ORIGINAL ARTICLE

Negative effects of calcium on magnesium and potassium benefit for adaptability of Chinese prickly ash (*Zanthoxylum bungeanum*) grown on poor soils

He-Chun Piao[1]

Abstract The aim of this study was to provide information about how calcium (Ca), magnesium (Mg) and potassium (K) respond to changes in the sugar concentrations and carbon isotopic compositions ($\delta^{13}C$) of Chinese prickly ash under field condition, therefore, to show why negative effect of Ca on Mg and K would be beneficial for adaptability of Chinese prickly ash grown on poor soils. Chinese prickly ash samples were collected in the six areas with different mean annual precipitation. Drought stress was evaluated via carbon isotope signatures. Additionally, concentrations of Mg, Ca, K and sugar concentrations in foliage, roots and soils were analyzed. Increased soil available Ca concentrations did significantly inhibit foliar Mg partitioning, implying that Ca did negatively affect Mg partitioning. Changes of foliar Mg concentrations were strongly controlled by variations of balance between soil available Ca and Mg. Thus, an accurate assessment of plant nutrient status should be useful for precision nutrient management in the fields. Magnesium deficiency did significantly induce foliar sugar accumulation, therefore, there were negative relationships between Mg concentrations and $\delta^{13}C$ values in foliage. In addition, increased sugar concentrations did significantly increase $\delta^{13}C$ values, implying that drought or water stress induced the accumulation of sugar in foliage. Linear and power function regression analysis revealed that negative effects of Ca on Mg and K should be responsible for accumulation of soluble sugar in foliage, which may enhance a plant's adaptability on poor soils.

Keywords Soil available Ca · Drought stress · Precipitation · Carbon isotope composition · Sugar concentration · Nutrient interaction

Introduction

Chinese prickly ash (*Zanthoxylum bungeanum*) is a shrub species, that is cultivated widely in China as a condiment and for medicinal purposes, making it one of the most important economic plants for local farmers (Li et al. 2009). Chinese prickly ash could produce economic benefit for farmers in areas where cereal productivity is very low because of its high drought resistance. Because of its high drought resistance, Chinese prickly ash plays an important role in the restoration of fragile ecosystems with poor soil (Piao et al. 2017), where the plant biomass is very low. The water–soil–plant relationships are an important determinant of the sustainability of biomass production (Gollany et al. 2015). In order to increasing the yield of fruits in *Zanthoxylum* various fertilizers are used by farmers. Bindraban et al. (2015) suggested that application of fertiliser consisted of unbalanced nutrient compositions on poor soils has shown limited impact on increase of yield. Fertiliser use efficiency can be deteriorated by soil factors, including moisture content, and by the interaction with soil nutrients, those interactions in plant and soil have enhanced or inhibited nutrient uptake (Gransee and Fuhrs 2013; Bindraban et al. 2015; Rhodes et al. 2018). Previous studies show that cationic antagonism exists between calcium (Ca), magnesium (Mg) and potassium (K) such that high levels of one or more of these nutrients can result in

✉ He-Chun Piao
piaohechun@vip.skleg.cn

1   State Key Laboratory of Environmental Geochemistry,
     Institute of Geochemistry, Chinese Academy of Sciences,
     Guiyang 550081, China

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decreased uptake of another, despite sufficient soil levels (Chang et al. 2010; Gransee and Fuhrs 2013; Ertiftik and Zengin 2017; Rhodes et al. 2018; Piao et al. 2020). For example, increased foliar K concentrations decrease foliar Ca and Mg concentrations (Rhodes et al. 2018); increasing K concentrations is associated with a decrease in Ca concentrations, while increasing Ca concentrations reduce that of Mg concentrations in anthurium at a whole plant level (Chang et al. 2010); antagonistic reaction between Ca and Mg and K may result in low absorption of K and Mg by plants from soils with high Ca concentrations even when levels of K and Mg should be adequate (Ertiftik and Zengin 2017). Because K is the counter-cation for nitrate transport in the xylem, the preferred uptake of nitrate in Chinese prickly ash can enhance foliar K concentrations with decreasing foliar Ca and Mg (Piao et al. 2017). Therefore, maintenance of a balance in response to changing nutrient status in the soil emerges as a critical feature of plant nutrients (Tang and Luan 2017; Piao et al. 2020).

Foliar $\delta^{13}C$ data could provide integrated information about how plants respond to drought conditions, those indirect methods could estimate the effect of drought on plant water status (Grant et al. 2012; Zhou et al. 2016). Under water shortage, the heavier ^{13}C taken up by plants increases due to closing stomata leading to an enrichment of ^{13}C in biomass (Klaus et al. 2016). Beena et al. (2018) reported that relatively early stomatal closure is shown to prevent water loss. The spatial variations in $\delta^{13}C$ values appear to be positively related to soil fertility and cation concentrations (Weitner et al. 2007). Thus previous results imply that soil Ca, Mg and K availability should influence variations of tissue carbon isotopic compositions. For example, the $\delta^{13}C$ values of tissue should decrease with increasing Mg content (Tränkner et al. 2016). In contrast, an increase in apoplastic Ca^{2+} concentrations could inhibit the stomatal opening (Rothwell and Dodd 2014), which would result in increased tissue $\delta^{13}C$ values. Potassium is a key actor of regulating stomatal aperture, and hence of the limitation of water loss (Zörb et al. 2014; Epron et al. 2015). Potassium is negatively related with $\delta^{13}C$ values, indicating a positive role of this nutrient on stomatal functioning (Tsialtas and Maslaris 2006).

A shortage of Mg decreases photosynthetic activity, chlorophyll synthesis and stomatal functioning (Yilmaz et al. 2017). Mg deficiency severely depresses sugar transport from source to sink (Yang et al. 2013). Therefore, the accumulation of sugar in foliage, due to impaired phloem loading under low Mg concentrations, reduces photosynthesis (Sami et al. 2016). Thus the accumulation of sugar in foliage is a major consequence of decreased Mg concentrations that can result in limited plant growth due to the regulation of photosynthetic activity (Verbruggen and Hermans 2013). However, K deficiency results in sugar accumulation in foliage (Zörb et al. 2014), Sugar induces stomatal closure, therefore, enhances a plant's adaptability under drought stress (Sami et al. 2016). Ca^{2+} is associated with stomatal closure, decreases Mg^{2+} concentrations, and inhibits CO_2 assimilation (Ahanger et al. 2014). This means that the uptake of Ca^{2+} and its delivery to the shoot are important in regulating stomatal behavior (Rothwell and Dodd 2014). It is apparent that the behavior of Ca affects photosynthesis and regulates stomatal behavior differently than Mg. The concentrations of Mg and Ca in foliage could be related to foliar $\delta^{13}C$ values through their involvement in plant transpiration, photosynthesis, and osmotic adjustment (Zhou et al. 2016; Tränkner et al. 2016). Therefore, it was hypothesised that the variations of Mg and Ca concentrations would differentially respond to changes of sugar concentrations, and therefore to changes of carbon isotope composition in foliage of Chinese prickly ash. The aim of this study was to provide information about how chemical composition, such as Ca, Mg, K, respond to changes in the soluble sugar, thus inducing variation of carbon isotopic compositions of Chinese prickly ash under field conditions, and to show why negative effect of Ca on Mg and K would be beneficial for adaptability of Chinese prickly ash grown on poor soils.

Materials and methods

Study sites

The study areas in this paper were widely distributed throughout a transitional zone ranging from Southwest China to East China (i.e., the Shandong Peninsula), in where the research previously conducted by Piao et al. (2018) examined the relationship between the nutritive quality (do not include Ca and Mg) of pods and seeds in *Zanthoxylum* and environmental factors, such as temperature and precipitation. Southern and eastern China is mainly dominated by southwest monsoons from the Indian Ocean and southeast monsoons from the Pacific Ocean, which produce high rainfall during the summer. Adult Chinese prickly ash samples were collected in the Huajiang (HJ, n = 22), Zunyi (ZY, n = 22), Chongqing (CQ, n = 8), Pingdingshan (PD, n = 10), Zoucheng (ZC, n = 12) and Laiwu (LW, n = 13) areas, which are located in order of decreasing mean annual precipitation (MAP) (Table 1). The sample sites were located in areas where soils have developed in mixed terrain, except for those in HJ, which have developed in limestone. The soil types in HJ, ZY and CQ were clay–sandy or sandy–clay loam. Soil is distributed highly heterogeneously in karst areas in Southwest China, where the plant biomass is very low, and soil organic carbon concentration is very low, therefore, soil is

Table 1 Soil parameters

Sampling sites	Huajiang (HJ)	Zunyi (ZY)	Congqing (CQ)	Pingdingshan (PD)	Zoucheng (ZC)	Laiwu (LW)
Latitude	25°38′N–25°41′N	27°48′N–27°57′N	29°10′N–29°14′N	33°56′N–33°59′N	35°20′N–35°25′N	36°06′N–36°26′N
	105°38′E–105°41′E	107°14′E–107°16′E	106°11′E–106°18′E	112°46′E–112°49′E	117°00′E–117°20′E	117°29′E–117°39′E
MAP (mm)	1200	1160	1035	730	780	710
MAT (°C)	18.4	15.6	18.2	15.0	14.1	13.4
Soil pH (H$_2$O)[a]	7.3 ± 0.8	6.9 ± 1.2	6.8 ± 0.7	7.7 ± 0.2	6.9 ± 1.2	7.9 ± 0.3
Org$_C$[b] (g kg^{-1})	24.4 ± 12.2	27.2 ± 8.6	37.1 ± 26.2	15.9 ± 6.0	11.7 ± 6.2	16.4 ± 10.1

MAP mean annual precipitation, *MAT* mean annual temperature

[a]Mean ± standard deviation

[b]Soil organic carbon

not fertile, not easy to till, and soaks up water easy runoff, local farmers call it poor soil. The Chinese prickly ash in these areas had fine roots that were more shallowly and widely rooted in the top 1–5 cm of soil. In PD, ZC and LW, the soils were sandy–clay loam or sandy loam, where deeper roots were expected. The parameters of the sampling sites are listed in Table 1. Soil samples were collected from depths ranging from 0 to 15 cm from six replicated plots of each soil sample and then were mixed thoroughly, homogenized, sieved (2 mm) to form a composite sample for each soil samples, and analysed for their available nutrients. Chemical fertilizer was not added to any of the sampling soils during the sampling year. Leaf samples were collected in late July in the HJ, ZY and CQ areas, while they were collected in early August in the PD, ZC and LW areas. The nutrient resorption process from foliage to seeds potentially occurs during seed development, foliar sampling time, therefore, must represent the farmers' harvesting time for obtaining condiments from fruits. Delay or advance of the harvesting time the seeds were not automatically separated from pods when drying the fruits.

Laboratory analysis

Plant samples for laboratory analysis were dried for 48 h at 60 °C and then were ground with a mortar and pestle. Soil organic carbon was determined using a CHNS autoanalyser (PE 2400–ll, Norwalk, CT, USA). Standard soil analysis methods were used to measure soil-extractable Ca, Mg and K using 1 M NH$_4$OAC (Thomas 1982). Plant samples were digested using nitric-perchloric acid and the concentrations of Ca, Mg and K analysed by the AAS method (PE900F, USA). To determine the content of soluble sugar, 0.25 g of air-dried material was extracted four times with distilled water at 75 °C. After each extraction, samples were filtered, and the filtrates were used to colorimetrically determine soluble sugar contents using the anthrone reaction (Piao and Liu 2011). Carbon isotopes were measured using a mass spectrometer (MAT 252 Finnigan, Bremen, GER). CO$_2$ generated in the combustion tubes was separated by cryogenic distillation, collected in breakseals and analyzed using a mass spectrometer (MAT 252 Finnigan, Bremen, GER). The ratio of heavy to light isotopes in the sample material (R$_{sample}$) was measured, using mass spectrometry, as the deviation from the isotopic ratio of a standard (R$_{standard}$), where R denotes the ratio of stable C isotopes (^{13}C/^{12}C), expressed in δ notation. For example, $\delta^{13}C$ (‰) = (R$_{sample}$/R$_{standard}$ − 1) × 1000; where R$_{sample}$ and R$_{standard}$ are the ^{13}C/^{12}C ratios of the carbon of the sample and the standard, respectively. The V–PDB ($\delta^{13}C$ = 0‰) serves as an international standard for stable C. The precision of the $\delta^{13}C$ analyses was ± 0.1‰.

Statistical analysis

Statistical analysis was conducted using the SPSS 12.0 software (SPSS Science, Chicago, USA). The significant differences of mean values of soil pH and soil organic carbon concentrations were determined by an independent-sample *t* test at six sampling areas. Pearson correlation coefficient was used to quantify the correlations between tissue Ca, Mg, K and soil Ca, Mg, K and mean annual precipitation (MAP) and between Ca, Mg, K, N and P concentrations in foliage and roots, and linear regression was used to assess the relationships of soil Ca or soil Ca/Mg with foliar $\delta^{13}C$, sugar and Mg concentrations in foliage, and between foliar Ca, Mg and foliar sugar, and between foliar $\delta^{13}C$ and foliar Ca, Mg, K, sugar concentrations. Although the correlations are significant, their relative value is very small in some cases of the linear regression. Therefore, the size effect of the correlation between the two variables is explaining only small % of the variability. Thus, a power function regression was used to
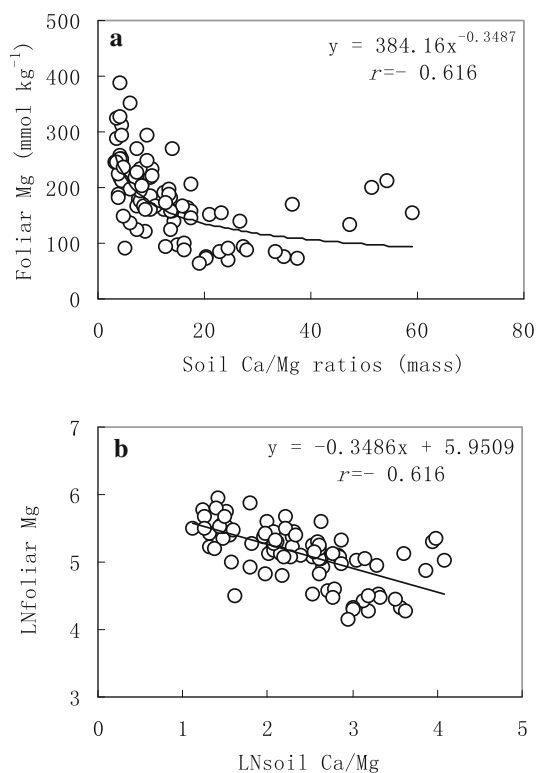
Fig. 1 Relationships of soil available Ca concentrations with foliar $\delta^{13}C$ values (**a**), with foliar sugar concentrations (**b**), and with foliar Mg concentrations (**c**), *$P < 0.05$; ***$P < 0.001$

Results

Relationships of soil available concentrations with tissue nutrients

Table 1 shows soil pH values, the highest average value of soil pH in LW did significantly differ from the lowest that in ZC, and soil organic carbon concentrations, their mean values in HJ, ZY and CQ were significantly high than that in PD, ZC and LW (Table 1, independent-sample t test table is not shown). Soil extractable Ca concentrations were highest in HJ soils developed from limestone and were lowest in ZC, which recorded the lowest soil pH values, indicating the presence of a significant relationship between soil Ca and pH ($r = 0.594$, $P < 0.001$, n = 87). Soil Mg concentrations varied significantly among sampling sites. The values of soil K concentrations in HJ, ZY, CQ and PD with lower latitude were higher than those in ZC and LW, but with extreme standard deviations. Soil Ca values were positively and significantly correlated with root Ca values, but not with foliar Ca values (Table 2). However, soil Mg concentrations were positively and significantly correlated with foliar Mg concentrations, but not with root Mg concentrations (Table 2). Soil K availability were positively and significantly correlated with the values of K in foliage and roots (Table 2). Soil available Ca concentrations were significantly and positively correlated with foliar $\delta^{13}C$ values (Fig. 1a) and foliar sugar concentrations (Fig. 1b). Linear regression showed significant and negative correlation between soil Ca and foliar Mg concentrations ($r = -0.417$, $P < 0.001$, n = 87) (Fig. 1c, Table 2), while power function regression did also show significant negative correlations between LNsoil Ca and LNfoliar Mg ($r = -0.389$, $P < 0.001$). But both soil Mg and soil K were not significantly correlated with foliar $\delta^{13}C$ values, foliar sugar concentrations, and foliar Ca concentrations, respectively. Foliar Mg concentrations did logarithmically decrease with increasing soil Ca/Mg ratios (Foliar Mg concentrations (mmol kg^{-1}) = 384.16 × soil
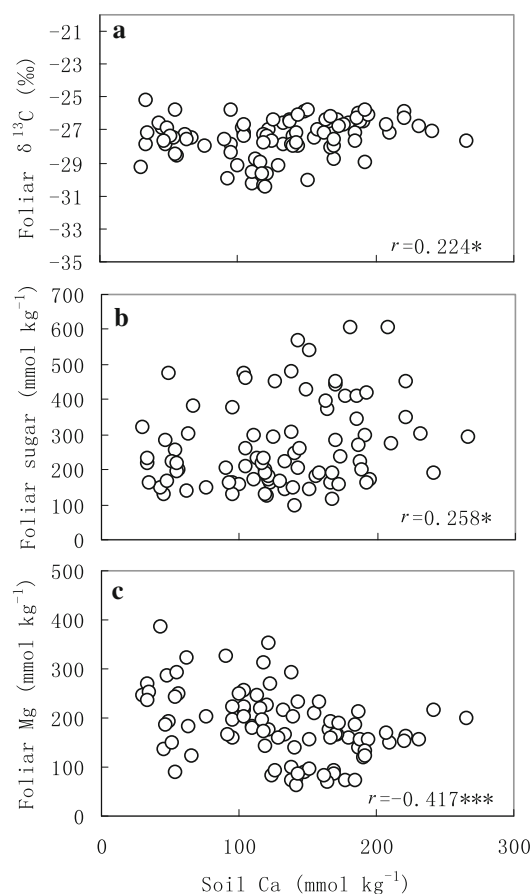
Ca/Mg ratios$^{-0.3487}$) ($r = -0.616$, $P < 0.001$, Fig. 2a), while power function regression also showed significant negative correlations between LNfoliar Mg and LNsoil Ca/Mg ratios (LNfoliar Mg concentrations = -0.3486 × LNsoil Ca/Mg ratios + 5.9509) ($r = -0.616$, $P < 0.001$, Fig. 2b, LN: logarithm). However, linear regression showed negative, but not significant, correlations between foliar Mg and soil Ca/Mg ratios ($r = -0.027$, $P > 0.05$). There were significant and positive correlations between soil Ca/Mg ratios and foliar $\delta^{13}C$ values (Fig. 3a). Linear regression showed significant and positive correlations between soil Ca/Mg ratios and foliar sugar concentrations ($r = 0.473$, $P < 0.001$, n = 87, Fig. 3b), while power

Table 2 Coefficients (r) of Pearson correlations between tissue Ca, Mg, K and soil Ca, Mg, K and mean annual precipitation (MAP) (n = 87)

	Foliar Ca	Foliar Mg	Foliar K	Root Ca	Root Mg	Root K
Soil Ca	0.146	− 0.417***	− 0.152	0.578***	− 0.062	− 0.190
Soil Mg	− 0.089	0.458***	− 0.155	− 0.230*	0.185	0.176
Soil K	− 0.014	− 0.127	0.229*	0.055	− 0.079	0.565***
MAP	− 0.106	0.453***	− 0.364***	0.351**	− 0.324**	− 0.154

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Fig. 2 Relationship between soil Ca/Mg ratios and foliar Mg concentrations (**a**), relationship between LNsoil Ca/Mg and LNfoliar Mg (**b**) (*LN* logarithm)
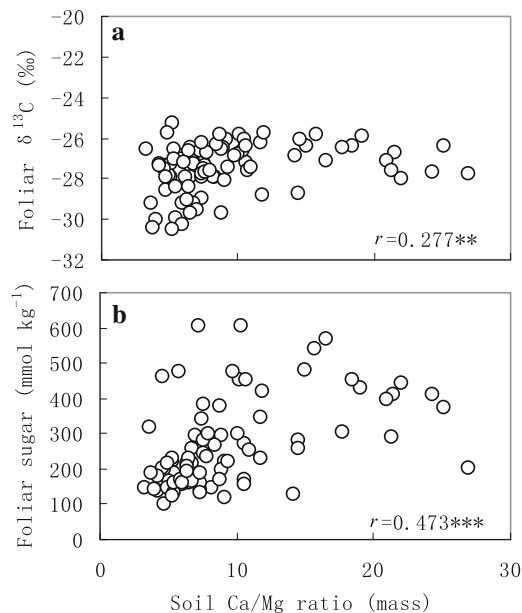
Fig. 3 Relationships of soil available Ca/Mg ratios with foliar δ^{13}C values (**a**), and with foliar sugar concentrations (**b**), $*P < 0.05$; $***P < 0.001$

function regression also showed significant and positive correlations between LNsoil Ca/Mg and LNfoliar sugar concentrations ($r = 0.279$, $P < 0.01$). Soil Mg

concentrations were significantly and negatively correlated with root Ca concentrations (Table 2), while soil Ca were not significantly correlated with root Mg concentrations (Table 2). Negative correlations were observed between MAP and foliar Ca concentrations, but not significantly, while root Ca values were positively and significantly correlated with MAP (Table 2), Positive correlations were observed between MAP and foliar Mg concentrations, while root Mg values were negatively correlated with MAP. However, foliar K concentrations were negatively and significantly correlated with MAP (Table 2).

Relationships between nutrients in tissue

The concentrations of foliar and root Ca were not significantly correlated with that of foliar and root Mg (Table 3). Foliar and root Ca concentrations were significantly and negatively correlated with foliar and root K concentrations, respectively. Except for root, foliar Ca concentrations negatively and significantly correlated with foliar N (nitrogen) and P (phosphorus) concentrations (Table 3). Foliar Mg concentrations were significantly and negatively correlated with foliar K concentrations ($r = -0.407$, $P < 0.001$), but there was positive, but not significant, relationships between root Mg and root K ($r = 0.117$). Linear regression showed that there were significant negative correlations between foliar Mg concentrations and foliar sugar concentrations ($r = -0.431$, $P < 0.001$, Fig. 4a), while power function regression also showed there were significant negative correlations between LNfoliar Mg and LNfoliar sugar ($r = -0.455$, $P < 0.001$). Linear regression showed there were significant positive correlations between foliar Ca concentrations and foliar sugar concentrations ($r = 0.262$, $P < 0.05$, Fig. 4b), while power function regression also showed significant positive correlations between LNfoliar Ca and LNfoliar sugar ($r = 0.293$, $P < 0.01$). However, foliar K concentrations were negatively, but not significantly, correlated with foliar sugar concentrations ($r = -0.121$).

Table 3 Coefficients (r) of Pearson correlations between Ca, Mg, K, N and P concentrations in foliage and roots (n = 87)

	Foliar Ca		Root Ca
Foliar Mg	− 0.022	Root Mg	− 0.076
Foliar K	− 0.544***	Root K	− 0.225*
Foliar N	− 0.315**	Root N	0.126
Foliar P	− 0.260*	Root P	− 0.043

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$
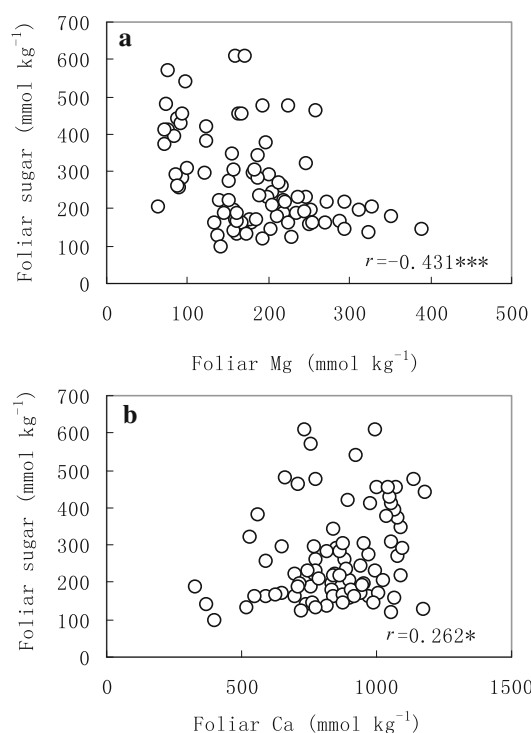
Fig. 4 Relationships of foliar sugar concentrations with foliar Mg (**a**), foliar Ca concentrations (**b**), *P < 0.05 ***P < 0.001

## Changes of δ¹³C values and variations of Mg, Ca, K and sugar concentrations

Foliar $\delta^{13}C$ values were positively and significantly correlated with those of foliar Ca (Fig. 5a): they were also negatively correlated with foliar Mg values, but not significantly (Fig. 5b). There were negative and significant relationships between foliar $\delta^{13}C$ values and foliar K concentrations (Fig. 5c). There were significant and positive relationships between foliar sugar concentrations and foliar $\delta^{13}C$ values (Fig. 6).

Discussion

Negative effects of Ca on Mg and K

The uptake and transport of Ca and Mg depend not only on plant transpiration but also on the availability of sufficient amounts of Ca and Mg in the soils (Dayod et al. 2010). However, Mg uptake by roots is subject to an antagonistic effect due to the high concentrations of Ca^{2+} in soils with relatively high pH values (Farhat et al. 2016b; Ertiftik and Zengin 2017). In the present study, increased soil available Ca did significantly result in decreasing foliar Mg concentrations, and increasing soil available Mg did significantly decrease root Ca concentrations, indicating there
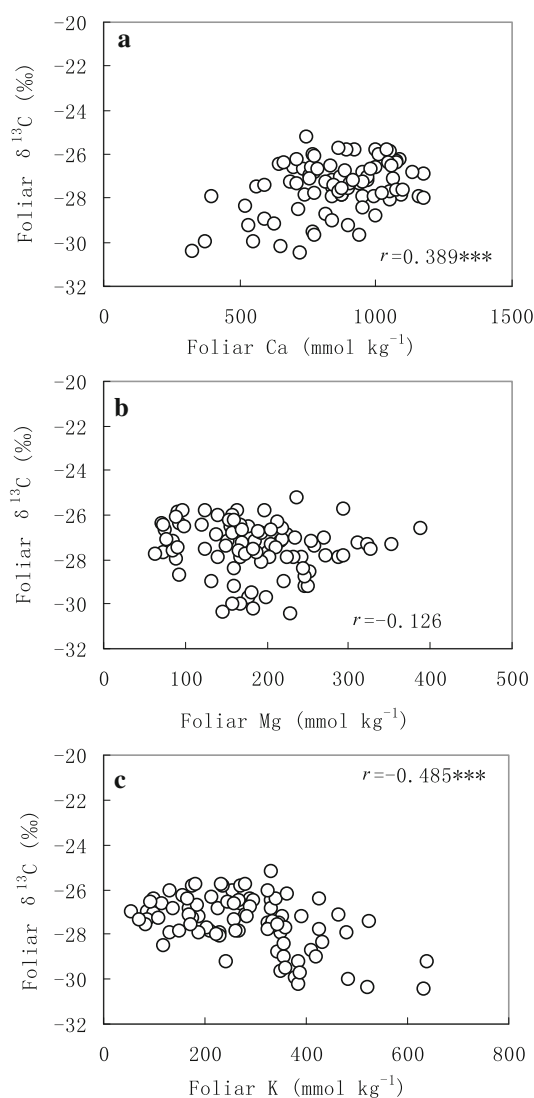
Fig. 5 Foliar Ca concentrations positively correlated with foliar $\delta^{13}C$ values (**a**), foliar Mg concentrations negatively correlated with foliar $\delta^{13}C$ values (**b**), foliar K concentrations negatively correlated with foliar $\delta^{13}C$ values (**c**), ***P < 0.001
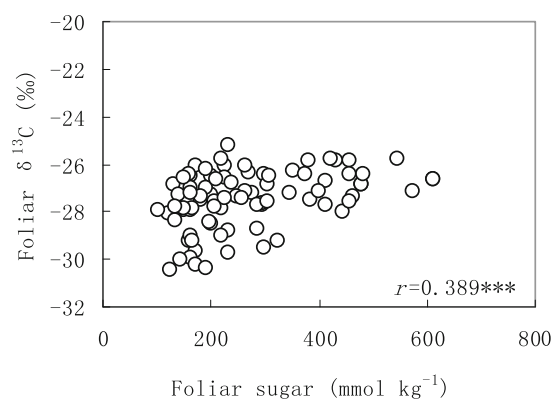
Fig. 6 Relationship between foliar sugar concentrations and foliar $\delta^{13}C$ values, ***P < 0.001

was the negative effect of Ca on Mg concentrations. Other results also show that competing cations such as Ca^{2+} do not only displace Mg^{2+} from the cation exchange sites and thus contribute to its leaching but also strongly inhibit its root uptake (Gransee and Fuhrs 2013). Therefore, Mg deficiency in the field is commonly caused by ionic antagonism (Rose et al. 2015). Plant uptake of Ca is inhibited by excess Mg in tissue (Kobayashi et al. 2005). Therefore, Kayama et al. (2009) suggested that Mg in roots was substituted for Ca, leading to a reduction in the concentration of Ca in roots. Variations in water availability also contribute to changes in Ca and Mg availability. For example, root Ca was positively correlated with MAP, while root Mg was negatively correlated with MAP, which may imply that Ca uptake had a negative effect on Mg uptake in the present study. Tang et al. (2015) reported that Ca uptake is found to have been considerably inhibited by excessive Mg, as Ca and Mg may have competed for the same transporters in the plasma membrane. Therefore, the balance between Mg and Ca is a critical factor for plant growth (Tang et al. 2015). Present study also showed that changes of foliar Mg concentrations were significantly controlled by the variations of soil Ca/Mg ratios, and foliar Mg concentrations could be evaluated from the following equation: foliar Mg concentrations (mmol kg^{-1})- $= 384.16 \times$ soil Ca/Mg ratios$^{-0.3487}$ or LNfoliar Mg concentrations $= -0.3486 \times$ LNsoil Ca/Mg ratios $+ 5.9509$. Holland et al. (2019) suggested that precision nutrient management requires accurate assessment of plant nutrient status.

In addition, the behavior of negative effect of Ca on K differed from that on Mg. Present study showed that increased soil available Ca did significantly inhibit Mg uptake, but not K uptake, The negative effect of high K on Ca uptake at the soil–root interface is a limiting factor for the amount of Ca loaded into the xylem at the root scale (Montanaro et al. 2014). It is demonstrated that Chinese prickly ash prefer nitrate, the increase of foliar K is accompanied by the decrease of Ca and Mg, because K is the favoured counter-cation for the transportation of nitrate in the xylem (Piao et al. 2017). Therefore, foliar K concentrations were significantly and negatively correlated with both Ca and Mg in foliage, respectively. Rhodes et al. (2018) also reported that increased foliar K concentrations decrease foliar Ca and Mg concentrations in sugarcane. Wakeel et al. (2016) reported that an addition of too much Ca and Mg can cause a K deficiency due to the competition between Ca, Mg and K, while an excessive application of K can also decrease the uptake of Ca and Mg (Schonewille 2013). In the present study, foliar K concentrations were significantly and negatively correlated with foliar Mg, implying that there was the negative effect of K on Mg partitioning in foliage because K is the favoured counter-

cation for the transportation of nitrate in the xylem (Piao et al. 2017).

Mickky et al. (2018) reported that water deficit increases total soluble sugars in alfalfa plants. Under drought stress, the higher accumulation of sugar significantly inhibits photosynthesis (Sami et al. 2016; Farhat et al. 2016a). Sugar accumulation in foliage is a major consequence of Mg shortage that could limit plant growth by the regulation of photosynthetic activity (Verbruggen and Hermans 2013; Farhat et al. 2016b), because Mg is involved in the source-to-sink transport of carbohydrates (Farhat et al. 2016a). Therefore, increase in the sugar concentrations in foliage, along with the photosynthetic structure must result in decreasing Mg concentrations in the present study, because Mg plays an important role as a central atom in chlorophyll during photosynthesis (Tanoi et al. 2014).

Relationships between the values of $\delta^{13}C$ and nutrient concentrations

In the present study, increased soil available Ca did significantly decrease foliar Mg concentrations, while significantly increase foliar $\delta^{13}C$ values. The shortage of Mg induced accumulation of sugar in foliage, thus resulting in higher $\delta^{13}C$ values. Therefore, there was a negative relationship between Mg concentrations and the values of $\delta^{13}C$ in foliage. Tränkner et al. (2016) suggested that the increase in nocturnal stomatal conductance results in the decrease of $\delta^{13}C$, and thus that discrimination against ^{13}C is significantly reduced under Mg deficiency. Values of $\delta^{13}C$ often increase when water availability is limited, due to stomatal closure and thus reduced transpiration (Grant et al. 2012). In the present study, foliar Ca concentrations were positively and significantly correlated with foliar $\delta^{13}C$ values: therefore, the increase in foliar Ca concentrations should result in increasing foliar $\delta^{13}C$ values. The concentration of Ca increase under drought stress, and the uptake and partitioning of Ca^{2+} are not affected by decreased transpiration, because efficient transpiration is not essential for long distance transport of Ca (Peuke and Rennenberg 2011). However, Zhu et al. (2010) reported that higher carbon isotope discrimination in foliage associated with higher stomatal conductance and stronger transpiration is related to high Ca content in foliage. A high Ca concentration in foliage is related to stronger transpiration (Zhu et al. 2010).

Potassium plays a key role in stomatal regulation, and its deficiency inhibits photosynthesis, which is more pronounced under high stomatal conductance (Erel et al. 2014). Those results suggested that the increase of foliar sugar should be accompanied by increasing Ca, and by decreasing Mg and K, resulting in increased $\delta^{13}C$ values, though some of them not significantly. Therefore, it was

concluded that the occurrence of negative effects of Ca on Mg and K should be associated with variation in plant transpiration, partitioning and photosynthesis-related processes under abiotic stress, including drought, water stress and soil fertility. Decreased foliar K concentrations did strongly increase foliar $\delta^{13}C$ values, but not foliar sugar, while decreased foliar Mg did strongly increase foliar sugar, but not foliar $\delta^{13}C$ in the present study. Therefore, the behavior of negative effect of Ca on K differed from that on Mg. Zörb et al. (2014) suggested that K deficiency also results in the accumulation of sugars in foliage, which is likely to be a consequence of impaired sucrose export from foliage, rather than a limitation of photosynthesis. Increased soil K concentrations did significantly increase K concentrations in foliage and roots. Potassium plays a central role in regulating stomatal aperture (Epron et al. 2015), and hence in the limitation of water loss (Zörb et al. 2014). Therefore, the increasing K should enhance water retention, resulting in lower foliar $\delta^{13}C$ values. A strong negative relationship between foliar $\delta^{13}C$ values and MAP can be found on a global scale (Diefendorf et al. 2010). Similar results show that MAP is negatively related to $\delta^{13}C$ in Inner Mongolia in China (Zhou et al. 2016). However, in the present study, foliar $\delta^{13}C$ values were not significantly correlated with MAP, thus implying that MAP could not solely reflect variations of drought or water stress in the sampling sites.

Conclusions

Soil available Ca concentrations were significantly and positively correlated with foliar $\delta^{13}C$ values. The values of foliar $\delta^{13}C$ were lower in Chinese prickly ash grown on lower soil Ca, indicating that water availability was impacted by soil characteristics. An increase of Mg concentrations caused decreasing the values of $\delta^{13}C$, but an increase of Mg concentrations tended to increase the values of $\delta^{13}C$ in foliage, indicating that Ca, Mg and K availability should differentially influence variations of carbon isotopic compositions under abiotic stress. Those results suggested that the behavior of the negative effect of Ca on Mg could be mainly related to accumulation of leaf sugar, therefore, increasing their $\delta^{13}C$ values, while the behavior of the negative effect of Ca on K should be associated with variation of water retention in foliage, thus influencing foliar $\delta^{13}C$ values in Chinese prickly ash. Although the negative interaction between Ca and Mg, K induced lower plant biomass it should be beneficial for the adaptability of Chinese prickly ash grown on poor soils through increasing leaf sugar concentrations. Therefore, nutrient balance- and water stress-related traits in plants had significant implications for growth and fitness. It was important that the phenomena of contrasting dynamics among nutrient composition in tissue should be considered for fertiliser formulations of specific nutrient composition in order to increasing the nutrient use efficiency for a plant's adaptability and plant growth.

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