

# Nutrient resorption in *Caragana microphylla* along a chronosequence of plantations: Implications for desertified land restoration in North China

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## ABSTRACT

Resorption of nutrients before leaf death and abscission is an important energy conservation mechanism employed by plants to endure nutrient limitation. However, leguminous N-fixing plants are able to acquire N through biochemical fixation, so are less dependent of soil N availability, and thus probably resorb less N. In the semi-arid Horqin Sandy Land of North China, *Caragana microphylla*, a leguminous N-fixing shrub, is the dominant plant species and is widely used in vegetation re-establishment programs to stabilize shifting sand. In this study, green- and senesced-leaf nutrient concentrations of *C. microphylla* were examined to compare nutrient resorption patterns along an age sequence of plantations (11, 19, 27 and 36 years, respectively) and to detect if nutrient resorption was affected by soil nutrient availability. The results showed that there were significant effects ( $p < 0.01$ ) of *C. microphylla* plantation age on nutrient resorption. N and P resorption efficiency decreased from 40% and 68%, respectively in the 11-yr old plantation to 32.0% and 55% in the 36-yr old plantation, while N and P concentrations of senesced leaves (indicators of resorption proficiency) increased from 17.5 and 0.56 mg g<sup>-1</sup>, respectively in the 11-yr old plantation to 24.8 and 0.91 mg g<sup>-1</sup> in the 36-yr old plantation. Furthermore, N and P resorption proficiency of individual shrubs were negatively related to available N and P in the soil under the shrub canopy within and among plantations. This indicates that more foliar N and P was resorbed in lower nutrient sites and implies that *C. microphylla* in nutrient-poor environments is less dependent on day-to-day nutrient uptake and thereby adapted to severely desertified regions. Additionally, *C. microphylla* in the present study showed incomplete resorption of nitrogen, which suggests senesced-leaf fall returns highly decomposable litter to the soil, and thereby indirectly improves soil nutrient availability. The restoration of desertified land, therefore, may be accelerated with plantations of the N-fixing leguminous shrub *C. microphylla*.

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## 1. Introduction

Nutrient resorption from senescing tissues, quantified by nutrient resorption efficiency (the proportion of nutrient resorbed from senesced leaves) or nutrient resorption proficiency (the level to which nutrient concentration is reduced in senesced leaves), is an important strategy employed by plants to overcome nutrient limitation in nutrient-poor ecosystems (Aerts, 1996; Killingbeck, 1996; Yuan and Chen, 2009). High resorption efficiency and proficiency enable plants to re-use internal nutrients rather than lose nutrients with leaf fall, thus facilitating plant growth, reproduction, and competitive ability (May and Killingbeck, 1992), especially

in nutrient-poor environments, where resorption from senescing tissues is essential in order for perennials to acquire their annual nutrient requirements (Aerts et al., 2007; Huang et al., 2012; Lu et al., 2012). It is, therefore, expected that plants inhabiting infertile environments would be more efficient and proficient at resorbing nutrients than those inhabiting fertile environments. Unfortunately, this hypothesis remains controversial and it has been supported by some studies (Pugnaire and Chapin, 1993; Yuan et al., 2005) and disputed by others (del Arco et al., 1991).

In severely desertified sandy land of North China, land desertification leads to substantial loss of topsoil nutrients (Zhao et al., 2006) and subsequently disappearance of plant species poorly adapted to nutrient-deficient environments (Liu et al., 1996). Poor soil nutrient availability, therefore, is regarded as the primary factor that limits plant colonization, growth and reproduction in these areas (Zuo et al., 2009a). Thus, in order to control land desertification, some native shrubs tolerant of nutrient-poor environments were selected and widely planted throughout severely desertified

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sites. Among these shrubs, leguminous species are preferred due to their  $N_2$ -fixation capacity, which facilitates their establishment on nutrient deficient soils (Zhao et al., 2011). There is evidence that growth of N-fixing plants is less dependent of soil nitrogen availability because N is readily available through biochemical fixation (Zahran, 1999). N-fixing plants also have greater concentrations of N in senesced leaves than plant species without  $N_2$ -fixation capacity (Killingbeck, 1993; Mao et al., 2011; Stewart et al., 2008; Tateno, 2003). This implies that N is not a limiting resource in some leguminous species and therefore may be not be highly resorbed during leaf senescence, even in nutrient-poor environments. In contrast, P may be substantially resorbed by leguminous species capable of N fixation when grown on nutrient deficient soils (Killingbeck, 1993; Stewart et al., 2008). However, there is a growing body of evidence showing significant variation of nitrogen resorption of leguminous N-fixing plants along soil nutrient gradients, suggesting that N-fixing leguminous plants probably also conserve more N in infertile environments than in fertile environments (Huang et al., 2008; Singh et al., 2005). Unfortunately, information on nutrient resorption patterns of leguminous N-fixing plants along soil nutrient availability gradients is very limited.

Here, we report a study that examined nutrient resorption patterns of a leguminous shrub *Caragana microphylla* along a chronosequence of plantations in Horqin Sand Land, North China. This shrub has a high  $N_2$ -fixation capacity (Zhang et al., 2009) and is widely planted throughout severely desertified sites to control land desertification in North China (Su et al., 2005; Zhang et al., 2006). Previous studies in Horqin Sand Land have shown improvements in soil nutrient availability and a gradient of increasing soil nutrient availability along a chronosequence of *C. microphylla* plantations (Cao et al., 2008; Su and Zhao, 2003). Furthermore, shrubs facilitated formation of 'fertile islands' under their canopies and thus led to great heterogeneity in soil nutrient availability. Even under shrub canopies, soil nutrient availability also varies with canopy size and topography (Zuo et al., 2009b). The objective of this study is to determine if foliar nitrogen and phosphorus resorption efficiency and proficiency in *C. microphylla* increases with soil nutrient availability. Since N-fixing plants are able to acquire N through biochemical fixation and are thus less dependent on soil nitrogen availability, we hypothesized that foliar N resorption efficiency and proficiency in *C. microphylla* would not greatly differ either along a chronosequence of plantations or among individual shrubs within each plantation. In contrast, we hypothesized that foliar P would be resorbed more efficiently and proficiently in the shrubs within the young plantations than those at the old plantations. Additionally, we hypothesized that P resorption would vary greatly with soil nutrient availability within plantations, due to the 'fertile island' effect causing variability in soil nutrient availability under distinct shrub canopies.

## 2. Materials and methods

### 2.1. Study site

The study was carried out at Yaoledianzi village (N 42°55' and E 120°41', 350 m above mean sea level) located in the south-west of Horqin Sandy Land, eastern Inner Mongolia, China and in a zone of continental semi-arid monsoon climate. The average annual temperature is 6.4 °C with monthly averages ranging from a minimum of −13.1 °C in January to a maximum of 23.7 °C in July. The yearly accumulated air temperature above 10 °C ranges from 3000 to 3400 °C. The frost-free period lasts 137–150 days per year. The mean annual precipitation is 362 mm, nearly 70% of which falls from June through August. The mean annual pan evaporation is 2000 mm. Prevailing wind directions are northwest in winter and

spring, and southwest to south in summer and autumn. The mean annual wind speed ranges from 3.4 to 4.1 m s<sup>−1</sup>.

In this area, the geomorphologic landscape is characterized by sand dunes alternating with gently undulating inter-dune lowlands. The soils are light yellow colored, very infertile and sandy with a coarse texture and loose structure. In this village, land desertification started in the 1950s with the disturbance of stabilized sandy land by extensive fuel wood gathering and grazing and reached the climax in the mid-1970s. At its peak, shifting and semi-shifting sand dunes made up 72% of the total land area (Su and Zhao, 2003). In order to curb desertification and alleviate its detrimental effects, large areas of *C. microphylla* plantations were gradually established on desertified sandy land around Yaoledianzi village beginning in the 1970s with the help of straw checkerboards as sand binders by the local government. Planting was arranged in belts oriented perpendicular to the prevailing wind direction with rows spaced 1.5–2 m apart and neighboring plant seedlings spaced 0.5 m apart. The details about plantations in the study site were described in Su and Zhao (2003). To date, an age series of 11-, 19-, 27- and 36-yr-old *C. microphylla* plantations is distributed throughout the sandy land surrounding the village. All the plantations have been lightly grazed by cattle and sheep in recent years.

### 2.2. Leaf and soil sampling

We selected 11-, 19-, 27- and 36-yr-old *C. microphylla* plantations, each with 3–5 replications for this nutrient resorption study. In all replicates of each plantation, we randomly marked 15 healthy, full sun-exposed individuals of *C. microphylla* to collect leaf and soil samples from. In July of 2008, 25–30 fully sunlit mature green leaves were randomly collected from each marked individual and a soil sample was taken under the canopy of the shrub using a 5-cm diameter soil auger at the 0–20 cm soil layer. In autumn (late September to early October), similar collections of senesced leaves from the same individuals were made. The leaves of a single shrub and soil samples under its canopy represented one sample unit. In total, we collected 15 pairs of leaf and soil samples from each plantation. Leaves with obvious signs of herbivory, galls or fungal attack were not sampled. Leaves that were clearly very thin (shaded canopy position) were also avoided. Senesced leaves were collected directly from plants rather than from leaf litter in order to avoid underestimates of N concentration in senesced leaves due to decomposition of leaf litter and leaching of leaf nutrients. Green and senesced leaf samples were immediately taken to the laboratory, and then oven-dried at 60 °C to constant weight and kept dry until analyses.

### 2.3. Root nodules sampling

We used numbers and dry weight of root nodules per unit volume of soil to evaluate the N-fixing capacity of each plantation. In each replicate of each plantation age, 10 shrubs were randomly selected to sample root nodules. Under each selected shrub canopy, 4 soil cylinders at 0–40 cm depth were sampled at 4 equidistant points around shrub base using a 10-cm diameter soil auger. The soil samples were transferred to the laboratory immediately and passed through a 2-mm sieve. The root nodules collected by the sieve were counted and then oven-dried at 60 °C for 48 h and weighed. The root nodules expressed as numbers and dry weight per unit volume of soil under the shrub canopy.

### 2.4. Leaf and soil chemistry

All leaf samples were ground using a centrifugal mill (Cyclotec Sample Mill; Tecator, Höganäs, Sweden) to obtain a uniform

particle size of <1 mm. N concentrations of green and senesced leaves were analyzed colorimetrically by the Kjeldahl acid-digestion method (UDK140 Automatic Steam Distilling Unit, Automatic Titroline 96, Italy). For P measurements, 2 ml of 36 N H<sub>2</sub>SO<sub>4</sub> and 3 ml of H<sub>2</sub>O<sub>2</sub> were added to a 20 mg sample of leaf material and heated at 360 °C for 4 h. After this mineralization step, P concentration was measured colorimetrically with an autoanalyzer (Evolution II; Alliance Instruments, Frépillon, France) using the molybdenum blue method (Grimshaw et al., 1989).

After the soil samples were brought to the laboratory, part of each soil sample was stored in a 0–4 °C refrigerator for later analysis of inorganic nitrogen (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N). The remaining sample was air-dried and passed through a 2-mm sieve. Soil pH and electrical conductivity (EC) were measured in a soil–water suspension (1:1 and 1:5 soil–water ratio, respectively) (Multiline F/SET-3, Germany). Part of the air-dried and sieved samples then ground and passed through a 0.25-mm sieve for C, N and P analysis. Organic C was determined using the Walkley–Black method of dichromate oxidation (Nelson and Sommers, 1982). Soil total N and total P were analyzed following the same procedure as leaf N and P measurements. The Olsen sodium bicarbonate method was used to measure soil available P. Inorganic nitrogen (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) was measured by the colorimetric method on fresh soil samples after extraction with 2 M KCl.

### 2.5. Data analysis

N and P concentrations in green and senesced leaves were used to calculate nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) on a mass basis (Killingbeck, 1996).

$$\text{PRE (\%)} = \left[ \frac{(P_{\text{green}} - P_{\text{sen}})}{P_{\text{green}}} \right] \times 100\%$$

$$\text{NRE (\%)} = \left[ \frac{(N_{\text{green}} - N_{\text{sen}})}{N_{\text{green}}} \right] \times 100\%$$

where  $N_{\text{green}}$  and  $N_{\text{sen}}$  represent N concentration in the green leaves and senesced leaves, respectively and  $P_{\text{green}}$  and  $P_{\text{sen}}$  represent P concentration in the green leaves and senesced leaves, respectively. It should be noted that calculating resorption efficiency based on leaf mass might underestimate nutrient resorption, due to probable changes in specific leaf mass resulting from resorption of soluble carbon compounds (Aerts, 1996). Estimates of proportional nutrient resorption based on leaf area may be more accurate than those based on leaf mass (Luyssaert et al., 2005). However, leaf area shrinkage also may occur during senescence and eventually underestimate resorption efficiency (van Heerwaarden et al., 2003). Therefore, mass-based NRE and PRE data were still used in this study. The nutrient concentrations in senesced leaves were considered a direct indicator of nutrient resorption proficiency (RP), which is defined as the absolute level to which N is reduced in senesced leaves (Killingbeck, 1996).

We employed one-way analysis of variance to test for differences in leaf nutrient concentrations, nutrient resorption efficiency, soil properties and root nodules among plantation ages. If the difference was significant, post hoc multiple comparisons were subsequently made using Turkey HSD test. Single linear regressions were used to test the power of soil available N and P under shrub canopies (within and among plantations) to predict green and senesced leaf N and P, and NRE and PRE of individual shrubs. All the data were transformed logarithmically to meet the assumptions of normality and homogeneity before analysis. Statistical analysis was performed using SPSS 16.0 for windows.

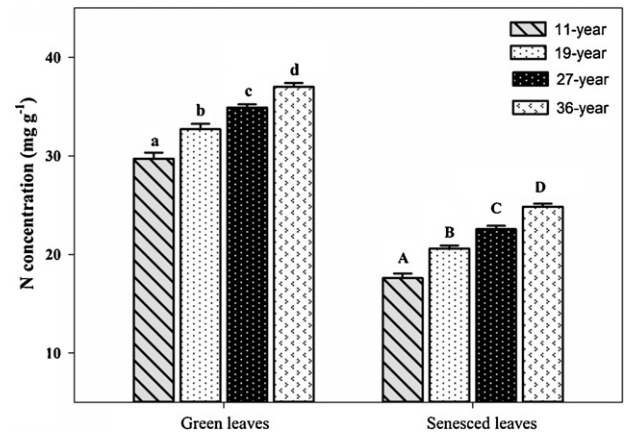


Fig. 1. N concentrations in green leaves and senesced leaves along an age sequence of *C. microphylla* plantations in Horqin Sand Land, North China. A one-way ANOVA was used to detect differences among green leaves ( $F = 41.6$ ,  $p < 0.001$ ) and senesced leaves ( $F = 78.6$ ,  $p < 0.001$ ) in different aged plantations. Significant difference among plantation ages are indicated by different letters (Turkey's test,  $p = 0.05$ ). Error bars are SE ( $n = 15$ ).

## 3. Results

### 3.1. Soil properties

Except soil pH value, there were significant differences ( $p < 0.001$ ) in organic C, total N, total P, available P, available N and EC of the soils at the 0–20 cm depth among the different plantation ages (Table 1). Soil organic carbon, total N, total P and EC at the 0–20 cm depth under the shrub canopy increased by 2.2-, 2.1-, 3.3- and 1.8-fold, respectively, along the chronosequence of *C. microphylla* plantations. Available N and P followed the same pattern with respect to plantation age, but with respective 1.77- and 1.35-fold increases in the soil under the canopy after 36 years of shrub growth, increased less than total N and total P (Table 1). This suggests that soil nutrient availability improved considerably with plantations of *C. microphylla*. However, numbers and dry weight of root nodules in 1-m<sup>-3</sup> of soil under the shrub canopy did not show obvious trends with increasing plantation age, with no significant differences ( $p > 0.05$ ) observed across the plantation chronosequence (Table 1). This implies that there is no apparent difference of N fixing capacity in *C. microphylla* across the chronosequence.

### 3.2. Leaf N and P concentrations and nutrient resorption

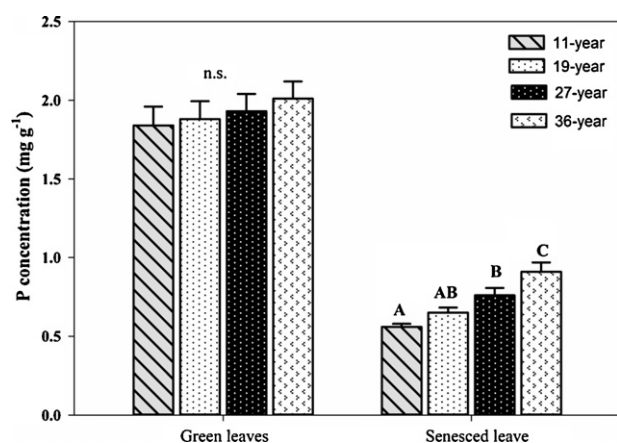
There were significant effects ( $p < 0.01$ ) on foliar  $N_{\text{green}}$ ,  $N_{\text{sen}}$  and NRE among ages of *C. microphylla* plantations (Figs. 1 and 3A). Mean N concentrations in green leaves varied between  $29.7 \pm 0.6 \text{ g kg}^{-1}$  in the 11-yr old plantation and  $37.0 \pm 0.4 \text{ g kg}^{-1}$  36-yr old plantation, increasing significantly ( $p < 0.01$ ) with development of *C. microphylla*. Meanwhile, mean N concentrations in senesced leaves, indicators of N resorption proficiency (NRP), significantly increased ( $p < 0.01$ ) by 29% along the age sequence. In other words, it appears that NRP significantly decreased with plantation age. In the 11-yr old plantation, nearly 40% of foliar N was resorbed during leaf senescence, which was significantly higher than 32% of NRE in the 36-yr old plantation and indicates that N was substantially resorbed by *C. microphylla* in lower nutrient sites.

In contrast, mean P concentration in green leaves varied little ( $p > 0.05$ ) among the plantation ages (Fig. 2). However, mean P concentration in senesced leaves increased from  $0.86 \pm 0.02 \text{ g kg}^{-1}$  in the 11-yr old plantation to  $1.23 \pm 0.06 \text{ g kg}^{-1}$  in the 36-yr old

**Table 1**Soil properties and root nodule counts along an age sequence of *C. microphylla* plantations in Horqin Sand Land, North China (means  $\pm$  SE,  $n = 15$ ).

	Age sequence				<i>F</i>	<i>p</i>
	11	19	27	36		
Organic C (g kg <sup>-1</sup> )	3.7 $\pm$ 0.2a	5.5 $\pm$ 0.1b	6.6 $\pm$ 0.2c	8.2 $\pm$ 0.3d	70.5	<0.001
Total N (g kg <sup>-1</sup> )	0.35 $\pm$ 0.02a	0.48 $\pm$ 0.01b	0.57 $\pm$ 0.02c	0.74 $\pm$ 0.04d	71.2	<0.001
Available N (mg kg <sup>-1</sup> )	5.7 $\pm$ 0.6a	7.6 $\pm$ 0.4bc	8.7 $\pm$ 0.4cd	10.1 $\pm$ 0.3d	16.9	<0.001
Total P (g kg <sup>-1</sup> )	0.09 $\pm$ 0.01a	0.17 $\pm$ 0.00b	0.22 $\pm$ 0.01c	0.30 $\pm$ 0.01d	93.5	<0.001
Available P (mg kg <sup>-1</sup> )	2.8 $\pm$ 0.1a	3.1 $\pm$ 0.1a	3.5 $\pm$ 0.1b	3.8 $\pm$ 0.1b	23.1	<0.001
pH (H <sub>2</sub> O)	7.77 $\pm$ 0.05	7.69 $\pm$ 0.05	7.63 $\pm$ 0.05	7.63 $\pm$ 0.06	1.6	0.202
Electrical conductivity ( $\mu$ S cm <sup>-1</sup> )	56.4 $\pm$ 2.4a	74.4 $\pm$ 2.8b	93.7 $\pm$ 2.3c	100.9 $\pm$ 1.9c	71.1	<0.001
Number of root nodules (No. m <sup>-3</sup> )	644.9 $\pm$ 83.8	700.6 $\pm$ 81.1	756.3 $\pm$ 102.7	668.7 $\pm$ 87.4	0.263	0.851
Weight of root nodules (g m <sup>-3</sup> )	81.48 $\pm$ 19.2	100.9 $\pm$ 18.5	125.7 $\pm$ 21.9	105.1 $\pm$ 23.9	0.675	0.573

Values followed by a different letter in rows mean significant differences among plantation age at 0.05 levels.

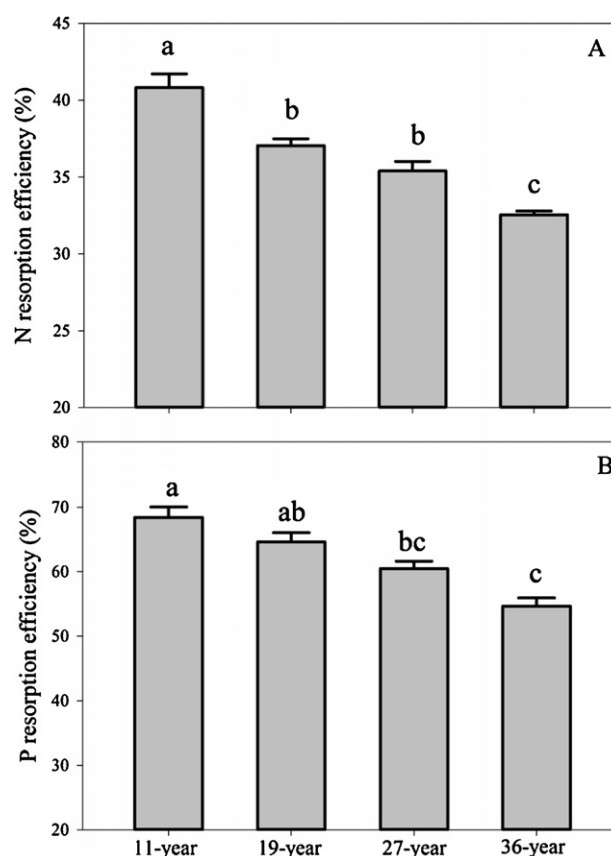
**Fig. 2.** P concentrations in green leaves and senesced leaves along an age sequence of *C. microphylla* plantations in Horqin Sand Land, North China. A one-way ANOVA was used to detect differences among green leaves ( $F = 0.428$ ,  $p = 0.733$ ) and senesced leaves ( $F = 14.3$ ,  $p < 0.001$ ) in different aged plantations. Significant differences among plantation ages are indicated by different letters (Turkey's test,  $p = 0.05$ ). Error bars are SE ( $n = 15$ ).

plantation, suggesting a significant decrease of P resorption proficiency along the plantation age sequence. PRE, was significantly higher than NRE in the corresponding plantation age and ranged from 56.9% to 65.5% along the chronosequence (Fig. 3B), indicating that more foliar P was also resorbed in lower nutrient sites.

### 3.3. Relationship between soil available nutrients, leaf nutrient concentration and nutrient resorption

N concentrations in green and senesced leaves of individual shrubs were positively related to soil available N under the shrub canopy within and among plantations (Fig. 4), suggesting that NRP decreased with increases in soil available N. In contrast, NRE was generally unrelated to soil available N within each plantation. Only NRE of individual shrubs in the 27-yr old plantation was negatively related to soil available N under the shrub canopy. However, when all NRE measurements from all plantations were regressed with soil available N, they negatively correlated (Fig. 4), indicating that foliar N was significantly resorbed during leaf senescence in low nutrient sites.

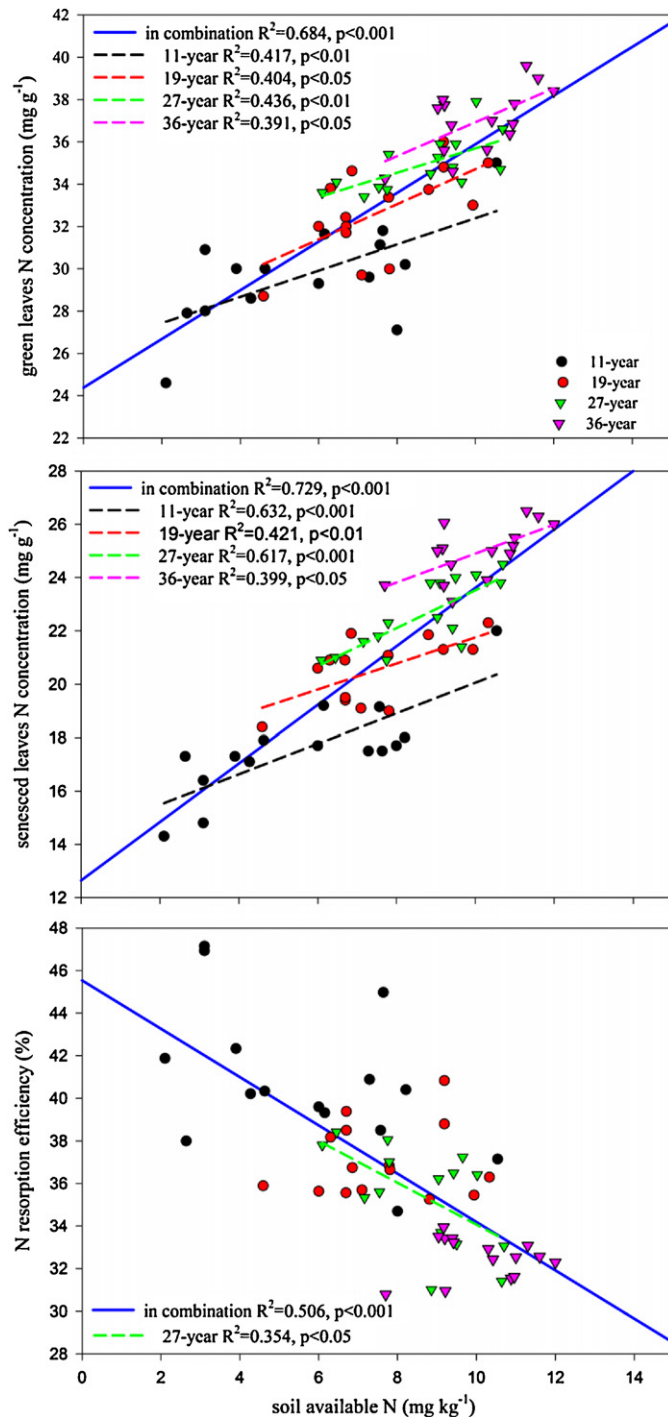
Similar relationships were displayed between leaf P concentrations and soil available P within and among plantations. While PRE did not show any relationship to soil available P within each plantation, when all PRE measurements from all plantations were regressed with soil available P, they, like N and NRE, also negatively correlated, suggesting efficient resorption of foliar P in low nutrient sites (Fig. 5).

**Fig. 3.** Foliar N and P resorption efficiency along an age sequence of *C. microphylla* plantations in Horqin Sand Land, North China. A one-way ANOVA was used to detect differences among P concentration of leaves in different aged plantations (for N:  $F = 33.43$ ,  $p < 0.001$ ; for P:  $F = 13.26$ ,  $p < 0.001$ ). Significant differences among plantation ages are indicated by different letters (Turkey's test,  $p = 0.05$ ). Error bars are SE ( $n = 15$ ).

## 4. Discussions

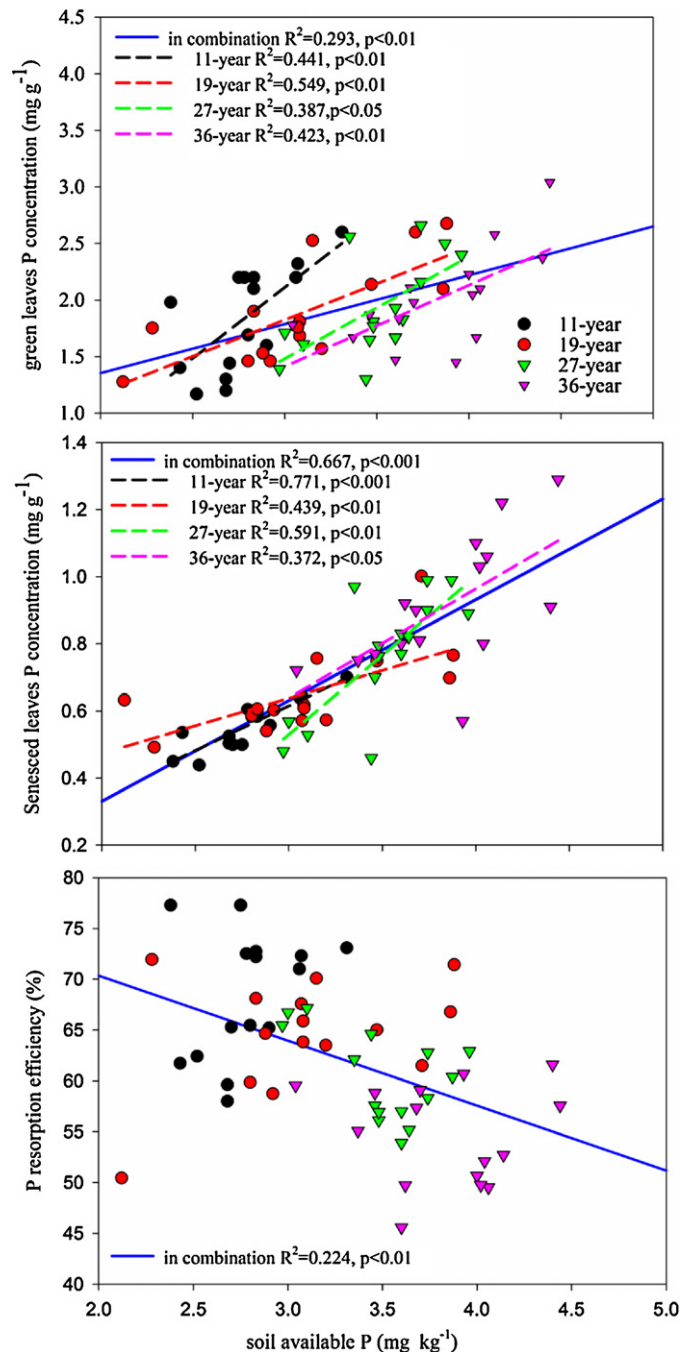
To the best of our knowledge, variation in nutrient resorption of N-fixing leguminous plants across nutrient gradients has mostly been overlooked because N-fixing plants are able to acquire N through biochemical fixation and thereby expected to resorb less N during leaf senescence, even in nutrient-poor environment. Instead, most researches focus on differences in nutrient resorption between N-fixing and non-N-fixing plants in nutrient-poor environments (Killingbeck, 1993; Stewart et al., 2008). Contrary to our first hypothesis, but in concordance with our second hypothesis, we found that the N-fixing leguminous shrub *C. microphylla* resorbed





**Fig. 4.** Predictive power of soil available N on green leaf N concentration, senesced N concentration and N resorption efficiency of four plantations. Only significant regressions are displayed.

foliar N and P less efficiently and proficiently in older plantation in comparison with young plantations. Since the *C. microphylla* N fixation capacity was similar across all plantations (Table 1), other factors could potentially have affected nutrient resorption in *C. microphylla* along plantation chronosequence. In the present study, soil available N increased with plantation age (Table 1), suggesting soil nutrient availability could be one of possible drivers of variation in nutrient resorption. Furthermore, our results showed that N concentration in green leaves increased with plantation age (Fig. 1).



**Fig. 5.** Predictive power of soil available P on green leaf P concentration, senesced P concentration and P resorption efficiency in four plantations. Only significant regressions are displayed.

Increasing N concentration with plantation age could be a direct consequence of increasing soil N supply because green-leaf N concentration, in some instances, reflects site fertility (Huang et al., 2008; Richardson et al., 2005; Yuan and Chen, 2010). It should be noted that plant age could influence photosynthetic capacity, growth rates and N economy (Chen and Klinka, 1997; Hikosaka, 2005; Vitousek, 1998), which are potential mechanisms behind nutrient resorption changes with plantation age. In this study, plant age would correspond to plantation age according to sampling methods. This implies that plant age other than soil nutrient availability could have affected nutrient resorption in *C. microphylla*.

along plantation chronosequence. However, positive relationships between soil nutrient availability and nutrient resorption, particularly nutrient resorption proficiency within each plantation suggest that nutrient resorption in *C. microphylla* is less dependent on plant age than soil nutrient availability. This result was supported by a recent N-addition study in steppe grasslands of Inner Mongolian (Huang et al., 2008), where N resorption of the N-fixing leguminous *Melissitus ruthenica* decreased along a gradient of increasing N-supplementation.

Deciduous plants appear to have the ability to resorb 50% or more of their foliar N and P during leaf senescence (Luyssaert et al., 2005; Yuan and Chen, 2009). Aerts (1996) reported an average of 54% N resorption for 115 deciduous trees and 50% P resorption for 98 deciduous trees and shrubs. In this study, N and P resorption efficiencies in *C. microphylla* were lower and higher, respectively, than those previously reported for trees and shrubs (Aerts, 1996), suggesting that foliar N was less efficiently resorbed relative to foliar P. This implies that N requirements may be partially balanced through symbiotic fixation in the leguminous shrub *C. microphylla*. It is suggested that nutrient deficiency stress, particularly low levels of available nitrate and ammonia, may stimulate the process of nodule formation by N-fixing plants (Zahran, 1999), and thus improve N shortage. However, previous studies have shown suppressed nodulation under conditions of soil P deficiency and drought stress (Leung and Bottomley, 1987; Singleton et al., 1985). It is therefore, expected that nodulation of *C. microphylla* may be suppressed in the loose sandy soil of severely desertified regions, where wind erosion leads to substantial loss of soil nutrients including P (Zhao et al., 2006) and low water holding capacity gives rise to frequent severe drought stress (Liu et al., 1996). As such, efficient and proficient resorption of nutrients seems more important for newly planted *C. microphylla* seedlings in severely desertified environments, which makes *C. microphylla* seedlings less dependent on day-to-day nutrient uptake and thereby facilitates plant growth and rapid development.

Killingbeck (1996), based on data from woody perennials, suggested that any values of nutrient resorption proficiency in deciduous species less than  $7 \text{ mg g}^{-1}$  for N and  $0.5 \text{ mg g}^{-1}$  for P could be considered “complete resorption”, and values greater than  $10 \text{ mg g}^{-1}$  for N and  $0.8 \text{ mg g}^{-1}$  for P could be considered “incomplete resorption”. If we adopt this threshold value, N concentrations in senescent leaves of *C. microphylla* in the present study show incomplete resorption of nitrogen. Our results for P concentrations in senesced leaves of *C. microphylla* ranged from 0.56 to  $0.91 \text{ mg g}^{-1}$  (Fig. 2), depending on plantation age, and suggest that P resorption in our study shifted from complete to incomplete along plantation chronosequence. The mean N and P concentrations of senesced leaves in the study ( $20.6 \text{ mg g}^{-1}$  and  $0.72 \text{ mg g}^{-1}$ ) were slightly higher than that of other evaluated N-fixing species ( $17.8 \text{ mg g}^{-1}$  and  $0.6 \text{ mg g}^{-1}$ , Stewart et al., 2008), indicating that the N-fixing leguminous shrub *C. microphylla*, as a species, has experienced weak selection for N and P conservation.

Incomplete N resorption by *C. microphylla*, even in 11-yr old plantations, contributes to the return of high quality litter to the soil, and thereby indirectly accelerates leaf litter decomposition and nutrient mineralization (Aerts et al., 2007; Lu et al., 2012). Thus, soil nutrient availability will be considerably improved, which can potentially create opportunities for settlement or development of otherwise subordinate or transient plant species (Tewksbury and Lloyd, 2001). This process may accelerate the restoration of desertified land after *C. microphylla* plantation initiation. In addition, our results showed that nutrient resorption proficiency of *C. microphylla* was negatively related to soil nutrient availability within each plantation, suggesting that an increase in soil fertility leads to highly concentrated nutrients in the leaf litter of the soil under

the shrub canopy, and thereby promotes the formation of ‘fertile islands’ under shrub canopies. This implies that the initiation of *C. microphylla* plantations may increase soil heterogeneity due to the return of higher-quality litter to the soil under shrub canopies, which potentially facilitates species diversity and buffers the community response to climate change (Baer et al., 2004; Fridley et al., 2011).

In summary, nutrient conservation strategies of the leguminous N-fixing shrub *C. microphylla* differed with age of plantation. Plants within older plantations seemed to be less efficient and proficient in resorbing N and P during leaf senescence than those in young plantations. This makes *C. microphylla* less dependent on day-to-day nutrient uptake and thereby facilitates plant growth and rapid development in severely desertified regions. Nevertheless, *C. microphylla* in the present study showed incomplete resorption of nitrogen, which should contribute to the return of highly decomposable litter to the soil, and thereby indirectly improve soil nutrient availability. Consequently, the restoration of desertified land may be accelerated with plantations of the N-fixing leguminous shrub *C. microphylla*.

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