Differences in Necromass and Carbon and Nitrogen Contents between Node and Internode Material of Dead Bamboo Culms in Two *Phyllostachys* Species

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Abstract

It is necessary to understand the heterogeneity in necromass and carbon (C) and nitrogen (N) contents within a dead bamboo culm before estimating these parameters in dead culms. This study determines differences in necromass and C and N contents between node and internode material of decomposing bamboo culms. We collected dead culms of *Phyllostachys bambusoides* and *P. pubescens* from 11 bamboo stands in central and south-western Japan, and determined the necromass per culm cylindrical volume (culm volume density), the C and N stocks per culm cylindrical volume (C and N densities), and the C and N concentrations of node and internode material. In both species the culm volume density was greater in node than internode, which led to a greater C density in node than internode, whereas the C concentration scarcely differed between the two. The N density was greater in node than internode material in both species, due to the difference in culm volume density, while the N concentration was also greater in node than internode. These differences remained unchanged with the degree of decomposition, because the dynamics of necromass and C and N were similar for node and internode materials. The decomposition process in node and internode resembles that in dead wood although variation in N dynamics is observed for *P. bambusoides*. When the greater culm volume density and C and N densities in node than internode were not taken into account, the necromass and C and N stocks in a dead bamboo culm decreased by 4.46–4.50, 4.51–4.59 and 9.47–10.83% respectively. We must sample numerous dead culms to mitigate node and internode differences. However, it might be better to take into account these differences when the number of dead culm samples is limited.

Discipline: Forestry and forest products

Additional key words: carbon dynamics, culm volume density, decomposition process, nitrogen dynamics

Introduction

Bamboo belongs to the subfamily Bambusoideae, containing 90 genera with > 1200 species that cover approximately 36780 km² worldwide²². The contribution of bamboo forests to carbon (C) and nitrogen (N) cycling cannot be ignored when considering the world carbon budget^{1,5}. Accordingly, the parties ratifying the United Nations Framework Convention on Climate Change (UNFCCC) are requested to submit data on C stock in the bamboo forests of their countries. Additionally, about 80% of bamboo forests lie within tropical regions of Asia¹⁵, which emphasizes the importance of understanding C and N cycling in bamboo

forests in the context of the recent decline and degradation of tropical forests.

Japan has 1592 km² of bamboo forests⁶: *Phyllostachys bambusoides* Sieb. et Zucc. and *P. pubescens* Mazel ex Houzeau de Lehaie are grown extensively for the commercial production of edible young shoots^{11,12,13}. These species are estimated to cover 36 and 56% respectively of the total bamboo forest area⁶. The Japanese government is held accountable to the Intergovernmental Panel on Climate Change (IPCC) for C stocks of the aboveground, belowground, deadwood, litter and soil components in these bamboo forests¹⁰, for which the regime of C and N stocks has been reported for all except the deadwood component^{12,13,16,24,25,26,28,29,30}. In bamboo stands, old culms die each

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year and new bamboo culms sprout^{11,31}. The dead culms remain standing for years, eventually falling and decomposing on the ground and contributing to C and N cycling as the deadwood component. However, the structure of bamboo culm tissue differs from that of woody species, featuring a large cavity surrounded by a silica-rich cortex^{9,21} (Fig. 1), which indicates the potential for the decomposition process of dead culm to differ from that of dead wood. The decomposition process is unknown for dead bamboo culms. Accordingly, there is a need to understand the decomposition process of dead culm before estimating the quantity of dead bamboo culms (hereinafter referred to as necromass) and their C and N stocks.

To estimate the necromass of dead wood in a forest ecosystem, the wood volume is multiplied by the wood density^{3,8,18,19,20,23,33}, while the C and N stocks are calculated by multiplying the necromass by the C and N concentrations in dead wood. This method is applicable to dead bamboo culms if the decomposition process, *i.e.* C and N dynamics, resemble those in dead wood. Ugawa et al.³² reported the necromass per culm cylindrical volume (hereinafter referred to as culm volume density), C and N stocks per culm cylindrical volume (hereinafter referred to as C and N densities), and the C and N concentrations for decomposing culm internodes: the changes in these parameters during decomposition resembled those of dead wood. However, the nodes were not accounted for.

Nodes and internodes are found in sequence in a bamboo culm (Fig. 1). The node contains a diaphragm that divides the cavity in the bamboo culm; node tissue has more intensive vascular bundle branching, shorter metaxylem vessels and fiber, and higher ash concentrations than internode material^{4,21}, which suggests that the culm volume density and C and N contents in nodes differ from those in the internode. Moreover, we should consider the possibility that the differences between node and internode change during decomposition. The morphology of the fibers in a bamboo culm differs between node and internode²¹, and culm fibers with broader layers of polylaminate walls degrade more easily². Accordingly, the decomposition process may differ between node and internode.

In this study we examine differences in culm volume density and C and N contents between node and internode. If differences between node and internode are observed, these may be related to the methodology of estimating the necromass and C and N stocks in dead culms. The impact of any differences between node and internode on estimates of necromass and C and N stocks in the entire bamboo culm were evaluated.

In this study, we aim to: (i) clarify the differences in culm volume density, C and N densities, and C and N concentrations, between node and internode; (ii) confirm the changes in the differences between node and internode dur-

Fig. 1. Upper node (UN), internode (IN) and lower node (LN) of a dead bamboo culm (DC) of *Phyllostachys pubescens*

The internode is formed by the culm wall surrounding a large cavity. The node contains a diaphragm, which is the plate that divides the cavity in the culm. For the analysis, we used the culm disks indicated by the dotted lines. Bar = 10 cm.

ing decomposition; and (iii) determine the effect of differences between node and internode on the necromass and C and N stock estimates for *P. bambusoides* and *P. pubescens*. Accordingly, we measured the culm volume density, C and N densities, and C and N concentrations of node and internode of dead bamboo culms collected from the bamboo stands of *P. bambusoides* and *P. pubescens* in central and south-western Japan.

Materials and Methods

1. Sampling

We randomly selected three *P. bambusoides* and eight *P. pubescens* stands in warm-temperate zones with high humidity and hot summers, as indicated by Kottek et al.¹⁷, located in central and south-western Japan where the two species are distributed (Fig. 2 and Table 1). From these stands, we randomly selected standing and fallen dead culms with two neighboring nodes (Fig. 1), and collected 18 dead *P. bambusoides* culms and 50 dead *P. pubescens* culms (Table 2), which were cut and transported to the laboratory.

2. Measurement and calculation of parameters

A dead bamboo culm might undergo trends involving consistent increases in culm volume density and N content from the bottom to the top of the culm^{7,27}. There is therefore a need to compare the parameters of two adjacent nodes with the internode material between them. The distance between two neighboring nodes, *i.e.* internode length, was measured and the culms were cut transversely into 3-cm-length disks in three positions (Fig. 1: lower node, middle-

Fig. 2. Locations of sampling stands

Samples of *Phyllostachys bambusoides* were taken from three stands (open circle) and *P. pubescens* from eight stands (solid circle).

position internode, and upper node).

The diameters of all the culm disks were measured, and the wall thicknesses of the internode disks were determined. The culm disks were then oven-dried at 70°C for 48 h and weighed. The dried culm disks were finely ground using a cutting mill and an agate mortar, and the C and N concentrations were measured using dry combustion methods with an NC analyzer (vario MAX CN; Elementar Analysensysteme GmbH, Hanau, Germany).

We calculated the cylindrical volume of the culm disk using Formula 1 below, where variables D and L denote the culm disk diameter and length (= 3 cm). For the internode,

the wall volume of culm disks was calculated using Formula 2 below, where variables D, L, and T denote the culm disk diameter, length (= 3 cm) and wall thickness. The culm volume density was determined by dividing the culm disk weight by its cylindrical volume. The wall density of the internode disk was determined by dividing the culm disk weight by the wall volume. We calculated the C and N densities of the culm disk by multiplying the culm volume density by the C and N concentrations.

$$\text{[Formula 1] Culm cylindrical volume} = \pi \left(\frac{D}{2} \right)^2 L$$

$$\text{[Formula 2] Wall volume} = \pi \left(\frac{D}{2} \right)^2 L - \pi \left(\frac{D}{2} - T \right)^2 L$$

3. Statistical analysis

Statistical analyses were conducted for each of the two bamboo species.

To examine differences in the culm volume density, C and N densities, and C and N concentrations between node and internode, the five parameters were each compared between pairs of culm disk positions (i.e. lower node, internode, and upper node) using Tukey's HSD test.

To confirm changes in how the five parameters differed between node and internode during decomposition, we calculated the lower and upper node-to-internode ratios of each parameter, to represent the difference between node and internode. We then analyzed the change in the lower and upper node-to-internode ratios against the wall density of internode, using a generalized linear mixed model with Gaussian error (Formula 3). Here, the wall density of the internode was used to indicate the degree of decomposition, because a decrease in wall density implies the loss of necromass during decomposition³², analogous to dead wood of tree species^{3,8,18,19,20,23,33}. A wall density of decomposing

Table 1. Community characteristics of each sampled stand of *Phyllostachys bambusoides* and *P. pubescens*

Species	Stand	Slope direction	Inclination (°)	Culm density (N ha ⁻¹)	DBH ^{*1} (cm)	Mean temperature ^{*2} (°C)	Precipitation ^{*2} (mm year ⁻¹)
<i>P. bambusoides</i>	PB1	NE	2	15200	4.3 ± 1.6	14.0	2205
	PB2	W	35	7200	7.3 ± 2.2	12.1	2252
	PB3	E	29	6900	7.2 ± 2.4	12.9	1794
<i>P. pubescens</i>	PP1	SE	22	5500	7.0 ± 1.3	10.8	1328
	PP2	N	3	5300	6.9 ± 1.7	13.5	1133
	PP3	N	3	8100	8.9 ± 2.1	13.2	2232
	PP4	N	36	5500	11.8 ± 2.0	15.2	1784
	PP5	S	28	9400	9.8 ± 1.9	15.0	1745
	PP6	N	32	4900	10.5 ± 1.7	11.2	1972
	PP7	E	27	6200	9.1 ± 1.9	14.6	1721
	PP8	W	27	9200	11.8 ± 2.1	12.9	1794

^{*1} Mean ± sample standard deviation of the diameter at breast height for living bamboo culms.

^{*2} Mean value in 1971–2000 (Japan Meteorological Agency¹⁴).

Table 2. Number and three characteristics (mean $\pm$ sample standard deviation) of dead culms sampled from each bamboo stand of *Phyllostachys bambusoides* and *P. pubescens*

Species	Stand	Number of samples	Internode length ^{*1} (cm)	Culm diameter ^{*2} (cm)	Wall density ^{*3} (mg cm ⁻³)
<i>P. bambusoides</i>	PB1	7	26.1 $\pm$ 8.6	4.7 $\pm$ 1.0	578 $\pm$ 64
	PB2	4	25.3 $\pm$ 3.1	5.7 $\pm$ 1.6	591 $\pm$ 49
	PB3	7	30.7 $\pm$ 5.8	5.8 $\pm$ 1.6	564 $\pm$ 142
	Total	18	27.7 $\pm$ 6.8	5.4 $\pm$ 1.4	576 $\pm$ 96
<i>P. pubescens</i>	PP1	4	14.5 $\pm$ 3.4	5.8 $\pm$ 1.0	431 $\pm$ 183
	PP2	5	18.8 $\pm$ 6.7	6.7 $\pm$ 1.7	515 $\pm$ 87
	PP3	7	21.2 $\pm$ 7.0	6.0 $\pm$ 1.1	542 $\pm$ 107
	PP4	3	24.7 $\pm$ 3.7	8.5 $\pm$ 2.9	506 $\pm$ 102
	PP5	8	17.1 $\pm$ 5.2	8.3 $\pm$ 1.8	529 $\pm$ 114
	PP6	5	27.6 $\pm$ 9.6	6.1 $\pm$ 1.5	681 $\pm$ 92
	PP7	6	17.5 $\pm$ 4.3	9.3 $\pm$ 2.1	555 $\pm$ 64
	PP8	12	21.2 $\pm$ 4.9	9.6 $\pm$ 1.9	491 $\pm$ 107
	Total	50	20.2 $\pm$ 6.5	7.8 $\pm$ 2.2	527 $\pm$ 117

^{*1} Distance between adjacent nodes.

^{*2} Diameter of mid-position internode.

^{*3} Wall density of mid-position internode, calculated by dividing the internode disk weight by the wall volume.

internodes might indicate a varying degree of decomposition among sampling stands because the initial wall density of internodes may differ among sampling stands. We therefore focused on detecting comprehensive changes in the node-to-internode ratios: the sampling stand was considered as both a random intercept and a random slope in distinguishing the variation among sampling stands. To further clarify the change in the five parameters during decomposition, we analyzed the change in each parameter for the internode, and lower and upper nodes versus the wall density of internode using a generalized linear mixed model with Gaussian error (Formula 4). The sampling stand was considered as both a random intercept and a random slope in distinguishing the variation among sampling stands.

[Formula 3] Lower and upper node-to-internode ratios = Wall density of internode + (Stand) + (Stand | Wall density of internode)

[Formula 4] Parameter of internode, lower and upper nodes = Wall density of internode + (Stand) + (Stand | Wall density of internode)

Finally, to determine the effect of the differences in the five parameters between node and internode on necromass and C and N stock estimates, we calculated the necromass and C and N stocks of a 3-cm-length disk for the internodes (hereinafter referred to as the internode value). We also calculated the intermediate value (hereinafter referred to as the node value) in necromass and C and N stocks between the

lower and upper nodes of 3-cm-length disks in each dead culm. Next, we calculated the necromass and C and N stocks in each dead culm using Formulas 5 and 6 (below), where the internode length is specified in centimeters. In Formula 5, we assumed a bamboo culm containing a node within an internode length. In Formula 6, we assumed a bamboo culm consisting solely of an internode. We then determined the mean value of the necromass and C and N stocks in dead culms with and without a node.

[Formula 5] Parameter of a bamboo culm with a node =

$$\text{Node value} + \left(\frac{\text{Internode value}}{3} \right) \times (\text{Internode length} - 3)$$

[Formula 6] Parameter of a dead culm without a node =

$$\left(\frac{\text{Internode value}}{3} \right) \times \text{Internode length}$$

All statistical analyses were performed using JMP 5.1 (SAS Institute, Cary, NC, USA).

Results and discussion

1. Differences in necromass and C and N contents between node and internode

The culm volume density was greater in node than internode (Table 3; for *P. bambusoides*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node; for *P. pubescens*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper

Table 3. Culm volume density, carbon (C) and nitrogen (N) densities, and C and N concentrations (mean $\pm$ sample standard error) in lower and upper nodes and internodes of dead culms of *Phyllostachys bambusoides* and *P. pubescens*

Species	Parameter	Number of samples	Lower node	Internode	Upper node
<i>P. bambusoides</i>	Culm volume density (mg cm ⁻³)	18	308 $\pm$ 21 ^a	227 $\pm$ 16 ^b	293 $\pm$ 19 ^a
	C density (mg cm ⁻³)	18	154 $\pm$ 10 ^a	113 $\pm$ 8 ^b	146 $\pm$ 10 ^a
	N density (mg cm ⁻³)	18	0.42 $\pm$ 0.03 ^a	0.21 $\pm$ 0.02 ^b	0.40 $\pm$ 0.03 ^a
	C concentration (g kg ⁻¹)	18	499 $\pm$ 1 ^a	497 $\pm$ 1 ^b	499 $\pm$ 1 ^a
	N concentration (g kg ⁻¹)	18	1.49 $\pm$ 0.18 ^a	1.00 $\pm$ 0.12 ^b	1.48 $\pm$ 0.18 ^a
<i>P. pubescens</i>	Culm volume density (mg cm ⁻³)	50	269 $\pm$ 9 ^a	208 $\pm$ 6 ^b	265 $\pm$ 9 ^a
	C density (mg cm ⁻³)	50	135 $\pm$ 4 ^a	104 $\pm$ 3 ^b	132 $\pm$ 4 ^a
	N density (mg cm ⁻³)	50	0.65 $\pm$ 0.04 ^a	0.41 $\pm$ 0.02 ^b	0.70 $\pm$ 0.04 ^a
	C concentration (g kg ⁻¹)	50	500 $\pm$ 0 ^a	500 $\pm$ 0 ^a	500 $\pm$ 0 ^a
	N concentration (g kg ⁻¹)	50	2.60 $\pm$ 0.22 ^a	2.14 $\pm$ 0.19 ^b	2.80 $\pm$ 0.22 ^c

These values were calculated using a generalized linear mixed model in which the sampling stand was incorporated as a random effect; the model formula was [Parameter = (Stand)]. Different letters indicate a significant difference between culm disk positions (Tukey's HSD test: $p \leq 0.050$)

node). This might be due to the diaphragm.

The C density was also greater in node than internode (Table 3; for *P. bambusoides*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node; for *P. pubescens*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node). The C density is calculated from the necromass and C concentration. In *P. pubescens*, the C concentration did not differ between node and internode ($p = 0.161$ in the lower node and $p = 0.079$ in the upper node). In *P. bambusoides*, the C concentration was greater in node than internode ($p < 0.001$ in the lower node and $p < 0.001$ in the upper node), but the mean difference between node and internode (i.e. 1.9 g kg⁻¹) was very small relative to the mean C concentration of about 500 g kg⁻¹. These results indicate that the C concentration has little influence on the difference in C density between node and internode, meaning the difference in C density between node and internode is due to the difference in culm volume density.

The N density was greater in node than internode (Table 3; for *P. bambusoides*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node; for *P. pubescens*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node). The N density is calculated from the necromass and N concentration. Interestingly, the N concentration was greater in node than internode (Table 3; for *P. bambusoides*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node; for *P. pubescens*, $p < 0.001$ in the lower node and $p < 0.001$ in the upper node). Thus, the difference in N density between node and internode is likely to be due to the difference in N concentrations as well as in culm volume density. The high N concentration corresponds to high ash concentrations in nodes of living culm, and may be related to physiological

function, e.g. intensive vascular bundle branching²¹.

2. Differences in necromass and C and N dynamics between node and internode

The node-to-internode ratio of the culm volume density remained unchanged with the wall density of the internode material, the indicator of the degree of decomposition (Fig. 3; for *P. bambusoides*, $p = 0.824$ in the lower node and $p = 0.748$ in the upper node; for *P. pubescens*, $p = 0.946$ in the lower node and $p = 0.958$ in the upper node). The culm volume density of the node and internode decreased with the degree of decomposition, although the p -value was not significant for the lower node of *P. bambusoides*, and was close to 0.050 (Fig. 4; for *P. bambusoides*, $p = 0.053$ in the lower node, $p = 0.025$ in the internode and $p = 0.045$ in the upper node; for *P. pubescens*, $p < 0.001$ in the lower node, $p < 0.001$ in the internode and $p < 0.001$ in the upper node). We therefore suggest that the decrease in necromass during decomposition is common between node and internode, so that the difference in culm volume density between node and internode is maintained. In dead wood, the difference in decomposition rates between heartwood and sapwood is explained by the difference in lignin and other antimicrobial extractives (e.g. polyphenols, terpenoids and tannins) rather than any difference in tissue or cell structures³⁴. Thus, the differences in tissues and cell structures between node and internode^{4,21} may not influence their decomposition rates.

The C density node-to-internode ratio remained unchanged with the degree of decomposition (Fig. 3; for *P. bambusoides*, $p = 0.825$ in the lower node and $p = 0.747$ in the upper node; for *P. pubescens*, $p = 0.946$ in the lower node and $p = 0.993$ in the upper node). The C density of

Fig. 3. Changes in lower and upper node-to-internode ratios of the culm volume density, carbon (C) and nitrogen (N) densities, and C and N concentrations versus the wall density of internode of dead culms in each bamboo stand of *Phyllostachys bambusoides* and *P. pubescens*

The wall density of internode material was used to indicate the degree of decomposition, and is shown on the x-axis in the reverse direction.

Fig. 4. Changes in culm volume density, carbon (C) and nitrogen (N) densities, and C and N concentrations of internode, lower and upper nodes versus the wall density of internode material of dead culms in each bamboo stand of *Phyllostachys bambusoides* and *P. pubescens*

The wall density of internode material was used to indicate the degree of decomposition, and is shown on the x-axis in the reverse direction. The dotted line is a significant regression line ($p < 0.05$), estimated using a generalized linear mixed model.

Table 4. Necromass and carbon (C) and nitrogen (N) stocks (mean $\pm$ sample standard error) in dead culms with and without a node, and their relative differences for dead culms of *Phyllostachys bambusoides* and *P. pubescens*

Parameter	<i>P. bambusoides</i>			<i>P. pubescens</i>		
	With a node	Without a node	Relative * difference	With a node	Without a node	Relative * difference
Necromass (g)	157.8 $\pm$ 26.8	150.7 $\pm$ 25.5	4.50%	208.3 $\pm$ 19.6	199.0 $\pm$ 18.8	4.46%
C stock (g)	78.5 $\pm$ 13.3	74.9 $\pm$ 12.7	4.59%	104.1 $\pm$ 9.7	99.4 $\pm$ 9.3	4.51%
N stock (g)	0.157 $\pm$ 0.032	0.140 $\pm$ 0.028	10.83%	0.359 $\pm$ 0.032	0.325 $\pm$ 0.029	9.47%

The necromass and C and N stocks were calculated using a generalized linear mixed model in which the sampling stand was incorporated as a random effect; the model formula was [Parameter = (Stand)].

* Percentage difference in the mean values of each parameter of dead culms with and without a node relative to the mean value of the parameter of dead culms with a node.

node and internode decreased with the degree of decomposition, although the p -value was not significant for the lower node of *P. bambusoides*, and was close to 0.050 (Fig. 4; for *P. bambusoides*: $p = 0.051$ in the lower node, $p = 0.043$ in the internode and $p = 0.025$ in the upper node; for *P. pubescens*, $p < 0.001$ in the lower node, $p < 0.001$ in the internode and $p < 0.001$ in the upper node). We therefore suggest that the decrease in C density during decomposition is similar for both node and internode, so that the difference in C density between node and internode is maintained. The C concentration of node and internode remained unchanged with the degree of decomposition (for *P. bambusoides*, $p = 0.087$ in the lower node, $p = 0.120$ in the internode and $p = 0.260$ in the upper node; for *P. pubescens*, $p = 0.653$ in the lower node, $p = 0.693$ in the internode and $p = 0.207$ in the upper node), which indicates that the decrease in C density is explained by the loss of necromass, which mainly comprises carbon. Thus, the common C dynamics of node and internode appear to derive from the common dynamics of their necromass.

The N density node-to-internode ratio remained unchanged with the degree of decomposition (Fig. 3; for *P. bambusoides*, $p = 0.891$ in the lower node and $p = 0.838$ in the upper node; for *P. pubescens*, $p = 0.760$ in the lower node and $p = 0.084$ in the upper node). The N density remained unchanged with the degree of decomposition in either node and internode (Fig. 4; for *P. bambusoides*, $p = 0.601$ in the lower node, $p = 0.814$ in the internode and $p = 0.722$ in the upper node; for *P. pubescens*, $p = 0.101$ in the lower node, $p = 0.161$ in the internode and $p = 0.339$ in the upper node). The common tendency for the N density to remain unchanged during decomposition should maintain the difference in N density between node and internode. However, the absence of any change in N density appears to have different causes in the two bamboo species. In *P. pubescens*, the N concentration increased with the degree of decomposition ($p < 0.001$ in the lower node, $p < 0.001$ in the internode and $p < 0.001$ in the upper node), which is due

to the loss of necromass, because the amount of N (i.e. N density) remained unchanged during decomposition. The lack of change in N density may result from the immobilization of N^{18,19,23}. In *P. bambusoides*, the N concentration did not increase ($p = 0.593$ in the lower node, $p = 0.491$ in the internode and $p = 0.423$ in the upper node) regardless of the decrease in culm volume density, although no change in N density during decomposition was detected. The lack of change in N density may therefore be attributable to the high variation in N dynamics.

3. Influence of differences in necromass and C and N contents on estimates of C and N stocks

Table 4 shows estimates of the necromass and C and N stocks in dead culms with and without taking into account the difference between node and internode. When the greater culm volume density in node than internode was not taken into account, the necromass was decreased by 4.50% in *P. bambusoides* and 4.46% in *P. pubescens*. Similarly, the C stock was decreased by 4.59% in *P. bambusoides* and 4.51% in *P. pubescens*. In the case of N stocks, the decrease was 10.83% in *P. bambusoides* and 9.47% in *P. pubescens*.

In actual surveys, we collect dead culm samples containing nodes randomly, which means the effect of differences between node and internode on estimates of necromass and C and N stocks is smaller than the percentages described above. The differences between node and internode need not be considered when estimating the necromass and C and N stocks in dead culms when numerous dead culms are sampled. Conversely, it might be better to take into account the differences between node and internode when the number of dead culm samples is limited due to the cost and time of field survey.

Conclusion

We have confirmed in this study the greater values in culm volume density, in C and N densities, and in N con-

centration in nodes than in internode material for two *Phyllostachys* species. However, these differences remained unchanged during decomposition, indicating homogeneity in the decomposition process between node and internode. The decomposition process in node and internode resembles that in dead wood although variation in N dynamics is observed for *P. bambusoides*. This means that the method of estimating C and N stocks of dead wood is also applicable to dead culms. The necromass and C and N stocks in dead bamboo culms are decreased by 4.46–4.50, 4.51–4.59 and 9.47–10.83% respectively when the node is not taken into account. The effect of differences between node and internode will be reduced when numerous dead culms are sampled. However, the differences between node and internode must be taken into account when the number of dead culm samples is limited. Bamboo forests are widely distributed worldwide, especially in tropical regions. It is important to recognize the differences between node and internode to estimate C and N stocks in these bamboo forests more accurately.

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