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Leaf nutrient resorption differs among canopy and understory plant species in subtropical *Eucalyptus* and *Acacia* plantations

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Abstract

Although plants are known to conserve nutrients by resorbing them from senescing leaves, how resorption of foliar macro- and micronutrients is affected by plant growth form (e.g., trees, shrubs, and ferns) and forest age are not well understood. The current study was conducted in four subtropical monoculture plantations: *Eucalyptus* and *Acacia* plantations in 14 and 35 years old, respectively. Leaf resorption efficiencies (REs) and resorption proficiencies (RPs) of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and manganese (Mn) of the canopy trees and understory shrubs and ferns were determined. N, P, and K but not Ca and Mn were generally resorbed from senescing leaves. RE was significantly higher for P than N, indicating that P was more limiting than N in the subtropical plantations. Nutrient REs did not differ with plantation age, while nutrient RPs generally tended to be lower in the 14-year-old than in the 35-year-old plantations. REs significantly differed among canopy and understory plant species with different growth forms, that is, NRE, PRE, and KRE values were much higher in woody plants (especially the canopy tree species) than in ferns. REs were correlated with foliar nutrient concentrations but not with soil nutrient concentrations. Our findings suggest that resorption of nutrients from senescing leaves differs among canopy and understory plants, and implicate that introducing native tree species into these plantations could be implemented for accelerating the community succession and further improving the multifunctionality.

KEYWORDS
biogeochemical cycling, land management, nutrient resorption, plantation age, southern China

1 | INTRODUCTION

Nutrient resorption from senescing leaves can improve plant nutrient use efficiency and is an essential nutrient preservation strategy of plants (Brant & Chen, 2015; Cleveland et al., 2013; Killingbeck, 1996). Nutrient resorption helps reduce plant reliance on soil nutrient availability, especially in nutrient-limited environments (Drenovsky et al., 2013; Jiang et al., 2012; Yuan & Chen, 2009). Nutrient transfers during leaf senescence change litter chemistry and decomposition, and thereby profoundly influence ecosystem biogeochemical cycling

(Aerts, 1996; Vergutz et al., 2012). Patterns of nutrient resorption and stoichiometry can also reflect the nutrient limitation status in terrestrial ecosystems (Du et al., 2020; Reed et al., 2012). Consequently, research on leaf nutrient resorption patterns can improve our understandings of plant internal nutrient cycling strategies, plant–soil feedback, and ecosystem nutrient management.

The site environment, especially soil nutrient status, greatly influences leaf nutrient resorption of plants (Miatto et al., 2016; Reed et al., 2012; Vergutz et al., 2012). It has been found that plants growing in nutrient-rich soil tend to have low nutrient resorption efficiency

(RE, e.g., Hidaka & Kitayama, 2011; Drenovsky et al., 2013; Xu et al., 2020). In phosphorus (P)-limited sites, RE of plants is generally higher for P than for nitrogen (N) (Hidaka & Kitayama, 2015; Urbina et al., 2021). Soil nutrient availability always changes with forest stand age (Brant & Chen, 2015; Yan, Zhu, & Yang, 2018). A previous study showed that leaf N and P resorption efficiency (NRE and PRE) are higher in the younger stands than in the older stands, and are negatively correlated with the accumulation of available N and P in the soil with stand development (Li et al., 2013). However, different and even opposite results are not lacking either. For instance, Zhang et al. (2018) found that NRE kept constant but PRE decreased with the aging of coastal plantations. The potassium (K) resorption efficiency (KRE) declined with the aging of Chinese fir plantations, while the NRE and PRE did not vary (Zhou et al., 2016). In addition, plant traits such as ecophysiological characteristics and relative growth rate of the canopy trees and understory species sometimes alter with forest stand development, and profoundly influence leaf nutrient resorption (Wu et al., 2020; Yuan & Chen, 2010). Foliar nutrient concentrations can also influence nutrient resorption, but the relationships are complex (Kobe et al., 2005; Qiu et al., 2020; Tong et al., 2020). Therefore, a clear consensus is lacking on how forest stand age affects nutrient resorption, which might be partly due to differences in plant species, research sites, or specific nutrient elements.

Nutrient resorption from senescing leaves varies greatly among plant growth forms (Aerts, 1996; Jiang et al., 2019). In forest ecosystems, the understory plants (e.g., shrubs, forbs, and ferns) have profound influences on ecological processes and ecosystem functioning (Ciarkowska & Miechówka, 2019; Sun et al., 2017; Yang et al., 2014). The nutrient REs of plants tend to vary among growth types with different leaf longevity and nutrient pool size (Vergutz et al., 2012). At the global scale, for example, nutrient REs are found to be lower for trees than shrubs (Yan, Zhu, & Yang, 2018; Yuan & Chen, 2009). Killingbeck et al. (2002) have demonstrated that differences in architecture and life history can help explain differences in nutrient resorption patterns of ferns versus woody plants. In a global estimate, Vergutz et al. (2012) reported nutrient REs are generally higher in ferns, forbs, and graminoids than in evergreen woody angiosperms, due to the nutrient pool size of nonleaf tissues plays an important role in determining nutrient resorption. Thus, we would expect that nutrient REs tend to be lower for the woody species especially the canopy trees than for the understory nonwoody species in forests. Plant features such as N_2-fixation capability play important roles in nutrient resorption. Several empirical experiments evidenced that N resorption is less in N-fixing species than in non-N-fixing species (e.g., Nongbri & Barik, 2020; Stewart et al., 2008; Zhao et al., 2017). Jiang et al. (2019) synthesized that non-N-fixing trees had higher NRE than N-fixing trees, while PRE showed an opposite trend across the planted forests worldwide. Research on nutrient resorption in forests has often focused on woody plants and especially on the canopy or overstory tree species, while the understory nonwoody species such as ferns have not been well assessed (Brant & Chen, 2015). Moreover, although many studies have assessed foliar resorptions of N and P during leaf senescence (e.g., Cleveland et al., 2013; Vitousek

et al., 2010), knowledge on the resorption patterns of other macro- and micronutrients, such as potassium (K), calcium (Ca), and manganese (Mn), is limited (Brant & Chen, 2015; Chen et al., 2021; Zhang et al., 2019), even though these elements are important for plant growth, enzyme formation, and microbial activity in decomposing leaf litter (Aponte et al., 2012; Berg, 2014; Santiago et al., 2012). In addition, plants might have different nutrient REs for different nutrient elements in order to meet the demand in nutrient balance for plant growth and reproduction (Du et al., 2017). It is therefore essential to assess the resorption patterns of nutrient elements besides N and P so as to increase our understanding of internal nutrient cycling in plants.

Plantations have expanded rapidly worldwide in the past several decades (Keenan et al., 2015; Liu, Wu, & Wang, 2014). As of 2020, the coverage of plantations was equivalent to approximately 3% of the total forest area of the globe (FAO, 2020). To restore degraded hilly land and to meet the demand for timber products, large areas of monoculture plantations have been established since the 1980s in southern China. Tree species such as *Eucalyptus* and *Acacia* are frequently selected in afforestation practices due to their fast-growing or N-fixing features (Ren et al., 2007). Currently, most of these plantations have low productivity and low biodiversity, and therefore provide inadequate forest goods and ecosystem services (Ren et al., 2021). Silviculture managements such as introducing indigenous plant species of different functional groups into the established plantations are needed to increase plant community diversity and improve ecosystem functions (Kimball et al., 2014; Su et al., 2019). With stand development, soil nutrient status may change and induce changes in plant nutrient use and conservation strategies. An understanding of plant nutrient resorption patterns during plantation development is required, but remains largely unknown, for sustainable plantation management, for example, the strategy making in introducing time and species selection, and so on.

In this study, we assessed the REs and RPs of N, P, K, Ca, and Mn for plants of different growth forms (i.e., canopy trees and understory shrub and ferns) in four subtropical monocultures: a 35-year-old and a 14-year-old plantation of the nonlegume *Eucalyptus urophylla*; a 35-year-old planation of the legume *Acacia mangium*; and a 14-year-old plantation of the legume *Acacia crassicarpa*. The two levels of plantations ages could represent the different development stage of *Eucalyptus* and *Acacia* plantations, that is, the 14-year-old plantations are already matured, while the canopy trees in the 35-year-old plantation are degraded (Lu et al., 2011, 2017). The primary objectives were to assess the nutrient resorption capacity of plants of different growth forms in typical plantations of different ages, and to improve our understanding on fertilization management in maintaining the large areas of established plantations in southern China based on the stoichiometric patterns of leaf nutrient resorption (Reed et al., 2012). Because soils in subtropical plantations are nutrient-impoverished in general but are especially impoverished in P (Wan et al., 2014; Wang et al., 2013), we tested the following hypotheses: (1) plants would resorb more P than N in the experimental plantations; (2) nutrient REs would be lower for the woody species than for the understory ferns;

and (3) nutrient REs would decrease with plantation development (age) and would be closely related to levels of foliar and soil nutrients.

2 | MATERIALS AND METHODS

2.1 | Study site and plant species

The study site was located at the Heshan National Field Research Station of Forest Ecosystem, Chinese Academy of Science (112°54′ E, 22°41′ N), Heshan City, Guangdong, South China. This area has a typical subtropical monsoon climate with a hot and humid summer, and cold and dry winter (Chen et al., 2010). The mean annual precipitation is about 1700 mm, and most rainfall occurs between May and September (Wang et al., 2009). The mean annual temperature is 21.7°C. The soil is lateritic red soil and classified as an Acrisol.

We selected four monoculture plantation forests. Two plantations were established with the non-N-fixing tree species *E. urophylla*; these plantations were either 35 or 14 years old at the time of the study. The other two plantations were established with the N-fixing tree species *A. mangium* or with *A. crassicarpa*; at the time of the study, the *A. mangium* planation was 35 years old and the *A. crassicarpa* planation was 14 years old. The 35-year-old plantations were established in 1984 and the 14-year-old plantations were established in 2015 on relatively homogenous hilly land with the goal of restoring the highly degraded ecosystems. All these plantations were then left to develop naturally without anthropogenic disturbance. Stand characteristics of these four plantations were shown in Table S1.

For the study of nutrient resorption patterns, we selected the canopy tree species, the understory shrub *Litsea cubeba*, and the ferns *Blechnum orientale* and *Dicranopteris dichotoma*. *E. urophylla* is an exotic tree species that grows rapidly and can tolerate nutrient-impoverished soils. *A. mangium* and *A. crassicarpa* are N-fixing tree species that are native to Australia. In this study, we assume that differences between *A. mangium* and *A. crassicarpa* with regard to nutrient resorption are unimportant, and we refer to both as *Acacia*, that is, we consider the study to have two kinds of canopy trees: *Eucalyptus* and *Acacia*. *L. cubeba* is a native shrub that is adapted to acidic soil and is a common shrub that grows in the understory of established plantations in subtropical China (Lu et al., 2011). *B. orientale* is a native fern in the Family Blechnaceae; it grows widely in southern China. *D. dichotoma* is a heliophyte in the fern family Gleicheniaceae; it is widely distributed in subtropical plantations where it forms a dense layer in the understories (Yang et al., 2021).

2.2 | Leaf and soil sampling and chemical measurement

In each plantation, five replicate plots (10 m × 10 m) were randomly designated for leaf and soil sampling. In each plot, healthy green, mature leaves, and senesced leaves were collected from five to six representative individuals (similar in height, DBH, or basal diameter)

of each of the studied species. In October 2019, the healthy mature leaves of the woody species were collected from the middle and lower outer crown of each individual (Zhou et al., 2016), while the mature photosynthetically active leaves of the fern species were collected from the fully developed fronds of each plant (Holub & Tůma, 2010). From October to December 2019, the senesced, newly shed leaves of the canopy trees and shrubs were collected by gently shaking their branches. For the ferns, we sampled the senesced photosynthetic leaves from the newly senesced fronds which were cut from the rhizome of the living individuals. None of the sampled mature or senesced leaves was damaged (except that mature fronds of the ferns were cut from the mother plant; we refer to fronds as leaves hereafter). In each plot of the studied plantations, the leaves of each species were combined to yield one sample of mature leaves per species per plot and one sample of senesced leaves per species per plot. In the laboratory, the harvested mature and senesced leaves were oven-dried at 105°C for 30 min and then at 65°C for 72 hr to a constant mass. Leaf samples were then milled to a fine powder for the determination of concentrations of C, N, P, K, Ca, and Mn. Concentrations of C and N were determined using the $K_2Cr_2O_7$-oxidation method and the Kjeldahl method, respectively. P concentration was measured spectrophotometrically after digestion with 98% (v/v) H_2SO_4 (Jones, 2001). Concentrations of K, Ca, and Mn were analyzed using an atomic absorption spectrometer (AAS, HITACHI JACO6-25, Hitachi Ltd., Japan; Gielen et al., 2016).

Six soil cores (4 cm diameter, 0–20 cm depth) were randomly collected and then combined to provide one composite soil sample per plot in each of the four plantations. After collection, soil samples were transported to the laboratory and passed through a sieve (2 mm mesh size) before chemical analysis. Half of each soil sample was stored at 4°C and was used for analyzing concentrations of NH_4^+-N and NO_3^--N. Soil NH_4^+-N and NO_3^--N were extracted from 10 g of fresh soil using 50 ml of 2 M KCl. Concentrations of soil NH_4^+-N and NO_3^--N were determined with a flow-injection auto-analyzer (FIA, Lachat Instruments, USA). The other half of each soil sample was air-dried and was used for analyzing chemical properties including pH; total N, P, K, Ca, Mn, available P and K (soil samples were ground to pass through a 0.15-mm sieve). Soil pH was determined in 1:2.5 (w/v) soil suspensions with a pH meter (Mettler Toledo, LE438, Shanghai). Soil total N was measured using the Kjeldahl acid-digestion method. Soil total P was measured colorimetrically with an ultraviolet spectrophotometer (Unico, UV-4800, Shanghai). Soil total K, Ca, and Mn were determined with an inductively coupled plasma optical emission spectrometer (ICP-OES). Soil available P was determined by the Olsen method after extraction in 0.5 M NaHCO₃. Soil available K was estimated with a flame photometer after extraction with neutral ammonium acetate. The determination of soil chemical properties followed with the method described by Liu et al. (1996).

2.3 | Data statistical analysis

Differences in soil properties among the four plantations were determined using one-way ANOVAs. Leaf nutrient RE was calculated as

TABLE 1 Soil chemical properties in the *Eucalyptus* and *Acacia* plantation with different ages

Soil property	*Eucalyptus* plantations		*Acacia* plantations	
	14-year-old	35-year-old	14-year-old	35-year-old
pH	4.07 ± 0.02^a	4.14 ± 0.06^a	4.09 ± 0.03^a	3.93 ± 0.02^b
NH_4^+-N (mg kg^{-1})	3.87 ± 0.20^a	1.57 ± 0.29^b	4.65 ± 0.33^a	1.70 ± 0.49^b
NO_3^--N (mg kg^{-1})	1.90 ± 0.26^c	6.02 ± 2.41^b	1.26 ± 0.43^c	11.49 ± 1.37^a
Available P (mg kg^{-1})	0.47 ± 0.09^b	0.70 ± 0.09^a	0.48 ± 0.03^b	0.82 ± 0.03^a
Available K (mg kg^{-1})	14.61 ± 1.26^b	31.25 ± 3.69^a	16.37 ± 2.11^b	36.38 ± 1.79^a
Total N (g kg^{-1})	0.91 ± 0.12^c	1.61 ± 0.15^a	1.26 ± 0.08^b	1.80 ± 0.09^a
Total P (g kg^{-1})	0.17 ± 0.01^b	0.20 ± 0.02^b	0.34 ± 0.01^a	0.20 ± 0.01^b
Total K (g kg^{-1})	5.38 ± 0.64^c	11.10 ± 2.15^b	4.03 ± 0.28^c	17.05 ± 1.39^a
Total Ca (g kg^{-1})	0.07 ± 0.02^b	0.18 ± 0.04^a	0.08 ± 0.01^b	0.08 ± 0.01^b
Total Mn (mg kg^{-1})	10.87 ± 1.88^c	22.28 ± 1.57^b	32.27 ± 0.16^a	17.47 ± 3.77^{bc}
Total N:P ratio	5.54 ± 0.89^b	8.27 ± 0.82^a	3.70 ± 0.14^b	8.93 ± 0.68^a

Note: Values are means ± SE. Means in a row followed by different letters are significantly different ($p < 0.05$)

$[(N_m - N_s)/N_m] \times 100\%$ (Killingbeck, 1996), where N_m and N_s represent nutrient concentrations in the mature leaves and senesced leaves, respectively. Nutrient resorption proficiency (RP) was defined as the concentrations of nutrients in the senesced leaves (Killingbeck, 1996). The normality of data was verified by Levene's test before statistical analysis, and all non-normal data were transformed to follow a normal distribution. We used two-way ANOVAs to assess the effects of plant species (or genus in the case of *Acacia*) and plantation age (35 and 14 years) on nutrient REs, N:P resorption ratio, nutrient RPs, nutrient concentrations in mature and senesced leaves, and nutrient stoichiometry in mature and senesced leaves. Least significant difference tests were used for multiple comparisons and significance was set at $p < 0.05$. Principal component analysis (PCA) was used to explore the variation in the RE of nutrients among different sites and species. The relationships between leaf REs and the nutrients in mature leaves, senesced leaves and soil, and the relationships between RPs and corresponding soil nutrients were determined using Pearson correlation analysis. Statistical analysis was performed with SPSS IBM version 22.0 for Windows and R 3.2.5 (R Development Core Team).

3 | RESULTS

3.1 | Soil chemical properties

Soil chemical properties differed among the plantations (Table 1). Soil pH in the 35-year-old *Acacia* plantation was much lower than in the other plantations. For both *Eucalyptus* and *Acacia*, concentrations of soil NO_3^--N, total N, available P, available K, total K, and total N:P ratio were much higher in the 35-year-old than in the 14-year-old plantations, while the opposite was true for soil NH_4^+-N concentration. The total P concentration in soil was higher in the 14-year-old *Acacia* plantation than in the other plantations, and the total Ca concentration in soil was higher in the 35-year-old *Eucalyptus* plantation than in the other plantations. The total Mn concentration in soil was significantly higher in the older than in the younger *Eucalyptus* plantation, but was significantly higher in the younger than in the older *Acacia* plantation.

3.2 | NRE, PRE, and NRE:PRE ratio

Across all the examined species investigated in this study, the average values of NRE, PRE, and NRE:PRE ratio were 32.3 ± 2.6%, 46.8 ± 3.6%, and 0.81 ± 0.10 in the *Eucalyptus* plantations, and 28.6 ± 2.3%, 41.4 ± 3.5%, and 0.78 ± 0.07 in the *Acacia* plantations (Figure 1). Leaf NRE and PRE were not significantly affected by plantation age but were significantly different among species in the *Eucalyptus* and *Acacia* plantations (Figure 1). In general, NRE and PRE were higher for the canopy tree species (i.e., *Eucalyptus* and *Acacia*) than for the other plant species. More specifically, NRE in the *Eucalyptus* plantation was higher for *Eucalyptus* than for *L. cubeba* (by 29.6%), *B. orientale* (by 124.0%), or *D. dichotoma* (by 127.5%) (Figure 1a). In the *Acacia* plantations, NRE was higher for *Acacia* than for *B. orientale* (by 111.7%) or *D. dichotoma* (by 114.7%) (Figure 1b). In both *Eucalyptus* and *Acacia* plantations, PRE values were much higher for the canopy species and for *L. cubeba* than for *B. orientale* or *D. dichotoma* (Figure 1c,d). For the 35-year-old plantations, NRE values of the canopy species were higher for *Eucalyptus* than for *Acacia*.

Averaged across all species, PRE was significantly higher than NRE ($p < 0.0001$), with the mean PRE values being approximately 1.45-times greater than the mean NRE values. NRE values were much lower than PRE values for the canopy species and *L. cubeba* in all plantations. However, there were no significant differences between NRE and PRE values for *D. dichotoma* in the *Eucalyptus* plantations and for either fern species in the *Acacia* plantations. The NRE:PRE ratios of the plant species were generally <1 with an average value of 0.796
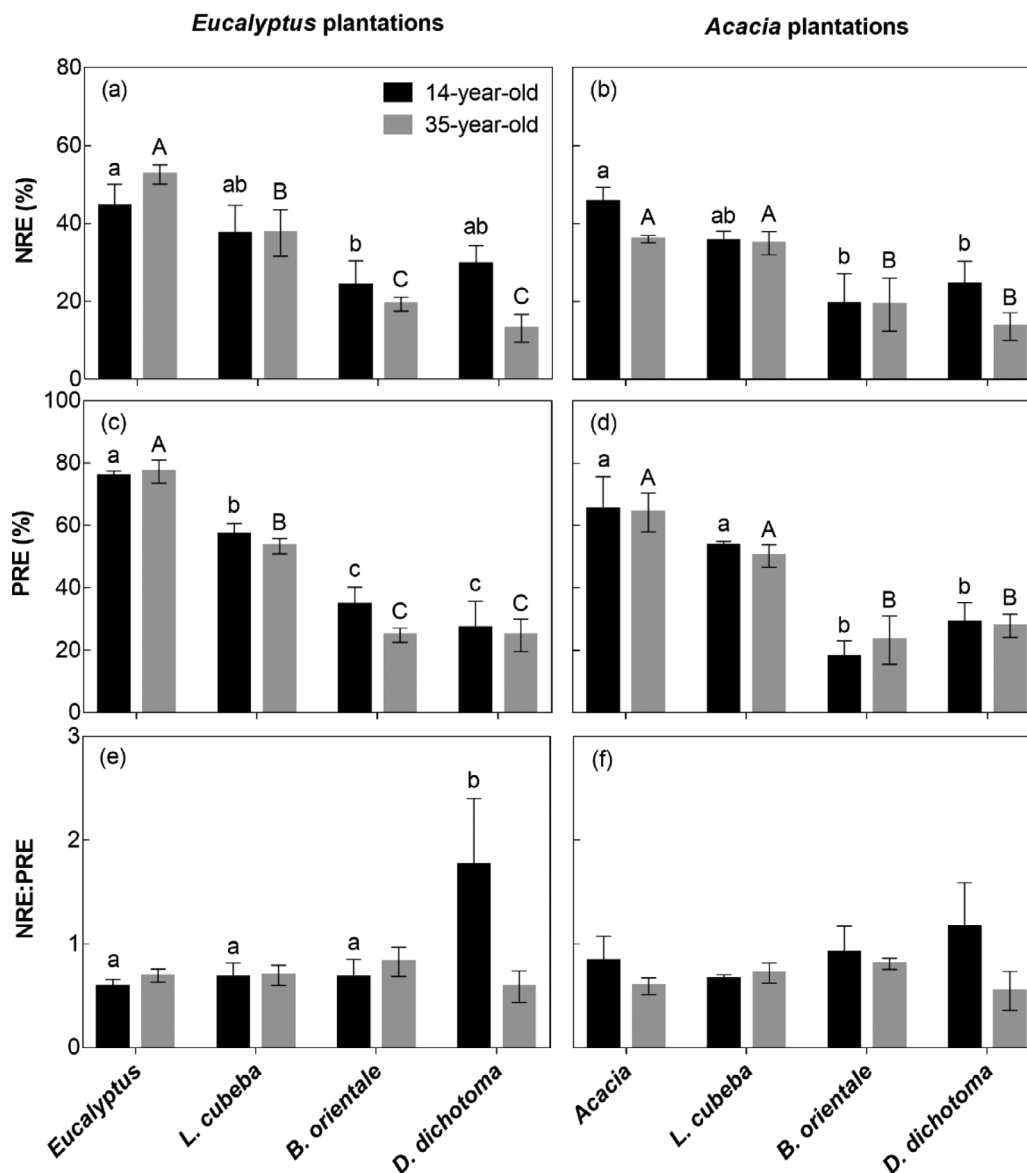
FIGURE 1 Resorption efficiency of nitrogen (NRE) (a,b) and phosphorus (PRE) (c,d), and the NRE:PRE ratio (e,f) in the 14- and 35-year-old *Eucalyptus* and *Acacia* plantations. Bars are means ± SE of five replicate plots. In each panel, the lower-case letters above the bars indicate a significant difference ($p < 0.05$) among the species in the 14-year-old plantation, while the upper-case letters above the bars indicate significant differences ($p < 0.05$) among the species in the 35-year-old plantation

across all species. Plantation age and species had no significant effects on the NRE:PRE ratio. The NRE:PRE ratio of *D. dichotoma* was much higher in the 14-year-old than in the 35-year-old *Eucalyptus* plantation (Figure 1e).

3.3 | KRE, CaRE, and MnRE

Across all species, the mean KRE was 20.6 ± 7.3% and 26.3 ± 6.7% in the *Eucalyptus* plantations and *Acacia* plantations, respectively. In all four plantations, *D. dichotoma* tended to accumulate K its senesced leaves, resulting in negative KRE values that were significantly lower than those of the other three species (Figure 2a,b). In general, KRE

was not significantly affected by plantation age, except that the KRE of *Eucalyptus* was much lower in the 14-year-old plantation than in the 35-year-old plantation ($p < 0.05$, Figure 2a). KRE values of the canopy species were significantly higher for *Eucalyptus* than for *Acacia* in the 35-year-old plantations.

Ca and Mn had generally accumulated in the senescent leaves, that is, the resorption values were negative. The mean CaRE and MnRE values were −66.8 ± 8.4% and −92.9 ± 11.4% in the *Eucalyptus* plantations, and −68.4 ± 8.4% and −47.7 ± 11.7% in the *Acacia* plantations. CaRE and MnRE were significantly affected by species. In the 35-year-old *Eucalyptus* and *Acacia* plantations, CaRE were significantly higher for the canopy tree species and *L. cubeba* than for *D. dichotoma* ($p < 0.05$, Figure 2c,d). In the 13-year-old *Acacia*
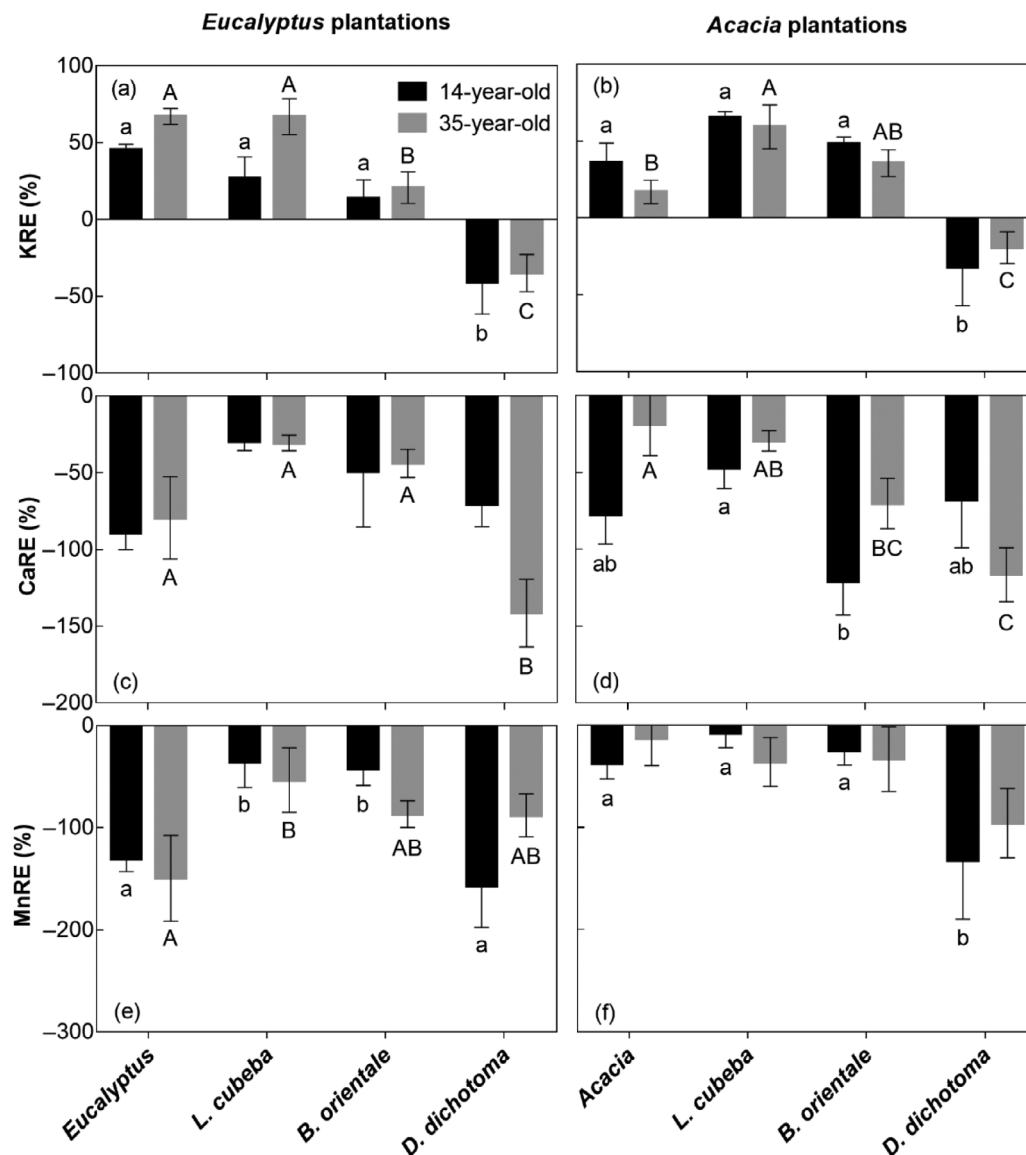
FIGURE 2 Resorption efficiencies of potassium (KRE) (a,b), calcium (CaRE) (c,d), and manganese (MnRE) (e,f) in the 14- and 35-year-old *Eucalyptus* and *Acacia* plantations. Bars are means ± SE of five replicate plots. In each panel, lower-case letters above or below the bars indicate significant differences ($p < 0.05$) among the studied species in the 14-year-old plantation, while upper-case letters above or below the bars indicate significant differences ($p < 0.05$) among the studied species in the 35-year-old plantation

plantation, the CaRE value was much higher for *L. cubeba* than for *B. orientale* ($p < 0.05$, Figure 2d). The CaRE value of *D. dichotoma* was higher in the 14-year-old than in the 35-year-old *Eucalyptus* plantation ($p < 0.05$, Figure 2c). MnRE values were much lower for *Eucalyptus* than for *L. cubeba* in the *Eucalyptus* plantations ($p < 0.05$, Figure 2e). In the 14-year-old *Acacia* plantation, the MnRE values were much lower for *D. dichotoma* than for the other species ($p < 0.05$, Figure 2f). In both the 14- and 35-year-old plantations, MnRE values of the canopy species were much lower for *Eucalyptus* than for *Acacia*.

PCA of the RE data indicated substantial differences in the nutrient reutilization among the investigated species, but the effect of forest age on the RE was not significant (Figure 3a). The first principal component (PC1) explained 35.72% and the second (PC2) explained 22.96% of the total variance in the RE. For the PC1 averaged across all species and plantation ages, PRE, NRE, KRE, and CaRE had

negative loading scores (Figure 3b). For the PC2 averaged across all species and plantation ages, the ratio of NRE:PRE had high positive loading scores, while MnRE had low negative loading scores (Figure 3b). The species with the highest NRE, PRE, and KRE values were *Eucalyptus* and *Acacia* on the left-hand side of Figure 3a, while *B. orientale* and *D. dichotoma* had the lowest values of NRE, PRE, and KRE on the right-hand side of Figure 3a.

3.4 | Relationships between REs and nutrient parameters in leaves and soils

Nutrient concentrations and related stoichiometry of the mature and senesced leaves are shown in Table S2. In the *Acacia* plantations, all of the foliar nutrient parameters were significantly affected by
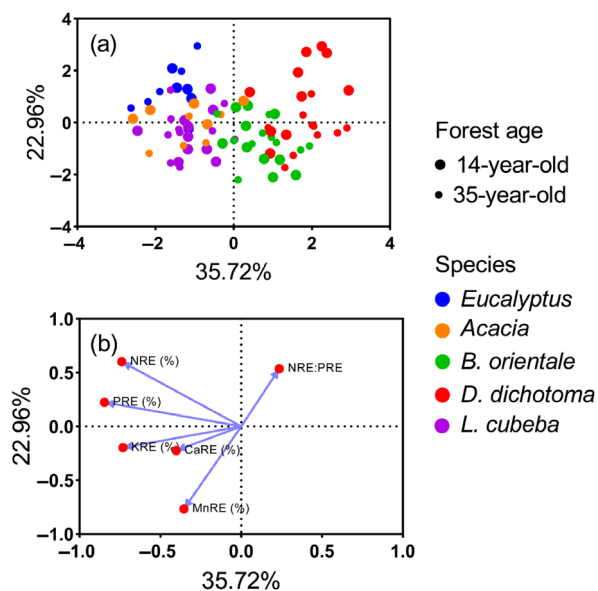
FIGURE 3 Principal component analysis (PCA) of resorption efficiency of nutrients among different species in the 14- and 35-year-old plantations: (a) scores; (b) loadings [Colour figure can be viewed at wileyonlinelibrary.com]

species. Plantation age had a significant effect on the senesced leaf K and Mn, on the mature leaf P and Mn, and N:P ratio, while species significantly affected all of the nutrient parameters except senesced leaf C and mature leaf N:P in the *Eucalyptus* plantation.

For all species pooled, both NRE and PRE were positively correlated with mature leaf N and P, and senesced leaf C:N and N:P, but were negatively correlated with the mature leaf C:N ratio and senesced leaf P (Figure 4). There were also significant negative relationships between NRE and senesced leaf N, and between PRE and mature leaf N:P ratio. KRE and MnRE were negatively correlated with senesced K and Mn, respectively (Figure 4). CaRE was positively correlated with mature leaf Ca (Figure 4). Among the studied plantations and averaged across all species, neither NRE nor PRE was correlated with soil parameters (i.e., NH_4^+-N, NO_3^--N, available P, total N, total P, and total N:P ratio) (Figure 5). Plant MnRE was positively correlated with soil total Mn concentration in the soil of the 35-year-old *Eucalyptus* and *Acacia* plantations (Figure 5k).

3.5 | Nutrient RPs and their relationships with soil nutrients

Overall, values of N and P resorption proficiency (NRP and PRP) were higher for *L. cubeba* and *B. orientale* than for the canopy species and *D. dichotoma* (Figure 6). K resorption proficiency (KRP) values were lower for *Eucalyptus* and *L. cubeba* than for the two ferns in the *Eucalyptus* plantations (Figure 6e), and KRP values were lower for *L. cubeba* than for the other species in the *Acacia* plantations (Figure 6f). In all four plantations, Ca resorption proficiency (CaRP) values of *D. dichotoma* were significantly lower than those of the

other species (Figure 6g,h). Mn resorption proficiency (MnRP) values of *Eucalyptus* and *L. cubeba* were much higher in the 14- and 35-year-old *Eucalyptus* plantation, respectively (Figure 6i). CaRP and MnRP values of *Eucalyptus*, MnRP values of *L. cubeba* and *B. orientale*, and *D. dichotoma* NRP were significantly lower in the 14-year-old than in the 35-year-old *Eucalyptus* plantation ($p < 0.05$). For the *Acacia* plantations, NRP, KRP, and MnRP values of *Acacia*, NRP, PRP, and MnRP values of *L. cubeba*, *B. orientale* KRP, and *D. dichotoma* MnRP were significantly lower in the young than in the old plantation ($p < 0.05$).

When all the plantations were pooled, NRP was negatively correlated with soil NH_4^+-N, but was positively correlated with soil total N and NO_3^--N (Figure 7a–c). Similarly, positive relationships between KRP and soil total K and available K were observed (Figure 7f,g). CaRP was negatively correlated with soil total Ca in both the 14-year-old and 35-year-old *Eucalyptus* plantations (Figure 7h).

4 | DISCUSSION

4.1 | Resorption patterns of foliar nutrients

On a global scale, mean foliar REs of N and P were reported to be 62.1% and 64.9%, respectively (Vergutz et al., 2012). Relative to those previously published values, the average REs of these two nonmetallic elements from senesced leaves were much lower, although mass loss correction factor was not involved for calculating REs of N and P in the current study. For the established canopy tree species in the current study, that is, *Eucalyptus* and *Acacia*, the average NRE values (44.7%) were lower while the average PRE values (70.6%) were higher than the values (59.0% and 60.2%, respectively) recently reported for planted forests worldwide (Jiang et al., 2019). The high PRE values support the inference that the established *Eucalyptus* and *Acacia* trees are highly dependent on internal P cycling in the subtropics (Drenovsky et al., 2013). Information on the REs of N and P and their stoichiometric pattern increases our understanding of plant resource-use strategies and nutrient limitation assessment (Du et al., 2020; Reed et al., 2012; Yuan & Chen, 2009). For plantation woody species in the present study, PRE values were significantly higher than NRE values, which is consistent with our first hypothesis that woody plants resorbed more P than N in the experimental plantations. Together with the NRE:PRE ratios (average = 0.796), our results indicate plants resorb more P than N from the senescing leaves and that plant growth is more limited by P than N in the subtropical plantations. The observed values of N:P ratios in mature and senesced leaves (>16, Table S2) further confirmed that P rather than N was limiting in these plantations, as indicated by Koerselman & Meuleman (1996).

KRE values in the current study averaged 23.5%, which was lower than the average KRE values reported by Vergutz et al. (2012) from a global dataset. For *D. dichotoma* in our study, more K was retained in senescent leaves than was resorbed from senescent to mature leaves. This was unexpected because, as a component of nucleic acids and

FIGURE 4 Pearson correlation coefficients between nutrient resorption efficiencies (i.e., NRE, PRE, KRE, CaRE, and MnRE) and nutrient concentrations and stoichiometric ratios in the mature and senesced leaves. Blue and red circles indicate positive and negative correlations, respectively. The darker the colour, the stronger the correlation. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$ [Colour figure can be viewed at wileyonlinelibrary.com]
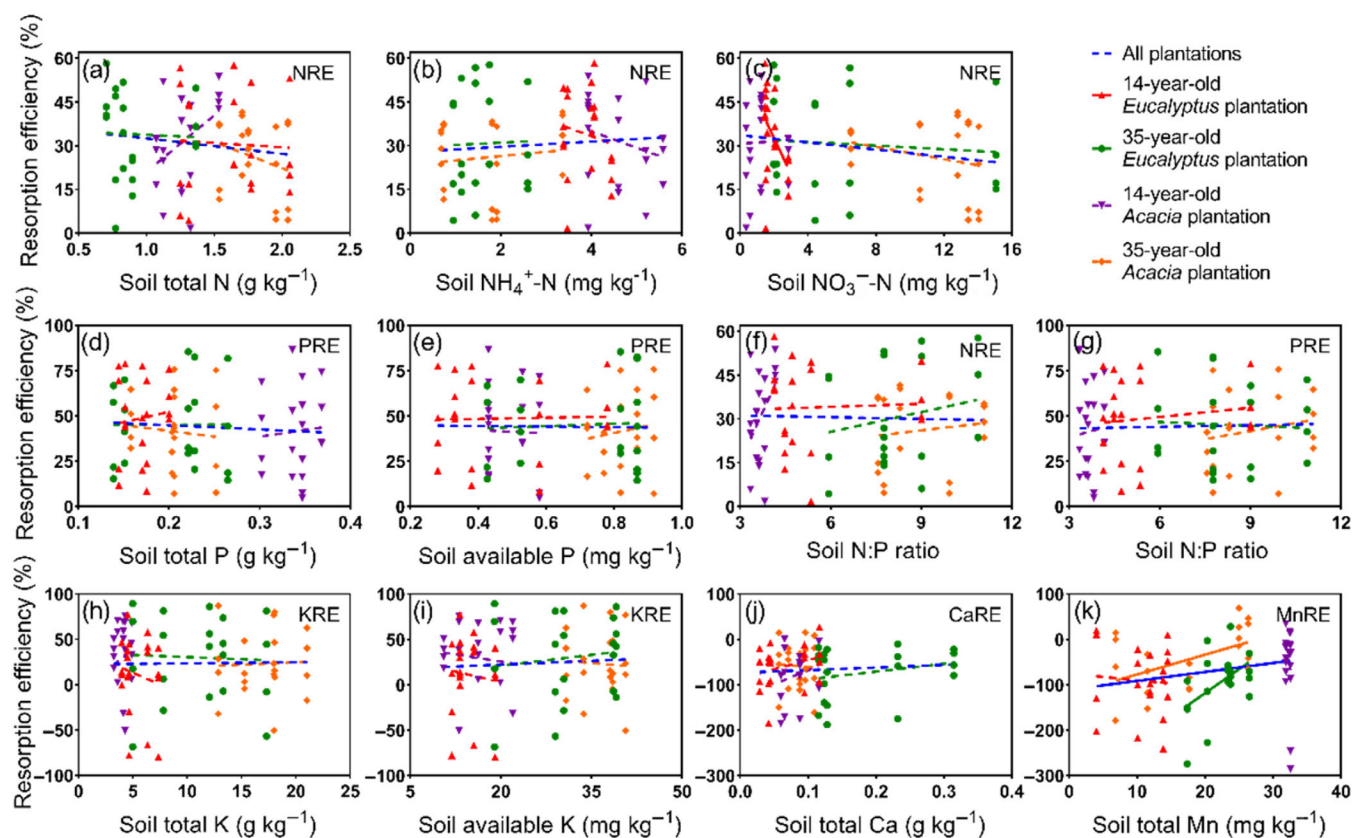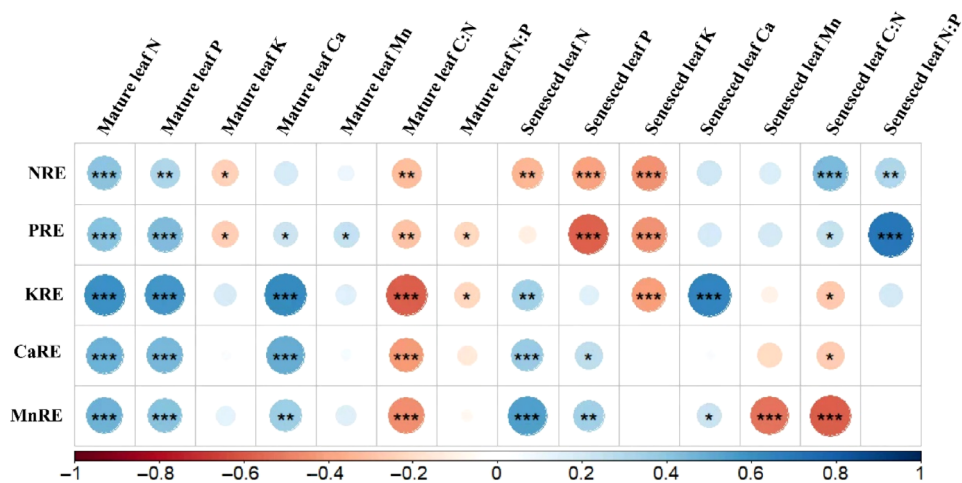
FIGURE 5 Relationship between resorption efficiencies of N (a,b,c,f), P (d,e,g), K (h,i), Ca (j), and Mn (k) and the corresponding nutrient concentrations in the soil [Colour figure can be viewed at wileyonlinelibrary.com]

proteins, K is generally resorbed preferentially during leaf senescence (e.g., Du et al., 2017; Zhang et al., 2019), and negative values for KRE have rarely been reported. Ca and Mn cations were not resorbed from the senesced foliage for any of the monitored plants in the present study, indicating that these two nutrients tend to be retained in the senescing leaves. Ca and Mn accumulation in senesced leaves was also recorded for mangrove species (Medina et al., 2015), deciduous oak species (Du et al., 2017), and karst region plants (Liu, Wu, &

Wang, 2014). The tendency that Ca is generally not be resorbed during leaf senescence has also been demonstrated in several reviews (van Heerwaarden et al., 2003; Vergutz et al., 2012). For example, Vergutz et al. (2012) reported that graminoids, evergreen and deciduous woody angiosperms in the polar region conserved Ca in the senesced leaves. The enrichment of Ca and Mn in senescent leaves might be attributed to the immobility of these structural elements within the plant (Fife et al., 2008; van Heerwaarden et al., 2003).
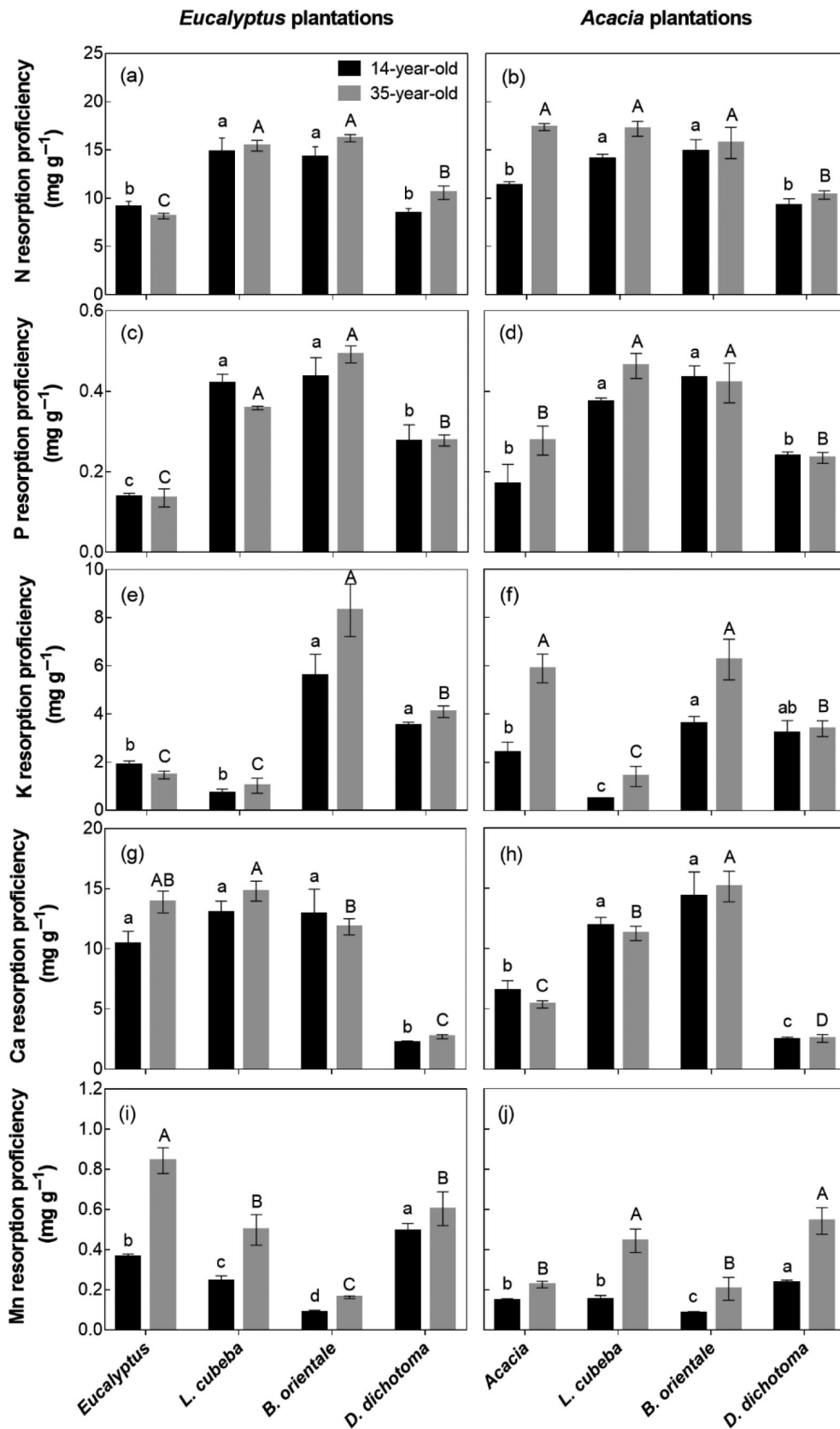
FIGURE 6 Resorption proficiencies of N (a,b), P (c,d), K (e,f), Ca (g,h), and Mn (i,j) in the 14- and 35-year-old *Eucalyptus* and *Acacia* plantations. Bars are means ± SE of five replicate plots. In each panel, lower-case letters above or below the bars indicate significant differences ($p < 0.05$) among the studied species in the 14-year-old plantation, while upper-case letters above or below the bars indicate significant differences ($p < 0.05$) among the studied species in the 35-year-old plantation
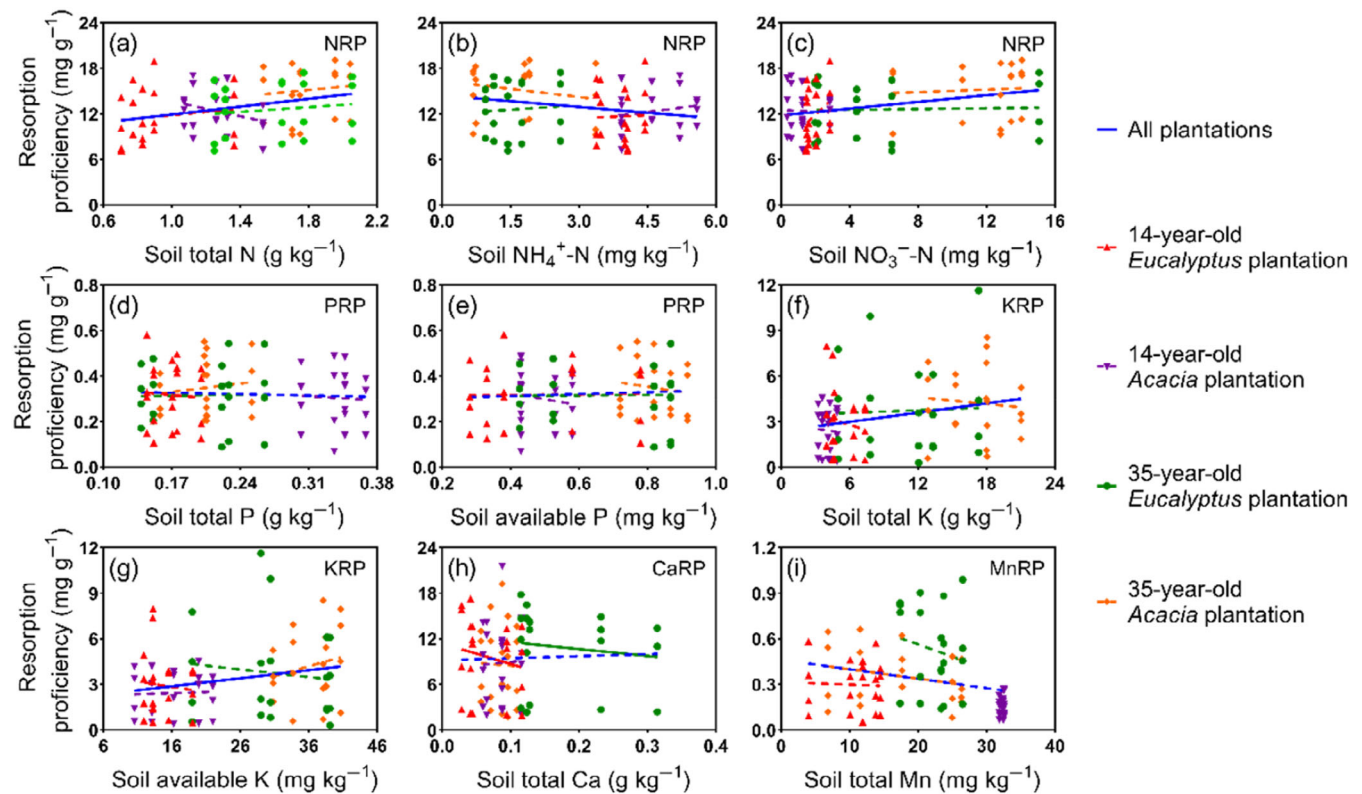
FIGURE 7 Relationships between resorption proficiencies of N (a,b,c), P (d,e), K (f,g), Ca (h), and Mn (i) and corresponding nutrients in the soil [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Effects of plantation developmental stage on nutrient resorptions

Young forests tend to require more nutrients than old forests. With forest development, plant growth rates as well as the nutrient demands are generally thought to decline, leading to declines in nutrient resorption (Brant & Chen, 2015). The latter inference, however, was not supported by our study. Contrary to part of our third hypothesis, we found that the REs of the examined nutrients remained constant with stand development in the *Eucalyptus* plantation and *Acacia* plantation, indicating that the established tree species and the typical understory plants did not alter their nutrient conservation strategies as plantations aged and soil chemical properties changed. Similar results for certain nutrient elements have been recently reported (Zhang et al., 2018; Zhou et al., 2016). Several previous studies revealed that forest stand age has important influences on nutrient resorption. In a chronosequence (7, 25, 85, and 139 years) of boreal forest stands, for instance, leaf NRE of trembling aspen was higher in younger stands than in older stands, suggesting greater conservation of N in younger, recently disturbed stands (Yuan & Chen, 2010). In contrast, N, P, and K REs increased with stand age from 8, 14 to 24 years (Ma et al., 2002). Yan, Lü, et al. (2018) also found that both NRE and PRE increased with the age of larch (*Larix kaempferi*) plantations. As indicated by Lu

et al. (2017), the resource acquisition rate of three subtropical forest plantations, including the *Acacia* plantation, turned to be constant after a quick increase in the first 5 years after planting. It is therefore reasonable that plantation age did not significantly affect leaf nutrient resorption in the current study.

In general, variations in nutrient resorption are potentially driven by changes in environmental conditions during forest stand development (Brant & Chen, 2015; Sun et al., 2016; Yuan & Chen, 2010). Our results showed that the concentrations of total N, available P, and NO_3^--N in soil increased while that of NH_4^+-N decreased with stand development in the *Eucalyptus* and *Acacia* plantations. However, neither NRE nor PRE was significantly correlated with the measured soil properties, indicating that, contrary to part of our third hypothesis, soil nutrient status did not substantially affect foliar nutrient resorption in the experimental subtropical plantations. Similarly, no significant correlations were found between soil nutrient levels and NRE in black locust forests (Deng et al., 2019). Zhou et al. (2016) also showed that nutrient REs were seldom affected by soil nutrient concentrations and stoichiometry. Dissimilar to RE of nutrients, RPs of N, K, and Ca were found to be related to corresponding nutrients in the soil in our study. The results indicated that nutrient RP may be more sensitive to altered soil nutrient availability than nutrient RE, which was also corroborated in previous studies (Kozovits et al., 2007; Lü et al., 2012).

4.3 | Variations in nutrient resorptions among plant growth forms

Leaf nutrient resorption depends on the transfer of nutrients from senescing leaves to stems, roots, or other plant tissues. The longevity and size of nutrient pools in senescing leaves might help explain the differences in resorption among different plant growth forms, and more specifically, why woody plants tend to have lower nutrient REs than nonwoody plants (Aerts, 1996; Brant & Chen, 2015; Vergutz et al., 2012). Disagreed with our second hypothesis, we found that woody plants and especially the canopy trees generally had much higher N and P REs than the two fern species in the subtropical plantations. Differences in nutrient resorption among species might also result from the relative energetic costs of resorbing nutrients from senescing leaves into live tissue versus taking-up nutrients from the soil (Wright & Westoby, 2003). Nutrient resorption by ferns has seldom been studied. Killingbeck et al. (2002) found that a winter-deciduous fern (*Dennstaedtia punctilobula*) was superior in resorbing nutrients, with both the NRE and PRE values of approximately 50%. In another study that considering dry mass loss during frond senescence, the deciduous fern *Athyrium distentifolium* transferred 44% of the P and 24% of the N from senescing tissue to living tissue (Holub & Tůma, 2010). The two fern species in the current study, in contrast, had relatively low values of NRE and especially of PRE (Figure 1). Our finding might be attributed to the studied ferns being evergreen, which generally have lower nutrient resorption values than deciduous plants (Aerts, 1996). At a global scale, NRE was found to be generally lower in trees than in shrubs, while PRE was similar between the two growth forms (Yuan & Chen, 2009). In the plantations of the current study, however, both the NRE and PRE values of the shrub *L. cubeba* were similar to those of the canopy *Acacia* trees but were much lower than those of the *Eucalyptus* trees. Trees generally absorb water and nutrients through small and fine roots at a deeper soil layer compared with shrubs and herbs (Kulmatiski et al., 2010). Furthermore, root distribution depth is generally deeper for pioneer trees than for middle- and late-successional trees in forests (Peng & Hao, 2005). Our previous study found that the carbon sequestration and nutrient accumulation in plants of these subtropical plantations fluctuated along a slowly decreasing path, after the dominant trees got matured (Lu et al., 2017). Simultaneously, the structural self-organization efficiencies of these subtropical plantations also slowed down after 20 years of development (Lu et al., 2015). Combined with the above results, our study implicated that introducing middle- and late-successional native tree species into these plantations could be implemented at this period for accelerating the community succession and further improving the multifunctionality of the plantations, without rising nutrient competition.

Foliar nutrient status has been used as an indicator of nutrient availability in attempts to explain nutrient resorption patterns (Liu, Liu, et al., 2014; Mediavilla et al., 2014). Although REs of N and P at a global scale were found to decrease with increases in the green leaf N and P status in terrestrial plants (Kobe et al., 2005; Vergutz et al., 2012), that was not the case in the current study. We found that NRE and PRE were positively correlated with N and P concentrations in the mature leaves, indicating that species with high N and P concentrations in green leaves tend to resorb more of the corresponding nutrients during leaf senescence than species with low N and P concentrations. Similar findings were reported in a national-scale study of forests in China (Xu et al., 2017). Previous studies have shown that leaf nutrient RE is largely controlled by the allocation patterns of nutrient fractions such as inorganic and organic P fractions rather than the total nutrient concentrations (Hidaka & Kitayama, 2011; Mao et al., 2015; Mayor et al., 2014). Further studies addressing nutrient fractions in leaves are needed to clarify the determinants of nutrient REs. In our study, additionally, both NRE and PRE were positively correlated with C:N and N:P ratios in senesced leaves; at the same time, NRE and PRE were negatively correlated with C:N ratio in mature leaves and P concentration in senesced leaves, indicating that NRE and PRE had similar response patterns to foliar nutrients. These findings also confirmed the idea that foliar resorption of one element could be driven by the availability of another element (See et al., 2015). In our study, all species tended to retain Ca and Mn in senescing leaves. CaRE was positively correlated with mature leaf Ca, suggesting that plants with lower concentrations of green leaf Ca tended to enhance its accumulation in senescent leaves. MnRE, in contrast, was primarily determined by the Mn concentration of senesced rather than mature leaves, such that MnRE was negatively correlated with senesced leaf Mn concentration.

In low-nutrient environments, selection favors plants with high nutrient resorption capabilities, which lead to low nutrient losses (de Campos et al., 2013; Ji et al., 2018; Richardson et al., 2008). Not all species in the present study had high PRE values even though they were growing and well established in P-deficient soils. The relatively low PRE values of the fern species suggest that the degree of P limitation might vary among species in the subtropical plantations. In agreement with previous studies (Deng et al., 2019; Killingbeck, 1996), our results indicated that nutrient resorption was closely related to the inherent features of species. Our results also indicated that foliar nutrient status rather than soil nutrient status might be a good indicator of nutrient RE in subtropical plantations.

In the current study, we determined nutrient resorption by plants based on sampling during a specific period in the dry season. Not all plant leaves, however, abscise simultaneously. In a recent study, See et al. (2019) demonstrated the N and P contents in newly senesced leaves decline throughout the autumn season, indicating that nutrient RE could be biasedly estimated from sampling on a single time point. For the evergreen species, leaf nutrient REs have also been found to vary with season (Zhou et al., 2016). There could also be large interannual variability in nutrient resorption by plants (Drenovsky et al., 2013). It follows that long-term experiments involving multiple sampling times of mature and senesced leaves should be conducted in order to quantity nutrient RE.

5 | CONCLUSIONS

Our results from subtropical plantations revealed that foliar REs varied greatly among nutrients, that is, N, P, and K were generally resorbed

from senescing leaves while Ca and Mn were retained by senescing leaves. Plants resorbed proportionally more P than N from the senescing leaves, such that PRE values were significantly higher than NRE values. Nutrient REs varied significantly among canopy and understory plant species with different growth forms, that is, woody plants and especially the canopy tree species generally had much higher NRE, PRE, and KRE values than the understory fern species, inferring that nutrient resorption capacity might be an inherent property of plant species. Because only one shrub species was selected in this study, inferences about differences among plant growth forms should be cautious. Nutrient REs remained constant with plantation age even though soil nutrient changed with plantation age. Soil nutrient levels evidently exerted minor control over N and P REs. Foliar nutrient levels were strongly correlated with REs and might be useful indicators of nutrient resorption in the subtropical plantations. Our findings demonstrate that subtropical *Eucalyptus* and *Acacia* plantations are more P-limited than N-limited, and that woody plants are highly dependent on internal P cycling. Results from this study implicate that introducing native tree species into these plantations could be implemented for accelerating the community succession and further improving the multifunctionality of the plantations.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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