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Allocation strategies of carbon, nitrogen and phosphorus following a gradient of wildfire severities

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Abstract

Wildfire is crucial in the regulation of nutrient allocation during the succession of boreal forests. However, the allocation strategies of carbon (C), nitrogen (N) and phosphorus (P) between leaves and fine roots in response to wildfire severities remain poorly studied. We aimed to explore the allocation strategies of C, N and P between leaves and fine roots among different fire severities. We selected four wildfire severities (unburned, low, moderate and high severity) after 10 years recovery in the Great Xing'an Mountains, northeast China, and compared C, N and P concentrations in leaves and fine roots of all species among fire severities using stoichiometry theory and allometric growth equations. Compared with unburned treatment, C concentrations in leaves and fine roots increased at low severity, and leaf N concentration was the greatest at high severity, but the lowest fine root N concentration occurred at high severity. Plant nutrient utilization tended to be P-limited at high fire severity according to the mean value of N:P ratio > 16. More importantly, C, N and P allocation strategies between fine roots and leaves changed from allometry to isometry with increasing fire severities, which showed more elements allocated to leaves than to fine roots with increasing fire severities. These changes in patterns suggest that the allocation strategies of elements between leaves and fine roots are of imbalance with the wildfire severity. This study deepens our understanding of nutrient dynamics between plant and soil in ecosystem succession.

Keywords allocation strategy, carbon, nitrogen and phosphorus, leaves and fine roots, wildfire severity

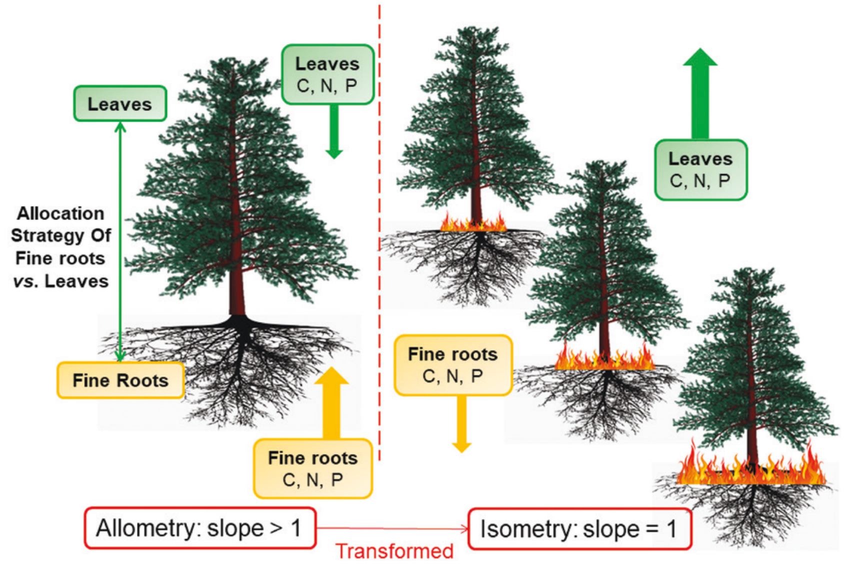
植物碳、氮、磷在不同火烧强度下的分配策略

摘要：森林野火是影响北方针叶林演替过程中养分分配规律的重要因素。然而，植物叶片和细根之间的碳(C)、氮(N)、磷(P)分配策略在不同强度森林野火后的研究尚不充分。本研究旨在探讨不同野火强度下叶片和细根间C、N、P的分配策略。运用化学计量学理论和异速生长方程，选取中国东北大兴安岭地区的4个不同火烧强度(未火烧、低、中、高)恢复10年后的火烧迹地为研究样地，比较不同火烧强度下各物种叶片和细根的C、N、P含量。研究结果表明，与未受到火烧的样地相比，轻度火烧迹地的植物叶片和细根C浓度增加，重度火烧迹地植物叶片N浓度最高，但是细根N浓度最低。N:P比值的平均值大于16的结果表示植物养分利用策略在高火烧强度下趋于P限制。更重要的是，随着火烧严重程度的增

加，细根与叶片间的C、N、P分配规律出现由异速生长向等速生长的转变，即随着火烧强度的增加，元素分配表现为对叶片的分配多于细根。这些结果表明，植物叶片和细根之间的元素分配策略在受到不同强度的野火干扰以后发生了失衡。本研究加深了我们对火后森林生态系统演替过程中植物与土壤养分动态的认识。

关键词：分配策略，碳，氮，磷，叶和细根，火烧强度

Graphical Abstract



INTRODUCTION

Wildfire is one of the main factors driving the regeneration processes in forest ecosystems (Bisbing *et al.* 2010; Liu *et al.* 2012), which disturbs the nutrient dynamic; thus, it affects ecosystem structure and functioning (Fang *et al.* 2015). Wildfire can decrease soil physical and chemical properties, where it lowers soil available nutrients and modifies soil nutrient circulation (Certini 2005; Holden *et al.* 2016; Hume *et al.* 2016). The changes of soil nutrients will influence the plant elemental concentration, which affects the nutrient utilization of different organs, such as leaves and roots (Deluca and Anna 2006). However, limited researches have been conducted on plant nutrient allocation strategies among different fire severities.

A previous study has revealed the effects of wildfire on plant growth with less consideration given to the impact of soil nutrient changes with fire severity in post-fire ecosystems (Fajardo and Gundale 2017). The early stage of wildfire regeneration (approximately 10 years) is a critical period for predicting the plant nutrient dynamics, ecosystem structure and succession trajectory (Hansen *et al.* 2016; Johnstone *et al.* 2010). Changes in soil nutrient status during this period have a vital role in the regeneration of vegetation (Hume *et al.* 2016; Turner *et al.* 2011). Burning usually leads to the losses of soil C, N and P (Schultz *et al.* 2008). The changes of soil N and P pool are different among fire severities (Walker *et al.* 2019). For example, previous studies have found the dynamic of soil N was affected by fire severities or frequencies (Hume *et al.* 2016; Pellegrini *et al.* 2018). Besides, the effects of wildfire on soil P vary greatly among different fire severities (Boby *et al.* 2010; Caon *et al.* 2014). High severity wildfire lowers the rate of soil mass loss and nutrient cycling process in comparison with low severity (Brennan *et al.* 2009). Hence, changes in the soil nutrients supply are closely related to the C, N and P concentrations of plants, which is reflected by their stoichiometric characteristics (Li *et al.* 2012).

Wildfire remarkably and disproportionately affects soil C, N and P pools, and fire severity also changes the nutrient status of plants (Cui *et al.* 2010; Hansen *et al.* 2016). Theories of ecological stoichiometry showed that the changes of elemental concentration and the ratio of elements can reflect the nutrient adaptation between plant and environment (such as C, N and P; Elser *et al.* 2010b; Zhang *et al.* 2018). After wildfire, ash from burned organisms remains on the surface; meanwhile, there is N deposition and P input during the recovery process (Fernández-Fernández *et al.* 2017). The increases of soil N and P availability in the burned area may boost plant growth in the ecosystem recovery process (Dijkstra and Adams 2015; Manuel *et al.* 2013). The N and P are fundamental components of genetic material and are tightly linked to many biochemical processes, such as photosynthesis, respiration and litter decomposition (Chen *et al.* 2013; Lebauer and Treseder 2008), and these processes are closely related to C dynamics (Elser *et al.* 2010b). For example, high soil N concentration can improve the plant C synthesis and thereby increase P requirement for photosynthesis (Niu *et al.* 2016). Moreover, excessive N can change the C distribution through altering photosynthetic rates because it may inhibit the root function and weaken the nutrient absorption of plants (Vernay *et al.* 2018). The same with leaves, fine roots also can show adaptation ability in the vital organs in the post-fire environment (Butler *et al.* 2018). However, few studies revealed the underlying mechanisms of the plant nutrients adaptation in the post-fire ecosystem. Thus, we hypothesized that wildfire may elicit the imbalance of C, N and P concentrations between leaves and fine roots.

Plants allocate nutrients effectively in order to maximize growth and ensure their metabolic activity in response to variations of the soil nutrients condition (Elser *et al.* 2010a; Enquist and Niklas 2002). Nutrient concentrations in different plant organs are tightly related to each other, and their allocation can be reflected by scaling relationship analyses (Yan *et al.* 2015). Plant organs may change nutrient utilization strategies to respond to the resource limitations (Ordoñez *et al.* 2010; Smithwick *et al.* 2012). It is worth noting that nutrient utilization of plant organs follows the optimal allocation theory, whereby a plant allocates more nutrients to the organ under nutrient limitation, yet allocates less nutrients to the organ under abundant nutrient resources (Minden and Kleyer 2014). For example, plants growing in arid conditions tend to allocate more N to leaves to augment their photosynthetic rate and water-use efficiency (Palmroth *et al.* 2013; Yang *et al.* 2015). Therefore, changes of nutrient supplies will affect plant biomass distribution (Freschet *et al.* 2015). Plants growing in high-nutrient conditions will allocate more nutrients to the leaf to capture sunlight, which will increase photosynthesis, while plants growing in low-nutrient conditions allocate more photosynthetic products to the root to increase nutrient acquisition (Freschet *et al.* 2015). Therefore, changes of the nutrient allocation between leaves and fine roots would reflect an important regulatory process for plants to adapt to the nutrient changes after wildfire. Thus, comparing with unburn treatment, we hypothesized that plant nutrient allocation between leaves and fine roots would be changed due to the different of nutrients supplying after wildfire.

Boreal forests as an important part of the global total carbon pool (Shuman *et al.* 2011) contribute a tremendous stock of terrestrial organic carbon (Wu *et al.* 2015). Frequent wildfires in boreal forests have profound influences on the plant nutrient utilizations, and even the forest ecosystem structure and functioning (Wu *et al.* 2013). Thus, understanding the nutrient circulation of fire-prone boreal forests is a key issue for post-fire management (Liu *et al.* 2012; Wu *et al.* 2014). As an important part of boreal forests, the Great Xing'an Mountains of northeastern China host the southern extension of the larch forests and account for 30% of China's timber production (Wang *et al.* 2010). *Larix gmelinii (Rupr.)* Kuzen is the dominant species in the Great Xing'an region. This forest therefore has immense value in terms of climate change and economy (Kong *et al.* 2015). Wildfire is an important ecological factor affecting forest succession in the Great Xing'an ecosystem, and this region retains the most complete burned sites in China (Hu and Zhou 2014; Wu *et al.* 2015). Currently, most studies in this region focused on soil and community composition regeneration after fire; however, the nutrient distribution between leaves and fine roots and the mechanisms by which they respond to soil nutrient are unclear.

Therefore, we wanted to answer the following scientific questions: (i) Could the soil nutrient be impacted among different fire severities? (ii) Would plant C, N and P stoichiometry be changed among fire severities? (ii) What is the allocation tendency of C, N and P between leaf and fine root following fire severities?

METHODS AND MATERIALS

Site description

This research was conducted in the Xilinji Forestry Bureau, near the town of Mohe in the Great Xing'an Mountains of northeastern China. The total forestry area was 18 367 m^2. The altitude of the experimental sites was 570–580 m. The climate was characterized by a long and severe winter, lasting up to 9 months where annual average precipitation was 500 mm and the mean annual air temperature was 5 °C. The number of forest species was fairly low in the area, especially at the vertical level of stratification (Hu *et al.* 2017). Dominant tree species included *Larix gmelinii*, *Pinus sylvestris* var. mongholica, *Picea koraiensis*, *Betula platyphylla* and two species of aspen (*Populus davidiana* and *Populus suaveolens*). Understory vegetation was dominated by shrubs, i.e. *Ledum palustre*, *Vaccinium vitis-idaea*, *Rhododendron dauricum*, *Vaccinium uliginosum* and *Eriophorum angustifolium* (Meng *et al.* 2017). Soils were classified as brown coniferous forest soil according to World Reference Base (2015).

The Great Xing'an ecosystem was primarily affected by natural wildfire disturbances because there were many combustible matters under canopy due to a low decomposition rate (Liu *et al.* 2012). The wildfire regime we selected occurred here in June 2009 and has not been fired again since then, for which historical records provided precise data. The wildfire type was characterized by surface fires. These undamaged burning sites provided scientific research sites for undertaking scientific experiments in the burned areas.

Field sampling

Fire severity was identified by the standard of composite burn index assessment protocol (Key 2006; Lentile *et al.* 2006), which was precisely provided by the post-fire investigation according to the historical records in July 2009. Specifically, investigators visually estimated the changes of coarse woody debris, black carbon, white ashes, char height, the mortality rate of tall trees and the proportion of fallen trees (Boby *et al.* 2010; Fang and Yang 2014; Key 2006; Table 1). At the end of July 2018, the four fire severities (each severity established three repeat plots) were categorized by composite burn proportion, which were unburned (UB), low (LB), moderate (MB) and high severity (HB) (Table 1). After fields investigated, 12 plots (20 m × 20 m) were established, with nine plots in the burned area (low, moderate and high severity) and another three plots in the unburned area. In addition, the forests type was *Larix gmelinii* forests in all plots before the burn.

Plant sampling

We sampled all tree and shrub species in the plot, as well as the dominant herb species (Table 1). In each plot, three repetitive individuals of each species growing under sufficient light conditions were selected. We obtained 56 plant samples of unburned, 44 samples of low severity, 32 samples of moderate severity and 24 samples of high severity. All plant samples included leaves and fine roots. We selected fresh intact leaf 80–100 g from each individual species from four orientations (the north and south, east and west). We manually grubbed the fine root (diameter < 2 mm) 40–60 g of each individual species within the depth of 2 m. Plant samples (including leaf and fine root) were cleaned carefully with distilled water. The samples were quickly transported to laboratory and kept at 4 °C and then oven-dried at 65 °C to constant weight in the laboratory and then ground to measure total C, N and P concentration.

Soil sampling

There are five soil replicates (four vertices and the center) in each sampling plot, and we collected three soil cores (aboveground plant material and live roots were removed) from each replicate at a depth of 0–20 cm, using a 25-cm-diameter metal soil corer. Fresh samples were placed in polyethylene zip-lock bags, stored in a cooler with ice and transported to the laboratory. Soil samples were air-dried and ground within 10 days after sampling.

Samples analyses

Chemical analyses

The C concentration of plants (leaves and fine roots) and soil were measured with an elemental analyzer (Vario MAX CN Elemental Analyzer, Elementar, Hanau, Germany). The N and P concentrations of plant and soil was measured by the ammonium molybdate method using a continuous-flow analyzer (AutoAnalyzer 3, Bran Luebbe, Hamburg, Germany), after H_2SO_4–H_2O_2 and Se–$CuSO_4$–K_2SO_4–H_2SO_4 digestion for plant and soil samples, respectively.

Data analyses

Reduced major axis (RMA, also called standardized major axis) regression was used to get the sloping exponent and constant of log–log linear functions

Table 1: Location and species information of study among fire severity grade

Fire severity	Composite burn proportion (%)	Site coordinates	Species numbers	Species
Unburned	0	52°32′01″ N 122°38′15″ E	14	*Larix gmelinii*; *Ledum palustre*; *Pyrola dahurica*; *Buxus sinica*; *Populus davidiana*; *Betula fruticosa*; *Betula platyphylla*; *Pinus sylvestris*; *Salix myrtilloides*; *Vaccinium uliginosum*; *Alnus mandshurica*; *Sambucus williamsii*; *Deyeuxia langsdorffii*.
Low	10–30	52°32′35″ N 122°38′50″ E	11	*Ledum palustre*; *Betula fruticosa*; *Vaccinium uliginosum*; *Larix gmelinii*; *Buxus sinica*; *Betula platyphylla*; *Rosa acicularis*; *Vaccinium uliginosum*; *Alnus mandshurica*; *Ribes nigrum*; *Filipendula palmata*.
Moderate	40–60	52°32′11″ N 122°38′19″ E	8	*Ledum palustre*; *Vaccinium uliginosum*; *Larix gmelinii*; *Betula fruticosa*; *Rhododendron dauricum*; *Betula platyphylla*; *Vaccinium uliginosum*.
High	70–90	52°32′31″ N 122°38′54″ E	6	*Vaccinium uliginosum*; *Ledum palustre*; *Larix gmelinii*; *Betula fruticosa*; *Betula platyphylla*; *Vaccinium uliginosum*.

(Warton *et al.* 2010). The data for C concentration in leaf and fine root were log-transformed. The allocation relationship of C in leaf and fine root was described by the equation:

$$\mathrm{Log}\,(Y) = \log\,(a) + b * \log\,(X) \qquad (1)$$

where X is the total C concentration of leaf and Y is the total C concentration of fine root; a is the intercept on the y axis, and b is the slope of the linear equation, represents the allometry exponent (Table 2). When $b = 1$, the relationship of X to Y is isometric; otherwise, the relationship is allometric. If $b > 1$, Y changes more than X, whereas $b < 1$ indicates that X changes more than Y (Warton *et al.* 2015). Allometry theory provides an approach to describe elemental distribution among plant organs (Kerkhoff *et al.* 2006). Confidence intervals of the slope were calculated according to the method of Pitman (1939). A likelihood ratio test was used to test the heterogeneity of the slope of total C at different fire severities. If there was heterogeneity in the slopes, *post hoc* comparisons were performed. Differences in the regression slopes among different fire severities were tested by multiple *post hoc* comparisons. The different slope of root *vs.* leaf along the common major axis indicated differences in nutrient allocation between leaf and root among different fire severities. Similar statistical analyses were conducted for N and P between leaves and fine roots among different fire severities. The statistical significance level was $P < 0.05$. All statistical analyses were performed using package of 'smatr' in R 3.3.2 (Warton *et al.* 2012).

Differences of C, N and P stoichiometry characteristic in soil, leaves and fine roots among fire severities were tested using one-way analysis of variance (ANOVA) with multiple comparisons of Duncan's post hoc tests using a general linear regression model (Figs 2 and 3). The significance level was set at $P < 0.05$. All statistical analyses were performed using R statistical software, version 3.3.2. We used aov() function and pairwise. t. test() function for the ANOVA analysis in R. All graphs were generated by SigmaPlot version 12.5 (Systat Software, San Jose, CA, USA, 2017).

RESULTS

Soil C, N and P stoichiometry among different fire severities

Fig. 1 shows the soil carbon and nutrient concentrations among different fire severities after 10-year wildfire. Soil C concentration was the highest at low severity, which increased by 67.0% compared with unburned. Soil C concentration was the lowest concentration at high severity. Soil N and P concentration shows

Table 2: Results of reduced major axis (RMA) regression on C, N and P concentrations of plant leaves and fine roots

Fine roots *vs.* leaves (Y *vs.* X)	Fire severity	b_{RMA}	95% CI	a_{RMA}	95% CI	R^2	P
Total C	UB	**2.50**a	(1.70, 3.68)	−4.21	(−6.87, −1.55)	0.36	0.03
	LB	1.29b	(1.16, 1.54)	−1.89	(−2.24, −1.37)	0.34	0.04
	MB	1.26b	(1.06, 1.56)	−4.23	(−5.46, −2.98)	0.68	0.02
	HB	1.23b	(1.10, 1.54)	−2.04	(−2.64, −1.45)	0.33	0.05
Total N	UB	**1.56**a	(1.05, 2.30)	−1.31	(−2.23, −0.37)	0.55	0.01
	LB	**1.31**b	(0.68, 2.53)	−0.95	(−2.37, 0.48)	0.96	0.005
	MB	1.18b	(0.61, 2.27)	−2.75	(−3.98, −1.52)	0.35	0.05
	HB	1.11b	(0.52, 2.35)	−2.77	(−4.21, −1.33)	0.45	0.04
Total P	UB	**1.92**a	(1.30, 2.83)	−0.55	(−0.83, −0.28)	0.37	0.04
	LB	0.79b	(0.41, 1.52)	−0.38	(−0.57, −0.19)	0.76	0.01
	MB	1.17ab	(0.79, 1.74)	−0.17	(−0.30, −0.04)	0.75	0.01
	HB	0.75b	(0.36, 1.58)	−0.34	(−0.51, −0.16)	0.34	0.05

Regression slope (b_{RMA}: allocation relationship between root and leaf) in bold are significantly different from 1 ($P < 0.05$). P-value in the last column indicates significant regression (all $P < 0.05$). Different letters indicate significant difference between different fire severities based on a likelihood ratio test ($P < 0.05$). Abbreviations: a_{RMA} = regression intercept; CI = confidence interval.

the same tendency with soil C concentration, which increased by 110.0% and 79.0%, respectively.

Variations in leaves and fine roots C:N:P stoichiometric characteristics among different fire severities

During the forest recovery, the concentrations of plant C, N and P were higher in leaves than those of fine roots ($P < 0.05$, Fig. 2). Compared with unburned, the C concentration of leaves and fine roots in burned areas significantly increased at low severity ($P < 0.05$, Fig. 2a and b). Compared with unburned, leaves N concentration was increased by 24.0% at high severity, but fine roots N concentration approached the lowest at high severity ($P < 0.05$, Fig. 2b and e). Fine roots P was significantly decreased after fire ($P < 0.05$, Fig. 2f).

The C:N, C:P and N:P ratios of leaves and fine roots in burned areas had different characteristics among fire severities (Fig. 3). Leaves C:N and C:P ratio significantly increased at moderate severity (Fig. 3a and b). The leaves N:P ratio significantly increased at high severity compared with unburned. The mean N:P ratio was lower than 14 at unburned, but it was higher than 16 at high severity (Fig. 3c). Fine roots C:N, C:P and N:P ratios among three fire severities were significantly higher than those at unburned ($P < 0.01$, Fig. 3d–f).

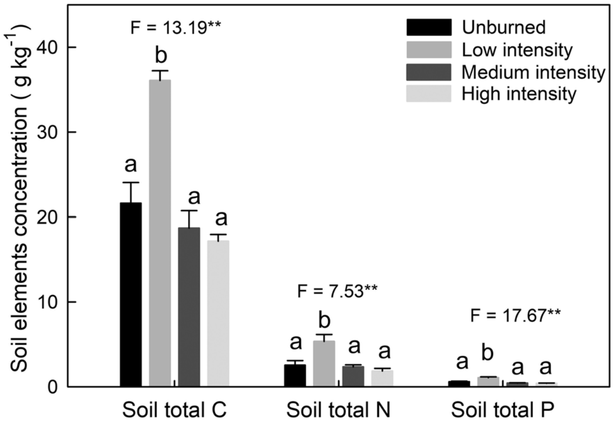


Figure 1: Differences in soil carbon (C), nitrogen (N) and phosphorus (P) concentration among fire severities. Error bars are standard errors. Different lowercase letters represent statistically significant differences among fire severities (**$P < 0.01$; *$P < 0.05$).

Scaling of C, N and P stoichiometry between leaves and fine roots among different fire severities

As shown in bold b_{RMA}, slopes from the RMA regressions of fine roots *vs.* leaves were significantly different from 1 for C at UB, N at UB and LB, as well as P at UB, suggesting an allometry growth relationship between fine roots and leaves (Table 2). As shown in different lowercase letters, the C, N and P allocation between fine roots and leaves transformed from allometry ($b_{RMA} > 1$) to isometry ($b_{RMA} = 1$) with severity increasing ($P < 0.05$). The slopes from the RMA regressions of fine roots *vs.* leaves at UB were larger than LB, MB and HB ($P < 0.05$, Table 2), which indicated that more C, N and P allocated in leaves at LB, MB and HB compared with unburned. However, more C, N and P were allocated in fine roots at UB. It obviously showed a changed elemental allocation between fine roots and leaves with increasing severity that transformed from allometry to isometry.

DISCUSSION

Soil C, N and P concentrations change in burned areas

Wildfire directly affects soil element volatilization and ash deposition, and further affects the soil nutrients among different severities (Boby *et al.* 2010; Wang *et al.* 2012). In our study, in 10-year regeneration after fire, total soil C, N and P concentrations significantly increased at low severity compared with unburn. As demonstrated in previous research, forest wildfire often changes the concentrations of nutrients in the soil, which plays an important role in the community successional processes (Ohlson *et al.* 2015; Smithwick *et al.* 2012). After low severity, acceleration of soil nutrient turns over due to burn and promotes soil microbial activity and increases soil N and P (Fajardo and Gundale 2017). Also, increasing plant and microorganism mortality rates can increase soil C (Fultz *et al.* 2016), which is usually higher than control area (unburned; Caon *et al.* 2014). Besides, a low severity often leads to an increase of soil organic N and ammonium nitrogen (Pellegrini *et al.* 2018). Additionally, P has a higher volatilization temperature compared with C and N, making P difficult to be volatilized at low severity (Toberman *et al.* 2014). The change of N and P supply in the disrupted ecosystem is an important ecological factor affecting plant growth and community recovery (Tarvainen *et al.* 2016). Thus, soil nutrient changes led to alterations of plant nutrient concentrations during the early recovery process in burned area, and the C, N and P concentration in leaves and fine roots achieved a dynamic balance.

Differential changes of C, N and P between leaves and fine roots in burned areas

The theory of ecological stoichiometry explains the nutrient interactions between biological organisms and environments (Elser *et al.* 2010a). Differences in C, N and P concentrations between leaves and fine roots are related to the requirements of functions (Kerkhoff *et al.* 2006). The main functions of leaves are light capturing and photosynthesis, while roots, especially fine roots, take in nutrients from soil (Ordoñez *et al.* 2010). The C and N concentration of leaves and fine roots showed significant differences among fire severities (Fig. 2). Compared with unburned treatment, both leaves and fine roots C significantly increased at low severity. As shown in a previous study, the increase of soil nutrients at low severity may result from the promotion of leaf biomass (Vitousek *et al.* 2010). Soil nutrients under low fire severities increase sharply, and plants adjust their nutrient allocation to adapt environmental changes, increasing leaf nutrient owing to N absorption saturation (Schreeg *et al.* 2014; Scoffoni *et al.* 2011). Combined with the stoichiometric distribution mechanism in the leaves and fine roots of most species, we also found that nutrient conditions in the burned area were conducive to promoting plant root growth (Venterink *et al.* 2003), thus increasing the root biomass. When compared with unburned treatment, leaf N concentration increased significantly at high severity, whereas the root N concentration was higher at low severity (Fig. 2). N is usually a major limiting nutrient to plant growth in forest ecosystems (Bünemann *et al.* 2018). At high severity, the soil N concentration was lowest, which was consistent with the results of Boerner *et al.* (2008). The less belowground accumulation of nutrients decreases soil nutrient supplement for leaves (Hansen *et al.* 2016). To ensure survival, plants take conservative growth strategies by investing more N in leaves than roots (Aerts and Chapin 2000); in line with a previous study, we found that fine roots N concentration was the lowest at high severity. The total P of fine roots in our study significantly decreased after burn. After burn, soil organic acid secretion increases soil acidification, causing a loss of soil available P (Yu *et al.* 2011). Under the above conditions, root P decreased, which damaged plant lateral root development and reduced root nitrogen absorption (Huanosto Magaña *et al.* 2009).

To get a better understanding of the physiological and evolutionary mechanisms of plant stoichiometric imbalance, we need to pay more attention to the ratio of plant elements in response to nutrient changes (Luo *et al.* 2016). The theory of stoichiometry points out that the amount of ecosystem C is controlled by the amount of ecosystem N and P; a lack of N and P

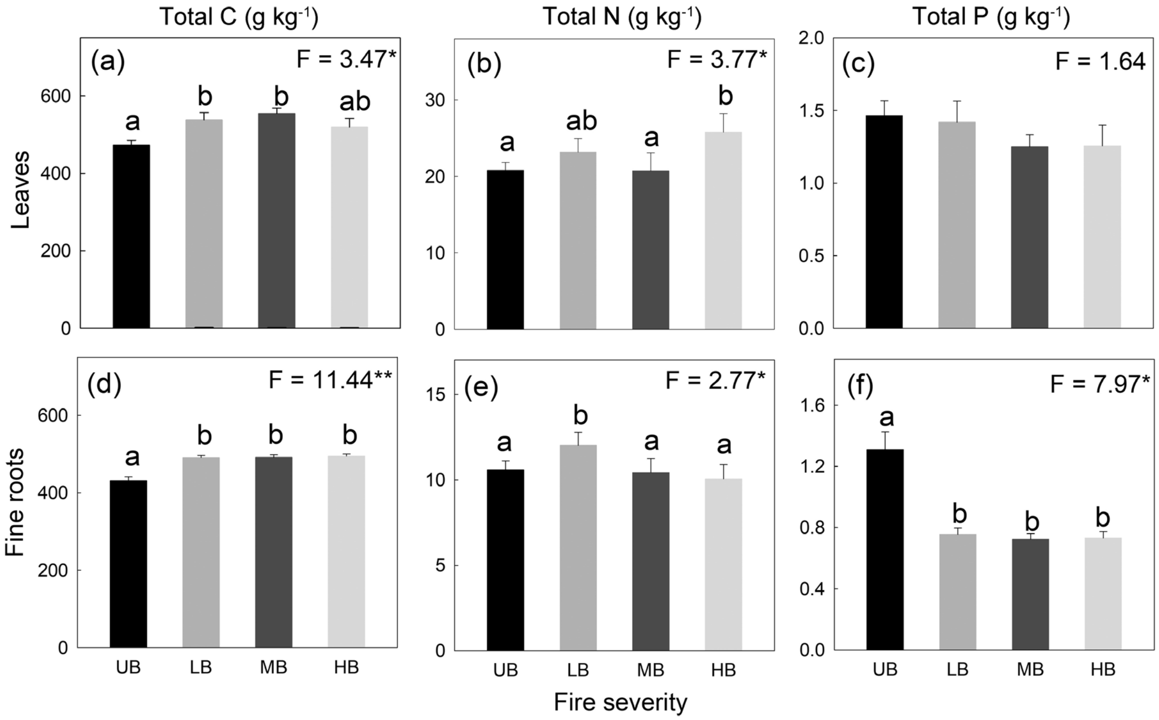


Figure 2: Changes of carbon (C), nitrogen (N) and phosphorus (P) concentration in leaves (**a**, **b**, **c**) and fine roots (**d**, **e**, **f**) among fire severities. UB, LB, MB and HB stand for unburned, low severity, moderate severity and high severity, respectively. Error bars are standard errors. Different lowercase letters indicate significant differences among different fire severities. $^{**}P < 0.01$; $^{*}P < 0.05$.

leads to a relative excess of C (i.e., greater C:N and C:P ratios), and a sufficient amount of N and P leads to a relative deficiency of C (i.e., smaller C:N and C:P ratios; Gusewell 2010). In this study, leaf C:N and C:P significantly increased at moderate severity because of the increase in absolute leaf C concentration and decrease in leaf N and P concentration. Leaf C:N and C:P represent the plants' ability to assimilate carbon using nutrient elements (Zhang *et al.* 2018). Wildfire in southern Ohio and Missouri in the USA also showed that fire led to changes in nutrient dynamics (Rietl and Jackson 2012). Our study better explains the significant changes in C:N ratio and C:P ratio of leaves and fine roots in boreal forests.

The concentration of leaf N and P eventually becomes fixed after long-term adaptation to the environment (Niklas 2006). A low leaf N:P ratio (<14) reflects a relative N limitation, while a high leaf N:P ratio (>16) reflects a relative P limitation; an N:P ratio between 14 and 16 is a transitional state (Gusewell 2010). Our results showed leaf N:P was more than 16 at the high severity compared with the unburned treatment, indicating the plants were generally relative restricted by P. Rarely, studies have shown the nutrient limitation during secondary vegetation succession (Du *et al.* 2011; Huang *et al.* 2013). In the early stage after fire, the nutrient restriction of plant transfers from N to P resulting from the gradual accumulation of N or loss of P (Göransson *et al.* 2014). Plants increase the demand for soil P during regeneration after wildfire disturbance, and a low input of P will lead to P limitation for plant growth (Huang *et al.* 2013; Mendes *et al.* 2012). Accordingly, plants nutrient utilization enhanced the P limitation at high fire intensity. Furthermore, compared with unburned treatment, the stoichiometric of both leaves and fine roots were uncoupled after burn.

C, N and P allocations between leaves and fine roots among fire severities

In the face of environmental changes, plants can adjust the nutrient concentration of their tissues (Reich and Oleksyn 2004). Soil nutrient limitations lead to decreases in aboveground biomass and plant productivity, thus affecting biomass distribution between above ground and below ground, which affected ecosystem carbon store (Niklas 2005). Under different fire severities, we observed that the C, N and P allocation between leaves and fine roots changed, which mainly showed an allometry pattern at unburned

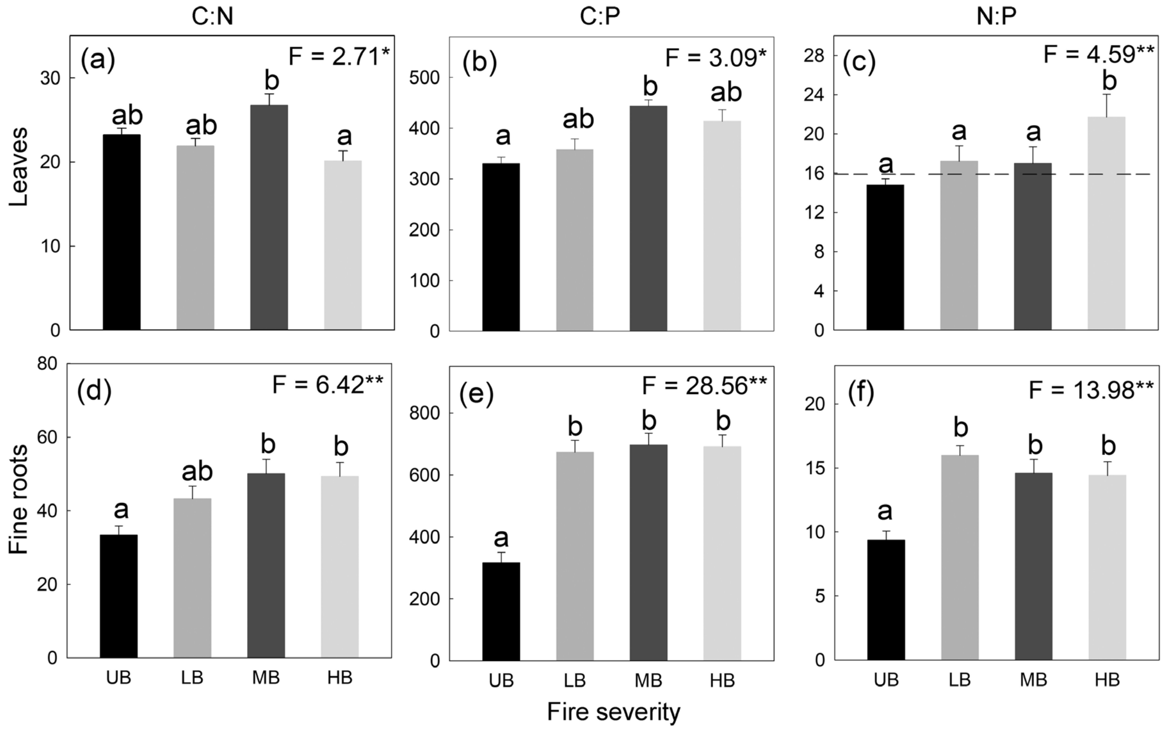


Figure 3: Changes of C:N, C:P and N: P ratio in leaves (**a**, **b**, **c**) and fine roots (**d**, **e**, **f**) among fire severities. UB, LB, MB and HB stand for unburned, low severity, moderate severity and high severity, respectively. Error bars are standard errors. Different lowercase letters indicate significant differences among different fire severities. The dashed horizontal line stands for N:P ratio = 16, above which indicates P limitation in subfigure (**c**). $^{**}P < 0.01$; $^{*}P < 0.05$.

treatment. The slopes of the RMA regressions of fine roots *vs*. leaves were significantly larger than 1 ($b_{\mathrm{RMA}} > 1$), which suggested that more nutrient invested in fine roots growth than in leaves growth in unburned areas (Table 2). In a former study on nutrient allocation strategies of plant organs, the scaling relationships of N and P tended to be allometric between leaf and non-leaf organs (Zhang *et al*. 2018). Our findings further supplemented the distribution mechanism that plants allocated more nutrients to fine roots growth in unburned area. Experiments of nutrient enrichment also show that high N enrichment can increase aboveground plant biomass, while low-nutrient treatment has negative effects on aboveground growth but promotes belowground biomass (Niklas 2006). Other studies provide further evidence that species can reduce leaf growth and allocate more nutrients to promote belowground growth under low-nutrient conditions (Kong *et al*. 2015; Mo *et al*. 2010).

Exploring plant nutrient allocation is therefore critical to understanding plant–soil interactions in the secondary succession ecosystems of burned areas. After burned, in our study, the C, N and P allocation strategies of fine roots *vs*. leaves transformed from allometry to isometry with increasing fire severity, which showed an uncoupled allocation after fire compared with those of unburned treatment. This transformation indicated more nutrient would be utilized by leaves than fine roots with increasing fire severity. On the one hand, with the increase of soil nutrient under low fire severity, nutrients in the soil usually determine the nutrient content of plants (Cui *et al*. 2010). When a plant is experiencing beneficial nutrient conditions, the photosynthetic efficiency of leaves may increase and the quantity of photosynthetic products consequently increase, which lead to more aboveground biomass (Ordoñez *et al*. 2010). After wildfire, the majority of shrubs allocate more N and P to leaves when plant nutrients increase, and further promote the photosynthetic ability to synthesize more carbohydrates (Lebauer and Treseder 2008). On the other hand, a study conducted in a forest in eastern China showed that deciduous species allocated more nutrients to leaves than evergreen shrubs with increases of nutrients (Yan *et al*. 2015). The results of species diversity in our study were partially agreed with the previous research in the *L. gmelinii* forests (Song and Liu 2019). In the *L. gmelinii* forests, regenerated species have a shorter leaf lifespan, which increases their photosynthetic rate during a short growing season in order to obtain as much light as possible (Chen *et al*. 2013; Elser *et al*. 2010a).

According to previous studies, more nutrients will be allocated to leaves to maintain the physiological functions to meet the recovery of species diversity (Zhao *et al.* 2020). Thus, differences in nutrient inputs in burned forest ecosystems can alter nutrient uptake, leading to an imbalanced redistribution of biomass between leaves and fine roots.

CONCLUSIONS

We explored the influences of fire severities on plant C, N and P concentrations and allocation strategies between leaves and fine roots. Compared with unburned treatment, the C concentration was maximum at low severity; leaf N concentration peaked at high severity, but fine roots N concentration was lowest at high severity. It showed P limitation for plant growth at high severity. Most importantly, the analyses of elemental allocation between fine roots and leaves showed more elements allocated to leaves than to fine roots with increasing severities. Therefore, the transformation of allocation slopes between leaves and fine roots reflected differences in nutrient allocation strategies after wildfire during the recovery processes. Furthermore, the above results indicated that wildfire affect nutrient cycling in forest ecosystems, and the adaptive strategies of leaves and fine roots in burned areas reflect interactions between plants and the environment, which provided a basis for post-fire ecosystem regeneration and management.

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Author contributions

Z.S. and Y.L. designed this research; Z.S. analyzed the results. Z.S. wrote the manuscript; Y.L. and Z.L. revised the manuscript.

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