

Nutrient uptake by mulberry and Chinese prickly ash associated with arbuscular mycorrhizal fungi

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Abstract Understanding how nutrient absorption processes in plants are related to arbuscular mycorrhizal (AM) association is critical for predicting the effects of AM symbiosis on elemental cycling for plants. Both mulberry (*Morus alba*) and Chinese prickly ash (*Zanthoxylum bungeanum*) are AM-associated plants, widely distributed in southwest China. It was hypothesized that if the nutrient absorption processes were efficiently associated with AM symbiosis in both mulberry and Chinese prickly ash, foliar nutrient concentrations—especially calcium (Ca)—would be primarily determined by the soil conditions in different regions. To investigate this, AM colonization levels of soils, nutrient levels in soils and leaves, and $\delta^{13}\text{C}$ values of leaves were analyzed for mulberry and Chinese prickly ash. In this study, spore density in soils with low pH was higher than that in soils with high pH. The average concentrations of sugar delivered to roots in both mulberry and Chinese prickly ash in soil with relatively low pH and soil extractable cations were higher than those in other areas. The values of foliar $\delta^{13}\text{C}$ in both mulberry and Chinese prickly ash in low soil-pH and soil extractable cations were lower than those in contrast areas, indicating that water availability was impacted by soil characteristics. The efficiency in AM-mediated processes might play an important role in translocation between soil nutrients and plant tissue. The results suggest uptake and translocation of nutrients, especially Ca, in AM-associated plants may be affected by

an efficiency of AM-mediated processes. Since Sr does not appear to be similarly affected, expressing Ca and other nutrient concentrations relative to Sr could be used to evaluate whether the uptake and translocation of Ca and other nutrients are affected by AM-mediated processes.

Keywords Arbuscular mycorrhizal fungi · Elemental ratio · Carbon isotopes · Mulberry · Chinese prickly ash

1 Introduction

A number of laboratory and field studies indicated that arbuscular mycorrhizal (AM) fungi was important in the uptake of nutrients, such as calcium (Ca), magnesium (Mg), potassium (K), nitrogen (N), and phosphorus (P), resulting in high levels of foliar nutrients in AM-associated plants (George et al. 1992; Taylor and Harrier 2001; Veresoglou et al. 2011; Doubková et al. 2012; Müller et al. 2013; Khabou et al. 2014; Xiao et al. 2014). Mulberry (*Morus alba*) and Chinese prickly ash (*Zanthoxylum bungeanum*) both provide economic benefits and ecosystem services in southwest China. Mulberry is a fast-growing species, while Chinese prickly ash is a slow-growing species; both easily adapt to calcareous and some loam soils and are able to form associations with AM fungi. Both mulberry and Chinese prickly ash possess natural defenses and characteristics that enable them to survive and even flourish under systems with anthropogenic disturbance, such as karst areas that have experienced environmental degradation. AM fungi contribute to plant adaptation and ecosystem sustainability by promoting a closed nutrient cycle (Rillig 2004; van der Heijden et al. 2008). AM fungi can also improve the water absorption capacity of plants (Evelin et al. 2009). The importance of AM fungi in

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enhancing host plant growth is well known (Smith and Read 1997; Gosling et al. 2006), and has been explained by the ability of the fungal extraradical hyphae to spread in soil and take up nutrients and water that are spatially unavailable to roots (Doubková et al. 2012).

Soil conditions can affect the response of plants to inoculation with AM fungi and influence the development of mycorrhizal associations (Orozco-Patiño and Medina-Sierra 2013). Soil pH has a significant effect on organisms and processes in the soil (Olsson et al. 2010), and plays an important role in AM growth; in turn, AM symbiosis regulates soil pH (Orozco-Patiño and Medina-Sierra 2013). Mårtensson et al. (2012) found AM fungal hyphae decrease in the soil with increasing soil pH. Furthermore, fungal growth is favored at low pH, while bacteria growth is favored at high pH (Bárceñas-Moreno et al. 2011). Soil acidity can directly affect AM fungal distribution, and in some cases soil acidification may restrict some fungal species in the soil (Guo et al. 2012). Base cation concentration and organic matter can also affect fungal distribution (Olsson et al. 2010). An et al. (2008) found that soil chemical properties, especially soil pH, are the major driving force for AM fungi communities in acid soils. Plants can acidify or alkalize the soil medium (Moody and Aitken 1997) thus affecting the optimal pH needed by AM species for proliferation in the roots (Orozco-Patiño and Medina-Sierra 2013). Mycorrhizal colonies can form and excrete organic substances by the extraradical hyphae and/or the roots of host plants, which can solubilize non-available nutrients, resulting in a strong capacity to mobilize nutrients absorbed by the host plant (Theuerl and Buscot 2010; Piao and Liu 2011).

Calcium and strontium (Sr) ions have many similar properties, including the same ionic charge, similar ionic radii, and the ability to form complexes and chelates of varying levels of solubility (Shtangeeva et al. 2011). Strontium is taken up by plants in similar ways to Ca; however, Sr and Ca accumulations in plants cannot be predicted simply from the behavior of Ca because Ca and Sr can interact competitively for uptake into biological systems (Shtangeeva et al. 2011). Because of the marked immobility of Ca^{2+} and Sr^{2+} within plants (Caines and Shennan 1999; Suárez 2010), root morphological features should be responsible for variations in Ca^{2+} and Sr^{2+} acquisition. Since plant-mycorrhiza associations are common, AM fungi's effects on plant nutrient availability should be taken into account in interpreting differences between Ca and Sr uptake. Mycorrhizal symbiosis does not modify Sr accumulation or transfer to host plants (Ladeyn et al. 2008). Van der Heijden et al. (2015) showed that the internal pool of Ca in trees is more active than previously thought based on Ca isotopic data. On acid soils a preferential uptake of Ca over Sr occurs, while on calcareous soils a preferential uptake of

Sr over Ca occurs (Poszwa et al. 2000), implying that the foliar Ca and Sr concentrations should differ in different regions for the same plant species. Soils with a high concentration of CaCO_3 significantly decrease root growth and alter the symbiosis development steps of the AM fungus (Labidi et al. 2012). Therefore, a relatively high efficiency in an AM-mediated process should be responsible for high foliar Ca and other nutrient concentrations, while a relatively low efficiency should be responsible for low Ca and other foliar nutrient contents (Piao and Liu 2011). The value of $\delta^{13}\text{C}$ is often increased when water availability is limited, as a result of stomatal closure and hence reduced transpiration (Grant et al. 2012). Limited transpiration rates result in low Ca and Sr concentrations in plant tissues (Funk and Amatangelo 2013). Therefore, Ca uptake and translocation by plants is driven by the transpiration stream (Clarholm and Skjellberg 2013). The ratios of foliar Ca/Sr versus soil Ca/Sr can express the degree to which Ca concentrations in plants have been discriminated over Sr relative to their soil resources (Blum et al. 2012). It was hypothesized that the differences in ratios of foliar Ca/Sr versus soil Ca/Sr in different regions should be determined by soil conditions. Thus, the objective of this study was to use measurements of stable carbon isotopes, and nutrient and sugar concentrations, to identify the parameters causing different foliar Ca and other nutrient concentrations in AM-associated plants of different regions.

2 Materials and methods

2.1 Research site

The study area is located in a transitional zone between lowland and hills in the mountainous terrain of the Guizhou Province of southwest China. Soil samples were collected in karst areas, where the geological environment is extremely fragile, the area overpopulated, and the economy backward, leading to serious land degradation in the form of karst rocky desertification and extensive exposure of basement rocks in some regions (Wang et al. 2004; Liu 2007; Li et al. 2013). Mulberry is a perennial tree, which is widely cultivated in China for leaves, fruit, medicine, and sericulture purposes. Chinese prickly ash is a shrub species that is also widely cultivated in China as a condiment and as medicine. Because of their high drought resistance, both mulberry and Chinese prickly ash have played an important role in economic development and adapting fragile ecosystem restoration.

The samples were divided into two groups for both mulberry and Chinese prickly ash. For mulberry, the first group included the samples collected from Libo soils (17 sites) and the second group samples collected from Huangping soils (16 sites). For Chinese prickly ash, samples

were collected from Zunyi soils (22 sites) and from Huajiang soils (22 sites). The sites were located in areas where soils developed in mixed terrains, except for the soils at Huajiang where the parent material was primarily limestone. The soil type was yellow Ultisols in all sampling areas, having a long land-use history as maize fields. Sample locations and environmental parameters for sampling sites are listed in Table 1. Soil samples were taken from 0 to 15 cm depth to provide an indication of available nutrients, with at least six replicated plots for each soil sample. Nurseries growing Chinese prickly ash seedlings varied in size from ~10 to 100 m². Under normal conditions, the farmers sow seeds in September and remove weeds at regular intervals. A chemical fertilizer was not added to any of the nursery soils after sowing seed. Belowground parts of mulberry trees grown on the sampling sites for less than 4 years were used in this study. All shoots (aboveground parts) were developed every year in the mulberry plantation for sericultural purposes. The leaf samples were collected in late May for mulberry, while the seedlings were collected in early September for Chinese prickly ash. Detailed samples of leaves and roots were taken.

2.2 Laboratory analysis

Plant samples for laboratory analysis were dried for 48 h at 60 °C and ground with a mortar and pestle. Total carbon (C) and N were determined with a CHNS autoanalyzer (PE 2400-II, Norwalk, CT, USA). Plant P was digested using nitric-perchloric acid and analyzed by the vanadomolybdate colorimetric method. Olsen extractable P (Olsen P) was measured by 0.5 M NaHCO₃ extraction (adjusted to pH 8.5 with NaOH) (Olsen et al. 1954). Total soil P was determined after combustion of 1 g soil for 2 h at 550 °C followed by digestion with 6 M HCl (Graetz et al. 1999). Standard soil analysis methods were used to measure soil extractable Ca, Mg, K, and Sr with 1 M NH₄OAC (Thomas 1982). The samples of both mulberry and Chinese prickly ash were sent to the Key Laboratory for Conservation and Utilization of Bio-resources of Yunnan University and examined for mycorrhizal colonization following the method of Li et al. (2005). Briefly, after clearing the roots with 10 % KOH, they

were acidified in lactic acid, stained with acid fuchsin, and subsequently examined for their level of colonization under a compound-light microscope (OLYMPUS-BX51, Japan) at magnification ×200 according to the method of McGonigle et al. (1990). For soluble sugar determination, 0.25 g of air-dried material was extracted four times with distilled water at 75 °C, modified from the method of Chinnasamy and Bal (2003) whereby water was used instead of 80 % ethanol, and the water temperature was 75 °C rather than boiling. After each extraction, samples were filtered, and the filtrates were used to determine soluble sugar colorimetrically through anthrone reaction (Piao and Liu 2011). The δ¹³C values of leaves were measured by combustion of ~2 mg C mixed with CuO at 850 °C in a vacuum-combustion system for 2 h. Carbon dioxide generated in the combustion tubes was separated by cryogenic distillation, then collected in break-seals and analyzed on a mass spectrometer (MAT 252 Finnigan, Bremen, Germany). The data are expressed relative to the international standard PDB as ‰. The precision for sample repeats was better than 0.2 ‰ for δ¹³C.

2.3 Statistical analyses

Statistical analysis was conducted using SPSS 12.0 software (SPSS Science, Chicago, USA). Differences between mean values of nutrient concentrations in samples between Libo and Huangping soils for mulberry, and between Zunyi and Huajiang soils for Chinese prickly ash were determined by a *t* test. Pearson correlation coefficients were performed to assess relationships between each plant tissue and soil parameters, and linear regression was used to assess relationships between foliar Ca/Sr ratios versus soil Ca/Sr ratios. For all statistical tests, differences were considered significant at *P* < 0.05.

3 Results

3.1 AM colonization level and number of spores

In this study, six samples were used for determining AM colonization levels for each plant species. Colonization levels

Table 1 Sampling locations and environmental conditions

		Coordinates	Mean annual air temperature (°C)	Mean annual precipitation (mm)	Average elevation (m)
Mulberry	Libo	25°17'N–25°30'N; 108°00'E–108°11'E	18.3	1320.5	560
	Huangping	26°46'N–26°56'N; 107°51'E–108°09'E	15.4	1114.2	840
Chinese prickly ash	Zunyi	27°48'N–27°57'N; 107°14'E–107°16'E	15.6	1160	830
	Huajiang	25°38'N–25°41'N; 105°38'E–105°41'E	19	1410	780

of AM fungi for mulberry were 16, 13, and 12 % in Libo soils; and 16, 32, and 9 % in Huangping soils. Colonization levels of AM fungi for Chinese prickly ash were 50, 82, and 86 % in Zunyi soils; and 17, 20, and 31 % in Huajiang soils. Six samples were used for determining AM spores for mulberry soils. The numbers of spores in 20 g dry soils were 33, 11, and 19 in Libo soils; and 16, 15, and 13 in Huangping soils.

3.2 Total carbon and sugar concentrations in plant tissues

The average concentration of foliar C in mulberry on Libo soils ($33.5 \pm 1.2 \text{ mol kg}^{-1}$) was similar to that on Huangping soils ($33.4 \pm 0.9 \text{ mol kg}^{-1}$), but the average concentration of root C in mulberry of Libo soils ($36.6 \pm 1.3 \text{ mol kg}^{-1}$) was significantly higher than that of Huangping soils ($35.0 \pm 2.7 \text{ mol kg}^{-1}$) ($P = 0.038$). For Chinese prickly ash, the average concentration of foliar C in Zunyi soils ($35.2 \pm 0.6 \text{ mol kg}^{-1}$) was significantly lower than that in Huajiang soils ($36.5 \pm 0.6 \text{ mol kg}^{-1}$) ($P = 0.000$), but the average concentration of root C in Zunyi soils ($36.5 \pm 0.7 \text{ mol kg}^{-1}$) was similar to that in Huajiang soils ($36.7 \pm 0.7 \text{ mol kg}^{-1}$) (Fig. 1a).

The average concentration of foliar sugar in mulberry in Libo soils ($340 \pm 138 \text{ mmol kg}^{-1}$) was significantly lower than that in Huangping soils ($530 \pm 285 \text{ mmol kg}^{-1}$) ($P < 0.05$). However, the average concentration of root sugar in mulberry in Libo soils ($628 \pm 217 \text{ mmol kg}^{-1}$) was significantly higher than that in Huangping soils ($458 \pm 219 \text{ mmol kg}^{-1}$) ($P < 0.05$). For Chinese prickly ash, the average concentration of foliar sugar in Zunyi soils ($226 \pm 39 \text{ mmol kg}^{-1}$) was slightly lower than that in Huajiang soils ($242 \pm 90 \text{ mmol kg}^{-1}$). The average concentration of root sugar in Zunyi soils ($262 \pm 115 \text{ mmol kg}^{-1}$) was slightly higher than that in Huajiang soils ($250 \pm 125 \text{ mmol kg}^{-1}$) (Fig. 1b).

3.3 Soil pH and soil extractable nutrients

Table 2 shows that the mean soil pH in Libo soils was significantly lower than that in Huangping soils. In the Chinese prickly ash plots, pH ranged from 5.49 to 8.12 in Zunyi soils, and from 6.79 to 8.10 in Huajiang soils. The mean soil pH in Zunyi soils was significantly lower than that in Huajiang soils (Table 3).

The average concentrations of extractable Ca in Libo soils growing mulberry was lower than that in Huangping soils, but the difference was not significant. The concentration of extractable Sr in Libo soils was slightly higher (not significantly) than that in Huangping soils (Table 2).

On average, the concentrations of extractable Ca in Zunyi soils growing Chinese prickly ash were lower than that in Huajiang soils, and the concentration of extractable Sr in

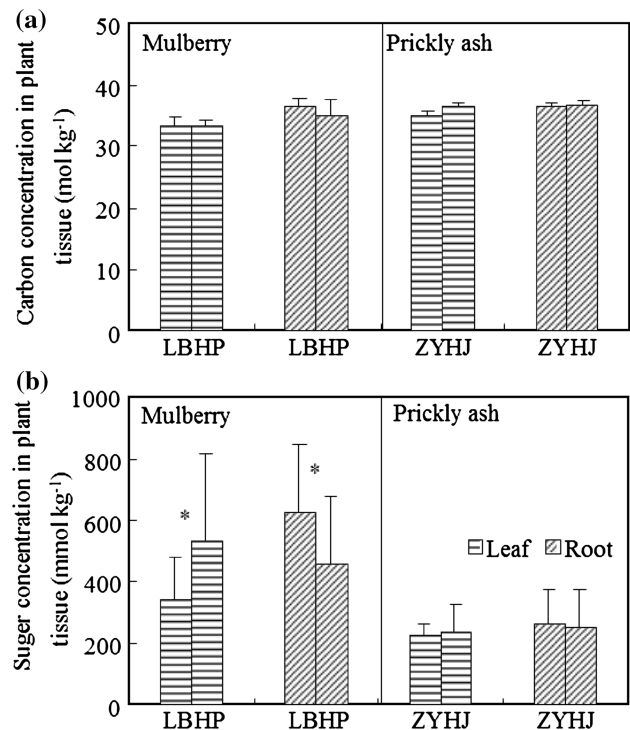


Fig. 1 a Carbon concentrations in leaves and roots of mulberry and Chinese prickly ash, and b sugar concentrations in leaves and roots of mulberry and Chinese prickly ash. LB Libo, HP Huangping, ZY Zunyi, HJ Huajiang ($*P < 0.05$)

Zunyi soils was significantly higher than that in Huajiang soils (Table 3).

3.4 Tissue chemistry and carbon isotopic compositions of leaves

The average concentration of foliar Ca in mulberry in Libo soils was relatively higher than that in Huangping soils (Table 4). For Chinese prickly ash, the mean value of foliar Ca in plants grown in Zunyi soils was higher than for those in Huajiang soils (Table 5). The average concentration of foliar Sr in mulberry in Libo soils was significantly higher compared to that found in Huangping soils (Table 4). The average concentration of foliar Sr in Chinese prickly ash in Zunyi soils was significantly higher than concentrations found in Huajiang soils (Table 5).

The average concentration of foliar N in mulberry grown on Libo soils was significantly lower than that in Huangping soils, but little difference of foliar Mg, K, and P concentrations was found between Libo and Huangping soils (Table 4). The concentrations of foliar N and K in Chinese prickly ash grown on Zunyi soils were significantly lower than those in Huajiang soils (Table 5). Except for Ca, Mg, and Sr, the average concentrations of root nutrients in mulberry (K, N, and P) did not differ between Libo and Huangping soils (Table 4). Except for N, the

Table 2 Mean values for soil pH; total N; P and Olsen P; organic C; and soil extractable Ca, Mg, K, and Sr concentrations in mulberry soils

	pH (H ₂ O)	Total N (mol kg ⁻¹)	Total P (mmol kg ⁻¹)	Olsen P (mmol kg ⁻¹)	Org C (mol kg ⁻¹)	Ext. Ca (mmol kg ⁻¹)	Ext. Mg (mmol kg ⁻¹)	Ext. K (mmol kg ⁻¹)	Ext. Sr (mmol kg ⁻¹)
Libo N = 17	4.92 (1.03)	0.12 (0.05)	20.9 (13.1)	1.8 (1.9)	2.64 (2.27)	50 (50)	6.6 (6.7)	1.6 (0.8)	0.069 (0.064)
Huangping N = 16	5.96 (1.08)	0.15 (0.10)	24.2 (10.4)	1.8 (1.2)	1.93 (1.28)	76 (38)	21.3 (12.9)	7.0 (6.2)	0.054 (0.023)
<i>t</i> test	<i>P</i> < 0.01	NS	NS	NS	NS	NS	<i>P</i> < 0.001	<i>P</i> < 0.001	NS

Ext. extractable, Org C soil organic carbon. Values in parentheses are standard deviations from the mean

Table 3 Mean values for soil pH; total N; P and Olsen P; organic C; and soil extractable Ca, Mg, K and Sr concentrations in Chinese prickly ash soils

	pH (H ₂ O)	Total N (mol kg ⁻¹)	Total P (mmol kg ⁻¹)	Olsen P (mmol kg ⁻¹)	Org C (mol kg ⁻¹)	Ext. Ca (mmol kg ⁻¹)	Ext. Mg (mmol kg ⁻¹)	Ext. K (mmol kg ⁻¹)	Ext. Sr (mmol kg ⁻¹)
Zunyi N = 22	7.35 (0.65)	0.18 (0.04)	29.8 (9.0)	1.3 (1.0)	2.88 (1.38)	140 (42)	9.1 (3.9)	4.9 (3.7)	0.23 (0.14)
Huajiang N = 22	7.68 (0.33)	0.23 (0.08)	40.5 (15.3)	1.5 (0.9)	2.81 (1.15)	187 (51)	12.8 (3.4)	13.5 (8.5)	0.12 (0.09)
<i>t</i> test	<i>P</i> < 0.05	<i>P</i> < 0.01	<i>P</i> < 0.01	NS	NS	<i>P</i> < 0.01	<i>P</i> < 0.01	<i>P</i> < 0.001	<i>P</i> < 0.01

Ext. extractable, Org C soil organic carbon. Values in parentheses are standard deviations of the mean

Table 4 Mean values for foliar and root Ca, Mg, K, Sr, P, and N in mulberry plants

	Ca (mmol kg ⁻¹)	Mg (mmol kg ⁻¹)	K (mmol kg ⁻¹)	Sr (mmol kg ⁻¹)	P (mmol kg ⁻¹)	N (mol kg ⁻¹)
Leaf						
Libo N = 17	445 (121)	203 (58)	587 (148)	0.55 (0.20)	124 (21)	2.99 (0.37)
Huangping N = 16	502 (109)	193 (88)	566 (155)	0.37 (0.17)	128 (25)	2.43 (0.49)
<i>t</i> test	NS	NS	NS	<i>P</i> < 0.01	NS	<i>P</i> < 0.001
Root						
Libo N = 17	106 (24)	62 (20)	175 (98)	0.33 (0.13)	57.5 (47.3)	0.80 (0.23)
Huangping N = 16	162 (91)	92 (50)	214 (99)	0.19 (0.11)	57.2 (24.7)	0.68 (0.26)
<i>t</i> test	<i>P</i> < 0.05	<i>P</i> < 0.05	NS	<i>P</i> < 0.01	NS	NS

Values in parentheses are standard deviations from the mean

average concentrations of root nutrients in Chinese prickly ash (Ca, Mg, K, Sr, and P) returned little difference between Zunyi and Huajiang soils (Table 5).

Foliar $\delta^{13}\text{C}$ in mulberry in Libo soils (-30.0 ± 0.5 ‰) was significantly lower than that in Huangping soils (-29.3 ± 0.7 ‰) ($P < 0.01$). For Chinese prickly ash, foliar $\delta^{13}\text{C}$ in Zunyi soils (-28.5 ± 1.4 ‰) was similar to that in Huajiang soils (-28.0 ± 0.8 ‰) (Fig. 2).

3.5 The ratios of foliar nutrient/Sr versus soil nutrient/Sr

The ratios of foliar nutrient/Sr versus soil nutrient/Sr are listed for mulberry and Chinese prickly ash in Table 6.

Significant differences were found in the ratios for foliar Ca/Sr, Mg/Sr, and K/Sr between Libo and Huangping soils and between Zunyi and Huajiang soils. The ratios of foliar P/Sr and foliar N/Sr were similar between Libo and Huangping soils and between Zunyi and Huajiang soils. The ratios of foliar and soil Ca/Sr, Mg/Sr, and K/Sr were generally higher than 1. The ratios for Ca/Sr of mulberry were higher in Libo soils (with mean soil pH value of 4.92) when compared to Huangping soils, which had a relatively high soil pH ($P < 0.05$). Similarly, the ratios for Ca/Sr of Chinese prickly ash were somewhat higher in Zunyi soils (with relatively low soil pH) than in Huajiang soils with a mean soil pH 7.68 ($P < 0.05$).

Table 5 Mean values for foliar and root Ca, Mg, K, Sr, P, and N in Chinese prickly ash

	Ca (mmol kg ⁻¹)	Mg (mmol kg ⁻¹)	K (mmol kg ⁻¹)	Sr (mmol kg ⁻¹)	P (mmol kg ⁻¹)	N (mol kg ⁻¹)
Leaf						
Zunyi N = 22	627 (131)	176 (67)	302 (124)	0.94 (0.45)	101 (44)	1.92 (0.28)
Huajiang N = 22	565 (114)	155 (46)	443 (148)	0.43 (0.26)	93 (21)	2.38 (0.46)
<i>t</i> test	NS	NS	<i>P</i> < 0.01	<i>P</i> < 0.001	NS	<i>P</i> < 0.001
Root						
Zunyi N = 22	162 (51)	100 (44)	210 (143)	0.61 (0.61)	61.3 (19.3)	0.87 (0.25)
Huajiang N = 22	168 (45)	109 (33)	268 (118)	0.27 (0.16)	55.0 (18.3)	1.12 (0.28)
<i>t</i> test	NS	NS	NS	NS	NS	<i>P</i> < 0.01

Values in parenthesis are standard deviations of the mean

4 Discussion

4.1 Ca behavior differs from Sr in soils

The limestone of the study area has a high concentration of Sr relative to aluminosilicate minerals (Jiang and Ji 2011). However, the concentrations of Sr in extractable fractions were lower in Huajiang soils developed from limestone than in the Zunyi soils developed on mixed terrains, indicating the intensive leaching of Sr relative to other nutrients during carbonate weathering and soil development in the karst area (Jiang and Ji 2011). Sr concentration in plants is maximized in soils with a low pH (Karpova and Gomonova 2006). Increasing soil pH with CaCO₃, especially in combination with application of organic fertilizers, can lead to changes in the soil chemical properties controlling Sr mobility, which results in a lower uptake of Sr by plants (Karpova and Gomonova 2006). Previous studies have indicated that soil nutrient availability is limited in high soil pH (Kerley 2000; Al-Karaki and Al-Omouh 2002). However, Stark et al. (2011) found that high soil pH usually parallels high soil extractable nutrient concentration, with important consequences for plants and

chemical quality of soil organic matter. This finding was supported, especially for Ca, by a study in southwest China (Piao and Liu 2012). While an acid condition might produce more soil nutrient availability, it might also lead to more soil nutrient loss through leaching. This is likely to be the main reason why the Sr leaching loss was more severe than that of other nutrients in both Libo and Huangping soils. Most soil nutrients in this study were relatively high in Zunyi and Huajiang—both soils with higher pH values. Soil organic C did not show a difference between the two soil groups in this study. In ion exchange on clays, Ca and Sr behave almost identically owing to the divalent charge and similar hydrated radius (Blum et al. 2008). In ion exchange on soil organic matter, Ca may be retained preferentially over Sr to a small degree (Baes and Bloom 1988; Blum et al. 2008), and the presence of soil microorganisms does not significantly enhance the retention of Sr in the organic system the way it does other elements (Parekh et al. 2008).

4.2 Relationship between AM fungi and nutrients distribution

Soil microorganisms, especially fungi, may contribute significantly to the long-term retention of elements in organic layers of forest soils, excepting Sr (Parekh et al. 2008). If the amounts of nutrients acquired by AM fungi are low, AM fungi have only a relatively minor impact on reducing nutrient leaching (van der Heijden et al. 2008). Using two-chambered pots where only AM fungal hyphae connected the chambers, Meding and Zamoski (2008) examined nutrient transfer between native plant species of grasses and forbs, and suggest that there is no evidence of significant Sr transfer between experimental plants via extraradical hyphae. However their results could be attributed to immobilization of Sr within plant tissues. It seems that the more severe leaching losses of Sr relative to other nutrients should be attributed to Sr acquisition and retention and not related to AM symbiosis.

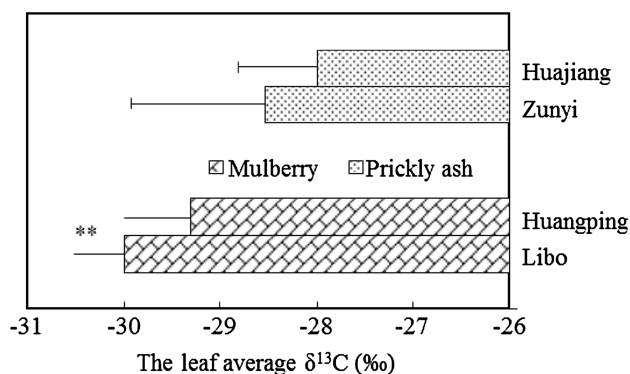


Fig. 2 Average foliar δ¹³C in Chinese prickly ash grown on Huajiang and Zunyi soils, and in mulberry grown on Huangping and Libo soils (***P* < 0.01)

Table 6 Ratios of foliar nutrient/Sr versus soil nutrient/Sr (mean \pm standard deviations)

Species		Ca/Sr	Mg/Sr	K/Sr	P/Sr	Po/Sr ^a	N/Sr
Mulberry	Libo (n = 17)	1.44 \pm 0.38	8.69 \pm 8.71	53.7 \pm 34.5	0.85 \pm 0.44	14.8 \pm 14.3	3.14 \pm 1.53
	Huangping (n = 16)	1.10 \pm 0.36	1.91 \pm 1.38	19.8 \pm 14.6	1.06 \pm 0.87	16.6 \pm 13.8	3.44 \pm 3.13
	<i>t</i> test	<i>P</i> < 0.05	<i>P</i> < 0.01	<i>P</i> < 0.001	NS	NS	NS
Prickly ash	Zunyi (n = 22)	1.05 \pm 0.23	4.72 \pm 2.19	17.8 \pm 11.3	0.84 \pm 0.43	29.0 \pm 20.2	2.32 \pm 1.09
	Huajiang (n = 22)	0.83 \pm 0.29	3.32 \pm 1.54	12.0 \pm 8.0	0.68 \pm 0.34	24.1 \pm 17.2	2.45 \pm 1.08
	<i>t</i> test	<i>P</i> < 0.05	<i>P</i> < 0.05	NS	NS	NS	NS

^a Po/Sr: ratios of foliar P/Sr versus soil Olsen P/Sr

There was little difference in AM colonization levels between mulberry and Chinese prickly ash. This supports previous research conclusions that there is no significant relationship between AM colonization levels and nutrient acquisition (Piao and Liu 2011; Piao et al. 2012). In this study, spore density in the Libo soils (with a relatively low soil pH and some soil nutrients) was higher than that in Huangping soils, which is consistent with the results of Aliasgharzadeh et al. (2001), who have reported a negative correlation between spore density and available soil Mg and Ca (Evelin et al. 2009). Guo et al. (2012) have found that high soil pH with CaCO₃ treatment significantly decreases root growth and alters the symbiosis development steps of the AM fungus *Rhizophagus irregularis*, such as germination, hypha elongation, root colonization rate, extraradical hyphal development, and sporulation. However the fungus is able to completely fulfill its life cycle (Labidi et al. 2012), which might influence the distribution of nutrients between soil and plants.

The AM fungal community structure is significantly influenced by environmental factors, especially soil moisture, pH, available N, and P (Wang et al. 2013; De Beenhouwer et al. 2015). The present data show that the average concentrations of sugar delivered to roots in both mulberry and Chinese prickly ash with relatively low soil pH and soil extractable N and P were higher than values in contrast areas. AM symbiosis depends on the host sugars for the formation, maintenance, and function of fungal structures (Zhu and Miller 2003). Root turnover can account for up to 40 % of the C input into soil and is clearly the major driver for soil microbiological processes (Richardson et al. 2009). The fungi are obligate symbionts and cannot survive without a photosynthate supply from the host plant (Smith et al. 2010). Therefore, acquisition of nutrients and growth responses depend on soluble photosynthate production and its concentration in the soil (Orozco-Patiño and Medina-Sierra 2013). Meanwhile, root exudates not only influence nutrient availability but also interact with soil microorganisms (Richardson et al. 2009). The amount of C allocated to AM processes is estimated to range from 4 to 20 % of a plant's total C budget (Smith and Read 1997).

Mårtensson et al. (2012) reported that the allocation of C to the extraradical AM hyphae decreases with increasing pH, ranging from not detectable to 1.2 $\mu\text{g } ^{13}\text{C g}^{-1}$ dry soil in the pH range of 5.5–8.5. CaCO₃ treatment of soil decreases chicory root growth (Labidi et al. 2012). This effect is more drastic in mycorrhizal roots than in non-mycorrhizal ones, which may be related to the allocation of a considerable portion of C by mycorrhizal roots to maintain fungal metabolism (Labidi et al. 2012). Mycorrhizal colonization can result in the excretion of organic substances by extraradical hyphae and/or roots of host plants, which can solubilize non-available forms of nutrients, resulting in a strong capacity to mobilize nutrients absorbed by the host plant (Theuerl and Buscot 2010; Piao and Liu 2011). Differences in sugar levels of plant tissues were found between Libo and Huangping soils, and between Zunyi and Huajiang soils. A key feature of AM-mediated processes is the transfer of photosynthate from the host plant to the AM fungal hyphae (Zhu and Miller 2003; Richardson et al. 2009; Piao and Liu 2011). For example, there is significantly less sucrose in both shoots and roots of summer wheat with AM fungus compared with summer wheat without AM fungus (Hawkins and George 2001). The efficiency of the AM-mediated processes was higher in both Libo and Zunyi soils than those in Huangping and Huajiang soils.

4.3 Relationship between water availability and Ca uptake and translocation

Arbuscular mycorrhizal symbiosis is beneficial in providing host plants with water, thus enhancing the tolerance of the host plants to water deficit (Bárcana et al. 2012). The value of $\delta^{13}\text{C}$ is often increased when water availability is limited, as a result of stomatal closure and hence reduced transpiration (Grant et al. 2012). Previous results show that plants under water stress increase their foliar $\delta^{13}\text{C}$ relative to those without water stress (Hubick et al. 1986; Farquhar et al. 1988). Values of $\delta^{13}\text{C}$ are not affected by irrigation or N treatments (Pascual et al. 2013). Both mulberry and Chinese prickly ash have the capacity to grow in a wide

range of environments. Under drought stress, the growth of mulberry is inhibited, but the trees are known to respond to the stress by increasing the root absorptive area and enhancing capacity for water retention (Huang et al. 2013). Mulberry trees have a high water demand owing to their fast growth rate and high metabolism (Guha et al. 2012), resulting in large biomass. The present results show that the values of foliar $\delta^{13}\text{C}$ in both mulberry and Chinese prickly ash in Libo and Zunyi soils, respectively, were relatively lower than those in Huangping and Huajiang soils. This indicates that water availability in both mulberry on Libo soils and Chinese prickly ash on Zunyi soils was higher than on Huangping and Huajiang soils, which would attribute to the higher efficiency of AM-mediated processes in the Libo and Zunyi soils due to different environmental characteristics, such as pH and soil nutrient distribution.

During water transport from root to leaf, divalent cations such as Ca and Sr undergo a series of exchange reactions at negatively charged sites on cell walls (Funk and Amantangelo 2013). Both Ca and Sr are immobile elements, meaning that they are not resorbed from a leaf once they have been assimilated (Karley et al. 2000), and therefore foliar Ca and Sr concentrations should be correlated with how much water is taken up over a leaf's lifetime (Funk and Amantangelo 2013). Low transpiration rates result in a small quantity of Ca and Sr in plant tissues, with implications for the nutritional quality of plants and for rates of biochemical cycling (Funk and Amantangelo 2013). Clarholm and Skjellberg (2013) reported that actual evapotranspiration is in control of the cycling of base cations, such as Ca and Mg, between soil and trees. Therefore, Ca uptake by tree roots is by passive movement in the mass flow of soil water driven by the transpiration stream.

4.4 The ratios of foliar nutrient/Sr versus soil nutrient/Sr

The ratios of foliar Ca/Sr versus soil Ca/Sr measure the degree to which Ca has been incorporated preferentially over Sr in plants relative to their soil presence (Blum et al. 2012). However, the bias toward Ca over Sr depends on soil conditions. The current data show that both mulberry grown at Libo and Chinese prickly ash at Zunyi had a relatively preferential uptake of Ca over Sr compared with contrast areas. Differences between Ca and Sr behavior were found during uptake of nutrients from soils, and might be caused by ion exchange processes during ascent in the xylem (Clarkson 1984). Our results show the ratios of foliar Ca/Sr versus soil Ca/Sr for both mulberry and Chinese prickly ash were higher on soils with relatively low pH and soil extractable cations, where the efficiency of AM-mediated processes would increase. This suggests that

relatively high efficiencies in the AM-mediated processes might be responsible for the high ratios of foliar Ca/Sr versus soil Ca/Sr in both Libo and Zunyi soils relative to the Huangping and Huajiang soils. Meanwhile, Sr is retained by cation exchange sites in stems to a greater extent than Ca, resulting in increased translocation of Ca relative to Sr in the leaves of plants (Poszwa et al. 2000; Dasch et al. 2006; Funk and Amantangelo 2013), which might be another cause for the difference of translocation.

The ratios of foliar Mg/Sr versus soil Mg/Sr and the ratios of foliar K/Sr versus soil K/Sr were also higher for soils with lower pH than for soils with higher pH for both mulberry and Chinese prickly ash (Tables 2, 6), a pattern repeated with the ratios of foliar Ca/Sr versus soil Ca/Sr. These results also indicate that both mulberry at Libo and Chinese prickly ash at Zunyi had a preferential uptake of Mg and K over Sr compared with contrast areas. As for the ratios of foliar P/Sr versus soil P/Sr and the ratios of foliar N/Sr versus soil N/Sr, there were no differences among regions, so these nutrients may be not suitable for assessing the effects of AM-mediated processes on uptake by mulberry and Chinese prickly ash.

5 Conclusion

Mulberry (*Morus alba*) and Chinese prickly ash (*Zanthoxylum bungeanum*) are important economic plants widely distributed in southwest China. In this study, the nutrients and AM-colonization level of soils as well as carbon isotopic compositions of leaves were investigated for mulberry and Chinese prickly ash growing in varied environmental conditions. The results suggested that the high efficiency in AM-mediated processes was responsible for the relatively high levels of foliar Ca, Mg, and K relative to Sr absorbed by mulberry and Chinese prickly ash grown on Libo and Zunyi soils, respectively, while the relatively low efficiency in AM-mediated processes was responsible for the low amount of foliar Ca, Mg, and K relative to Sr in others areas. Water availability also affects ratios of foliar Ca/Sr versus soil Ca/Sr. Since uptake and translocation of Ca and Sr in AM plants might be influenced by an efficiency of AM-mediated processes, expressing Ca concentration relative to Sr could be used to evaluate whether the nutrient could be affected by AM-mediated processes. However the ratios of foliar Ca/Sr versus soil Ca/Sr could vary with species and environmental conditions, including temperature and precipitation. More research on these processes in the future will improve the interpretation of foliar elemental ratios as an index for evaluating AM-mediated processes and elemental cycling on the Earth's surface.

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