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ORIGINAL PAPER

Changes in foliar nitrogen resorption of *Phyllostachys edulis* with culm development

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Abstract Leaf nitrogen resorption is very important to *Phyllostachys edulis* development because the withdrawn nitrogen can help newly emerging and growing culms. However, few studies have focused on the ontogenetic changes in leaf nitrogen resorption of *P. edulis*. Here, we examined the variability in mature leaf nitrogen concentrations (N_m), nitrogen resorption efficiency (NRE) and proficiency (NRP or N_s) and leaf-level nitrogen use efficiency (NUE) of the current-, 3rd- and 5th-year culms in *P. edulis* stands under extensive management. Analyses of variance and correlation indicated that patterns of N_m, NRP, NRE and NUE were markedly affected by culm age and leaf nitrogen status. N_m, N_s and NRE were significant higher in younger (current-year) culms with 1-year lifespan leaves, while NUE was markedly higher in older (3rd- or 5th-year) culms with 2-year lifespan leaves. Significant linear correlations between N_m and NRP, NRE and NUE, N_m and NUE, N_s and NRE were found for each culm age, and N_m was significantly positively correlated to NRE for all culms pooled. Higher proficiency in older culms led to higher NUE and lower NRE, these relationships can be modulated by N_m, which in turn, is restrained by leaf N availability and acquisition. Our results revealed that at the intraspecific level, *P. edulis* can adjust its leaf NRE, NRP, and leaf-level NUE in concert with culm development. Understanding nitrogen resorption characteristics and NUE of *P. edulis* can help decision-makers design appropriate deforestation strategies and achieve precise N fertilization for sustainable bamboo forest management.

Keywords *Phyllostachys edulis* · Nitrogen resorption efficiency · Nitrogen resorption proficiency · Nitrogen-use efficiency · Extensive management · Culm development · Precision fertilization

Abbreviations

NRE	Leaf nitrogen resorption efficiency
NRP	Leaf nitrogen resorption proficiency
NUE	Leaf-level nitrogen-use efficiency
N_m	Nitrogen concentrations in mature leaves

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N_s	Nitrogen concentrations in senescent leaves
L1	One-year lifespan leaves
L2	Two-year lifespan leaves

Introduction

Variation in leaf functional traits among different groups may play an adaptive role in the successful survival of plants under diverse environments because leaf functional traits can lead to pronounced effects on leaf function (Wang et al. 2015). Nitrogen resorption from senescing leaves is an important mechanism that plants use to conserve nitrogen in nitrogen-poor sites (Aerts 1996; Killingbeck 1996; Stackpoole et al. 2008). Nitrogen resorption can be quantified by the fraction of nitrogen resorbed from senescing leaves (nitrogen resorption efficiency or NRE) or by the nitrogen concentration in senescing leaves (nitrogen resorption proficiency or NRP) (Killingbeck 1996). Both resorption efficiency and proficiency determine leaf-level nitrogen-use efficiency (NUE) (Eckstein et al. 1999), and they change with a large number of variables, such as plant and soil nutrient status, species, latitude, temperature, precipitation, and so on (Kobe et al. 2005; Wang et al. 2014; Yuan and Chen 2009). In many terrestrial ecosystems, nitrogen availability is one of the primary restrictions for plant growth and net primary productivity (LeBauer and Treseder 2008; Magnani et al. 2007; Yuan et al. 2006). As fast-growing and high-yield plantation, the amount of nitrogen needed for the yearly growth of new culms and rhizomes in *P. edulis* stand in the spring of on-years (i.e., mass flowering years) was about 123.1 kg ha^{-1} and only 29.3 kg ha^{-1} in the spring of off-years, respectively (Li et al. 1998). Therefore, nitrogen resorption might be very important for *P. edulis* stand development.

Some studies on nitrogen resorption and NUE have revealed significant interspecific variability (Escudero and Mediavilla 2003; Killingbeck 1996; Li et al. 2010; Yuan et al. 2005), which can be influenced by numerous factors, including plant and soil nutrient availability (Wang et al. 2014; Yuan and Chen 2009), nitrogen additions (Li et al. 2010), soil water status (Pugnaire and Chapin 1992). Moreover, even for the same plant, significant differences between ages can be observed (Mediavilla et al. 2014; Pastor-Pastor et al. 2015; Wang et al. 2014), which might be explain because differences in age among individuals might provoke a marked variability in plant structure and functioning (McConnaughay and Coleman 1999; Yen and Lee 2011). For example, green leaves of adults tend to have higher nitrogen concentrations, which allows for a higher percentage that can be resorbed during senescence, and they have higher NRE than leaves at the initial stages of the life cycle (Mediavilla et al. 2014). Wang et al. (2014) found that leaf NRE in *Medicago sativa* (lucerne, alfalfa) rose and then dropped as the stand aged. Leaf NRE and NRP of *Populus tremuloides*, however, decreased as stands aged in a chronosequence (Yuan and Chen 2010). Leaves of young species tend to contain more nitrogen, which allows higher photosynthetic efficiency (Niinemets 2004), and are closer to an acquisitive strategy in nutrient utilization than those of mature individuals (Mediavilla et al. 2013). Pastor-Pastor et al. (2015) used a relative age index to show that nitrogen in green and senescing leaves of *Physaria mendocina* (Brassicaceae) decreases with plant age, while NRE does not change and NUE increases. Therefore, leaf nitrogen resorption characteristics also significantly vary with plant age.

China, where bamboo originated, has the world's richest bamboo resource with about 500 species (Di and Wang 1996), accounting for one-third of the total global bamboo species. Among these species, *P. edulis* grows and propagates vigorously, is high-yielding and regenerates easily, and stands rapidly form and dominate secondary forests. The species now covers an area of more than 3.87 million ha, about 71.9% of the country's total area of bamboo forests according to China's 7th national forest continuous inventory.

Phyllostachys edulis is a predominantly asexual, monopodial giant bamboo (Li et al. 2003). After emergence, 500–3000 new culms elongate rapidly and reach the top of the canopy by early summer (May) in *P. edulis* stands (Ueda 1960). In on-years, the number and size of new culms emerging and surviving in the bamboo stands markedly exceed those in off-years. On-year and off-year often alternates, forming a regular biennial cycle and this pattern appears to be correlated with the peculiar leaf age structure of the stand. The leaf lifespan of *P. edulis* is 2 years (L2), except in current-year culms where it is only 1 year (L1), and all leaves on a culm are the same age. Two-year-old leaves and leaves in current-year culms are dropped in January to April when new culms emerge and elongate (Li et al. 1998) (Table 1).

Foliar nitrogen resorption in *P. edulis* under extensive management in China has been studied from various perspectives. For example, Lin et al. (2004, 2005) studied the nutrient retranslocation efficiency during leaf senescence in 2-year-old culms of *P. edulis*, the monthly nitrogen retranslocation efficiency on the basis of concentration was about 21.71%. Li et al. (1998) also reported the characteristic of NRE from 2-year-old senescing leaves in this bamboo. They found that from the 2-year-old senescing leaves, about 43% of N was withdrawn from April 1 to April 24 1995. Previous studies showed that leaf NRE of other plants is significantly influenced by plant age (Wang

Table 1 Culm ages and leaf phenologies of *P. edulis* in April (Li et al. 1998)

Culm age	Leaf phenology	Leaf lifespan
Newly emerging culms	No leaves	–
Current-year culms	Shedding leaves (1-year old)	1 year (L1)
2nd-, 4th-, 6th- and 8th-year culms	Retaining new (1st-year) leaves	2 year (L2)
3rd-, 5th-, 7th- and 9th-year culms	Shedding old (2nd-year) leaves	2 year (L2)

et al. 2014; Yuan and Chen 2010), leaf age or leaf lifespan (Escudero and Mediavilla 2003; Pastor-Pastor et al. 2015), and nutrient availability (Yuan et al. 2005). However, differences in NRE, NRP and NUE among different age culms and different types of leaf lifespan, and their relationships with leaf nitrogen availability have yet to be quantified. Are there significant differences in nitrogen resorption characteristics among culm ages? Do nitrogen resorption characteristics differ significantly between the leaves of the two leaf lifespans for this bamboo species? How does leaf NRE NRP and NUE of *P. edulis* vary with culm age? These studies are rather descriptive, and little is known for *P. edulis*.

To resolve these issues, we determined leaf nitrogen concentrations in mature and senescent leaves from different-aged culms in an extensively managed forest of *P. edulis*. The specific objectives of this study were to (1) quantify and compare the foliar N resorption characteristics and patterns in different age culms and leaf lifespans of *P. edulis* under extensive management in southern China; (2) determine any correlations among nitrogen-use characteristics (e.g., N_m, NRE, NRP and NUE), and (3) elucidate the mechanisms that regulate nitrogen use in *P. edulis*.

Materials and methods

Study site

Research was conducted at Shuangzhen Forest Farm, Wenfang Town, Guixi County, Jiangxi Province, China (27°54′52″N, 117°21′19″E), known as China's "bamboo capital". The climate is subtropical monsoon. The slope at the study sites ranged from 20° to 33°, and the altitude ranged from 800 to 1000 m above mean sea level. Mean annual precipitation is 2135.3 mm. There is an annual average of 228 frost-free days. The average minimum and maximum air temperatures occur in January (− 12.9 °C) and July (36 °C). The average air temperatures of the coldest and hottest month occurs in January (0 °C) and July (29.3 °C). The soil in the study area, derived from Quaternary red clay, is classified as Ultisol according to the American soil taxonomy, USDA classication (Soil Survey Staff 1999), with pH 4.7–5.2, N 0.036–0.359%, P 0.021–0.064%, and organic matter content of 1.92–7.75% in the upper of 30 cm. The *P. edulis* forest had a crown density of 0.75, bamboo density of 2528 culm hm^{-2}, mean height of 15.3 m and mean diameter at breast height of 10.9 cm. The understory consisted of *Alangium chinense* and *Ilex latifolia* with *Lophatherum gracile* and *Woodwardia japonica* in the herb layer.

Sampling and chemical analysis

To collect leaf samples, we established a study plot (30 m × 200 m) in a *P. edulis* pure forest under extensive management at the Shuangzhen Forest Farm in July 2013. Forty-five sample culms each of current-, 3rd- and 5th-year culms ($\geq$ 6-year culms are the main age for cutting in bamboo stands in China) were chosen and labeled in the strip after the tally, i.e., 15 replications for each age of culms, 15 replications for 1-year lifespan leaves, and 30 replications for 2-year lifespan leaves. Then 50 pieces of mature leaves and senescent leaves from the same culm on the upper canopy of each labeled culm were collected on August 14, 2013 and February 14, 2014, respectively, using pruning shears attached to a pulley and an extensible pole. Fully expanded leaves are considered to be mature, and senescent leaves are those in which an abscission layer has formed at the base of the petiole, preventing further nutrient withdrawal (Norby et al. 2000). Senescent leaves are easily identified by having different pigmentation (often yellow or red) than mature green leaves, and can be removed by a gentle flick of the branch or leaf (Wright and Westoby 2003). Senescent leaves were collected directly from culms rather than from leaf litter here. Leaves collected from the same culm were then pooled into one bulk sample for mature leaves and one sample for senescent leaves of each individual. Leaves with distinct evidence of substantial mechanical damage or biotic alteration (e.g., leaves with insects, bird droppings, disease) were not sampled, and bias in terms of leaf length, width, shape and colour was minimized. The leaf samples were immediately taken to the laboratory, oven-dried at 80 °C for at least 48 h, then finely ground in a RETSCH mill to pass through a 2-mm mesh screen for later analysis. Subsamples of mature and senescent leaves were digested using a sulfuric acid-hydrogen peroxide flux, then nitrogen concentration was determined using the micro-Kjeldahl method (Yoshida et al. 1971). Each test was done three times, and the error among three replications was less than 2%. Therefore, the leaf nitrogen concentration of each leaf sample was the mean value of the three replications.

Calculations

Nitrogen concentrations in senescent leaves (N_s) were used directly as an indicator of the NRP, which is defined as the absolute level to which nitrogen is decreased in senescent leaves (Killingbeck 1996). Nitrogen resorption efficiency (NRE, %) was calculated on a mass basis (Killingbeck 1996), and leaf-level nitrogen-use efficiency (NUE, g g^{-1}) was estimated according to Vitousek (1982) as:

$$\mathrm{NRE} = [(N_m - N_s)/N_m] \times 100 \qquad (1)$$

$$\mathrm{NUE} = 1/[N_m(1 - \mathrm{NRE})] \qquad (2)$$

where N_m is the nitrogen concentrations in mature leaves and N_s is that in senescent leaves.

Statistical analyses

Data were analyzed using SPSS programme version 13.0 (SPSS, Chicago, IL, USA). Differences between mean values were evaluated by a one-way analysis of variance (ANOVA); data were assessed using Tukey's honestly significant difference multiple range tests), and relationships between the various variables were analyzed using the model $y = ax + b$ using Excel 2007 (Microsoft, Redmond, WA, USA).

Results

Variation in culm ages

Culm age of *P. edulis* has significant effects ($p < 0.01$) on N_m, N_s, NRE and leaf-level NUE. N_m and N_s in current-year culms were significantly higher than those of 3rd- and 5th-year culms respectively (Table 2, Fig. 1), while its leaf-level NUE (75.4 g g^{-1}) was significantly lower than that of 3rd-year culms (102.8 g g^{-1}) or 5th-year culms (93.3 g g^{-1}), and there were no significant differences in N_m, N_s and leaf-level NUE between 3rd- and 5th-year culms. For NRE, the lowest foliar NRE (53.7%) was found in 5th-year culms and highest in current-year culms (61.7%); no significant differences were found between current- and 3rd-year culms (Table 2, Fig. 1).

Variation in leaf lifespans

With the development of the culm, the leaf of *P. edulis* changes lifespan from 1 year to 2 years after the leaves on current-year culms drop. To determine any effects of this change on nitrogen-use characteristics during culm growth, we compared the two leaf lifespans for leaf N_m, NRP, NRE and NUE, and found them to differ significantly for N_m, N_s, NRE and NUE. N_m and N_s of 1-year lifespan leaves were significantly higher than those of 2-year lifespan leaves, so was NRE. On the contrary, leaf-level NUE (75.4 g g^{-1}) of 1-year lifespan leaves was significantly lower than that (98.0 g g^{-1}) of the 2-year lifespan leaves (Table 3, Fig. 2).

Relationships among N_m, N_s, NRE and NUE

N_m, N_s, NRE and NUE were plotted against each other to examine whether there were possible relationships between these variables. Significant positive linear correlations were found between N_s and N_m within and among the three ages of culms (Fig. 3a). In contrast, NRE was negatively correlated to N_s within and among the ages of culms (Fig. 3c), indicating that decreasing N_s can increase foliar NRE. NRE was generally unrelated to N_m within each culm age. However, when all NRE measurements from all three ages of culms were regressed with N_m, they positively correlated ($r = 0.3409$, $p < 0.05$, Fig. 3b), indicating that the higher the nitrogen level in the leaf tissue, the greater the percentage translocation capacity.

Similarly, negative relationships were displayed between leaf-level NUE and N_m within and among the three ages of culms (Fig. 4a), while leaf-level NUE were positively correlated with foliar NRE within and among culm ages (Fig. 4b).

Discussion

Our study indicates that nitrogen-use characteristics (N_m, NRP, NRE and NUE) of current-, 3rd- and 5th- year *P. edulis* culms were significantly influenced by culm age and leaf nitrogen status, and those characteristics were correlated with each other. As the culm develops, it also changes its leaf lifespan from 1 year to 2 years after the leaves on current-year culms drop. *Phyllostachys edulis* seem to have a higher potential for nitrogen resorption during the initial stages of their life cycle, and more proficiency in nitrogen use in older culms, perhaps because culms in early ontogenetic stages are more prone to acquire and utilize resources at a faster rate than older culms. Significant linear correlations between N_m and NRP, NRE and NUE, N_m and NUE, N_s and NRE were found for each culm age, and N_m was significantly positively correlated to NRE for all culms pooled together. Higher nitrogen resorption proficiency in older culms led to higher NUE and lower NRE, and these relationships can be modulated by N_m, which, in turn, is regulated by nitrogen availability and acquisition.

Table 2 Nitrogen concentrations in mature leaves (N_m) and in senescent leaves (N_s), nitrogen resorption efficiency (NRE) and leaf-level nitrogen-use efficiency (NUE) from culms of different ages in *P. edulis* stands

Culm ages	N_m (mg g^{-1})	N_s (mg g^{-1})	NRE (%)	NUE (g g^{-1})
Current-year culms	35.1 (2.4) Aa	13.4 (1.6) Aa	61.7 (3.3) Aa	75.4 (8.9) Bb
3rd-year culms	26.1 (3.6) Bb	10.1 (2.1) Bb	61.5 (4.7) Aa	102.8 (18.8) Aa
5th-year culms	23.7 (2.5) Bb	11.0 (1.7) Bb	53.7 (4.5) Bb	93.3 (15.7) Aa
F	66.54	13.92	16.70	12.83
p	< 0.001	< 0.001	< 0.001	< 0.001

Values are means with SD in parentheses

Means followed by different capital or lowercase letters within a column differed significantly at $P < 0.01$ and $P < 0.05$, respectively, in equal *N* Tukey honestly significant (HSD) tests

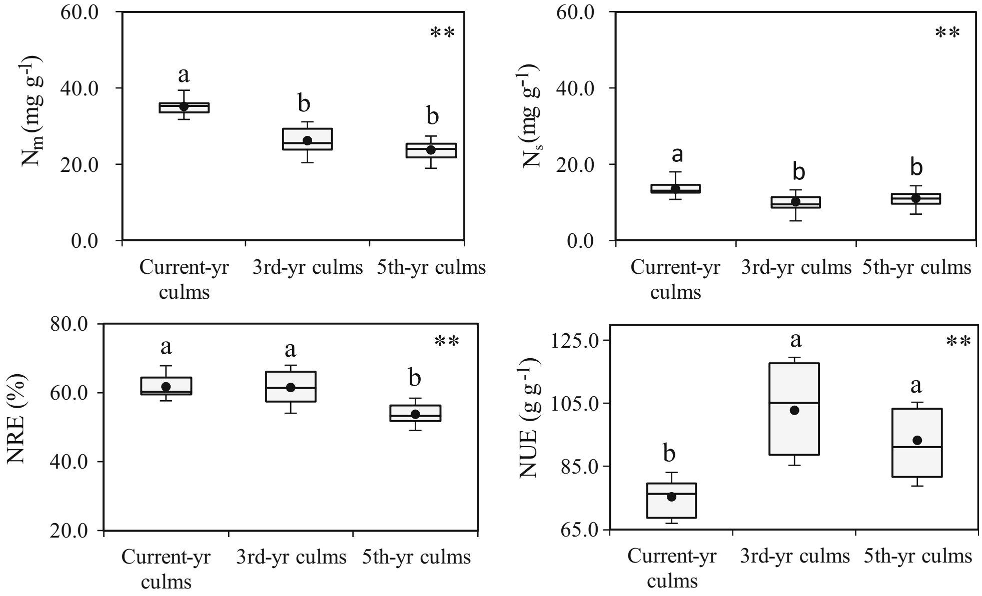


Fig. 1 Nitrogen concentrations in mature leaves (N_m) and in senescent leaves (N_s), nitrogen resorption efficiency (NRE) and leaf-level nitrogen-use efficiency (NUE) for *P. pubescens* in culms of different ages. *$P < 0.05$; **$P < 0.01$

Table 3 Nitrogen concentrations in mature leaves (N_m) and in senescent leaves (N_s), nitrogen resorption efficiency (NRE) and leaf-level nitrogen-use efficiency (NUE) of different lifespan leaves in *P. edulis* stands

Leaf lifespan	N_m (mg g^{-1})	N_s (mg g^{-1})	NRE (%)	NUE (g g^{-1})
1 year	35.1 (2.4) Aa	13.4 (1.6) Aa	61.7 (3.3) Aa	75.4 (8.9) Aa
2 year	24.9 (3.3) Bb	10.5 (1.9) Bb	57.6 (6.1) Aa	98.0 (17.7) Bb
F	115.589	25.390	5.946	21.660
p	< 0.001	< 0.001	< 0.05	< 0.001

Values are means with SD in parentheses

Means followed by different capital or lowercase letters within a column differed significantly at $P < 0.01$ and $P < 0.05$, respectively, in equal *N* Tukey honestly significant (HSD) tests

N_m, NRP, NRE and NUE of different age culms

In this study, the NRE of *P. edulis* ranged from 43.1% to 68.6% and averaged about 59.0%. These values were much lower than those based on leaf mass in other studies for herb species (Carrera et al. 2003; Quested et al. 2003; Van Heerwaarden et al. 2003). However, the average NRE of 59.0% for the three culm ages here was good compared with the reported average NRE based on a large number of graminoids worldwide (58.5%) (Aerts 1996) or herbs in northern China (55.1%) (Yuan et al. 2005). Our results indicated that the NRE of *P. edulis* in subtropical China

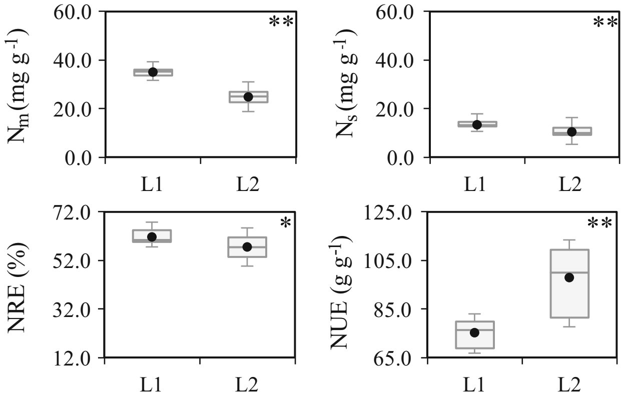


Fig. 2 Nitrogen concentrations in mature leaves (N_m) and in senescent leaves (N_s), nitrogen resorption efficiency (NRE) and leaf-level nitrogen-use efficiency (NUE) of 1-year lifespan leaves (L1) and 2-year lifespan leaves (L2) for *P. pubescens*. $^*P < 0.05$; $^{**}P < 0.01$

was at the higher end of the values reported by Aerts (1996) and Killingbeck (1996) for a wide range of ecosystems, and Huang et al. (2007) for 50 other tree species in subtropical China. These results might be explained by the fact that species with a long average leaf lifespan tend to have higher leaf nutrient resorption efficiency than species with short lifespan (Aerts and Chapin 2000). *Phyllostachys edulis*, even it is a perennial grass species, has a much longer leaf lifespan than trees. The average NRE and N_m (28.3 mg g^{-1}) for the three ages of culms of *P. edulis* were much higher than those of this bamboo species reported by Li et al. (1998), which might be due to the growing stage of the mature leaves when they were sampled. Their mature leaves were collected at the beginning of April 1995. In fact, 2-year-old leaves and leaves on current-year culms of this bamboo begin dropping about in January; thus some nitrogen might have moved to other parts before sampling in the 1998 study by Li et al. (Aerts and Chapin 2000; Pastor-Pastor et al. 2015).

Previous studies have demonstrated that nutrient resorption from senescing leaves and extended leaf longevity are important strategies to conserve nutrients for plants in general (Hemminga et al. 1999), and in low-input systems plants tend to be more conservative when they grow (Mediavilla et al. 2013). Plants with long lifespan tend to have bigger leaf thickness and smaller specific leaf area (England and Attiwill 2006) and higher leaf dry mass per unit area (Poorter et al. 2009), lower nutrient concentrations (Wright and Westoby 2003) and lower photosynthetic capacity (Niinemets 2004). These leaf characteristics have been connected with lower growth rates (Chapin 1991), an adaptive response to enhancing nitrogen limitation (Nacry et al. 2013). In this context, we proposed the question whether leaf nitrogen use and conservation could be influenced by culm age for *P. edulis*. Our results showed that culm age have a significant effect on N_m, NRP, NRE and leaf-level NUE, and even on the leaf lifespan, and older (3rd- or 5th-year) culms have more efficiency in the use of nitrogen than younger (current-year) culms.

Current-year culms with a 1-year lifespan leaves had higher N_m than did 3rd- and 5th-year culms with 2-year lifespan leaves, likely because plants in the initial ontogenetic stages can usually acquire and utilize resources at a faster rate than adults (Mediavilla et al. 2013). This result agreed well with a previous suggestion that N_m decreases with increasing leaf lifespan or stand age (Pastor-Pastor et al. 2015; Wright and Westoby 2003), while Chen et al. (2004) reported that the foliar N concentrations did not show a consistent change with age. However, there was no significant difference in N_m between 3rd- and 5th-year culms, which was inconsistent with previous suggestions that N_m increased as plants grow older (Li et al. 2013; Yuan and Chen 2010), while it agreed well with reports that N_m was highest in current-year culms of *P. edulis* (Su 2012; Wu et al. 2005).

In addition, 3rd- and 5th-year culms had significant higher NRP (lower N_s) than current-year culms. Killingbeck (1996) suggested that plants with lower N_s (< 7.0 mg g^{-1}) are highly proficient, while those with higher N_s (> 10.0 mg g^{-1}) are weakly proficient. According to this suggestion, *P. edulis* can be categorized as the weakly proficient plant because the N_s of the three ages of culms were all greater than 10.0 mg g^{-1}, and 3rd- or 5th-year culms might be more proficient than current-year culms. A possible explanation for this result is that *P. edulis* was an acquisitive plant, as 500–3000 new culms per ha emerge and elongate each year in this bamboo stands, and current-year culms tend to be more acquisitive, a characteristic associated with lower nitrogen proficiency at the leaf level (Freschet et al. 2010). The higher acquisition capacity of current-year culms might be a consequence of lower costs of acquisition compared with the cost of nitrogen resorption. As culm developing, acquisition capacity decreases (Hodge 2004), while its cost exceeds that of resorption (Fisher et al. 2010; Wright and Westoby 2003).

As regards changes in proficiency, we found foliar NRE of current-year culms was significantly higher than that of 3rd- or 5th-year culms (Table 2, Fig. 2), these results were consistent with the finding that NRE is higher for leaves in younger *P. tremuloides* stands than in older stands (Yuan and Chen 2010). While Wang et al. (2014) also reported that leaf NRE rose and then dropped as the lucerne stand aged, and Mediavilla et al. (2014) observed that the species seem to have a lower potential for N resorption during the initial stages of their life cycle. This is probably because leaf nutrient resorption characteristics vary with species and their experimental objectives differed from ours. Here,

Fig. 3 **a** Relationship between N concentrations in senescent and mature leaves; **b** relationship between NRE and N concentration in mature leaves; **c** relationship between NRE and N concentration in senescent leaves. ◆ Current-year culms, ● 3rd-year culms, ▲ 5th-year culms

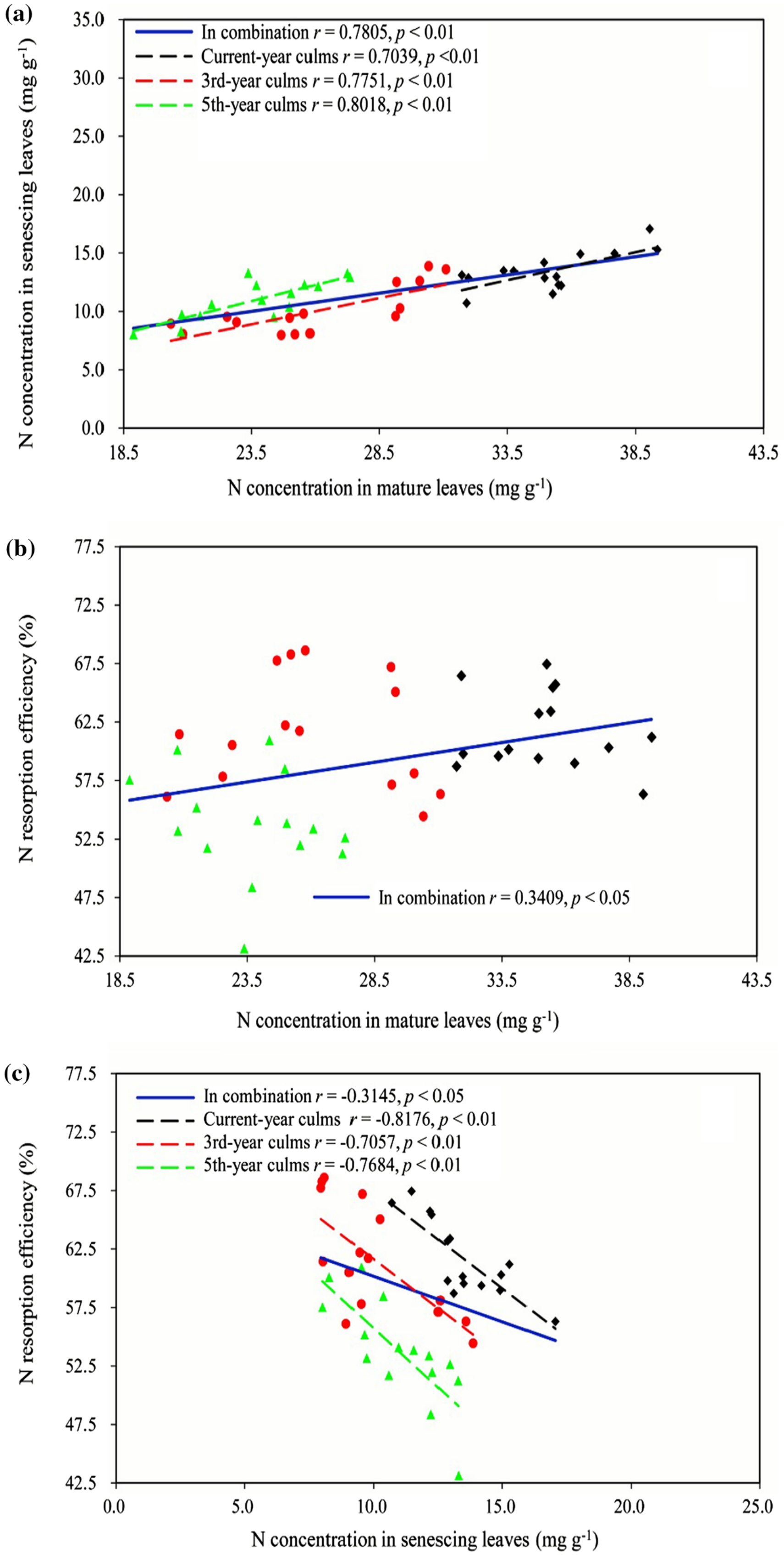
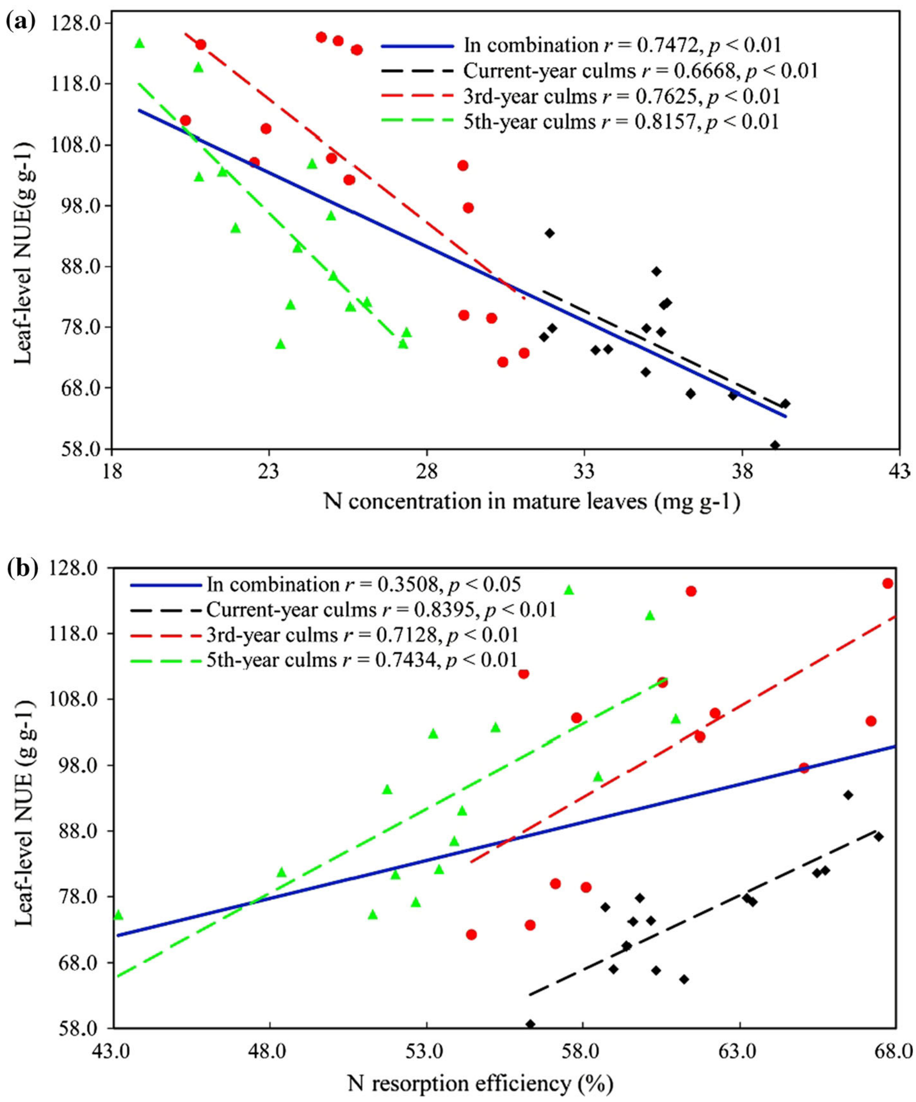


Fig. 4 **a** Relationship between leaf-level N-use efficiency (NUE) and N concentration in mature leaves. **b** Relationship between leaf-level NUE and N resorption efficiency (NRE). ◆ Current-year culms, ● 3rd-year culms, ▲ 5th-year culms



the NRE, NRP and NUE did not significantly increase or decrease with the culm age chronosequence, which is inconsistent with the results of Yuan and Chen (2009), but agrees with the finding for *P. edulis* stands that 5 years after shooting will be the optimal time to harvest *P. edulis* cums because culms older than 5 years will stop producing shoots and their consumption begins to exceed their accumulation (Zhou 1989).

Previous studies have suggested that a greater leaf lifespan is one mechanism to enhance nutrient-use efficiency (Chabot and Hicks 1982; Loveless 1961; Pastor-Pastor et al. 2015); thus, variation in leaf lifespan appears to play a vital role in determining the leaf-level NUE of *P. edulis* in the nitrogen-limited environment here. Why do older culms with 2-year leaf lifespan have significantly higher NUE than younger culms with leaves with 1-year lifespans? Vitousek (1982) and Pastor-Pastor et al. (2015) suggested resorption proficiency was the main factor determining this change. In older culms, lower acquisition may thus lead to lower N_m, and, in turn, lower N_m may lead to higher resorption proficiency and higher leaf-level NUE.

Correlations among the nitrogen-use characteristics in leaves

Previous studies have been inconsistent regarding correlations among nitrogen-use characteristics (e.g., N_m, NRE, NRP and NUE). For example, Yuan et al. (2005) reported that NRE and N_s increased with N_m, and NUE decreased; NRP decreased with NRE, and NUE increased. Wang et al. (2014) also found that nitrogen concentration in green leaves increased significantly with increasing NRE, and nitrogen concentration in senesced leaves decreased in lucerne stands. On the contrary, Kobe et al. (2005) and Vergutz et al. (2012) observed that globally, NRE decreased with increased leaf nitrogen status, while Aerts

(1996) and Cai and Bongers (2007) found no relationships between NRE and leaf nutrition status for trees and lianas. In the present study, there were markedly positive relationships between N_m and N_s for culms at each age, as well as between NRE and NUE. Significant negative relationships between N_s and NRE, NUE and N_m for each age of the culms, as well as a significant positive relationships between N_m and NRE for all three ages, suggested that plants with higher N_m were capable of resorbing a higher percentage of nitrogen from senescing leaves.

It is well-known that NUE covers a suite of physiological processes, including the relationship between plant nutrient content and its growth velocity (Small 1972) and the allocation of nutrients between litterfall and resorption pathways (Vitousek 1982). Thus, NUE was influenced by many factors (e.g., plant nitrogen status, soil fertility, light, nitrogen application) (Yasumura et al. 2002). As to leaf nitrogen-use characteristics, some reports showed that leaf-level NUE of plants was increased with NRE (Aerts and Chapin 2000; Yuan et al. 2005) and decreased with foliar nitrogen concentration (Cordell et al. 2001; Yuan et al. 2005). Those reported results agreed well with our results. Moreover, Yuan et al. (2005) thought that cumulative photosynthetic NUE at the leaf level will mainly determine NUE at the plant level because leaf is the only organ conducting carbon assimilates for plants. For *P. edulis*, spring shoots had lower photosynthetic capacity, and the leaf is the only organ conducting carbon assimilation after leaf flush on current-year culms (Cui et al. 2012). Therefore, leaf-level NUE could be regarded as a proxy estimate of NUE at the whole-plant level for *P. edulis*.

Plant leaf nitrogen resorption and utilization is a complicated process (Birk and Vitousek 1986), and all nutrient elements closely influence each other during plant growth and development (Wang et al. 2014). The present study failed to establish solid correlations between nitrogen-use characteristics and culm age, but still provides some clues on leaf nitrogen resorption patterns in *P. edulis* from the viewpoint of leaf nutrient status. We have identified a few questions as directions for future further investigation: Are there any significant differences in N_m of current-year culms between on- and off-years? Does leaf NRE increase with an increase in mean residence time of a nutrient? Are there any correlations between NRE and other elements in leaf? Does soil nutrient availability influence the leaf NRE of this bamboo? Answers to these questions are relevant for applied research on sustainable management of *P. edulis*.

Implications for bamboo stand management

Management practices can have significant impacts on the soil and plant nutrient availability, leaf nitrogen resorption efficiency, proficiency and nitrogen-use efficiency (Rejmánková 2005; Kozovits et al. 2007; Henderson and Jose 2012). And Li et al. (1998) reported that fertilization can increase leaf nitrogen concentration. Plants can increase the retention time of nutrients in their leaves by increasing leaf longevity and/or retranslocation efficiency (Escudero et al. 1992). *Phyllostachys edulis* is such a plant. Our results indicate that significant linear correlations between N_m and NRP, NRE and NUE, N_m and NUE, N_s and NRE were found for current-year, 3rd-year and 5th-year culms, N_m was significantly positively correlated to NRE for all culms together, and higher nitrogen proficiency for *P. edulis* led to higher NUE and lower NRE. These relationships could be modulated by N_m, which, in turn, is limited by leaf nitrogen availability and acquisition. Therefore, understanding the nitrogen resorption characteristic and nitrogen-use efficiency of *P. edulis* can aid in the design of appropriate deforestation strategies for *P. edulis* forest management. In practice, to balance the input and output of nutrients and to sustain the high productivity of a *P. edulis* forest, the cutting target should be culms 6 years old and older.

Another major application of our results was precision fertilization in *P. edulis* forests. Because the increasing demand for bamboo can only be met in the future by sustaining the high productivity of bamboo forests (Zhang et al. 2010), more and more bamboo forests are now intensively managed, and the excessive fertilization is causing serious problems (e.g., degradation or even death of the bamboo forests, water pollution, and decline in soil quality) (Shen et al. 2000). As a result, precision fertilizer technology was developed (Makowski et al. 2001). Therefore, the amount of available recycled nitrogen can be estimated using our results after determining leaf nitrogen availability, and we can the estimate the fertilizer norm for *P. edulis* pure forest after synthesizing the input, output and reserve of nitrogen.

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