Catena 183 (2019) 104186

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena

Response of forest species to C:N:P in the plant-litter-soil system and stoichiometric homeostasis of plant tissues during afforestation on the Loess Plateau, China

Xuejuan Bai[a], Baorong Wang[b], Shaoshan An[a,*], Quanchao Zeng[c], Haixin Zhang[c]

[a] State Key Laboratory of Soil Erosion and Dry Land Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Yangling 712100, China
[b] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Science and Ministry of Water Resources, Yangling 712100, China
[c] College of Natural Resources and Environment, Northwest A&F University, 712100 Shaanxi, China

ARTICLE INFO

Keywords:
Plant
Litter
Soil
Ecological stoichiometry
Stoichiometry homeostasis
Loess Plateau

ABSTRACT

As the "Grain for Green" project goes on in the Loess Plateau, some drawbacks, such as the low survival rate, the appearances of dry soil layers and little old trees are appearing, especially for introduced tree species. Ecological stoichiometry, which indicates the balance of elements and the flow of energy, plays a vital role in exploring biogeochemical cycling in ecosystems. To investigate the carbon (C), nitrogen (N) and phosphorus (P) balance and flow of energy, the stoichiometry characteristics and stoichiometry homeostasis for introduced and natural forests on the Loess Plateau, four typical forests were selected, including three introduced forests composed of *Robinia pseudoacacia* (*R. pseudoacacia*), *Pinus tabuliformis* (*P. tabuliformis*) and *Platycladus orientalis* (*P. orientalis*) and a natural forest composed of *Quercus wutaishansea* (*Q. wutaishansea*) and the C, N and P in the plant-litter-soil system were measured. The results showed that the C, N and P contents and C:N:P in leaves, branches, fruits, litters and soils varied widely and were influenced strongly by forest species. The N content in *R. pseudoacacia* leaves, branches, fruits and litters and the soil C, N and P contents in *Quercus wutaishansea* were higher than those in other forest species. The soil C:N:P stoichiometry in *Quercus wutaishansea* was higher than that in introduced forest species, while the reverse was found for plant tissues and litter C:N:P. According to the leaf N:P, with the exception of *R. pseudoacacia*, growth of the other three forest species was limited by N. The N, P and N:P homeostasis exist in trees, especially in *Quercus wutaishansea*, forest species and plant tissues had significant effects on the strength of homeostasis. Overall, the results of C, N and P content and stoichiometric homeostasis revealed that the natural forest was more adaptable to the arid environment in the Loess Plateau compared to the introduced forests.

1. Introduction

The Loess Plateau, one of the most vulnerable ecosystems in the world, located in northern China, is characterized by the arid and nutrient-poor and has the largest loess accumulation and excessive desertification. A series of measures focused on soil and water conservation have been carried out in this region, including a major project known as "Grain for Green" that was launched in 1999. By the end of the 2000s, the forest increased from 14.8% to 21.7% in this region (Fu et al., 2017). However, since that time, some problems have appeared, such as low survival rate, the appearance of dry soil layers and few mature trees, especially for the introduced forests. In contrast, the growth conditions for the natural forest are relatively good. Thus, the material and energy circulation processes in the plant-soil system should be explored to form a deep understanding of the ecological characteristics and functions of the natural and introduced forest species.

Ecological stoichiometry, the balance of carbon (C) and elemental nutrients, mainly includes nitrogen (N) and phosphorus (P) in interactions and processes, especially in terrestrial ecosystems (Sterner and Elser, 2002). All living things are based on C, which provides the structural basis of plants, composing a relatively stable 35% of the dry

---

* Corresponding author at: State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Xinong Road, #26, Yangling 712100, Shaanxi Province, China.
E-mail addresses: bxj@nwafu.edu.cn (X. Bai), shan@ms.iswc.ac.cn (S. An).

https://doi.org/10.1016/j.catena.2019.104186
Received 9 April 2019; Received in revised form 3 June 2019; Accepted 23 July 2019

plant biomass (Liu et al., 2011). N is a plant bio-element and plays an important role in plant growth, photosynthesis and litter decomposition (Daufresne, 2004). P is responsible for cell structure and is a component of DNA and RNA, and P promotes C:N assimilation and transpiration (Tilman, 2004; Bai et al., 2012). C:N:P stoichiometry, focusing on the balance and interaction of C, N and P in ecological processes (Mooshammer et al., 2014; Ren et al., 2016), has been often used to explore the relationships and feedbacks between above- and belowground components of ecosystems (Sophie et al., 2015; Damien et al., 2016; Zeng et al., 2017; Yang et al., 2018). For example, soil C:N, C:P and N:P ratios may vary with different plant communities with different substrate inputs (Fanin et al., 2013; Zechmeister-Boltenstern et al., 2015). Moreover, soil C:N:P ratio reflects soil fertility, regulates plant growth and affects plant nutrient state (Bui and Henderson, 2013; Fan et al., 2015). Several studies have explored the stoichiometric characteristics of plant tissues at regional or global scales to examine nutrient cycling and elemental limitations of plants (Güsewell, 2004; Reich and Oleksyn, 2004; Han et al., 2005; Yuan et al., 2011). Elser et al. (2000a) reported extensive variations in the C:N, C:P and N:P ratios in leaves, they found that leaf C:N and C:P ranged from 5 to 100 and 250 to 3500, respectively, which were significantly higher than fresh water biomass, while leaf N:P (5–56) was similar to fresh water biomass. Evidence from many studies has shown that the leaf N:P ratio can reflect N- or P-limitation in ecosystems (Güsewell, 2004; Reich, 2005; Richardson et al., 2008; Fan et al., 2015; Zhang et al., 2019). However, determination of the stoichiometry in plant-litter-soil systems remains to be elucidated, such as how tree species and vegetation composition influence C and nutrient (N and P) redistribution between the plant, litter and soil and how N- or P-limitation changes in different tree species. Moreover, existing studies have mainly focused on the C:N:P stoichiometry in leaves, but for other plant tissues, such as branches and fruits, C:N:P stoichiometry has not been studied extensively.

If the stoichiometric composition of organisms does not change with variation in resource stoichiometry, the system can be considered strictly homeostatic, while if the nutrient content of a consumer is passively mirrored by resource nutrient content, the system is non-homeostatic (Sterner and Elser, 2002). "Homeostasis is the essence of life" (Sterner and Elser, 2002), but in early stoichiometric theory, photoautotrophs, especially cyanobacteria and algae, were considered to have very weak stoichiometric homeostasis. Sterner and Elser (2002) proposed a continuously variable regulation parameter (H) to quantify the degree of stoichiometric homeostasis of a particular organism. This parameter was calculated with the following equation:

$$H = 1/S \tag{1}$$

In Eq. (1), S is the slope of $\ln N_R$ vs. $\ln N_C$, $\ln P_R$ vs. $\ln P_C$, or $\ln N{:}P_R$ vs. $\ln N{:}P_C$ (R represents resources and C represents the consumer). Many studies have examined variations in elemental or stoichiometric homeostasis in response to nutrient supply across a wide range of taxa, including bacteria (Makino et al., 2003), fungi (Levi and Cowling, 1969), algae (Rhee, 1978) and grasslands (Yu et al., 2011). As reported, stoichiometric homeostasis was positively correlated with the function and stability of vegetation (Yu et al., 2010). The strength of stoichiometric homeostasis in climax communities is higher than that in subdominant species (Hooper et al., 2005). Thus, stoichiometric homeostasis is related to the adaptation of the vegetation. Does elemental or stoichiometric homeostasis exist for trees? In addition, how does elemental or stoichiometric homeostasis respond to natural and introduced forest species?

Previous studies have explored variation in the ecological stoichiometry of soils, leaves and roots in plantations of different ages and grassland communities on the Loess Plateau (Zeng et al., 2017; Yang et al., 2018). However, studies on the relationships of C, N and P stoichiometry between the above- and below-ground components of certain forest types in this region are lacking. Moreover, exploring the stoichiometric homeostasis of C, N and P in plant tissues will illustrate the sustainable development countermeasures of natural and introduced forest species and provide a scientific basis for adjusting vegetation restoration strategies on the Loess Plateau.

Three typical introduced forests composed of *Robinia pseudoacacia* (*R. pseudoacacia*), *Pinus tabuliformis* (*P. tabuliformis*) and *Platycladus orientalis* (*P. orientalis*) and one natural forest composed of *Quercus wutaishansea* (*Q. wutaishansea*) were selected for our study. Plant tissues, litter and soil samples were sampled to explore C, N and P contents, stoichiometry and stoichiometric homeostasis on the Loess Plateau, China. We hypothesized the following: (i) the C, N and P contents in the plant-litter-soil system have different trends in the natural and introduced and forest species; (ii) the C:N:P stoichiometry in the plant-litter-soil system has different trends and the N- or P-limiting conditions differ among the selected forest species; and (iii) trees have stoichiometric homeostasis, which differs among tree species and plant tissues.

2. Materials and methods

2.1. Study area

The study area is located in the northeast forest area of Ziwuling (36°03′52″–36°04′49″ N, 109°09′54″–109°10′48″ E) (Fig. 1), an ecologically important forest on the central Loess Plateau (Table 1). The elevation is 1173.8–1195.5 m; the study area has a warm temperate monsoon climate, and the annual average temperature from 1980 to 2015 was10.4 °C. The average annual precipitation is 500–620 mm, and the rainy season occurs in July to September, which accounts for approximately 60% of the total precipitation; the annual average humidity is 63%–68%, and the frost-free period is 110–150 days. The zonal soil is cambisol according to the WRB soil taxonomy. With the implementation of the "Green for Grain" project, certain forest species have been established in the region. The main forest species are *R. pseudoacacia*, *P. tabuliformis*, and *P. orientalis* in the introduced forests; *Q. wutaishansea* is a natural forest species and the climax community in this region.

2.2. Experimental design

Samples were collected in late August and early-September during the period of vegetative growth. Three plots (70 m ∗ 40 m) that were separated by at least 1 km were selected for each forest species with similar latitude, longitude, altitude and coverage; all selected trees in the plots in the Ziwuling mountains were approximately 25 years old. In addition, 3 subplots of 20 m ∗ 20 m were selected in each plot for a total of 36 subplots.

To collect plant samples (leaf, branch and fruit), 5 trees that had similar health and age were selected randomly and evenly in each subplot. For each selected tree, we collected 5 branches from the inner, middle and outer parts of each crown canopy, and mature leaves, branches and fruits that were without plant diseases or insect pests were selected and then brought back to the lab. A total of108plant samples (4forest species × 3 plots × 3 subplots × 3) were collected. Then, we collected the newly fallen and undecomposed leaf litter in the litter layer. The weight of each plant and litter sample was approximately 350 g. In every subplot, we collected 6 cores from 0 to 20 cm of the soil layer with a soil auger (diameter of 5 cm) after peeling off the litter surface following the "S" route; we mixed the cores evenly to form the soil sample before returning to the lab, and a total of 72 soil samples were collected.

2.3. Laboratory analysis

After returning to the lab, the plant and litter samples were oven-dried for 30 min at 105 °C and then dried at 65°Cfor approximately 72 h to a consistent weight, sieved through a 0.15-mm sieve after grinding with a ball mill and stored in a cool and dry place until analysis. The soil samples were air-dried for approximately7 days and then sieved through 2-mm and 0.15-mm mesh sieves after grinding with a ball mill.

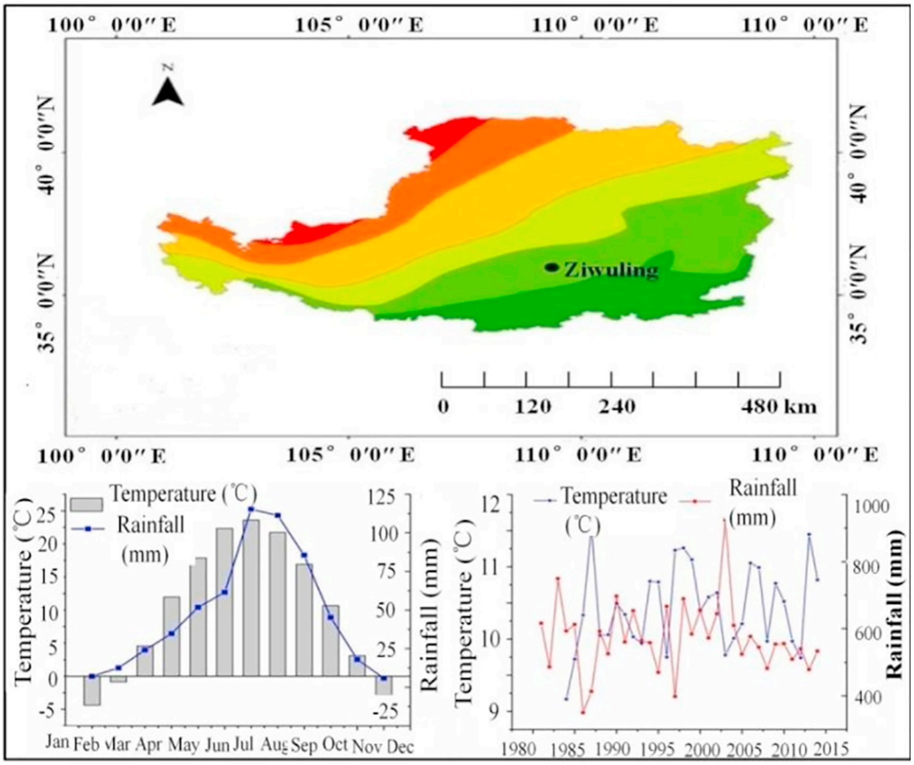

Fig. 1. The location, annual mean temperature and annual mean precipitation at the Ziwuling station on the Loess Plateau.

The organic C content in the soils and plants was measured using the potassium dichromate volumetric method (Bao, 2010). To measure the plant total P and N, the samples were digested initially with $H_2SO_4$and H_2O_2 (Bao, 2010), then the total P and total N contents were measured using the colorimetric (UV spectrophotometer) and micro-Kjeldahl method, respectively. To determine total N content of the soil, soil samples were digested initially with a H_2SO_4-mixed catalyst and then through the Kjeldahl acid-digestion method (KDY-9830) to determine the N content in the boiling fluids (Bao, 2010). Total P content of the soil was determined through molybdenum-blue colorimetry after digestion by $HClO_4$-H_2SO_4 and then measured through calorimetric analysis (Spectrophotometer UV-2300 from Techcomp Com (Shanghai, China)).

2.4. Data processing

The method proposed by Persson et al. (2010) to determine the degree of stoichiometric homeostasis of an organism was used. Regression analyses were conducted for N ($1/H_N$), P ($1/H_P$) and N:P ($1/H_{N:P}$) for leaves, branches, and fruits in the selected forest species. Since the slope was expected to be equal to or > 0,one-tailed tests with $\alpha = 0.1$ were used. If the regression relationship was nonsignificant ($p > 0.1$), 1/H was set to zero, and the organism was considered to be 'strictly homeostatic'. Species with $1/H = 1$ were considered not homeostatic. All datasets with significant regressions and $0 < 1/H < 1$ were classified as $0 < 1/H < 0.25$ 'homeostatic', $0.25 < 1/H < 0.5$ 'weakly homeostatic', $0.5 < 1/H < 0.75$ 'weakly plastic', or $1/H > 0.75$ 'plastic'. All data were described by the average value and standard deviation (SD). We have checked the data for homogeneity of the variances and normality. All analyses were conducted with SPSS 20.0 (SPSS Inc., Chicago, IL, USA). Scheffe's test was used to determine the differences in content and stoichiometry of C, N and P among the five forest species. Differences at $p < 0.05$ were considered statistically significant. Principal component analysis (PCA) was conducted using Canoco 5.0. All figures were drawn using Origin Pro 2018 (Origin Lab Corporation).

Table 1
The basic information of the plots and soil characteristics among different forest species.

Forest species	Sample plot number	Longitude	Latitude	Elevation (m)	Cove degree (%)	BD ($g\cdot cm^{-3}$)	Mean plant height (m)	Mean DBH (cm)
R. pseudoacacia	1	109°10′15″E	36°04′24″N	1188.4	73	1.02	8.82	41
	2	109°10′36″E	36°04′44″N	1190.2	72	1.03	8.85	41
	3	109°09′54″E	36°04′32″N	1195.5	75	1.03	8.89	41
P. tabuliformis	1	109°10′17″E	36°04′47″N	1186.4	71	1.06	7.77	38
	2	109°10′48″E	36°04′41″N	1185.9	74	1.08	7.74	37
	3	109°10′14″E	36°04′36″N	1183.7	78	1.07	7.78	39
P. orientalis	1	109°10′11″E	36°04′44″N	1173.8	74	1.04	6.43	40
	2	109°10′13″E	36°04′49″N	1175.3	75	1.03	6.3	41
	3	109°09′7″E	36°03′52″N	1174.7	76	1.04	6.6	40
Q. wutaishansea	1	109°08′59″E	36°05′15″N	1262	68	1.14	7.75	33
	2	109°08′37″E	36°04′20″N	1302	65	0.98	7.8	32
	3	109°09′27″E	36°05′25″N	1256	62	1.04	8.21	30

Note: BD: bulk density; *R. pseudoacacia*: *Robinia pseudoacacia*; *P. tabuliformis*: *Pinus tabuliformis*; *P. orientalis*: *Platycladus orientalis*; *Q. wutaishansea*: *Quercus wutaishansea.*

3. Results

3.1. Content of organic C, total N and total P in the plant-litter-soil system

As shown in Table 2, forest species had significant effects on the content of C, total N and total P in the plant-litter-soil system, but the differences between natural and introduced forest species were not obvious. Overall, the C content in *R. pseudoacacia* was lower than that in other forest species in the plant-litter-soil system. The leaf C content in *P. tabuliformis*, *P. orientalis* and *Q. wutaishansea* was significantly higher than the leaf C content in *R. pseudoacacia*. Branch C content in *P. tabuliformis* was 13.2%, 6.1% and 6.4% higher than that in *R. pseudoacacia*, *P. orientalis* and *Q. wutaishansea*, respectively. The fruit C content in *P. orientalis* and *Q. wutaishansea* was significantly higher than that in *R. pseudoacacia* and *P. tabuliformis.* The litter C content in *P. tabuliformis* was 1.26, 1.06 and 1.16 times higher than the litter C content in *R. pseudoacacia*, *P. orientalis* and *Q. wutaishansea*, respectively. The soil C content in *Q. wutaishansea* was 2.84, 1.59 and 1.18 times higher than that in *R. pseudoacacia*, *P. tabuliformis* and *P. orientalis*, respectively. Overall, the C content in leaves was higher than that in branches, fruit, litter and soil except for *R. pseudoacacia*.

In contrast to organic C content, N content in *R. pseudoacacia* was higher than that in other forest species in the plant-litter-soil system. The leaf N in *R. pseudoacacia* was 3.08, 2.82 and 1.92 times higher and the fruit N was 4.16, 4.20 and 3.85 times higher than that in *P. tabuliformis*, *P. orientalis* and *Q. wutaishansea*, respectively. In contrast, the soil N content in *R. pseudoacacia* was significantly lower than the soil N content in other forest species. Similar to N content, the leaf and fruit P contents in *R. pseudoacacia* were significantly higher than those in other forest species. The difference in soil P content among the selected forest species was not significant, ranging from 0.55 to 0.61 g/kg^{-1} (Table 2).

3.2. Ecological stoichiometry in the plant-litter-soil system

Overall, differences in C:N:P in the plant-litter-soil system were not obvious between the natural and introduced forest species. However, the leaf C:N:P ratios in the different forest species were significantly different. Across all the data, leaf C:N varied from 13.93 to 52.07 with *P. tabuliformis* > *P. orientalis* > *Q. wutaishansea* > *R. pseudoacacia* and differed significantly ($p < 0.05$) (Table 2). *P. orientalis* leaf C:P was the highest followed by *P. tabuliformis* then *Q. wutaishansea* and *R. pseudoacacia*. The leaf C:P in *P. orientalis* and *P. tabuliformis* was significantly higher than that in *Q. wutaishansea* ($p < 0.05$). Other than for *R. pseudoacacia*, values of leaf N:P in the other three plantations were smaller than 10; *R. pseudoacacia* leaf N:P was 12.2 followed by 6.94 for *Q. wutaishansea*, 6.08 for *P. orientalis* and 5.35 for *P. tabuliformis*.

Overall, the branch C:N and C:P were higher than the C:N and C:P in leaves, litter, fruit and soil. Similar to leaf C:N, *P. tabuliformis* litter C:N was the highest and was 4.07, 1.81 and 3.62 times higher than those in *R. pseudoacacia*, *P. orientalis* and *Q. wutaishansea*, respectively. The litter C:P ratio varied from 239.04 to 356.26 with *P. tabuliformis* > *P. orientalis* > *R. pseudoacacia* > *Q. wutaishansea.* The trend of the litter N:P ratio was exactly opposite to that of litter C:N and ranged from 3.80 to 12.19, and it was higher than those in leaves, branches, fruit and soil. Although the soil C and N contents were highly variable in the investigated forest species, the soil C:N ratios were remarkably consistent and varied from 9.59 to 11.97. Soil C:P was significantly smaller than leaf, branch, fruit and litter C:P. With the consistent soil P content, the soil N:P ranged from 1.14 to 2.92.

3.3. Stoichiometric homeostasis

The results of the degree of stoichiometric homeostasis of N, P and N:P in leaves, branches and fruit are shown in Figs. 2–4. For N content, the leaves of the four forest species and the branches and fruit of *P. tabuliformis* and *Q. wutaishansea* were categorized as 'strictly homeostasis' ($p > 0.1$) (Fig. 2). The fruit in *R. pseudoacacia* was 'weakly homeostatic', the branches in *R. pseudoacacia* were 'plastic' with $1/H = 1.36$ (Fig. 2a). The branches and litter of *P. orientalis* were 'weakly plastic' and 'weakly homeostatic', respectively.

For P content, the leaves, branches and fruit of *R. pseudoacacia*, the leaves and branches of *P. tabuliformis*, the leaves of *P. orientalis* and the leaves and fruit of *Q. wutaishansea* were categorized as 'strictly homeostasis' ($p > 0.1$) (Fig. 3). The fruit of *P. tabuliformis* was 'weakly homeostatic' with $1/H = 0.43$. The branches and fruit of *P. orientalis* were 'plastic' and 'weakly plastic', respectively. The branches of *Q. wutaishansea* were classified as 'homeostasis'.

For N:P stoichiometry, the leaves of *R. pseudoacacia*, the branches of *P. tabuliformis*, the leaves and fruit of *P. orientalis* and the leaves,

Table 2
Characteristics of the C, N and P contents and stoichiometry in the plant-litter-soil system among different forest species.

Forest species	Sample plot number	Carbon content (g/kg)	Nitrogen content (g/kg)	Phosphorus content (g/kg)	C:N	C:P	N:P
R. pseudoacacia	Leaf	413.94 ± 23.96Ba	29.74 ± 1.79Aa	2.43 ± 0.27Aa	13.95 ± 0.94Cc	171.77 ± 17.91Cc	12.31 ± 0.96Aa
	Branch	423.49 ± 22.87Ca	8.53 ± 2.19Ac	1.06 ± 0.19Bc	52.80 ± 12.94Ca	414.27 ± 84.46Aa	8.00 ± 1.00Ab
	Fruit	431.15 ± 33.18Ca	24.49 ± 2.42Ab	2.53 ± 0.21Aa	17.77 ± 2.18Cb	171.51 ± 17.04Dc	9.69 ± 0.47Aa
	Litter	398.22 ± 30.83Db	17.10 ± 2.06Ab	1.43 ± 0.32Bb	23.75 ± 4.09Cb	291.94 ± 69.96Bb	12.19 ± 1.31 Da
	Soil	6.76 ± 1.36Cc	0.70 ± 0.08Cd	0.61 ± 0.04Ad	9.63 ± 1.05Ac	11.12 ± 2.63Ad	1.14 ± 0.18Cc
P. tabuliformis	Leaf	495.48 ± 19.88Aa	9.67 ± 1.25Ca	1.81 ± 0.21Ca	52.07 ± 6.64Ad	277.26 ± 26.11Ab	5.40 ± 0.82Bb
	Branch	488.07 ± 20.99Aa	4.63 ± 0.80Bb	1.36 ± 0.31Ab	108.11 ± 17.76Aa	377.56 ± 93.13Ba	3.55 ± 0.90Bc
	Fruit	452.77 ± 29.52Bb	5.88 ± 1.32Bb	1.28 ± 0.19Cb	82.25 ± 25.20Ac	362.57 ± 73.50Ba	4.56 ± 0.73Bb
	Litter	501.02 ± 33.65Aa	5.34 ± 0.65Cb	1.42 ± 0.19Bb	96.75 ± 10.31Ab	356.26 ± 40.44Aa	3.80 ± 0.53Ca
	Soil	12.04 ± 1.83Bc	1.25 ± 0.13Bc	0.58 ± 0.09Ac	9.59 ± 0.89Ae	21.13 ± 4.59Ac	2.21 ± 0.48 Bd
P. orientalis	Leaf	483.81 ± 25.92Aa	10.55 ± 0.46Ca	1.73 ± 0.10Ca	46.01 ± 3.66Ab	279.89 ± 20.18Ab	6.10 ± 0.42Bb
	Branch	458.00 ± 16.55Bb	5.10 ± 0.5Bc	1.09 ± 0.22Bc	92.29 ± 14.91Ba	434.64 ± 77.84Aa	4.78 ± 0.88Bb
	Fruit	474.47 ± 34.11Aa	5.83 ± 1.16Bc	1.11 ± 0.18Dc	83.86 ± 15.62Aa	434.06 ± 63.88Aa	5.30 ± 0.98Bb
	Litter	474.35 ± 49.88Ba	8.81 ± 0.90Bb	1.48 ± 0.09Bb	53.51 ± 5.09Bb	321.37 ± 39.11Bb	5.97 ± 0.72Ba
	Soil	16.20 ± 2.61Ac	1.53 ± 0.19Ad	0.55 ± 0.05Ad	10.62 ± 0.26Ac	29.46 ± 4.36Ac	2.77 ± 0.39Ac
Q. wutaishansea	Leaf	486.79 ± 19.00Aa	15.42 ± 1.29Ba	2.22 ± 0.22Ba	31.81 ± 2.99Bb	221.97 ± 22.89Bc	7.00 ± 0.85Bb
	Branch	456.54 ± 23.92Bb	5.13 ± 0.43Bb	1.06 ± 0.15Bc	89.64 ± 9.52Ba	441.22 ± 67.33Aa	4.96 ± 0.81Bb
	Fruit	468.57 ± 29.73Aa	6.37 ± 0.43Bb	1.75 ± 0.17Bb	73.76 ± 4.27Ba	270.98 ± 31.39Cb	3.68 ± 0.43Bc
	Litter	431.37 ± 12.87Cc	16.26 ± 1.53Aa	1.83 ± 0.22Ab	26.74 ± 2.45Cb	239.04 ± 27.41Cb	8.98 ± 1.10Aa
	Soil	19.18 ± 2.14Ad	1.60 ± 0.14Ac	0.55 ± 0.03Ac	11.96 ± 0.59Ac	35.00 ± 4.30Ad	2.92 ± 0.27Ad

Note: *R. pseudoacacia*: *Robinia pseudoacacia*; *P. tabuliformis*: *Pinus tabuliformis*; *P. orientalis*: *Platycladus orientalis*; *Q. wutaishansea*: *Quercus wutaishansea.* Different capital letters indicate significant differences among different forest species and different lower case letters indicate significant differences in the leaves, branches, fruits, litter and soil.

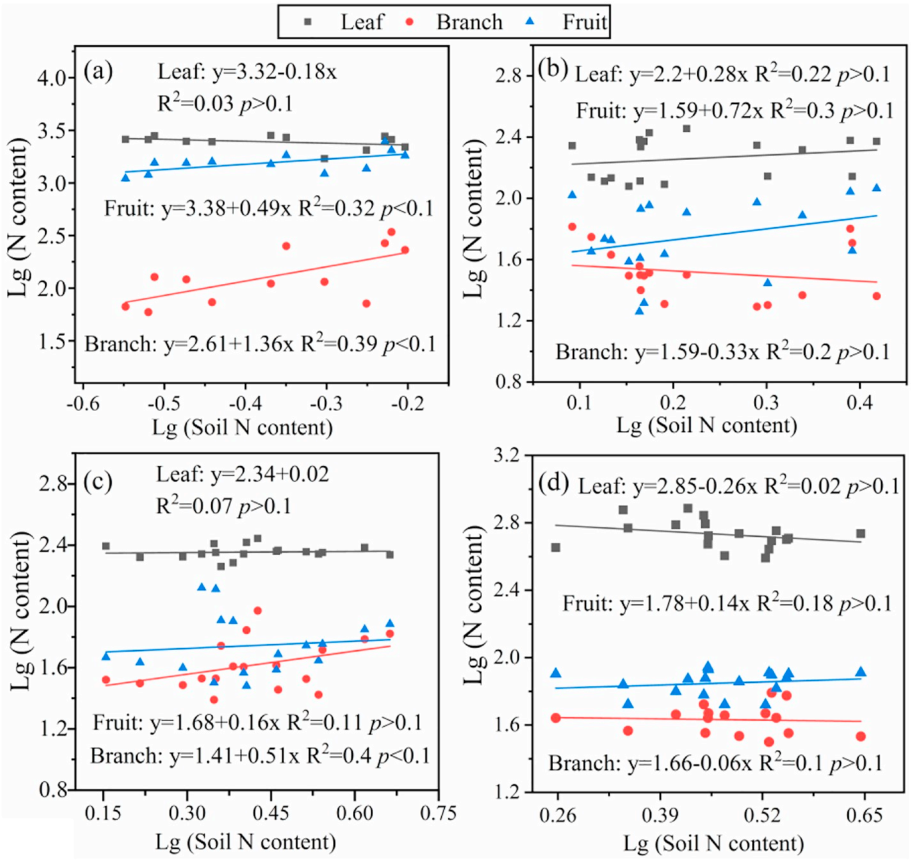

Fig. 2. Relationships between $\log_{10}$-transformed N content in plants, litter and soil for (a) *Robinia pseudoacacia*; (b) *Pinus tabuliformis*; (c) *Platycladus orientalis*; and (d) *Quercus wutaishansea*.
One-tailed tests with $\alpha = 0.1$ were used. If the regression was nonsignificant ($p > 0.1$), 1/H was set to zero, and the organism was considered to be 'strictly homeostatic'. Species with $1/H = 1$ were considered not homeostatic. All datasets with significant regressions and $0 < H < 1$ were categorized as: $0 < 1/H < 0.25$: 'homeostatic'; $0.25 < 1/H < 0.5$: 'weakly homeostatic'; $0.5 < 1/H < 0.75$: 'weakly plastic'; $1/H > 0.75$ 'plastic'. For $1/H > 1$, 1/H close to 1 indicates weak or no stoichiometric homeostasis, and 1/H much larger than 1 indicates 'homeostatic'.

branches and fruit of *Q. wutaishansea* were identified as 'strictly homeostasis' ($p > 0.1$) (Fig. 4). The branches of *R. pseudoacacia* and *P. orientalis* showed 'homeostasis' with 1/H of 4.62 and 3.78, respectively. The fruit of *R. pseudoacacia* and the leaves and fruit of *P. tabuliformis* were 'weakly homeostatic'.

3.4. Relationships of C, N and P contents and ecological stoichiometry in the plant-litter-soil system

Relationships among the C, N and P content and ecological stoichiometry in the plant-litter-soil system are shown in Fig. 5. The principal component analysis (PCA) results showed that, except for *P. orientalis*, the leaf C, N, P and branch C, N were significantly correlated in the selected forest species (Fig. 5a). Moreover, fruit P had a significant positive influence on branch C. The leaf, litter and fruit N:P were significantly positively correlated, especially in *R. pseudoacacia* (Fig. 5b). Branch C:N, C:P and N:P were significantly positively correlated, litter C:N significantly affected both leaf and fruit C:N and C:P, especially in *P. orientalis* and *P. tabuliformis*. In addition, leaf, litter and fruit N:P were significantly negatively correlated with leaf and fruit C:N, C:P and litter C:N.

4. Discussion

4.1. C, N and P contents in the plant-soil-litter system

The C, N, and P contents significantly differed in the plant-soil-litter system and among forest species, which was consistent with our first hypothesis and previous studies (Han et al., 2005; Mulder and Elser, 2009; Chen et al., 2016). Except for *R. pseudoacacia*, leaf C content in the forest species was higher than the average leaf C content of 126 plant species in the Loess Plateau (Zheng and Shangguan, 2006) and higher than the global average leaf C content (461.60 g·kg^{-1}) (Elser et al., 2000b). Overall, except for *R. pseudoacacia*, the leaf N contents were smaller than values in a related study in the Loess Plateau region (24 g·kg^{-1}) and smaller than the average leaf N content nationwide (Elser et al., 2000b; Reich and Oleksyn, 2004; Han et al., 2005). The lower leaf N content maybe due to the arid soil; plants only absorb available nitrogen that is highly mobile (NH_4^+ and NO_3^-), which would leach as the vegetation is relatively sparse and rainfall is concentrated in the loess hill. The plant N and P contents in *R. pseudoacacia* were higher than those in the other three forest species. Higher plant N content in *R. pseudoacacia* may result from it being a fast-growing leguminous species that can compensate for the lack of leaf N, caused by an insufficient soil nitrogen supply, through fixing atmospheric N via rhizobium. Except for *P. orientalis*, leaf P contents were all higher than those reported by Zheng and Shangguan (2006) in the Loess Plateau (1.60 g·kg^{-1}) and higher than those reported by Han et al. (2005), who measured leaves of 753 species nationwide. Higher content of leaf N or P indicates higher photosynthetic rate, faster growth rate and stronger resource competitive ability, and higher C content results in larger specific leaf weight and lower photosynthetic and growth rates but stronger defense capabilities (Niklas and Cobb, 2005).

Forest soil C and nutrient contents are closely related to the species and growth status of the covered vegetation and mineralization of litter (Freschet et al., 2013). Trends of soil C and N were the same among our studied forest species, which results from both soil C and N, the vital components of soil organic matter and being closely associated (Redfield, 1958). Hyvonen et al. (2008) conducted a long-term localization experiment in 15 forests and showed that, to some extent, the input of C can improve soil N accumulation with a simultaneous increase soil C mineralization with increased N input. Our study suggested that soil N content in Ziwuling is higher than that in other regions of the Loess Plateau (0.77 g/kg) with the exception of *R. pseudoacacia* (Liu, 2013).

Nutrients and soil water content are the main factors hindering

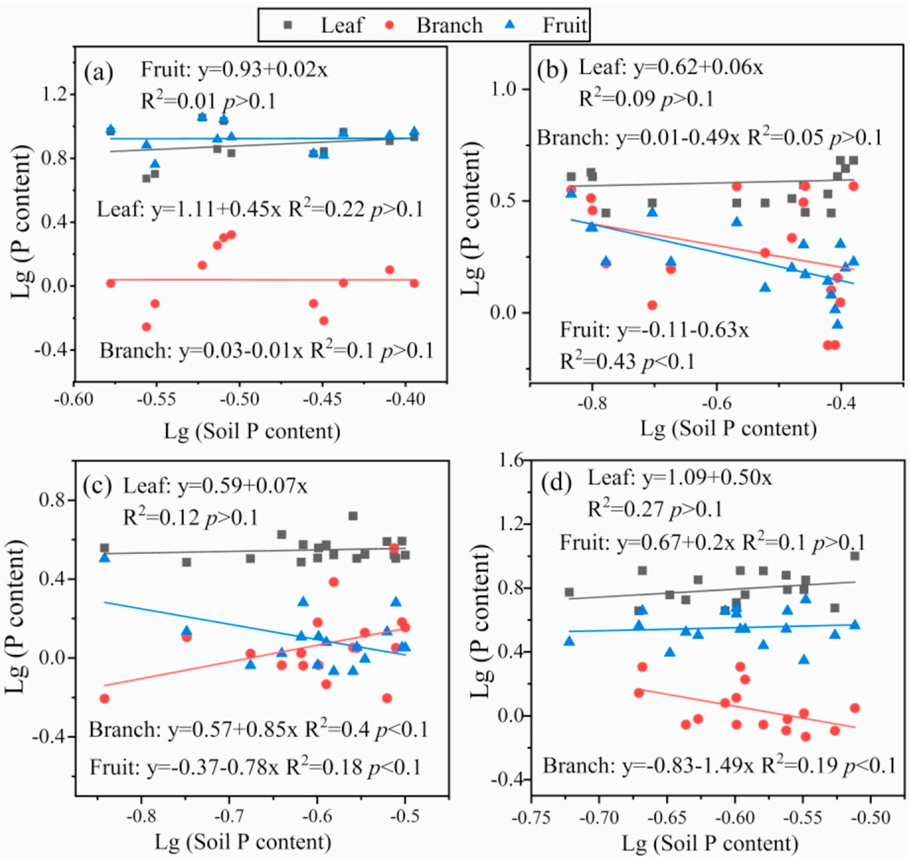

Fig. 3. Relationships between $\log_{10}$-transformed P content in plants, litter and soil for (a) *Robinia pseudoacacia*; (b) *Pinus tabuliformis*; (c) *Platycladus orientalis*; and (d) *Quercus wutaishansea*.

vegetation growth in the Loess Plateau. Across the entire data set, leaf and soil C, N and P contents in *Q. wutaishansea* were relatively higher than the introduced forest species, which demonstrates that *Q. wutaishansea* forests the natural climax community, are able to prevent wind-water erosion and other adverse environmental conditions. Further, our results indicated that the growth rate and nutrient absorption capacity of *Q. wutaishansea* exceeded the introduced tree species under the nutrient deficient conditions on the Loess Plateau. As previously reported, compared to the introduced forest, the water deficit was not as serious for the natural forest but this deficit did not affect the development and succession of natural vegetation (Yang et al., 2012). On the Loess Plateau, the existing natural vegetation has been preserved during hundreds of years of natural development and adaptation and is a stable system with coexisting trees, shrubs and grasses and a sustainable distribution of species with the ability to self-regulate that formed over long-term succession (Yang et al., 2012).

4.2. C, N and P stoichiometry in the plant-soil-litter system

C:N:P be used as an effective tool to analyze coupled relationships and differences between each element in the plant-soil system (Sterner and Elser, 2002; Zhang et al., 2011). The C, N and P stoichiometry showed clear trends among the selected forest species, which was consistent with our second hypothesis. The leaf C:N ranged from 13.92 to 45.88 with an average of 33.65, which was higher than the global average leaf C:N (22.5), while the average leaf C:P was smaller than the global average leaf C:P (469.16) (Elser et al., 2000b). The results indicated that these forest species have higher P utilization rates and lower N utilization efficiency. The Growth Rate Hypothesis suggests that the growth rate of an organism is negatively related to C:N and C:P (Sterner and Elser, 2002). The growth rate of *Q. wutaishansea* was higher than the introduced forest species as the C:N and C:P of *Q. wutaishansea* were relatively smaller than in the introduced forests.

In this study, the N:P ratios for plant tissues ranged from 3.55 to 12.31, which were smaller than the average N:P ratio of terrestrial plant species in their natural field sites (12 − 13) (Elser et al., 2000b; Güsewell, 2004). The relatively low N content resulted in smaller N:P in our study site. Growth of vegetation requires photosynthetic products, and protein synthesis requires ribosomes, which contain large amounts of N and P (van Duren and Pegtel, 2000). Therefore, the leaf N:P ratio is usually used to evaluate nutrient limitation (Sterner and Elser, 2002; Schreeg et al., 2014; Mayor et al., 2017). Güsewell (2004) found that when leaf N:P was smaller than 10, vegetation was relatively N-limited, and when leaf N:P was larger than 20, vegetation was relatively P-limited, and if leaf N:P ranged from 10 to 20, vegetation was limited by N or P depending on the plant species. According to Güsewell (2004), leaf N:P ranged from 5.35 to 12.21, which indicates that, except for *R. pseudoacacia*, the other forest species are all N-limited. In addition, by measuring > 753 species, Han et al. (2005) found that the growth of vegetation was usually limited by N in China. The leaf N:P was significantly positively correlated with fruit and, in particular, litter N:P (Fig. 5), which indicated that litter N:P ratio could be used as an indicator of soil nutrient availability in forests. Further, fertilizer experiments should be conducted to test the validity of this idea in the future.

The stoichiometric ratios of C:N:P varied within communities during plant ontogeny because nutrient use strategies significantly differed among plant life forms and vegetation types (Koerselman and Meuleman, 1996; Schreeg et al., 2014). In general, litter C:N is negatively correlated with litter decomposition rate (Sariyildiz and Anderson, 2003). The litter C:N of *P. tabuliformis* and *P. orientalis* was higher than that in *R. pseudoacacia* and *Q. wutaishansea*, which was

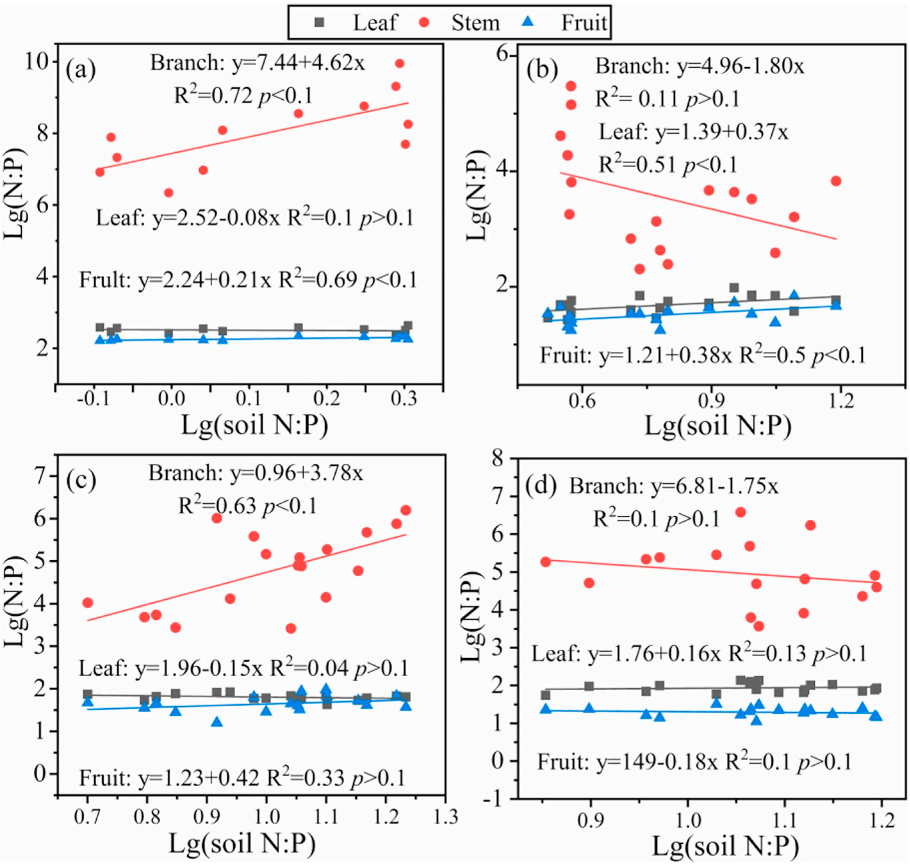

Fig. 4. Relationships between $\log_{10}$-transformed N:P stoichiometry in plants, litter and soil for (a) *Robinia pseudoacacia*; (b) *Pinus tabuliformis*; (c) *Platycladus orientalis*; and (d) *Quercus wutaishansea*.

consistent with studies showing that the litter decomposition rate in deciduous broad-leaved forests was higher than in evergreen coniferous forests (Taylor et al., 1989; Berg, 2014).

The stoichiometry of soil C, N and P varied widely, and forest species had a critical influence on the soil C, N and P stoichiometry (Fig. 4), which is consistent with previous research (Mulder and Elser, 2009; Chen et al., 2016). The average soil C:N value was 10.74, which is similar to the average value across China (11.0) (Tian et al., 2010), but

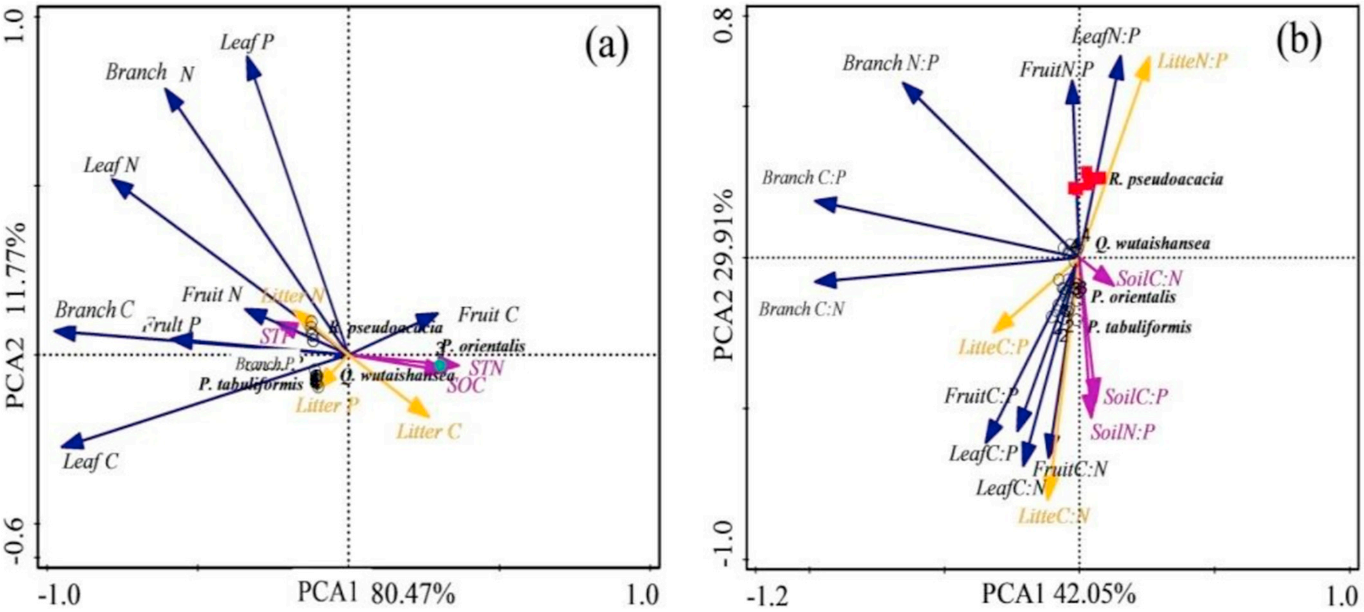

Fig. 5. In Fig. 5(a), PCA was used to identify the relationships of C, N and P contents in the plant-litter-soil system. PCA axes 1 and 2 explained 80.47% and 11.77% of the variation, respectively. In Fig. 5(b), PCA was used to identify the relationships of C, N and P stoichiometry in the plant-litter-soil system. PCA axes 1 and 2 explained 42.05% and 29.91% of the variation, respectively.

smaller than the value globally (13.33) (McGroddy et al., 2004). The average soil C:P (24.89) and N:P (2.28) were both smaller than the average value across China (Tian et al., 2010). The results indicated that soil P was relatively high in the study area.

4.3. Stoichiometric homeostasis of plant tissues

Ecological stoichiometry has often presumed flexible homeostasis for autotrophs and strict homeostasis for animals (Sterner and Elser, 2002). However, emerging research indicates that the situation is more complicated (Persson et al., 2010; Yu et al., 2010; Wang et al., 2018). Sterner and Elser (2002) found that the limiting element (N in our study) is the main regulator of homeostasis. In this study, the leaf, stem and fruit N contents in *Q. wutaishansea* and *P. tabuliformis* were categorized as 'strictly homeostasis'. Even though *Q. wutaishansea* and *P. tabuliformis* were limited by N, plants may change the availability and utilization efficiency of the limiting element through a variety of physiological and biochemical mechanisms to maintain the nutrient content of their bodies and the stability of related characters (Hesson et al., 2004). Although *R. pseudoacacia* is a leguminous species, the *R. pseudoacacia* fruit and branches were 'weakly homeostatic'. Yu et al. (2010) found that species-level stoichiometric homeostasis was positively correlated with the stability of vegetation as the species with a high degree of homeostasis may be more conservative in their use of nutrients improving their adaptation to arid conditions. As previously reported, the species with the highest degree of N homeostasis consistently had the relatively highest growth rates (Yu et al., 2012) and well-developed storage systems (Johnson et al., 2008; Yu et al., 2010). Therefore, resource utilization and storage functions of these species mitigated environmental variations (Aerts and Chapin, 2000), resulting in spatiotemporal stability in abundance (Tilman et al., 2006).

Moreover, except for the branches and fruit of *P. orientalis*, which were 'plastic' and 'weakly plastic', respectively, the other plant tissues had P homeostasis in the selected forest species. Our results revealed that forest species on the Loess Plateau had a considerable range in the strength of N and P homeostasis and did not generally support the concept of close association with environmental nutrient supply originally emphasized in stoichiometric theory. The degree of elemental and stoichiometric homeostasis appeared to differ among plant tissues for the same plant, which reflects a fundamental trade-off in nutrient investment and allocation (Yu et al., 2011; Gu et al., 2017). Except for the leaf N:P in *P. tabuliformis*, the leaf N, P and N:P homeostasis in other forest species were characterized as 'strictly homeostasis'. Leaves are the main photosynthetic organ and thus are important for plant growth and biomass accumulation; therefore, nutrient contents are constrained with a certain range to provide optimal physiological traits (Aerts and Chapin, 2000; Wang et al., 2018).

Compared to N or P alone, the N:P stoichiometric homeostasis was better for evaluating the homeostasis condition of plants, as the stoichiometric homeostasis reflects the consumption of nutrients by organisms and the storage capacity of nutrients during the period of growth (Blouin et al., 2012). The N:P stoichiometry of plant tissues in *Q. wutaishansea* was 'strictly homeostasis'. For the growth and development of plants, maintenance of stable elements in their bodies in a changeable environment is advantageous for survival (Blouin et al., 2012). This result may reflect that the natural forest has more developed modulation systems than introduced species or that the natural species contain more functional materials, which allows them to respond more quickly to different nutrient regimes.

Overall, our results and the results from previous studies demonstrate that the degree of stoichiometric homeostasis for trees and herbs is higher than phytoplankton (Persson et al., 2010), indicating a stronger stoichiometric homeostasis in higher plants than in lower plants. These results verified our third hypothesis that stoichiometric homeostasis exists for trees, and the degree of stoichiometric homeostasis was clear among plant tissues. In summary, the combined results of N and P homeostasis and N:P stoichiometric homeostasis indicate that *Q. wutaishansea* is more adaptable to the arid and N-limited environment on the Loess Plateau.

5. Conclusions

This study comprehensively explored the content, stoichiometry and stoichiometric homeostasis of C, N and P in the plant-litter-soil system among different forest species on the Loess Plateau, China. The results showed that C, N and P contents and stoichiometry varied significantly among different forest species and in the plant-litter-soil system. Overall, C, N and P contents of *Q. wutaishansea* plant tissues were relatively higher than those of the other three forest species. In addition, *Q. wutaishansea* played an important role in improving soil C and N contents. The soil C:N:P stoichiometry for *Q. wutaishansea* was higher than that for introduced forest species, while leaf and litter C:N:P stoichiometry for introduced forest species was higher than that for *Q. wutaishansea*. For leaf N:P, with the exception of *R. pseudoacacia*, the growth of the forest species was limited by N. N, P and N:P homeostasis was found in tree tissues, especially in *Q. wutaishansea*. Forest species and plant tissues have critical effects on the strength of homeostasis. Based on plant-soil C, N and P contents and elemental and stoichiometric homeostasis, *Q. wutaishansea* is more adaptable to the arid and N-limiting environment on the Loess Plateau. Our results indicated that natural forest vegetation development is superior to introduced forests for adaptation to the water-depleted and nutrient-poor environment.

Acknowledgments

The Acknowledgments should be: This study was supported by the National Natural Science Foundation of China (41877074) and the National Science Foundation for Young Scientists of China (41701317).

References

Aerts, R., Chapin III, F.S., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv. Ecol. Res. 30, 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1.

Bai, Y., Wu, J., Clark, C.M., Pan, Q., Zhang, L., Chen, S., Han, X., 2012. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. J. Appl. Ecol. 49, 1204–1215. https://doi.org/10.1111/j.1365-2664.2012.02205.x.

Bao, S.D., 2010. Soil and Agriculture Chemistry Analysis. China Agriculture Press, Beijing.

Berg, B., 2014. Decomposition patterns for foliar litter–a theory for influencing factors. Soil Biol. Biochem. 78, 222–232. https://doi.org/10.1016/j.soilbio.2014.08.005.

Blouin, M., Mathieu, J., Leadley, P.W., 2012. Plant homeostasis, growth and development in natural and artificial soils. Ecol. Complex. 9, 10–15. https://doi.org/10.1016/j.ecocom.2011.11.001.

Bui, E.N., Henderson, B.L., 2013. C:N:P stoichiometry in Australian soils with respect to vegetation and environmental factors. Plant Soil 373, 553–568. https://doi.org/10.1007/s11104-013-1823-9.

Chen, Y., Chen, L., Peng, Y., Ding, J., Li, F., Yang, G., 2016. Linking microbial C:N:P stoichiometry to microbial community and abiotic factors along a 3500-km grassland transect on the Tibetan plateau. Glob. Ecol. Biogeogr. 25, 1416–1427. https://doi.org/10.1111/geb.12500.

Damien, F., Kathryn, P., Kerrilyn, C., Marco, K., Fiona, R., Roger, A., Ram, D., 2016. Ecological stoichiometry controls the transformation and retention of plant-derived organic matter to humus in response to nitrogen fertilization. Soil Biol. Biochem. 99, 117e127. https://doi.org/10.1016/j.soilbio.2016.05.006.

Daufresne, T., 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. Nature 429, 171–174. https://doi.org/10.1038/nature02454.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., et al., 2000a. Nutritional constraints in terrestrial and freshwater food webs. Nature 408, 578–580. https://doi.org/10.1038/35046058.

Elser, J., Sterner, R., Gorokhova, E., Fagan, W., Markow, T., Cotner, J., Harrison, J.F., Hobbie, S.E., Odell, G.M., Weider, L.W., 2000b. Biological stoichiometry from genes to ecosystems. Ecol. Lett. 3, 540–550. https://doi.org/10.1111/j.1461-0248.2000.00185.x.

Fan, H., Wu, J., Liu, W., Yuan, Y., Hu, L., Cai, Q., 2015. Linkages of plant and soil C:N:P stoichiometry and their relationships to forest growth in subtropical plantations. Plant Soil 392, 127–138. https://doi.org/10.1007/s11104-015-2444-2.

Fanin, N., Fromin, N., Buatois, B., Hättenschwiler, S., 2013. An experimental test of the hypothesis of non-homeostatic consumer stoichiometry in a plant litter-microbe system. Ecol. Lett. 16, 772. https://doi.org/10.1111/ele.12108.

Freschet, G.T., William, K., Cornwell, D.A., Wardle, T.G., Elumeeva, W.L., Benjamin, G., Jackson, V.G., Onipchenko, N.A., Soudzilovskaia, J.T., Johannes, H.C., 2013. Linking litter decomposition of above- and below-ground organs to plant–soil feedbacks worldwide. J. Ecol. 101, 943–952. https://doi.org/10.1111/1365-2745.12092.

Fu, B.J., Wang, S., Liu, Y., Liu, J.B., Liang, W., Miao, C.Y., 2017. Hydrogeomorphic ecosystem responses to natural and anthropogenic changes in the Loess Plateau of China. Ann. Rev. Earth Planet. Sci. 45, 223–243. https://doi.org/10.1146/annurev-earth-063016-020552.

Gu, Q., Zamin, T.J., Grogan, P., 2017. Stoichiometric homeostasis: a test to predict tundra vascular plant species and community-level response to climate change. Arct. Sci. 3, 320–333. https://doi.org/10.1139/AS-2016-0032.

Güsewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance. New Phytol. 164, 243–266. https://doi.org/10.1111/j.1469-8137.2004.01192.x.

Han, W., Fang, J., Guo, D., Zhang, Y., 2005. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. New Phytol. 168, 377–385. https://doi.org/10.1111/j.1469-8137.2005.01530.x.

Hesson, D.O., Agren, G.I., Anderson, T.R., et al., 2004. Carbon sequestration in ecosystems: the role of stoichiometry. Ecology 85, 1179–1192. https://doi.org/10.1890/02-0251.

Hooper, D.U., Chapin, F.S., Elser, J.J., Hector, A., Inchausti, P., Lavorel, S., et al., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35. https://doi.org/10.1890/04-0922.

Hyvonen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G., Linder, S., 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogechemistry 89, 127–137. https://doi.org/10.1007/s10533-007-9121-3.

Johnson, N.C., Rowland, D.L., Corkidi, L., Allen, E.B., 2008. Plant winners and losers during grassland N-eutrophication differ in biomass allocation and mycorrhizas. Ecology 89, 2868–2878. https://doi.org/10.1890/07-1394.1.

Koerselman, W., Meuleman, A.F., 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450. https://doi.org/10.2307/2404783.

Levi, M.P., Cowling, E.B., 1969. Role of nitrogen in wood deterioration VII. Physiological adaptation of wood-destroying and other fungi to substrates deficient in nitrogen. Phytopathology 59, 460–468. https://doi.org/10.1016/S0959-4752(01)00019-6.

Liu, Z.P., 2013. Spatial Distribution of Soil Nutrients and the Impact Factors Across the Loess Plateau of China [D]. The University of Chinese Academy of Sciences.

Liu, R., Zhao, H., Zhao, X., Drake, S., 2011. Facilitative effects of shrubs in shifting sandon soil macro-faunal community in Horqin Sand Land of Inner Mongolia, Northern China. Eur. J. Soil Biol. 47, 316–321doi: https://doi.org/10.1016/j.ejsobi.2011.07.006.

Makino, W., Cotner, J.B., Sterner, R.W., Elser, J.J., 2003. Are bacteria more like plants or animals? Growth rate and substrate dependence of bacterial C:N:P stoichiometry. Funct. Ecol. 17, 121–130. https://doi.org/10.1046/j.1365-2435.2003.00712.x.

Mayor, J.R., Sanders, N.J., Classen, A.T., Bardgett, R.D., Clément, J.C., Fajardo, A., 2017. Elevation alters ecosystem properties across temperate treelines globally. Nature 542, 91–96. https://doi.org/10.1038/nature21027.

McGroddy, M.E., Daufresne, T., Hedin, L.O., 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. Ecology 85, 2390–2401. https://doi.org/10.1890/03-0351.

Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S., Richter, A., 2014. Stoichiometric imbalances between terrestrial decomposer communities and their resources: mechanisms and implications of microbial adaptations to their resources. Front. Microbiol. 5. https://doi.org/10.3389/fmicb.2014.00022.

Mulder, C., Elser, J.J., 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. Glob. Chang. Biol. 15, 2730–2738. https://doi.org/10.1111/j.1365-2486.2009.01899.x.

Niklas, K.J., Cobb, E.D., 2005. N, P, and C stoichiometry of Eranthishyemalis (Ranunculaceae) and the allometry of plant growth. Am. J. Bot. 92, 1256–1263. https://doi.org/10.2307/4126089.

Persson, J., Fink, P., Goto, A., James, M.H., Jayne, J., Satoshi, K., 2010. To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119, 741–751. https://doi.org/10.1111/j.1600-0706.2009.18545.x.

Redfield, A.C., 1958. The biological control of chemical factors in the environment. Am. Sci. 46, 205–211. https://doi.org/10.1086/646891.

Reich, P.B., 2005. Global biogeography of plant chemistry: filling in the blanks. New Phytol. 168, 263–266. https://doi.org/10.1111/j.1469-8137.2005.01562.x.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and in relation to temperature and latitude. Proc. Natl. Acad. Sci. U. S. A. 101, 11001–11006. https://doi.org/10.1073/pnas.0403588101.

Ren, C., Zhao, F., Kang, D., Yang, G., Han, X., Tong, X., et al., 2016. Linkages of C:N:P stoichiometry and bacterial community in soil following afforestation of former farmland. For. Ecol. Manag. 376, 59–66. https://doi.org/10.1016/j.foreco.2016.06.004.

Rhee, G., 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnol. Oceanogr. 23 (1), 10–25. https://doi.org/10.4319/lo.1978.23.1.0010.

Richardson, S.J., Allen, R.B., Doherty, J.E., 2008. Shifts in leaf N:P ratio during resorption reflect soil P in temperate rainforest. Funct. Ecol. 22, 738–745. https://doi.org/10.1111/j.1365-2435.2008.01426.x.

Sariyildiz, T., Anderson, J.M., 2003. Interactions between litter quality, decomposition and soil fertility: a laboratory study. Soil Biol. Biochem. 35, 391–399. https://doi.org/10.1016/s0038-0717(02)00290-0.

Schreeg, L.A., Santiago, L.S., Wright, S.J., Turner, B.L., 2014. Stem, root, and older leaf N:P ratios are more responsive indicators of soil nutrient availability than new foliage. Ecology 95, 2062–2068. https://doi.org/10.1890/13-1671.1.

Sophie, Z., Katharina, M.K., Maria, M., Jordi, S., Wolfgang, W., 2015. The application of ecological stoichiometry to plant–microbial–soil organic matter transformations. Ecol. Monogr. 85, 133–155. https://doi.org/10.1890/14-0777.1.

Sterner, R.W., Elser, J.J., 2002. Ecological Stoichiometry: The Biology of Elements From Molecules to the Biosphere. Princeton University Press.

Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70, 97–104. https://doi.org/10.2307/1938416.

Tian, H., Chen, G., Zhang, C., Melillo, J.M., Hall, C.A., 2010. Pattern and variation of C:N:P ratios in China's soil: a synthesis of observational data. Biogeochemistry 98, 139–151. https://doi.org/10.1007/s10533-009-9382-0.

Tilman, D., 2004. Niche trade-offs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. PNAS 101, 10854–10861. https://doi.org/10.1073/pnas.0403458101.

Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441, 629–632. https://doi.org/10.1038/nature04742.

van Duren, I.C., Pegtel, D.M., 2000. Nutrients limitations in wet, drained and rewetted fen meadows: evaluation of methods and results. Plant Soil 220, 35–47. https://doi.org/10.1023/a:1004735618905.

Wang, J.Y., Wang, J.N., Guo, W.H., Li, Y.G., Geoff, G., Wu, T.G., 2018. Stoichiometric homeostasis, physiology, and growth responses of three tree species to nitrogen and phosphorus addition. Trees 32, 1377–1386. https://doi.org/10.1007/s00468-018-1719-7.

Yang, L., Wei, W., Chen, L.D., et al., 2012. Response of deep soil moisture to land use and afforestation in the semi-arid Loess Plateau, China. J. Hydrol. 475, 111–122. https://doi.org/10.1016/j.jhydrol.2012.09.041.

Yang, Y., Liu, B.R., An, S.S., 2018. Ecological stoichiometry in leaves, roots, litters and soil among different plant communities in a desertified region of Northern China. Catena 166, 328–338. https://doi.org/10.1016/j.catena.2018.04.018.

Yu, Q., Chen, Q., Elser, J.J., He, N., Wu, H., Zhang, G., Han, X., 2010. Linking stoichiometric homoeostasis with ecosystem structure, functioning and stability. Ecol. Lett. 13, 1390–1399. https://doi.org/10.1111/j.1461-0248.2010.01532.x.

Yu, Q., Elser, J., He, N., Wu, H., Chen, Q., Zhang, G., Han, X., 2011. Stoichiometric homeostasis of vascular plants in the Inner Mongolia grassland. Oecologia 166, 1–10. https://doi.org/10.1007/s00442-010-1902-z.

Yu, Q., Wu, H., He, N., Lu¨, X., Wang, Z., Elser, J.J., Wu, J., Han, X., 2012. Testing the growth rate hypothesis in vascular plants with above- and below-ground biomass. PLoS One e32162, 7. https://doi.org/10.1371/journal.pone.0032162.

Yuan, Z., Chen, H.Y., Reich, P.B., 2011. Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. Nat. Commun. 2, 344. https://doi.org/10.1038/ncomms1346.

Zechmeister-Boltenstern, S., Keiblinger, K.M., Mooshammer, M., Penuelas, J., Richter, A., Sardans, J., et al., 2015. The application of ecological stoichiometry to plant-microbial-soil organic matter transformations. Ecol. Monogr. 85, 133–155. https://doi.org/10.1890/14-0777.1.

Zeng, Q.C., Lal, Rattan, Chen, Y.N., An, S.S., 2017. Soil, leaf and root ecological stoichiometry of Caragana korshinskii on the Loess Plateau of China in relation to plantation age. PLoS One e0168890, 12. https://doi.org/10.1371/journal.pone.0168890.

Zhang, G.M., Han, X.G., Elser, J.J., 2011. Rapid top-down regulation of plant C:N:P stoichiometry by grasshoppers in an Inner Mongolia grassland ecosystem. Oecologia 166, 253–264. https://doi.org/10.1007/s00442-011-1904-5.

Zhang, W., Liu, W.C., Xu, M.P., Deng, J., Han, X.H., Yang, G.H., Feng, Y.Z., Ren, G.X., 2019. Response of forest growth to C:N:P stoichiometry in plants and soils during *Robinia pseudoacacia* afforestation on the Loess Plateau, China. Geoderma 337, 280–289. https://doi.org/10.1016/j.geoderma.2018.09.042.

Zheng, S., Shangguan, Z., 2006. The spatial distribution pattern of plant leaf nutrient composition in Loess Plateau. Prog. Nat. Sci. 16, 965–973.