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Log decay of *Picea abies* in the Swiss Jura Mountains of central Europe

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Abstract

The key importance of coarse woody debris (CWD) for biodiversity is well acknowledged. However, its role in terrestrial nutrient and carbon cycles is less studied, in particular in central Europe. We analysed the decay process of spruce *Picea abies* (L.) Karst., the most common tree species in Switzerland. The aims were: (i) to examine the usefulness of ultrasonic wave measurements for characterising of decay processes; (ii) to assess changes in physical and chemical variables of CWD during the decay process in relation to site-specific humus forms. We analysed 25 logs, five per decomposition class within a five-class system, for their density, moisture, C, N and P contents, lignin and cellulose. We also applied ultrasonic measurements to the radial axis of decaying logs using the Sylvatest-Duo® tool. In addition, we described eight soil profiles below the sampled logs and analysed the soil samples for total C, N and P and water pH. All the soils sampled were classified as humiferous Brunisol (eutric Cambisol) with various humus types.

The propagation speed of ultrasonic waves was found to be directly proportional to the average tree density and inversely proportional to C content. These preliminary results point out the potential usefulness of this technique for further studies of wood decay. Wood density was found to decrease during wood decay (434–308 mg g^{-1}), whereas moisture increased (94–258%). Carbon and lignin concentrations remained stable, while N and P contents both increased between classes 3 and 5 (N: 0.41–1.26 mg g^{-1} and P: 0.01–0.06 mg g^{-1}).

These general decay patterns are in accordance with previous studies of other tree species and of *P. abies* in other geographic regions. However, we did find some site-specific patterns, e.g. N and P were lower and wood density declined less than in other studies. Climatic factors at the study site slow down biological activity and they also seem to explain the morphology of the humus forms and their variations. We found no concordance between the humus morphology and the wood-decay state. We recommend performing long-term experiments in Central European forests to investigate the different factors that may influence CWD decomposition, such as edaphic and climatic conditions, in a controlled way.

Keywords: Dead wood; Spruce; Decomposition; Nutrients; Humus; Brunisol; Ultrasonic waves; Sylvatest-Duo®

1. Introduction

Coarse woody debris (CWD) is an important structural and functional component of forest ecosystems (Harmon et al., 1986). It affects soil development, reduces erosion, stores carbon, nutrients and water, acts as germination sites for the forest vegetation, and serves as a major habitat for saproxylics. There is, however, less knowledge about the role of CWD in terrestrial nutrient and carbon cycles. Climate change is expected to lead to more frequent and more severe disturbances and thus more CWD. It is, therefore, becoming increasingly important to understand the roles and dynamics of dead wood in ecosystem carbon and nutrient cycles.

The majority of studies of CWD decay dynamics have been undertaken in the coniferous forests of North America (e.g. Lambert et al., 1980; Sollins et al., 1987; Yin, 1999) or northern Europe (e.g. Krankina and Harmon, 1995; Temnuhin, 1996; Krankina et al., 1999; Naesset, 1999a,b; Harmon et al., 2000). Recent findings concerning the input, accumulation, and decay of CWD in northern coniferous forests are summarized in Laiho and Prescott (2004). The decomposition of CWD has only recently been studied in other geographic regions (e.g. southern Indiana USA: Idol et al., 2001; south-eastern Australia: Mackensen and Bauhus, 2003; New Zealand: Ganjegunte et al., 2004; Ecuador: Wilcke et al., 2005). In central Europe, however, little is known about these processes, even for the

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most common trees species. To forecast, e.g. the potential for biodiversity or the quantity of CO_2 stored under different management regimes, we need to understand the dynamics of dead wood decay in European temperate forests better. The few studies concerning CWD decay processes have mainly focussed on beech *Fagus sylvatica* L. (Christensen and Vesterdal, 2003; Van Hees, 2003; Ódor and Standovár, 2003).

Assessments of CWD decomposition are often made on the basis of a visual classification. CWD classification methods generally include several decay stages from hard to soft to buried wood (see, e.g. Maser et al., 1979; Sollins, 1982; Lee et al., 1997; Naesset, 1999b). In order to quantify the decomposition process in a more objective way, it may be more straightforward to measure target variables. One method that involves ultrasonic measurements to characterize the wood quality of timber has been described by Sandoz (1989). This technique has also been used to evaluate the mechanical properties of trees (Combe, 1997; Bailleres et al., 1998; Carrasco and Oliveira, 1999) and to detect internal wood decay in living standing trees (Niemz et al., 1998; Lin et al., 2000). To the best of our knowledge, this technique has never been used to characterize CWD or log decay. However, it may be a useful tool for complementing visual decay classifications, since it can be used to obtain rapidly non-destructive quantitative measurements in the field.

The overall aim of this study was to find out more about the decomposition process of spruce *Picea abies* (L.) Karst., the most common tree species in temperate forests in Switzerland. The specific objectives of this paper are: (i) to examine the usefulness of ultrasonic wave measurements for the characterisation of decay processes and (ii) to assess changes in physical and chemical variables of CWD during the decomposition process in relation to site-specific humus forms.

2. Methods and material

2.1. Study site

The experimental data for this study was collected in the Jura Mountains in Switzerland (46°36′ latitude north and 6°19′ longitude east). The major part of the Jura Mountains are covered by sub-alpine forests, dominated by spruce (*P. abies*), mixed with beech (*F. sylvatica* L.), fir (*Abies alba* Mill.) and maple (*Acer pseudoplatanus* L.). The study site is a part of a protected forest area in the canton of Vaud, which covers an area of 355 ha. The sample trees were taken within an east-exposed homogeneous area of 12 ha with an average slope of 11°, between 1370 and 1470 m a.s.l. The average annual temperature between 1961 and 1990 was 5.3 °C (−2 °C in January and 13.4 °C in July) and the annual average precipitation was 1274 mm. The soils of the study site are covered by snow during at least 4 months per year and first layers may be frozen. In spring when snow melts, soils are water-saturated. The type of soil considered in the present study is a humiferous Brunisol on karst, according to the official French classification (Baize, 1998), that corresponds to an Eutric Cambisol in the FAO classification (FAO, 1989). The upper layers are calcareous free or partly decalcified because of the heavy precipitation and the fissured rocks (intense water leaching).

2.2. Sampling

The sampling scheme was based on the choice of 25 logs, i.e. five logs per decomposition class, according to the five-class system of Maser et al. (1979) (Table 1). Each log was visually assessed for its degree of decomposition and served as the centre of a circular plot 500 m^2 in area. On each plot we inventoried all the lying and standing dead trees with the following characteristics: length $\geq$ 1 m and diameter at the thicker end $\geq$ 10 cm (lying trees); diameter at breast height $\geq$ 10 cm (standing trees). On each log, two diameters were measured with a slide calliper, one at the base of the trunk ($d_1 = 2r_1$) and the other at the end ($d_2 = 2r_2$). The overall length (l) was also recorded. For snags we recorded their diameter and length. The volume was calculated using the equation for a cone-shaped object:

$$V = \frac{\pi l}{3}(r_1^2 + r_1 r_2 + r_2^2)$$

To carry out the necessary physico-chemical analyses one cross-section, 5–10 cm thick, was extracted from each log using a chainsaw. The samples were cut in October at a temperature of 10–11 °C and a relative air humidity of 100%. They were stored in the laboratory at ambient temperature for 2 days inside plastic bags to avoid loss of moisture. Under these conditions the water loss in the wood is negligible (F. Perrin, pers. commun.).

Table 1
Five-class system of log decomposition according to Maser et al. (1979)

Log characteristics	Log decomposition classes				
	1	2	3	4	5
Bark	Intact	Intact	Trace	Absent	Absent
Twigs <3 cm	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft, blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Color of wood	Original color	Original color	Original color to faded	Light brown to faded brown or yellowish	Faded to light yellow or gray
Portion of log on ground	Log elevated on support points	Log elevated on support points but sagging slightly	Log is sagging near ground	All of log on ground	All of log on ground

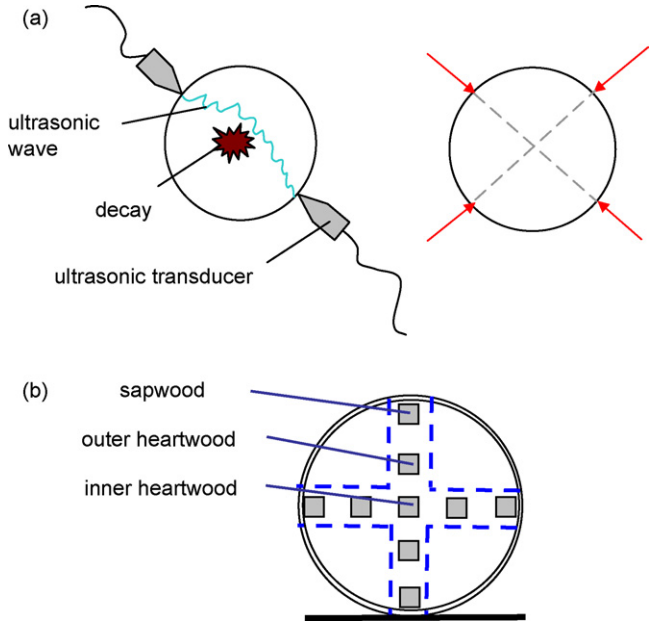

Fig. 1. (a) Ultrasonic wave measurements with the Sylvatest-Duo® tool and (b) sampling within cross-sections for physical and chemical analyses.

As a reference, we chose 10 living trees inside the study area near the circular plots. One cylindrical sample 3 cm in diameter and 3.5 cm in length was extracted from the sapwood of each selected tree to determine its density, humidity and nitrogen (N), phosphorus (P) and organic carbon (C) contents.

To determine the soil's humus forms, a total of eight subsites were chosen with respect to the previously defined classes of wood decomposition (from class 2 to class 5). At each subsite, the soil profile was determined and classified, and soil samples were collected for further chemical analyses.

2.3. Ultrasonic wave measurements

The decomposition stage was assessed with the Sylvatest-Duo® tool (http://www.cbs-cbt.com/TECH/index_s_en.html, 22 January 2007). We applied ultrasound to the radial axis of logs. Each 1-m portion of a log was screened with two measurements on two radial orthogonal axes, i.e. perpendicular to the tree axis (Fig. 1a). Living trees were measured at breast height. Then, the average speed per sample tree was computed. For a healthy tree, the ultrasound speed on the radial axis is nearly constant, i.e. 1600 m s^{-1} for a spruce tree with a diameter of 0.60 m (Y. Benoît, pers. commun.). In order to standardize data for ultrasonic wave speed, we computed for each tree the speed for a diameter of 60 cm.

2.4. Physical and chemical analyses

For the physical analyses small wooden cubes (2.5 cm per side) were cut from the sampled wood cross-sections at three positions corresponding to the sapwood, outer and inner heartwood (Fig. 1b). They were weighed and put in an oven at 105 °C for at least 3 days until they obtained a constant weight. Moisture was calculated as a percentage of dry weight at 105 °C. The density was measured by the standardized method for determining wood density ISO 3131: 1975 (http://www.iso.org/iso/en/, 22 January 2007) and expressed in kg m^{-3}.

In order to carry out the chemical analyses, a representative part of the cross-sections was cut into small pieces, and then dried at 60 °C for 3 days until their weight remained constant. Then, these pieces were ground to powder to analyse the cellulose and lignin content through gravimetry (Colin, 1973). N and P were determined through the modified Kjeldahl method of Chapman and Pratt (1961), and the organic C using a carbon analyzer (Casumat 8-Adge, Wösthoff, Germany).

The wood mass was calculated by multiplying computed volume by the average bulk density of each decay class. In order to account for mass losses during wood decay, we multiplied initial concentrations (in mg g^{-1}) by the average bulk density of each decay class and expressed them as kg m^{-3}.

For the characterisation of the soil's humus forms, the total N and organic C were measured in the same way as for the wood samples. Total P in soil was measured following a Kjeldahl oxidation and was determined at 880 nm using the molybdate acid procedure (Murphy and Riley, 1962). We also measured water pH (1:2.5).

2.5. Statistics

Data from logs within the same decay classes were pooled. Means were calculated for each decay class and for each position (sapwood, outer and inner heartwood; Fig. 1b) per decay class. In the results section, all the means are given with their standard error. We tested for differences between decay class means by univariate ANOVA and for significance between groups ($p < 0.05$) using the Duncan's multiple range test. All statistics were executed with the STATISTICA 6.0® software.

3. Results

3.1. Total volume and mass

The mean diameter at the thicker end of the 25 studied logs was 37.7 ± 3.2 cm (range 13–68 cm). We recorded 10.2 ± 5.0 m^3 ha^{-1} of snags and 30.2 ± 3.6 m^3 ha^{-1} of logs. These volumes were not distributed homogeneously within decay classes. Among snags, 4.1 m^3 ha^{-1} belonged to class 1, 3.5 m^3 ha^{-1} to class 2, 1.9 m^3 ha^{-1} to class 3 and 0.9 m^3 ha^{-1} to class 4. No snags of class 5 were recorded. For logs, we observed 6.4 m^3 ha^{-1} in class 1, 9.6 m^3 ha^{-1} in class 2, 6.7 m^3 ha^{-1} in class 3, 5.1 m^3 ha^{-1} in class 4, and finally 2.4 m^3 ha^{-1} in class 5.

The estimated total mass of dead wood was 15.7 t ha^{-1} (snags: 4.2 t ha^{-1} and logs: 11.6 t ha^{-1}). C, N and P amounts in CWD represented 7.7 t ha^{-1} of C (snags: 2.0 t ha^{-1} and logs: 5.7 t ha^{-1}), 8.7 kg ha^{-1} of N (2.1 and 6.6 kg ha^{-1}), and 0.5 kg ha^{-1} of P (0.1 and 0.4 kg ha^{-1}).

3.2. Ultrasonic wave measurements

The propagation speed of the ultrasonic waves was highest for living trees (1450 ± 47 m s^{-1}) and diminished with

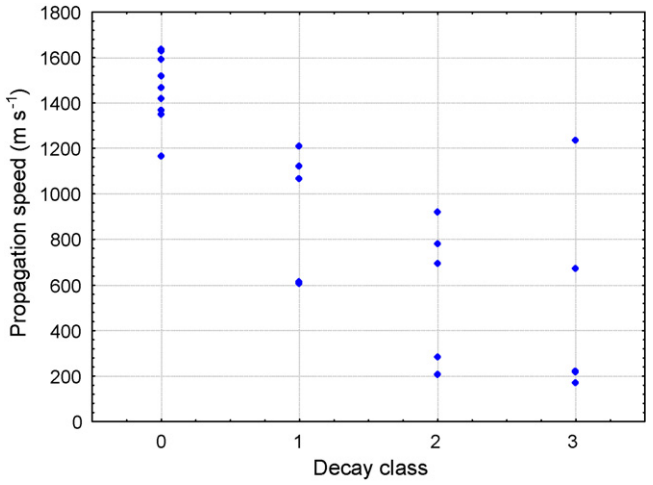

Fig. 2. Mean propagation speed (m s^{-1}) of the ultrasonic waves per sampled tree. Data standardized for a tree 60 cm in diameter.

advanced tree decay (class 1: 923 ± 130 m s^{-1}; class 2: 576 ± 141; class 3: 503 ± 204 m s^{-1}; Fig. 2). It was difficult to measure decay classes 4–5, as there was no compact wood structure. The soft and powdery wood texture of rotten logs hinders the traversal of ultrasonic waves. The trees of decay class 1 with a low speed of only about 600 m s^{-1} (Fig. 2) were trees affected by brown-rot fungi pockets. Even though they had been generally classified as decay class 1 visually, some parts of these logs usually had symptoms of more decay. In contrast, one log of class 3 had a high propagation speed (1200 m s^{-1}). This tree was characterized by a high heterogeneity of decay (some twigs, but little bark remaining). For trees of decay classes 1–3, the average wave speed per tree was positively correlated to average tree density ($r = 0.65$, $p = 0.008$, $n = 15$) and negatively to C concentration [mg g^{-1}] ($r = -0.53$, $p = 0.044$, $n = 15$).

3.3. Density and moisture

Wood density decreased steadily with advancing decay, varying between 434 ± 8 kg m^{-3} (class 1) and 308 ± 13 kg m^{-3} (class 5); Table 2. The tendency to decrease was accentuated after decay class 3. Density did not differ in the sapwood, and in the outer and inner heartwood (Table 3).

The moisture content significantly increased with advancing decay from $52 \pm 8\%$ of dry mass (class 2) to $258 \pm 38\%$ (class 5; Table 2). When samples of each decay class were pooled according to their position within a log (i.e. sapwood, outer and inner heartwood), we found significant differences in the water content. The sapwood of decay class 1 ($144 \pm 11\%$) contained more water than the outer ($63 \pm 10\%$) and inner heartwood ($31 \pm 4\%$) (Table 3). For more advanced decay classes, the water content of the sapwood ($129 \pm 32\%$; class 4) was still similar to the wood of slight decay, whereas the inner heartwood was much more humid ($266 \pm 65\%$, class 4). Standard deviations were generally higher for logs in advanced decay states.

We also analysed the water content in samples of the same log. Within the sapwood and the heartwood of each log, the water content was the same (data not shown).

Table 2
Mean physical and chemical data for *Picea abies* logs, ranging from living trees through subsequent wood decay states, and for humus (O-layers) material

	Living trees			Decay classes												O-layers			ANOVA (classes 1–5)	
				1			2			3			4			5					
	Mean	S.E.	*n*	Mean	S.E.	*n*	Mean	S.E.	*n*	Mean	S.E.	*n*	Mean	S.E.	*n*	Mean	S.E.	*n*	Mean	S.E.	*n*	*F*	*p*
Density (dry mass) (kg m^{-3})	412	9.8	10	434(a)	8	37	404(ab)	8	34	382(b)	9	37	315(c)	12	19	308(c)	13	11	n.a.	n.a.	n.a.	21.77	<0.001
Moisture (%)	126	3.8	10	94(ab)	10	37	52(a)	8	34	84(a)	11	37	135(b)	27	19	258(c)	38	11	n.a.	n.a.	n.a.	16.82	<0.001
Organic carbon (mg g^{-1})	470	1	10	477(a)	3	5	490(a)	5	5	491(a)	6	5	504(a)	13	5	502(a)	14	5	391	30	11	1.41	0.256
Nitrogen (mg g^{-1})	0.38	0.02	10	0.45(a)	0.07	5	0.56(a)	0.10	5	0.41(a)	0.05	5	0.75(a)	0.12	5	1.26(b)	0.22	5	13.53	0.84	11	7.34	<0.001
Phosphorus (mg g^{-1})	0.04	0.003	10	0.05(ac)	0.02	5	0.02(ab)	0.01	5	0.01(b)	0.01	5	0.04(abc)	0.01	5	0.06(c)	0.01	5	0.35	0.03	11	3.52	0.025
Lignocellulose (mg g^{-1})	n.a.	n.a.	n.a.	782(a)	12	5	729(b)	6	5	759(ab)	15	5	749(ab)	21	5	752(ab)	14	5	n.a.	n.a.	n.a.	1.71	1.188
Lignin (mg g^{-1})	n.a.	n.a.	n.a.	310(a)	4	5	304(a)	12	5	337(a)	22	5	399(a)	56	5	410(a)	53	5	n.a.	n.a.	n.a.	1.87	0.155
Cellulose (mg g^{-1})	n.a.	n.a.	n.a.	474(b)	9	5	429(b)	17	5	429(b)	37	5	354(b)	70	5	344(b)	51	5	n.a.	n.a.	n.a.	1.66	0.199
Hemicellulose (mg g^{-1})	n.a.	n.a.	n.a.	229(c)	12	5	217(c)	19	5	193(c)	16	5	192(c)	17	5	186(c)	12	5	n.a.	n.a.	n.a.	1.40	0.269
C:N	1272	64	10	1165(a)	198	5	986(a)	182	5	1297(a)	169	5	789(ac)	130	5	478 (c)	84	5	30.8	3.7	11	3.87	0.017
N:P	9.2	0.8	10	11.5(b)	2.4	5	24.6(b)	5.4	4	38.3(b)	26.7	2	20.9(b)	3.2	4	20.1(b)	1.8	5	40.0	2.3	11	1.99	0.148
Lignin:N	n.a.	n.a.	n.a.	619(d)	146	5	855(d)	189	5	663(d)	128	5	780(d)	106	5	472(d)	131	5	n.a.	n.a.	n.a.	1.07	0.393

Statistical tests were applied to data from decay classes 1–5. n.a.: not analysed. Where letters are the same (abc), the Duncan test showed no significant difference.

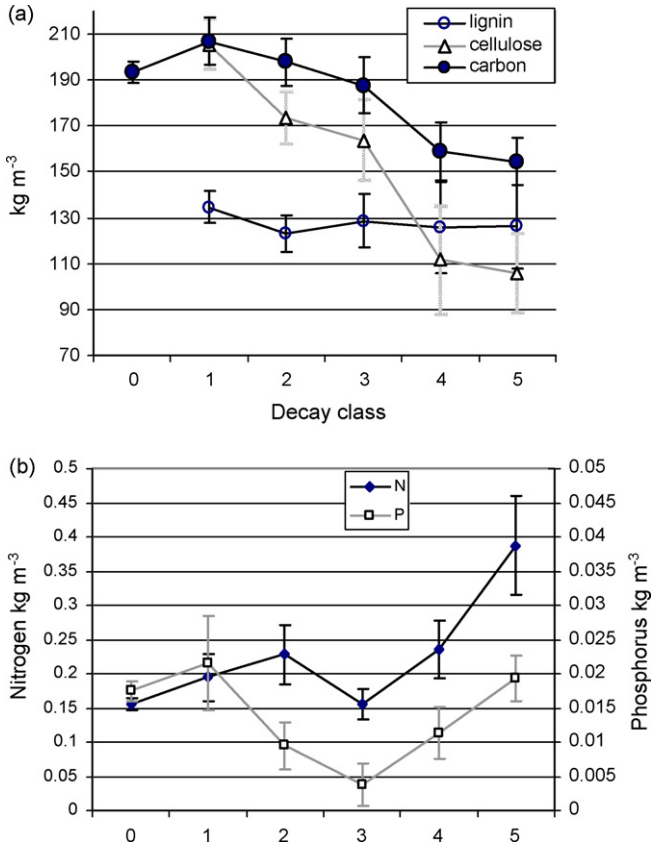

Fig. 3. (a) Evolution of organic carbon, lignin and cellulose and (b) N and P dynamics of coarse woody debris (logs) over decay classes in kg m^{-3}. *X*-axis: decay classes 1–5, 0 = living trees. *Y*-axis: N on the left *Y*-axis, and P on the right *Y*-axis. Means and standard errors.

3.4. Nutrients in wood and soil

3.4.1. Wood

While the total organic C concentration changed little with decay state, between 470 ± 1 mg g^{-1} (living trees) and 502 ± 14 mg g^{-1} (advanced decay), and without any significant variation (Table 2), the C content per volume unit decreased steadily (Fig. 3a). The cellulose content decreased from 474 ± 9 mg g^{-1} (class 1) to 344 ± 51 mg g^{-1} (class 5), although this was statistically not significant (Table 2). Conversely, the lignin concentration increased from 310 ± 4 mg g^{-1} (class 1) to 410 ± 53 mg g^{-1} (class 5), although this was also not statistically significant. The lignin:cellulose ratio increased from 0.65 (class 1) to 1.19 (class 5).

Both, the N concentration and the N content per volume unit in the logs remained quite constant as decay proceeded until the advanced decay class 5, where N levels increased sharply and significantly (Table 2 and Fig. 3b). The C:N ratio remained high at the beginning of wood decay (1272 ± 64; living trees), but decreased significantly for advanced wood decay states (class 3, 1297 ± 169; class 4, 789 ± 130; class 5, 478 ± 84). In contrast, a significant P loss occurred between classes 1 and 3 (0.05 ± 0.02 to 0.01 ± 0.01 mg g^{-1}), followed by an accumulation until class 5 (0.06 ± 0.01 mg g^{-1}). The N:P ratio increased significantly from living wood (9.2 ± 0.8) to intermediate (24.6 ± 5.4; class 2) and advanced decay classes (20.1 ± 1.8; class 5; ANOVA $F_{5,24} = 4.56$, $p = 0.0046$), though the variation during wood decay, i.e. excluding living trees, was not significant (Table 2).

3.4.2. Soil

Marked morphological variations were observed in the humus forms, which were classified as oligomull, dysmull, amphimull, hemimoder or dysmoder, according to Jabiol et al. (1995). Table 4 presents the chemical compositions of the humus forms representative of four wood decay classes (2–5). There were high levels of organic C (339–490 mg g^{-1}) in the organic layers. The proportions of N were also relevant and more than 10 mg g^{-1} in the O-layers, except for the (OLn-OLv) layer (class 4, 7.9 mg g^{-1}). The C:N ratio may reach high values (61.7 in the OLn-OLv layer in a hemimoder), but is around 20–30 in the O-layers.

4. Discussion

We have been able to identify some significant physical and chemical patterns in dead wood decomposition, in spite of the

Table 3
Density (in kg m^{-3}) and moisture (in % of dry mass) of *P. abies* sapwood and heartwood logs

	Living trees	Decay classes					ANOVA (classes 1–5)	
		1	2	3	4	5	*F*	*p*
(a) Density								
Sapwood	412(9.8/10)	423(13/16)	397(19/14)	389(11/14)	326(18/6)		4.604	0.01
Outer heartwood	n.a.	440(13/16)	400(18/14)	378(16/16)	312(13/8)	303(15/6)	10.5	<0.01
Inner heartwood	n.a.	447(23/5)	429(13/6)	377(32/5)	323(44/4)	307(23/5)	5.427	<0.01
F		0.615	0.526	0.176	0.136	0.027		
p		0.546	0.595	0.838	0.873	0.872		
(b) Moisture								
Sapwood	126 (3.8/10)	144 (11/16)	63 (17/14)	118(24/14)	129(32/6)		3.708	0.02
Outer heartwood	n.a.	63 (10/16)	43(7/14)	66 (11/16)	119(48/8)	251(49/6)	11.08	<0.01
Inner heartwood	n.a.	31 (4/5)	46 (15/6)	61(20/5)	196(71/4)	266(65/5)	6.75	<0.01
F		24.700	0.721	2.639	0.563	0.031		
p		<0.001	0.493	0.086	0.580	0.863		

Mean values with S.E. and sample number in brackets. Statistical tests were applied to decay classes 1–5 data. n.a.: not analysed.

Table 4
Soil profiles (description and chemical composition) relative to wood decay classes

Wood decay class	Humus form	Soil profile (layers)	Thickness (cm)	C (mg g^{-1})	N (mg g^{-1})	C:N	pH	Total P (mg g^{-1})
2	Hemimoder	OLn-OLv	1	n.d.	n.d.	n.d.	n.d.	n.d.
		OFm	2	456	15.1	30.1	n.d.	0.28
		OF	4	423	15.0	28.3	n.d.	0.33
		Aci	5	186	10.1	18.4	4.7	0.334
		Aci Sci	16	100	5.4	18.7	6.2	0.25
2	Dysmoder	OFm	0.5	441	12.5	35.2	n.d.	0.26
		OH	4	343	15.8	21.7	n.d.	0.41
3	Oligomull	OF	0.5	n.d.	n.d.	n.d.	n.d.	n.d.
		Aci	2.5	187	11.1	16.9	5.8	0.33
		Aci Sci	6	155	9.3	16.7	6.2	0.31
4	Hemimoder	OLn-OLv	1	490	7.9	61.7	n.d.	0.24
		OLv-OF	2	458	12.3	37.4	n.d.	0.27
		OFm	4	342	13.2	25.8	n.d.	0.45
		Aci	5	219	11.9	18.5	6.8	0.57
		Aci Sci Dca	16	190	n.d.	n.d.	7.4	0.56
		Scih Rca 1	15	181	10.0	18.1	7.4	0.53
		Scih Rca 2	24	148	8.5	17.4	7.5	0.54
4	Hemimoder	OFm	2	n.d.	n.d.	n.d.	n.d.	n.d.
		Aca	5	n.d.	n.d.	n.d.	n.d.	n.d.
		Aca Cca	10–43	247	13.2	18.7	7.2	0.56
4	Amphimull	OLn	0.5	n.d.	n.d.	n.d.	n.d.	n.d.
		OLv-OF	1	473	12.9	36.5	n.d.	0.38
		OFm	2–4	454	15.8	28.7	n.d.	0.41
		OFm Aci	3–5	351	17.9	19.7	5.6	0.59
		Aci	8–?	248	14.3	19.2	6.9	0.70
5	Dysmull	OF	1	n.d.	n.d.	n.d.	n.d.	n.d.
		A	2	141	8.3	17.0	6.0	0.34
		Aci Sci	2	121	7.7	15.6	6.9	0.35
		Aca Sca	5	126	7.2	17.4	7.2	0.40
5	Oligomull	OLv-OFm	1	339	10.3	32.8	n.d.	0.24
		OF	0.5	n.d.	n.d.	n.d.	n.d.	n.d.
		Aci	1.5	146	7.3	19.9	6.4	0.26
		Sci	n.d.	109	4.7	23.2	6.7	0.16

O: organic layer; L: fresh litter; F: fragmented litter; A: organo-mineral layer; S: layer of rock alteration; R: hard rock not fragmented; D: hard rock fragmented; n: young litter; v: old litter; m: presence of fungi; ci: calcium saturated; ca: calcareous. C: organic carbon; N: nitrogen; P: phosphorus. n.d.: not determined (too little material).

small sample size (five logs per decomposition class, i.e. a total of 25) and high between-tree variation.

4.1. Decay determination using Sylvatest

The Sylvatest-Duo® tool detected differences in log decay through the measurement of the propagation speed of ultrasonic waves. Above decay class 3, when logs were in an advanced state of decomposition, the waves could not, in most cases, traverse the porous wood and Sylvatest-Duo® then did not give any signal. This instrument is not helpful if it is used for longitudinal measurements or in wood in an advanced state of decay (classes 4 and 5). For classes 1–3, however, it enabled a more differentiated assessment of the decay state than visual classification only. First, it allows within-log decay to be described in some detail, since measurements can be applied at different log sections separately. Secondly, it is possible to calculate a percentage of tree decay by comparing the measured wave speed with a reference speed for intact trees, depending both on tree diameter and species. By doing this, the classification of decay becomes quantitative and thus less subjective than just a visual classification. Ultrasonic measurements are non-destructive, rapid to execute and can be applied in the field on entire logs, without collecting any wood samples. Since they correlate with average tree density and C content, they are an easy way to obtain some quantitative information on tree decay rapidly.

Our preliminary results are promising and we recommend more such investigations to develop reliable estimations of tree decay percentages. In particular, an inventory of reference speeds for intact trees of different species should be produced.

4.2. Changes in physical properties of wood with decay

We found the general trends over decay classes for water content and wood density were similar to those found in

previous studies in other regions. The density loss observed in our study (434–308 kg m^{-3}), however, was smaller than values reported for spruce *P. abies* in northern European forests (350–110 kg m^{-3} in Harmon et al., 2000; 410–140 kg m^{-3} in Naesset, 1999b). The reason for our higher density values for advanced decay classes may be in part methodological because, with our method, it was not possible to measure the density of wood with a completely powdery texture. We actually measured the density of the most compact remaining wood fragments in our classes 4 and 5 samples, and thus possibly overestimated it. In addition, loss of density over time does not fully account for the loss of biomass in a dead tree because it does not include the loss of volume due to fragmentation (e.g. Krankina and Harmon, 1995). Both reasons mentioned, however, do not fully explain the differences in density loss when compared to Harmon et al. (2000) or Naesset (1999a).

As in previous studies, moisture was found to significantly increase during wood decay. In our study this was from 94% to 258% of dry weight. In the case of *Pinus radiata* the water content varied from 61% to 256% during decomposition (Mackensen and Bauhus, 2003). Sollins et al. (1987) reported changes of 90–335% for western hemlock *Tsuga heterophylla*, and 65–356% for Douglas-fir *Pseudotsuga menziesii*. We observed a growing variability in moisture during log decay, possibly because of the increasing influence of varying factors on logs with ground contact (moisture of the forest soil, ground surface, microtopography, etc.).

Water content varied considerably, according to position in the log (i.e. sapwood, outer or inner heartwood), reflecting high within-tree heterogeneity. A significant loss of moisture in the sapwood occurred between classes 1 and 2, when the bark starts to become detached. Between-tree heterogeneity was also high (large standard errors of the mean values). However, the water contents of samples in the same position within a tree (e.g. sapwood) were homogeneous (half of the samples had coefficients of variation smaller than 10%). Such subtle differences cannot be detected by visual classification systems.

4.3. Changes in chemical properties of wood with decay

The organic C concentrations (mg g^{-1}) of wood did not vary significantly throughout the decay process, remaining between 48% and 50%. They are similar to those measured for other coniferous species (Ganjegunte et al., 2004; Lambert et al., 1980; Sollins et al., 1987). In contrast, the C content per volume unit steadily decreased during decay, rising the complex question of C fluxes, yet beyond the scope of this paper. Lignin concentrations increased from 310 to 410 mg g^{-1} during wood decay, whereas cellulose concentrations decreased from 474 to 344 mg g^{-1}. Preferential degradation of carbohydrates (by brown rot fungi) with a concomitant increase in the concentration of aromatic compounds in CWD has been reported in many studies (e.g. Lambert et al., 1980; Ganjegunte et al., 2004). The relatively slower degradation of lignin compared to cellulose indicates that lignin can act as an important long-term source of soil organic carbon (Ganjegunte et al., 2004).

The N concentration of decaying wood is of special interest because of its key role in the function of terrestrial ecosystems. We observed a three-fold increase in N concentration (Table 2) and a net N accumulation (Fig. 3b) during decay, which is similar to the finding of other studies (Krankina et al., 1999; Lambert et al., 1980; Sollins et al., 1987). A number of factors may have contributed to the N accumulation between living trees and decay 5 class logs: (i) as the material became increasingly fragmented, it also became more accessible to microflora (Sollins et al., 1987); (ii) fungi probably retained the N of the original substrate in the shrinking wood mass through immobilization; (iii) fungi may have translocated N from the at least 10-times N-richer forest soil into C-rich wood via their mycelia; (iv) the microbial biomass increased with advancing decay, and bacterial N-fixation may have occurred within the rotting logs (Lambert et al., 1980). The N concentrations in the wood in our study were low (0.41–1.26 mg g^{-1}) in comparison with those in other studies of conifer decay (1.7–5.4 mg g^{-1} *P. abies* in Krankina et al., 1999; 1.5–8.6 mg g^{-1} *Abies balsamea* in Lambert et al., 1980; 9–24 mg g^{-1} *Pseudotsuga menziesii* in Sollins et al., 1987). In Krankina et al. (1999), however, samples for chemical analyses, unlike in our study, also contained bark, which has been shown to be much more nutrient-rich than wood. Their initial nutrient concentration values are thus relatively higher than values from studies where the bark is separated from wood. It is possible that the soils in our study site contained less N (13.5 mg g^{-1} on average in the O-layers) than soils in the studies mentioned above (e.g. 32.5 mg g^{-1} in N-rich humus in Lambert et al., 1980), and the N availability for living trees may, therefore, be limited. Both the N and P levels measured in our soil samples were similar to those observed by Dominguez et al. (2001) in forest soils in the Jura Mountains.

P amounts decreased until class 3 and then rose until above those in living trees. A similar trend has been reported for *Pseudotsuga menziesii* (Sollins et al., 1987), whereas in other studies the P contents were found to remain the same during the period of decay (e.g. Ganjegunte et al., 2004). Like for N, P concentrations in wood (0.01–0.06 mg g^{-1}) were lower than in other conifer decay studies (0.072–0.365 mg g^{-1} for *P. abies* in Krankina et al., 1999; 0.061–0.428 mg g^{-1} for *Abies balsamea* in Lambert et al., 1980; 0.04–0.11 mg g^{-1} for *Pseudotsuga menziesii* in Sollins et al., 1987). Phosphorus concentration in the O-layers (0.35 ± 0.03 mg g^{-1}) was higher than it was in class 5 logs (0.06 ± 0.01 mg g^{-1}), which means there is an opportunity for P to move from the soil into the wood. We believe that organo-mineral layers with a high pH (around 7.5) as observed in this study may strongly fix P to the mineral matrix. Stumm and Morgan (1981) demonstrated a P fixation on calcic phosphates at pH 7–8. Consequently, P is not readily available for vegetation to take up. Only a small proportion of P could be absorbed by fungi which are known to be great transporters of P, especially mycorrhizae (Lee and Pankhurst, 1992; Miller et al., 1995). As a consequence, in our study, the higher P amounts recovered in decay class 5 trees may be due to an active transfer from the soil into the wood via fungi hyphae, as for N.

Because both N and P often are limits to biological activity, the relative accumulation rates of both elements are of interest. For both N and P, the possible transfer of nutrients may help fungi to develop and grow, which would, in turn, enhance wood decomposition. The N:P ratio in wood for class 1 was 11.5 (9.2 for living trees). This went up to 26.7 for class 3 and then converged again, ending up, towards 20.1 for class 5. Convergence towards an N:P ratio of 20 seems to be common during log decay (Sollins et al., 1987; Laiho and Prescott, 2004).

4.4. Site-specific humus forms and decay patterns

All the soil types described in our study site belong to the same unit classification (humiferous Brunisol, i.e. eutric Cambisol). However, we noticed an important variation in the morphology of their humus forms: five types of well-drained humus forms were identified. Among the different factors involved in this variation in morphology, neither the underlayers' chemical composition (Aci layer) nor variation in the decay of the CWD lying on the corresponding humus layers can explain it. We hypothesize that the variations in humus forms in our site could result from local microclimatic variations (humidity due to microtopography, for example) that influence the soil biological activity. However, larger and more systematic sampling would be needed to confirm this.

The morphology of the humus forms identified means that the breakdown of the litter and the transformation and incorporation of organic matter are quite slow. Various factors (which do not exclude each other) could explain the slow decay in organic matter, for instance the soil parameters (texture, pH), the climatic conditions (low average temperatures, high precipitation, hydric stress, persistence of snow cover) or the litter quality.

P. abies CWD in our study site had very low N and P concentrations: i.e. about four to five times lower than *P. abies* in Russian boreal forests (see Krankina et al., 1999). Species low in N decay slower than those high in N (Harmon et al., 1986), which may possibly also affect decay rates amongst different tree populations within the same species. The snag mineralization rates of spruce in the Jura Mountains are probably rather low. Firstly, we observed only a small loss in density during the decay process. It is possible that the logs, which were in an advanced state of decay (classes 4 and 5), were exposed to physical fragmentation (e.g. by freezing and unfreezing) much more than to biological decay by microbes. Secondly, the N and P levels in our study were low. Their changes in level indicate a time lag for mineralization since there was a net P loss and no N accumulation until class 3 (Fig. 3b). From class 3 upwards, the concentrations of both nutrients increased, with a concomitant decrease in cellulose concentration.

Like the humus forms discussed above, the site-specific CWD decay patterns we found may well be due to local climatic conditions, which could explain some of the differences from the patterns noted in other studies. Long winters, cool summers, and a short vegetation period are likely to slow down the soil biological activity necessary for wood decay. Some of the processes contribute to nutrient immobilization and input, such as growth of fungi and bacteria, root colonization and atmospheric N fixation (Krankina et al., 1999).

5. Conclusion

We assessed changes in physical and chemical variables during the log decay of spruce *P. abies* trees in the Swiss Jura Mountains. The Sylvatest-Duo® tool, based on non-destructive ultra-sonic wave measurements, which had previously been used to evaluate the mechanical properties of living trees, proved helpful in characterising wood in decay stages 1–3. The propagation speed of ultrasonic waves was directly proportional to the average tree density and inversely proportional to the C content. These preliminary results suggest that this technique is potentially useful for further studies of wood decay.

The general trends in log decay we found were comparable with patterns reported for other conifer tree species and for *P. abies* at different latitudes and longitudes. However, some characteristics, such as low N and P contents, were site specific and differed from previous data for *P. abies* in other regions. Our results did not show any correlation between the state of wood decay and the humus form. We recommend establishing long-term experiments in Central European forests that will allow a controlled investigation of the different factors that may influence CWD decomposition, such as edaphic and climatic conditions. A better knowledge of the functional roles and dynamics of the CWD in forest ecosystems would help us to improve our understanding of terrestrial nutrient cycles and carbon sequestration. To this end, biological processes and the role of soil fauna (earthworms and microarthropods) and soil microorganisms, especially fungi, still need to be investigated.

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