Determining the Necessity of Applying N and P Fertilizer in a Mature Subtropical Torreya Grandis Orchard

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Research

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Abstract

Background In managed orchards, fertilizer treatments facilitate both high productivity and environmental pollution. Because economic profit takes priority over environmental cost, increasing amounts of chemical nitrogen and phosphorus fertilizer have been used in mature subtropical Torreya grandis orchards. However, given the magnitude of global nitrogen deposition, it’s worth considering whether heavy fertilizer treatment is necessary.

Methods To elucidate the balance between T. grandis nutrient demands and the fertilizer supply, we determined the C, N, and P foliar and soil concentrations ([C], [N], [P]) at five orchards undergoing long-term varied intensity fertilizer treatments.

Results After documenting the dynamic variation of available plant nutrients and the corresponding resorption efficiency, we found that increasing the fertilizer supply elevated foliar [P], yet foliar [C] and [N] remained stable. Because T. grandis was already equipped with a high nutrient content, the increased foliar [P] levels decreased C:P and N:P ratios. These results demonstrate that extra fertilizer in the N-saturated environment disturbs P-limitation. Furthermore, we also found that fertilizer supply failed to improve carbon accumulation, which in addition to soil nutrient content and leaf [P], highly impacted productivity.

Conclusions Thus, based on the results of this study, there are ample reasons to propose rejecting N addition in the present orchards, and we recommend organic management as a more conducive method to realize sustainable development.

Introduction

In order to facilitate a rapid increase in soil nutrients and guarantee profitable productivity, escalating amounts of chemical nitrogen (N) and phosphorus (P) rich fertilizer have been applied in T. grandis orchards, without any scientific management guidance. N and P are key nutrients that play pivotal roles in controlling plant growth and litter decomposition as well as the ecosystems’ biochemical cycles (Finzi et al. 2011; Penuelas et al. 2013; You et al. 2018). However, indiscriminate use of chemical fertilizers has caused abnormally high concentrations of N and P to accumulate in the soil, which has severely stressed the terrestrial plants’ physiological processes. Furthermore, the excessive use of chemical fertilizer has also generated serious adverse environmental consequences, such as non-point source pollution (Sun et al. 2019) and N induced soil acidification (especially due to NH4+), both of which have been observed in multiple ecosystems (Fernández-Escobar et al. 2009; Zhao and Zeng 2019; Zhu and Chen 2002). It should be noted that soil acidification further changes ecosystem biogeochemistry, which increases cationic nutrient leaching and thereby reduces plant productivity (Dai et al. 2017; Zhang et al. 2016).

In the field conditions, N input to an N-limited ecosystem, such as boreal forests, will improve net primary productivity (NPP) through a direct fertilizing effect on vegetation (Lebauer and Treseder 2008a). as a direct result from global change, N deposition in many regions of the world (i.e., United States, western
Europe, and China) currently exceeds 10 kg N ha\(^{-1}\) yr\(^{-1}\), especially in tropical and subtropical areas (Liu et al. 2013; Meunier et al. 2016), where over 80–120 kg N ha\(^{-1}\) yr\(^{-1}\) has been reported (Yu et al. 2016). Therefore, as N deposition levels continue to accelerate, N-limitation has been subsequently alleviated (Tao and Hunter 2012), and there is a high likelihood that the ecosystem is shifting to an N-enriched status (Yu et al. 2018). N deposition has also changed the soil stoichiometry by accelerating the soil P cycle in tropical and subtropical forests. Specifically, excessive N in temperate forests has been shown to alter the biogeochemical cycles of essential plant nutrients (Ferretti et al. 2015; Gilliam et al. 2016; Sardans et al. 2016a), but it also introduced P-limitation in forest ecosystems (Du et al. 2020; Du et al. 2016; Güsewell 2004; Vitousek et al. 2010). Fang et al. (2019) reported N saturation in three subtropical sites and noted that P deficiency is becoming progressively more problematic. Anthropogenic alternation of regional P and N cycling has led to large areas of southern China forests transmuting due to human-induced P-limitation (Du et al. 2016). Thus, NPP has transformed from being N limited to P limited in many forest ecosystems (LeBauer and Treseder 2008b).

Under intensive management, long-term addition of balanced compound fertilizer (e.g., N:P:K = 15:15:15) may cause excess P in orchards, as plants generally require less P than N (Macy 1936). P is an essential element for nucleic acids and membrane lipids. Although P sensing and signaling are not fully understood, there appears to be a series of physiological processes in plants that are either stimulated or suppressed in response to P supply (Fang et al. 2009). Unlike the immobile N in the plant cell wall, most leaf P is hydrolyzable and, therefore, more easily resorbed (Ågren 2008; McGroddy et al. 2004). In fact, due to its indiscriminate uptake, greater variability of foliar P has been reported even if it's not needed at that growth stage (Ostertag 2010). Species in P-poor environments, such as subtropical evergreen trees, are equipped with a corresponding adaptation mechanism, which makes them more susceptible to toxic eutrophication under excessive P addition (Musick 1978).

Soil N and P availability when combining with N deposition and/or external addition can influence forest productivity and ecosystem processes (Elser et al. 2000; Finzi et al. 2011). Trees may keep leaf nutrient concentrations and their ratios stable by modulating the nutrients coming from branches, roots or senescent leaves (Cernusak et al. 2010; Yan et al. 2016). Recently, foliar N and P concentration stoichiometry ratios (i.e., N/P, C/N, C/P) have been used to indicate soil N- and/or P-limitations to plant growth (Aerts and Chapin III 1999; Güsewell 2004; Koerselman and Meuleman 1996). In addition, nutrient resorption [nitrogen (NRE) and/or phosphorus (PRE)] from senescing plant tissues and the proficiency of nutrient conservation (Lin et al. 2010) are also widely used as indicators in studies of nutrient cycling between the plants and soil in fluctuating environments. Generally, nutrients would transfer from senescent leaf to trunk before falling off, thereby maintaining the plant nutrients at a favorable level. The NRE and PRE might depend on the type of nutrient limitation (Güsewell 2005) and vary in response to the plant’s intrinsic genetic characteristics (Sadanandan Nambiar and Fife 1991; Silla and Escudero 2003). NRE/PRE is commonly employed to determine the relative limitation between N and P; as NRE/PRE values >1 imply a stronger N-limitation at the ecosystem scale (Du et al. 2020). However, previous studies
predominantly focused on the effect of single N or P addition on leaf nutrients or resorption; thus, the
effect of intensive P addition on PRE in subtropical forests is not well understood.

Due to the high economic value of its nuts, T. grandis has become one of the most important commercial
tree species in southeast China. During the past three decades, the planting area of T. grandis has
steadily increased. As a result, farmers are facing escalating economic pressure, which has led to
excessive fertilizer consumption, and ultimately deterioration of the soil’s physical and chemical
properties. Thus, it is critical to determine the optimal amount of fertilizer necessary to achieve ideal
growth. A comprehensive understanding of fertilizer impact on crop quantity and soil quality is critical for
improving fertilizer treatment strategies in economic considerations and maintaining a healthy soil
environment. To solve the above problems, we examined the C, N, and P stoichiometry of soil as well as
green and senescent leaf of a mature T. grandis, in five orchards plots with varying fertilizer treatments.
The objective of this study was to: 1) evaluate whether the continuously increasing N deposition in
subtropical forests has alleviated the N-limitation, making P the limiting factor restricting plant growth;
(2) determine the optimal fertilizer supply; and (3) assess whether large amounts of fertilizer, i.e., N
and/or P, negatively impacts the plants. These results are expected to provide fertilization guidelines and
recommendations to help farmers reduce costs and soil pollution, while ensuring optimal production.

Materials And Methods

Study site

The study was conducted at the origination locale of T. grandis — Chinese Torreya Forest Park (29.69-
29.73°N, 120.49-51°E), in Zhuji city, Zhejiang Province, China. The physical and chemical properties of
the soil in the study area consisted of: organic carbon (OC) − 18.2 g/kg; total N (TN) − 1.67 g/kg; total P
(TP) − 1.56; hydrologic N (HN) − 132 mg/kg; and Olmes-P (AP) − 225 mg/kg. The soil was acidic with a
pH = 3.67 ± 0.12 and was characterized as Hapludult soil type with respect to Soil Taxonomy (Gong et al.
2007). T. grandis trees of 130 years old growing in orchards with a density of 22–55 trees per hectare
were selected as the study object. The average tree height was 7.8 ± 0.5 m (mean ± SD), the diameter at
breast height (DBH) was 46.2 ± 2.2 cm, the average crown breadth or trees was 6.0 ± 0.6 × 7.0 ± 0.5 m.

Nutrients addition

Fertilization was applied in each study orchard during the growing season. Different amounts of
compound fertilizer with an N: P₂O₅: K₂O proportion ratio of 15:15:15 (a N: P: K content ratio of
1:0.44:0.83) were used as the nutrient addition treatments. The experimental design included five
treatments and three replicates, totaling 15 100 m x 100 m plots. The control group was designated “F0”,
which received no fertilization. The four nutrient addition treatments were designated as F1-F4, forming
an increasing fertilization gradient. Each plot had 12–15 mature T. grandis plants, and were subjected to
the same management practices except for nutrient addition. Fertilizer treatments were detailed in
Table 1, and fertilization was applied twice, each in April and July, at a depth of 10 cm below the soil’s surface. Organic fertilizer was applied in plots F1, F2, and F4, in order to provide more organic matter.

| Fertilizer treatments | F0 CK | F1 Low | F2 Medium | F3 Medium | F4 High |
|-----------------------|-------|--------|-----------|-----------|---------|
| CF (kg/hm²)           | 0     | 120    | 240       | 320       | 480     |
| OF (kg/hm²)           | 0     | 40     | 80        | 0         | 160     |
| N (kg/hm²)            | 0     | 18     | 36        | 48        | 72      |
| P (kg/hm²)            | 0     | 7.9    | 15.8      | 21.1      | 31.7    |
| Nᵢ (%)                | 7.9   | 7.6    | 8         | 7.5       | 8.9     |
| Pᵢ (%)                | 14.4  | 29.3   | 20.7      | 11.6      | 24.3    |

**Sample collection and measurements**

**Soil samples** were collected at the same time when leaf samples were collected. Each soil sample was a mixture of three soil collections from a 0–20 cm depth, and each location was randomly selected along the diagonal of each plot. The soil was dried and sifted to measure the particle size distribution and other soil chemical properties. In each plot, **three green leaf sample groups (30 leaves for each group)** were collected from the apricus healthy shoots of random plants in the middle of the canopy. Similarly, three 1 m x 1 m **litter** collection boxes were arranged along the diagonal of each plot. Both sample sets - the green leaf samples and the mixed litter samples were individually oven-dried at 60 °C to a constant weight, then they were respectively ground up and sieved through a 1 mm mesh screen for further analyses.

The foliar and soil nutrient properties (i.e., Total N, Total P, hydrolysable N, Olsen-P, and soil organic carbon) as well as soil pH were measured in accordance with national forestry industry standards, as shown in Table 2.
### Table 2
Measurement standard referred in this study

| Standard      | Administration                                                                 |
|---------------|--------------------------------------------------------------------------------|
| LY/T 1237–1999| National Forestry and Grassland Administration, 1999                           |
| LY/T 1239–1999| National Forestry and Grassland Administration, 1999                           |
| LY/T 1271–1999| National Forestry and Grassland Administration, 1999                           |
| LY/T 1228–2015| National Forestry and Grassland Administration, 2015                           |
| LY/T 1232–2015| National Forestry and Grassland Administration, 2015                           |

### Data analysis

To examine the relative nutrient limitation among the treatments, we calculated nutrient resorption efficiency (NuRE) using the following equation:

\[
NuRE = 1 - \frac{N_{\text{senescent}}}{N_{\text{green}}} \times MLCF \times 100\%
\]

where, \(N_{\text{green}}\) and \(N_{\text{senescent}}\) are the nutrient concentrations ([N], [P]) in green and senesced leaves, respectively, and MLCF is the mass loss correction factor with a value of 0.780 for evergreen species (Vergutz et al. 2012).

Given the large data set collected, we also tested the relationships between log-transformed nutrient stoichiometry of green and senescent leaves, by applying a type II linear regression model (SMA, standardized major axis; \(Y \sim X\)) using the lmodel2 package in R (3.6.1). \(Y\) is the \([C], [N], [P]\) or stoichiometry ratios in the foliar samples and \(X\) is the related variables in the senescent leaves; slope > 1 indicated dependence of \(Y\) variation on \(X\), slope < 1 indicated an independence of \(Y\) on \(X\), and slope = 1 indicated a synchronous change of \(X\) and \(Y\).

Significant difference of each dependent variable (C, N, P stoichiometry of soil, foliar and nutrient resorption) among fertilizer treatments were tested by one-way analysis of variance (ANOVA) followed by Least Significant Difference (LSD) and Tamhane's T2. Distance correlation analysis was performed to assess the nutrient content correlation among the soil, green leaves, and senescent leaves. Results were considered significant when \(P<0.05\). All statistical analysis was performed using the SPSS software (version 20.0, SPSS Inc., Chicago, USA) and R (3.6.1).

### Results
Effects of fertilization on soil nutrient characteristics

Fertilization treatments significantly affected soil chemical properties. Soil nutrient stoichiometry showed a strong positive correlation with the nutrient addition gradient (Fig. 1). Concentrations were ranged from 18.17 ~ 34.17 g/kg (OC), 1.67 ~ 3.38 g/kg (TN), 1.56 ~ 4.45 mg/kg (TP), 132 ~ 299 mg/kg (HN), and 225 ~ 1081.00 mg/kg (AP) depending on the specific treatment. Compared to the control, adding fertilizer increased the soil’s TN, TP, HN, and Olsen-P by a maximum of 102%, 185%, 127%, and 380%, respectively. The addition of organic fertilizer raised the soil pH in samples F1, F2, and F4 above that of F0 and F3. Yet, by comparing samples F0, F2, and F3, it is apparent that organic fertilizer had no significant effect on soil organic carbon (SOC) content. Finally, as the fertilizer concentration increased, the soil N:P and C:P significantly decreased (Figs. 1g, h), but C:N (11.00 ± 0.87) remained stable throughout the four experimental treatments.

Effects of fertilizer on foliar nutrient characteristics

Fertilizer treatment increased foliar nutrient contents, which depended on the nutrient element and growing status (Fig. 2). Generally, green leaf uniformly exhibited a higher nutrient concentration than senesced leaf (Fig. 2), but different nutrient elements, [C], [N], and [P], showed different patterns. For green leaf, although [N] and [C] tended to be the highest under medium fertilizer treatments, there was little difference in nutrient contents in response to the different fertilizer supply intensities. In contrast, [P] exponentially increased with the fertilizer supply gradient (F2-F4) and tended to maximize under the high level fertilizer treatment (F4). For senescent leaf [C], [N], and [P], the resorption proficiency trend paralleled with that of the green leaf, although the magnitudes differed. Compared to the control, high level fertilizer supply increased [P] by 102% and 57% of green and senescent leaves, respectively. Similar to green leaf, there was no significant difference in [C] and [N] among different treatments in senescent leaf. Senescent leaf [P] under high level fertilizer supply (F3 and F4) was slightly higher than that of the other treatments. Green leaf [P] was significantly correlated with soil inorganic nitrogen concentration (indicated by soil HN) rather than inorganic phosphorus (indicated by soil Olsen-P) (Table 3), while there was no correlation of leaf [N] with either soil P or N content.

| Table 3 | Pearson correlation coefficients of the nutrients in leaves and soil |
|---------|---------------------------------------------------------------|
|         | Soil TN  | Soil TP  | Soil HN  | Soil Olsen-P | SOC   |
| Leaf P  | 0.789**  | 0.809**  | 0.906*  | 0.541        | 0.691** |
| Leaf C:P| -0.564*  | -0.548*  | -0.917* | -0.507       | -0.476  |
| Leaf N:P| -0.582*  | -0.549*  | -0.900* | -0.488       | -0.512  |

** and * indicate statistical significances at α 0.01 and 0.05
The C:N ratio of both green (2.15 ± 0.05) and senescent (2.47 ± 0.09) leaves showed no apparent change among the treatments (Fig. 3). The significant increase in [P] led to big variations of N:P and C:P in green and senescent leaves, which declined with increasing fertilizer addition, excluding the control group. The highest nutrient utilization efficiency indicated by C:P and C: N were 27.92 (F1) and 2.21 (F1) in the green leaf. In addition, there was no correlation between foliar N or P with soil pH values.

**Discussion**

**Effect of fertilizer on soil condition**

Long-term N deposition and fertilization could elevate soil nutrient concentration beyond the demand of plant, altering the soil nutrient cycles (Huang et al. 2007). Because most soils in subtropical areas is severely acidic, improper and excessive use of fertilizers could further deteriorate soil physical, chemical, and biological properties, especially aggravating soil acidification and soil hardening. Decreases in soil pH caused by fertilizers are likely to reduce soil microbial and enzyme activities, which subsequently reduces organic matter mineralization and ultimately reduces “chemical facilitation” (Yang 2018). In this study, adding organic fertilizer effectively improved soil acidification (Fig. 1) and validated previous reports that organic fertilizer addition plays a positive role in soil acidification improvement in subtropical forests (Fang et al. 2019; Pang et al. 2019; Wang et al. 2014). However, unlike other studies, the improvement in our experiment was not related to the amount of organic fertilizer, but instead, it was negatively related to the amount of compound fertilizer (Chai et al. 2019). It is generally accepted that organic matters can increase available soil nutrients, which, however, was not significant in our study. The possible cause was attributed to the form of added N (NH$_4$NO$_3$), which lowered the positive priming effect of carbon inputs on mineralization of organic matters in soil (Chen et al. 2018).

**Effect of fertilizer on plant C, N, and P stoichiometry**

The primary goal of this research was to evaluate whether *T. grandis* requires fertilization or whether adding additional nutrients through fertilization can improve tree nutrition. In the present study, we found that fertilization tended to increase the green and senescent leaves [C], [N], and [P], but only the increase in [P] was statistically significant (Fig. 2). Furthermore, the average values of [N] and [P] were clearly higher than the corresponding values of global flora (Han et al. 2005; Reich and Oleksyn 2004) and most woody species in southeast China (Wu et al. 2012). Plants reduce nutrient resorption to the largest extent when the environmental nutrient availability exceeds their demands (Wright and Westoby 2003). The fact that foliar [N] remained stable, despite the increased nutrient supply, may indicate diminished N-limitation to plant growth, which can be explained by a plant behavior developed from adjusting to nutrient abundant environments. Only leaf [P] showed a significant increase under increasing fertilizer supply, resulting in a distinct decrease in C:P and N:P ratios. Therefore, our findings support our first hypothesis that long-term fertilization, combined with increasing nitrogen deposition, results in a N-enriched and P-limited environment. This result also confirms that N-limitation has been generally alleviated in the
subtropical forest; while P-limitation in the study area was aggravated by N enrichment (Han et al. 2005; See et al. 2015; Wang et al. 2014).

The soil nutrients pool (TN, TP, HN, and SOC), under long-term fertilizer treatment, was much higher than that in other subtropical areas (Kou et al. 2016; Zhang et al. 2017). Long-term soil nutrient enrichment resulted in much higher *T. grandis* foliar nutrient (N and P) contents (Tang et al. 2018a) than other subtropical evergreen trees (Yan En-Rong et al. 2010); the average N and P values of 753 terrestrial species were 18.6 and 1.21 g/kg, respectively (Han et al. 2005). Due to the different N and P utility patterns in physiological process, regardless of species and site fertilizer supply, plants are able to store a greater percentage of inorganic P than N. Thus, following fertilizer treatment, foliage accumulated more P than N (Ostertag 2010). It was also observed that some plant species growing in P-limited environments might not downregulate P uptake when a higher supply of P is available (Ostertag 2010; Shane and Lambers 2007; Standish et al. 2007). When the environment P supply shifts from P-limited to non-limited condition, the plants may undergo an excessive P uptake, even to saturated or toxic levels. Hence, foliar [P] usually displays a much higher variation after fertilizer treatment. Therefore, it is not surprising that the foliar [P] nearly doubled after a high fertilizer treatment compared to the control group (Fig. 2). Given the generally low bioavailability of P in subtropical soils, *T. grandis* may have developed as an efficient mechanism to take up and accumulate P in response to the strong selective pressure (Chapin III et al. 1990; Ingestad 1974; Mulligan and Sands 1988). Unlike previous studies (Huang et al. 2016; Sardans et al. 2016b; Zhang et al. 2019), leaf [N] of *T. grandis* didn't change much in response to the increasing soil [N] availability, which implied that fertilizer treatments had no effect on *T. grandis* N absorption (Figs. 1 and 2). In this scenario, relatively stable leaf [C] and [N], but increased leaf [P] led to opposite trends between C:P and N:P and soil nutrients (Fig. 1; Table 3).

Stoichiometry homeostasis was used to analyze plant composition, ecosystem function, and nutrient limitation, especially for key elements such as C, N, and P ratios (Allen and Gillooly 2009; Hessen et al. 2004). Generally, plants uptake nutrients in appropriate proportions to maintain nutritional balance, depending on physiological consumption (Phoenix et al. 2012; Sardans et al. 2016b). The inherently higher variability of P concentration in plants, relative to N, was illustrated in a survey of European wetlands (Güsewell and Koerselman 2002). Similarly, our findings demonstrated that the correlations between foliar [P], [C], [P], and [N] were decoupled due to a more sensitive response of foliar [P] to fertilizer supply (Figs. 2 and 3). This suggests that the balance of biogeochemical C, N, and P cycles were broken by the fertilizer treatments, which could decrease ecosystem stability (Demars and Edwards 2007) and alter the N and P cycles (Yuan and Chen 2015), leading to degenerative feedback between the plant and ecosystem (Sistla and Schimel 2012). Under these circumstances, foliar [P] or the N:P ratio may not reflect the actual demands of the plant under P addition conditions (Greenwood et al. 2008). Although many studies indicate that the N:P ratio of mature leaves have been widely used to diagnose plant growth nutrient limitations, with thresholds (such as 10 and 20) to classify the plants into N-limited, N and P co-limited, and P limited plants (Güsewell 2004; Rejmánková 2005; Xu et al. 2017).
Furthermore, contrary to previous research (Li et al. 2016), fertilizer treatment in this study also failed to increase the aboveground biomass (indicated by a stable carbon sequestration) of *T. grandis*. Moreover, the fertilizer significantly reduced the C:P (indicating the P utilization efficiency in productivity) of *T. grandis* in this study, suggesting that the P utilization efficiency of plants was reduced by the increased nutrient supply (Dijkstra et al. 2016). Our analysis suggested that both P and N fertilizer might be unnecessary for *T. grandis*.

**Effect of fertilizer on plant nutrient resorption**

| Y      | X      | Slope | Intercept | $R^2$  |
|--------|--------|-------|-----------|--------|
| Leaf N | soil TP| 0.24  | 1.26      | 0.63*  |
| Leaf N | Soil HN| 0.21  | 0.87      | 0.48*  |
| Litter N | Leaf N | 0.9   | 0.25      | 0.72** |
| Litter P | Soil TP| 0.69  | -0.02     | 0.59*  |
| Litter C | Leaf C | 1.63  | -1.12     | 0.51*  |
| Leaf C | SOC    | 0.18  | 1.42      | 0.88** |
| Leaf C:P | Leaf P     | -1.03 | 1.70      | 0.99** |
| Leaf C:P | Leaf P    | -1.02 | 1.36      | 0.98** |
| PRE    | Leaf P  | -1.02 | 1.36      | 0.98** |

* and ** are 2-tail sig. $P<0.1$ and 0.05

Acquisition (root uptake) and conservation (resorption from senescent tissue) are two important biological strategies for plants to maintain balanced nutrition where soil nutrition is deficient. These processes are also important in cycling nutrients between the soil and plants (Killingbeck 1986). Choosing between alternative strategies for plants depends on the cost (time and energy) of each process and the species characteristics. Short-term experiments have demonstrated that generally, plants will reduce nutrient utilization efficiency when the availability of that nutrient increases in the plant's natural environment (Yuan and Chen 2015). While the relationship between foliar resorption and soil nutrient concentration is not consistent (Aerts 1996; Aerts and Chapin III 1999; Yuan 2015). Our results indicated a constant NRE, which further verified our supposition concerning N enrichment in the orchard (Fig. 4a). However, increased P migration from senescent leaf to green leaf (PRE) in response to increasing fertilizer supply conflicts with the negative correlation between fertilizer treatment and nutrient resorption (Yuan and Chen 2015). This counterintuitive result from a single-resource conservation standpoint has been observed in previous studies (Boerner 1986; Sabaté et al. 1995); yet multiple-element
theory much appropriately explains variability in foliar nutrient resorption (See et al. 2015). Based on a Pearson correlation analysis, we found that green leaf [P] was not related to soil [Olsen-P], but it was highly correlated with soil N content (Table 3). It should be noted that the root system can directly uptake inorganic nutrients (Olsen-P and hydrolysable nitrogen) and therefore plays a more important role in nutrient absorption than organic nutrients. This inorganic nutrient preference may help explain the absence of a common trend in studies comparing P resorption to soil P availability (Aerts 1996; Aerts and Chapin III 1999). Under the circumstances, although the soil and leaves were characterized by a higher [P] compared to other studies of evergreen trees (Tang et al. 2018b), N enrichment was responsible for the amplified P-limitation (Fig. 4b), which subsequently elevated leaf P uptake (Agüero et al. 2014; Tian et al. 2019). The standardized major axis (SMA) analysis showed that leaf [P] is independent of soil [P], which supports the above hypothesis. Strong dependencies, indicated by a slope > 1, were found only between senescent [C] and leaf [C] (Table 4). For an evergreen species with a long leaf life span, T. grandis exhibited a more conservative P use strategy as opposed to the external root uptake strategy, regardless of soil P availability. Similar results were also reported in some non-mycorrhizal species (Laliberté et al. 2012). This mechanism allows plants to maintain a higher nutrient absorption efficiency with relatively less cost (energy and time) but lowers the utilization efficiency and productivity (Wright and Westoby 2003).

**Conclusion**

As N deposition and long-term fertilizer treatment intensified, there was a significant increase in the soil N and P, which improved leaf N and P concentrations. In our study area, N enrichment was indicated by stable and decoupling relationships between the soil and leaf [N]. Although T. grandis has a high level of leaf [N] and [P], N enrichment amplified the physiological P limitation (deficiency). Unfortunately, the present fertilizer modes did not seem to enhance productivity (C fixation). Excessive fertilizer application both wastes resources and negatively impacts nutrient uptake and soil physicochemical properties. Thus, we recommended rejecting N fertilizer addition and increasing application of organic fertilizer as needed. Although P-limitation was demonstrated in this study area, whether the P was deficient in the soil requires further exploration through a single-P element control experiment.

**Abbreviation**
| Abbreviations | Definitions                      |
|---------------|----------------------------------|
| T. grandis    | Torreya grandis                  |
| C             | Carbon                           |
| N             | Nitrogen                         |
| P             | phosphorus                       |
| [C]           | Carbon concentration            |
| [N]           | Nitrogen concentration           |
| [P]           | Phosphorus concentration         |
| NPP           | Net primary productivity         |
| NRE           | Nitrogen resorption efficiency   |
| PRE           | Phosphorus resorption efficiency |
| RR            | Relative nutrient resorption     |

**Declarations**

**Ethics approval and consent to participate**

Not applicable.

**Consent for publication**

Not applicable.

**Availability of data and material**

All data generated or analysed during this study are included in this published article.

**Competing interests**

The authors declare that they have no competing interests.

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Authors' contributions

All the authors listed have contributed significantly to this research work and approved to submit this manuscript to your journal. Specifically, Dr. Yini Han, conducted the data analysis, and data interpretation and drafted the manuscript; Dr. Songheng Jin instructed the field experiment design, data interpretation; Dr. Geofeng Gao and Tonggui Wu helped develop ideas and revised the manuscript; Dr. Wenjing Chen and postgraduate Yongliang Ji helped in field experiment design and data collected.

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Figures
Figure 1

Relationship between nutrient supply and soil nutrient contents. SOC, TN, TP, HN, Olsen-P denote total soil organic C, Total N, Total P, Hydrolysable N, and Available P, respectively. Error bars refer to ±1 standard error, P<0.05, n=3
Figure 2

Effect of different fertilizer treatments on the leaves (left) and litters (right) nutrient contents (OC, N and P). Error bars refer to ±1 standard error (a, b, c, d above each row indicate the differences in fertilizer treatments, P<0.05.)
Figure 3

Green leaf stoichiometry under different fertilizer treatments. Error bars refer to ±1 standard error (a, b above each row indicate the differences in fertilizer treatments, P<0.05.)
Figure 4

Nutrient resorption efficiency of N, P: a) NRE and PRE and b) relative nutrient resorption (RR) of T. grandis under different fertilizer treatments. The letters above or below each row indicate the differences in fertilizer treatments, P<0.05.