did leaf and acorn K concentrations, whereas all four trophic levels showed significant decreases in Mg content with both MAT and MAP ( $P < 0.05$ – $0.001$ ). Leaf and acorn Ca : Mg showed significant relationships with LAT and MAT ( $P < 0.05$ – $0.01$ ). The K : (Mg + Ca) ratio in soils and weevil larvae increased linearly with MAP ( $P < 0.05$ ), and acorn K : (Mg + Ca) ratio varied in a concave manner ( $P < 0.001$ ). Our results suggest that variations of Ca, Mg and K in plant tissues and weevil larva across a study area of 20° LAT range were largely driven by climatic factors, and that Mg concentration changes in all four trophic levels with climate (and LAT) largely drive changes in soil, plant and consumer ratios between Mg, Ca and/or K. These results provide information on possible effects of climate change on nutrient dynamics in terrestrial ecosystems.

**Additional keywords:** eastern Asia, ecological stoichiometry, ecosystem processes, herbivore insects, leaching.

Received 15 March 2015, accepted 27 October 2015, published online 21 December 2015

## Introduction

Magnesium (Mg), calcium (Ca) and potassium (K) are three essential metal elements, playing important roles in a variety of biochemical and physiological activities of organisms (Kirkby and Pilbeam 1984; Whitehead 2000; Jammická *et al.* 2007; Sardans and Peñuelas 2015). Magnesium plays a critical role in phloem loading, transport of photoassimilates into sink organs, photosynthesis, enzyme activation, and formation and utilisation of ATP in plants, and bone formation, hormone regulation and cell replication in animals (Rude and Gruber 2004). Emerging evidence suggests that Mg concentration in plants is decreased as a result of higher levels of photosynthesis induced by increasing CO<sub>2</sub> (Loladze 2014), leading to lower available Mg for consumers. Lower Mg intakes as a global trend might contribute to some human illness such as osteoporosis and

cardiovascular disease (CVD) and higher mortality rates (Rude and Gruber 2004; Rosanoff 2013).

Potassium is essential to photosynthesis, chlorophyll function and many enzyme actions in plants (Marschner 1995) and is essential for health in animals and humans, especially in relation to Mg and Ca (Grunes and Welch 1989; Suter 1999; Aburto *et al.* 2013). Potassium also protects plants during water deficiency (Sardans *et al.* 2012). Both soil K and plant K have long been studied because of their importance to crop production (Hewitt and Smith 1974). Recently, the characteristics of K dynamics in terrestrial ecosystems on a global scale have been stressed (Tripler *et al.* 2006; Sardans and Peñuelas 2015).

Calcium plays structural roles in the cell wall and membranes, influencing plant growth and development (Marschner 1995; Hepler 2005). In the vacuole, Ca<sup>2+</sup> provides a counter-cation

for inorganic and organic anions, allowing plant cells to store, digest and detoxify metabolites (White and Broadley 2003). In animals, ~98–99% of the Ca resides in bones and teeth, with the other 1–2% in various soft tissues or extracellular fluids. Extracellular fluids have important physiological roles (Grace 1983), and the concentration of Ca in plasma and extracellular fluids is tightly regulated by homeostatic mechanisms (Underwood and Suttle 1999) that respond to Mg status (Rude 1993).

It is important to consider adequacy of these three elements in soils and organisms, as well as their ratios in both ecological and physiological processes. For example, low Mg concentration can lead to grass tetany in animals, with symptoms largely due to low Mg in food or a high K level, which can decrease efficiency of Mg and Ca absorption by the animals. Thus, in livestock cultivation, K : Mg and K : (Mg + Ca) ratios are often used as an indication of grass tetany (Mayland and Grunes 1979; Wilkinson and Stuedemann 1979). In humans, both rising dietary and intracellular Ca : Mg ratios have shown trends towards greater risks of human diseases (Resnick 1992; Rosanoff 2010). It is thus appropriate and promising to use elemental ratios of Ca, Mg and K as potential tools in ecological stoichiometry.

There are complex differences in how these elements interact in plants and animals and in their response to environmental factors. For example, Ca is almost immobile when leaves are senescing whereas K can be largely withdrawn from the leaves (Tripler *et al.* 2006; Vergutz *et al.* 2012) during senescence. Application of K fertilisers can affect the concentrations of Ca and Mg in soils; however, changes in soil K can yield opposite trends of Ca and Mg concentrations in some plants (Whitehead 2000). With such diverse responses to ecological conditions and physiological processes, these three elements can behave quite differently in ecosystems of varying environmental conditions.

There is much site-specific literature concerning effects of the dynamics and availability of soil K, Ca and Mg on plants and animals in terrestrial ecosystems (e.g. Whitehead 2000). In soils, all three elements are subject to loss by leaching, particularly in tropical and subtropical biomes, resulting in Mg-, Ca- and K-deficient soils in low-latitude areas (Gong 1993). In addition, their availability can vary with water condition (Valipour 2012; Valipour *et al.* 2015). It is thus not surprising that Mg concentration has been found to vary significantly in the soils, plants and herbivore insects across temperate and subtropical biomes (Sun *et al.* 2013). However, no consistent trend was observed for Ca and K concentrations in the soils and leaves of plants along a precipitation gradient in a tropical biome (Austin and Vitousek 1998).

Studies on how these elements and their ratios co-vary across trophic levels in a regional area across which climate and soil properties vary (i.e. along a large geophysical–geochemical gradient) are still lacking (Sun *et al.* 2013). It is worth exploring how the variations of K, Ca and Mg along a climate gradient affect the K–Mg–Ca stoichiometry of soils, plants and their consumers in terrestrial ecosystems. Macroclimatic variation along latitudinal gradients provides an excellent natural laboratory to investigate the role of the potential impacts of climate change on terrestrial organisms (De Frenne *et al.* 2013) and may similarly serve to explore ecological impacts on inter-species trophic levels. On both regional and global scales,

temperature and water availability are typically the primary climatic factors influencing the variation of stoichiometric traits (Reich and Oleksyn 2004; Han *et al.* 2005; Liu *et al.* 2006), and they are generally indexed with mean annual temperature (MAT, °C) and precipitation (MAP, mm). In this regard, latitude (LAT) can be employed to represent the combined effect of MAT and MAP.

In previous studies, little attention has been given to the patterns of variation in K, Ca and Mg ratios at different trophic levels of ecosystems across biomes. In addition, host–parasite interactions fundamentally differ from prey–predator interactions with regard to the biological relationships (Hall *et al.* 2008; Hecheinger *et al.* 2011). It is not clear how K, Ca and Mg ratios vary along a parasitism food chain. In this study, samples of soils, leaves, acorns and parasite weevil (*Curculio davidi* Fairmaire) larvae were collected in Chinese cork oak (*Quercus variabilis* Blume) forests across temperate to subtropical China, and the concentrations of K, Ca and Mg were measured. Our objective was to show how K, Mg and Ca stoichiometric traits in soils, plants and weevil larvae vary across these multiple trophic levels along the climate gradient from temperate to subtropical biomes, a gradient that mimics the dynamics of climate change.

## Methods

### *Study site and sampling design*

The study area extended from temperate areas in north-eastern and northern China to subtropical areas in central and southern China. For the climatic factors, soils, and vegetation, detailed information can be found in Sun *et al.* (2012, 2013).

Leaf and soil samples were generally collected in middle August. At each site, a sampling plot (20 m by 20 m) was chosen at a south-facing slope. We divided each plot into five subplots. From each of the five subplots, we randomly took five samples from the topsoil (0–10 cm in depth) to compose one bulk soil sample for each subplot.

In each plot, five dominant trees were selected. We selected branches in the mid-crown of each sample tree, and picked fully healthy leaves. Acorns were collected under each sample tree during the period September–October. We used ~25 acorns without weevil damage for each sample to measure Ca, Mg and K concentrations, and stored the rest at room temperature for 1–5 days for incubating weevil larvae. Larvae were collected within 12 h of emergence from acorns.

### *Sample preparation and chemical analysis*

All samples were oven-dried (soils, leaves and acorns at 65°C, larvae at 55°C) for 72 h. Soil, leaf and acorn samples were ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA), and passed through a 1.6-mm sieve. Weevil larvae were processed by using a ball mill to homogenise samples. All samples were kept cool and dry until chemical analysis.

The samples were digested using trace-metal-grade nitric and perchloric acid, and then they were measured for Ca, Mg and K using inductively coupled plasma-atomic emission-spectrometry (ICP-OES) (model no. iCAP6300, Thermo Fisher Scientific, Waltham, MA, USA).

### Climate data

Geographical position was recorded using a global positioning system (MobileMapper, Thales USA, Arlington, VA, USA). Mean annual temperature (MAT) and mean annual precipitation (MAP) were estimated using a global climate dataset with a resolution of 1 km by 1 km obtained from <http://www.worldclim.org/>.

### Statistical analyses

Reduced major axis regressions were performed using the program RMA (Bohonak and van der Linde 2004). Linear regressions were used to describe the relationships between soil, leaf, acorn and weevil larva Ca, Mg, K, Ca:Mg, K:(Mg+Ca) and K:Mg ratios with LAT, MAT and MAP, and non-linear models were applied when linear regression failed to describe the relationship. To overcome the problems caused by collinearity among explanatory variables, and disentangle the independent contribution and joint contribution of explanatory variables to the response-variable factors, we used hierarchical partitioning to explore the contribution of different factors to explain stoichiometric variations (Heikkinen *et al.* 2004). Hierarchical partitioning was conducted by using the R package 'hier.part' (Walsh and MacNally 2003). All statistical analyses were performed by using R 3.1.3 (R Development Core Team 2014).

### Results

Table 1 shows the mean concentrations of K, Ca, Mg, and their ratios plus the coefficients of variation for all samples from all plots and subplots, regardless of latitude. The K concentration increased across all trophic levels, Ca increased from soils to leaves and from acorns to weevil larvae, whereas Mg decreased from soils to plant tissues and increased from acorns to weevil larvae (Table 1). Leaf K:Mg ratio was more than two times that of soil and leaf Ca:Mg ratio more than seven times that of soil, whereas leaf K:(Ca+Mg) was lower than that of soil (Table 1). Acorn K:Mg ratio was three times that of leaves and weevil larvae, and acorn K:(Ca+Mg) displayed a similar pattern (Table 1), with the acorn ratio nine times that of leaves and more than four times that of weevil larvae. Acorn Ca:Mg showed an opposite pattern, being one-quarter that of leaves and one-half that of weevil larvae (Table 1).

Variability of K, Ca, Mg concentrations and their ratios across the trophic levels decreased distinctly from soil (coefficient of variation (CV) 61–128%) to plant tissue (CV 14–41% for oak leaves, 9–27% for acorns), and increased to weevil larvae (CV 11–77%) (Table 1).

Figure 1 shows trends of K, Ca and Mg for soil, leaf, acorn and weevil larvae. The concentration of K in leaves, acorns and

weevils significantly increased with LAT, and K concentrations in both plant tissues decreased with increasing MAT and MAP ( $P < 0.05$ ). Soil Ca and Mg significantly increased with LAT, and decreased with MAT and MAP ( $P < 0.05$ ), whereas for plant tissue Ca, only acorn Ca decreased with LAT. Concentration of Mg in all trophic levels (leaves, acorns and weevil larvae) increased with LAT and decreased with both MAT and MAP. Leaf and acorn Ca:Mg ratio significantly decreased with LAT, and leaf Ca:Mg increased with MAT (Fig. 2). Soil and weevil larvae K:(Ca+Mg) significantly increased, whereas acorn K:(Ca+Mg) displayed a binomial curve with increasing MAP (Fig. 2).

A substantial fraction of variation in the three elements in leaves, acorns and weevil larvae could be explained by the factors (LAT, MAT, MAP, plus soil nutrients for plant tissues and acorn nutrients for weevil larvae) (Fig. 3). Variations in K, Ca and Mg of leaf, acorn and weevil larva were largely by driven by LAT, but the variation in leaf K also by MAT and MAP, and the variation in acorn K also by soil K, followed by MAT and MAP (Fig. 3). It was noteworthy that acorn K:(Ca+Mg) ratio significantly varied with MAP following a quadratic equation ( $r^2 = 0.57$ ,  $P < 0.001$ ), with the lowest ratio at MAP = 1000 mm.

### Discussion

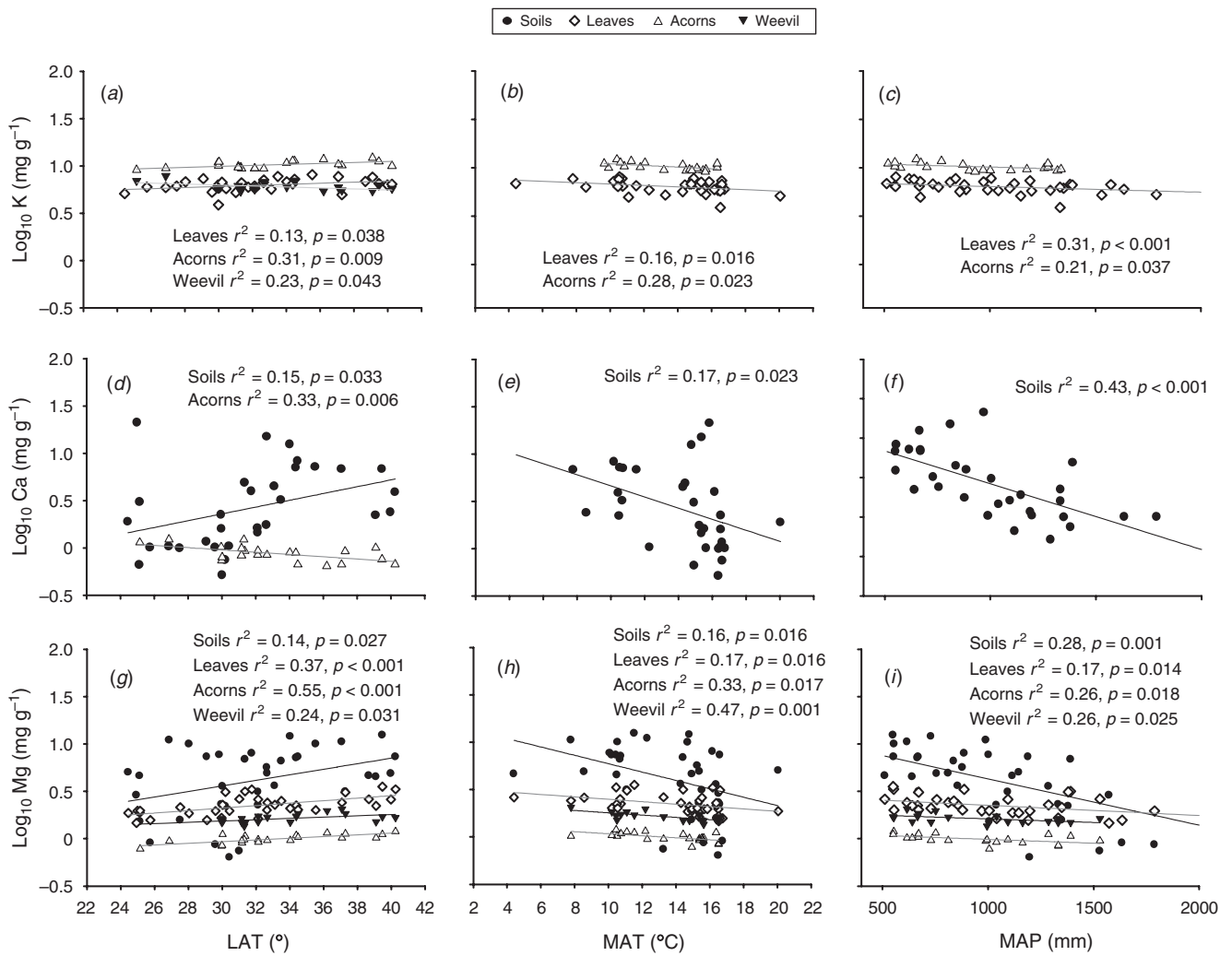
This paper is the first effort to explore the stoichiometric traits of K, Ca and Mg in relation to climatic factors in a terrestrial parasitism food chain across temperate and subtropical biomes. The characteristics of Mg in soils, leaves, acorns and weevil larvae in relation to environmental variables have been discussed by Sun *et al.* (2013). Here, the discussion will focus on differences in variation between K, Ca and Mg across temperate and subtropical biomes. The status of K, Ca and Mg and the influential factors are considered together because of their similar properties in physiological and ecological processes in terrestrial ecosystems (Whitehead 2000).

#### Lower variability of K, Ca and Mg in acorns

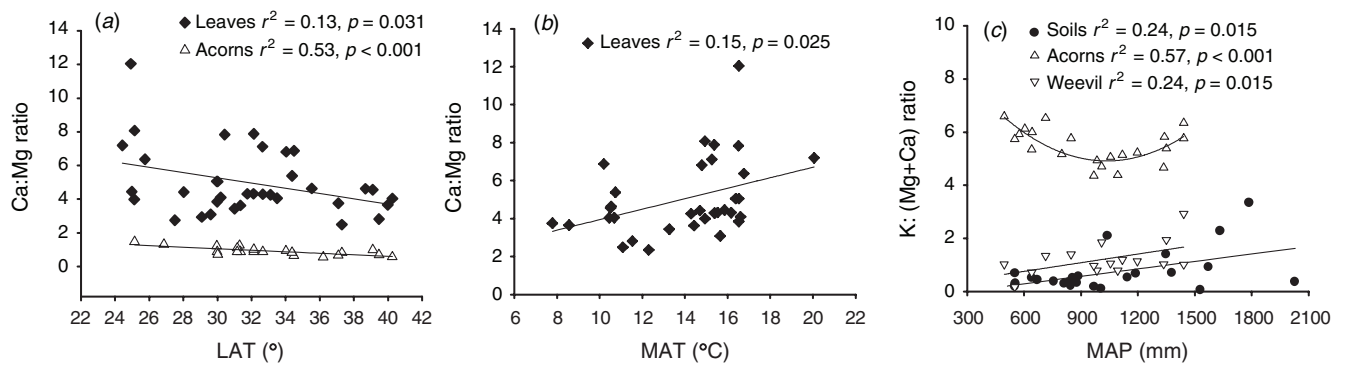
Acorns showed lowest variability in K, Ca and Mg concentrations, as well as their ratios, compared with soils, leaves and weevil larvae. This suggests an important phenomenon, that as a reproductive organ, seeds have stronger conservation in stoichiometric compositions, perhaps in relation to their function of providing optimal energy and nutrients for seedlings. Among the three elements, K showed lower variability than Ca and Mg in leaves, acorns and weevil larvae. Compared with the Ca:Mg ratio, K:Mg and K:(Ca+Mg) ratios had lower variability in leaves, acorns and weevil larvae.

**Table 1.** Mean ( $\text{mg g}^{-1}$ ) and coefficient of variation (CV, %) of K, Mg and Ca concentrations and their ratios in soils, leaves, acorns and weevil larvae in *Q. variabilis* forests across eastern China

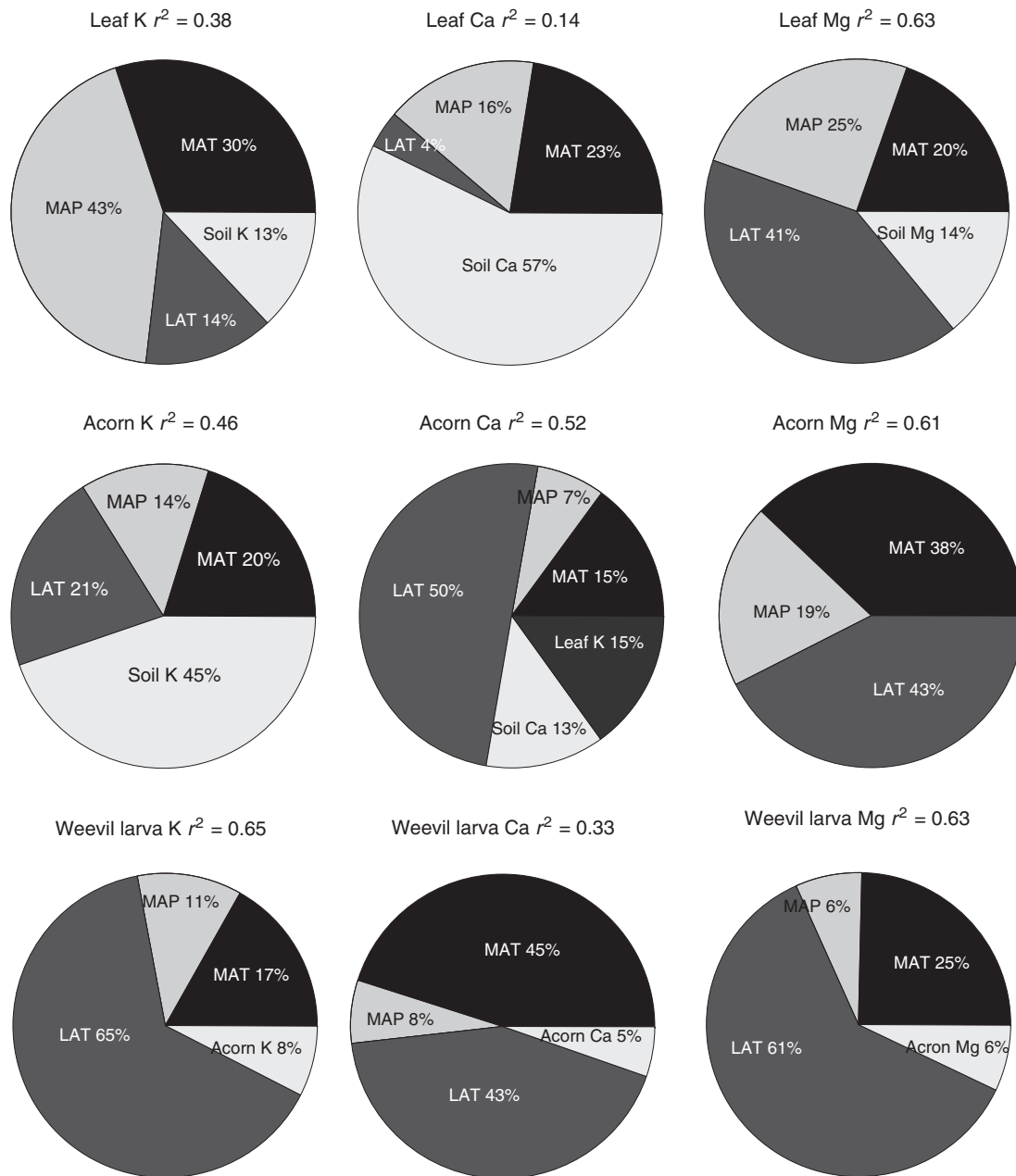
	K		Ca		Mg		K:Mg		Ca:Mg		K:(Ca+Mg)	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Soils	4.52	61	4.23	113	6.68	75	1.37	128	0.68	76	0.85	110
Leaves	6.33	14	9.19	26	2.00	25	3.33	28	4.90	41	0.59	25
Acorns	10.30	9	0.89	19	1.00	11	12.04	24	1.18	27	5.48	12
Weevil larvae	6.07	11	4.43	77	1.78	36	3.58	16	2.38	51	1.22	40



**Fig. 1.** Trends of (a–c) K, (e–f) Ca and (g–i) Mg concentrations in soils ( $n=34$  for K, 31 for Ca, 34 for Mg), leaves ( $n=36$  for all), acorns ( $n=21$  for all) and weevil larvae ( $n=18$  for all) with latitude (LAT), mean annual temperature (MAT), and mean annual precipitation (MAP) across eastern China.



**Fig. 2.** Trends of Ca:Mg and K:(Mg+Ca) ratios in soils ( $n=24$  for K:(Ca+Mg)), leaves ( $n=33$  for Ca:Mg and K:(Ca+Mg)), acorns ( $n=21$  for K:(Ca+Mg)) and weevil larvae ( $n=16$  for K:(Ca+Mg)) along the (a) latitude (LAT), (b) mean annual temperature (MAT), and (c) mean annual precipitation (MAP).



**Fig. 3.** Fraction of variance of K, Ca and Mg in leaves ( $n=36$ ), acorns ( $n=21$ ) and weevil larva ( $n=18$ ) explained by latitude (LAT), climatic factors (mean annual temperature (MAT) and precipitation (MAP)), and soil nutrients for leaves and acorns or acorn nutrients for weevil larva. The fractions are of variance explained by the full model ( $r^2$ ) and the respective contributions of the individual predictors to the whole model.

According to phenotypic plasticity theory, such variability of K, Ca and Mg concentrations in leaves, acorns and weevil larvae along the climate gradient can be mostly ascribed to environmental control (Agrawal 2001), implying high sensitivity to change in environmental variables in the context of global change. This is confirmed by the large fractions of variation explained by environmental variables (Fig. 3).

#### *Differential patterns of K, Ca and Mg variation along the climate gradient*

Magnesium concentration in all different trophic levels (leaves, acorns and weevil larvae) in this food chain consistently varied with environmental variables (Fig. 1*g–i*), but this was not true for K and Ca (Figs 1, 3). In leaves, a closer relationship has been observed between Mg concentration and precipitation than other nutrient elements (such as N, P, Ca and K) in tropical



Hawaiian forests (Austin and Vitousek 1998). The present study indicates that such a pattern also occurred in acorns (plant reproductive organ) and weevil larvae (heterotroph) (Fig. 1). To a certain extent, the strong relationship between leaf Mg and climate seen in this study might be due to the function of Mg in photosynthesis, which is highly controlled by temperature and water (Ågren and Weih 2012). However, this does not explain the strong pattern of Mg variation in acorn and weevil larva with climate. One underlying cause might be a functional physiological homeostasis of Mg with temperature, whereby higher Mg concentration in organisms could prevent cold injury at higher latitudes where cold winter is experienced by both acorns and weevil larvae (Sun *et al.* 2013). However, a strong homeostasis of Ca in plasma and extracellular fluids (Underwood and Suttle 1999) may also explain the lack of variability in Ca concentration of plant tissues (and weevil larvae) in the face of significant soil Ca variability along this climate gradient. Although Ca showed no change in leaf, acorn or weevil trophic levels, K showed variability in leaves and acorns but not weevils as either temperature or precipitation varied.

Among K, Ca and Mg ratios in different trophic levels, several significant relationships were observed for Ca:Mg and K:(Ca+Mg) with environmental variables (such as LAT, MAP or MAT) (Fig. 2), but no significant relationship between K:Ca or K:Mg and environmental variables was observed. In particular, contrasting with linear relationships between MAP and K:(Ca+Mg) in soils and weevil larvae, acorn K:(Ca+Mg) ratio displayed a concave curve with MAP, with the lowest ratio at MAP=1000 mm. Such MAP sites are in the transition zone between warm-temperate and subtropical areas, showing that increasing precipitation has differential effects on acorn K:(Ca+Mg) in two climate biomes. The results also suggest that variation in Mg concentration of soils, leaves, acorns and weevil larvae with climate exerts an important influence on variations in K, Ca and Mg stoichiometric traits along the climate gradient.

We speculate on possible causes of the main patterns with the aim of motivating additional research to identify mechanisms. We found that soil Mg concentration and K:Mg ratio (data not shown) varied more with MAP than with MAT, possibly because the large hydrated radius of the Mg cation makes it more prone to leaching than other biologically active cations (Hermans *et al.* 2004). The strong association between soil Mg and precipitation is consistent with previous among- and within-species comparisons (Johansson 1995; Austin and Vitousek 1998; Han *et al.* 2011). The geographical variation in organism Mg content that we have documented is likely driven by a combination of resource availability and demands for functional performance related to climate factors. Leaf Mg, which was strongly associated with soil Mg as well as LAT, MAP and MAT, depends largely on Mg availability and factors influencing oak growth rate. Acorn Mg content was high at high latitude, possibly because plants may allocate more Mg to reproductive tissues to ensure rapid development at high latitude with its low temperature and short growing seasons. We found that weevil Mg was only weakly related to the variation in Mg content in its food source, acorns. Therefore, high weevil Mg

content at high-latitude sites with short growing seasons and low temperatures may point to a process of Mg sequestration that meets physiological demands of exposure to a high diurnal range of temperature, because Mg plays an important role in temperature regulation in animals (Nowell and White 1963; Pratihari and Kundu 2009). Surprisingly, any climate-correlated variation in K:Mg ratio was dampened, presumably by plant physiological regulation and allocation strategies, and thus there was no cascade upward of K:Mg influence to higher trophic levels.

#### *Dissimilarity of K, Ca and Mg relationships with environmental variables*

The variations of K, Ca and Mg concentrations in soils, plant tissues and herbivorous insects is differentially explained by environmental variables, implying their differences in responding to change in environmental conditions. For instance, for the variation in leaf K concentration, 43% could be explained by MAP and only 13% by soil K, but for acorn K, an opposite pattern occurred (Fig. 3) and soil K accounted for 45% of variability. In addition, for most cases in Fig. 3, LAT explained a relatively larger fraction of variation, maybe because it represented combined effects of MAT, MAP and soil elements. For weevil larvae in particular, the variation in K, Ca and Mg concentrations was explained more by LAT and MAT than by acorn nutrients (i.e. food resources), showing an important homeostasis in the face of changing climatic factors via metabolism.

#### **Conclusions**

This study is the first to illustrate the across-trophic variation of stoichiometric traits of three macro-metal elements (K, Ca and Mg) in a terrestrial food chain across temperate and subtropical biomes. Our results suggest distinct variations in stoichiometric traits of these three elements in plant tissues and weevil larvae, and that the variation in Mg concentration exerts a dominant influence on the variation in K:Mg, Ca:Mg and K:(Ca+Mg) ratios in different trophic levels. In particular, acorn K:(Ca+Mg) ratio appeared to vary with MAP in a concave manner, with the lowest ratio at the transition zone between warm temperate and subtropical biomes. Whereas significant variation in Mg concentration existed in all trophic levels along the climate gradient, no such significant variation was evident for Ca concentrations in leaves, acorns or weevil larvae and none for K in weevils with environmental variables. Compared with nutrients in soil (for leaves and acorns) and those in acorns (for weevil larvae), temperature or precipitation was more influential on the variation in K, Ca and Mg in plant tissues and weevil larvae, suggesting that climatic factors highly influence the status of K, Ca and Mg via metabolism regulation.

This study considered K, Ca and Mg stoichiometry in weevil larvae across wide areas. In future work, attention should be paid to how these elements vary for weevil larvae, pupae and adults in different climate conditions so that we can have a more complete understanding of the stoichiometric status of these three elements in the whole life cycle of a parasitic consumer.

Our findings broaden the knowledge of the variation of K, Ca and Mg stoichiometric traits in different trophic organisms and their relation to environmental variables in the context of global change.

## Acknowledgements

This work was financially supported by the National Natural Science Foundation of China (NSFC 31270640, 31270491, 71333010) and the National Key Technology R & D Program (2013BAD11B01).

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