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Research Article

Changes in carbon, nitrogen and phosphorus stoichiometry in decaying logs with gap positions in a subalpine forest

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Abstract

Aims The redistribution of forest gaps based on solar radiation and precipitation (mainly rainfall and snowfall) can create heterogenous microenvironments inside and outside the gaps. Here, we investigated the effects of forest gaps on carbon (C), nitrogen (N) and phosphorus (P) stoichiometry in decaying logs by altering the microenvironments.

Methods Minjiang fir (*Abies faxoniana*) logs of decay classes I–V were incubated *in situ* on the floor under the gap center (GC), gap edge (GE) and closed canopy (CC) in a subalpine forest in the eastern Qinghai-Tibet Plateau. The C, N and P concentrations in decaying bark, sapwood and heartwood were measured in August from 2013 to 2016.

Important Findings Our results showed that the N concentration in bark decreased from the CC to the GC, while the opposite trend was found in sapwood and heartwood. Additionally, the C/N ratio in sapwood and heartwood of decay classes IV and V decreased from the CC to the GC, and the N/P ratio in heartwood of decay class V increased from the CC to the GC, implying that forest gaps have strong effects on C/N/P stoichiometry in highly decayed logs. Briefly, highly decayed logs are more susceptible to the microenvironment, and the proportion of highly decayed logs under the CC or the GC should be appropriately adjusted if necessary.

Keywords forest gap, decaying log, carbon, nutrients, subalpine forest, *Abies faxoniana*

亚高山森林倒木碳氮磷化学计量特征随林窗位置的变化

摘要：森林林窗对太阳辐射和降水(主要是降雨和降雪)的再分配可造成林窗内外微环境条件的异质性。本研究旨在通过改变微环境，测试林窗对倒木碳(C)、氮(N)和磷(P)化学计量比的影响。在青藏高原东部的亚高山森林中，将I–V腐解等级的岷江冷杉(*Abies faxoniana*)倒木分别置于林窗中心(GC)、林窗边缘(GE)和郁闭林下(CC)进行原位培养，分别于2013–2016年8月测定了腐烂树皮、边材和心材的C、N、P含量。研究表明，树皮N浓度从CC到GC呈下降趋势，而边材和心材则表现出相反的趋势。此外，边材和心材IV、V腐解等级的C/N从CC到GC呈下降趋势，心材V腐解等级的

N/P从CC到GC呈增加趋势，这表明森林林窗对高度腐解等级倒木的C/N/P化学计量比有强烈影响。简而言之，高度腐烂的倒木更容易受到微环境的影响，必要时应适当调整郁闭林下或林窗中心的高度腐烂的倒木比例。

关键词：森林林窗，倒木，碳，养分，亚高山森林，岷江冷杉 (*Abies faxoniana*)

INTRODUCTION

Decaying logs and their concomitant gaps are widely distributed in forest ecosystems (Harmon *et al.* 1986), and both play vital roles in conserving biodiversity (Tinker and Knight 2000), maintaining site fertility (Wiebe *et al.* 2014), promoting soil development and forest regeneration (Forrester *et al.* 2012) and the cycles of carbon (C) and nutrients (Laiho and Prescott 2004). Interestingly, fallen logs are exposed in different microenvironments due to the formation of forest gaps, and as a consequence, an inevitable and close linkage between the position of canopy gap and the dynamics of C and nutrients in decaying logs can be observed. Therefore, fully understanding the dynamics of C and nutrients in decaying logs under different gap positions is key to reveal the roles of both gaps and fallen logs in C and nutrient cycling. To our knowledge, no available information has been provided on the effects of gap positions on the C and nutrient dynamics in decaying logs.

C, nitrogen (N) and phosphorus (P) are three of the most abundant basic bioelements in decaying logs (Smyth *et al.* 2016), and their concentrations and stoichiometric ratios can indicate the decay status (Wojciech *et al.* 2019). Accordingly, the changes in the decaying environment lead to different degrees effects on C/N/P stoichiometry in fallen logs (Shorohova and Kapitsa 2014). The redistribution of the canopy and gaps on solar radiation and precipitation (rainfall and snowfall) can create more heterogeneous microenvironments inside and outside the gaps (Gray *et al.* 2002; Wu *et al.* 2018), leading to the higher-surface temperature and lower-moisture conditions in the canopy gap than in the closed canopy (CC) (Forrester *et al.* 2012). Additionally, changes in the light regime will affect the colonization and growth of epiphytic and epixylic plant communities (Liu and Bao 2006). Consequently, forest gaps can directly affect the leaching and mineralization of C, N and P in the decaying logs by changing the moisture and temperature (Chen *et al.* 2000) and indirectly affect their C/N/P stoichiometry by altering the epixylic plant communities (Chang *et al.* 2019). Previous

fallen log decay experiments have been conducted under closed canopies (Harmon *et al.* 2000; Prescott *et al.* 2017; Yang *et al.* 2010), or have focused on the carbon dynamics of coarse woody debris in forest gaps (Forrester *et al.* 2015); however, the effects of the gap position on the stoichiometry of C, N and P of fallen logs remain unknown.

Log quality is an intrinsic factor that determines the dynamics of C, N and P during logs deposition in response to forest gaps. Generally, log quality varies with the decay class (Chang *et al.* 2015), implying that the dynamics of C, N and P during logs deposition in response to forest gaps will vary with the decay class. There are no clear signs of decomposition in newly formed logs (Ganjegunte *et al.* 2004), and the microbial community structure in the early decomposition stage is relatively simple (Chang *et al.* 2014). However, highly decayed logs have larger specific surface areas in contact with the forest floor, and sediment adsorption becomes easier (Barker 2008). Additionally, large amounts of active organic C and nutrients released from highly decayed logs enhance the permeability of fallen logs and promote microbial growth (Boddy 2001; Zalamea *et al.* 2007). Consequently, monitoring the responses of log C, N and P stoichiometry to the gap position will be helpful for deeply understanding the roles of fallen logs and forest gaps in the cycles of C and nutrients.

We hypothesized that (i) forest gaps would change the stoichiometric ratios of C, N and P in decaying logs and that (ii) forest gaps would lead to stronger effects on the C, N and P stoichiometry in highly decayed logs. To test these hypotheses, we conducted a 3-year of fallen log incubation experiment in field in a subalpine coniferous forest on the eastern Qinghai-Tibet Plateau, China. In this region, Minjiang fir (*Abies faxoniana*) is the dominant tree species. Minjiang fir logs of decay classes I–V were incubated on the forest floor under the gap center (GC), gap edge (GE) and CC, and the concentrations of C, N and P in decaying bark, sapwood and heartwood were measured from 2013 to 2016. The objective of this study was to assess the roles of both forest gaps and decaying logs

on the biogeochemical cycles of C, N and P in forest ecosystems.

MATERIALS AND METHODS

Site description

Our study was conducted at the Long-Term Research Station of Alpine Forest Ecosystems (102°53′–102°57′ E, 31°14′–31°19′ N, 2458–4619 m a.s.l.) in Li County, Sichuan Province, southwestern China. The region is a transitional area between the Tibetan Plateau and the Sichuan Basin (Yang *et al.* 2005). The annual mean temperature and precipitation are approximately 2–4 °C and 850 mm, respectively (Chang *et al.* 2019). The seasonal soil freeze–thaw period begins in early November and lasts until April of the following year. The soil is classified as Cambisols and Primosols (Xiao *et al.* 2014).

The tree layer in the study area consists mainly of Minjiang fir (*A. faxoniana*), cypress (*Sabina saltuaria*), larch (*Larix mastersiana*) and red birch (*Betula albo-sinensis*), and Minjiang fir accounts for 80% of the total stand basal area in the experimental forest site (Xiao *et al.* 2014). The main understory shrubs include willow (*Salix paraplesia*) and azalea (*Rhododendron lapponicum*). Canopy gaps account for 23% of the test site (Wu *et al.* 2013).

Experimental design

According to our previous investigations (Chang *et al.* 2019; He *et al.* 2015; He and Yang 2020), the treatments were assigned to a primary Minjiang fir forest (102°53′ E, 31°14′ N, 3582 m) in August 2013. Three plots (25 m × 25 m in size) with similar slope aspect, slope degree, canopy closure and tree height were established. In each plot, an approximately elliptical forest gap with an area of approximately 50–60 m² was selected, and the GE and CC were set along the same slope according to the location of the GC.

Based on a system of five decay classes (Yan *et al.* 2005) and the detailed description of decay class divisions in Chang *et al.* (2019), the following classes were used: I: cambium still fresh, less than 1 year dead; II: cambium starting to decay; III: the shape of the cambium is not complete, and the bark is separated; IV: no bark, and the heartwood is rotten, oval and V: partial collapse, difficult to identify the shape. Forty-five Minjiang fir logs (9 logs from each decay class) were collected from a primary Minjiang fir forest for the experiment. Among these, the logs

of decay classes II–V were collected from the primary coniferous forest, and three standing Minjiang fir trees (40 cm in diameter) in each subplot were felled to create the fallen log representing the start of the decay process. Each fallen trunk from the stem base to 8 m in length was cut into 6 sections (120 cm in length) (Prescott *et al.* 2017) and carefully placed into three gap positions in each plot. Two sections in the same gap positions in each plot were from the same fallen trunk, and one was used in this study. All the log sections were arranged in the order of the decay classes. There were 270 sections of decaying logs in total, and 30 sections were incubated on the forest floor in the same gap position in each plot. In total, 135 sections of decaying logs were used in this study.

Sampling and analysis

The concentrations of C, N and P in the fallen logs in 2013 served as the initial values. After 1 year of *in situ* incubation, log samples were collected (once a year) during the growing period (August 20) from 2014 to 2016. In each of the GC, GE and CC plots, one 2-cm-thick disk was cut from each log and transported to the laboratory following the procedure for collecting samples for microbial analysis described in Chang *et al.* (2019). Based on previous studies (Cardoso and Pereira 2017; Chang *et al.* 2019), after delivery, sapwood and heartwood were distinguished roughly according to the color depth of the disk. Sapwood samples were extracted around the disk along the edge, and heartwood samples were extracted from the center of the disk. Approximately 200-g samples of each bark, sapwood and heartwood section were oven-dried to constant weight at 65 °C, and the oven-dried samples were ground and sieved through a 2.0-mm mesh. Subsequently, the concentrations of C, N and P in the samples were measured by the methods of dichromate oxidation, Kjeldahl digestion (KDN, Top Ltd., Zhejiang, China) and phosphomolybdenum yellow spectrophotometry (TU-1901, Puxi Ltd., Beijing, China), respectively.

Additionally, the air temperature was measured at 2-h intervals throughout the study period (15 August 2013–15 August 2016) using iButton DS1923-F5 recorders (iButton DS1923-F5, Maxim/Dallas Semiconductor, Sunnyvale, CA, USA). To protect the recorders from direct sunlight and precipitation, the recorders were placed in a litterbag (nylon, 20 cm × 20 cm, 0.5-mm mesh size) and hung on trees in a subplot of each plot. To characterize the temperatures dynamics, we calculated the daily temperature from 2013 to 2016 (Fig. 1).

Figure 1: Dynamics of daily air temperatures at the GC, GE and CC in a subalpine coniferous forest in the eastern Qinghai-Tibet Plateau from August 2013 to August 2016.

Calculations and statistical analysis

The stoichiometric ratios of C/N, C/P and N/P in the decaying logs were calculated on an elemental mass basis.

A repeated-measure general linear model was used to test the mixed effects of the decay classes, gap positions and sampling time on the C, N and P concentrations and the C/N/P stoichiometric ratios of the decaying bark, sapwood and heartwood. The decay classes and gap positions were set as fixed factors, and the sampling time was set as random factor. According to the results of previous studies, there are great differences in the matrix quality (C, N and P concentrations, lignin and cellulose) and microbial community (fungi and bacteria) of different structural components of decaying logs (Chang *et al.* 2015, 2017). Therefore, the bark, sapwood and heartwood were analyzed separately in this study. For the specific sampling times, one-way ANOVA (analysis of variance) and least significant difference tests were used to evaluate the differences in the C, N and P concentrations in the decaying logs at different gap positions and from different decay classes. Levene's test for homogeneity of variance was performed before conducting ANOVA, and the data were log-transformed if required. The correlations between the C, N and P concentrations and the C/N/P stoichiometric ratios in the decaying logs with the air temperature were analyzed by Pearson correlation analysis. ANOVA and Pearson correlation analysis were performed using SPSS 20.0 (IBM SPP Statistics Inc., Chicago, IL, USA), and the data were presented as graphs in Origin Pro9.0 (OriginLab, Northampton, MA, USA). Differences were considered significant at the $P < 0.05$ level for all analyses.

RESULTS

Concentrations of C, N and P in the decaying logs

The C concentration in decaying logs decreased slightly from the CC to the GC (Fig. 2), while after the 3-year incubation experiment, the interaction between decay classes and gap positions gave a significant effect on the C concentration only in sapwood ($P < 0.05$, Table 1). Meanwhile, the interaction between time and gap positions gave a significant effect on C concentration in decaying bark and heartwood ($P < 0.05$, Table 1).

The effects of the gap position on the N concentration varied greatly with decay class, structural component and sampling time (Fig. 2). The bark N concentration decreased significantly from the CC to the GC, but the opposite pattern was found in sapwood of decay classes IV and V (Fig. 2). Meanwhile, a significant difference in the N concentration in decaying logs was also observed among gap positions ($P < 0.05$). In addition, the interaction between time and gap positions showed a significant effect on the N concentration in decaying bark and heartwood ($P < 0.05$, Table 1).

Similar to the N concentration, the effect of gap position on the P concentration depended greatly on structural component and decay class of the log (Fig. 2). Overall, the bark P concentrations varied slightly among the gap positions, the interaction between decay classes and gap positions showed a significant effect on the P concentration only in the sapwood ($P < 0.05$), and the interaction between time and gap positions showed no significant effect on the log P concentrations ($P > 0.05$, Table 1).

Stoichiometric ratios of C, N and P in decaying logs

The stoichiometric ratios of C, N and P varied greatly with gap positions and structural components (Fig. 3). In general, the C/N ratio in sapwood and heartwood of decay classes IV and V under the CC was higher than that under the GC. Significant differences in the C/N ratio in the advanced-decay logs were observed among different gap positions. After 3 years of incubation, the C/N ratio in sapwood of decay class V under the GC, GE and CC were 160, 184 and 193, respectively, while the C/N ratio in heartwood of decay class V under the GC, GE and CC were 218, 254 and 246, respectively. Repeated-measures ANOVA indicated that the

Figure 2: Dynamics of carbon (C), nitrogen (N) and phosphorus (P) concentrations in decaying logs under the GC, GE and CC (mean $\pm$ SD, $n = 3$). I–V: decay classes I, II, III, IV and V. Different uppercase letters represent significant differences among different gap positions in the same decay class and sampling time ($P < 0.05$). Different lowercase letters represent significant differences among different decay classes in the same gap position and sampling time ($P < 0.05$).

interaction between time and gap positions showed a significant effect on C/N ratio only in heartwood ($P < 0.05$, Table 1).

Slight effects on the C/P ratio in decaying logs were observed among the gap positions (Fig. 3). After 3 years of incubation, the C/P ratio in heartwood of decay class V under the GC, GE and CC were 7451, 6513 and 5230, respectively. Repeated-measures ANOVA indicated that the interaction between the time and the gap positions showed a significant effect on C/P ratio in the sapwood and heartwood ($P < 0.05$, Table 1).

Similarly, the effect on the N/P ratio in the decaying logs was slight between gap positions, except for the decaying wood of decay class V (Fig. 3). After 3 years of incubation, the N/P ratio in sapwood of decay class V under the GC, GE and CC were 30, 17 and 26, respectively, while the N/P ratio in heartwood of decay class V under the GC, GE and CC were 34, 26 and 21, respectively. Repeated-measures ANOVA indicated that the interaction between the time and the gap positions showed no significant effect on log N/P ratio ($P > 0.05$, Table 1).

The concentrations of C and P in decaying logs were negatively correlated with the air temperature inside and outside the forest gaps, as were the ratios of C/N and C/P, and the significance varied with structural components of the log (Table 2). Strong positive correlations between N concentration and C/N ratio for all the structural components and air temperatures were found.

DISCUSSION

Consistent with our hypotheses, the results indicated that the formation of forest gaps changed the C, N and P stoichiometry in the decaying logs, and the effect of forest gaps on the C, N and P stoichiometric ratios in the decaying logs varied with decay classes and structural components. Additionally, the gap position gave stronger effects on the C, N and P stoichiometric ratios in highly decayed logs. Therefore, forest gaps caused by the natural aging of trees, climate change, natural disasters and human disturbance (Allen *et al.* 2010; Anderegg *et al.* 2015) can give to different degrees of effects on log C, N and P stoichiometry

Table 1: Results (*F* values) of repeated-measures ANOVA testing the effects of decay classes (DC), gap positions (GP), sampling time (T) and their interactions on C, N and P concentrations and C/N/P stoichiometric ratios of decaying logs

Structural components	Factors	C (g·kg ⁻¹)			N (g·kg ⁻¹)			P (g·kg ⁻¹)			C:N			C:P			N:P		
		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>	
Bark	DC	162.305	<0.001		33.985	<0.001		2.878	0.082		73.235	<0.001		8.894	0.002		0.238	0.791	
	GP	14.572	<0.001		48.545	<0.001		7.490	0.004		11.578	0.001		2.404	0.119		0.190	0.829	
	T	136.571	<0.001		238.783	<0.001		0.997	0.375		267.467	<0.001		8.856	0.001		21.288	<0.001	
	DC × GP	0.581	0.681		14.186	<0.001		0.764	0.562		8.758	<0.001		0.867	0.503		3.326	0.033	
	DC × T	10.894	<0.001		3.126	0.027		0.538	0.709		4.734	0.004		1.954	0.131		1.222	0.319	
	GP × T	3.146	0.026		3.122	0.027		0.406	0.803		1.863	0.138		0.384	0.819		0.904	0.472	
	DC × GP × T	0.559	0.758		8.252	<0.001		2.139	0.057		2.529	0.027		2.525	0.027		3.248	0.007	
Sapwood	DC	1081.002	<0.001		129.888	<0.001		0.710	0.592		253.062	<0.001		13.622	<0.001		23.485	<0.001	
	GP	10.745	<0.001		37.661	<0.001		1.246	0.302		32.861	<0.001		3.548	0.041		2.751	0.080	
	T	69.924	<0.001		47.358	<0.001		14.026	<0.001		33.927	<0.001		6.653	0.004		23.292	<0.001	
	DC × GP	2.885	0.017		5.048	<0.001		2.361	0.042		2.069	0.072		3.041	0.013		4.888	0.001	
	DC × T	5.430	<0.001		15.912	<0.001		5.423	<0.001		4.028	<0.001		4.463	<0.001		0.868	0.548	
	GP × T	2.052	0.098		2.474	0.054		2.164	0.084		0.911	0.442		1.713	0.159		2.144	0.102	
	DC × GP × T	1.754	0.060		1.452	0.149		1.937	0.034		0.747	0.697		1.864	0.043		1.567	0.107	
Heartwood	DC	410.361	<0.001		214.817	<0.001		0.608	0.660		178.114	<0.001		3.465	0.019		58.853	<0.001	
	GP	6.475	<0.001		18.760	<0.001		0.900	0.417		12.353	<0.001		0.945	0.400		11.478	<0.001	
	T	47.818	<0.001		73.078	<0.001		0.581	0.454		41.482	<0.001		3.066	0.054		16.724	<0.001	
	DC × GP	0.772	0.630		6.352	<0.001		1.041	0.428		2.913	0.016		3.286	0.008		6.379	<0.001	
	DC × T	1.631	0.142		23.827	<0.001		1.086	0.381		12.177	<0.001		3.684	0.001		3.015	0.007	
	GP × T	4.728	0.002		4.223	0.004		1.320	0.273		3.285	0.017		2.012	0.104		1.981	0.109	
	DC × GP × T	0.490	0.942		3.268	<0.001		0.858	0.618		2.143	0.017		0.859	0.616		1.012	0.457	

Bold values indicate that the effects of the treatment on the measured parameters are significant.

Figure 3: Dynamics of the ratios of C/N, C/P and N/P in decaying logs under the GC, GE and CC (mean $\pm$ SD, $n = 3$). I–V: decay classes I, II, III, IV and V. Different uppercase letters represent significant differences among different gap positions in the same decay class and sampling time ($P < 0.05$). Different lowercase letters represent significant differences among different decay classes in the same gap position and sampling time ($P < 0.05$).

Table 2: Pearson correlation coefficients of average air temperature in August of each year with annual C, N and P concentrations, and C/N/P stoichiometric ratios in bark, sapwood and heartwood of decaying logs

		C	N	P	C/N	C/P	N/P
Bark	AT	−0.436**	0.307**	−0.200	−0.457**	−0.072	0.430*
Sapwood	AT	−0.145	0.206*	−0.880	−0.127	−0.131	0.282**
Heartwood	AT	−0.134	0.184*	−0.225**	−0.149	−0.154	0.245**

Abbreviation: AT = air temperature. Bold values indicate that the effects of the treatment on the measured parameters are significant. * $P < 0.05$, ** $P < 0.01$.

in decaying logs, implying that both forest gaps and fallen logs play crucial roles in C, N and P cycling in forest ecosystems.

Differential responses of the C, N and P concentrations in decaying woods to the gap position

Only a slight effect of the gap position on the C concentration in decaying logs was observed. The same trend was reported by Forrester *et al.* (2012), who found that canopy gaps exceed the respiration rate of coarse woody debris by 18% due to the high-surface temperature and low-moisture conditions in the canopy gap. The results can likely

be explained by the fact that thicker snow covers the surfaces of logs for a relatively longer period in the forest gaps (He *et al.* 2015), leading to higher and steadier winter temperatures and moisture levels due to snow insulation, which benefits microbe-driven log decomposition. Additionally, the C concentrations of the sapwood and heartwood showed a downward trend during the decay process, but that of bark did not. It is likely that the bark C concentration is affected by root exudates of epixylic vegetation and plant residues. However, the effects of epixylic vegetation and plant residues on the bark C dynamics need to be further investigated.

The bark N and P concentrations were lower under the GC than under the CC, while the sapwood N concentration was higher under the GC than under the CC. N and P may be supplied from the substrate, litter accumulated on moist soil and throughfall (Wiklund 2003). Ni *et al.* (2018) and Wu *et al.* (2015) reported that the formation of forest gaps promotes the decomposition of organic matter and the release of N and P. It is likely that the invasion and reproduction of microorganisms (Glassman *et al.* 2018), such as azotobacteria, and nitrogen deposition (Carter *et al.* 2017) alter the N concentration of logs. Additionally, several studies have demonstrated that a substantial decrease in the microbial biomass occurs in forest gaps (Bauhus 1996; Ni *et al.* 2018). Thus, the characteristics of the microbial community structure in different structural components undergo relatively independent changes during the decomposition process (Chang *et al.* 2014), resulting in different nutrient release patterns.

More significant effects of the gap position on the N and P concentrations of the sapwood and heartwood were observed in the highly decayed logs. Wojciech *et al.* (2019) found that logs of decay classes I and II showed no clear signs of decomposition and had no or only weak effects on soil properties. Barker (2008) and Progar *et al.* (2000) indicated that a low water content leads to less microbial colonization in decay classes I and II of Douglas fir. Additionally, in our study, the P concentration increased from the CC to the GC in the early-decay sapwood and heartwood but decreased from the CC to the GC in the advanced-decay wood. The decrease of the microbial biomass under forest gaps might be attributed to a decline of ectomycorrhizal hyphae (Brumme 1995). Some hyphae of wood-decaying fungi transfer nutrients from the soil to highly decayed logs (Clinton *et al.* 2009), and the decomposition of organic material leads to relative P enrichment (Manzoni *et al.* 2010). However, early decaying sapwoods have been shown to be rich in low-molecular weight sugars and have high carbon activities, and these conditions are suitable for the growth of bacteria (Clausen 1996). In addition, P is likely recycled during the decomposition process, which could hinder the release of P to the soil (Wardle *et al.* 2004). Therefore, there are abundant species of microorganisms in highly decayed logs (Prewitt *et al.* 2014), which are greatly influenced by the microenvironment.

The effects of gap position on C/N/P stoichiometry in decaying logs

Significant differences in the C, N and P stoichiometric ratios in decaying logs were observed among the gap positions. Decaying bark of decay classes II and III under the GC was characterized by higher ratios of C/N and C/P than those under the CC. These results are similar to those from a foliar litter study (Ni *et al.* 2015). Moreover, the effects of the gap position on the C, N and P stoichiometric ratios in the sapwood and heartwood varied with the decay class. According to previous studies, the C/N/P stoichiometry of coarse woody debris is approximately 14103:40:1 (Harmon *et al.* 1986; Zechmeister-Boltenstern *et al.* 2015). In our study, the bark, sapwood and heartwood all had lower ratios than the reported value, which may be due to the low temperature in the subalpine forest, leading to slow decomposition of logs. Moreover, Sinsabaugh *et al.* (2009) have found that the growth of microorganisms is restricted when C:N > 27 or C:P > 186. In our study, the growth of microorganisms was limited by the N and P concentrations during the decomposition of fallen logs. In addition, compared with sapwood and heartwood, bark had a lower C concentration and a higher N and P concentrations, which lead to lower C/N/P stoichiometric ratios. In addition, Laiho and Prescott (2004) have observed that the critical N/P ratio of coarse woody debris is approximately 20 in coniferous forests, and the initial N/P ratio could predict the dynamics of N and P. In this study, the N/P ratio in decaying bark was greater than 20, and the bark N and P concentration decreased significantly from the CC to the GC, which indicates that the accumulation rate of N/P in bark is greater under the CC. Meanwhile, the initial N/P ratios in the sapwood and heartwood of decay classes IV and V were greater than 20, while the N concentration of sapwood and heartwood increased from the CC to the GC, which indicates that the accumulation rate of N/P in sapwood and heartwood is greater under the GC. Together, the effects of the gap position on the stoichiometric ratios of C, N and P in decaying logs varied greatly with structural components and decay class of the log.

CONCLUSIONS

Forest gap position changed the C, N and P stoichiometry in decaying logs in the forest ecosystem, which depended on the decay stage and structural components of the logs. Specifically, the N

concentration in decaying bark decreased from the CC to the GC, while the opposite trend was found in sapwood and heartwood. Moreover, the C/N ratio in sapwood and heartwood of decay classes IV and V decreased from the CC to the GC, and the N/P ratio in heartwood of decay class V increased from the CC to the GC, implying that forest gaps gave stronger effects on C/N/P stoichiometry in highly decayed logs. Although the forest gaps promoted the decomposition of organic matter, a slight effect was observed in the 3-year decomposition experiment. Briefly, highly decayed logs are more susceptible to the microenvironment. In order to better maintain soil fertility and promote soil development and forest regeneration, the proportion of highly decayed logs under the CC or the GC should be appropriately adjusted if necessary.

Authors' Contributions

W. Y. and B.T. conceived and designed the experiment and contributed resources; Q. W. completed laboratory analysis experiment and wrote the paper. B.T., Z. W., C. C., and R. C. participated in field sampling. W. Y., and H. L. revised the paper. All authors have read and agreed to the published version of the manuscript.

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

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