

A chronosequence of wood decomposition in the boreal forests of Russia

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Abstract: Coarse woody debris (CWD), represented by logs and snags >10 cm in diameter and >1 m in length, was sampled at eight sites in Russian boreal forests to determine the specific density of decay classes and decomposition rates. Tree species sampled included *Abies siberica* Ledeb., *Betula pendula* Roth., *Betula costata* Trautv., *Larix siberica* Ledeb., *Larix dahurica* Turcz., *Picea abies* (L.) Karst., *Picea obovata* Ledeb., *Picea ajanensis* Fisch., *Pinus koraiensis* Sieb. et Zucc., *Pinus siberica* Ledeb., *Pinus sylvestris* L., and *Populus tremula* L. The mean densities for decay classes 1 through 5 ranged from 0.516 to 0.084 g·cm⁻³, respectively. Annual decomposition rates varied among the species, and for logs, decomposition rates ranged from 4.2 to 7.8% for *B. pendula*, 2.6 to 4.9% for *Picea* spp., 2.7 to 4.4% for *Pinus sylvestris*, 1.5 to 3.1% for *Larix* spp., and 1.5 to 1.9% for *Pinus koraiensis* and *Pinus siberica*. Logs decomposed faster than snags. Among the sites examined, temperature and precipitation did not correlate with decomposition rates, which is consistent with other studies in the boreal region. Globally, a positive correlation between decomposition and mean annual temperatures was found, with decay-resistant trees less responsive than those with low decay resistance.

Résumé : Les débris ligneux grossiers, c'est-à-dire les billes et les chicots >10 cm de diamètre et >1 m de longueur, ont été échantillonnés dans huit stations situées dans la forêt boréale russe pour déterminer la densité spécifique par classe de décomposition ainsi que le taux de décomposition. Les espèces d'arbres échantillonnées incluent : *Abies siberica* Ledeb., *Betula pendula* Roth., *Betula costata* Trautv., *Larix siberica* Ledeb., *Larix dahurica* Turcz., *Picea abies* (L.) Karst., *Picea obovata* Ledeb., *Picea ajanensis* Fisch., *Pinus koraiensis* Sieb. & Zucc., *Pinus siberica* Ledeb., *Pinus sylvestris* L. et *Populus tremula* L. La densité spécifique moyenne pour les classes 1 à 5 varie respectivement de 0,516 à 0,084 g·cm⁻³. Le taux annuel de décomposition varie selon l'espèce et, dans le cas des billes, varie de 4,2 à 7,8 % pour *B. pendula*, de 2,6 à 4,9 % pour *Picea* spp., de 2,7 à 4,4 % pour *Pinus sylvestris*, de 1,5 à 3,1 % pour *Larix* spp. et de 1,5 à 1,9 % pour *Pinus koraiensis* et *Pinus siberica*. Les billes se décomposent plus rapidement que les chicots. Dans les stations étudiées, la température et la précipitation ne sont pas corrélées avec le taux de décomposition, ce qui corrobore les autres études menées dans les régions boréales. Globalement, une corrélation positive a été observée entre la décomposition et la température annuelle moyenne, les arbres résistants à la carie étant moins influencés que les arbres avec une moins grande résistance à la carie.

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Introduction

Forests play a key role in the global carbon cycle (Dixon et al. 1994). The degree to which forest ecosystems serve as a carbon sink or source is still unknown, in part, because of the complexity of the ecological processes taking place in these ecosystems and our inadequate understanding of them. Coarse woody debris (CWD) is a major source of uncertainty. While live wood inventories are common around the globe, the dead wood pool is usually overlooked by large-scale inventories (Kukuev et al. 1997; Harmon et al. 2001; Krankina et al. 2002); it thus represents a carbon pool of an unknown size and dynamics. The decomposition of dead wood is among the major controls of carbon (C) retention in forest ecosystems. Narrowing the uncertainty in dead wood decomposition rates can significantly improve our under-

standing of C dynamics in forest biomes. The CWD pool is controlled by the ecological processes of disturbance, decomposition, and succession (Harmon et al. 1987), and examination of these processes is crucial for understanding how the CWD pool and forest ecosystems in general contribute to the global carbon cycle.

This study is part of a larger scientific effort assessing C accumulation, storage, and release by coarse woody detritus in the forests of Russia. The results of regional assessment of CWD stores were published previously (Krankina et al. 2002). To understand current and future dynamics of the woody detritus pool, one needs to know not only the stores but also the turnover or decomposition rates. Decomposition is a major link in C cycling in forest ecosystems; yet it is poorly studied, especially compared with photosynthesis and forest growth. Decomposition of dead wood is only grossly similar to fine-litter decomposition, making it difficult to extrapolate from the latter form of detritus. While our knowledge of woody detritus stores in Russia has improved (Krankina et al. 2002), information on the decomposition rates is still very limited.

This study analyzes the decay-class system required to estimate CWD stores, examines the patterns and dynamics of CWD decomposition using a chronosequence approach

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Fig. 1. Study sites and tree species sampled: 1, *Abies siberica*; 2, *Betula costata*; 3, *Betula pendula*; 4, *Larix* spp.; 5, *Pinus sylvestris*; 6, *Pinus siberica* – *Pinus koraiensis*; 7, *Populus tremula*; 8, *Picea* spp.



(Harmon et al. 1987; Harmon and Sexton 1996), and explores environmental controls on decomposition rates of the major tree species in the Russian boreal forest. We also compare our results with those of other studies and put the decomposition rates we found in a global context.

Methods

This study had two interrelated parts: (i) calculation of decay-class specific density of CWD for the common tree species in eight forest regions of Russia (Fig. 1), and (ii) estimation of decomposition rates in a subset of four regions (St. Petersburg, Krasnoyarsk, Irkutsk, and Khabarovsk). For logistical reasons, the selection of regions and locations for sampling was driven by inventory plans of regional forest inventory enterprises. Common tree species were identified in each region using the regional summaries of forest inventory data (State Committee for Forestry Publishers 1990). A set of climatic variables was used to explain regional differences in decomposition rates; thus only the four regions included in decomposition study were included in Table 1 and are briefly described below.

Data from the St. Petersburg region of northwestern Russia were collected during the field seasons of 1993 and 1996 (Harmon et al. 2000). The study site is located within 100 km southeast of St. Petersburg. The climate of the region is cool maritime (Table 1) with cool, wet summers and

long, cold winters (Krankina et al. 1999). *Picea abies* (L.) Karst. and *Pinus sylvestris* L. are the most common tree species in the region.

Data from the Krasnoyarsk region were collected during the 1997 field season in the Chunoyarskii Forest Management Enterprise (FME) located in the northeast part of the region. The FME is within the Angara province of the southern taiga and is dominated by *Larix siberica* Ledeb. – *Pinus sylvestris* forests. The climate is moderately cold and continental (Table 1).

Data from the Irkutsk region were collected during the 1998 field season in the Ol'khonskii and Bayandaikskii FMEs, located along the northwest bank of Lake Baikal and approximately 120 km west of Lake Baikal, respectively. The climate in this region is severe continental and permafrost is common (Table 1). Forests in the south are primarily composed of *Pinus sylvestris*. At higher elevations *Larix siberica*, *Pinus siberica* Ledeb., and *Picea obovata* Ledeb. are common and are mixed with *Abies siberica* Ledeb.

The Khabarovsk site, located in the Khorskii FME, was sampled during the 1999 field season. The eastern mountainous part includes the Sikhote-Alin Range and occupies 90% of the FME's territory. The western lowland portion of the FME is in the southwestern part of the Amur Lowland. A continental climate is prevalent with a dry, cold winter (Table 1). Seventy-four to 82% of the precipitation occurs during the warm part of the year, with the mountainous parts

Table 1. Study regions where chronosequences of coarse woody debris decomposition were developed.

Region	Coordinates	Mean annual temperature (°C)	Annual precipitation (mm)	Degree-days*	Sum of precipitation (mm) [†]
St. Petersburg	59°N, 31–32°E	3.4	708	1152.3	363
Krasnoyarsk	56°N, 93°E	–3.2	361	1195.3	241
Irkutsk	52°N, 104°E	–0.6	216	1129.1	182
Khabarovsk	49°N, 140°E	–1.9	909	1706.6	741

*Annual sum of temperatures >5°C.

†For days with temperatures >5°C.

getting considerably more precipitation than the lowlands. Favorable conditions for plant growth promote the growth of a wide range of plant species, including *Pinus koraiensis* Sieb. et Zucc., *Picea obovata*, *A. siberica*, and a diverse hardwood tree flora (Usenko 1969).

Density sampling

In each study region we located sample snags (standing dead) or logs (dead laying on the ground) to cover the full range of decomposition stages in selected major tree species. Only logs and snags with a length-to-diameter ratio of >10 were sampled to reduce the effects of elevated end decay (Harmon and Sexton 1996). The selected CWD pieces were categorized into one of five decay classes based on visual characteristics linked to the degree of decomposition: the presence of leaves, twigs, branches, or bark cover on branches and bole; sloughing of wood; collapsing and spreading of log (indicating the transition from round to elliptic form); friability of wood; and mobility of branch stubs (Triska and Cromack 1980; Graham and Cromack 1982; Sollins 1982; Harmon and Sexton 1996). Biological indicators of decomposition such as moss cover, presence of fungal fruiting bodies, and presence of insect galleries were also noted. Log dimensions, including length, base and top diameters, and current diameter at breast height (DBH), were recorded.

Each selected log or snag was divided into four sections of similar length. If the sampled log was short (e.g., in more advanced decay classes), it was divided into only two or three sections. The diameter at both ends of each section was recorded with a precision of 1 cm, and the section length and total tree length were recorded with a precision of 10 cm. From the end of each section, a disk (cross-section sample) was cut with a chainsaw for use in determining the density of wood and bark. The outermost diameter, longitudinal thickness, radial depth of rot, and radial thickness of bark were measured at four points on each disk to the nearest 0.1 cm, and averages for each disk were calculated. Bark was separated from wood, and the wet mass of each tissue was determined. Wedge-shaped bark and wood subsamples (~50 g) were taken from each disk, weighed, placed in cloth bags, and air dried to stop decomposition. All wet sample masses were measured in Russia on a portable electronic scale to the nearest 0.1 g. Dry masses of subsamples were determined in the U.S. laboratory after oven drying at 55°C to a constant mass (precision 0.01 g). The dry mass of wood and bark for each disk was calculated from the wet masses of these tissues and the ratio of dry-to-wet mass determined

for the subsample. Then the density of the disk was calculated as ratio of its dry mass to volume.

The current density of each CWD piece was calculated as an average of disk densities weighed by the section volumes to give greater weight to disks from the lower part of each log or snag. First, the volumes of wood and bark were calculated for each section. The total volume of each section was computed as the sum of its bark and wood volumes, and the total current volume of a piece was calculated as the sum of section volumes. Then current masses of wood and bark in each section were calculated by multiplying their volume in each section by the corresponding tissue density (usually from the upper disk in a section, except for the top section). The total mass of each section was computed as the sum of its bark and wood masses. The total current mass of an entire piece of CWD was calculated as the sum of section masses. Finally, the mean CWD density for each log and snag was computed as a ratio of the total current mass of a piece to its total current volume. Using this method, density was calculated for a total of 970 logs and snags sampled over the course of 5 years (1993 and 1996–1999) (Table 2).

Chronosequence of decomposition

A chronosequence approach was used to estimate CWD decomposition dynamics (Harmon and Sexton 1996). While the same procedure was used to collect and process samples for decay-class density and decomposition rate estimation, the latter required, in addition, an estimate of time since death (i.e., time elapsed from the date of tree death to the date of tree sampling) and information on mass loss via fragmentation (Harmon et al. 2000). We were able to determine the time since death for 693 logs and snags. The dating of logs relied on local records of catastrophic events, data from permanent growth and yield plots, the age of young stands regenerating after a disturbance, the age of trees growing on logs, the age of fire scars on living trees, and the age of scars left by fallen trees.

To account for fragmentation and volume losses, we reconstructed the original tree volume from bole length and DBH either measured directly or after reconstruction in the field. Several methods were used for the latter purpose. For pieces missing bark at breast height, DBH was adjusted using the bark/wood thickness ratios from other parts of the bole. For boles with missing bark and some wood fragmentation, DBH without bark, missing bark thickness, and radial thickness of missing wood were estimated (Harmon and Sexton 1996). For example, if the DBH location of a piece was severely damaged, diameter at the tree base was ad-

Table 2. Mean densities ($\text{g}\cdot\text{cm}^{-3}$) (with SE in parentheses) and sample sizes of coarse woody debris by decay class for major tree species of Russia (logs and snags combined).

Species	Decay class				
	1	2	3	4	5
<i>Abies siberica</i>	0.285 (0.016), $n = 9$	0.320 (0.012), $n = 9$	0.257 (0.024), $n = 8$	0.204 (0.021), $n = 10$	0.173 (0.025), $n = 7$
<i>Betula costata</i>	0.516 (0.007), $n = 13$	0.333 (0.037), $n = 3$	0.194 (0.012), $n = 10$	0.120 (na), $n = 2$	0.084 (na), $n = 2$
<i>Betula pendula</i>	0.474 (0.005), $n = 46$	0.370 (0.009), $n = 48$	0.237 (0.014), $n = 34$	0.148 (0.012), $n = 43$	0.108 (0.010), $n = 29$
<i>Larix</i> spp.	0.455 (0.007), $n = 43$	0.424 (0.009), $n = 45$	0.368 (0.013), $n = 41$	0.162 (0.008), $n = 25$	0.109 (0.008), $n = 20$
<i>Pinus sylvestris</i>	0.362 (0.005), $n = 43$	0.338 (0.006), $n = 50$	0.269 (0.009), $n = 51$	0.172 (0.012), $n = 31$	0.122 (0.006), $n = 29$
<i>Pinus siberica</i> – <i>Pinus koraiensis</i>	0.336 (0.006), $n = 29$	0.322 (0.006), $n = 30$	0.252 (0.011), $n = 25$	0.146 (0.008), $n = 12$	0.109 (0.007), $n = 10$
<i>Populus tremula</i>	0.339 (0.017), $n = 9$	0.287 (0.019), $n = 13$	0.247 (0.023), $n = 12$	0.135 (0.011), $n = 3$	na
<i>Picea</i> spp.	0.358 (0.006), $n = 42$	0.335 (0.010), $n = 39$	0.236 (0.010), $n = 39$	0.139 (0.010), $n = 26$	0.108 (0.006), $n = 14$

justed using taper equations. The original volume was determined using local volume tables based on the reconstructed DBH and tree height (Tret'yakov et al. 1952; USSR Federal Forestry Committee 1961; Koryakin 1990).

The current mass of each log or snag was compared with its estimated initial mass to determine decomposition rates. The original total mass was calculated by one of two methods. When data for the density of undecayed wood and bark were available for given species and region (Borovikov and Ugolev 1989), they were used as the initial density, and the total mass was determined as the product of the initial total tree volume and this undecayed density. In most cases, however, the original total mass was determined by using the initial total tree volume and density of wood and bark measured on two freshly cut live trees. Then the percent mass remaining was calculated for each log and snag.

Statistical analysis

All statistical analyses were performed on the level of the entire CWD piece. The density of the entire log or snag was used to calculate mean CWD densities by decay class. For multivariate analysis, the visual characteristics of each log or snag were analyzed, and for decomposition rate constants of mass loss over time, the entire log or snag was analyzed.

The raw data set for the analysis of decay-class specific density included a total of 970 observations representing 8 regions, 14 species, and 5 decay classes defined by fragmentation and biotic indicators, and 2 positions reflecting the physical situation of a dead tree: snag or log. Sample sizes varied among regions, species, decay classes, and positions, leading to an unbalanced design. To better balance the sample sizes, Moscow and Nizhnii Novgorod were combined into a single central European region, and Novosibirsk and Tomsk were combined into a single western Siberian region, while species of the same genera were combined into *Larix* spp. and *Picea* spp. *Pinus siberica* and *Pinus koraiensis* were combined into a group of Russian white pines. The observations for *Quercus* spp. were removed because of the small sample size ($n = 7$). The resulting data set had total of 963 observations, organized by 6 regions, 8 species, 5 decay classes, and 2 positions. These data were plotted and examined for outliers. Nine such observations were detected and removed to create a final data set with 954 observations.

To determine which variables (decay class, species, region, and position) had a significant effect on density ($\alpha = 0.05$), a stepwise regression (GLM procedure) was used (SAS Institute Inc. 1990; Ramsey and Schafer 1997). The CLASS statement was applied to the categorical variables region, species, and position (log vs. snag).

Comparisons of mean CWD density among all decay classes within each species group, mean CWD density among species within each decay class, and mean CWD density among the regions within each species, decay class, and position were performed using the GLM procedure with LSMEANS statement for uneven sample sizes and the Tukey–Kramer p value adjustment for multiple comparisons at $\alpha = 0.05$ (SAS Institute Inc. 1990; Ramsey and Schafer 1997). Further, we compared the estimates of mean CWD density between logs and snags for each species within each decay class and region using a t test.

Multivariate analysis of visual characteristics

Multivariate analysis (ordination) was used to examine the continuous changes in CWD visual characteristics occurring as a result of decomposition. For the purpose of this analysis, data were represented in two matrices. The so-called “qualitative” matrix was 970 rows by 21 columns with each row representing a sampling unit (log or snag of a particular species and decay class) and each column representing the visual presence–absence of a CWD characteristic. The “quantitative” matrix was 970 rows by 5 columns in size with each row representing a sampling unit and each column representing species, age, decay class, density, and percent bark cover. The latter matrix contained a mix of categorical variables (decay classes and log or snag tree species) that were used for overlays on the ordination, as well as quantitative variables (percent bark cover on bole, time since death, and density) that were used for correlations with ordination axes. The only transformation applied to this data set was dividing the bark cover in the qualitative matrix by 100.

PC-ORD (McCune and Mefford 1999) outlier analysis was used to check for potential outliers. Thirty such observations were found that were more than two standard deviations from the centroid, but only nine of these were removed as they had incomplete or unreliable records of CWD indicators. The final data set had 961 observations.

Nonmetric multidimensional scaling (NMS) analysis with rotation of the axes was used as the ordination method. We decided to use NMS, as it performs better than other ordination methods with nonlinear distributions and presence–absence data. Rotation of the axes increased the interpretation of the strongest gradient and more clearly revealed patterns in the data distribution with decay class and species overlays from the quantitative matrix.

Numerous preliminary runs indicated that the so-called “quick and dirty autopilot” mode within the “quick and dirty” part of the PC-ORD program was appropriate for our analysis. The PC-ORD settings for this mode included a maximum number of 75 iterations, an instability criterion of 0.001, three axes at the start, five real runs, and 20 randomized (Monte Carlo) runs. To represent similarity, the Sorensen distance measure was used. The final NMS run was set to use two dimensions, no step-down in dimensionality, one real run, and no Monte Carlo test (randomized runs).

Decomposition rate constants

The data set for the analysis of decomposition rate constants included a total of 684 observations, organized by 4 regions, 10 species, and 2 positions. A regression of percent mass remaining over time since death was run for each species, region, and position. Then the plots of residual versus predicted values were examined for outliers. The two potential outliers found were snags that had low wood density at an early stage of decomposition resulting from extensive heart rot probably present when the trees were still alive. These two observations were removed, thus leaving the final data set with 682 observations.

A stepwise regression (GLM procedure) on untransformed data was run to determine which variables had a significant ($\alpha = 0.05$) effect on percent mass remaining. The CLASS

statement was applied to the categorical variables region, species, and position.

Then, the coefficients of the negative exponential equation (Olson 1963) describing the decomposition process for the sampled species in each region were determined:

$$Y_t = Y_0 e^{-kt}$$

where Y_t is the percent dry mass remaining at time t (years), Y_0 is the initial dry mass (%), and k is the decomposition rate constant (year^{-1}).

Linear regression (PROC REG procedure) was run after percent mass remaining (Y_t) was log transformed. For comparison with other studies a second regression was used that forced the Y intercept through 100%.

The resulting regression equations were examined for differences using the “comparison of regression lines” procedure, regressing the percent dry mass remaining by regions (CLASS statement was applied to region variable) over time since death. The significance of differences was determined at $\alpha = 0.05$. A similar procedure was applied to the comparison of decomposition rates of logs and snags. Finally, we identified species that showed a pattern of decomposition that departed from the single-exponential curve (*Betula costata* Trautv., *Picea ajanensis* Fisch., and *Pinus koraiensis*). For these species the decomposition process was divided into three phases based on time since death and percent mass loss. Then, we fitted a simple-exponential regression for each phase of each species and determined the regression coefficients.

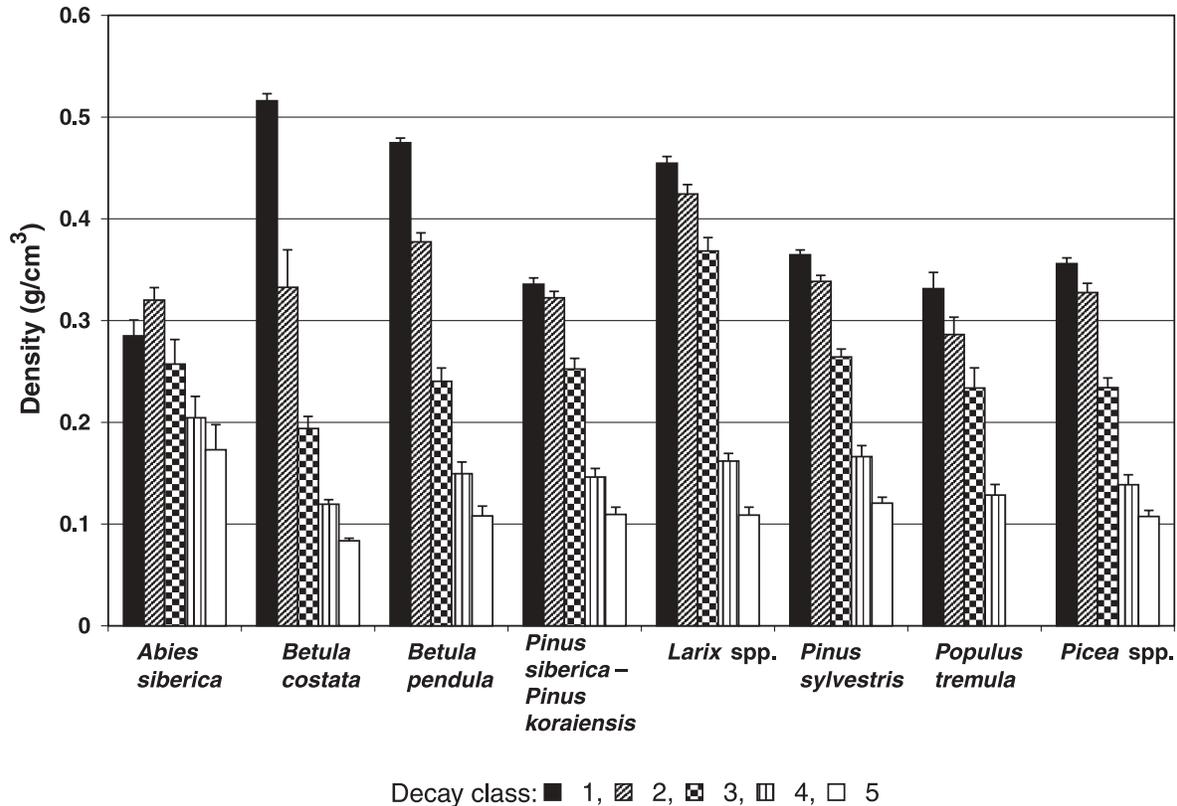
To determine the effect of climatic characteristics on decomposition rates, we examined the relationship between decomposition rates and mean annual temperatures and precipitation. We also examined the correlation between decomposition rates and the annual sum of daily air temperatures above 5°C (degree-days), as well as the correlation between decomposition rates and amount of precipitation over the time period with the temperatures above 5°C.

Results

Decay-class specific density

A decrease in mean CWD density from decay class 1 to decay class 5 was observed in all species except *A. siberica*, which had a slight increase from decay class 1 to decay class 2. Most species showed little change in mean CWD density between decay classes 1 and 2, the most change among 2, 3, and 4, and less between 4 and 5 (Fig. 2). In addition, species became more similar in density as decay class increased (Fig. 2, Table 2). All of the independent variables (decay class, species, position, region), including most of their interactions, had significant effects on density ($p = 0.0001$ to 0.0068). As expected, decay class explained the most variation in density (68.0%). Species was the next most important factor explaining an additional 6.1% of the variation, and the interaction term (decay class \times species) explained an additional 7.1% of the variation, indicating that differences among decay classes varied from species to species. Thus, decay class, species, and their interaction together explained 81.2% of the variation associated with CWD density. In all species, the standard deviations of density increased with ad-

Fig. 2. Mean specific density (with standard error bars) of coarse woody debris by species and decay class.



vancing decomposition, reached maximum in decay class 3, and then declined towards decay class 5.

The comparison of decay classes within each species indicated that there was an overlap of adjacent decay classes especially for decay classes 1 and 2 and for decay classes 4 and 5 (Fig. 2). The comparison of species within each decay class showed that the differences in CWD density observed among species in early decay classes decreased as the decomposition process progressed from decay class 1 to decay class 5, with no statistically significant differences in estimates of mean CWD density observed among species as early as decay class 4 (Fig. 2).

Although position (snag vs. log) and region explained a small part of variation in CWD density (1.1 and 0.9%, respectively), p values for these variables indicated that their effect on density was still significant ($p = 0.0001$). Therefore, we compared (i) logs and snags within each decay class, species, and region, and (ii) regions within each decay class, species, and position. This indicated that mean CWD density of logs and snags in decay class 1 does not differ for most species or regions. *Betula* spp. did not show any difference in mean CWD density between logs and snags for any decay class or region, while conifers such as *Larix* spp., *Picea* spp., and *Pinus siberica - Pinus koraiensis* exhibited differences in decay classes 2 and 3. There were no significant differences among the estimates of mean density of CWD sampled in different regions.

Multivariate analysis of CWD visual characteristics

Scree-plot and the Monte Carlo stress results indicated that a two-dimensional NMS solution was the most appro-

priate for these data. An axes rotation of one degree resulted in the first axis having the highest coefficient of determination (r^2), explaining 87.8% of the variance in the data, while second axis explained only 12.2%. This axis rotation also led to an increased correlation between the variables from the qualitative matrix and scores on the first ordination axis (Table 3). Variables associated with early stages of decomposition (bark on bole, bark on branches, branches, and twigs) had lower negative scores, whereas variables associated with late stages of decomposition (heartwood friable, sapwood sloughing, and sapwood friable) had higher positive axis scores. Very low negative values indicate strong negative correlation, while high positive values indicate strong positive correlation, and values close to zero indicate little correlation with the ordination axes. Variables from the quantitative matrix had a strong correlation with the first ordination axis, with density and percent bark cover having negative correlation coefficients of -0.754 and -0.648 , respectively, which decreased as scores on the first ordination axis increased. Time since death was positively correlated with axis 1 ($r = 0.528$), having higher scores on the ordination axis 1 with older logs and snags. These correlations, as well as an overlay of variables from the quantitative matrix on the qualitative matrix with decay class as a grouping variable (Fig. 3), all support the idea that the first ordination axis is a decomposition gradient. The distribution of the observations in the ordination shows intermixing of decay class 1 and 2 and decay class 4 and 5 observations.

There were no significant differences among five best-represented species in terms of the variables correlated with the scores on ordination axis one (Table 4). However, corre-

Table 3. Variables in the approximate sequence of their appearance on the ordination axes, and correlation coefficients (r) between them and scores on the ordination axes.

Axis 1		Axis 2	
Variable*	r	Variable*	r
BARKBOLE	-0.746	BARKBR	-0.312
BARKBR	-0.733	TWIGS	-0.299
BRANCHES	-0.716	NEEDLES	-0.261
TWIGS	-0.700	BRANCHES	-0.215
BCOVER	-0.648	SCATTER	-0.177
NEEDLES	-0.459	BCOVER	-0.172
BEETLES	-0.393	COLLAPSE	-0.138
WOODBORER	-0.129	HWFRIAB	-0.082
CONKS	-0.109	STUBSMOV	-0.065
LICHENS	0.073	BROWNROT	-0.028
ANTS	0.115	BARKBOLE	-0.018
CASEHARD	0.211	CASEHARD	-0.01
WHITEROT	0.464	MOSS	0.073
STUBSMOV	0.623	LICHENS	0.078
SCATTER	0.647	SAPFRIAB	0.118
MOSS	0.659	ANTS	0.127
BROWNROT	0.697	CONKS	0.159
COLLAPSE	0.718	SAPSLOUG	0.159
HWFRIAB	0.743	WHITEROT	0.261
SAPSLOUG	0.763	BEETLES	0.346
SAPFRIAB	0.858	WOODBORER	0.381

*ANTS, presence-absence of carpenter ants; BARKBOLE, presence-absence of bark on boles of logs and snags; BARKBR, presence-absence of bark on branches; BCOVER, percent bark cover on boles of logs and snags; BEETLES, presence of bark beetles or their galleries; BRANCHES, presence-absence of branches; BROWNROT, presence-absence of brown rot in the log or snag tissues; CASEHARD, presence-absence of a hard wooden shell on decayed logs or snags; COLLAPSE, indicated whether or not log could support its own weight; CONKS, presence-absence of conks; HWFRIAB, presence-absence of friable heartwood; LICHENS, presence-absence of lichens on the surface of logs or snags; MOSS, presence-absence of moss on the surface of logs or snags; NEEDLES, presence-absence of needles or leaves; SAPFRIAB, presence-absence of friable sapwood; SAPSLOUG, indicated whether or not process of sapwood sloughing takes place; SCATTER, indicated whether or not logs had an elliptical cross section; STUBSMOV, indicated whether logs were rotten enough so the branch stubs could be moved; TWIGS, presence-absence of twigs; WHITEROT, presence-absence of white rot in the log or snag tissues; WOODBORER, presence-absence of wood borers or their galleries.

lation coefficients of birch bark cover (-0.257) and bark on bole (-0.200) (Table 4) were low and indicate little change in birch bark presence on bole and percent bark cover over the course of decomposition. This contrasts with the coniferous species, which have a high correlation of these variables with first ordination axis, with correlation coefficients ranging from -0.635 to -0.801 and from -0.724 to -0.854 for bark cover and bark on bole, respectively.

Decomposition rate constants

Decomposition rate constants, based on percent mass remaining, ranged from 0.015 to 0.078 year⁻¹ for logs and

from 0.077 to -0.020 year⁻¹ for snags (Table 5). All of the independent variables examined (time since death, position, and region), including some of their interactions, had a significant effect on percent mass remaining ($p = 0.0001$ to 0.0045). As expected, time since death explained the most variation in percent mass remaining (50.3%). Position was the next most important factor, explaining an additional 8.6% of the variation. In general, the decomposition rates of logs were higher than those of snags. Species explained an additional 6.4% of the variation, while regions explained only an additional 0.5%. The interaction term time since death \times species was highly significant ($p = 0.0001$), explaining an additional 8.4% of the variation. This indicates that differences in the percent mass remaining among species increased with time elapsed since tree death.

The Y intercepts of the exponential equations describing the decomposition process in logs and snags fluctuated between 41 and 131%. Theoretically, an intercept below 100% indicates a high initial decomposition rate, while an intercept above 100% indicates a lag in decomposition in the early stages of decay (Harmon et al. 1995). However, the low intercept Y_0 of 41% and associated low decomposition rate coefficient (k) of 0.011 year⁻¹ for *Betula* spp. in the St. Petersburg region were probably caused by the small number of *Betula* logs sampled during the first 6 years of decomposition. The equation describing the decomposition process in *B. pendula* logs of the St. Petersburg region was therefore modified by forcing the regression through the Y intercept of 100%. The resulting decomposition rate coefficient of 0.054 year⁻¹ was used in the subsequent statistical analysis.

A comparison among the decomposition rate constants within each species and position indicates that some of the decomposition rates were not significantly different from each other (Table 6). The most similar rates were in the white pine group: the log decomposition rate of *Pinus siberica* was not different from the log decomposition rate of *Pinus koraiensis* ($p = 0.1355$), and the snag decomposition rate of these species was not different either ($p = 0.837$).

Although all of the species had decomposition rates calculated for logs and snags separately, we compared decomposition rates of logs and snags only for species and regions with a similar time since death range of the sampled pieces of CWD, specifically *Picea ajanensis* in the Khabarovsk region (1-71 and 2-77 years since death for snags and logs, respectively) and *Pinus siberica* (2-65 and 0-65 years) and *L. siberica* (1-65 and 1-90 years) in the Irkutsk region. This was essential to avoid bias associated with sample distribution over the time since death range. While decomposition rates of logs and snags were not significantly different for *Picea ajanensis* ($p = 0.121$), they were different for *Pinus siberica* and *L. siberica* ($p = 0.002$ and 0.001, respectively).

Ranking species by their decomposition rate constants indicates that *B. pendula* is the fastest decaying species in all regions, usually followed by *Picea* spp. and *Pinus sylvestris*, with *Larix* spp. and *Pinus siberica* - *Pinus koraiensis* being the most decay-resistant species (Table 5). A similar ranking holds when decomposition rates are obtained by forcing the intercept of the negative exponential curve through 100%.

Betula costata, *Picea ajanensis*, and *Pinus koraiensis* log data showed a departure from a single-exponential curve.

Fig. 3. Overlay of variables from the “quantitative” matrix on the “qualitative” matrix with decay class as the grouping variable and density, time since death, and percent bark cover as vectors.

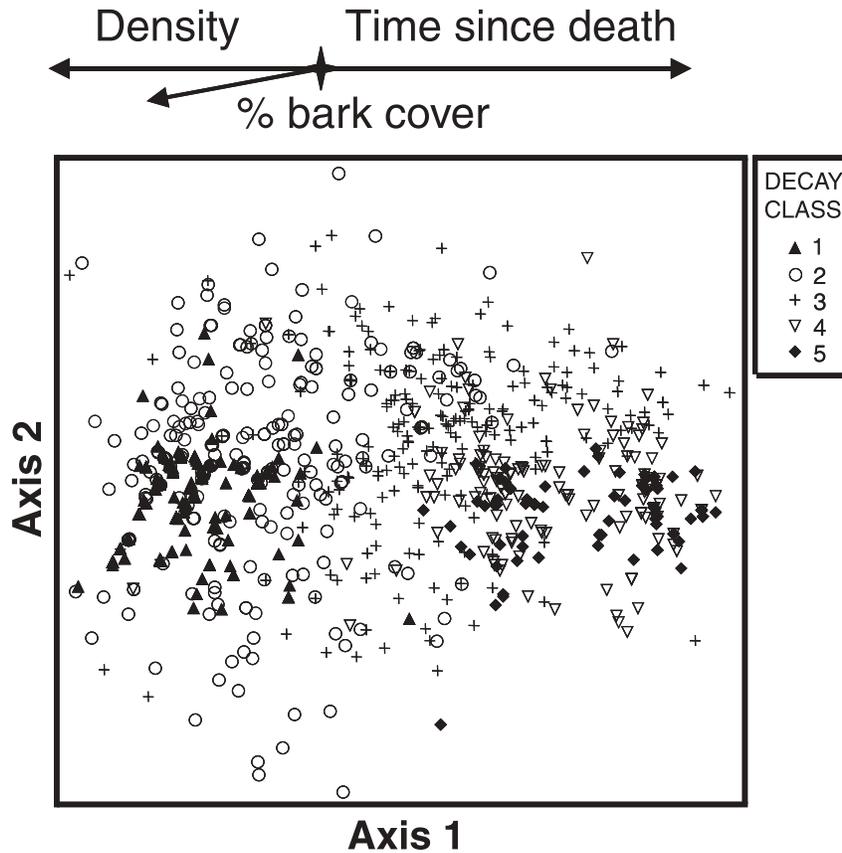


Table 4. Correlations of indicator variables (in ascending order) with scores on ordination axis 1 for five major taxa.

<i>Betula pendula</i>		<i>Pinus siberica – Pinus koraiensis</i>		<i>Larix spp.</i>		<i>Picea spp.</i>		<i>Pinus sylvestris</i>	
Variable	<i>r</i>	Variable	<i>r</i>	Variable	<i>r</i>	Variable	<i>r</i>	Variable	<i>r</i>
BRANCHES	-0.817	BARKBOLE	-0.854	BARKBOLE	-0.814	BARKBOLE	-0.724	BARKBOLE	-0.792
BARKBR	-0.799	BARKBR	-0.795	BCOVER	-0.801	BARKBR	-0.702	BRANCHES	-0.776
TWIGS	-0.707	BCOVER	-0.788	BRANCHES	-0.769	BRANCHES	-0.663	BARKBR	-0.708
NEEDLES	-0.435	TWIGS	-0.787	BARKBR	-0.710	BCOVER	-0.635	BCOVER	-0.704
BCOVER	-0.257	BEETLES	-0.739	TWIGS	-0.704	TWIGS	-0.567	TWIGS	-0.694
LICHENS	-0.226	NEEDLES	-0.650	BEETLES	-0.660	BEETLES	-0.496	NEEDLES	-0.519
BARKBOLE	-0.200	BRANCHES	-0.586	NEEDLES	-0.429	NEEDLES	-0.395	BEETLES	-0.435
BEETLES	-0.008	WOODBORER	-0.444	WOODBORER	-0.331	LICHENS	-0.151	WOODBORER	-0.148
ANTS	0.023	CONKS	-0.356	CONKS	-0.214	WOODBORER	-0.113	CONKS	-0.092
WOODBORER	0.038	CASEHARD	0.102	ANTS	0.094	CONKS	-0.100	ANTS	0.148
CONKS	0.075	ANTS	0.166	LICHENS	0.175	ANTS	0.102	CASEHARD	0.272
CASEHARD	0.215	LICHENS	0.259	CASEHARD	0.311	CASEHARD	0.254	WHITEROT	0.404
WHITEROT	0.479	WHITEROT	0.563	STUBSMOV	0.543	WHITEROT	0.441	LICHENS	0.420
BROWNROT	0.496	SCATTER	0.652	WHITEROT	0.544	MOSS	0.477	SCATTER	0.642
MOSS	0.549	COLLAPSE	0.667	SCATTER	0.730	BROWNROT	0.546	STUBSMOV	0.667
STUBSMOV	0.665	STUBSMOV	0.668	MOSS	0.746	SCATTER	0.567	MOSS	0.668
SAPSLOUG	0.669	MOSS	0.703	COLLAPSE	0.766	COLLAPSE	0.617	SAPSLOUG	0.722
SCATTER	0.683	HWFRIAB	0.767	HWFRIAB	0.787	SAPFRIAB	0.638	BROWNROT	0.754
COLLAPSE	0.787	BROWNROT	0.810	BROWNROT	0.834	SAPSLOUG	0.657	HWFRIAB	0.780
HWFRIAB	0.793	SAPSLOUG	0.859	SAPFRIAB	0.862	STUBSMOV	0.680	COLLAPSE	0.797
SAPFRIAB	0.846	SAPFRIAB	0.870	SAPSLOUG	0.874	HWFRIAB	0.686	SAPFRIAB	0.881

Note: See Table 3 for a description of the variables. *r*, coefficient of correlation.

Table 5. Decomposition rate constants (with SE in parentheses) and regression coefficients of percent mass remaining over time of decomposition for the major tree species in four forest regions of Russia.

Species	Region	Snags					Logs				
		Y_0 (%)	k (year ⁻¹)	n	Adj. r^2	k_{100} (year ⁻¹)	Y_0 (%)	k (year ⁻¹)	n	Adj. r^2	k_{100} (year ⁻¹)
<i>Betula pendula</i>	St. Petersburg	92.68	0.027 (0.008)	7	0.64	0.037 (0.007)	100.00	0.054 (0.013)	11	0.62	0.054 (0.013)
	Krasnoyarsk	106.53	0.056 (0.009)	13	0.78	0.051 (0.005)	107.08	0.061 (0.006)	28	0.81	0.058 (0.003)
	Irkutsk	108.11	0.052 (0.009)	17	0.67	0.039 (0.006)	86.56	0.042 (0.004)	41	0.75	0.047 (0.002)
<i>Betula costata</i>	Khabarovsk	130.92	0.077 (0.022)	7	0.64	0.052 (0.011)	118.73	0.078 (0.008)	20	0.82	0.069 (0.005)
	Khabarovsk	108.63	0.071 (0.003)	7	0.99	0.063 (0.004)	79.13	0.030 (0.003)	23	0.81	0.036 (0.003)
	St. Petersburg	118.35	0.044 (0.018)*	6	0.50	0.014 (0.009)*	82.48	0.026 (0.003)	20	0.78	0.032 (0.003)
<i>Picea abies</i>	Krasnoyarsk	98.53	-0.0006 (0.0043)*	8	-0.16	0.0006 (0.002)*	110.58	0.049 (0.006)	31	0.68	0.045 (0.003)
<i>Picea ajanensis</i>	Khabarovsk	125.24	0.035 (0.003)	14	0.92	0.031 (0.003)	96.59	0.028 (0.002)	39	0.83	0.029 (0.001)
<i>Pinus sylvestris</i>	St. Petersburg	103.85	0.037 (0.009)	14	0.56	0.032 (0.005)	81.76	0.027 (0.005)	42	0.46	0.033 (0.003)
<i>Larix siberica</i>	Krasnoyarsk	97.13	-0.020 (0.011)*	8	0.26	-0.009 (0.010)*	120.60	0.044 (0.003)	31	0.85	0.038 (0.002)
	Irkutsk	103.25	0.004 (0.003)	19	0.03	0.001 (0.002)*	111.20	0.036 (0.003)	35	0.84	0.032 (0.002)
	Krasnoyarsk	101.45	0.004 (0.005)*	8	-0.04	0.003 (0.003)*	90.23	0.023 (0.002)	30	0.85	0.025 (0.001)
<i>Larix dahurica</i>	Irkutsk	102.49	0.010 (0.001)	28	0.64	0.010 (0.001)	99.72	0.031 (0.002)	42	0.83	0.031 (0.002)
	Khabarovsk	93.56	0.009 (0.012)*	10	-0.05	0.013 (0.003)	80.70	0.015 (0.002)	26	0.66	0.019 (0.002)
	Irkutsk	88.02	0.003 (0.001)	17	0.33	0.006 (0.001)	88.55	0.019 (0.002)	33	0.66	0.021 (0.002)
<i>Pinus koraiensis</i>	Khabarovsk	86.66	0.003 (0.002)*	12	0.02	0.009 (0.002)	86.79	0.015 (0.001)	35	0.87	0.017 (0.001)

Note: Regression equation $Y_t = Y_0 e^{-kt}$, where Y_t is the percentage of the mass remaining at time t (years), Y_0 is the initial mass in percent dry mass, k is the decomposition rate constant when Y_0 is not forced to 100%, and k_{100} is the decomposition rate constant when Y_0 is forced to 100%.

*The coefficient is not significantly different from zero ($\alpha = 0.05$).

The decomposition of each of these species could be represented as a three-phase process, namely a slow phase, a rapid phase, and a moderately slow phase (Fig. 4). The duration of each phase and the decomposition rate constants varied among the species (Table 7).

Mean annual temperatures and precipitation exhibited no obvious correlation with decomposition rates. No obvious correlation was detected between decomposition rates and degree-days (annual sum of temperatures ($T > 5^\circ\text{C}$) or decomposition rates and the precipitation sum over the period with $T > 5^\circ\text{C}$. The decay-resistant species (i.e., *Larix* spp. and *Pinus siberica* – *Pinus koraiensis*) showed a negative correlation with the sum of precipitation over the period with $T > 5^\circ\text{C}$. No correlation with degree-days, however, was detected for *Larix* spp. and *Pinus siberica* – *Pinus koraiensis* or for any other coniferous species.

Discussion

Decay classification

The five-class system used to assign logs and snags to decay classes was consistent in most aspects with that used in other studies (Triska and Cromack 1980; Christensen 1984; Harmon et al. 1987; Storozhenko 1992; Pyle and Brown 1999). The decay class description adopted from Fogel et al. (1973), MacMillan et al. (1977), and Maser et al. (1979) worked well for most coniferous species; however, it had to be modified for *B. pendula*, a species that retains its bark through the entire decomposition process (Krankina et al. 1999). Presence of bark on *B. pendula* prevented sapwood and heartwood from sloughing, thus introducing secondary differences between this species and conifers: the presence of beetles, traces of wood borers, and conks can be detected in more advanced decay classes in *Betula* CWD than in conifers. Also, the difference between *B. pendula* and conifers was indicated by early occurrence (decay class 1) of white rot in *Betula* logs and snags, while the appearance of this type of rot in conifers was not recorded until decay class 2. Not all hardwoods, however, behave like *B. pendula*. Some lose bark rapidly. Maple (*Acer* spp.) and oak (*Quercus* spp.) in the hardwood forests of Connecticut were found to lose most of their bark by decay class 2 (Pyle and Brown 1999). A similar pattern was observed in our study for *B. costata* in the Russian Far East.

Case hardening is often observed in coniferous logs of decay classes 3 to 5. This condition occurs when outer tissues dry out while inner tissues continue to decompose, thus forming an inner friable material surrounded by a hard shell. Pyle and Brown (1998) suggested that case hardening most likely occurs on snags of *Acer* and *Quercus* that have been standing for a long time. Harmon et al. (1995) indicated that case hardening is typical for logs and snags in seasonally dry tropical forests. In our study, case hardening was associated with decay classes 3, 4, and sometimes 5 of *Larix*, *Pinus*, and especially *Picea* logs that were found in the areas damaged by catastrophic disturbances (windthrow in particular) and were suspended in the air for some part of the decomposition process.

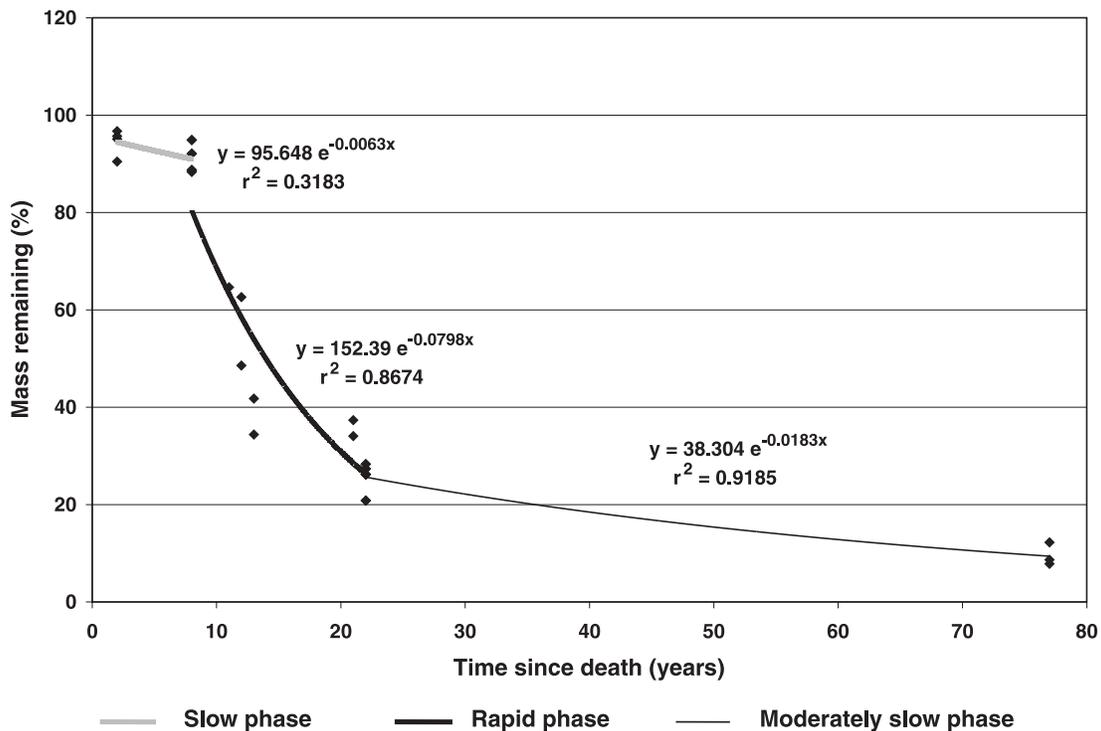
The five decay class system did not completely eliminate the ambiguity associated with borderline logs. The most difficult decision we faced in the field was separating logs from

Table 6. Differences in mean decomposition rate (k , year⁻¹) (SE in parentheses) between regions for species or groups of species.

Species	Region	Snags	Logs
<i>Betula pendula</i>	St. Petersburg	0.027 (0.017)a	0.054 (0.013)ab
	Krasnoyarsk	0.056 (0.007)ab	0.061 (0.006)a
	Irkutsk	0.052 (0.014)ab	0.042 (0.004)b
	Khabarovsk	0.077 (0.014)b	0.078 (0.009)a
<i>Betula costata</i>	Khabarovsk	0.071 (0.003)	0.030 (0.003)
<i>Picea abies</i> , <i>Picea obovata</i> , <i>Picea ajanensis</i>	St. Petersburg	0.044 (0.037)ab	0.026 (0.005)a
	Krasnoyarsk	-0.0006 (0.011)b	0.049 (0.006)b
	Khabarovsk	0.035 (0.002)a	0.028 (0.002)a
<i>Pinus sylvestris</i>	St. Petersburg	0.037 (0.007)a	0.027 (0.003)a
	Krasnoyarsk	-0.020 (0.027)ab	0.044 (0.005)b
	Irkutsk	0.004 (0.003)b	0.036 (0.004)ab
<i>Larix siberica</i> , <i>Larix dahurica</i>	Krasnoyarsk	0.004 (0.007)	0.023 (0.002)a
	Irkutsk	0.010 (0.001)	0.031 (0.002)b
	Khabarovsk	0.009 (0.013)	0.015 (0.003)c
<i>Pinus siberica</i> , <i>Pinus koraiensis</i>	Irkutsk	0.003 (0.002)	0.019 (0.002)a
	Khabarovsk	0.003 (0.001)	0.015 (0.001)a

Note: Means followed by different letters differ significantly between regions at $\alpha = 0.05$.

Fig. 4. Mass loss by *Betula costata* logs in Khabarovsk region. Separate exponential curves show three phases of decomposition (slow, rapid, and moderately slow).



decay classes 2 and 3 as well as logs from classes 4 and 5 from each other. The same problem has been common in other studies. Pyle and Brown (1998) indicated that 15% of the logs assigned to decay classes 2 and 3 were not consistent with the calculated decay-class specific density. This inconsistency may be associated with the variability of decay class 3, as indicated by the maximum standard deviation of decay-class specific density in this decay class. The time

since death distribution of logs by decay class also supports the idea, as logs in the middle of the decay class sequence have a larger time since death range.

On the other hand, the overlap observed between adjacent decay classes, indicated both by densities (Table 2) and the ordination results (Fig. 3), contradicts the idea that decay class 3 has maximum overlap with other decay classes. The overlap in density is highest in decay classes 1 and 2 and de-

Table 7. Decomposition rate constants (SE in parentheses) for three phases of decomposition of *Betula costata*, *Picea ajanensis*, and *Pinus koraiensis* logs in Khabarovsk study region.

Species	Phase of decomposition	Duration of a phase (years)	Y_0 (%)	k (year ⁻¹)	p^*	n	Adj. r^2
<i>Betula costata</i>	Slow	8	95.65	0.006 (0.004)	0.1452	8	0.20
	Rapid	14	152.39	0.080 (0.008)	0.0001	16	0.86
	Moderately slow	55	38.30	0.018 (0.002)	0.0002	8	0.90
<i>Picea ajanensis</i>	Slow	8	90.80	-0.008 (0.008)	0.3317	10	0.0075
	Rapid	24	122.76	0.045 (0.006)	0.0001	24	0.68
	Moderately slow	45	83.15	0.026 (0.008)	0.0096	14	0.39
<i>Pinus koraiensis</i>	Slow	12	95.42	0.011 (0.003)	0.0053	14	0.45
	Rapid	33	121.27	0.034 (0.005)	0.0001	19	0.68
	Moderately slow	115	39.31	0.0086 (0.0028)	0.0215	8	0.55

Note: Regression equation $Y_t = Y_0 e^{-kt}$, where Y_t is the percentage of the mass remaining at time t (years), Y_0 is the initial mass in percent dry mass, k is the decomposition rate constant when Y_0 is not forced to 100%.

* p values are for the comparison of the decomposition rate constant to zero.

decay classes 4 and 5 with these pairs being statistically similar. Similarly, the NMS ordination indicates that decay classes 1 and 2 as well as 4 and 5 occupy the same ordination space. Although decay class 3 overlaps other decay classes, it occupies a different space in the ordination. Interestingly, Storozhenko (1992) noted in a five decay class system for spruce that decay class 3 was the most distinct. In a study of coastal forests of Vancouver Island, Preston et al. (2002) found no statistical differences in density between decay classes 1 and 2 and between classes 4 and 5 for some species, while for others, no statistical differences in density were found among the first three decay classes.

CWD density changes with decay class

Different patterns in density change with decay class have been observed. Various sources report a gradual decrease in density with decay class (Triska and Cromack 1980; Shorohova and Shorohov 1999). Harmon et al. (1987) indicated that density of white fir (*Abies concolor* (Gord. & Glend.) Lindl.) decreased gradually, whereas for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) and incense cedar (*Calocedrus decurrens* (Torr.) Florin.) density remained fairly constant until decay class 4. The latter pattern was also reported by Torres (1994) for logs of swamp titi (*Cyrilla racemiflora* L.) in tropical forests of Puerto Rico. For *Acer* and *Quercus* logs, Hale and Pastor (1998) indicated a small decrease from decay class 1 to decay class 2 and a more dramatic decrease from decay class 2 to decay class 4. The decrease in CWD density we observed from decay class 1 to decay class 5 was similar to that reported by Hale and Pastor (1998) with exception that we also observed no decrease in density from decay class 4 to decay class 5 for most species. Snags of *Larix* spp. and *Pinus koraiensis* showed a different pattern of decay in our study than other species, maintaining almost constant density until decay class 3. In some instances there was an increase in density of snags from decay class 1 to decay class 2, similar to that reported by Sanders and Wein (2000), and this is probably associated with shrinkage caused by excessive drying.

We suggest there are four different patterns in CWD density loss. The first one is exemplified by *B. pendula*, as observed in our study with a gradual, almost linear density decrease from decay class 1 to decay class 5. This gradual

decrease is attributed to prolonged bark presence preventing inner tissues from drying and simultaneous decomposition of sapwood and the absence of decay-suppressing substances in the heartwood of *Betula*. The second pattern is found in species with decay-resistant heartwood, as typified by *Pinus siberica* – *Pinus koraiensis*, *Pinus jeffreyi*, *Larix* spp., *Calocedrus decurrens*, *Cyrilla racemiflora*, and *Malnikaria* spp. (Harmon et al. 1987; Torres 1994). For these species basically no change in density is observed until decay class 4, because bark and less-resistant sapwood slough off as they decompose leaving solid, long-lived, decay-resistant, and dense heartwood. The third pattern we associate with such species as *Pinus sylvestris*, *Picea* spp., and *Pseudotsuga menziesii* (Mirb.) Franco, where the heartwood is not very decay resistant or the sapwood-to-heartwood ratio is high even for mature trees. In this case, decomposition starts from the outside and goes through three phases (slow, rapid, and moderately slow) (Harmon et al. 2000). The observed density change is small between decay classes 1 and 2, which often is associated with a drying effect due to shrinkage or slow colonization by decomposing organisms. Significant density decrease is observed through decay classes 3 and 4, and slight density decline, from decay class 4 to 5, which is probably due to slow decomposition of the remnant decay-resistant tissues. Finally, the fourth pattern is associated with species susceptible to heart rot similar to oak and maple studied by Hale and Pastor (1998) in Minnesota. CWD decomposition in this case is complex as the decay of log or snag proceeds simultaneously from the inside out as well as from the outside in. Initial CWD density of such trees might be lower than that of sound trees. Density loss in these species might be initially fast because part of the heartwood is already affected by rot.

Decomposition rate constants

The single-exponential curve (Olson 1963) does not always adequately describe the CWD decomposition process (Hale and Pastor 1998; Harmon et al. 2000; Sanders and Wein 2000). Many species decompose slowly at first because of the high moisture content, decay-resistant heartwood, or the long time required for decomposer organisms to become established (Grier 1978; Harmon et al. 2000). A phase of slow decomposition (Hale and Pastor 1998;

Harmon et al. 2000) is often modeled with a time lag (Grier 1978; Naesset 1999; Harmon et al. 1995). To account for this pattern, the process can be broken into more uniform periods. Hale and Pastor (1998), for example, calculated decomposition by decay classes. This approach resulted in moderately slow decomposition rates for decay class 1 logs, slow for decay class 2, increased rates for decay class 3, and an even higher rates for decay class 4 logs. Harmon et al. (2000) used a decomposition vector approach to estimate decomposition dynamics for a range of decay classes. This approach suggested three distinct phases in log decomposition: slow, when colonization by decomposers occurred; fast, a period of rapid mass loss; and slow, when mass losses from highly decayed wood are minor. We also tried to determine the decomposition rates for each of three decomposition phases of *B. costata*, *Picea ajanensis*, and *Pinus koraiensis* by fitting an exponential curve through the mass loss data associated with each phase. This indicated decomposition rates of 0.0063, -0.0084, and 0.011 year⁻¹ for the first phase (essentially 0 for *Betula* and *Picea*), 0.080, 0.045, and 0.034 year⁻¹ for the second phase, and 0.018, 0.026, and 0.0086 year⁻¹ for the third phase for *Betula*, *Picea*, and *Pinus* decomposition, respectively.

The decomposition rates determined in this study were species dependent and within the range determined by other researchers for Russia, Norway, and northern China (Table 8). *Betula pendula* had the highest decomposition rate among all species in all these studies. *Pinus siberica* – *Pinus koraiensis* and *Larix* spp. were the slowest decomposing species studied, and this is attributed to the decay-resistant heartwood as well as to the large size of the trees we sampled. Large diameter is often associated with low surface area to volume ratio, which prolongs the colonization process by wood-destroying organisms and reduces the sapwood-to-heartwood ratio (Harmon et al. 1986). Moreover, previous work in Russian forests indicates that the decomposition rate is negatively correlated with the size of CWD (Tarasov 1999). Although it is true that *Pinus siberica*, *Pinus koraiensis*, and *Larix* had the largest logs and snags sampled, the presence of decay-resistant heartwood is considered the main reason for the low decomposition rates of these species (Scheffer and Cowling 1966; U.S. Forest Products Laboratory 1967; Panshin and de Zoew 1970; Marra and Edmonds 1996). The other species sampled had decomposition rates within the range of those of *Betula* and *Pinus koraiensis*. Similarly, Alban and Pastor (1993) found a significant effect of species on the decomposition rate with quaking aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), red pine (*Pinus resinosa* Ait.), and jack pine (*Pinus banksiana* Lamb.) listed in descending order of decomposition rates.

The differences in decomposition rates between logs and snags observed in our study correspond with the results of other researchers. Onega and Eickmeier (1991) indicated that the decomposition rate of logs was higher than the rate of snags of *Acer saccharum* Marsh. in Tennessee. There might be two explanations for this phenomenon. First, the time since death of the sampled snags is often short making it difficult to accurately detect losses in density or volume. Second, snag decomposition may be slower than that of logs

because of insufficient moisture in snag tissues resulting from the microclimatic differences. Compared with conifers, *B. pendula* logs and snags had similar decomposition rates, a pattern that may be caused by bark retention in the latter genus.

Factors affecting decomposition rate constants

Moisture has been observed to have a profound nonlinear effect on decomposition in laboratory studies (Chen 1999; Hicks 2000). At low levels of moisture the decomposition rate is low. When moisture increases to the point of saturation or waterlogging, most decomposers are unable to respire because of a lack of oxygen. Field measurements suggest that moisture is important in some ecosystems. For example, Harmon et al. (1987) found an inverse relationship between decomposition rate and annual precipitation for conifer boles in the western U.S. This is consistent with laboratory studies that indicate excess moisture reduces aeration (Harmon and Chen 1991). Conversely, Marra and Edmonds (1996) found that excess moisture did not control seasonal variations of decomposition in the field.

Temperature appears to be a more consistent factor than moisture for determining decomposition rate (Marra and Edmonds 1996). Temperatures approaching the freezing point, for example, arrest fungal growth and bacterial activity, although this does not eliminate decay completely. There is also an indication that the activity of fungi increases approximately two- to three-fold for every 10°C rise in temperature (Q_{10} factor) (Panshin and de Zoew 1970; Chen 1999; Hicks 2000). Laboratory tests of the relationship between decomposition rate and temperature indicate an increase in decomposition rate with temperature, followed by a sharp drop once the temperature exceeds an optimum value of approximately 40°C (Chen 1999; Hicks 2000).

Our study, however, did not find any of the abovementioned relationships between decomposition rate and climatic conditions. This may be explained by the fact that the data were collected over a narrow range of conditions. All the sites were located in the southern taiga zone, and thus differences in temperature and precipitation were likely too small to have effects on decomposition rates. This hypothesis is supported by our statistical analysis (stepwise regression), which indicated that region (which may include some aspects of temperature and precipitation differences) explained only 0.5% of the variation in percent mass remaining.

However, for tropical forests, Chambers et al. (2000) found a high correlation between decay rates and mean annual temperatures with a Q_{10} of 2.4. A compilation of global decomposition rate data, including those from our study, suggests that while there is not a significant effect of temperature on decomposition for decay-resistant species ($Q_{10} = 0.8$), there is a significant temperature effect on decay-susceptible species with a Q_{10} of 2.4 (Fig. 5). Thus, the decomposition rate of decay-susceptible species appears to increase exponentially as the mean annual temperature increases. The curve describing the relationship for decay-susceptible species may be broken into two parts, with a minor response for temperatures ranging between -5 and 15°C and a dramatic increase for temperatures above 15°C. If a

Table 8. Comparison of mean decomposition rates (SE in parentheses) determined in this study with published values from the same regions.

Species	Region	Reference	k (year ⁻¹)	k_{100} (year ⁻¹)
<i>Betula pendula</i>	St. Petersburg	This study*	0.054 (0.013) [§]	0.054 (0.013) [§]
			0.027 (0.008)	0.037 (0.007)
			0.035 (0.013) [¶]	0.053 (0.009) [¶]
		Shorohova 2000 [†]	0.058	0.054
		Harmon et al. 2000*		0.046 [¶]
		Tarasov 1999 [†]		0.026–0.051 ^{‡‡}
<i>Picea abies</i>	St. Petersburg	This study*	0.026 (0.003) [§]	0.032 (0.003) [§]
			0.044 (0.018)	0.014 (0.009)
			0.028 (0.003) [¶]	0.036 (0.002) [¶]
		Shorohova 2000 [†]	0.031	0.027
		Harmon et al. 2000*		0.033 [¶]
		Tarasov 1999 [†]		0.019–0.033 ^{‡‡}
Southeast Norway	Naesset 1999 [†]	Krankina and Harmon 1995*	0.028–0.041 ^{**}	0.034 [¶]
			0.033 ^{††}	
<i>Pinus sylvestris</i>	St. Petersburg	This study*	0.027 (0.005) [§]	0.033 (0.003) [§]
			0.037 (0.009)	0.032 (0.005)
			0.029 (0.004) [¶]	0.033 (0.003) [¶]
		Harmon et al. 2000*		0.035 [¶]
		Tarasov 1999 [†]		0.014–0.023 ^{‡‡}
		Krankina and Harmon 1995*		0.033 [¶]
Krasnoyarsk	This study*	This study*	0.044 (0.003) [§]	0.038 (0.002) [§]
			–0.020 (0.011)	–0.009 (0.010)
Tomsk	Wirth et al. 2000 [‡]	This study*	0.042 (0.003) [¶]	0.038 (0.002) [¶]
				0.034
<i>Pinus koraiensis</i>	Khabarovsk	This study*	0.015 (0.001) [§]	0.017 (0.001) [§]
			0.003 (0.002)	0.009 (0.002)
			0.015 (0.001) [¶]	0.017 (0.001) [¶]
	Changbai, China	Harmon and Chen 1991 [†]	0.016 [§]	
Changbai, China	Harmon and Chen 1991 [‡]	0.023 [§]		

*The decomposition rate was determined based on percent mass loss.

[†]The decomposition rate was determined based on percent density loss.

[‡]The decomposition rate was determined based on input-to-biomass ratio.

[§]The decomposition rate was determined for logs only.

^{||}The decomposition rate was determined for snags only.

[¶]The decomposition rate was determined for logs and snags combined.

**The lower decomposition rate limit is associated with a diameter range of 7 to 10 cm; the upper limit, with diameters >25 cm.

^{††}The decomposition rate is the average for all cross-sections sampled.

^{‡‡}The decomposition rate range is associated with a diameter range of 10 to 50 cm.

Q_{10} is calculated for each part, it is 1.41 for temperatures below 15°C and 3.06 for those above 15°C. These Q_{10} values indicate little effect of temperature on decomposition rates in cold and moderately cold climates but a significant increase in decomposition rates in subtropical and tropical climates. The cause of this increase in decomposition is yet to be determined, but we hypothesize that this occurs as a result of the appearance of insect comminators (termites in particular) that are generally absent in colder climates.

Conclusions

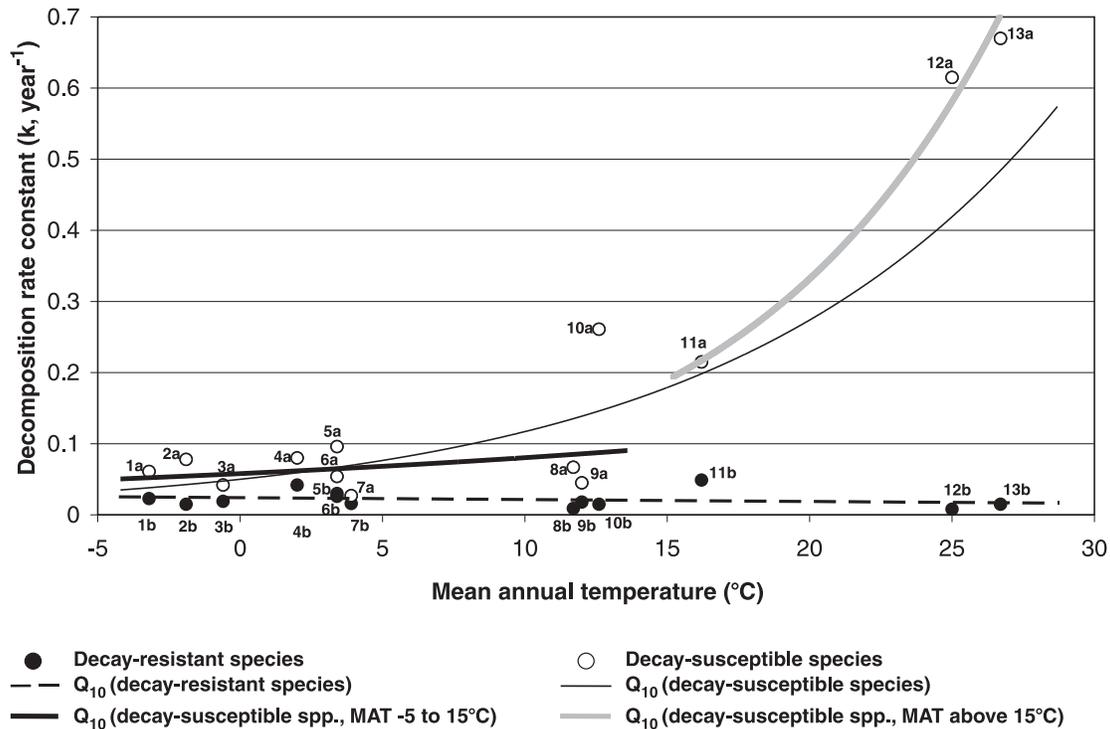
The major tree species in the boreal forests of Russia showed diverse decomposition patterns and different characteristics associated with decay classes. The most significant

differences in mean CWD density were associated with decay classes and species, making regional and positional differences of lesser concern for CWD inventories. The differences in mean CWD density among species declined with increasing decay class, indicating that species identification of CWD in advanced stages of decomposition is of minor importance.

The order of increasing CWD decomposition rate constants (k) among species was *Betula pendula* > *Picea* spp. > *Pinus sylvestris* > *Larix* spp. > *Pinus siberica* – *Pinus koraiensis*. Differences in decomposition rates of logs and snags indicated that disturbances creating snags increase overall turnover time of CWD.

No effect of climatic conditions on decomposition rates was found within the study area. Examination of the most

Fig. 5. Decomposition rate constants of decay-susceptible and decay-resistant species over mean annual temperature (MAT) in different regions of the globe. Number indicates site; decay-susceptible species are labeled “a”, decay-resistant species are labeled “b”. 1a, *Betula pendula*, Krasnoyarsk region (this study); 1b, *Larix siberica*, Krasnoyarsk region (this study); 2a, *Betula pendula*, Khabarovsk region (this study); 2b, *Pinus koraiensis*, Khabarovsk region (this study); 3a, *Betula pendula*, Irkutsk region (this study); 3b, *Pinus siberica*, Irkutsk region (this study); 6a, *Betula pendula*, St.-Petersburg region (this study); 6b, *Picea abies*, St.-Petersburg region (this study); 4a, *Populus tremuloides*, north-central Minnesota (Alban and Pastor 1993); 4b, *Pinus banksiana*, north-central Minnesota (Alban and Pastor 1993); 5a, hardwoods (maple, ash, birch, beech), New Hampshire (Arthur et al. 1993); 5b, *Abies balsamea*, New Hampshire (Lambert et al. 1980); 7a, hardwoods, western Oregon (Turner et al. 1995); 7b, *Thuja plicata*, western Oregon and Washington (Sollins et al. 1987); 8a, *Tilia amurensis*, China (Harmon and Chen 1991); 8b, *Pinus koraiensis*, China (Harmon and Chen 1991); 9a, *Acer* spp., Indiana (MacMillan 1988); 9b, *Quercus* spp., Indiana (MacMillan 1988); 10a, *Diospyros virginia*, North Carolina (Mattson et al. 1987); 10b, *Robinia pseudoacacia*, North Carolina (Mattson et al. 1987); 11a, *Eucalyptus calophylla*, western Australia (Brown et al. 1996); 11b, *Pinus pinaster*, western Australia (Brown et al. 1996); 12a, *Bursera simaruba*, Mexico (Harmon et al. 1995); 12b, *Manikara zapota*, Mexico (Harmon et al. 1995); 13a, fast decomposing species, central Amazon (Chambers et al. 2000); 13b, slow decomposing species, central Amazon (Chambers et al. 2000).



decay-resistant and decay-susceptible species at a global level suggests that while there is little or no correlation between mean annual temperature and decomposition rates of decay-resistant species, for decay-susceptible species there is a positive correlation with temperature, which appears once a mean annual temperature of 15°C is reached.

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