Wildfire alters the linkage between total and available soil C:N:P ratios and the stoichiometric effects on fine root growth in a Chinese boreal larch forest

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Abstract

Background and aims Wildfire is a primary driver of forest ecosystem functioning, and fire-induced changes in nutrient cycling and the balance of multiple nutrients may influence plant growth response to burning. However, the relationship between total and available soil stoichiometry and stoichiometric effects on the growth of fine roots following forest fires remain unclear.

Methods We measured the total and available soil C, N, and P concentrations, their ratios, and fine root biomass (FRB) at unburned control, 1-year-postfire, and 11-year-postfire sites in a Chinese boreal larch forest. We analyzed the relationship between soil stoichiometry and FRB.

Results Wildfire significantly reduced the total and available soil C:N:P ratios and FRB immediately postfire. Eleven years postfire, most indicators recovered to the prefire levels except for total soil C:P and N:P ratios, and available C:N ratio. Wildfire increased the associations between total and available soil C:N:P ratios, as well as between FRB and soil C:N:P ratios, but reduced the relationship between FRB and soil nutrient supply. However, these effects became weaker over time.

Conclusions The effects of wildfire on biogeochemical processes in boreal ecosystems extend to the relationship between total and available soil stoichiometry. Wildfires strengthen the linkage between fine roots and soil stoichiometry but weaken the effects of soil nutrient supply in the Great Xing’an Mountains. Therefore, the effects of wildfire on the coupling of soil C, N, and P cycling can produce a more complex soil-plant interaction in the early succession stage of boreal larch forest.

Keywords Disturbance · Fire · Soil nutrients · Plant-soil interaction · Belowground biomass

Introduction

Wildfire is a dominant natural disturbance in boreal forests, annually burning 1% of the forest area (Stocks et al. 1998) and influencing the elemental cycling and balance within forest ecosystems (Bond-Lamberty et al. 2007; Cavard et al. 2019), which may further affect the responses of forest regrowth and production
Fire-induced stoichiometric shifts in the balance of C, N, and P elements in soils can also influence soil biotic processes, plant nutritional status, and forest productivity (Butler et al. 2019; Toberman et al. 2014). Some studies reported that prescribed fire could alter foliar N and P concentrations and N:P ratios through its effects on the amount and balance of available soil nutrients in subtropical flatwoods (Schafer and Mack 2014) and tropical forests (Butler et al. 2016). In contrast, a meta-analysis study showed that fire effects on the plant N:P ratios were not related to changes in available soil nutrients (Dijkstra and Adams 2015). However, these studies generally concentrated on the effects of soil nutrient status on aboveground plant tissues (i.e., leaves) and neglected the effects on belowground roots, particularly fine roots. Fine roots (i.e., roots <2 mm in diameter) are important in C flow and biogeochemical cycling in terrestrial ecosystems (Matamala et al. 2003; Yuan and Chen 2010). For instance, fine roots are the primary organ for plants to absorb water and nutrients from the soil and serve as a major channel of C below ground (Kyaschenko et al. 2019). Due to fast turnover rates, fine root mortality and decomposition can release large amounts of nutrients to the soil (Gill and Jackson 2000). Previous studies have shown that the amount of C and nutrients cycled to the soil from fine roots may equal or exceed those from aboveground litter (Norby et al. 2000), although fine root biomass contributes only a small part of the total forest biomass (Vogt et al. 1996). However, despite the close linkage between fine roots and soil environments, the response of fine root growth to fire-induced stoichiometric shifts in soils remains unclear.

In this study, we examined the effects of wildfire on total and available soil C, N, and P concentrations and their stoichiometric ratios among three study sites (control, 1-year-postfire, and 11-year-postfire) in the Great Xing’an Mountains in China and determined the effects of fire-induced changes in soil stoichiometry on fine root biomass (FRB). The Great Xing’an Mountains are at the southern boundary of the Eurasian boreal forests, and more than 70% of the forested area contains Dahurian larch (Larix gmelinii Rupr.; Xu 1998). Wildfire is the primary natural disturbance in these forests and regulates ecosystem structure and function (Cai et al. 2013). Recently, several studies have evaluated the effects of wildfire on forest productivity (Liu and Yang 2014), soil physicochemical
and biological properties (Kong et al. 2015; Kong et al. 2019; Xiang et al. 2015), and available soil nutrient composition (Kong et al. 2018). However, the relationships between total and available soil stoichiometry and stoichiometric effects on the growth of fine roots following fire are unclear. Specifically, we will focus on (1) the dynamics of available and total soil C, N, and P concentrations and their ratios along a temporal gradient of fire history; (2) the relationships between total and available soil C:N:P stoichiometry; and (3) the response of fine root growth to fire-induced changes in soil C:N:P stoichiometry and nutrient supply. We expected that wildfire would decrease soil C:N:P ratios due to greater loss of C to the atmosphere and larger release of N and P to the soil through burning fuels. We also expected that wildfire would strengthen the relationships between total and available soil C:N:P stoichiometry due to the enhanced fire-driven recycling of those elements, but such relationships would weaken over time. Finally, given that wildfire shifted the soil C:N:P stoichiometry, we expected that fine root growth would be more responsive to soil C:N:P stoichiometry than the individual changes in soil nutrient elements immediately after fire exposure.

Materials and methods

Study site and sampling

The study area is located in the Huzhong National Natural Reserve (approximately 167, 213 ha) in the Great Xing'an Mountains in northeastern China (51°17′42″N, 122°42′14″E to 51°56′31″N, 123°18′05″E). The area has a terrestrial monsoon climate with a long and severe winter. The mean annual temperature is −4.7 °C, and the annual mean precipitation is 495 mm. The soils of the region are classified as brown coniferous forest soils in the Chinese soil taxonomy. Soils developed under a cold temperate and humid climate. Soils are shallow (10–30 cm) and nutrient-poor. Topographic characteristics in the region include small, gently sloping uplands (0–15°) scattered with wide valleys (Xu 1998). Topography also affects soil development and characteristics. South-facing slopes have shallower and dry soils and are prone to surface runoff erosion, whereas north-facing slopes and valley bottoms typically have deep and moist soils (Xu 1998). The dominant over-story tree species are Dahurian larch (L. gmelinii), white birch (Betula platyphylla), and aspen (Populus davidiana). The Great Xing’an Mountains are usually affected by frequent forest fires. From 1990 to 2010, a total of 167 forest fires occurred, each burning an area of more than 200 ha in this region (Liu et al. 2012). Most fires mainly occurred in late spring and early summer. In the Huzhong Natural Reserve, two wildfires caused by extreme weather conditions started on June 7th, 2000 and June 26th, 2010, and burned approximately 8700 and 700 ha, respectively.

To examine the postfire changes in soil nutrient status and the effects of these changes on fine root growth along a temporal gradient, we selected sample plots based on fire history. Additionally, to evaluate the overall wildfire effects on soils, we considered sampling areas covering a range of fire severities and topographic positions. This study had one unburned control and two fire history levels (i.e., 1-year-postfire and 11-year-postfire). We carefully chose the unburned area so that its prefire vegetation, topography, and soil properties were similar to those of the two burned areas (Table 1). The unburned area is a mature larch forest that hasn’t been burned in nearly 80 years, according to records of the management committee of the Huzhong National Natural Reserve. We collected a total of 60 soil samples (12 control samples, 24 1-year-postfire samples, and 24 11-year-postfire samples) from the end of July to the middle of August 2011. Within each of the 60 plots (40 m × 40 m), we collected soils from 5 points (4 vertices and the center) at surface mineral soil depths of 0–15 cm. For each plot, the samples from the five points were mixed into one composite sample, resulting in a total of 60 composite samples. All samples were placed in a cooler with ice bags and then transported to the laboratory (Carter and Gregorich 2008).

Soil nutrient supply and fine root sampling

The soil nutrient supply was measured by inserting plant root simulator probes (PRS®, Western Ag Innovations, Saskatoon, SK, Canada) into the PVC tubes for in situ incubation. The PRS® probes can absorb ions from the soil similar to plant uptake of nutrients. As a convenient and economical soil analysis tool,
PRS® technology has been widely applied in agro-nomic, forestry, and ecological research. Each pair of probes consists of cation and anion exchange resin membranes, which concurrently adsorb cations (e.g., NH$_4^+$) and anions (e.g., NO$_3^-$ and PO$_4^{3-}$). The cation probes are saturated with Na$^+$ and the anion probes are saturated with HCO$_3^−$. Measurements of these probes are $\mu$g element 10-cm$^2$ per 15-cm depth.

Within each sample plot, we randomly selected two of five soil sampling points as in situ measurement locations (Fig. 1). At each in situ location, we buried a sharpened open PVC (polyvinyl chloride plastic) tube (10-cm diameter and 20-cm long) into the soil (20-cm depth) as an external root exclusion cylinder (Fig. 1). Then, we vertically inserted one pair of PRS® probes in each PVC tube. The 60 pairs of probes were kept for three weeks in situ during the growing season. Then, all probe pairs were removed, washed immediately with distilled water, and placed in zipseal plastic bags. Finally, all probes were shipped to Western Ag Innovations, Saskatoon, SK, Canada on ice for analysis; the two probe pairs from the same plot were pooled for elution and analysis.

Fine roots were sampled using the soil-coring method (inside diameter 10-cm PVC tube). In this study, the probe pair and soil core were incubated together in the same PVC tube. After incubation, one pair of probes was removed, the PVC tubes were pulled out by carefully excavating the soil, and finally, a root sample was collected from each tube. The fine root samples from the same plot were mixed as one sample. On the same day, we carefully washed the roots in water to eliminate adhering soil. The live fine roots (< 2 mm in diameter) were separated by hand from the samples, and the dead roots were discarded. The sorting of dead and live roots was carried out based on root color, where living roots were white and dead roots were dark (Brassard et al. 2011). Then, the root samples were oven-dried at 70 °C for 48 h and weighed.

### Laboratory methods

The soil samples were screened over a 2-mm sieve and then divided into two parts: one part was stored at 4 °C for the extractable N and soil dissolved organic carbon (DOC) analysis; the other was air-dried and then finely ground for the analysis of total soil carbon (TC), phosphorus (TP), nitrogen (TN), and available phosphorus (AP). Soil TP was determined using the perchloric/sulfuric acid digestion method and the Mo-Sb antiscatterphotography method (Lu 2000). Soil TC and TN were determined by dichromate oxidation and titration with ferrous ammonium sulfate (Walkley and Black 1934). The concentrations were measured as % and were used to calculate the stoichiometric ratios. Soil DOC was determined by a Liquid TOC analyzer (Elementar Liqui TOC, Elementar Co., Hanau, Germany). We used soil extractable inorganic N and P concentrations as indicators of available soil N (AN) and P, respectively. To measure soil extractable inorganic N (including NH$_4^+$ and NO$_3^-$), a 10-g fresh soil sample was extracted.
in 40 mL 2 M KCl by shaking the sample for 1 h at 160 r/min. Extracts were filtered with Whatman No.1 filter paper pre-leached with 2 M KCl and deionized water. The resulting extracts were kept frozen until analysis. Ammonium and nitrate concentrations were measured using a Continuum Flow Auto Analyzer 3 (Bran+Luebbe, Norderstedt, Germany; Carter and Gregorich 2008). Soil AP was extracted by shaking soil for 30 min with 0.1 M NaHCO₃ (1:20 w:v), and PO₄³⁻ was measured by the molybdenum blue method.

Calculations and statistical analysis

On a mass basis, we calculated total soil C:N:P ratios using TC, TN, and TP concentrations and obtained available soil C:N:P ratios using DOC, AN, and AP concentrations. We checked the data for normality and homogeneity of variance. One-way ANOVA was used to determine how wildfire affected the soil C, N, and P concentrations and their stoichiometry, and fine root biomass. A Games-Howell post hoc test was used to identify differences in the soil C, N, and...
P concentrations, C:N:P ratios, and FRB among the control, 1-year-postfire, and 11-year-postfire sites. Spearman rank-order correlation analysis was used to identify the correlations between total and available soil C, N, and P concentrations. The relationships between total and available soil C:N:P stoichiometry, and between FRB and soil C:N:P stoichiometry and the supply of soil N and P for each study site were reflected through simple linear regression analysis. In this study, all statistical analysis was conducted with the R statistical package (version 3.2.4; R Core Team 2016), and the significance level was $\alpha < 0.05$.

Results

The effects of wildfire on soil C, N, and P concentrations and their stoichiometric ratios

Wildfire had different effects on the soil C, N, and P concentrations (Table 2). Compared with the control, wildfires showed no significant effects on the soil TC and TN concentrations at either the 1-year-postfire or 11-year-postfire sites. The soil TP concentration was 82% and 50% higher than that of the control at the 1-year-postfire ($p < 0.0001$) and 11-year-postfire sites ($p = 0.002$), respectively. The soil DOC concentration was 34% and 22% lower than that of the control at the 1-year-postfire ($p < 0.0001$) and 11-year-postfire sites ($p = 0.001$), respectively. However, wildfire significantly increased soil AN and AP concentrations by 59% and 26%, respectively, at the 1-year-postfire

Table 2 Total and available soil C, N, and P concentrations at the control (n = 12 plots), 1-year-postfire (1-YPF, n = 24 plots), and 11-year-postfire (11-YPF, n = 24 plots) sites

| Total soil | Control | 1-YPF | 11-YPF | F   | p   |
|------------|---------|-------|--------|-----|-----|
| TC (%)     | 8.14 ± 0.79a | 6.32 ± 0.43a | 7.96 ± 0.65a | 2.86 | 0.065 |
| TN (%)     | 0.37 ± 0.03a | 0.33 ± 0.02a | 0.38 ± 0.03a | 1.07 | 0.349 |
| TP (%)     | 0.05 ± 0.005b | 0.09 ± 0.006a | 0.07 ± 0.004a | 14.05 | <0.0001 |
| Available soil | | | | |
| DOC (mg kg$^{-1}$) | 473.2 ± 15.4a | 310.0 ± 21.1b | 370.7 ± 19.4b | 14.04 | <0.0001 |
| AN (mg kg$^{-1}$) | 32.15 ± 1.76b | 51.12 ± 3.06a | 34.00 ± 1.27b | 26.84 | <0.0001 |
| AP (mg kg$^{-1}$) | 22.46 ± 1.63b | 28.40 ± 1.70a | 21.25 ± 1.57b | 6.85 | 0.002 |

Values in the Table 2 are means ± standard error (s.e.); different letters between three sites in a row represent significant differences at 0.05 levels (one-way ANOVA or Post hoc Games-Howell test). TC total soil carbon, TN total soil nitrogen, TP total soil phosphorus, DOC soil dissolved organic carbon, AN soil extractable nitrogen, AP soil extractable phosphorus.

Table 3 Total and available soil C:N, N:P, and C:P ratios at the control (n = 12 plots), 1-year-postfire (1-YPF, n = 24 plots), and 11-year-postfire (11-YPF, n = 24 plots) sites

| Total soil | Control | 1-YPF | 11-YPF | F   | p   |
|------------|---------|-------|--------|-----|-----|
| C:N        | 21.84 ± 1.01a | 18.30 ± 0.66c | 20.96 ± 0.69ab | 6.57 | 0.002 |
| N:P        | 8.21 ± 0.86a | 3.96 ± 0.27c | 5.36 ± 0.47b | 15.71 | <0.0001 |
| C:P        | 175.5 ± 17.1a | 75.2 ± 6.4c | 113.5 ± 10.7b | 19.11 | <0.0001 |
| Available soil | | | | |
| C:N        | 15.35 ± 1.12a | 6.23 ± 0.67c | 10.70 ± 0.68b | 48.62 | <0.0001 |
| N:P        | 1.54 ± 0.16a | 1.96 ± 0.15a | 1.77 ± 0.21a | 1.17 | 0.317 |
| C:P        | 23.21 ± 2.81a | 11.74 ± 1.15b | 19.82 ± 2.16a | 9.45 | 0.0002 |

Values in the Table 3 are means ± standard error (s.e.); different letters between three sites in a row represent significant differences at 0.05 levels (one-way ANOVA or Post hoc Games-Howell test).
Wildfire had significant effects on the soil C:N:P stoichiometry at the two burned sites relative to the control (Table 3). At the 1-year-postfire site, wildfire greatly reduced the total soil C:N, N:P, and C:P ratios, by 14%, 57%, and 49%, respectively. Eleven years postfire, the total soil C:N ratios recovered to the prefire level. In addition, the total soil N:P and C:P ratios increased over time but were still significantly lower at the 11-year-postfire site than at the control site. Similarly, at the 1-year-postfire site, the available soil C:N and C:P ratios were 60% ($p < 0.0001$) and 50% ($p = 0.0002$) lower than those of the control, respectively. At the 11-year-postfire site, the available soil C:N ratios were still significantly lower than those of the control ($p = 0.012$), whereas the available soil C:P ratios recovered to the prefire levels. Additionally, wildfire showed little effect on the available soil N:P ratios at the two burned sites.

Relationships between total and available soil C:N:P stoichiometry

Wildfire significantly affected the relationship between available and total soil nutrient pools (Fig. 2). The soil TC and TN concentrations were positively correlated with each other at the two burned and control sites (all $p$ values <0.0001). The soil TC concentration was significantly correlated negatively with the DOC concentration at the control site, and positively related to the AN concentration at the 11-year-postfire site. There were no significant relationships between soil TC and TP and DOC concentrations at the control and 1-year-postfire sites. Comparatively, the soil TN concentration was not related to the available and total soil C and P concentrations at the two burned and control sites but was significantly correlated positively with the soil AN concentration only at the 11-year-postfire site. The soil TP concentration was significantly correlated with the soil AP and DOC concentrations at the 1-year-postfire site but was not correlated with other soil indicators at the control and 11-year-postfire sites. The soil AP concentration was significantly correlated negatively with the soil DOC concentration at the control site.

Wildfire greatly altered the relationships between the total and available soil C:N:P ratios (Fig. 3). At the control site, there was a marginal relationship between the total and available soil C:N ratios ($R^2 = 0.317$, $p = 0.056$; Fig. 3A), while the relationship was significantly positive at the 1-year-postfire ($R^2 = 0.212$, $p = 0.031$; Fig. 3D) and 11-year-postfire sites ($R^2 = 0.189$, $p = 0.030$; Fig. 3G). The available soil C:P ratios did not change with the total soil C:P ratios at the control site (Fig. 3B), but increased with the total soil C:P ratios at the 1-year-postfire site ($R^2 = 0.356$, $p = 0.002$; Fig. 3E). Eleven years postfire, the relationship between the total and available soil

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**Fig. 2** Spearman’s rank correlation coefficients ($r$) between total and available soil C, N, and P concentrations at the control (n = 12 plots), 1-year-postfire (1-YPF, n = 24 plots), and 11-year-postfire (11-YPF, n = 24 plots) sites. * $p < 0.05$, ** $p < 0.01$
C:P ratios recovered to the control levels (Fig. 3H). Similarly, the relationship between the total and available soil N:P ratios was not significant at the control site (Fig. 3C) but was significantly positive at the 1-year-postfire site ($R^2 = 0.243$, $p = 0.014$; Fig. 3F). However, there was no significant relationship between the total and available soil N:P ratios at the 11-year-postfire site (Fig. 3I).

Response of fine root biomass to fire-induced changes in soil nutrient supply and C:N:P stoichiometry

Wildfire significantly affected the soil nutrient supply (Fig. 4). At the 1-year-postfire site, soil N and P supplies increased by 210% ($p = 0.001$) and 157% ($p = 0.010$) compared with the control, respectively. Soil N and P supplies declined to the prefire levels at the 11-year-postfire site. The fine root biomass was 67% and 58% lower than that of the control at the 1-year-postfire ($p = 0.014$) and 11-year-postfire ($p = 0.031$) sites, respectively (Fig. 5).

Wildfire affected the relationship between fine root growth and soil nutrient status (Figs. 6, 7). At the control site, FRB increased with soil N supply ($R^2 = 0.615$, $p = 0.002$; Fig. 6A) but did not change with soil P supply (Fig. 6B). In contrast, soil N and P supplies showed no significant effects on FRB at the two burned sites (Fig. 6). Fine root growth showed different responses to the soil C:N ratios ($R^2 = 0.343$, $p = 0.006$; Fig. 7A), but did not change with the total soil C:P or N:P ratios or available C:N:P stoichiometry. At the 1-year-postfire site, FRB...
increased with the total soil C:N:P stoichiometry and available C:N and C:P ratios (all \( p \) values <0.05; Fig. 7A-E). However, there was no significant relationship between FRB and the available N:P ratios (Fig. 7F). At the 11-year-postfire site, there was a significant but weak relationship between FRB and the total soil C:N ratios (\( R^2 = 0.215, p = 0.019 \); Fig. 7A). Comparatively, there were no significant relationships between FRB and the total soil C:P or N:P ratios or available C:N:P stoichiometry (Fig. 7B-F). In total, the linkage between fine root growth and soil C:N:P stoichiometry was closer at the 1-year-postfire site than at the 11-year-postfire and control sites.

**Discussion**

The effects of wildfire on soil C, N, and P concentrations and their stoichiometric ratios

In this study, the total soil C and N concentrations were not significantly different at the control and two burned sites (Table 2) because wildfire-induced C and N loss mainly focuses on vegetation, woody debris and the O horizon and has little effect on the surface mineral soil (Johnson et al. 2007; Nave et al. 2011). Numerous studies have shown that fire has little effect on soil TC and TN contents (Adkins et al. 2019; Johnson et al. 2007; Wirth et al. 2002). However, soil TC loss was higher than soil TN loss one year after the fire (Table 2) because a large portion of soil organic N survives following low soil burned severity fire (Certini 2005). Thus, this greater decrease in soil TC than TN immediately following the fire resulted in a significant reduction in the total soil C:N ratio (Table 2). Then, the total soil C:N ratios increased to the prefire level with time since fire due to inputs.
of C and N from the return of understory vegetation (e.g., herbaceous annual plants), litterfall, and vegetation root turnover from the regenerating stands (Alexander et al. 2018; De Long et al. 2016; Yuan and Chen 2013), and biological fixation (Harden et al. 2003). However, in a boreal jack pine forest in central
Canada, Hume et al. (2016) reported that the postfire total soil C:N ratio in the mineral layer exerted no significant changes with time since fire but that in the forest floor increased with stand age because substantial litter accumulated on the forest floor and provided organic matter for the soil.

In contrast to the small changes in soil TC and TN after fire, the soil TP concentration greatly increased at the 1-year-postfire site (Table 2), suggesting that wildfires promote P cycling by burning vegetation and forest floors, as found by Schaller et al. (2015). This confirms that previous work that showed mature or old boreal forests may not be able to maintain a positive P balance because P is derived mainly from the geochemical weathering of bedrock and over time becomes increasingly bound in more stable forms by calcite minerals (Buendía et al. 2014; Huang et al. 2017; Walker et al. 1983). The nonproportional changes in total soil C, N, and P resulted in significant reductions in the total soil C:P and N:P ratios immediately after fire (Table 2). Over time, the total soil C:P and N:P ratios significantly increased but still were lower in the 11-year-postfire stand than in the control, suggesting long-term effects of wildfire on the balance of soil C, N, and P cycling. Similarly, Hume et al. (2016) reported that a 15-year-postfire stand had lower total soil C:P and N:P ratios than mature stands in a boreal forest in central Canada, and attributed the reductions to the increase in soil TP. In this study, the soil TP concentration at the 11-year-postfire site was significantly lower than that at the 1-year-postfire site, suggesting substantial P losses in the burned area. Several studies have reported that a postfire P decrease could be related to surface runoff or erosion (Blake et al. 2010; Bodí et al. 2012) because most fire-increased P can accumulate in surface soils (Certini 2005; Lagerström et al. 2009). Chen et al. (2015) reported that wildfire could weaken soil anti-scourability and increase the risk of runoff erosion (Blake et al. 2010; Bodí et al. 2012) because most fire-increased P can accumulate in surface soils (Certini 2005; Lagerström et al. 2009). Chen et al. (2015) reported that wildfire could weaken soil anti-scourability and increase the risk of runoff erosion, especially in severely burned areas in Chinese boreal larch forests. In our study, the burned areas experienced heavy rains in the first two growing seasons following the fire, which would have likely affected the distribution of ash-P across landscape positions and could even have caused a decrease in soil P. Another possible explanation is that part of the available P in soil could be utilized by regenerated plants and bound in plant tissues. These processes could have been responsible for the P loss with time since fire in this study. Our results indicate that wildfire could not only greatly release P into the soil by burning plant biomass and forest floors but also lead to substantial P loss because the fire-caused removal of most forest floors at hillslope positions may be vulnerable to runoff erosion (Chen et al. 2015; Pereira et al. 2016). Therefore, postfire engineering measures such as mulching forest residues may be needed to reduce and even stop soil erosion and ensure soil recovery (Fernández and Vega 2016).

Compared with the changes in total soil C, N, and P pools after fire, wildfires exerted greater effects on their available pools in the Great Xing’an Mountains, suggesting that available pools of soil C, N, and P were more responsive to wildfire than their total pools. In fact, fire-produced ash with abundant available nutrients mainly deposits on the surface soil and thus provides some nutrients for soils (Bodí et al. 2012). As a consequence, available soil N and P greatly increased immediately after fire (Table 2), but most C in biomass and litter could be volatized into the atmosphere during burning except for pyrogenic carbon left on the surface soil (Kane et al. 2010). In this study, we found that the soil DOC at the 1-year-postfire site was significantly lower than that at the control site. Such nonproportional changes in available soil C, N, and P concentrations resulted in great reductions in available soil C:N and C:P ratios, which may promote microbial growth and activities and thus increase mineralization of SOM (Wei et al. 2020). However, the change in available soil N:P ratios at the 1-year-postfire site was small relative to the control, which may have been related to the concurrently substantial increases in soil N and P supplies in the recently burned soils (Fig. 4). This was not consistent with Butler et al. (2017), who found that recently burned soils had significantly lower labile soil N:P ratios in Australian eucalypt forests. This discrepancy may be related to the differences in measurement method and ecosystem type. Butler et al. (2017) used water-hot-extractable C, N, and P as labile soil pools of these elements, whereas soil AN and AP in our study were extracted by using 2 M KCl and 0.5 M NaHCO₃, respectively. Additionally, soils in Australian eucalypt forests are low-P and thus have high N:P ratios in unburned areas, while burning caused a greater increase in labile P than N and thus resulted in lower labile soil N:P ratios (Butler et al. 2017). Eleven years postfire, the available soil
N:P ratios increased relative to the 1-year-postfire site, but the difference was not significant. In contrast, Kong et al. (2018) observed a significantly higher available soil N:P ratios in the 11-year-postfire larch stand. This seemingly inconsistency may be attributable to the difference in measurement method, as Kong et al. (2018) used the PRS® probe (plant root simulator probes, Western Ag Innovations, Saskatchewan, SK, Canada) incubation method to estimate initial pools of plant-available soil N and P, and used them to calculate available N:P ratios. Nevertheless, these two studies reached similar conclusions that wildfire effects on available soil N:P ratios were not significant both in the short and long terms. In contrast to the small change of available soil N:P ratios postfire, the available soil C:P ratios significantly increased to the prefire level at the 11-year-postfire site, whereas the available soil C:N ratios were still significantly lower than that of the control, suggesting that wildfire could exert a relatively long-term effect on available soil stoichiometry. The changes in available soil C:P and C:N ratios may be attributed to the slow recovery rate of soil DOC and large declines in AN and AP (Table 2). We found that soil AN and AP decreased to prefire levels eleven years postfire, suggesting that burned soils lost substantial N and P possibly because of leaching, erosion, and plant uptake (Durán et al. 2008). Compared with AN, the AP decrease was greater because biological fixation can replenish some available N in soil (De Long et al. 2016; DeLuca et al. 2008). These results indicate that wildfire could exert greater effects on available soil stoichiometry, which may produce profound effects on the mineralization of soil organic C (Shuman et al. 2017) and plant growth.

Relationships between total and available soil C:N:P stoichiometry

At the control and two fire history sites, the relationship between total and available soil C:N:P stoichiometry was significant only at the 1-year-postfire site, but it was rather weak (all $R^2$ values <0.4; Fig. 3), which may be related to the large variation in the data (Clark and Avery 1976) resulting from the large sample areas covering various fire severities and topographic positions. These results were consistent with our expectation that wildfire could strengthen the relationship between available and total soil stoichiometry. This supports the idea that burning forest floors could enhance biogeochemical cycling of soil C, N, and P due to the improvement of postfire soil environments (Adkins et al. 2019; Santín et al. 2016). At the 1-year-postfire site, there were lower available soil C:N:P ratios, suggesting a sufficient nutrient supply that could satisfy the microbial demand for optimal available C:N:P ratios and thus promote recovery of the bacterial community (Wei et al. 2020). Our previous study in the Great Xing’an Mountains also showed that the bacterial community structure could rapidly recover to the prefire levels because burned soils had higher pH, AN and suitable moisture (Xiang et al. 2014), which may create beneficial conditions for SOC decomposition. The bare surface soils at the 1-year-postfire site had lower total C:N:P ratios, indicating that SOC may be vulnerable to microbial decomposition (Sistla and Schimel 2012). These processes can be responsible for the closer link between available and total soil C:N:P stoichiometry. To the best of our knowledge, this is the first study to show the effects of wildfire on the relationship between total and available soil stoichiometry in boreal forest ecosystems. This novelty is critical for our in-depth understanding consequences of the wildfire biogeochemical effects.

Responses of fine root growth to soil N and P supply and C:N:P stoichiometry following fire

In this study, fine root biomass significantly increased with soil N supply at the control site but did not change with soil N and P supplies at the two burned sites (Fig. 6), suggesting that wildfires could alter soil-plant interactions. This was likely due to substantial increases in available soil N and P following fire (Table 2), which may be excessive for regenerating vegetation. Another possible explanation was reduced plant uptake after fire because we observed that almost all vegetation was killed by burning and that regenerated vegetation was sparse at the two burned sites. Thus, fire fertilization effects not only alleviate N limitation but also supply sufficient N and P for regenerating plant growth in the Great Xing’an Mountains. Dijkstra and Adams (2015) also found that fire had the potential to enhance or alleviate the magnitude of N and P limitation in plants.

Despite no significant relationship between FRB and soil nutrient supply at the site burned one year
before, soil C:N:P stoichiometry significantly affected fine root growth at the recently burned site relative to the control and 11-year-postfire sites, suggesting that FRB was more responsive to fire-induced changes in soil resource stoichiometry than to increases in their absolute amounts. This supports the idea that soil C:N:P ratios can regulate plant growth and indicate plant nutrient status (Fan et al. 2015; Zhang et al. 2019). Fires can release substantial available N and P, which may not only potentially promote plant growth but also enable plants to optimize their tissue N:P ratios (Dijkstra and Adams 2015). In fertile burned areas, fine roots with optimal C:N:P ratios likely affect soil nutrient status because they can return nutrients to soils through rapid turnover rates (Kyaschenko et al. 2019). Yuan and Chen (2010) reported that fine roots contained 50.9 kg ha\(^{-1}\) of N and 3.63 kg ha\(^{-1}\) of P, and their mortality contributed 18–58% TN to forest soils. Therefore, these processes may be attributable to explaining the changes in the relationship between fine root growth and soil stoichiometry immediately after fire. Assuming that the interaction between fine roots and soil stoichiometry increases following fire in boreal forests, additional research should focus on the postfire relationships between soil stoichiometry and fine root turnover and stoichiometry.

Conclusions

Our study suggests that available pools of soil C, N, and P are more responsive to wildfires than total pools, and soil C:N:P ratios are more sensitive to wildfires than individual elements in the Great Xing’an Mountains. The nature of these responses may be attributed to the different potentials of these elements to volatilize during burning and their rates and manners of recovery after fire. Wildfires can exert a relatively long-term effect on soil stoichiometry. Our results suggest that wildfire strengthens the linkage between total and available soil C:N:P ratios, similar to the relationship between fine root growth and soil C:N:P ratios. Furthermore, we found that fine root growth was regulated by the soil N supply before the fire in this forest ecosystem, while this effect was small following the fire. These results suggest that wildfire could alleviate N limitation. These findings indicate that wildfires can profoundly disrupt or even decouple the biogeochemical cycling of C, N, and P in the soil and produce a more complex soil-plant interaction in the early succession stage of boreal larch forest. Future studies on the relationships between postfire soil stoichiometry and forest ecosystem structure and function are needed to improve the understanding of soil-plant interactions in response to wildfire in boreal forest ecosystems.

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Declarations

Conflict of interests The authors declare that they have no competing interests.

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