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published in
Forest Ecology and Management
2020

DOI (link to publisher)
10.1016/j.foreco.2020.118411

document version
Publisher's PDF, also known as Version of record

Forest Ecology and Management 475 (2020) 118411

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tissue type and location within forest together regulate decay trajectories of *Abies faxoniana* logs at early and mid-decay stage

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ARTICLE INFO

Keywords:
Canopy gap
Density loss correction
Bark
Heartwood
Microclimate
pH

ABSTRACT

Deadwood decomposition plays a crucial role in global carbon and nutrient cycles. Factors controlling deadwood decomposition at local scales could also have strong effects at broader scales. We tested how trait variation within stems (i.e. tissue types) and forest habitat heterogeneity (i.e. location within forest) together influence the deadwood decay trajectory and decay rate. We conducted an *in situ* decomposition experiment of *Abies faxoniana* logs in an alpine forest on the eastern Qinghai-Tibetan Plateau, decomposing logs from a series of decay classes I-III (on a 5-class scale) for five years on the forest floor in canopy gap, gap edge and under closed canopy (each sized 25 ± 3 × 25 ± 3 m). We found strong differences in density and chemical composition between tissue types at least across decay classes I-III, which revealed the distinct contribution of each tissue type to carbon and nutrient cycling. There were remarkable interactions of tissue types and locations within forest. We found bark always decomposed faster than wood, while heartwood can decompose faster than sapwood in canopy edge and canopy gap. Locations within forest influenced the best fit decay model and decay rate of bark and sapwood in the same way, while it had no corresponding effects for heartwood decay dynamics. The largest difference in $T_{0.25}$ and $T_{0.4}$ (time to 25% and 40% mass loss) between locations were 1.52 and 3.21 (bark), 19.41 and 37.61 (wood overall), 31.82 and 60.15 (sapwood), and 12.86 and 22.84 (heartwood), respectively. We also found that pH was significantly negatively related with sapwood and heartwood mass loss, demonstrating that pH can potentially be applied to evaluate sapwood and heartwood mass loss when density correction is difficult to achieve at least at early to mid-decay stages. However, whether pH is a powerful predictor of decomposition trajectory across more species and biomes remains to be tested. We strongly recommend that further model predictions of coarse log decay include radial positions within stem and locations within forest as factors to increase the reliability of carbon budget estimates.

1. Introduction

Deadwood is a large carbon stock in the world's forest biomes (Pan et al., 2011), and its decay rate could greatly influence the role of forests in the global carbon cycle (Oberle et al., 2019). Therefore, a better understanding of factors influencing the decay rates, and its accurate estimation, are necessary to predict the contribution of forest ecosystems to the global carbon balance, and to provide guidance for forest management. Climate, wood traits and decomposers are traditionally thought to be the predominant controls on decay rates (Harmon et al., 1986), with the prevailing perception that wood traits and decomposers mainly dominate at small spatial scales. However, mounting evidence suggests that these factors could also control decomposition of dead plant matter at larger scales (Bradford et al., 2017; Hu et al., 2018). Trait variation within stems originating from the functional difference of different tissue types (heartwood, sapwood, bark) might predict a great proportion of variation in deadwood decay rates; indeed stoichiometric and structural deadwood traits vary greatly intraspecifically, including within individual stems, besides interspecifically (Hu et al., 2018). Variation in forest canopy cover, driven

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https://doi.org/10.1016/j.foreco.2020.118411
Received 23 April 2020; Received in revised form 28 June 2020; Accepted 7 July 2020
Available online 20 July 2020
0378-1127/

by treefall gap dynamics, could provide an additional control of deadwood decomposition by regulating microclimate and microhabitat (Brazee et al., 2014; Crockatt and Bebber, 2015). To estimate the magnitudes and relative importance of these controls, we focused on how deadwood decay dynamics vary with stem radial position and how the radial variation-based decay process varies across different forest canopy cover environments.

Clear divergence in wood density, chemical composition and anatomical composition, such as vessel size, fibers wall thickness, and axial parenchyma fraction from the centre of a stem (pith; if present), via heartwood and sapwood, towards the outermost shell (bark) has been found in living trees, including the mass and volume ratios between these parts (Chave et al., 2009; Reyes-García et al., 2012; Rungwattana et al., 2018). However, little attention has been paid to the afterlife effect of these traits on decomposition, except for a few recent studies on bark versus wood (Dossa et al., 2016; Dossa et al., 2018). Empirical studies have revealed that species-specific and organ-based variation in deadwood traits can drive carbon cycling (Weedon et al., 2009; Zanne et al., 2015; Hu et al., 2018), whereas the effects of radial trait variation within stems, especially between heartwood and sapwood, on carbon cycling are always overlooked. Even though there is an emerging awareness about radial differences in the decomposing process (Bütler et al., 2007; van der Wal et al., 2015), and even though the decomposition of different radial parts may respond differently to climate regimes and disturbance, nearly all models for wood decomposition still lump together heartwood and sapwood, and sometimes bark as well. Differentiation between bark, sapwood and heartwood is necessary to mechanistically understand the decay dynamics of whole tree logs and their drivers.

Treefall gap dynamics are a key aspect of natural succession on a decadal time scale (Parker, 1995; Bin L, 2010), thus the decomposition of fallen tree probably proceeds along with the succession of the canopy gap, in which the environmental conditions and species biodiversity (including decomposers) are simultaneously changing (Ozanne et al., 2003; Forrester et al., 2012). Because of the physiochemical heterogeneity within tree stems and the different degrees of environmental exposure of their different layers, the decomposition of heartwood, sapwood and bark might respond differently to gap-associated heterogeneity within forest. For instance, bark is always directly exposed to the ambient conditions with additional organic acid and nutrient input from decomposing litter and invertebrate residues (Harmon et al., 1986), and input of aromatic secondary metabolites produced by epixylic bryophytes and lichens (Sedia and Ehrenfeld, 2005; Xie and Lou, 2009). Moreover, bark is easy to crack and peel off (Kéérik, 1974) in canopy gaps where the moisture content tends to fluctuate much more than under canopy cover. This process in turn exposes the sapwood more to the ambient than the heartwood. However, besides such a theoretical conjecture, there is little if any quantitative evidence on the canopy gap effects on decomposition of different tissue types. A detailed understanding of these interactions would help to accurately quantify the current role of forests to the global carbon cycle and specifically to consider whether inclusion of gap-related canopy cover combined with tissue type is needed for such quantification.

The decay class classification method is commonly employed to assess deadwood decomposition, as it is easily measured and time saving; however it is a subjective method (Bütler et al., 2007; Harmon et al., 2011). Several alternative approaches have been developed for more objective and precise estimates of deadwood decay dynamics (Kueppers et al., 2004; Kahl et al., 2009; Larjavaara and Muller-Landau, 2010). Wood density is the most commonly used indicator to quantify decay stage, but it is often challenging to measure in a representative way and is prone to artefacts (Chang et al., 2020). Here, we test whether the more easily-measured tissue pH could be used as an alternative predictor of decay stages, especially for gymnosperms which usually have a lower pH than angiosperms (Liu et al., 2019; Tao et al., 2019). The mechanism underpinning the increase in decaying coniferous debris may include the formation of oxidation products of coniferyl alcohol (i.e. the building units of lignin in coniferous tree), and microbial biomass-derived chemical structures (Mattson and Koutler-Andersson, 1941; Miltner et al., 2012). The succession of microbial organisms and epiphytes could also acidify the decomposing deadwood (Baldrian, 2008; Hagemann et al., 2010). Tree stumps of *Picea abies* were shown to steadily decrease in pH with progressing decay (Cornelissen and Karssemeijer, 1987), but we do not know if this relation also applies to the deadwood decomposition of different tissue types of other conifer tree species. Therefore, the power of pH as an alternative predictor trait of wood decay stage will be tested, with respect to the different coniferous tissue types and locations within the forest.

In the present study, we studied decay dynamics in logs of the dominant tree *Abies faxoniana* in an alpine forest located at the transition zone from the Tibetan Plateau to the Sichuan Basin, which is a region subject to relatively fast climate warming (Yang et al., 1992). We incubated stem logs of a series of decay stages *in situ* under closed canopy, at canopy edge and in canopy gap for five years and compared their decay dynamics in three different tissue types. We are aiming to answer two research questions: (i) is there a long-term difference in density and chemical composition within tissue types along decomposition, and do the decay rates and best-fit decay model vary with these tissue types? (ii) how does locations within forest affect log decay of *A. faxoniana* and will the tissue types respond differently to such forest canopy heterogeneity? We also explore (iii) whether pH of each tissue type is negatively correlated with its mass loss, thus could be a substitute to predict the decay status of logs. To answer these questions, we use the method that combines the sampling and simultaneous short-term decomposition of logs from several decay stages. Then we model the decay process by an iterative optimization procedure (Freschet et al., 2012) to derive the best fit predictive model.

2. Materials and methods

2.1. Study area

Both the log sample collection and incubation took place at the Long-term Research Station of Alpine Forest Ecosystems (102.88–102.95° E, 31.23–31.32° N, altitude 2458–4619 m) in Li County, Sichuan, south-western China. The research station is located in the transition zone from the Tibetan Plateau to the Sichuan Basin. The mean annual temperature and precipitation are approximately 2–4 °C and 850 mm, respectively. The soils include Cambisols and Primosols. Large amounts of woody debris (53 t/ha) (Xiao et al., 2016) are accumulated in this region because of low microbial activity (Chang et al., 2017) and play crucial roles in maintaining soil fertility, holding freshwater, and facilitating biodiversity. *Abies faxoniana Rehder & E. H. Wilson*, *Sabina saltuaria (Rehder & E. H. Wilson) W. C. Cheng & W. T. Wang*, *Betula albo-sinensis* Burkill and *Larix mastersiana* Rehder & E. H. Wilson dominate the tree canopy in this region. In the target plots the average proportion of *A. faxoniana* basal area is almost 80% of total stand basal area (Xiao et al., 2016).

2.2. In situ decomposition and sampling

The *in situ* decomposition experiment was located in the permanent plot (31.23° N, 102.88° E, 3582 m a.s.l., sized 100 m × 100 m) in primary *A. faxoniana* forest, which was manipulated for monitoring long-term log decomposition. Within this permanent plot, three decomposition subplots were positioned under closed canopy (“canopy”), in the canopy edge (“edge”) and in canopy gaps (“gap”) along the downwind direction (3 replications × 3 locations = 9 subplots). Each location within the forest was sized 25 (± 3) × 25 (± 3) m. The crown density in the closed canopy was more than 0.8. The canopy gap subplots were established in forest gaps of approximately 40 m diameter.

The air temperature at 1.3 m height under closed canopy, in canopy edge and canopy gap ranged between −15.0 to 24.5 °C, −17.0 to 27.8 °C, and −17.3 to 27.5 °C respectively during the whole year.

Estimating long-term log decomposition requires measurements of logs covering a wide range of decay status. Here we used decay classes I-III classified according to the modified criteria of Rouvinen (Rouvinen et al., 2002; Campbell and Laroque, 2007). Logs in decay class I (reference log, 35 ± 5 cm in diameter) were newly cut down living trees (mimicking natural treefall due to windthrow) to ensure a very precise starting point of decomposition for the study. Logs in decay class II had slightly decayed xylem, while the structure of logs in decay class III were still mostly intact but with loose xylem. Logs in decay classes IV and V were excluded from this study, as they were already losing much of their structure. Logs with diameter of 35 ± 5 cm in decay class II and III were also collected in the *A. faxoniana* forest. All the logs were sawed into 120 cm in length on-site because heavy long logs are difficult to transport in the forest and would be easily damaged during transportation. We also sawed three 2-cm thick disks randomly when sawing the 120-cm length log per decay class. In total, 81 logs of *A. faxoniana* were collected and carefully transported to the permanent plot with minimum damage to the bark and underlying wood. Three decay series of logs were manipulated at each subplot (3 decay classes × 3 replications × 3 subplots × 3 locations = 81 logs) on August 2013 (T_0). Nine disks across three decay classes were sawed and taken to the laboratory for initial trait measurement.

At the five-year harvest (August 2018, T_5), three 2-cm thick disks per decay class, i.e. one disk per log, were collected from gap, edge, and under forest canopy (27 disks), respectively. Wood and bark samples extracted from the disk were immediately stored in separate sealed bags for trait analyses and area measurement (Materials and Methods 2.3). Between the two harvests, we also collected disks four times one year to monitor seasonal dynamics of microbial community, carbon and nutrient cycles because the decomposing process in natural and under disturbance are both highly season-specific in high-frigid forest ecosystem (Chang et al., 2017; Chang et al., 2019). To estimate the measured effects (i.e. tissue types and forest positions in this study) on log decomposition, we set seasonal sawing as control variable in our study which could influence the decay process. Thus, the logs used for sawing disks were randomly selected and marked at T_0, and then undergone subsequent sequential sampling. For more details see (Chang et al., 2019).

2.3. Sapwood and heartwood density measurement

Sapwood and heartwood density were measured separately in our study. The heartwood can be distinguished by colour difference and looseness especially after decomposition has started. Two different methods for determining wood density were applied at T_0 and T_5 because of volume depletion at T_5 (see Chang et al., 2020). We used the water replacement method to estimate sapwood and heartwood volume at T_0 (Eq. (1)) because the wood was still intact. To achieve a high accuracy, we measured the volume with a precision electronic auto balance (ESJ200-4A, Longteng, Shenyang, PR China, max = 200 mg, d = 0.1 mg) based on Archimedes' principle which states that the upward buoyant force exerted on a body immersed in a fluid is equal to its weight. Three blocks (2 × 2 × 2 cm) from each tissue (i.e heartwood and sapwood) were randomly extracted from the disk and then saturated for 24 h with demineralized water. Adherent water was blotted from the wet blocks using tissues before measurement. First, we placed a pin and a tank of water on the balance, and then tared. Second, with the pin to submerge the blocks into the tank, and record the displaced mass (g). Any water loss was be avoided after the balance reading was cleared, and until the reading was recorded. The initial densities of sapwood and heartwood (WD_1) in decay classes I-III are shown in Table 1. Density in decay class I (i.e. undecomposed) was defined as the reference density:

$$WD_1 = \frac{M}{V_{wat}} \quad (1)$$

M: oven-dry mass (60 °C, g); V_{wat}: water replacement volume (cm^3)

A combined drawing-scanning method was applied at T_5 to estimate the original sapwood and heartwood volumes of more decomposed samples. We placed a sampled disk (without bark) onto a horizontal white sheet of paper with a ruler for scaling next to it; then took a photograph of the disk cross section and the ruler from straight above. We scanned the picture using Image J software (https://imagej.nih.gov/ij/download.html) and drew the outline of the disk and the heartwood. For portions that had strongly decomposed (i.e. without intact outline), we reconstructed the original outline based on the intact or less decomposed part of the disk (see Chang et al., 2020). We then calculated the area inside the outline of the disk and heartwood by Image J using the ruler for scale. The sapwood area equals the difference between disk area and heartwood area. The volume of sapwood and heartwood equals their respective area multiplied by the thickness of the disk. After estimating the volume, all the sapwood and heartwood subsamples were separately oven dried (60 °C) in paper bags. The density equals the oven dry mass divided by the volume (Eq. (2)):

$$WD_2 = \frac{M}{V_{ds}} \quad (2)$$

M: oven-dry mass (60 °C, g); V_{ds}: volume measured by drawing-scanning combined methods (cm^3)

2.4. Bark density measurement

We measured bark density in two different ways. One was the water replacement method (g/cm^3, see above). The other method, used for deriving mass loss, employed dry mass per area (MA, g/cm^2). Bark samples of decay classes I to III at T_0 (see Table 1) were measured in both ways, while the samples at T_5 were only measured by the second method. The density was calculated as the average of three representative sub-samples from each disk. For details about this method see Chang et al. (2020).

2.5. Relative density and fraction mass loss transformation

The decay class system was only used for logs at T_0. For each decay class, WD_1 WD_2 and MA were transformed to relative density, which was defined as the density divided by the reference density. Fraction mass loss equals the percentage of density loss compared to reference density. Fraction mass loss of wood is calculated on the basis of sapwood and heartwood fraction mass loss in combination with the area ratio of sapwood to heartwood.

2.6. pH measurement and other chemical analyses

Three blocks (2 × 2 × 2 cm) from heartwood (and sapwood) were randomly extracted from the disk and three pieces (2 × 2 cm) of bark were randomly collected for measurement. Subsamples from each component were milled into powder after having been oven-dried at 65 °C. pH was measured by mixing powder and demineralized water (mass ratio 1:8). After 1 h of shaking, the supernatant was measured using a pH meter (PHS-25CW, Bante Instrument, Shanghai, PR China). Carbon, nitrogen and phosphorus contents were measured by dichromate oxidation, Kieldahl digestion (KDN, Top Ltd., Zhejiang, China) and phosphomolybdenum yellow spectrophotometry (YU-1901, Puxi Ltd., Beijing, China) method, respectively. Cellulose and lignin were measured by the acid detergent lignin method.

2.7. Data analysis

All analyses were conducted in R (version 3.6.1). To explore the

Table 1
Variation in initial density (T_0) of *A. faxoniana* bark, sapwood and heartwood with different decay classes (I-III).

Decay class	Bark g/cm^2	Bark g/cm^3	Sapwood g/cm^3	Heartwood g/cm^3
I (reference density)	0.706 ± 0.045	0.541 ± 0.037 ^{a}	0.493 ± 0.006 ^{ab}	0.443 ± 0.038^{b}
II	0.530 ± 0.026	0.396 ± 0.016	0.423 ± 0.047 ^{a}	0.307 ± 0.021^{b}
III	0.333 ± 0.087	0.419 ± 0.034	0.317 ± 0.006 ^{a}	0.247 ± 0.031^{b}

Density is shown as means ± SD (n = 3). One-way ANOVA tests were applied between bark, sapwood and heartwood in decay class I (reference density), and between sapwood and heartwood in decay classes II and III respectively. Values followed by the same letter within a row indicate there was no significant difference between heartwood and sapwood at $P = 0.05$ level.
Bark density were both expressed as dry mass per volume (g/cm^3) and dry mass per area (g/cm^2), sapwood and heartwood density were only expressed as dry mass per volume (g/cm^3, Eq. (1)).

difference in sapwood and heartwood density along decay class I-III, we first used linear regression with tissue type and decay class as independent variables and then performed an ANOVA test within each decay class. We used a PERMANOVA analysis to test difference in chemical composition with tissue types (bark vs sapwood vs heartwood) and visualizing the dissimilarity using Non-metric multidimensional scaling (NMDS) analysis based on Bray Curtis dissimilarity matrix. Spearman's correlation coefficients were calculated for the relationships of fraction mass loss between bark and wood, between sapwood and heartwood, and between fraction mass loss and pH across initial decay classes for each forest location. The commands ADONIS and METAMDS command in package vegan (Oksanen et al., 2016) were used for the PERMANOVA analysis and NMDS anlysis, respectively. All the data was visualized using package ggplot2 (Wickham, 2016).

We modelled the decay process of each tissue type over time by an iterative optimization procedure in which data for all three initial decay classes were employed (Freschet et al., 2012). Briefly, all WD and MA data were standardized first to give relative values ranging from 1 to 0. The 'n' vector (number of decay classes) was 3 and the decomposition years were 5. We applied three alternative models, i.e. the classic exponential (Olson, 1963), sigmoid and linear decay model (Table A1), to the relative density data to estimate decay dynamics. For each deadwood series, once the optimization procedures had been performed for each alternative model, the goodness of fits to the model were compared using the value of Akaike Information Criterion (AIC) and the Root Mean Squared Error (RMSE). The lower AIC and RMSE scores indicated which model was better supported by the data. For detailed information about the iterative optimization procedure see Freschet et al. (2012). From the chosen models we calculated the estimated time taken for each tissue type to lose 25% ($T_{0.25}$) or 40% ($T_{0.40}$) of its original mass loss respectively based on the regression model, which broadly corresponded with the range of mass losses between 40% and 80%. By comparing $T_{0.25}$ or $T_{0.40}$ we can test the relative decay rate of each woody tissue between different locations within forest, across different functional forms for the decay dynamics.

3. Results

3.1. Changes in density and chemical composition along decay classes in different log tissues

Bark density (g/cm^3) was higher than heartwood density in decay class I (Table 1, $P < 0.05$), whereas sapwood density was intermediate (P greater than 0.05). The difference in density between sapwood and heartwood became stronger in decay classes II and III, with significantly higher sapwood density observed in comparison to heartwood density. There was also an obvious difference in chemical composition between bark, sapwood and heartwood in all three decay classes (Fig. 1, Table A.2, PERMANOVA, $P < 0.05$). The average ratio of heartwood to sapwood transverse area was 1:4. Bark density (g/cm^3) increased in decay class III while dry mass per area (g/cm^2) decreased as decay advanced, which hints at failure of the former method in predicting bark decay status.

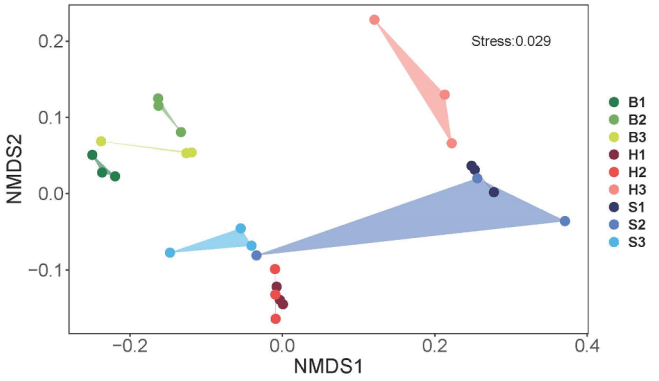

Fig. 1. Variations in chemical composition of *A. faxoniana* bark (B), sapwood (S) and heartwood (H) in different decay classes based on NMDS analysis. Arab number showed the decay class. pH, carbon, nitrogen, phosphorous, cellulose and lignin content (values see Table A.2) were included in the analysis. All the chemicals were measured at the first harvest (T_0).

3.2. Decay patterns varied with log tissues and forest positions

The fraction mass loss varied greatly along the radial positions within the stem (Fig. 2). The fraction mass loss between bark and wood, and between sapwood and heartwood both were positively correlated. Bark always had higher fraction mass loss (using the area-based method) than the paired wood overall, whereas heartwood tended to have a higher fraction mass loss than the paired sapwood, especially at the more advanced decay classes.

Our regression model results (Fig. 3, Table A.3) showed that bark, wood overall and sapwood within wood followed similar decay models in response to forest location, being best represented by sigmoidal model below forest canopy and by single exponential decay in canopy edge and gap. Both bark, wood and sapwood decomposed faster below forest canopy, whereas there was hardly any difference between canopy edge and canopy gap. Our results also showed that the heartwood decay model did not vary with forest location (i.e. single exponential was always the best fit), whereas the decay rate in canopy edge was significantly faster than in the other positions. Heartwood always decomposed faster than sapwood except under closed canopy.

$T_{0.25}$ was 5.72-fold higher and $T_{0.40}$ was 5.71-fold higher in wood than in bark (Table 2). The biggest difference (7.77-fold) was observed in canopy gap. Variation in $T_{0.25}$ and $T_{0.40}$ was on average 1.62-fold and 1.58 higher respectively in sapwood than in heartwood. However, location within forest caused large deviations from this mean: $T_{0.25}$ and $T_{0.40}$ of sapwood were almost half that in heartwood below closed canopy, while it was 1.62 ~ 4.11 ($T_{0.25}$) and 1.58–4.11($T_{0.40}$) -fold higher in sapwood than in heartwood in canopy edge and canopy gap.

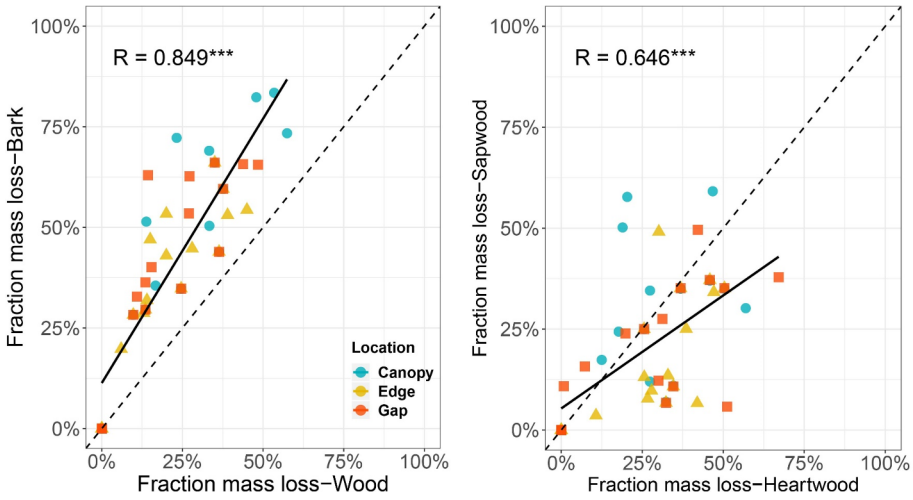

Fig. 2. Relationships of fraction mass loss between *A. faxoniana* (a) bark and wood, and (b) sapwood and heartwood along decay classes I-III across two harvests. Tissue samples collected in each decay class were transformed into fraction mass loss via reference density. Each spot represents the paired tissue fraction mass losses of one log. Regression lines (solid line) are only performed for relationships. Black lines are performed for general relationships across locations within forest, whereas blue, yellow and red lines are performed for relationships at different locations within forest. *R*: Spearman's correlation coefficient across locations within forest. *** $P < 0.001$. Dashed line is 1:1 line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. pH as a predictor for log decomposition

A significant negative correlation was observed between fraction mass loss and pH in heartwood ($R = -0.52$, $P < 0.001$) and sapwood ($R = -0.37$, $P < 0.01$) (Fig. 4). There was no correlation between fraction mass loss and pH in bark, because pH remained stable as decay advanced. The patterns of each tissue type showed no difference among the locations within forest.

4. Discussion

4.1. Variation in decomposition within stem

We found a generally faster decay rate in bark than in the overall wood, which is common across tree species (Shorohova and Kapitsa, 2014; Chang et al., 2020). We also found a faster decay rate in heartwood than in sapwood, with a highly site-specific ratio (compared with 1) between them, reflecting a strong interaction of intrinsic and extrinsic drivers. Fast-decaying heartwood compared to sapwood was previously reported for decomposing *Quercus* spp. and *Picea abies* (Schowalter, 1992; Bütler et al., 2007), even though *Quercus* is generally considered to have very recalcitrant heartwood compared to sapwood (Lavisci et al., 1991; Brischke et al., 2009). Studies about heartwood decay have mostly been neglected as the general perception is that it is less permeable to liquid and gas, often impregnated with recalcitrant secondary compounds (Cornelissen et al., 2012; Song et al., 2014) and surrounded by sapwood, leading to a low decay rate. However, our results confirm that heartwood can be relatively easily decomposed in at least some species. One possible reason for the site-specific faster decay of *A. faxoniana* heartwood is the relatively low

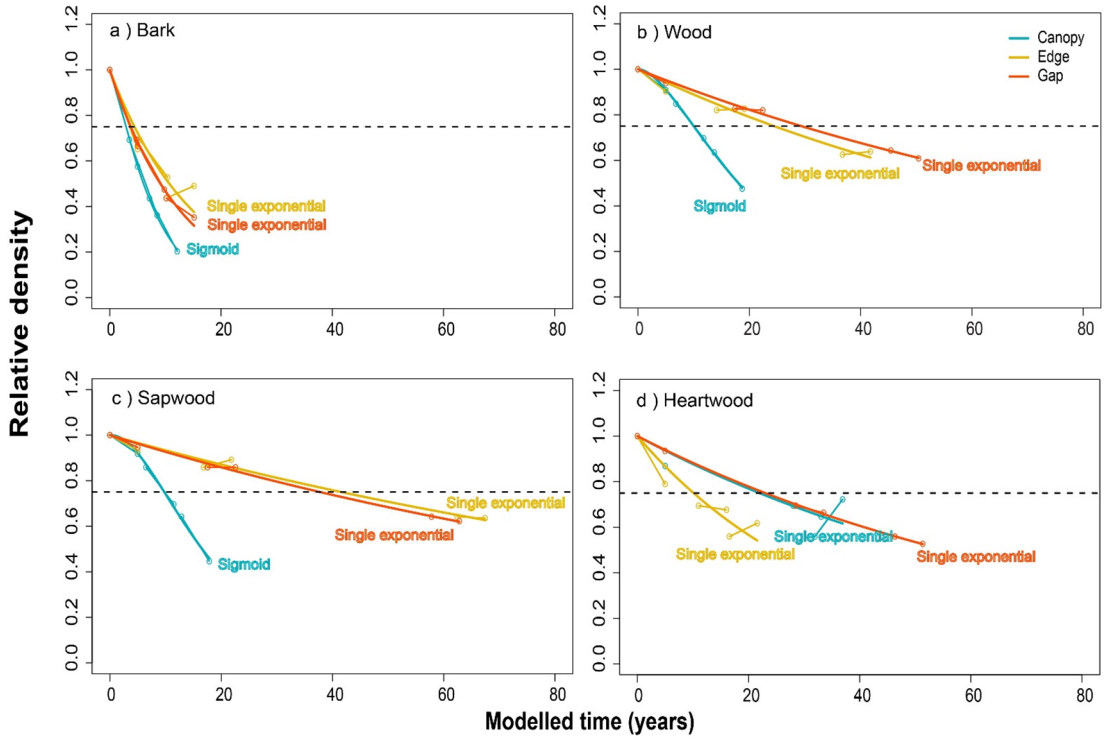

Fig. 3. Comparisons of best-fit decay models between different locations within forest in each *A. faxoniana* tissue. The dashed line was Y = 0.75. The corresponding modelled time ($T_{0.25}$) was provided in Table 2. The function type was provided next to the regression line in the same colour. Parameters of each function are provided in Table A.1 and the regression results were provided in Table A.3.

Table 2
Prediction of time taken for each tissue of *A. faxoniana* to lose 25% ($T_{0.25}$) and 40% ($T_{0.40}$) of its original mass within three locations (Canopy, Edge and Gap) in an alpine fir forest in the eastern Qinghai-Tibetan Plateau. Time was calculated on the basis of the best fit model (see Fig. 2).

Predicted time (year)	Tissue types	Locations			Average
		Canopy	Edge	Gap	
$T_{0.25}$					
	Bark	2.94	4.46	3.79	3.73
	Wood	10.02	24.53	29.43	21.33
	Sapwood	9.78	41.60	37.81	29.73
	Heartwood	21.96	10.12	22.98	18.35
$T_{0.4}$					
	Bark	4.71	7.91	6.72	6.45
	Wood	14.65	43.55	52.26	36.82
	Sapwood	13.72	73.87	67.13	51.58
	Heartwood	38.99	17.96	40.80	32.59

density of heartwood (0.44 g/cm^3) compared with that of sapwood (0.49 g/cm^3) at the beginning of decomposition. The relative higher phosphorus (P) content and lower lignin content in heartwood compared with sapwood (Table A.2) may also contribute to its higher decomposability of the former. Also, the still rather low-density sapwood might not form a strong barrier to environmental influences on heartwood decomposition. The high P concentration and extremely low total phenol concentration (0.0007–0.003%, unpublished data) in heartwood also suggest that endophytes may already exist in the heartwood before tree death, and they could initiate heartwood decomposition soon after the tree falls down without a lag time (Song et al., 2017). Consequently, variation in substrate density and chemical composition could strongly drive variation in the decay process.

Our results also showed a strong difference in chemical composition between bark, sapwood and heartwood even at the mid decay stage (decay class III), and the variation at this advanced stage remained stronger than the variation of the same woody tissue between different decay classes. The long lasting after-life effect of these woody tissues indicate that each tissue type plays a distinct role in carbon and nutrient cycling at least during the first half period of the decay process. The nutrient rich and easily decomposed bark can act as a rapidly available nutrient source, increasing the soil quality within a short period. Furthermore, the element release rate should be faster than we estimated as bark fragmentation along with decomposition was not included in the present study (Shorohova and Kapitsa, 2014; Chang et al., 2020). The relatively slower decaying sapwood and heartwood can act as an important long-term source of soil organic carbon and habitats for diverse organisms. Moreover, our findings also hint that previous studies using wood blocks to explore decay dynamics could be subject to a large bias when using species with a strong radial variation in wood quality. Compared with previous studies, our methods greatly increased the accuracy in modelling deadwood decay by separating sapwood and heartwood decay, whereas it is tough work to estimate the area of each tissue type if more tree species with various diameters were included. Hereby, we suggest to pre-build a database about the proportions of sapwood and heartwood area concerning tree species, diameters, growth environment and other factors affecting sapwood and heartwood area (Kampe and Magel, 2013).

Wood density may be an important negative correlate for decomposability across angiosperm species (e.g. Liu et al., 2015) but not across gymnosperms (Weedon et al., 2009). These inconsistencies may arise because wood density itself is not a causal driver of decomposability but confounded with other structural and chemical drivers. However, within individual trees the trend of the radial density gradient could have a strong power in predicting the desynchronized decay type within the stem. Both radially increasing and decreasing wood density gradients exist widely across forest ecosystems (Preston et al., 2006; Hietz et al., 2013). The density gradient reflects the life history of

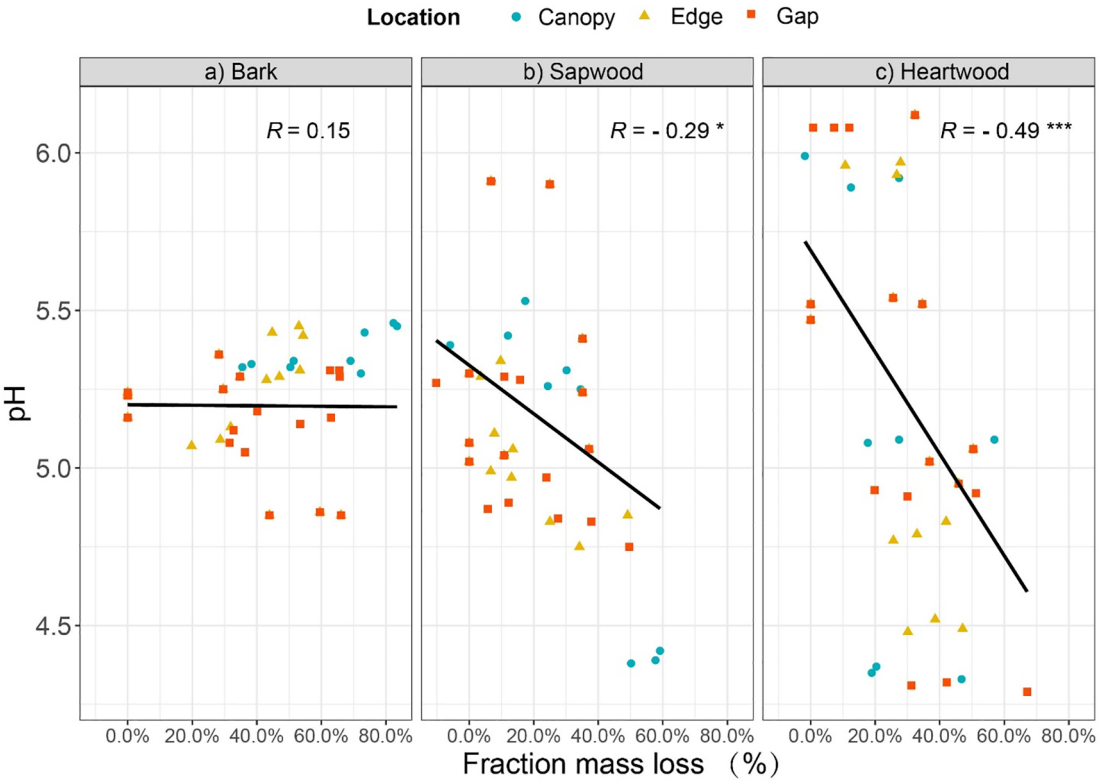

Fig. 4. Relationships between fraction mass loss and pH in *A. faxoniana* tissues along decay classes I-III across two harvests. Tissue samples collected in each decay class were transformed into fraction mass loss via reference density. *R*: Spearman's correlation coefficient. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Regression lines (solid line) were only performed for relationships.

the tree individuals; denser outer wood tends to be produced to confer mechanical stability, especially in excessively wind-exposed forest and the forest with heavy winter snow load on the canopy. Thus, we predict that tree species with higher density, less decomposable sapwood as compared to heartwood may converge in the high-altitude region. An extreme expression of this is deadwood becoming hollow (or filled with highly decomposed, mushy heartwood) during decomposition. This is for instance seen in the pioneer species *Betula albo-sinensis* in our study region. Hollow trunks could play crucial roles in harbouring biodiversity on a decadal time scale, and this function may be particularly important by sheltering soil fauna from warm and dry conditions that are frequent in canopy gaps with their strong solar exposure. Further study should include more species in the alpine region to make a general test of the relative decay rates between sapwood and heartwood, and to inform forest managers about which tree species have fast decaying heartwood, which could help to promote biodiversity.

4.2. Canopy gap effects on log decay

We quantified the canopy gap effects on the decay mode and decay rate considering the radial wood and bark trait variation within the stem, which is also the main novelty and highlight of our study compared with previous studies. There was a slight difference in the pathway into which location within the forest regulates the decomposition of different tissue types, with bark and sapwood decomposing faster and following a different curve (i.e. sigmoid versus exponential) under closed canopy relative to canopy gap and edge. In contrast, heartwood decomposed faster at the canopy edge as compared to under closed canopy or in the gap. One previous study also found both faster wood and bark decay in the closed canopy compared with canopy gap by comparing the average decay class in each location within forest (Forrester et al., 2012). One possible reason for the relatively fast decay of bark and sapwood in canopy could be the high abundance and richness of decomposers living in the canopy such as bark beetles and sapwood-boring ambrosia beetles (Vodka and Cizek, 2013; Lachat et al., 2016), which could consume deadwood directly themselves and promote its microbial colonization. We hypothesize the interaction between locations within forest and radial tissue types on decay rate is also related to gap age, gap size, geographic location and time point that decay started, all of which can influence soil and air temperature, moisture, solar radiation, carbon and nutrient cycling regimes (Prescott, 2002; Muscolo et al., 2014). For instance, soil nutrient availability always increased during the first 3–5 years after canopy gap creation (Prescott, 2002), followed by a strong nutrient leaching by rain erosion and snow-cover melting especially in the high latitude and altitude regions. Combined with the results from previous studies (Prescott, 2002), we suggest to add deadwood to the canopy gap to weaken the pulse in the soil nutrient content.

4.3. pH as a potential predicator

Changes of deadwood traits over time as estimates for decay stage (which in turn can be a component of estimates of decay rates) have received considerable attention (Campbell and Laroque, 2007; Kahl et al., 2009; Larjavaara and Muller-Landau, 2010). However, these methods generally represent estimates of wood density, which is often not a reliable estimator of decay stage without correction for volume loss (Chang et al., 2020). From our results, we can conclude that, at least in *A. faxoniana*, changes in pH during decomposition represent the mass loss to some degree, although the scatter around the regression lines for sapwood and heartwood is large and it did not work for bark at all. Bark pH was stable during decomposition, suggesting that chemical changes other than the formation of organic acids took place. Attempts to quantify sapwood or heartwood decomposition by following individual deadwood over time and/or reconstructing the volume are practical only for the early to middle phases of the decay process. While both wood density and pH come with problems to infer decay stages or rates from, the combined usage of (preferably volume-corrected) wood density and pH, here applied only for early to mid-decay, can possibly help to obtain better estimates also at later decay stages. While here we successfully demonstrate the relationship between pH and mass loss with respect to deadwood of a typical conifer, whether or not there is a similar trend in other conifers and in (angiosperm) hardwood tree species ranging in initial pH, or in foliar litter or other types of plant debris, still needs to be tested further.

5. Conclusion

We found a long-lasting afterlife effect of density and chemical composition between tissue types on decay dynamics. We also demonstrated that there is strong asynchronicity in decay rate and in the best-fit decay model within the *A. faxoniana* stem (bark versus sapwood versus heartwood) along the gradient from closed forest to forest gap by using density correction methods. Furthermore, we recommend that more studies focus on tree species with easily decomposed heartwood, as their decomposing stems may serve as shelter for the fauna especially at high latitudes with strong solar radiation and strong gap dynamics owing to frequent abiotic disturbances. Additionally, we recommend using pH as an assistant for gauging decay rate when density measurement is difficult to achieve for sapwood and heartwood at least at early to mid-decay stage. Although based on one tree species only, our findings indicate that future studies predicting the response of deadwood decomposition to landscape level environmental variation, e.g. due to forest canopy gap dynamics, should consider the variation in decay rates between tissue types within the stem. This may be highly relevant for understanding the impact of human-induced changes in forest disturbance regimes, e.g. due to climate change or logging, on carbon cycling.

Author contributions

WQY, CHC and JHCC convinced conceptualization. CHC and JTW analysed data. CHC led the writing of the manuscript. All authors made contributions to data collection via field work or lab work. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was financially supported by the National Nature Science Foundation of China (31570445). C. Chang received a PHD grant (201706910019) from the China Scholarship Council.

Appendix A

See Tables A.1–A.3.

Table A.1
The regression models that were used to predict the decay process of *A. faxoniana* in an alpine fir forest in the eastern Qinghai-Tibetan Plateau and the regression results.

Sigmoid	$Y = 1\text{-}(1\text{-}e^{at})^b$
Single exponential	$Y = e^{kt}$
Linear	$Y = mk + b$

t is time in years and a, b, k and m are parameters to be estimated. All models assume Y = 1 at t = 0 (i.e. the wood samples with highest initial density represents 'fresh' woody debris at the beginning of decomposition).

Table A.2
The initial content of chemicals at *A. faxoniana* bark, sapwood and heartwood with different decay classes.

Tissue types	Decay class	pH	C (mg/g)	N (mg/g)	P (mg/g)	Cellulose (mg/g)	Lignin (mg/g)
Bark	I	5.21 ± 0.04	370.8 ± 6.3	5.6 ± 1.1	0.21 ± 0.04	169.3 ± 18.6	331.5 ± 17.8
	II	5.30 ± 0.06	385.8 ± 7.0	6.8 ± 1.6	0.13 ± 0.00	151.7 ± 11.0	430.0 ± 24.5
	III	4.85 ± 0.01	422.4 ± 17.8	5.5 ± 1.6	0.16 ± 0.01	191.4 ± 14.4	411.5 ± 6.6
Sapwood	I	5.13 ± 0.15	561.2 ± 25.7	1.5 ± 0.3	0.01 ± 0.00	319.2 ± 29.0	309.2 ± 10.3
	II	5.62 ± 0.50	542.1 ± 35.4	1.0 ± 0.8	0.04 ± 0.03	299.5 ± 36.1	296.5 ± 22.9
	III	5.24 ± 0.18	529.8 ± 3.3	2.4 ± 0.5	0.12 ± 0.04	274.5 ± 4.6	329.1 ± 15.2
Heartwood	I	5.50 ± 0.03	582.9 ± 0.5	1.4 ± 0.2	0.09 ± 0.01	392.8 ± 18.3	254.4 ± 31.6
	II	5.73 ± 0.34	573.1 ± 0.6	1.6 ± 0.5	0.08 ± 0.00	380.4 ± 6.9	255.6 ± 62.5
	III	5.01 ± 0.06	540.1 ± 20.0	4.1 ± 2.7	0.04 ± 0.01	234.3 ± 86.5	367.7 ± 50.6

Values of each chemical content were shown as means ± SD (n = 3); All the chemicals were measured at the first harvest (T_0).

Table A.3
Regression results of each tissue type with different locations based on the three decay models (Table A.1). Values in bold represent the best fit model.

Tissue types	Locations	AIC	RMSE	k (b)	a	Model
BARK	Canopy	**−40.199**	**0.005**	**1.343**	**−0.150**	**sigmoid**
		−26.988	0.018	−0.119		expo
		−16.070	0.045	−0.071		linear
	Edge	−9.717	0.065	1.000	−0.065	sigmoid
		−11.717	**0.065**	**−0.065**		**expo**
		−7.161	0.095	−0.040		linear
	Gap	−24.302	0.019	1.000	−0.076	sigmoid
		−26.302	**0.019**	**−0.076**		**expo**
		−40.199	**0.005**	**1.343**	**−0.150**	**sigmoid**
WOOD	Canopy	**−40.001**	**0.005**	**1.894**	**−0.065**	**sigmoid**
		−20.591	0.031	−0.029		expo
		−26.669	0.019	−0.025		linear
	Edge	−20.282	0.027	1.000	−0.012	sigmoid
		−22.282	**0.027**	**−0.012**		**expo**
		−20.655	0.031	−0.009		linear
	Gap	−31.200	0.011	1.000	−0.010	sigmoid
		−33.200	**0.011**	**−0.010**		**expo**
		−31.355	0.013	−0.008		linear
SAPWOOD	Canopy	**−32.071**	**0.010**	**2.316**	**−0.082**	**sigmoid**
		−16.864	0.043	−0.030		expo
		−21.505	0.029	−0.026		linear
	Edge	−22.060	0.023	1.000	−0.007	sigmoid
		−24.060	**0.023**	**−0.007**		**expo**
		−23.358	0.025	−0.005		linear
	Gap	−30.541	0.012	1.000	−0.008	sigmoid
		−32.541	**0.012**	**−0.008**		**expo**
		−30.928	0.013	−0.006		linear
HEARTWOOD	Canopy	−9.696	0.065	1.000	−0.013	sigmoid
		−11.696	**0.065**	**−0.013**		**expo**
		−10.956	0.070	−0.007		linear
	Edge	−11.445	0.057	1.000	−0.028	sigmoid
		−13.445	**0.057**	**−0.028**		**expo**
		−11.168	0.068	−0.019		linear
	Gap	−43.570	0.004	1.000	−0.013	sigmoid
		−45.570	**0.004**	**−0.013**		**expo**
		−34.504	0.010	−0.010		linear

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