Changes in plant nutrient utilization during ecosystem recovery after wildfire

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A B S T R A C T

Wildfire is the primary natural disturbance in boreal forest ecosystems. It substantially changes soil nutrient conditions and plant nutrient dynamics. After a wildfire, various plant strategies of nutrient utilization are fundamental to ecosystem recovery processes. Stability of plant nutrients reflects the ability of plants possessing relatively constant elemental concentrations in the face of nutrient changes, which can be calculated by the value of "nutrient homeostasis". However, the mechanism of how nutrient homeostasis mediates plant community recovery in post-fire ecosystems remains unknown. The dominant tree species that survived after fire and the new emergence of regenerated tree species are the important components of a plant community during the recovery process. Our primary objective was to elucidate the nutrient homeostasis trade-off between dominant and regenerated species over years after recovery. Five treatments, namely, 2 year, 10 year, 20 year, 30 years after moderate burning severity, and unburned forests, were designed in the boreal forests of Great Xing'an Mountains, Northeast China. Compared with unburned forests, wildfire lowered the average value of homeostasis of plant nutrients (N and P). Moreover, the mean homeostasis value of the dominant species (i.e., *Larix gmelinii*) was higher than that of the regenerated species (i.e., *Betula platyphylla*). The slope of relationship between nutrient homeostasis and recovery years of the regenerated species was higher than that of the dominant species, suggesting that the nutrient homeostasis in the regenerated species recovered more quickly than dominant species after recovery. Compared with the dominant species, changes in the regenerated species' homeostasis can explained more to the changes of species diversity during the years after recovery. This study revealed plant nutrient adaptation in different species and different plant organs with years after wildfire and highlighted the importance of nutrient homeostasis in plant adaptation strategies and the recovery of plant community.

1. Introduction

As one of the major drivers of ecosystem structure and function, especially in boreal forests, wildfire plays a vital role in nutrient cycling, plant adaptation, and plant community recovery (Alcaniz et al., 2018; Augustine et al., 2014). Frequent wildfires in boreal forests considerably influence post-fire ecosystem recovery because it changes plant nutrient utilization and circulation (Liu et al., 2012; Wu et al., 2014, 2015). Wildfire changes nutrient supply, which may regulate nutrient utilization in plants during the recovery process (Bento-Gonçalves et al., 2012; Marañón-Jiménez et al., 2013; Tessler et al., 2013). Nutrient homeostasis, an aspect of plant nutrient adaptation strategy, refers to the ability of plants possessing relatively constant elemental concentrations in the face of nutrient supply changes (Elser et al., 2010). Understanding the mechanism underlying the recovery of post-fire ecosystems, that is, how fire-induced changes in soil nutrients affect plant nutrient homeostasis during recovery processes, is important in projecting the dynamics of plant growth (Elser et al., 2010; Güsewell and Gessner, 2009) and community structure (Sterner and Elser, 2002). However, the mechanisms underlying ecosystem recovery after wildfire are not well understood. Thus, it is urgent to reveal the plant nutrient adaptation strategies over recovery periods in post-fire forests.

Previous studies stated that wildfires might decrease soil nutrients and then modify plant nitrogen (N) and phosphorus (P) concentrations (Dijkstra and Adams, 2015). Some studies reported that wildfires tend to alleviate N and P shortage in plants during recovery periods (Certini, 2005; Song and Liu, 2019). Changes in plant nutrients in post-fire ecosystems may be important to the dynamics of species richness, community structure, and ecological functions during the recovery periods (Elser et al., 2010). For example, high amounts of soil nutrients can increase leaf N concentration and facilitate plant carbon (C) synthesis in early recovery periods (approximately <10 years), thereby increasing community productivity (Butler et al., 2017). Changes in nutrients after wildfire may favor some species, for example, a pioneer shrub species (*Ledum palustre* Linn.) (Song and Liu, 2019). However, our understanding of plant nutrient adaptation after years of recovery is limited.

Some studies demonstrated that nutrient homeostasis varies with species, plant compartments (aboveground part vs. belowground part), and plant growth stages. Alterations in plant N and P may change plant growth rate and some physiological processes, such as photosynthesis and respiration (Chen et al., 2013; LeBauer and Treseder, 2008). For some vascular plants, high values of homeostasis indicate stable nutrient utilization (Yu et al., 2015). Homeostasis of plant N is consistently greater than that of P (Güsewell and Gessner, 2009). Furthermore, plants with a greater homeostatic value are assumed to be more conservative in nutrient utilization than plants with a lower homeostatic value. However, the role of homeostasis in organismic and ecological processes remains poorly understood in a changing nutrient environment, such as in areas disturbed by wildfires. As far as we know, plant nutrient homeostasis is not always conservative once nutrient conditions change. Therefore, because of alternations in soil nutrients under wildfire, we predicted that plant nutrient homeostasis in burned areas would change over time after recovery.

Plant nutrient adaptation strategies play a fundamental role in modulating the relationship between species diversity and community structure (Knops et al., 2002). Nutrient homeostasis, one of the important parts in plant nutrient adaptation strategies, in response to alterations of species diversity was broadly used to predict plant nutrient adaptation strategies (Wang et al., 2018; Yu et al., 2015). In boreal forests, wildfire substantially changes plant communities, and it is usually beneficial to the growth of regenerated tree species that emerge after wildfire, such as birch (Pausas et al., 2004). Birch trees usually adopt fast-growing strategies with low homeostasis to rapidly recruit after moderately severe fire (Burnham et al., 2017; Kronzucker et al., 1996). Compared with regenerated trees species, the dominant tree species that survive after fire (i.e., larch trees) usually take conservative strategies with high nutrient homeostasis (Kobayashi et al., 2007; Song and Liu, 2019). The trade-off between dominant species of high homeostasis and regenerated species of low homeostasis may be important in predicting changes in species diversity, an important aspect of community structure recovery (Fernandes, 2013; Santana et al., 2013). Most importantly, there has relatively simple community structure in Great Xing'an Mountain. Previous studies verified that the nitrogen utilization of two species strongly correlated to changes in species diversity in different burn intensities, especially among regenerated trees species (Song and Liu, 2019). The nutrient adaptations of dominant species and regenerated species are important to the recovery period of post-fire ecosystems. However, these adaptations are rarely reported. Thus, we hypothesized that regenerated species may play a more important role than dominant species over years of recovery period after wildfire.

Boreal forests are the important type of terrestrial forest ecosystems (Shuman et al., 2011). This forest type contributes to maintaining species diversity and carbon sequestration (Kong, 2015). Wildfire is the main ecological factor affecting forest succession and management in this region. Currently, most previous studies in this post-fire region focused on the recovery of community composition. However, the mechanisms of plant nutrient utilization in response to soil nutrient changes remain a critical knowledge gap in ecology. We aimed to address this knowledge gap in boreal forests in Northeast China under moderate fire severity. We explored the following scientific questions: (1) Does the N and P homeostasis of both dominant and regenerated species differ with recovery periods? (2) How does plant leaf and fine root nutrient homeostasis respond over years after recovery? (3) Whose nutrient homeostasis could better reflect the dynamics of community diversity after wildfire?

2. Materials and methods

2.1. Site description

This study was conducted at Xilinji Forestry Bureau, which is located in the Great Xing'an Mountains, Northeastern China. The climate is characterized by a long and severe winter, the mean annual air temperature ranges from $-6\,°C$ to $1\,°C$, and the mean annual precipitation is 500 mm. The dominant tree species are *Larix gmelinii* (Rupr.) Kuzen, *Pinus sylvestris* Linn. var. *mongholica* Litv., *Picea koraiensis* Nakai, *Betula platyphylla* Suk., and two species of aspen, namely, *Populus davidiana* Dode and *P. suaveolens* Fisch. Understory shrubs are dominated by *L. palustre* Linn., *Vaccinium vitis-idaea* Linn., *Rhododendron dauricum* Linn., *V. uliginosum* Linn., and *Eriophorum angustifolium* Honck (Meng et al., 2017). Soils are classified as brown soil (Wrb, 2015).

The Great Xing'an Mountains have larch forests, which account for 30% of China's timber production (Wang et al., 2010). The trees that survived after wildfire were defined as the dominant tree species in boreal forests because they are important in the climax of succession. The newly emerged tree species that occupied a high important value after wildfire were defined as regenerated tree species (Kobayashi et al., 2007). *L. gmelinii (Rupr.)* Kuzen is the dominant species, whereas *B. platyphylla* Suk is the regenerated tree species in the Great Xing'an region. The Great Xing'an Mountains have a relatively simple community structure. The number of common species in this region is < 10. The Great Xing'an Mountains are usually affected by natural wildfires because of the accumulation of combustible matter on the forest floor. Fire regimes are characterized by surface fires mixed with stand-replacing crown fires (Liu et al., 2012). Accurate records of fire provided the background for us to categorize the recovery phases in this area.

2.2. Study design

Fire severity refers to the severity of organic material consumed or vegetation mortality directly caused by a fire (Lentile et al., 2006). The classification of fire severity followed the standard of composite burn index assessment protocol (Kay et al., 2008; Lentile et al., 2006). Specifically, fire severity was estimated according to changes in coarse woody debris, black carbon, char height, mortality rates of tall trees, and proportions of fallen trees (Boby et al., 2010; Fang and Yang, 2014; Kay et al., 2008). After investigations, we determined that the burn proportion ranging from 41% to 70% as moderate fire severity. On the basis of largely accurate historical records, five treatments were selected according to recovery periods, including four burned treatments (fire occurred in 2015, 2007, 1997, and 1987) and one unburned treatment. Each treatment had three replicates. The treatments were presented as year 2 (2a), year 10 (10a), year 20 (20a), and year 30 (30a) after recovery, and unburned forests (>80a) hereafter. In this study, 2a and 10a were viewed as early recovery periods, 20a and 30a as the medium recovery periods, and unburned forests as the longest recovery period. The altitude of the site ranges from 570 m to 580 m. The forest type in this study was *L. gmelinii* forests prior to the occurrence of wildfires. All treatments had similar topography and environmental factors (more details are presented in Table S1).

2.3. Field sampling

2.3.1. Plant sampling

In July and August 2017, 15 plots (20 m × 20 m) were sampled, 12 plots of which were in the burned treatments (2a, 10a, 20a, and 30a), and 3 plots were in the unburned forests. Species diversity index was calculated by determining the number of species in each plot to obtain the data of diameter at breast height (DBH), height and frequency of all trees, canopy density, and frequency of shrubs and herbs. Two species, namely, *L. gmelinii* Kuzen as the dominant species and *B. platyphylla* Suk as the regenerated tree species, were sampled in each quadrat, in which five individuals of each species were randomly selected. Totally, we obtained 30 plant samples from unburned forests, 2a, 10a, 20a, and 30a, respectively. Fresh intact leaves (80–100 g) from each individual species were selected, and then the fine roots (80–100 g, diameter <2 mm) of each individual species were manually grubbed. The samples were quickly transported to the laboratory and stored at 4 °C. Plant samples, including leaves and fine roots, were carefully cleaned with distilled water and then dried in an oven at 65 °C to constant weight in the laboratory. The samples were ground to 0.15 mm for chemical analyses.

2.3.2. Soil sampling

Three soil sites in each plot were selected. The sites were located at two points and in the middle on the diagonal of each plot. Three soil cores were sampled from each site at a depth of 0–20 cm by using a metal auger with an inner diameter of 5 cm. The cores were then composited into one sample. Each treatment had three replicated plots. Accordingly, nine soil samples were obtained in each treatment (results of determination of soil nutrients are shown in Supplementary Figure S1). Fresh samples were placed in polyethylene zip-lock bags, stored in a cooler with ice, and transported to the laboratory within 8 h. Afterward, they were preserved at 4 °C. Chemical analyses of the soil samples were completed in 10 days after sampling.

2.4. Samples analyses

2.4.1. Chemical analyses

The total N and P concentrations of plant and soil samples were measured via the ammonium molybdate method by using a continuous-flow analyzer (AutoAnalyzer 3, Bran Luebbe, Hamburg, Germany) after Se–CuSO$_4$–K$_2$SO$_4$–H$_2$SO$_4$–H$_2$O$_2$ digestion for soil and H$_2$SO$_4$–H$_2$O$_2$ digestion for plant samples (Lin et al., 2011; Zhao et al., 2016).

2.4.2. Data analyses

Over different years after recovery, the homoeostatic regulation ability of the two species was estimated by calculating the homoeostatic regulation coefficient (H) according to the following equation: $y = cx^{1/H}$ (Sterner and Elser, 2002), where y is the total N or P concentrations of leaf (or fine root) in each year after recovery, respectively; x is the total N or P concentrations of soil (normalized to dry mass); and H is the calculated parameter. H_N (or H_P and $H_{N:P}$) was defined as the homeostasis of leaf and root using N (or P and N:P) from soil. In the equation, c is a constant. Values of H and c were obtained from the relationship between y and x via regression analysis (Table S2). A high value of H indicated strong homeostasis in nutrient utilization. With regard to species diversity indexes (Shannon index, Pielou index, and Simpson index), the importance values of each tree, shrub, and herb species were calculated. Relative abundance, relative height, and relative frequency of tree species were calculated on the basis of DBH, tree height, and species frequency. Relative abundance and relative frequency of shrubs (and herbs) were calculated using canopy density and species frequency, respectively. According to the importance values of each species, the value of Shannon index, Pielou index, and Simpson index was calculated using the "vegan" package in R3.3.2 (R Core Team, 2017).

Plant homoeostasis for a given plant nutrient content was estimated using the equation $y = cx^{1/H}$, where differences in H between species type were tested via ANOVA with Duncan's post hoc tests (Fig. 1). Generalized linear mixed model (GLMM) was used to analyze the relationship between nutrient homeostasis and recovery time by using the plot ID as a random effect. This analysis was conducted in different species. A GLMM was fitted using the "lme4" package and the "lmer ()"function in R3.3.2 (Figs. 2 and 3). Variation partition, which was conducted using the "vegan" package in R3.3.2, was used to estimate the effects of the two species' H on Shannon index, Pielou index, and Simpson index (Fig. 4). The significance level was set at $P < 0.05$. All graphs were generated by SigmaPlot (Systat Software, San Jose, CA, USA, 2017).
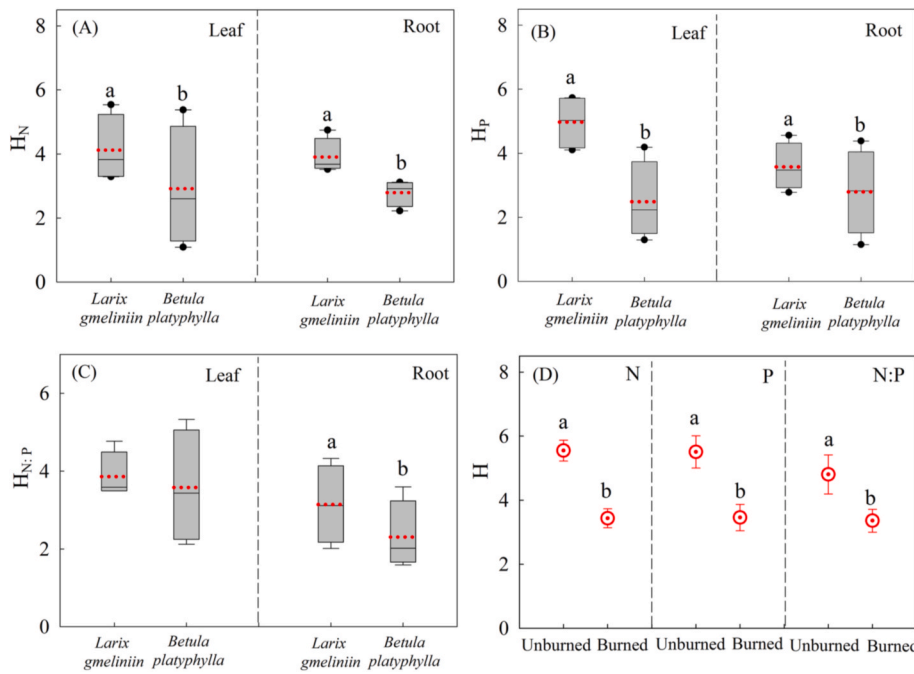
3. Results

3.1. Changes in homeostasis of the dominant species (Larix gmelinii) and the regenerated species (Betula platyphylla) after wildfire

For N and P, the mean value of H was significantly higher in the dominant species (*Larix gmelinii*) than that in the regenerated species (*Betula platyphylla*) after wildfire (Fig. 1A and B, $P < 0.05$). The mean H value of N and P in the leaves was greater than that in the roots. Specifically, the mean H_N of *Larix gmelinii* leaves was 4.12 ± 1.06, which was greater than that of the roots (3.91 ± 0.56). Similarly, the mean H_N of *Betula platyphylla* leaves was 2.92 ± 1.08, which was also greater than that of the roots (2.79 ± 0.41). The mean H_P of *Larix gmelinii* and *Betula platyphylla* leaves was 4.97 ± 0.86 and 2.49 ± 1.22, respectively, which were greater than those of the roots (3.57 ± 0.74 and 2.40 ± 1.33, respectively). $H_{N:P}$ showed the same pattern. Moreover, the average nutrient H of the plants in unburned forests was higher than that after wildfire (Fig. 1D).
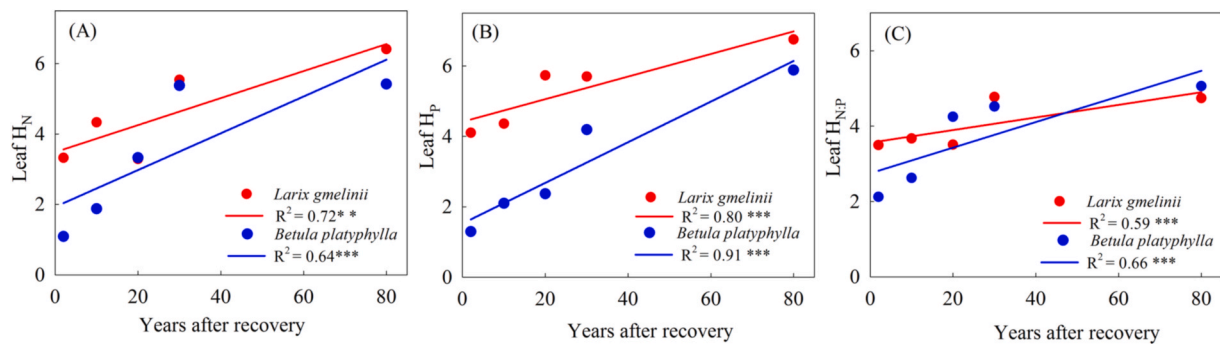
3.2. Relationships of organ homeostasis with years after recovery in the dominant species (Larix gmelinii) and the regenerated species (Betula platyphylla)

Among the five recovery periods, leaf homeostasis for N, P, and N:P was significantly and positively correlated with years after recovery (Fig. 2). The leaf H_N of the dominant species (*Larix gmelinii*) significantly increased over years after recovery with a slope of 0.036 ($P < 0.05$; Fig. 2A), and the slope was lower than that of the regenerated species (*Betula platyphylla*) (slope = 0.051, $P < 0.05$; Fig. 2A). With regard to leaf P, the H_P of the dominant species (*Larix gmelinii*) significantly increased over years after recovery with a slope of 0.030 ($P < 0.05$; Fig. 2B), which was also lower than that of the regenerated species (*Betula platyphylla*) (slope = 0.057, $P < 0.05$; Fig. 2B). The same pattern of leaf $H_{N:P}$ occurred in these two species; the slope was 0.017 and 0.034 for *Larix gmelinii* and *Betula platyphylla*, respectively ($P < 0.05$; Fig. 2C). In general, the slope between leaf H and years after recovery in the regenerated species (*Betula platyphylla*) was steeper than that in the dominant species (*Larix gmelinii*).

Similar patterns were observed for H_N, H_P, and $H_{N:P}$ in the roots (Fig. 3). Among the five recovery periods, root H for N, P, and N:P was significantly and positively correlated with years after recovery. Moreover, the increase in the relationship between root H and years after recovery in the dominant species (*Larix gmelinii*) was lower than that in the regenerated species (*Betula platyphylla*). Specifically, the root H_N of both the dominant species and the regenerated species significantly increased over years after recovery with a slope of 0.026 and 0.032, respectively ($P < 0.05$; Fig. 3A). With regard to root P, the H_P of both the dominant species (*Larix gmelinii*) and the regenerated species (*Betula platyphylla*) significantly increased over years after recovery with a slope of 0.020 and 0.039, respectively ($P < 0.05$; Fig. 3B). Additionally, the relationship between root $H_{N:P}$ and years after recovery was significantly linear in the regenerated species with a slope 0.030 ($P < 0.05$; Fig. 3C).

Fig. 1. Changes in homeostasis values of the dominant species (*Larix gmelinii*) and regenerated species (*Betula platyphylla*). Boxes stand for plant nutrient homeostasis after recovery (Fig. 1A–C). Dots stand for nutrient homeostasis in unburned and burned treatments (year 2, year 10, year 20, and 30 years after moderate burning severity) (Fig. 1D). Different lowercase letters indicate significant differences between treatments ($P < 0.05$). The red dashed line in box plots stands for mean value of plant nutrient homeostasis. Error bars are standard errors. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 2. Bivariate relationships between leaf homeostasis and years after recovery for the dominant species (*Larix gmelinii*) and the regenerated species (*Betula platyphylla*). Leaf H_N, H_P, and $H_{N:P}$ represent leaf N, P, and N:P homeostasis values obtained for each species, respectively. *: $P < 0.05$.
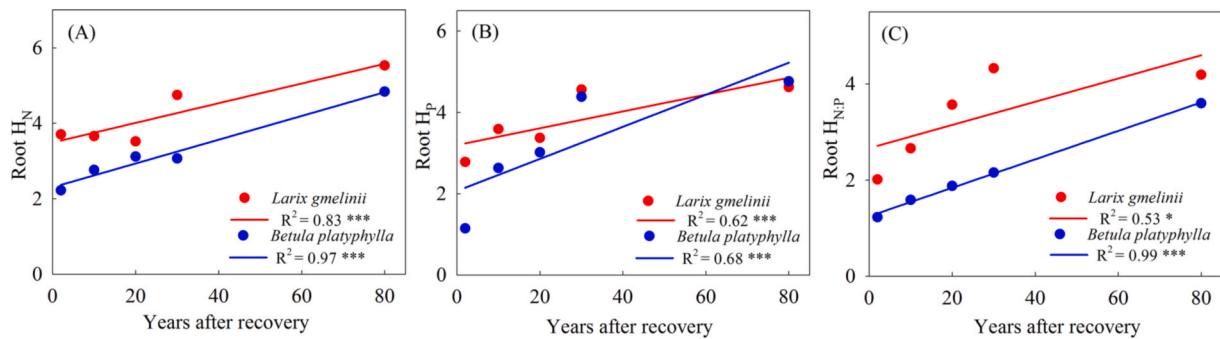

Fig. 3. Relationships in root H of the dominant species (*Larix gmelinii*) and the regenerated species (*Betula platyphylla*) at different years after recovery. Root H_N, H_P, and $H_{N:P}$ represent root N, P, and N:P homeostasis value for each species, respectively. *: $P < 0.05$.

3.3. Relative contribution of the nutrient homeostasis of both the dominant and the regenerated species to species diversity

The values of Shannon index, Pielou index, and Simpson index represent the species' richness, dominance, and evenness in the community, respectively. Moreover, these indexes reflect species

composition and community structure (Heemsbergen et al., 2004). The H of the dominant species had a strong effect on Shannon index (33.13%) and Simpson index (30.09%) (Fig. 4A and C). However, the effects of the dominant species were slightly lower than those of the regenerated species' H on the two indexes (33.80% and 32.57%; Fig. 4A and C). Conversely, the effects of the dominant species' H (42.43%,
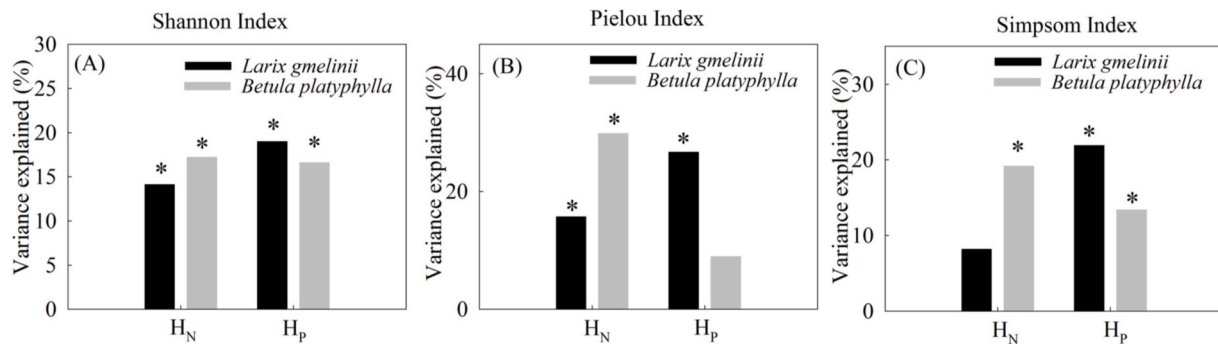
Fig. 4. Variation partitioning analyses of the effects of dominant species' (*Larix gmelinii*) H and regenerated species' (*Betula platyphylla*) H on Shannon index, Pielou index, and Simpson index. H_N and H_P represent N and P homeostasis value, respectively. *: $P < 0.05$.

Fig. 4B) on Pielou index were larger than those of the regenerated species (38.88%, Fig. 4B).

The H_N of the regenerated species always had higher effects on species diversity than that of the dominant species (Fig. 4A–C). By contrast, the H_P of the dominant species always had higher effects on species diversity than that of the regenerated species.

4. Discussion

This study revealed the nutrient adaptation of different plant species in various plant organs over several years after wildfire. The results demonstrated that plant nutrient homeostasis in the regenerated species recovered more quickly than that in the dominant species over several years after recovery. This result suggested that the regenerated species predominantly influenced the species diversity and the subsequent community recovery in ecosystems after wildfire. This study highlighted the importance of nutrient homeostasis in plant adaptation strategies and in the recovery of community structure. The present results advance our current understanding of plant adaptation strategies after wildfire disturbance.

4.1. Changes in plant nutrient homeostasis in post-fire ecosystems

Wildfire leads to volatilization and ash deposition, as well as further changes soil nutrient conditions (Boby et al., 2010; Wang et al., 2012). Changes in N and P supply can influence plant growth and community recovery (Tarvainen et al., 2016). In the present study, wildfire lowered the average nutrient homeostasis of plants in burned forests compared with those in unburned forests. Greenhouse and field studies reported that plant nutrient homeostasis is not usually conservative once environmental nutrient conditions change, which are usually unstable in nutrient utilization (i.e., low homeostasis) (Wang et al., 2018; Yu et al., 2015). Moreover, nutrient homeostasis differs among organs, which reflects a fundamental trade-off in nutrient investment within a plant (Gu et al., 2017; Yu et al., 2011). Our results revealed that the mean homeostasis value of N and P in the leaves was greater than that in the roots likely because the most active organs have a greater ability than less active parts in maintaining important functions during plant growth, such as by increasing the uptake of a limited resource (Minden and Kleyer, 2014). Our findings supported the assumption that leaves are characterized by greater stoichiometric homeostasis than stems and roots. These findings bear a strong similarity with those of previous studies conducted in greenhouse (Schreeg et al., 2014; Wang et al., 2018). but it was one of initiate results in burned area.

Nutrient homeostasis varies among tree species. After wildfire, the mean homeostasis values of N and P for the dominant species (*Larix gmelinii*) were higher than those for the regenerated species (*Betula platyphylla*). Different interspecies homeostasis probably results from phylogenetic differences in resource acquisition and retention between tree species. Some of the regenerated trees species in our research site,

such as birch, usually adopt fast-growing strategies with low homeostasis to rapidly recruit after wildfire (Lin et al., 2011). *Betula platyphylla* has a rapid resource acquisition (fast recovery) strategy and, therefore, it can more likely adapt to a changing environment compared with *Larix gmelinii*, which has a resource retention (slow recovery) strategy.

4.2. Recovering pattern of homeostasis in two species over years after recovery

Plant nutrient absorption appears to be sensitive to years after recovery in post-fire ecosystems. In this study, nutrient homeostasis in both the leaves and roots was positively correlated with years after recovery. Soil nutrient conditions gradually increase over several years of recovery after the occurrence of wildfire of moderate severity (Wright and Sutton-Grier, 2012). The value of plant nutrient homeostasis is closely related to changes in soil nutrients, a condition that may reflect plant nutrient adaptation strategies (Yu et al., 2010a). These flexible growth strategies of plants would facilitate resource reallocation among organs to adapt to the changing environment by rapidly increasing N and P absorption efficiency (Muqaddas et al., 2015; Scoffoni et al., 2011). Specifically, soil nitrogen substantially decreases in the early years after recovery (Fig. S1), and plant nutrients show a low homeostatic strategy in response to severe environmental changes (Aerts and Chapin III, 1999). With increasing years after recovery, limitations in soil nutrients ameliorate after the recovery of understory community (Scalenghe et al., 2015). As nutrient supply increases, plant organs with a higher metabolic activity than other plant parts tend to be more homeostatic, and N and P could be optimally utilized for plant growth or reproduction (Song and Liu, 2019; Wang et al., 2018; Yan et al., 2016). The relationship between organs' nutrient homeostasis in response to nutrient alterations over time after wildfire was established herein. Nevertheless, further research is warranted to determine the generality of the mechanisms underlying the relationships observed in this study.

The increase in slope value of the relationship between organs' homeostasis and years after recovery for the dominant species (*Larix gmelinii*) was lower than that for the regenerated species (*Betula platyphylla*) (Figs. 2 and 3). This result suggested that nutrient homeostasis in the regenerated species recovered more quickly than that in the dominant species over several years after recovery. This result may be attributed to the observation that plant species with a higher stoichiometric homeostasis (Fig. 1) are more conservative for nutrients, whereas plants with a lower stoichiometry homeostasis are more flexible in nutrient utilization (Avolio et al., 2014; Elser et al., 2010). In grasslands, species have a higher nutrient homeostasis, which reflect a more conservative nutrient utilization, than other species under changing environments (Yu et al., 2010b). Therefore, the experimental results discussed above partly explain an important physiological mechanism for species changes in burned areas.

On the one hand, as the results shown in Fig. 1, the mean homeostasis value of the dominant species was higher than that of the regenerated

species after wildfire. We proposed that plant species with a high organ homeostasis in an ecosystem would have a higher stability in abundance (Yu et al., 2015). Elemental concentrations in plant organs are more stable in dominant species than that in regenerated species (Karimi and Folt, 2006) possibly because regenerated species have a higher metabolic activity than dominant species, thereby allowing the regenerated species to respond more quickly than older plants. On the other hand, in disturbed ecosystems under N addition, the biomass of species with a low homeostasis more rapidly increase than that of species with a high homeostasis (Bai et al., 2010), suggesting that the former, such as regenerated species, has a relatively greater growth rate than the latter. Furthermore, dominant species generally have a conserved stoichiometry under soil nutrient changes. Hence, dominant species are also less sensitive to alterations of soil resources in post-fire environments (Dijkstra and Adams, 2015). Thus, an altered nutrient environment can promote the regrowth of species with a low homeostasis to allow the community to rapidly recover.

4.3. Relative contribution of the two species' homeostasis to species diversity

Plant nutrient adaptation may be related to vegetation growth and regeneration, which further influence species diversity and community structure (Elser et al., 2010). In this study, the dominant species' H had a positive effect on Shannon index (33.13%) and Simpson index (30.09%), which was lower than that of the regenerated species (33.80% and 32.57%, respectively; Fig. 4A and C). The links between nutrient homeostasis and species diversity suggested that changes in homeostasis may reflect plant nutrient utilization and adaptation strategies (i.e., nutrient concentrations and nutrient use efficiency) (Song and Liu, 2019). The adaptation strategies were based on the physiological properties of larch (*Larix gmelinii*) and birch (*Betula platyphylla*). The flexible adaptation of recruited birch is an important factor that reflects quick recovery processes in post-fire forests (Johnstone et al., 2010, 2011). Changes in nutrients have been proved as the most important influencing factor on birch abundance, where a low nutrient homeostasis leads to a great proportion of recruits. However, in larch-dominated boreal forests, the growth property of birch under different nutrient conditions is mainly promoted over short-to long-term recovery periods (Liu et al., 2012; Schulze et al., 2012). Thus, our results suggested that differences in plant nutrient homeostasis at the species level may influence the recovery of boreal forests dominated by regenerated tree species (i.e., birch). Thus, this study proved that the homeostasis of the regenerated tree species is more important than that of the dominant species in predicting species diversity over time after recovery in post-fire ecosystems.

Moreover, the H_N of the regenerated species had greater effects on species diversity than that of the dominant species. The H_P of the dominant species had greater effects on species diversity than that of the regenerated species (Fig. 4). These different contributions of H_N and H_P to diversity may be partly due to differences in ecophysiology between the regenerated species and the dominant species, such as metabolism (Dubey et al., 2017). The regenerated species with a more rapid N utilization and a lower H_N more quickly responded to environmental changes than the dominant species; by contrast, the dominant species with a more conservative N utilization and a higher H_N responded more slowly than the regenerated species (Yu et al., 2015). Our results suggested that N availability at short timescales may be a more important driver of ecosystem recovery than P in post-fire ecosystems. However, in the long term, the P utilization of the dominant species can become a more important factor than N utilization (Elser et al., 2007). We expected that dominant species with a high H_P may have an advantage as environmental P availability increases, and thus it may promote the ability to increase species diversity (Butler et al., 2017). Thus, this study demonstrated that the species with a strong N or P homeostasis might be vital for species diversity in short-to long-term recovery periods.

5. Conclusions

We demonstrated that N and P homeostasis after wildfire of moderate severity remarkably differed among organs, species, and years after recovery because of changes in soil nutrient conditions. Our findings revealed that nutrient homeostasis in the regenerated species recovered more quickly than that in the dominant species over several years after recovery. Changes in the regenerated species' homeostasis contributed more to species diversity than those of the dominant species over several years after recovery, especially the homeostasis of N. This study also demonstrated that the species with a strong N or P homeostasis might be vital for species diversity recovery after wildfire. Thus, this study suggested that the nutrient homeostasis of different species in an environment driven by wildfire would result in profound consequences to community recovery processes. This study advances our current understanding of plant adaptation strategies in a post-fire ecosystem.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.112994.

Author statement

Zhaopeng Song carried out the analyses and wrote the manuscript. Huixia Tian provided the dataset and revised the manuscript. Yanhong Liu designed this research. Zhaoli Li and Yiqi Luo revised the manuscript. All authors heavily involved in writing.

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