Leaf Calcium Form Differences in Camellia sect. Chrysantha under Limestone and Acidic Soil Habitats: Postprint

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Abstract

Investigating the leaf calcium form characteristics of Camellia sect. Chrysantha plants across different habitats facilitates a deeper understanding of their adaptation mechanisms to soil calcium and provides a reference for conservation measure formulation. Using Camellia sect. Chrysantha from 10 limestone soil habitats and 4 acidic soil habitats as research subjects, we determined the calcium content and pH of their habitat soils, along with the contents of calcium nitrate and calcium chloride, water-soluble organic acid calcium, calcium pectate, calcium phosphate and calcium carbonate, calcium oxalate, calcium silicate, and total calcium in plant leaves from these habitats. The results showed that: (1) Both soil calcium content and soil pH in limestone soil habitats were extremely significantly ($P<0.01$) higher than those in acidic soils. (2) In limestone soil habitats, leaf calcium forms of Camellia sect. Chrysantha plants were dominated by calcium oxalate (41.17%), whereas in acidic soil habitats, calcium pectate (43.10%) was dominant. Except for calcium nitrate and calcium chloride, and calcium pectate, all leaf calcium forms and total calcium contents in limestone soil Camellia were extremely significantly ($P<0.01$) higher than those in acidic soil Camellia. (3) Correlation analysis results revealed that most leaf calcium form contents were extremely significantly ($P<0.01$) positively correlated with soil pH and soil calcium content, indicating that the soil environment exerts an important influence on leaf calcium form characteristics of Camellia sect. Chrysantha plants. (4) One-way ANOVA results demonstrated extremely significant ($P<0.01$) differences in leaf calcium form contents among species, indicating that leaf calcium form characteristics exhibit diversity during the species differentiation process of Camellia sect. Chrysantha plants. (5) Cluster analysis based on leaf calcium form characteristics showed that 14 Camellia species could be grouped into 3 major categories. In summary, differences in

leaf calcium forms of Camellia sect. Chrysantha plants under different habitat backgrounds may result from the combined effects of soil environment and genetic factors.

Full Text

Difference in Calcium Speciation of Leaves of Golden Camellia Species from Calcareous Soil and Acidic Soil Habitats

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Abstract

Investigating the characteristics of calcium speciation in leaves of golden Camellia species across different habitats can deepen our understanding of their adaptation mechanisms to soil calcium and provide a reference for developing conservation measures. This study examined 10 golden Camellia species from calcareous soil habitats and 4 from acidic soil habitats, measuring soil calcium content and pH, as well as leaf contents of calcium nitrate and chloride, water-soluble organic calcium, calcium pectate, calcium phosphate and carbonate, calcium oxalate, calcium silicate, and total calcium. The results showed: (1) Both soil calcium content and pH in calcareous habitats were extremely significantly higher ($P<0.01$) than those in acidic soils. (2) In calcareous habitats, calcium oxalate (41.17%) was the dominant leaf calcium form in golden Camellia species, whereas calcium pectate (43.10%) predominated in acidic habitats. Except for calcium nitrate/chloride and calcium pectate, all leaf calcium forms and total calcium content were extremely significantly higher ($P<0.01$) in calcareous-soil species compared to acidic-soil species. (3) Correlation analysis revealed that most leaf calcium forms were extremely significantly ($P<0.01$) positively correlated with soil pH and soil calcium content, indicating that soil environment exerts an important influence on leaf calcium speciation characteristics. (4) One-way ANOVA showed extremely significant ($P<0.01$) interspecific differences in all leaf calcium forms, suggesting considerable variation in calcium speciation traits during species differentiation. (5) Cluster analysis based on leaf calcium speciation characteristics grouped the 14 golden Camellia species into three major categories. In summary, differences in leaf calcium speciation among golden Camellia species from different habitats likely result from the combined effects of soil environment and genetic factors.

Keywords: golden Camellia, soil environment, calcium adaptation, cluster analysis, karst plant

Introduction

Calcium is an essential nutrient element for plant growth that promotes development, photosynthesis, and stress resistance. However, excessive calcium can cause cellular toxicity, making it a double-edged element for plants [?, ?]. In plants, calcium exists primarily in several chemical forms: calcium nitrate and chloride, water-soluble organic calcium, calcium pectate, calcium phosphate and carbonate, calcium oxalate, and calcium silicate [?, ?]. In high-calcium environments, some dominant plants have evolved calcium tolerance mechanisms to avoid toxicity, such as secreting excess calcium through specialized glands [?, ?, ?], forming calcified roots to control calcium uptake at the source [?, ?], or regulating physiological active substances to adapt to high-calcium conditions [?, ?]. Karst regions, also known as karst areas, represent typical high-calcium environments where calcium plays a crucial role in the ecosystem [?, ?]. Most plants in these regions have developed calcicole, lithophytic, and xerophytic characteristics [?, ?], making karst habitats a hotspot for studying plant adaptation to high-calcium environments [?, ?, ?, ?].

The golden Camellia group (*Camellia* sect. *Chrysantha* Chang) comprises evergreen shrubs or small trees in the family Theaceae. Due to their scarce germplasm resources and high ornamental value, golden Camellias are known as the "giant panda of the plant kingdom" and "queen of the tea family" [?, ?]. They also possess significant medicinal value for anti-tumor, antioxidant, antihypertension, anti-inflammatory, and anti-allergic properties [?, ?]. In August 2021, all species in the golden Camellia group were listed as nationally protected wild plants (second-class) in China' s National Key Protected Wild Plants List. More than 20 species of golden Camellia have been reported and recognized in China, mainly distributed in southwestern Guangxi. Most species inhabit karst calcareous soils, while a few grow in acidic soils [?, ?]. In natural environments, no golden Camellia species has been found to grow in both calcareous and acidic soil habitats simultaneously [?, ?]. Based on habitat soil type, they can be divided into calcareous-soil and acidic-soil golden Camellias. Artificial introduction experiments show that most calcareous-soil species can grow normally in acidic soils, whereas acidic-soil species struggle to adapt to calcareous environments [?, ?]. This high habitat specificity may be related to their calcium adaptation mechanisms [?, ?]. However, previous research on golden Camellias has focused primarily on morphological characteristics [?, ?, ?], medicinal components [?, ?, ?], cultivation techniques [?, ?, ?], and genetic diversity [?, ?, ?], leaving the calcium adaptation mechanisms under different habitats poorly understood.

Therefore, this study investigated 10 calcareous-soil and 4 acidic-soil golden

Camellia species, measuring soil calcium content and pH, as well as various leaf calcium forms. The main objectives were: (1) to determine whether leaf calcium speciation differs between habitats; (2) to assess whether soil factors significantly influence leaf calcium speciation; and (3) to characterize leaf calcium speciation traits among golden Camellia species. The findings will enhance understanding of calcium adaptation mechanisms and provide a scientific basis for conservation efforts.

Materials and Methods

1.1 Experimental Materials Fourteen golden Camellia species were selected from their main natural distribution areas , including 10 calcareous-soil species: *Camellia impressinervis* (CIM), *C. longzhouensis* (CLO), *C. limonia* (CLI), *C. grandis* (CGR), *C. pubipetala* (CPU), *C. perpetua* (CPE), *C. terminalis* (CTE), *C. flavida* (CFL), *C. pingguoensis* (CPI), and *C. huana* (CHU) [Note: formerly *C. tianeensis*, now merged with *C. huana*], and 4 acidic-soil species: *C. tunghinensis* (CTU), *C. nitidissima* (CNI), *C. euphlebia* (CEU), and *C. parvipetala* (CPA). At each sampling site, three healthy adult plants of similar growth condition were selected. From each plant, approximately 100 g of one-year-old mature leaves were collected from four directions (east, south, west, north), yielding 42 leaf samples total. Corresponding surface soil (0–20 cm) samples of approximately 1 kg were collected from around the plant roots.

1.2.1 Determination of Leaf Calcium Speciation Leaf samples were processed in the laboratory by deactivating enzymes at 105°C for 30 minutes, drying at 80°C for 12 hours, crushing, and sieving through a 100-mesh screen. Leaf calcium speciation was determined following the method of Qi et al. (2013) with minor modifications. Briefly, 0.5000 ± 0.0005 g of leaf powder was placed in a 50 mL centrifuge tube with a cap, 20 mL of 80% ethanol was added, and the mixture was shaken in a 30°C water bath for 1 hour, then centrifuged at 4,000 $r \cdot min^{-1}$ for 10 minutes. The supernatant was filtered into a 50 mL volumetric flask, and the extraction was repeated twice more with 10 mL of 80% ethanol for 1 hour each time. After centrifugation and filtration, the solution was diluted to volume with 5% HCl. This procedure was then repeated sequentially with distilled water, 1 $mol \cdot L^{-1}$ NaCl, 2% acetic acid, and 0.6% HCl to obtain five extracts. The remaining residue was transferred to a clean tall beaker, heated on a hot plate to evaporate the liquid, and 5 mL of nitric-perchloric acid mixture (4:1, V/V) was added in a fume hood, soaked overnight at 50°C. The next day, another 10 mL of the acid mixture was added, a small glass funnel was placed at the bottle mouth, and the sample was digested at 80°C for 30 minutes, then at 150°C for 1 hour, and finally at 180°C until brown fumes turned white. After the white fumes dissipated and the liquid evaporated completely, 15 mL of 0.2% HNO_3 was added in two portions, heated to dissolve precipitates, cooled, transferred to a 25 mL volumetric flask, diluted with 0.2% HNO_3, and filtered

through a 0.45 m membrane to obtain the residual calcium extract. Blanks and standard samples were digested simultaneously for quality control. Atomic absorption spectrophotometry was used to determine calcium nitrate and chloride (AIC-Ca), water-soluble organic calcium (H_2O-Ca), calcium pectate (NaCl-Ca), calcium phosphate and carbonate (HAC-Ca), calcium oxalate (HCl-Ca), and calcium silicate (Res-Ca) in the six extracts. Total leaf calcium (Tot-Ca) was calculated as the sum of all six calcium forms.

1.2.2 Soil Index Determination Soil samples were air-dried, cleaned, mixed, ground, and sieved through a 100-mesh screen. Soil pH (Soil-pH) was measured using a glass electrode method: 10 g of soil was placed in a 50 mL beaker, 25 mL of deionized water was added, stirred for 1 minute, left to stand for 30 minutes, and the pH of the supernatant was measured. Soil calcium content (Soil-Ca) was determined by microwave digestion-flame atomic absorption spectrophotometry: 0.1 g of soil was digested with 4 mL concentrated HNO_3 and 2 mL HF in a microwave sample preparation system, and calcium content was measured by atomic absorption spectrophotometry after digestion.

1.3 Data Analysis Statistical analyses were performed using SPSS v23.0. Independent samples t-tests were used to compare soil environments and leaf calcium speciation between calcareous-soil and acidic-soil golden Camellias. Spearman correlation coefficients were calculated to examine relationships between leaf calcium forms and soil indices, with significance testing. One-way ANOVA was used to compare leaf calcium speciation among different golden Camellia species, followed by Duncan' s multiple range test. Cluster analysis of leaf calcium speciation characteristics was performed using the Flexclust package in R (Dolnicar & Leisch, 2014) with Ward' s hierarchical clustering method and Euclidean distance.

Results

2.1 Comparison of Soil Environment and Leaf Calcium Speciation Between Calcareous-Soil and Acidic-Soil Golden Camellias T-test results showed that both pH and calcium content in calcareous habitats were extremely significantly higher ($P<0.01$) than in acidic soils , indicating substantial differences between the two habitat soil environments. In leaves, except for calcium nitrate/chloride and calcium pectate, the remaining four calcium forms and total leaf calcium were all extremely significantly higher ($P<0.01$) in calcareous-soil golden Camellias than in acidic-soil species. The relative proportions of leaf calcium forms in calcareous-soil species were: calcium oxalate (41.17%), calcium pectate (27.67%), calcium silicate (16.36%), calcium phosphate and carbonate (13.82%), water-soluble organic calcium (0.61%), and calcium nitrate/chloride (0.37%). In acidic-soil species, the order was: calcium pectate (43.10%), calcium

oxalate (28.70%), calcium phosphate and carbonate (17.13%), calcium silicate (10.16%), calcium nitrate/chloride (0.53%), and water-soluble organic calcium (0.37%). Notably, calcium nitrate/chloride and water-soluble organic calcium contents were low in both groups, each accounting for less than 1% of total leaf calcium.

2.2 Correlations Between Soil Indices and Leaf Calcium Speciation Correlation analysis revealed correlation coefficients (R) between soil indices and leaf calcium forms ranging from 0.12 to 0.95 [Figure 1: see original paper]. Soil pH was extremely significantly positively correlated with soil calcium content ($P<0.01$). Soil pH showed extremely significant positive correlations ($P<0.01$) with all leaf calcium forms except calcium nitrate/chloride. Soil calcium content was significantly ($P<0.05$) or extremely significantly ($P<0.01$) positively correlated with total leaf calcium, water-soluble organic calcium, calcium oxalate, calcium silicate, and calcium phosphate/carbonate, but not significantly correlated with calcium nitrate/chloride or calcium pectate ($P>0.05$). Total leaf calcium was significantly correlated ($P<0.05$) with all six calcium forms, with the strongest correlations with calcium oxalate ($R=0.95$) and calcium silicate ($R=0.92$), indicating these two forms have the greatest influence on total leaf calcium. Calcium oxalate and calcium silicate were highly correlated ($R=0.82$), and calcium phosphate/carbonate showed correlations of 0.70 and 0.71 with calcium oxalate and calcium silicate, respectively, suggesting interrelationships among calcium forms.

2.3 Interspecific Comparison and Cluster Analysis of Leaf Calcium Speciation One-way ANOVA revealed extremely significant differences ($P<0.01$) in all leaf calcium forms and total calcium among the 14 golden Camellia species [Figure 2: see original paper]. Calcium nitrate/chloride content was highest in *C. limonia* (50.48 $mg \cdot kg^{-1}$), significantly higher than other species. Water-soluble organic calcium and calcium pectate contents were highest in *C. pingguoensis* (56.41 $mg \cdot kg^{-1}$) and *C. terminalis* (1,739.33 $mg \cdot kg^{-1}$), respectively. Calcium phosphate/carbonate content was highest in *C. terminalis* (1,087.00 $mg \cdot kg^{-1}$) and lowest in *C. nitidissima* (358.83 $mg \cdot kg^{-1}$), with three acidic-soil species (*C. nitidissima*, *C. euphlebia*, *C. tunghinensis*) showing significantly lower ($P<0.05$) contents than most calcareous-soil species. Similarly, calcium oxalate was highest in *C. terminalis* (2,743.67 $mg \cdot kg^{-1}$) and lowest in *C. nitidissima* (268.5 $mg \cdot kg^{-1}$), while calcium silicate was highest in *C. pingguoensis* (1,164.23 $mg \cdot kg^{-1}$) and lowest in *C. nitidissima* (53.21 $mg \cdot kg^{-1}$). The three acidic-soil species (*C. nitidissima*, *C. euphlebia*, *C. tunghinensis*) showed consistent leaf calcium profiles with significantly lower ($P<0.05$) calcium oxalate and silicate contents compared to calcareous-soil species. In contrast, *C. parvipetala* showed calcium speciation patterns similar to calcareous-soil species, with no significant differences ($P>0.05$) in most calcium forms.

Cluster analysis of calcium speciation characteristics among the 14 species re-

vealed three major groups [Figure 3: see original paper]: Group I—low total leaf calcium with calcium pectate as the dominant form, including *C. euphlebia*, *C. tunghinensis*, and *C. nitidissima*; Group II—moderate total leaf calcium with calcium pectate and calcium oxalate as co-dominant forms, including *C. flavida*, *C. pubipetala*, *C. longzhouensis*, *C. impressinervis*, and *C. perpetua*; Group III —high total leaf calcium with calcium oxalate as the dominant form, including *C. limonia*, *C. grandis*, *C. pingguoensis*, *C. terminalis*, *C. huana*, and *C. parvipetala*.

Discussion and Conclusion

As a vital nutritional organ, studying leaf calcium speciation characteristics helps reveal mechanisms of calcium enrichment and adaptation to habitat soil conditions. Cao et al. (2011) reported average total leaf calcium contents of 1,216.82 $mg \cdot kg^{-1}$ for karst region plants and 767.94 $mg \cdot kg^{-1}$ for non-karst plants, with common karst trees such as *Liquidambar formosana* (1,173.25 $mg \cdot kg^{-1}$), *Cinnamomum parthenoxylon* (1,024.87 $mg \cdot kg^{-1}$), and *Toona sinensis* (963.63 $mg \cdot kg^{-1}$). Qi et al. (2013) reported leaf calcium speciation in 11 herbaceous *Primulina* species, with average total leaf calcium of 2,285.6 $mg \cdot kg^{-1}$ from limestone calcareous soils, 1,379.3 $mg \cdot kg^{-1}$ from sandstone acidic soils, and 1,329.1 $mg \cdot kg^{-1}$ from Danxia landform soils. In this study, total leaf calcium contents reached 5,287.10 $mg \cdot kg^{-1}$ and 3,008.35 $mg \cdot kg^{-1}$ for calcareous-soil and acidic-soil golden Camellias, respectively—substantially higher than plants from the aforementioned regions, indicating strong calcium enrichment capacity in golden Camellia species. Beyond species differences, this strong enrichment ability may partly reflect ecological niche advantages. For instance, Xie et al. (2007) found that different forest layers in karst ecosystems showed varying calcium uptake capacities, with shrub layers exhibiting stronger calcium enrichment than herb layers. The significantly higher total leaf calcium in calcareous-soil golden Camellias likely relates to the abundant calcium content and high pH of their habitat soils, suggesting that long-term adaptation to different habitats may have fostered unique calcium enrichment and adaptation mechanisms.

Regulating internal calcium speciation composition represents another important mechanism for plant adaptation to different calcium environments. Cao et al. (2011) found that karst plants primarily contained calcium pectate (27.91%-32.82%) in leaves, while non-karst plants were dominated by calcium oxalate (33.69%-34.34%). However, our results showed the opposite pattern: calcareous-soil golden Camellias were dominated by calcium oxalate (41.17%), while acidic-soil species were dominated by calcium pectate (43.10%). This discrepancy may arise from extensive variation in calcium speciation among different species and even among populations of the same species [**?**, **?**]. Additionally, foliar elemental stoichiometry may show dynamic variation influenced by developmental stage, climate, and topography [**?**, **?**, **?**]. Previous studies indicate that calcium oxalate primarily functions to regulate cellular calcium levels; under high-calcium con-

ditions, some dominant species can combine excess free Ca^{2+} with oxalic acid to form stable calcium oxalate crystals, whose morphology, size, and quantity vary with environmental calcium concentration, thereby avoiding calcium toxicity [**?**, **?**, **?**]. This may represent one adaptation mechanism of calcareous-soil golden Camellias to high-calcium environments. Calcium pectate, an active calcium form mainly present in cell walls, has been shown to maintain intracellular calcium stability in low-calcium acidic sandstone soils, ensuring normal calcium requirements for plant growth [**?**, **?**]. Therefore, the calcium pectate-dominated distribution in acidic-soil golden Camellias may facilitate better adaptation to low-calcium environments.

The influence of soil environment on plant calcium uptake has long been a research focus [**?**, **?**, **?**]. In golden Camellias, we observed significant ($P<0.05$) positive correlations between most leaf calcium forms and both soil pH and soil calcium content, indicating that high-calcium, high-pH environments promote accumulation of various calcium forms. Calcium nitrate/chloride showed no significant correlations with soil pH or calcium content, likely because these forms are metabolized rapidly and have short residence times in plants, making them less influenced by soil conditions [**?**, **?**]. Correlation analysis also revealed interactions among calcium forms: total leaf calcium was most strongly influenced by calcium oxalate and calcium silicate, while the extremely significant positive correlation between these two forms ($R=0.82$, $P<0.01$) may suggest mutual promotion in golden Camellia tissues. However, few studies have reported correlations among plant calcium forms, and our results provide a valuable reference for research on leaf calcium speciation diversity.

The extremely significant interspecific differences ($P<0.01$) in total leaf calcium and all calcium forms indicate substantial differentiation of calcium speciation traits during diversification of golden Camellia species. To quantify these characteristics, we performed hierarchical clustering on the 14 species, which revealed that, except for *C. parvipetala*, the three acidic-soil species formed one group, while calcareous-soil species were further divided into two groups. Leaf chemical composition often shows phylogenetic conservatism during species differentiation; for example, recent studies on *Dysosma* species found that over 90% of leaf compound contents were closely related to interspecific phylogenetic relationships [**?**, **?**]. Leaf calcium speciation traits in golden Camellias may also be regulated by phylogenetic relationships. For instance, Xiao et al. (2014) used ISSR markers to analyze genetic relationships among 29 golden Camellia species, finding close phylogenetic relationships between *C. terminalis* and *C. pingguoensis*. Studies by Liu et al. (2019) using SNP markers and Lu et al. (2021) using SCoT markers both showed close phylogenetic relationships among *C. nitidissima*, *C. tunghinensis*, and *C. euphlebia*. These molecular results align with our clustering based on leaf calcium speciation, suggesting that phylogenetic relationships may influence calcium speciation traits. Notably, *C. parvipetala* clustered most closely with *C. huana*, consistent with Jiang et al. (2020)' s clustering based on petal polyphenol composition, though this relationship was not confirmed in previous phylogenetic studies [**?**, **?**]. This may relate to *C.*

parvipetala' s habitat (soil pH=5.86, soil calcium=1,473.75 $mg \cdot kg^{-1}$) being transitional between acidic and calcareous soils, or to other soil factors such as organic matter content, nutrient elements, and microorganisms [**?**, **?**].

In conclusion, differences in leaf calcium speciation among golden Camellia species from different habitats likely result from combined effects of soil environment and genetic factors. For future introduction, cultivation, and conservation of golden Camellia species, efforts should be made to match cultivation soil conditions to native habitats as closely as possible, with particular attention to soil pH and calcium content to avoid calcium toxicity or deficiency.

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Note: Figure translations are in progress. See original paper for figures.