Trees (2018) 32:1377–1386
https://doi.org/10.1007/s00468-018-1719-7

ORIGINAL ARTICLE

# Stoichiometric homeostasis, physiology, and growth responses of three tree species to nitrogen and phosphorus addition

Jingyuan Wang[1] · Jiannan Wang[1] · Weihong Guo[1] · Yingang Li[2] · G. Geoff Wang[3] · Tonggui Wu[1,3]

Received: 2 February 2018 / Accepted: 6 June 2018 / Published online: 11 June 2018

## Abstract

***Key message*** **Homeostatic regulation coefficient (*H*) exists for trees and the tree species with higher *H* are more stable in physiological and growth responses to nutrient addition.**

**Abstract** Stoichiometric homeostasis, indicated by the homeostasis regulation coefficient (*H*), is closely related to evolutionary stage, and can reflect physiological and biochemical adaption of organisms to environmental changes. However, stoichiometric homeostasis is seldom studied in trees. In this case study, three tree species, two angiosperms (*Quercus acutissima* and *Sapium sebiferum*) and one gymnosperm (*Metasequoia glyptostroboides*), were chosen to calculate the *H* of nitrogen ($H_N$), phosphorus ($H_P$), and nitrogen:phosphorus ($H_{N:P}$) after soil N and P addition. The responses of physiology, growth, and biomass to nutrients addition were also determined. The value of *H* ranged from 5.03 to 21.28 for all organs of the three tree species. *H* was significantly different among tree species ($P = 0.010$), and was all higher than that of herbs, which may result from phylogenetic differences (angiosperms:gymnosperms) and life form differences (trees:herbs). While having the largest *H* value, *Q. acutissima* had the smallest response ratio of physiology (effective quantum yield of PSII), growth (height, root collar diameter), and biomass to soil N and P addition, which indicated that species with stronger stoichiometric homeostasis showed better adaption to environment changes. Our results successfully expanded the stoichiometric homeostasis theory to trees, and provided a link between stoichiometric homeostasis and response of plant traits to environmental changes.

**Keywords** Stoichiometric homeostasis · N and P addition · Physiology · Growth and biomass · Tree seedlings

## Introduction

Ecological stoichiometry is the study of the balance of multiple chemical elements [mainly nitrogen (N) and phosphorus (P)] and energy in ecological interactions (Elser et al. 2000; Reich and Oleksyn 2004; Elser and Hamilton 2007; Zhang et al. 2017). Stoichiometric homeostasis, the central concept of ecological stoichiometry, is defined as the ability of organisms to keep their nutrient composition relatively constant regardless of changing environmental nutrients. When nutrients restrict the growth of plants, plants can use a variety of physiological mechanisms to improve the availability and efficiency of nutrient restriction, thereby maintaining the stability and related functions of nutrient levels in the body (Hessen et al. 2004). At the individual level of plant, the homeostatic regulation coefficient (*H*) indicates the ability of stoichiometric homeostasis (Sterner and Elser 2002; Yu et al. 2010; Gu et al. 2017). If the value of *H* is higher, it means that the content of nutrients in the plant is

---

Communicated by U. Luettge.

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s00468-018-1719-7) contains supplementary material, which is available to authorized users.

✉ Tonggui Wu
wutonggui@caf.ac.com

[1] East China Coastal Forest Ecosystem Long-Term Research Station, Research Institute of Subtropical Forestry, Chinese Academy of Forestry, Hangzhou 311400, Zhejiang, People's Republic of China

[2] Zhejiang Academy of Forestry, Hangzhou 310023, People's Republic of China

[3] Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634-0317, USA

more stable (Hessen et al. 2004; Yu et al. 2011; Peng et al. 2016).

In early studies, stoichiometric homeostasis has been focused on algae (Rhee 1978; Hall et al. 2005), fungi and bacteria (Makino et al. 2003; Danger and Chauvet 2013), and animals (DeMott and Pape 2005; Persson et al. 2010), and in recent years, on seed plants (Yu et al. 2010, 2015; Dijkstra et al. 2012; Wang et al. 2016b; Gu et al. 2017). In general, the stoichiometric homeostasis is closely related to evolutionary stage (Williams and Silva 1996; Demars and Edwards 2007; Stock and Verboom 2012; Yu et al. 2014): plants are found to be more homeostatic than algae and fungi, but lower than animals (Sterner and Elser 2002; Jaenike and Markow 2003; Makino et al. 2003; Yu et al. 2011). For seed plants, the largest and most diverse groups within the plant kingdom, the stoichiometric homeostasis theory has been mostly investigated and validated in herbs (Yu et al. 2010, 2011, 2015; Xing et al. 2016; Jiang et al. 2014, 2017), and it remains unknown if the stoichiometric homeostasis theory is underlying success of other growth forms (shrubs or trees) (Yu et al. 2015). Also, it is not clear if there exist differences in stoichiometric homeostasis among life forms (e.g., trees, shrub, and herb), phylogenesis (e.g., angiosperms and gymnosperms) and among different organs of plants.

Stoichiometric homeostasis also reflects physiological, biochemical, and growth adaption of organisms to environmental changes (Hessen et al. 2004; Elser et al. 2010; Xing et al. 2016), which is related to the ecological strategies and fitness of the species (Gusewell and Bollens 2003). Previous studies found that species or communities with stronger homeostasis would have higher stability. For example, plant $H$ for nitrogen ($H_N$) and N:P ($H_{N:P}$) were found to be positively related to species dominance (calculated by biomass) in grassland ecosystems (Yu et al. 2010, 2015; Dijkstra et al. 2012); and community $H$ was also positively correlated with community production and stability (Yu et al. 2010; Gu et al. 2017). Moreover, stoichiometric homeostasis has been validated primarily to be predictive of species responsiveness, expressed by response ratio (RR), to environmental changes, such as RR of species relative cover to soil water limitation and addition (Yu et al. 2015), and RR of species biomass to temperature increase (Gu et al. 2017). However, we are not clear if stoichiometric homeostasis can be predictive of the response of plant physiology to environmental changes (Zeng et al. 2013).

Here, we proposed two hypotheses: (1) constant homeostatic regulation coefficient ($H$) exists for trees and differs among tree species; (2) tree species with higher $H$ are more stable in physiological and growth responses to soil N and P addition. To verify the two hypotheses, we selected three tree species (*Quercus acutissima* Carruth., *Sapium sebiferum* [L.] Small, and *Metasequoia glyptostroboides* Hu & W.C. Cheng) seedlings to calculate the $H$ value through N and P addition, and to analyze the response of physiology, growth, and biomass to alterations in soil N or P.

## Materials and methods

### Experimental materials and design

Two angiosperms (*Q. acutissima* and *S. sebiferum*) and one gymnosperm (*M. glyptostroboides*), which are distributed widely in subtropical China, were selected. Four hundred seedlings for each species, from the nursery at Research Institute of Subtropical Forestry in Hangzhou, China, were chosen and transplanted to plastic pots, 26 cm in diameter and 30 cm deep, in February 2016. The soil pH and the bulk density are 6.07 and 1.04 g $cm^{-3}$, respectively, and soil is composed of 35% sand, 37% silt, and 28% clay. A total of 5.5 kg soil, with low organic matter (2.83 g $kg^{-1}$), available nitrogen (3.42 mg $kg^{-1}$) and available phosphorus (4.08 mg $kg^{-1}$), was filled into each pot. All transplanted seedlings were acclimated for 1 month in a greenhouse. Two hundred and sixteen average seedlings were then selected for each species for study.

N and P addition experiments were designed: N addition as urea (0, 0.25, 0.5, 0.75, 1, 1.5 g N per pot) and P addition using calcium superphosphate (0, 0.2, 0.4, 0.8, 1.2, 2 g P per pot). The fertilizer was dissolved in 0.5 L of water and then evenly sprayed on the soil surface of the pot. Each treatment had three replicates, each replicate had 6 plants, and a total of 216 pots (3 replicates × 6 plants × 6 nutrient levels × 2 experiments) were used for each tree species. For each treatment, the prescribed amount of fertilizer per plot was added in three installments: 40% on the day of experiment started, 30% on the 20th day after experiment started, and 30% on the 40th day after experiment started. A pallet was placed under each pot, and any water drained to the pallet during watering was poured back to pot to prevent the loss of nutrition in the basin. All treatments are identical except for nutrients addition.

### Measurements and sampling

Seedling height and root collar diameter (RCD) were recorded with a ruler and digital vernier caliper, respectively, before the experiment and each month after the experiment started (Supplementary Appendix Tables 1, 2). Chlorophyll fluorescence parameters were measured with a portable fluorometer (PAM 2100, Walz, Germany) on dark-adapted leaves in the 5th month after the experiment started.

All experimental trees were harvested in the 6th month after the experiment started. Roots, stems and leaves were separated, weighed, sampled, oven dried at 60 °C for 3 days to constant weight, and reweighed to determine dry mass. Subsequently, the dried samples were ground and homogenized in a mill, after which they were stored in a sealed plastic bag until analysis.

Plant N and P concentrations (mg $g^{-1}$) were determined by the Semimicro–Kjeldahl method and colorimetrically by the phosphomolybdic blue method, respectively (Lu 2000). The soil available N and P concentrations were calculated based on N and P added.

### Data analysis and statistics

To estimate the strength of plant homeostasis for a given measurement of plant nutrient concentrations, we used a regression analysis to fit the data to the homeostatic model equation (Sterner and Elser 2002):

$$y = cx^{1/H},$$

where $y$ is the N or P concentration or N:P ratio of plants, $x$ is N or P concentration or N:P in the environment, $x$ is the total soil available N or P concentrations or N:P in this study, $c$ is a constant, and $H$ is homeostatic regulation coefficient. The values of $H$ and c were obtained when we analyzed the relationship between $y$ and $x$ using a regression analysis.

The growth of seedling height, root collar diameter, and biomass were calculated based upon the differences of height, root collar diameter, and biomass before and after the experiment, respectively. PSII photochemistry is considered to be the most sensitive part of the photosynthetic pathway to environmental stress (Zha et al. 2017), and effective quantum yield of PSII (Y(II)) is an important parameter of photochemical reaction which reflects actual efficiency of PSII (Feng et al. 2015). Therefore, we selected Y(II) as a physiological index in this study. The basic parameters such as RCD, seedling height and Y(II) of the three tree species were shown in the Supplementary Appendix Table 3. In this experiment, the response of plant physiology and growth indices for the three tree species to soil N and P addition were expressed by the response ratio (RR) of (Y(II)), growth (height, RCD) and biomass. This was determined using the following equation modified by Yu et al. (2015):

$$\mathrm{RR} = (T_{\max} - \mathrm{CK})/\mathrm{CK},$$

where $T_{\max}$ is the maximum value of each index for the tree species under soil N and P addition, and CK is the value of each index for the tree species in the control.

Plant nitrogen use efficiency (NUE) and phosphorus use efficiency (PUE) were calculated as follows (Cao and Zhang 2000):

$$\mathrm{NUE\,(PUE)} = \frac{\text{Total biomass}}{\text{Total nitrogen (phosphorus) absorption}},$$

where total biomass was the sum of the biomass of leaves, stems and roots (g), and total nitrogen (phosphorus) absorption was the sum of nutrient uptake by the three organs (mg).

Three-way ANOVA was used to test the variations of $H$ across species, organs, and elements (i.e., N, P, N:P). Statistical analyses were performed using the software IBM SPSS Statistics 20 (2011, ver. 20; SPSS Inc., USA).

## Results

### Stoichiometric homeostasis regulation coefficient for three tree species

The homeostasis regulation coefficient of N ($H_N$) varied from 5.03 to 14.71, with ranges from 7.46, 5.03, 5.71 for *M. glyptostroboides* to 13.33, 14.71, 8.77 for *Q. acutissima* for leaf, stem and root, respectively (Fig. 1, Table 1). The homeostasis regulation coefficient of N:P ($H_{N:P}$) showed more variations than N, ranged from 6.58 to 21.28, with minimum values of 6.58, 10.87, 7.52 for *S. sebiferum*, and maximum values of 21.28, 17.09, 13.51 for *Q. acutissima* for leaf, stem and root, respectively (Fig. 3). The homeostasis regulation coefficient of P ($H_P$) was not well fitted, except for leaf of *Q. acutissima* ($H_P = 16.67$) (Fig. 2a).

$H$ differed significantly among the three tree species ($P = 0.010$; Table 2), and the $H_{N:P}$ was larger than $H_N$ for the three tree species ($P = 0.043$; Table 2). Moreover, the $H$ varied insignificantly among organs ($P = 0.475$; Table 2).

### Response ratio of leaf chlorophyll fluorescence to soil N and P addition

Response ratio of effective quantum yield of PSII [$RR_{Y(II)}$] was found to be significantly different among the three tree species ($P = 0.000$), and *Q. acutissima* had the lowest $RR_{Y(II)}$ to soil N and P addition (Fig. 4).

### Response ratio of growth and biomass to soil N and P addition

Response ratio of height ($RR_{Height}$), root collar diameter ($RR_{RCD}$), and biomass ($RR_{Biomass}$) were all significantly different among the three tree species ($P = 0.010$, $P = 0.023$, $P = 0.002$, respectively). *Q. acutissima* also had lowest $RR_{Biomass}$ and $RR_{RCD}$ under soil N and P addition (Figs. 5, 6).

**Table 1** The homeostatic regulation coefficient (*H*) for different species in the present study and previous studies

| Life form | Leaf | | | Stem | | | Root | | | References |
|---|---|---|---|---|---|---|---|---|---|---|
| | $H_N$ | $H_P$ | $H_{N:P}$ | $H_N$ | $H_P$ | $H_{N:P}$ | $H_N$ | $H_P$ | $H_{N:P}$ | |
| Trees | | | | | | | | | | |
| Three trees | 7.46–13.33 | | 6.58–21.28 | 5.03–14.71 | | 10.87–17.09 | 5.71–8.77 | | 7.52–13.51 | This study |
| Herbs | | | | | | | | | | |
| Twelve herbs | 3.53–7.68 | 2.60–5.60 | 2.62–10.29 | | | | | | | Yu et al. (2010, 2011) |
| Three herbs | 1.50–7.67 | 2.00–14.22 | 0.63–19.23 | 0.18–1.56 | 0.33–14.12 | 0.60–4.25 | 1.12–3.96 | 1.10–5.25 | 1.00–3.83 | Jiang et al. (2014) |
| One herb | 3.03–4.76 | 2.17–7.14 | 1.82–11.11 | | | | | | | Peng et al. (2016) |
| Four herbs | | | < 5.00 | | | | | | | Xing et al. (2016) |
| Five herbs | | | 4.28–9.60 | | | | | | | Dijkstra et al. (2012) |

## Discussion

### Stoichiometric homeostasis regulation coefficient for trees

Stoichiometric homeostasis, such as elements' stoichiometry, is associated closely with evolutionary stage (Williams and Silva 1996; Stock and Verboom 2012; Yu et al. 2014; Halvorson and Small 2016). In this study, the homeostatic regulation coefficient (*H*) was calculated with the stoichiometric *H* model (Sterner and Elser 2002) for the three tree species through N and P addition. The values ranged from 5.03 to 14.71 for $H_N$ and from 6.58 to 21.28 for $H_{N:P}$ among the three tree species. Ranges of leaf $H_N$ (7.46–13.33), leaf $H_{N:P}$ (6.58–21.28) and root $H_N$ (5.71–8.77), root $H_{N:P}$ (7.52–13.51) for the three tree species were higher than those of herbs in grasslands (leaf $H_N$: 2.50–8.80; leaf $H_{N:P}$: 3.00–12.16; root $H_N$: 2.95–9.00; root $H_{N:P}$: 2.19–14.00) (Yu et al. 2011), than herbs in wetlands (leaf $H_N$: 1.50–7.67; leaf $H_{N:P}$: 0.63–19.23; root $H_N$: 1.12–3.96; root $H_{N:P}$: 1.00–3.83) (Jiang et al. 2014), and than other herbs in previous studies (Table 1). Woody plants showed lower variation in leaf N and P concentrations and N:P than herbs (Zhao et al. 2014), which may be influenced by distinct life strategies among life forms. Slow-growing woody species are likely to be competitors or stress tolerators with relatively conservative stoichiometric traits; however, fast-growing herbs exhibit more flexibility for leaf stoichiometric traits (Gusewell 2004).

Stoichiometric homeostasis also varied among tree species. The *H* values for *Q. acutissima* and *S. sebiferum* are higher than those for *M. glyptostroboides*, which is probably resulting from the phylogenetic differences among tree species. Angiosperms have a rapid resource acquisition (fast return) strategy and, therefore, it is easier to adapt to a changing environment compared to gymnosperms, which have a resource retention (slow return) strategy (Royer et al. 2010). These differences in resource acquisition and retention are all owing to phylogenetic differences in conducting tissues (Gomez Ros et al. 2007).

Stoichiometric homeostasis appeared to exhibit different degrees among organs for the same plant, which reflect a fundamental tradeoff in nutrient investment and allocation (Yu et al. 2011; Gu et al. 2017). Leaves are the main photosynthetic organs in plants and thus it is eminently important for growth and biomass accumulation; therefore, nutrient concentrations were constrained in a certain range to provide the optimal physiological traits (Aerts and Chapin 2000; Lambers et al. 2008; Yan et al. 2016). Roots, acting as nutrient reservoirs, supply enough N and P to above ground organs when plants are lack of nutrient, and store excess N and P when plant are not lack of

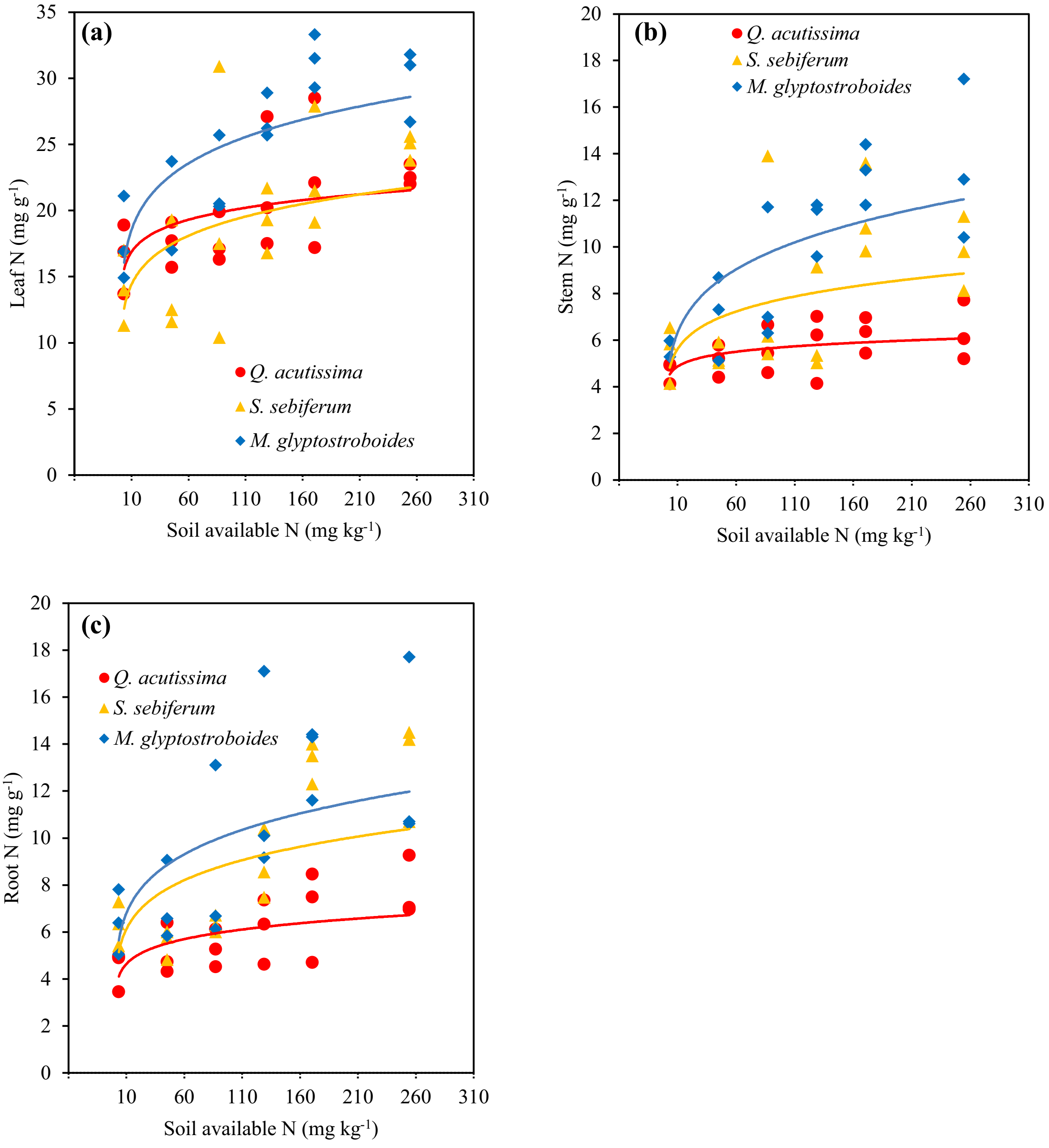

**Fig. 1** Relationships between seedling N concentrations and soil available N contents for three tree species. **a** Leaf. *Q. acutissima:* $y=14.188x^{0.0753}$, $H=13.33$, $R^2=0.334$, $P=0.012$; *S. sebiferum:* $y=10.759x^{0.1270}$, $H=7.87$, $R^2=0.329$, $P=0.013$; *M. glyptostroboides:* $y=13.627x^{0.1339}$, $H=7.46$, $R^2=0.602$, $P=0.000$. **b** Stem. *Q. acutissima:* $y=4.1562x^{0.0684}$, $H=14.71$, $R^2=0.289$, $P=0.021$; *S. sebiferum:* $y=4.0558x^{0.1411}$, $H=7.09$, $R^2=0.299$, $P=0.019$; *M. glyptostroboides:* $y=3.9964x^{0.1992}$, $H=5.03$, $R^2=0.602$, $P=0.000$. **c** Root. *Q. acutissima:* $y=3.5673x^{0.1144}$, $H=8.77$, $R^2=0.401$, $P=0.005$; *S. sebiferum:* $y=4.2104x^{0.1630}$, $H=6.13$, $R^2=0.400$, $P=0.005$; *M. glyptostroboides:* $y=4.5542x^{0.1746}$, $H=5.71$, $R^2=0.438$, $P=0.003$

nutrient; therefore, roots had lower *H* than organs aboveground (Cernusak et al. 2010; Yan et al. 2016). While, leaves and stems had higher, but insignificant, *H* compared to roots in this study that may be the reservoir role of roots not needing to act at the seedling stage (Yang 2011; Peng et al. 2016).

Previous studies reported that smaller variations in plant N:P when compared to plant N and P concentrations across plant species in a given site and for the same species across sites (Han et al. 2005; Wu et al. 2014), due to the similar biochemical pathways of N and P (Sterner and Elser 2002). Therefore, plant N:P was more constant than plant N and P concentrations (Yu et al. 2011; Jiang et al. 2014). In our study, $H_{N:P}$ was also significantly higher than $H_N$. However, $H_P$ was not obtained except in the leaves of *Q. acutissima* in this study, which may be because plant P concentration is

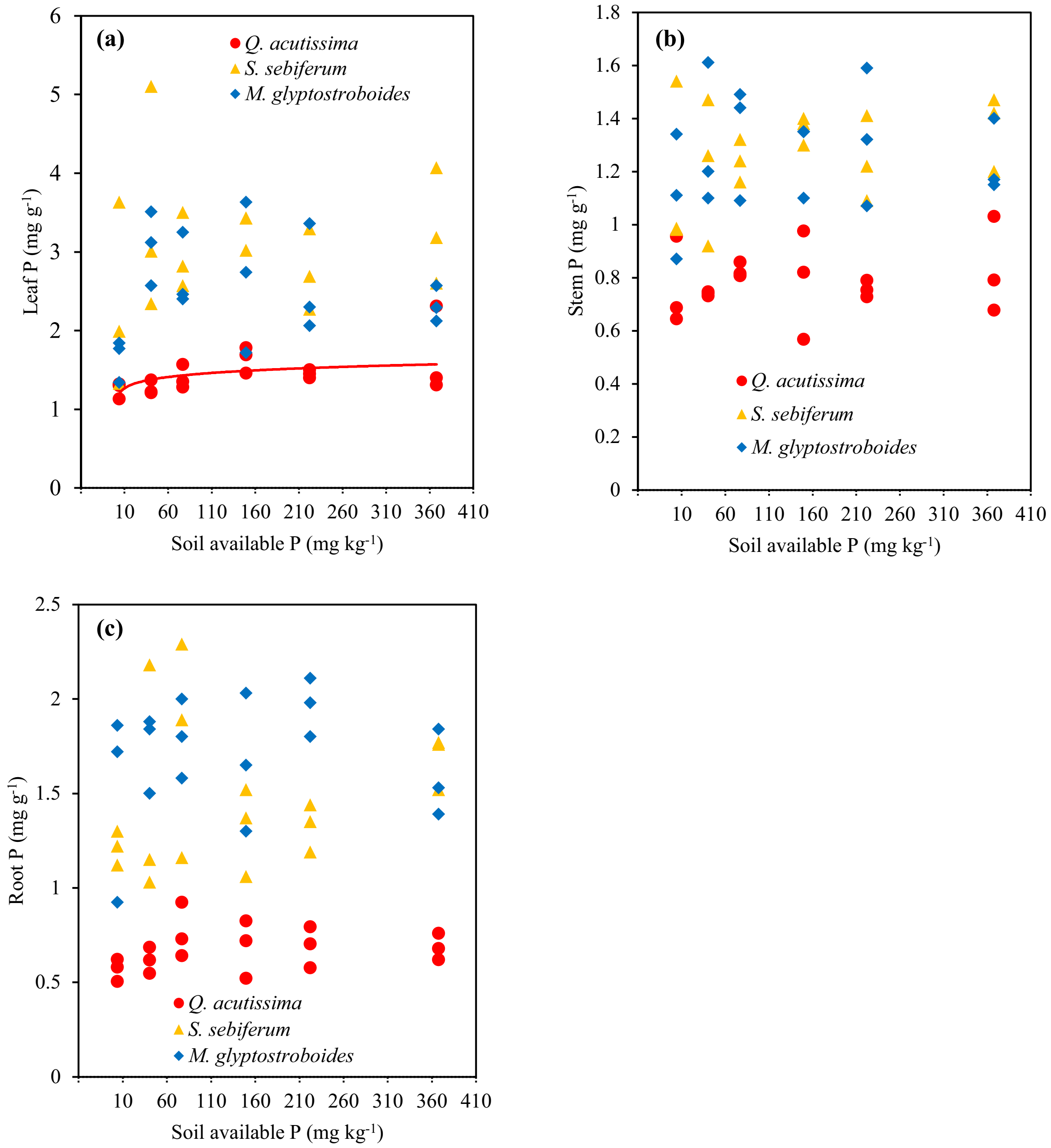

**Fig. 2** Relationships between seedling P concentrations and soil available P contents for three tree species. **a** Leaf. *Q. acutissima:* $y = 1.1044x^{0.0597}$, $H = 16.67$ $R^2 = 0.298$ $P = 0.019$. No H was detected for *S. sebiferum* and *M. glyptostroboides*. **b** Stem. No H was detected for each tree species. **c** Root. No H was detected for each tree species

more variable than N concentrations and N:P, which indicated that seedlings growth was mainly limited by soil N, not soil P (Reich and Oleksyn 2004; Yuan et al. 2011; Gu et al. 2017; Zhang et al. 2017).

Our results and previous studies together indicated that the value of *H* for trees and herbs were also higher than phytoplankton (average $H = 1.88$) (Persson et al. 2010), suggesting a stronger stoichiometric homeostasis in higher plants than in lower plants. These results verified our first hypothesis that *H* exists for trees and differs among tree species, thus extended the stoichiometric homeostasis theory to trees. Whether mature trees have same homeostasis regulation coefficients to seedlings remains unclear. It seems reasonable that mature trees could exhibit similar stoichiometric homeostasis to seedlings, because they have similar nutrient absorption and transport pathways. The stoichiometric homeostasis of mature trees will be validated in our future experiment. Moreover, we also confirmed that trees were more

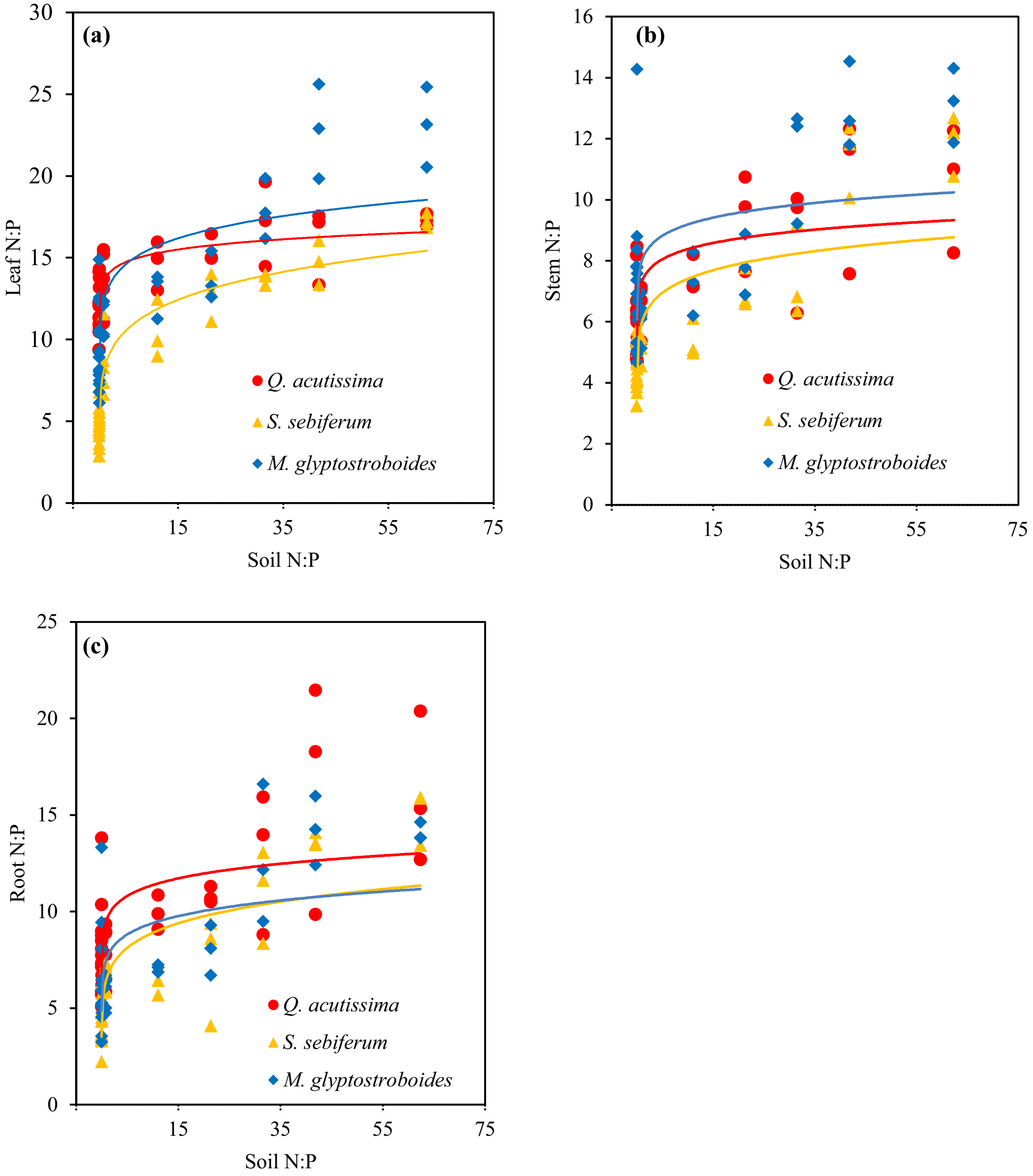

**Fig. 3** Relationships between seedling N:P and soil N:P for three tree species. **a** Leaf. *Q. acutissima:* $y=13.663x^{0.047}$, $H=21.28$ $R^2=0.632$ $P=0.000$; *S. sebiferum:* $y=8.244x^{0.152}$, $H=6.58$ $R^2=0.899$ $P=0.000$; *M. glyptostroboides:* $y=12.508x^{0.095}$, $H=10.53$ $R^2=0.660$ $P=0.000$. **b** Stem. *Q. acutissima:* $y=7.326x^{0.059}$, $H=17.09$ $R^2=0.524$ $P=0.000$; *S. sebiferum:* $y=5.993x^{0.092}$, $H=10.87$ $R^2=0.673$ $P=0.000$; *M. glyptostroboides:* $y=8.020x^{0.059}$, $H=16.89$ $R^2=0.342$ $P=0.000$. **c** Root. *Q. acutissima:* $y=9.597x^{0.074}$, $H=13.51$ $R^2=0.462$ $P=0.000$; *S. sebiferum:* $y=6.558x^{0.133}$, $H=7.52$ $R^2=0.717$ $P=0.000$; *M. glyptostroboides:* $y=7.575x^{0.094}$, $H=10.64$ $R^2=0.500$ $P=0.000$

homeostatic than herbs, and stoichiometric homeostasis was closely related to life form and phylogenesis in plants.

### Stoichiometric homeostasis relations to responsiveness of tree physiology, growth, and biomass to soil N and P addition

Plant $H$ was found to be positively correlated with species dominance, and stability in a grassland ecosystem (Yu et al.

**Table 2** The ANOVA results for the effects of species, organs, and elements on *H* in the experiments

| Species | | Organs | | Elements | |
|---|---|---|---|---|---|
| *Q. acutissima* | 14.78 ± 4.18 | Leaf | 11.18 ± 5.53 | N | 8.46 ± 3.37 |
| *S. sebiferum* | 9.38 ± 4.37 | Stem | 11.95 ± 5.12 | N:P | 12.77 ± 4.84 |
| *M. glyptostroboides* | 7.68 ± 1.69 | Root | 8.71 ± 2.96 | | |
| Species | $F = 6.288$, $df = 2$, $P = 0.010$ | | | | |
| Organs | $F = 0.783$, $df = 2$, $P = 0.475$ | | | | |
| Elements | $F = 4.807$, $df = 1$, $P = 0.043$ | | | | |

Values of *H* are expressed by mean ± SD. The degrees of freedom (*df*) for the numerator are given in the table

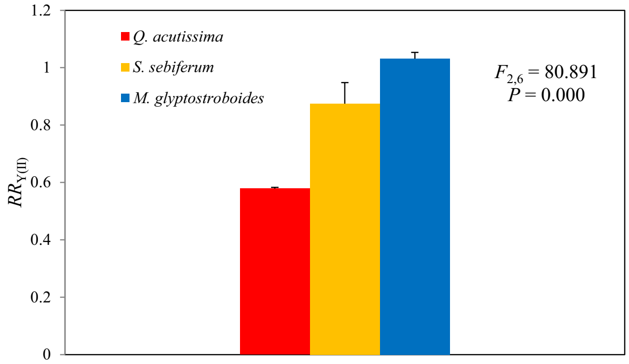

**Fig. 4** RR of leaf chlorophyll fluorescence for three tree species to soil N and P addition

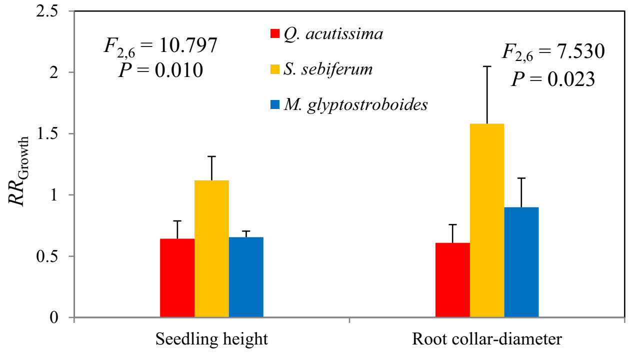

**Fig. 5** RR of growth for three tree species to soil N and P addition

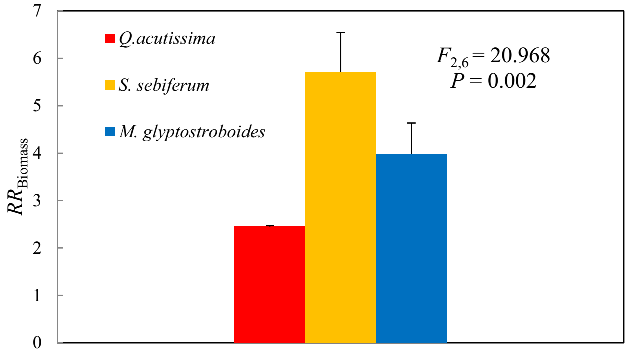

**Fig. 6** RR of biomass for three tree species to soil N and P addition

2010) and in a tundra ecosystem (Gu et al. 2017). Meanwhile, species with the highest *H* responded the least (was most constant) in relative cover or biomass to environmental changes, while the species with lowest *H* responded the most (Yu et al. 2015; Gu et al. 2017). In this study, the same result was also found for RR of plant physiology and growth to soil N and P addition.

Compared to the other two species, ranges of leaf N and P concentrations were more narrow for *Q. acutissima* under soil N and P addition (Supplementary Appendix Table 3). Leaf N and P concentrations are associated closely to plant physiology, such as photosynthesis and fluorescence (Dubey et al. 2017). Since Y(II) is an indicator of the intrinsic efficiency of PSII and can effectively reflect photosynthetic efficiency, the magnitude and variation characteristics of its parameter values are often used to judge and speculate on the resistance of plants to environmental factors (Yang et al. 2002; Chen et al. 2013; Yao et al. 2013). In this experiment, $RR_{Y(II)}$ for *Q. acutissima* was the smallest among the three tree species which indicated that external environment stress had less impact on the growth of *Q. acutissima* than the other two tree species. Additionally, we also found that $RR_{Height}$ and $RR_{RCD}$ of *Q. acutissima* were also relatively low, compared to the other two species. This suggested that the growth traits of plants presented a similar trend with that of Y(II), perhaps because the changes of chlorophyll synthesis have effect on the photosynthesis of plants and accumulation of photosynthetic products, which in turn change the growth of plants and their resistance (Liu and Liu 2010; Malhi et al. 2015; Wang et al. 2016a). Furthermore, although the nutrient content of *Q. acutissima* was relatively low, the value of NUE and PUE were higher than those of the other two tree species (Supplementary Appendix Table 4), which indicates that the adaptability of *Q. acutissima* is stronger (Leng et al. 2009). Therefore, *Q.acutissima*, with the largest *H* values, remained relatively more stable in physiology, growth and biomass under soil N and P addition compared to the other two species. This demonstrated that plants with stronger stoichiometric homeostasis were more conservative nutrient users (lower nutrient content), and strong stoichiometric homeostasis might be vital for species in stress environments, such as over fertilization, and thus might be crucial ecophysiological mechanisms strengthening their stability (Yu et al. 2010, 2011). This result is consistent with previous studies where soil water and air temperature were manipulated (Yu et al. 2010, 2015; Gu et al. 2017). Here, we confirmed the second hypothesis that tree species with higher *H* are more stable in physiological and growth responses to soil N and P addition.

## Conclusion

The homeostatic regulation coefficient (*H*) existed and showed significant differences for the three tested tree species. *Q. acutissima*, with highest *H*, was more constant in responsiveness of physiology, growth and biomass to soil N and P addition. Our study has successfully extended stoichiometric homeostasis theory to trees, and provides a link between stoichiometric homeostasis and response of plant traits to environmental changes. Furthermore, these results should be authenticated further for other tree species and other stress environments.

**Author contribution statement** TW was responsible for funding acquisition and resources. TW and YL conceptualized the study. WG and JW performed the data curation and investigation. JW and GW wrote original draft. All authors read and approve the final manuscript.

**Acknowledgements** This work was supported by the Fundamental Research Funds for the Central Non-profit Research Institution of CAF (CAFYBB2014ZD002) and National Natural Science Foundation of China (31770756).

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a reevaluation of processes and patterns. Adv Ecol Res 30:1–67

Cao J, Zhang FS (2000) Phosphorus uptake and utilization efficiency in seedlings of different wheat genotypes as influenced by water supply at low soil phosphorus availability. Acta Phytoecologica Sinica 24:731–735

Cernusak LA, Winter K, Turner BL (2010) Leaf nitrogen to phosphorus ratios of tropical trees: experimental assessment of physiological and environmental controls. New Phytol 185:770–779

Chen C, He XD, Qin JZ, Lui GH (2013) Comparison of chlorophyll fluorescence Fv/Fm characteristics of four michelia trees. J Anhui Agric Univ 40:32–37

Danger M, Chauvet E (2013) Elemental composition and degree of homeostasis of fungi: are aquatic hyphomycetes more like metazoans, bacteria or plants? Fungal Ecol 6:453–457

Demars BO, Edwards AC (2007) Tissue nutrient concentrations in freshwater aquatic macrophytes: high inter-taxon differences and low phenotypic response to nutrient supply. Freshw Biol 52:2073–2086

DeMott WR, Pape BJ (2005) Stoichiometry in an ecological context: testing for links between Daphnia P-content, growth rate and habitat preference. Oecologia 142:20–27

Dijkstra FA, Pendall E, Morgan JA, Blumenthal DM, Carrillo Y, Lecain DR, Follett RF, Williams DG (2012) Climate change alters stoichiometry of phosphorus and nitrogen in a semiarid grassland. New Phytol 196:807–815

Dubey P, Raghubanshi AS, Dwivedi AK (2017) Relationship among specific leaf area, leaf nitrogen, leaf phosphorus and photosynthetic rate in herbaceous species of tropical dry deciduous in Vindhyan highlands. Ann Plant Sci 6:1531–1536

Elser JJ, Hamilton A (2007) Stoichiometry and the new biology: the future is now. PLoS Biol 5:e181

Elser J, Sterner R, Gorokhova E et al (2000) Biological stoichiometry from genes to ecosystems. Ecol Lett 3:540–550

Elser JJ, Fagan WF, Kerkhoff AJ, Swenson NG, Enquist BJ (2010) Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytol 186:593–608

Feng T, Chen SS, Gao DQ, Liu GQ, Bai HX, Li A, Peng LX, Ren ZY (2015) Selenium improves photosynthesis and protects photosystem II in pear (*Pyrus bretschneideri*), grape (*Vitis vinifera*), and peach (*Prunus persica*). Photosynthetica 53:609–612

Gomez Ros LV, Gabaldon C, Pomar F, Merino F, Pedreno MA, Ros Barcelo A (2007) Structural motifs of syringyl peroxidases predate not only the gymnosperm-angiosperm divergence but also the radiation of tracheophytes. New Phytol 173:63–78

Gu Q, Zamin TJ, 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

Gusewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266

Gusewell S, Bollens U (2003) Composition of plant species mixtures grown at various N:P ratios and levels of nutrient supply. Basic Appl Ecol 4:453–466

Hall SP, Smith VH, Lytle DA, Leibold MA (2005) Constraints on primary producer N:P stoichiometry along N:P supply ratio gradient. Ecology 86:1894–1904

Halvorson HM, Small GE (2016) Observational field studies are not appropriate tests of consumer stoichiometric homeostasis. Freshw Sci 35:1103–1116

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

Hessen DO, Ågren GI, Anderson TR, Elser JJ, Ruiter PC (2004) Carbon sequestration in ecosystems: the role of stoichiometry. Ecology 85:1179–1192

Jaenike J, Markow TA (2003) Comparative elemental stoichiometry of ecologically diverse Drosophila. Funct Ecol 17:115–120

Jiang LL, He S, Wu LF, Yan YF, Weng SF, Liu J, Wang WQ, Zeng CS (2014) Characteristics of stoichiometric homeostasis of three plant species in wetlands in Minjiang estuary. Wetl Sci 12:293–298

Jiang LL, Zeng CS, Shao JJ, Zhou XH (2017) Plant nutrient dynamics and stoichiometric homeostasis of invasive species *Spartina alterniflora* and native *Cyperus malaccensis* var. *brevifolius* in the Minjiang River estuarine wetlands. Chin J Plant Ecol 41:450–460

Lambers H, Chapin S III, Pons TL (2008) Plant physiological ecology. Springer, New York

Leng HN, Chen YT, Duan HP, Rao LB, Wang YJ, Hu YX (2009) Effects of phosphorus stress on the growth and nitrogen and phosphorus absorption of different formosan sweet gum provenances. Chin J Appl Ecol 20:754–760

Liu DL, Liu SM (2010) Comparative drought resistance of different varieties of *Zanthoxylum bungeanum*. Agric Res Arid Areas 28:183–189

Lu RK (2000) Methods of soil and agro-chemical analysis. China Agriculture Science Technology Press, Beijing, pp 127–332

Makino W, Cotner J, Sterner R, Elser J (2003) Are bacteria more like plants or animals? Growth rate and resource dependence of bacterial C:N:P stoichiometry. Funct Ecol 17:121–130

Malhi Y, Doughty CE, Goldsmith GR et al (2015) The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. Glob Chang Biol 21:2283–2295

Peng HY, Chen YH, Yan ZB, Han WX (2016) Stage-dependent stoichiometric homeostasis and responses of nutrient resorption in *Amaranthus mangostanus* to nitrogen and phosphorus addition. Sci Rep 6:37219

Persson J, Fink P, Goto A, Hood JM, Jonas J, Kato S (2010) To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119:741–751

Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. Proc Natl Acad Sci USA 101:11001–11006

Rhee GY (1978) Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition and nitrate uptake. Limnol Oceanogr 23:10–25

Royer DL, Miller IM, Pepper DJ, Hickey LJ (2010) Leaf economic traits from fossils support a weedy habit for early angiosperms. Am J Bot 97:438–445

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton

Stock WD, Verboom GA (2012) Phylogenetic ecology of foliar N and P concentrations and N:P ratios across Mediterranean-type ecosystems. Glob Ecol Biogeogr 21:1147–1156

Wang JY, Tang HL, Gong W, Hu W, Gou GJ (2016a) Effects of water and fertilizer coupling on growth, nutrients absorption and fertilizer use of *Zanthoxylum bungeanum* Maxim‘Hanyuan’seedling. J Nanjing For Univ 40:33–40

Wang M, Larmola T, Murphy MT, Moore TR, Bubier JL (2016b) Stoichiometric response of shrubs and mosses to long-term nutrient (N, P and K) addition in an ombrotrophic peatland. Plant Soil 400:403–416

Williams PJR, Silva J (1996) The natural selection of the chemical elements: the environment and life’s chemistry. Oxford Press, Clarendon

Wu T, Wang GG, Wu QT, Cheng XR, Yu MK, Yu WW XB (2014) Patterns of leaf nitrogen and phosphorus stoichiometry among *Quercus acutissima*, provenances across China. Ecol Complex 17:32–39

Xing W, Shi Q, Liu H, Liu G (2016) Growth rate, protein: RNA ratio and stoichiometric homeostasis of submerged macrophytes under eutrophication stress. Knowl Manag Aquat Ecosyst 417:25

Yan Z, Guan H, Han W, Han T, Guo Y, Fang J (2016) Reproductive organ and young tissues show constrained elemental composition in *Arabidopsis thaliana*. Ann Bot 117:431–439

Yang G (2011) The relationship between growth and water absorption about two conifer seedlings in Gongga Mountain. Ph.D. Theses. Chinese Academy of Science

Yang CW, Peng CL, Duan J, Lin GZ, Chen YZ (2002) Responses of chlorophyll fluorescence and carotenoids biosynthesis to high light stress in rice seedling leaves at different leaf position. Acta Botanica Sinica 44:1303–1308

Yao CH, Ai JN, Cao XP, Xue S (2013) Salinity manipulation as an effective method for enhanced starch production in the marine microalga *Tetraselmis subcordiformis*. Bioresour Technol 146:663–671

Yu Q, Chen Q, Elser JJ et al (2010) Linking stoichiometric homoeostasis with ecosystem structure, functioning and stability. Ecol Lett 13:1390–1399

Yu Q, Elser JJ, He N, Wu H, Chen Q, Zhang G, Han X (2011) Stoichiometric homeostasis of vascular plants in the Inner Mongolia grassland. Oecolocgia 166:1–10

Yu GR, Li XR, Zhao N, He NP, Wang QF (2014) Theoretical linkage between ecological stoichiometry with the coupled cycle of carbon, nitrogen and water in terrestrial ecosystems. Quat Sci 34:881–890

Yu Q, Wilcox K, Pierre KL, Knapp K, Han X, Smith MD (2015) Stoichiometric homeostasis predicts plant species dominance temporal stability and responses to global change. Ecology 96:2328–2335

Yuan ZY, Chen HY, Reich PB (2011) Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. Nat Commun 2:344

Zeng DP, Jiang LL, Zeng CS, Wang WQ, Wang C (2013) Reviews on the ecological stoichiometry characteristics and its applications. Acta Ecol Sin 33:5484–5492

Zha TS, Wu YJ, Jia X et al (2017) Diurnal response of effective quantum yield of PSII photochemistry to irradiance as an indicator of photosynthetic acclimation to stressed environments revealed in a xerophytic species. Ecol Indic 74:191–197

Zhang H, Yang X, Wang J, Wang GG, Yu M, Wu T (2017) Leaf N and P stoichiometry in relation to leaf shape and plant size for *Quercus acutissima* provenances across China. Sci Rep 7:46133

Zhao N, He N, Wang Q, Zhang X, Wang R, Xu Z, Yu G (2014) The altitudinal patterns of leaf C:N:P stoichiometry are regulated by plant growth form, climate and soil on Changbai Mountain, China. PLoS one 9:e95196