Time since death and decay rate constants of Norway spruce and European larch deadwood in subalpine forests determined using dendrochronology and radiocarbon dating

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Abstract

Due to the large size (e.g. sections of tree trunks) and highly heterogeneous spatial distribution of deadwood, the time scales involved in the coarse woody debris (CWD) decay of *Picea abies* (L.) Karst. and *Larix decidua* Mill. in Alpine forests are largely unknown. We investigated the CWD decay dynamics in an Alpine valley in Italy using the chronosequence approach and the five-decay class system that is based on a macromorphological assessment. For the decay classes 1 to 3, most of the dendrochronological samples were cross-dated to assess the time that had elapsed since tree death, but for decay classes 4 and 5 (poorly preserved tree rings) radiocarbon dating was used. In addition, density, cellulose and lignin data were measured for the dated CWD. The decay rate constants for spruce and larch were estimated on the basis of the density loss using a single negative exponential model, a regression approach and the stage-based matrix model. In the decay classes 1 to 3, the ages of the CWD were similar and varied between 1 and 54 years for spruce and 3 and 40 years for larch with no significant differences between the classes; classes 1 – 3 are therefore not indicative for deadwood age. This seems to be due to a time lag between the death of a standing tree and its contact with the soil. We found distinct tree species-specific differences in decay classes 4 and 5, with larch CWD reaching an average age of 210 years in class 5 and spruce only 77 years. The mean CWD rate constants were estimated to be in the range 0.018 to 0.022 y^{-1} for spruce and to about 0.012 y^{-1} for larch. Snapshot sampling (chronosequences) may overestimate the age and mean residence time of CWD. No sampling bias was, however, detectable using the stage-based matrix model. Cellulose and lignin time trends could be derived on the basis of the ages of the CWD. The half-lives for cellulose were 21 y for spruce and 50 y for larch. The half-life of lignin is considerably higher and may be more than 100 years in larch CWD. Consequently, the decay of *Picea abies* and *Larix decidua* is very low. Several uncertainties, however, remain: ^{14}C dating of CWD from decay classes 4 and 5 and having a pre-bomb age is often difficult (large age range due

to methodological constraints) and fall rates of both, European larch and Norway spruce are missing.

Keywords: coarse woody debris, decay constants, Norway spruce, European larch, subalpine forests, cellulose, lignin

1 Introduction

The quantity and residence time of deadwood or coarse woody debris in Alpine forests are crucial in assessing the carbon cycle to ensure sustainable management of forests. Coarse woody debris (CWD) is defined as large-sized deadwood pieces, such as stems of dead trees lying on the forest floor, standing dead trees and stumps, big branches and wood boles in all stages of decomposition. Deadwood plays an important role in maintaining biodiversity in forest ecosystems (Müller and Bütler, 2010) as well as storing carbon (Di Cosmo et al., 2013), and contributing to nutrient cycle processes (Palviainen et al., 2010). The amount of deadwood varies greatly from managed to natural forests. In managed European Alpine forests, for example, the average stock of deadwood is estimated to be about 26 m^3 ha^{-1}, while in old growth Alpine coniferous forests it can be up to 150 – 190 m^3 ha^{-1} (Barbati et al., 2014). Residence time for deadwood (e.g. Krüger et al., 2014) — from the moment the tree reaches the forest floor until it loses 95 % of the mass — can range from decades to several hundred years, depending on intrinsic and external factors. These factors include the dimensions of the log, the wood chemistry and the site conditions, in particular the mean annual temperature and soil moisture.

Until now, various different sampling designs have been used to determine the time since death to estimate the decay rate of deadwood. Long-term studies can provide reliable results (Müller-Using and Bartsch, 2009), but the slow decay dynamics of wood usually require a decadal observation period. Bond-Lamberty and Gower (2008) used the ratio of deadwood mass input into the pool of initial deadwood to estimate its decay rate based on a 7-years observation period. Such time sequences (chronosequence) offer ideal scenarios to study deadwood dynamics. If windthrow, fire regeneration and harvest events are known, the starting point in the timeline of the decay process can be specified. However, the exact year of such events is often uncertain which means precisely dating a tree's death is critical. Dendrochronology can be a helpful tool to determine the year of death, and the technique has been used in several studies to determine the time elapsed since tree-death (Campbell and Laroque, 2007, Lombardi et al., 2008, 2013). Other researchers have used radiocarbon dating to date the last recognizable ring of deadwood. For example, Kueppers et al. (2004) estimated the turnover time of lodgepole pine along a subalpine elevation gradient and Krüger et al. (2014) compared tree-ring cross-dating and radiocarbon dating, demonstrating that the two techniques produce comparable results. The decay rate can be estimated by relating the time-since-death to the density loss or mass loss of deadwood during a given time period (e.g. Busse, 1994; Melin et al., 2009). The decay rate is commonly expressed through a decay constant *k*, which indicates the density loss or mass loss per year. This constant is derived from a decay model (Harmon, 1986), which can be most simply expressed by the equation

$$x_t = x_0 \, e^{-kt} \quad (1)$$

(single-negative-exponential model), where x_t is the density or mass of deadwood at a given time, and x_0 is the initial density or mass (Jenny et al., 1949; Olson, 1963). Other decay models have also been developed that take wood decomposition into account (reviewed by Mackensen et al., 2003). Several authors (Minderman, 1968; Wider and Lang, 1982; Means et al., 1985) consider the different wood components, e.g. bark, sapwood, heartwood and chemical compounds, and combine them in multiple-exponential equations. Other authors (e.g., Harmon et al., 1986) consider the time elapsed from the death of a standing tree to the moment when it falls and comes in contact with the forest floor (lag-time models). In several environments, e.g. on dry mountain slopes, the time lag between death and contact with the forest floor can last for almost the entire decay process

(Kueppers et al., 2004). A few models take not only the losses due to heterotrophic respiration and leaching into account, but also losses due to fragmentation (Mackensen et al., 2003).

One of the most important components of deadwood is coarse woody debris. Because the spatial distribution of CWD is highly heterogeneous, only little quantitative data about its long-term decay dynamics are available for European Alpine forests. Decay models in Europe have, therefore, rarely been parameterised using empirically derived decay constants. In the field, the different stages of CWD decomposition are often described by so-called decay classes (as defined by Hunter, 1990) through a visual assessment of the wood status (Lombardi et al. 2013). In a previous study, Petrillo et al. (2015) demonstrated that the Hunter classification is particularly suitable for describing changes in the physical-chemical characteristics of European larch (*Larix decidua* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) deadwood in alpine environments. The physical-chemical properties of deadwood changed distinctly during decay and correlated well with the 5 decay classes. Furthermore, no substantial differences between spruce and larch decay patterns were found, although the wood chemistry of the living trees differed slightly between these two species (significant differences were found in the cellulose content, with 45.1% for spruce and 39.4% for larch; these differences were, however, negligible already in decay class 1; Petrillo et al., 2015). European larch and spruce are widespread in the Alps. Although C-stocks in soils are substantial (e.g. Johnston et al., 2004), CWD is a non-negligible C reservoir in subalpine forests (Sandström et al., 2007). Consequently, it is thus very important to know which time scales are involved in CWD decay. Jebrane et al. (2014) showed that Scots pine is more decay resistant than European larch, which suggests that the decay rate of pine is lower. Some species of larch are, however, considered economically valuable due to their hard, heavy and decay-resistant wood (Parker, 1993), which implies that residence time of larch CWD should be longer.

The aim of our work was to find out; i) which time scales are involved in CWD decay of *P. abies* and *L. decidua* in the Alps and ii) how these time scales correlate with the five-decay class system.

We hypothesised that the CWD decay of these coniferous trees is relatively slow (due to, e.g. the nutrient availability for macro and micro-organisms being unfavourable).

2 Materials and methods

2.1 Site description

The study area is located in the north-eastern Italian Alps, in Val di Sole and Val di Rabbi (Fig. 1; Table 1). The climate of the valleys ranges from temperate to alpine (above the timberline), the mean annual temperature from 8.2 °C at the valley floor to about 0 °C at 2400 m a.s.l., and the mean annual precipitation from approximately 800 to 1300 mm (Sboarina and Cescatti, 2004). The geological substrate is paragneiss debris in all sites. The soil units are Cambisols, Umbrisols and Podzols (WRB: IUSS working group, 2014). The soil properties at each site could be taken from a previous study (Egli et al., 2006). The timberline is close to 2000 – 2200 m a.s.l., with the forests dominated by Norway spruce and, at the highest altitudes, by European larch.

2.2 Sampling protocol

Norway spruce and European larch CWD was sampled at eight sites ranging in altitude from 1200 m a.s.l. to 2000 m a.s.l. In spring and summer 2013, wood cores from living trees and cross sections of CWD were taken from all sites. At each site, 5 or 6 living trees were sampled in two directions per each tree at 130 cm height (breast height) using an incremental corer (0.5 cm in diameter; Suunto, Finland). The wood cores were wrapped in paper and transported to the laboratory, where they were air dried, fixed onto a flat wooden support and sanded in order to obtain a smooth surface for tree-ring measurements. Before sampling, each CWD was first classified relative to the decay stage. The classification was done *in situ* using the five-class classification system of Hunter (1990)

(Table 2), which is based on visual, geometric and tactile features and considers the presence/absence of twigs and bark, the shape of the log section, and the deadwood structure. To sample CWD, a circular area of 50 m radius was explored at each plot. In total, 177 CWD samples were collected (46 of them were dated). At the highest sites, the forests consisted predominantly of larch trees. In addition, one lower site on the south-facing slope (S7) also had a predominantly larch forest. All other sites are spruce dominated. Samples were taken randomly either using a manual saw or, in more advanced stages of decay, simply by hand. If necessary, they were wrapped up with tape to preserve their structure during transport to the laboratory, where they were air dried and sanded. For CWD in more advanced decay stages (decay class 4 and 5), a 25 cm x 30 cm bag was filled. The samples were then oven-dried at 50 °C, but not sanded. To establish a master chronology, 83 wood cores were taken from living trees, 29 from larch and 54 from spruce. Two cores were taken from each tree. In three cases, one of the two cores taken from the same tree was too damaged to be measured (one at N02, one at S06 and one at S07). Furthermore, two outliers were excluded from the master chronology, namely one measured core at S07 and one at S08. CWD was dated using 46 cross sections from deadwood (18 from larch and 28 from spruce).

2.3 Dendrochronological dating

At each site, the 10 or 12 wood cores taken from living trees were used to build a reference (master) ring-width chronology for each species. Tree rings were first counted and then measured using the LINTAB tree-ring-width measurement device (RINNTECH e.K., Heidelberg, Germany), coupled together with a stereomicroscope (Leica, Germany). The two ring-width measurements from the same tree were first cross-checked and then incorporated into a single average master chronology for each species and for each site. To maximise the common signal, one outlier per species was excluded from the relative master chronology. These two tree-ring measurements exhibited a poor correlation with the other, probably due to an elevated number of missing rings. The statistical software TSAP-win™ (Time Series Analysis Program, RINNTECH e.K., Heidelberg, Germany) was used to calculate the *Gleichläufigkeit*, GLK (Kaennel and Schweingruber, 1995), i.e. the agreement between two ring-width series. The correlations among all the ring-width series of living trees and CWD were statistically assessed using the software COFECHA (Holmes et al., 1986). EPS (expressed population signal; Wigley et al., 1984) was calculated using the statistic software R. The deadwood cross-sections were measured from the most external ring to the pith, along three or four different radial directions. The individual CWD series (i.e. floating chronologies) were matched to the master chronology of the corresponding species. We visually and statistically checked the deadwood series using the GLK to obtain the highest value with the master chronology and to date the year of death of the tree from which the deadwood originated.

2.4 Radiocarbon dating

The CWD of the decay classes 4 and 5 was too degraded to be dated through tree-ring analysis as their wood structure was too altered and the tree rings were no longer visible. In such cases, the outermost part of the CWD was sampled and ^{14}C-dated (Fig. 2-A and 2-B). We selected a small fragment of 1 to 2 cm^3 in volume from the outermost part assumed to have contained the last- tree rings produced before the tree died (Fig. 2-C and 2-D). This small fragment was gently cleaned with a brush to remove any non-woody elements, such as particles of soil or vegetation like moss. The organic samples were cleaned using an acid-alkali-acid (AAA) treatment. The samples were then heated under vacuum in quartz tubes with CuO (oxygen source) to remove any absorbed CO_2 in the CuO. The tubes were evacuated, sealed and heated in the oven at 900 °C to obtain CO_2. The CO_2 of the combusted sample was mixed with H_2 (1:2.5) and catalytically reduced over iron powder at 535 °C to elemental carbon (graphite). After reduction, the mixture was pressed into a target so that carbon ratios could be measured by Accelerator Mass Spectrometry (AMS) using the 0.2 MV radiocarbon dating facility (MICADAS) of the Laboratory of Ion Beam Physics at the Swiss Federal Institute of Technology of Zurich (ETHZ).

The calendar ages were obtained using the OxCal 4.2 calibration program (Bronk Ramsey, 2001, 2009) based on the IntCal 13 calibration curve and for modern samples the Bomb 13NH1 curve (Reimer et al., 2013; Hua et al., 2013) was used. Several samples (before 1950 AD) had a widely calibrated age range. For these samples, we used the age range with the highest probability of confining the time elapsed since death very strictly.

2.5 Determining the cellulose and lignin

To obtain α-cellulose (Boettger et al., 2007), 10 mg of powdered wood were weighed in Teflon pockets for chemical and thermal treatments. All wood (sapwood and heartwood) was homogenised prior to chemical analysis. We decided to use this procedure, because it was not possible to distinguish between sapwood and heartwood for the most decayed stages. Samples were first washed in a 5% NaOH solution at 60 °C for two hours and then for an additional two hours with fresh 5 % NaOH solution (the NaOH solution was discarded each time), before finally being rinsed three times using boiling distilled water (see also Petrillo et al., 2015). The samples were then washed in a 7 % $NaClO_2$ solution at 60 °C for 30 hours, changing the solution at least every 10 hours and then rinsed three times with boiling distilled water. The pockets were dried in the oven at 50 °C and the cellulose content was determined as the difference between the initial weight and dried samples. The so-called Klason lignin (lignin insoluble in strong acid; Dence and Lin, 1992) was determined gravimetrically after a sequential extraction in which 0.2 g of each sample was washed three times with 5 ml of distilled water at 80 °C. After each washing, the samples were centrifuged for 10 min at 4500 rpm, dried in the oven at 80 °C and washed three times with 5 ml of ethanol. They were then centrifuged again (10 min. at 4500 rpm) and the supernatant was discarded. After being dried at 60 °C in the oven, 60 mg of each sample were treated with 0.6 ml 72 % H_2SO_4 in a warm (30 °C) bath for one hour, and then, after adding 16.8 ml of distilled water, in an autoclave at 120 °C for one hour. Subsequently, the samples were filtered and the filtrate used to determine of the acid-soluble lignin. The insoluble lignin was dried in the oven at 105 °C and determined as the difference between the dry and initial weight.

In total, the cellulose and lignin content was measured for 177 CWD samples.

2.6 Estimating decomposition rate constants on the basis of density loss

In a previous investigation (Petrillo et al., 2015), the density of the deadwood samples was measured. To estimate the decay constants, the average densities in class 1 and in class 5 (the earliest and latest decay stages) were used and the single-negative exponential model of Jenny et al. (1949) applied (see eq. 1). Equation 1 was then solved for the decay constant *k* according to equation 2:

$$k = \frac{-\ln\left(x_t / x_0 \right)}{t} \qquad (2)$$

where x_t is the density of each deadwood sample at a given time (i.e. the estimated time elapsed since death), and x_0 the initial density (0.45 g cm^{-3} for *Picea abies* and 0.59 g cm^{-3} for *Larix decidua*).

The density of all CWD samples was then compared to the related ages to derive the overall decomposition rates. A similar procedure was applied to cellulose and lignin to derive compound-specific decomposition rates of CWD.

Calculating mean residence time in decay classes from a single time point sample, rather than using longitudinal long-term data, tends to overestimate residence time due to a higher probability of inclusion of slow-decaying trees (Kruys et al., 2002). Consequently, snapshot sampling may overestimate the age and mean residence time of CWD. Thus, the decay rate could be underestimated. Calculating the overall CWD decay rates by using density values along a chronosequence risks, therefore, that a certain amount of error is introduced. This bias can be corrected using the proposed approach of Kruys et al. (2002). The mean residence time of CWD in a particular decay class is

$$E_m = \frac{\sum_{i=1}^{N} b_{mi}}{N} \qquad (3)$$

where b_{mi} is the residence time of tree i in a specific decay class m and N = trees present during the time period. The estimator of E_m is:

$$\hat{E}_m = \frac{\sum_{i=1}^{n_m} \frac{b_{mi}}{c\, b_{mi}/T}}{\sum_{i=1}^{n_{tot}} \frac{1}{cl_i/T}} = \frac{n_m}{\sum_{i=1}^{n_{tot}} \frac{1}{l_i}} \qquad (4)$$

with c = proportion of the logs existing at time point t, n_m = number of trees from which samples were taken in decay class m, n_{tot} is the total number of sampled trees and l_i is the total residence time of each tree across all decay classes. The expressions cb_{mi}/T and cl_i/T are the probabilities of including units b_{mi} and l_i in the sample, respectively. According to Kruys et al. (2002) it was assumed that all wood samples were taken half-way through their residence time in that class. The parameter l_i was calculated as age_i/x; age_i is the measured time since death of tree i and

$$x = \frac{r_m}{2} + \sum_{k=1}^{m-1} r_k \qquad (5)$$

where x is the sum of proportions, r_k, assigned to classes preceding the class of tree i plus 50% of the proportion assigned to tree i's class, r_m. $\hat{E}_m$ can be calculated iteratively for the different classes. Convergence occurred after 5 – 10 iterations.

3 Results

3.1 Living chronologies

Two master chronologies for spruce and larch were obtained extending over 164 and 141 years, respectively (Fig. 3). The spruce chronology ranged from 1848 to 2012 AD (Fig. 3) and the larch chronology from 1871 to 2012 AD. The tree-ring widths of the same species correlated well among each other with a high GLK. When considering each individual plot, the GLK values were highest at S09 (larch), with a mean GLK of 0.70 (± 0.1) and lowest at N01 (spruce) with a mean GLK of 0.58 (± 0.13). The series inter-correlation coefficients obtained using COFECHA were 0.535 for spruce and 0.641 for larch (Pearson correlation, all series above 0.3281 were significant; 99% confidence interval). The EPS values (Fig. 3B) were in most cases above (or close) to 0.85 (a threshold value for noise-free chronology; Wigley et al., 1984), except for *Picea abies* for the period of 1870 – 1910 AD. Spruce and larch, however, had quite different growth patterns with a Pearson correlation coefficient of 0.274 when comparing the two species-specific master chronologies. The spruce chronology indicated that the trees grew homogeneously throughout the whole observation period, while larch seemed to be more sensitive to climate with marked high and low growth periods (positive and negative pointer years, Fig. 3). Furthermore, the negative and positive pointer years were not synchronous in the larch and spruce master chronologies. Even though more larch trees were sampled at south-facing sites and at higher elevation, we can exclude a bias due to an unbalanced sample distribution. Within the same homogenous climatic region similar growth pattern are found (Carrer and Urbinati, 2006). The differences between the two master chronologies are rather influenced by the different phenology of the two species. Larch is a deciduous tree, with a deep rooting system, while spruce is evergreen and has a shallow root system. Furthermore, the larch master chronology is cyclically influenced by outbreaks of the larch bud defoliator *Zeiraphera diniana* Gn. that result in the abrupt occurrence of extremely narrow tree rings which are not observed for spruce (Esper, 2007). The growth pattern of some trees, however, differed considerably from that of the master chronology, possibly due to the specific growth conditions of the individual trees, e.g. if their growth was very suppressed because of competition. Such outliers were excluded from the chronologies.

3.2 Age of coarse woody debris (CWD)

Most of the samples of the decay classes 1 – 3 could be dendrochronologically dated, but those of decay classes 4 and 5 had to be radiocarbon dated because of the poorly preserved tree rings (Tables 3 and 4). In the first three decay classes, the CWD ages of spruce and larch seem to be in a similar range. The values vary from 1 to 54 years. Interestingly, the average age of CWD does not seem to increase from class 1 to 3. The average age was around 10 – 20 years for all decay classes assuming a relatively fast decay. In decay classes 4 and 5, the average and maximum ages of CWD were usually higher for larch than for spruce. In decay class 4, spruce CWD has an average of about 42 years (median 43 years; Fig. 4) and larch CWD an average of 87 years (median 45 years). In decay class 5, the average age of spruce CWD increases to 77 years and the age of larch CWD to 210 years. This shows that larch wood, particularly in the decay classes 4 and 5, is much more resistant to rotting than spruce. Several CWDs had an age of around 200 years. The calibration of radiocarbon dates for such ages is, however, complicated by the so-called plateaus that give rise to a relatively wide range of calibrated ages. To minimise the array of possibilities, we used the age range with the highest probability for confining the time elapsed since death more strictly.

3.3 Relations between year since death, decay class and physical-chemical properties of deadwood

The physico-chemical data for the CWD (n = 177) are given in Petrillo et al. (2015) and Tables 3 and 4 so that the density and the cellulose and lignin contents could be plotted as a function of the decay class and age of the CWD (Fig. 5). Since the relationship between the age of the CWD and physical-chemical characteristics was rather stochastic for the decay classes 1 – 3, they were grouped and their average was used for further analysis. The decrease in density and cellulose concentrations and the simultaneous increase in lignin definitely proceed faster for the spruce CWD than for the larch CWD (Fig. 5). An exponential function best describes the trends in the cellulose and lignin concentrations with time.

The stage-based matrix model of Kruys et al. (2002) was applied to calculate the *k*-values (Table 5) as a function of tree species and decay stage (summed decay classes)., Using the classical chronosequence approach, the decay rate constants per year (y^{-1}) were, furthermore, calculated for each dated sample based on the density loss of spruce and larch CWD (Table 6). For spruce, we obtained an average value of 0.018 (y^{-1}) and for larch 0.012 (y^{-1}; cf. Table 6). The *k*-values were non-normally distributed. Using the Kruskal-Wallis statistical test, we assessed the effects of the factors elevation, exposition, MAT (mean annual temperature), MAP (mean annual precipitation), species and decay class on the *k*-values. None of these parameters significantly influenced the decay rate constant. Nonetheless, the range of *k*-values on south-facing plots seem to be slightly higher than those on the north-facing plots, which suggests the decomposition rates are faster on south-exposed slopes (Fig. 6). In addition, the *k*-values were estimated by comparing the CWD density with their age and by plotting an exponential regression curve (not shown). This approach resulted in lower k-values: 0.012 y^{-1} for spruce and 0.005 y^{-1} for larch. The mean residence time and half-lives are summarised in Table 7. The differences in mean residence time and rate constants between Kruys' model and the more classical approach (chronosequence) using equation 1 are small (Table 6). Kruy's model gave slightly higher decay constants for Norway spruces (0.022 y^{-1}) and the same values (0.018 y^{-1}) for European larch (variant a) in Table 6).

4 Discussion

Although the five-decay class system is well suited to describe changes in the physical and chemical properties of deadwood (Lombardi et al., 2008), no real differences in the age of the CWD classes 1 – 3 could be found. The CWD in decay class 4 and 5 was, however, clearly older. This implies that the first three decay classes are not clearly related to deadwood age. Similarly, Lombardi et al. (2013) found no relationship between the age of CWD and the chemical properties of decay classes 1 – 3. The main explanation for this unexpected finding is that there is probably a time lag between the death of a standing tree and its contact with the soil (Kueppers et al., 2004; Zielonka, 2006; Lombardi et al., 2013). Standing dead trees, i.e. snags, can remain upright for several years and decay much more slowly than fallen dead trees (Yatskov et al., 2003). Such an effect overshadows a clear age trend in decay. If the species-specific fall rates were known the decay rates could be better assessed. Unfortunately, the fall rates of snags of the studied tree species are unknown at the investigated sites. To our knowledge, no data about fall rates of snags of either species, *Picea abies* (Norway spruce) and *Larix decidua* Mill. (European larch), are available. In this respect, the data situation in North America is much better. A good overview is given for example in Hilger et al. (2012) and Dixon (2015). According to Hilger et al. (2012), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine larch (*Larix lyallii* Parl.) have similar snag fall rates. Due to morphological, ecological and physiological similarities, we have to assume (but we finally cannot prove it) that Norway spruce and European larch should exhibit a similar reaction to Engelmann spruce and subalpine larch. As a consequence, no particular difference in the fall rate between European larch and Norway spruce is to be expected. Therefore, difference in the decay rates between European larch and Norway spruce are hypothesised not to be due to different fall rates.

Angers et al. (2012), however, observed that the wood density in snags in boreal forests already decreases after a few years. Decay rates they calculated are comparable to those in our study. The density loss in standing dead trees could be due to the activity of cerambycid larvae, while the activity of the wood decomposers, mainly fungi, was impeded in snags due to the lack of moisture. The discrepancy between the macromorphology of deadwood (and consequently decay class) and the age of deadwood seems therefore to be related to the individual tree death history. Shortly after tree death, in fact, the wood is rapidly colonized by fungi (Zielonka, 2006). The CWD in classes 4 and 5 showed a relation to deadwood age that seems to be species-specific since larch CWD is older than spruce in both classes. With respect to the CWD ages in our study, classes 1 to 3 appear to be a single group, while classes 4 and 5 are different. The oldest sample (larch CWD) was about 244 years old – a surprisingly old age for wood lying on the forest floor (i.e. not buried). Spruce CWD in decay classes 4 and 5 seem to be significantly younger than larch CWD. Few empirical assessments of time since the death of a tree have been made in Europe. Krüger et al. (2014) used both dendrochronology and radiocarbon dating to assess the time since death of Norway spruce in Bavarian forests. They estimated a total residence time of 61 to 62 years for this species. Our values are slightly lower. One major problem in determining the age using ^{14}C are the sometimes large age ranges obtained after calibration (due to plateaus) for samples having a pre-bomb age. We used the ranges with the highest probabilities (varying from 50 to 82.2%; Table 4; commonly the age 1-σ range, i.e. 68% is considered) for CWD dated to the time period before the bomb peak. Consequently, this procedure introduces an uncertainty. According to Krüger et al. (2014), radiocarbon analysis and dendrochronological cross-dating revealed a similar year of tree death for samples having a post-bomb age. The results of Krüger et al. (2014) suggest that both methods are suitable for the age determination of CWD. In Atlantic Canada, Campbell and Laroque (2007) found an age of 56 to 84 years (depending on the investigated sites) in the latest decay stage (decay class 5; Black spruce and Balsam fir). Lombardi et al. (2008) estimated stumps of beech and silver fir in decay class 3 to be 55 and 59 years which is close to our findings.

The decay rates reflect the determined ages of the CWD; and spruce therefore had a higher decay rate constant than larch. Consequently, decay rates are species specific due to, among others things, the initial differences in the physical-chemical properties of the wood of the living trees and in environmental factors. Larch has, for example, a higher density (cf. Fig. 5) and a lower nutrient content than spruce (Petrillo et al., 2015). Shorohova et al. (2014) also found that decay rates can strongly vary among tree species. The decay rate (i.e. 0.032 y^{-1}) they found for spruce was slightly higher than that in our study (Fig. 6). The variability of the decay rates given in the literature may also arise from using different mathematical models or different methods to determine wood density or the age of the CWD. According to Hale and Pastor (1998), the decay rates of oak and maple logs (in a temperate forest) varied between 0.00 and 0.18 y^{-1} (their dating of the logs, however, was based on estimates). The decay rates of tree species in a Mediterranean area (Australia; Brown et al., 1996) varied in the range of 0.05 up to 0.22 y^{-1}, while in a cool-continental climate (Alban and Pastor, 1993), decay rates were 0.042 and 0.055 for red and jack pine, respectively, 0.07 for spruce and 0.08 y^{-1} for aspen. Fukusawa et al. (2014) estimated decay rates by using the annual input of CWD divided by the CWD accumulation, and obtained a value of 0.036 y^{-1}. With the chronosequence approach, however, the rates were in the order of 0.020 – 0.023 y^{-1}.

The determined decay rates for spruce and larch in our investigation seem to be very low (Table 6). As pointed out by Kruys et al. (2002), the chronosequence approach, and thus the snapshot sampling, may overestimate the CWD age and consequently residence time. Thus, the decay rate may be underestimated. It seems, however, that this error is not overwhelmingly distinct in our case or even absent. The approach according to Kruys et al. (2002) and variant a) in Table 6 gave similar results. The regression approach (variant b) in Table 6) probably slightly underestimated the decay rates.

Using mass losses instead of density losses to estimate the decay rates may result in higher values, because the losses for fragmentation are added to the mineralisation losses (Yin, 1999). This might explain why our decay rate constants were lower than those in some other studies (Rock et al., 2008; Herrmann et al., 2015). Moreover, the decay rates are sensitive, at a regional scale, to climatic conditions such as temperature and precipitation (Shorohova et al., 2014), although the decay rates for a mean annual temperature of 0 to 10 °C are, however, quite similar, and rates below 0.04 y^{-1} are often reported (Mackensen et al., 2003). Soil temperature was found to be the main explanatory variable for differences in the decay rates of standard wood, such as aspen and pine (Risch et al., 2013). Although the data are too limited to draw clear conclusion, some of the differences in the decay rates we observed are likely to be due to environmental factors. On south-facing sites, for instance, we found that the decay rates were slightly, but not significantly, higher than those on north-facing sites (Fig. 6), which is comparable to Shorohova’s et al. (2014) observations.

Although our measured k values are very low, they fit reasonably well to those of the recent compilation of Russel et al. (2015). For environments having a mean annual temperature of < 10 °C, the decay rate constants are usually < 0.1 (median value is 0.027 for such sites). The compilation of Russel et al. (2015), however, only considers two sites having *Picea abies* (k values = 0.044 and 0.027; Krankina et al., 1999; Næsset, 1999) and none for larch. Together with our results, a residence time of about 20 – 90 years for *Picea abies* in subalpine (boreal) climates might be suggested.

The concentrations of cellulose and lignin in the CWD are given as a function of time in Fig. 5. Due to the faster decomposition of cellulose, lignin is relatively enriched. Lignin, however, also decomposes with time. To unravel the decay behaviour of these compounds, a multiple-exponential model was applied (Means et al., 1985; Mackensen et al., 2003), with the general form:

$$x = x_1 e^{-k_1 t} + x_2 e^{-k_2 t} \ldots + x_n e^{-k_n t} \quad (6)$$

where x_t is the density or mass of deadwood at a given time and $x_{1\ldots n}$ are partitioned parameters. The portioning of cellulose and lignin is solved graphically using their mass per unit volume over time, and fitting them to an exponential regression curve. From this, the half-life of cellulose or lignin in the CWD could be calculated:

$$t_{1/2} = \frac{\ln(1/2)}{-k} \quad (7)$$

where $t_{1/2}$ is the half-life and k is the decay constant (obtained from the exponential regression curve). Using the k-values in Fig. 7, the following half-lives were obtained:

a) for cellulose: 21 years (spruce) and 50 years (larch)

b) for lignin: 91 years (spruce) and 481 years (larch)

Means et al. (1985) were able to derive k-values for cellulose values of 0.0109 to 0.0117 y^{-1} for Douglas-fir logs (in a cool to temperate climate), although age determination (or estimation) was done differently. This would give rise to half-lives in the range of 59 to 64 years. With k-values in the range of 0.0039 to 0.0045 y^{-1} (Means et al., 1985), the half-life of lignin would be in the range of 154 – 178 years. In this specific case, the overall decay rates were between 0.006 and 0.0073 y^{-1}. Although cellulose is relatively easily degradable by (micro)organisms, it may persist astonishingly long in larch trees (several decades). Lignin may have a half-life of more than hundred years. These half-lives may be shorter if the decay is related to mass losses and not to density.

In decay classes 4 and 5, the CWD starts to become more and more part of the soil. The further fate of CWD compounds strongly depends on their interaction with the mineral soil. The introduced organic matter into soils can be either further degraded or stabilised to a certain extent. The persistence of organic matter in soils is largely due to complex interactions between the organic matter and its environment, such as the interdependence of compound chemistry, reactive mineral surfaces, climate, water availability, soil acidity, soil redox state and the presence of potential degraders in the immediate micro-environment (Schmidt et al., 2011). Together with physical protection, organo-mineral interactions are generally thought to be the main mechanism for SOM stabilisation (e.g., Nierop et al., 2002; Kleber et al., 2005; Marschner et al., 2008).

5 Conclusions

The first 3 decay classes do not seem to reflect the age of the CWD, but they are relevant for the description of its decay stage. The time lag between the death of a standing tree and its contact with the soil overshadows a clear age trend. Taking classes 1 – 3 as one group and relating them to the decay classes 4 and 5, a time trend with increasing decay stage can then be detected. This time trend also closely correlates to the wood density, and the cellulose and lignin content. The oldest CWD age of a larch tree reached the considerable age of 244 years. We used a chronosequence approach and applied several calculation techniques to estimate the overall decay rate constants of European larch and Norway spruce. The stage-based matrix model of Kruys et al. (2002) that corrects for sampling bias was in good agreement with the often-used single-negative-exponential model. The regression approach probably underestimated slightly the decay rates. The decay rate constant for spruce seems to be in the range of 0.018 to 0.022 (y^{-1}) and for larch it is about 0.012 (y^{-1}). The rates seemed to be slightly higher on south-facing sites (although this was not statistically significant). An effect of the altitude on the decay rates was, however, not discernible. Using the dating approach (dendrochronology and ^{14}C-dating), the behaviour of cellulose and lignin as a function of time could be assessed. Our findings demonstrate that lignin in larch may persist particularly long, with a mean residence time of > 100 years. This indicates that turnover rates of CWD organic matter are even in a comparable range to that of SOM.

More empirical data is, however, needed to ascertain our findings. A major issue is that fall rates between European Larch and Norway spruce could not be compared. Furthermore, the preparation and precise dating of CWD is time-consuming, cost intensive and in some cases also difficult (particularly samples with a pre-bomb age in decay classes 4 and 5). Since CWD represents an important forest carbon pool, improving the informative potential of the decay classes (including the dating of the CWD) would contribute to sustainable forest management and make carbon accounting easier.

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Table 1. Characteristics of the study sites.

Plot ID	Elevation (m a.s.l.)	Aspect (°N)	Slope (°)	MAP[a] (mm y^{-1})	Parent material	Dominating tree species	Land use	Soil classification (WRB) (Egli et al., 2006)
North-facing sites								
N01	1180	340	31	950	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
N02	1390	0	28	1000	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
N03	1620	0	29	1060	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Endoskeletic Cambisol (Dystric)
N04	1930	20	12	1180	Paragneiss debris, moraine material	*Larix decidua*	Originally used as pasture	Episkeletic Podzol
South-facing sites								
S06	1185	160	31	950	Paragneiss debris	*Picea abies*	Ex-coppice, natural forest (ecological forestry)	Episkeleti-Endoleptic Cambisol (Chromi-Dystric)
S07	1400	145	33	1000	Paragneiss debris	*Larix decidua*	Natural forest (ecological forestry)	Dystri-Endoskeletic Cambisol
S08	1660	210	33	1060	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Skeletic Umbrisol
S09	1995	160	25	1180	Paragneiss debris	*Larix decidua*	Ex pasture, natural forest	Skeletic Umbrisol

[a]MAP = mean annual precipitation (Sboarina and Cescatti, 2004)

Table 2. The five decay-class system of log decomposition (according to Hunter, 1990).

Log features	Decay classes 1	2	3	4	5
Bark	Intact	Partially absent	Absent	Absent	Absent
Twigs	Present	Partially absent or absent	Absent	Absent	Absent
Shape of radial section	Round	Round	Round	Oval	Very oval
Colour	Original	Original	Faded in the external part	Reddish brown or faded	Reddish or faded
Texture of wood	Intact	Intact	Soft outer layer, intact inner part	Small pieces, soft	Powdery or fibrous, very soft
Contact with soil	Log elevated on what remains of branches	Log in contact with soil	Log in contact with soil	Log in contact with soil	Log in contact with soil and partially buried

Table 3. Typical properties and ages of Norway spruce and European larch CWD in class 1 – 3. Ages were obtained mostly from dendrochronological measurements and a few* from ^{14}C-dating (Detail of ^{14}C-dating cf. Appendix A).

Plot	Tree species	Decay class	Density (g cm^{-3})	Cellulose (%)	Lignin (%)	Year of death	CWD age
N03	Norway spruce	1	0.32	34.8	22.4	2009	4
S08	Norway spruce	1	0.40	31.3	33.2	1992	21
N01	Norway spruce	1	0.45	43.4	22.0	1988	25
N02	Norway spruce	1	0.44	41.4	23.3	1969	44
N03	Norway spruce	2	0.39	41.4	35.9	2006	7
N03	Norway spruce	2	0.44	28.4	25.0	2004	9
N03	Norway spruce	2	0.39	27.8	25.9	2004	9
S08	Norway spruce	2	0.36	38.2	23.1	2003	10
N02	Norway spruce	2	0.11	39.2	14.2	1996	17
N03	Norway spruce	2	0.43	40.8	21.5	1993	20
N01	Norway spruce	2	0.39	28.2	24.3	1970	43
N02	Norway spruce	2	0.67	27.8	25.9	1959	54
N03	Norway spruce	3	0.48	43.6	23.4	2012	1
N03	Norway spruce	3	0.38	36.6	24.2	2005	8
N03	Norway spruce	3	0.39	37.4	10.7	2005	8
N01	Norway spruce	3	0.30	22.3	35.1	1979	34
N02	Norway spruce	3	0.48	33.5	24.6	1970	43
S09	European larch	1	0.60	37.2	21.1	2010	3
N04	European larch	1	0.59	44.2	16.9	1973	40
S07*	European larch	1	0.31	21.2	39.6	2007	6
S07	European larch	2	0.58	20.2	38.0	2010	3
S09	European larch	2	0.53	37.3	31.0	2000	13
S07*	European larch	2	0.30	30.4	40.6	2003	10
S07*	European larch	3	0.27	6.7	63.0	2004	9
S09*	European larch	3	0.60	4.2	40.8	1973	40
S09*	European larch	3	0.33	23.3	58.4	1968	45

Table 4. Typical properties and radiocarbon data of the deadwood samples (decay classes 4 and 5) as a function of site and tree species.

UZH number	ETH number	Sample code	Site	Tree species	Decay class	Density (g cm^{-3})	Cellulose (%)	Lignin (%)	^{14}C-age years	±1σ	δ^{13}C ‰	±δ^{13}C ‰	cal AD 2 σ	Average age[1] years	cal AD[2] years (probability)	Average age[1] years
UZ 6210	ETH-56612	37A	N4	European larch	4	0.26	34.6	27.9	-2931	29	-23.6	1	1962-1974	45		
UZ 6211	ETH-56613	34A	N4	European larch	4	0.40	1.0	47.2	170	31	-24.4	1	1658-1950	209	1720-1819 (50%)	244
UZ 6213	ETH-56615	50A	S9	European larch	4	0.15	2.3	43.2	-659	31	-26.5	1	1957-2003	33		
UZ 6219	ETH-56853	95A	S7	European larch	4	0.21	16.7	38.4	-860	25	-25.5	1	1957-1998	36		
UZ 6227	ETH-56861	209	S7	European larch	4	0.33	0.0	47.2	-2545	25	-25.3	1	1962-1976	44		
UZ 6228	ETH-56862	214	S7	European larch	4	0.33	16.5	28.7	60	25	-23.9	1	1695-1919	206	1867-1919 (53.3%)	120
UZ 6212	ETH-56614	45B	S9	European larch	5	0.34	25.9	29.4	183	31	-27	1	1650-1950	213	1726-1815 (51.5%)	243
UZ 6224	ETH-56858	202	S9	European larch	5	0.25	0.0	58.1	140	25	-28.9	1	1669-1944	207	1798-1944 (52.6 %)	142
UZ 6264	ETH-60747	33	N4	European larch	5	0.28	0.0	49.4	185	25	-29.4	1	1656-1950	220	1728-1810 (54.7 %)	244
UZ 6214	ETH-56616	69A	S6	Norway spruce	4	0.13	23.3	25.2	-1331	30	-31.3	1	1958-1989	40		
UZ 6215	ETH-56849	72A	S6	Norway spruce	4	0.37	0.0	51.7	-2120	25	-23.6	1	1961-1980	43		
UZ 6216	ETH-56850	84A	S8	Norway spruce	4	0.16	32.4	29.1	-4080	25	-27	1	1966-1967	47		
UZ 6220	ETH-56854	97B	N2	Norway spruce	4	0.26	28.1	36.1	-3720	25	-31.4	1	1967-1968	46		
UZ 6221	ETH-56855	98A	N3	Norway spruce	4	0.26	0.0	67.0	-290	25	-19.7	1	1955-2009	31		
UZ 6226	ETH-56860	206	N3	Norway spruce	4	0.29	28.5	20.5	-2150	25	-23.9	1	1962-1979	43		
UZ 6217	ETH-56851	87A	S8	Norway spruce	5	0.13	1.5	66.8	130	25	-26.1	1	1677-1940	205	1800-1940 (59.5%)	143
UZ 6218	ETH-56852	89A	S8	Norway spruce	5	0.27	17.6	27.7	-615	25	-24.6	1	1956-2004	33		
UZ 6222	ETH-56856	106A	N1	Norway spruce	5	0.19	4.3	68.5	-1665	25	-25.2	1	1959-1984	42		
UZ 6223	ETH-56857	197	N1	Norway spruce	5	0.19	0.0	40.2	-4595	25	-24	1	1963-1965	49		
UZ 6225	ETH-56859	205	N2	Norway spruce	5	0.19	0.0	44.3	10	25	-22.9	1	1699-1916	206	1879-1916 (82.2 %)	116

[1] Calculated as the mean value between the maximum and minimum age (2 σ). For this range of years (2 σ), associated probabilities are summed to 95.4 %

[2] For samples dated in the period before the bomb peak and giving a wide calibrated age range, the age is also calculated for the most important calibrated time-range associated to the highest, corresponding probability (in brackets)

Table 5. Mean residence time and decay constants calculated using the stage-based matrix model of Kruys et al. (2002)

Decay class	No of samples		Mean residence time		Decay constant (y^{-1})	
	Spruce	Larch	Spruce	Larch	Spruce	Larch
1	4	3	77	80	0.013	0.012
1+2	8	3	36	47	0.027	0.021
1+2+3	4	3	28	67	0.036	0.015
1+2+3+4	6	6	63	116	0.016	0.009
1+2+3+4+5	5	3	63	254	0.016	0.004

Table 6. CWD decay parameters based on a) equation 1, b) the regression approach and c) stage-based matrix model of Kruys et al. (2002)

	Average decay constant *k* (y^{-1})	Residence time* (y)	Half-life* (y)
a)			
Norway spruce	0.018	56	39
European larch	0.012	83	58
b)			
Norway spruce	0.012	84	58
European larch	0.005	222	154
c)			
Norway spruce	0.022	45	32
European larch	0.012	83	58

*calculated from the average decay constant

Appendix A. Radiocarbon data of the deadwood samples of the decay classes 1 – 3.

UZH number	ETH number	Sample code	Site	Tree species	Decay class	C14 age	±1σ	$\delta^{13}C$ ‰	$\pm\delta^{13}C$ ‰	Cal AD ±1σ	Average age years
UZ-6258	ETH-60741	L_10_c1_1	S7	European Larch	1	-435	25	-25.7	1	2006-2009	6
UZ-6260	ETH-60743	S07_dc2_92	S7	European Larch	2	-590	25	-26.9	1	2002-2004	10
UZ-6261	ETH-60744	S07_dc3_96	S7	European Larch	3	-545	25	-26.4	1	2003-2005	9
UZ-6262	ETH-60745	S09_cl3_46	S9	European Larch	3	-2865	25	-29.3	1	1973-1974	40
UZ-6263	ETH-60746	S09_cl3_48	S9	European Larch	3	-2775	25	-23.8	1	1962-1974	45

[1)] Calculated as the mean value between the maximum and minimum age (1 σ). For this range of years (1 σ), associated probabilities summed to 68.2 %

Figure captions

Fig. 1. Location of the study area with the major vegetation units and investigation sites. Data source: Museo delle Scienze (Trento), CORINE Landcover (Joint Research Center of the European Union) and scilands GmbH. The site label N indicates north-facing sites and S south-facing sites.

Fig. 2. Cross section of (A) spruce deadwood in the field (site N03) and (B) larch deadwood (site S07). Examples (C and D) of deadwood fragments classified as decay class 4 dated using radiocarbon (outermost part of the wood piece).

Fig. 3. Master chronologies for spruce and larch to cross-date the deadwood (A) and the expressed population signal (EPS) for segments of constant periods (B). A noise-free chronology is achieved with an EPS > 0.85 (dashed line; Wigley et al., 1984)

Fig. 4. Box plots of the larch and spruce deadwood age as a function of decay class.

Fig. 5. Relation between the age of spruce and larch CWD and density (A), cellulose % (B) and lignin % (C). The decay classes 1 – 3 were grouped together due to their similar age (Fig. 4).

Fig. 6. Calculated decay rate constants (k) as a function of tree species and site exposure.

Fig. 7. Empirically determined exponential regression curves (principle of multiple-exponential model) for partitioning the decay behaviour of cellulose (A) and lignin (B).

Fig. 1

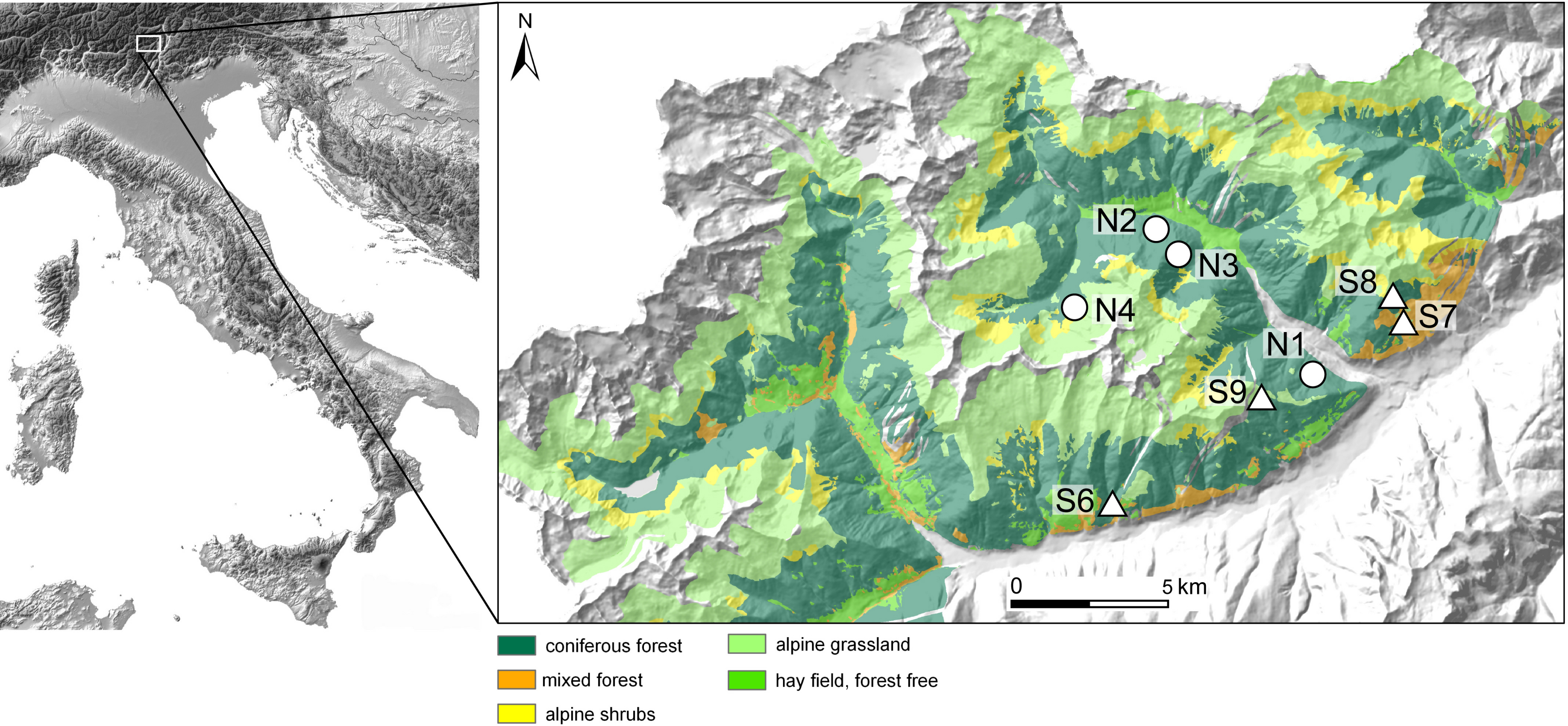

N
N2
N3
N4
N1
S8
S7
S9
S6
0
5 km
coniferous forest
mixed forest
alpine shrubs
alpine grassland
hay field, forest free

Fig. 2

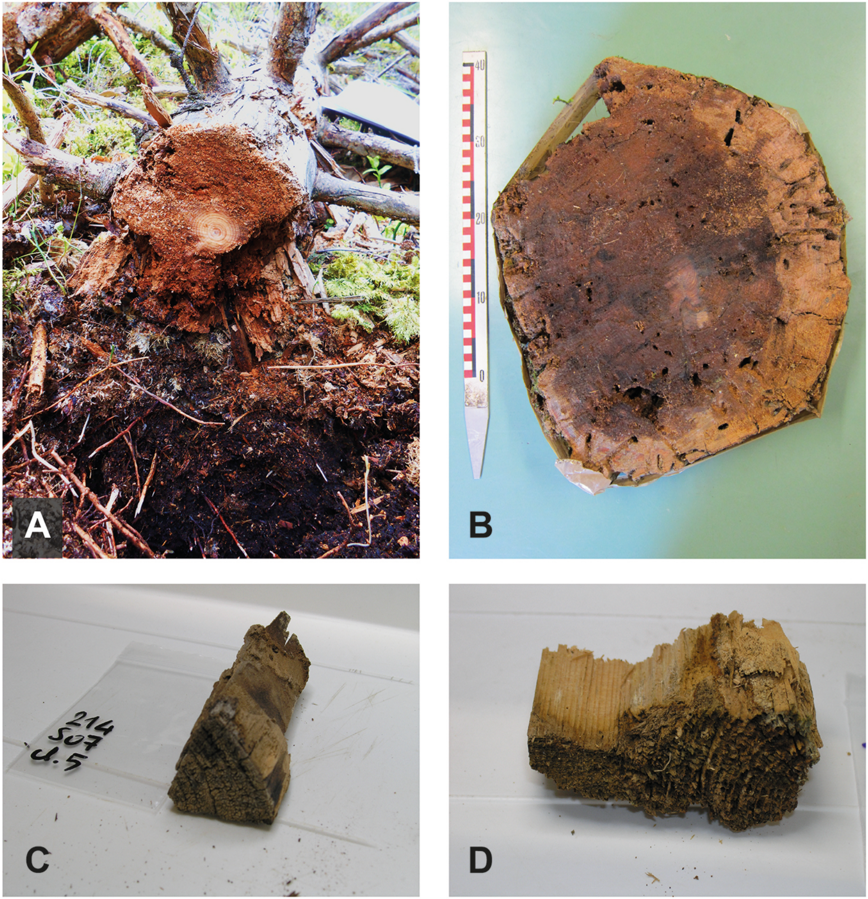
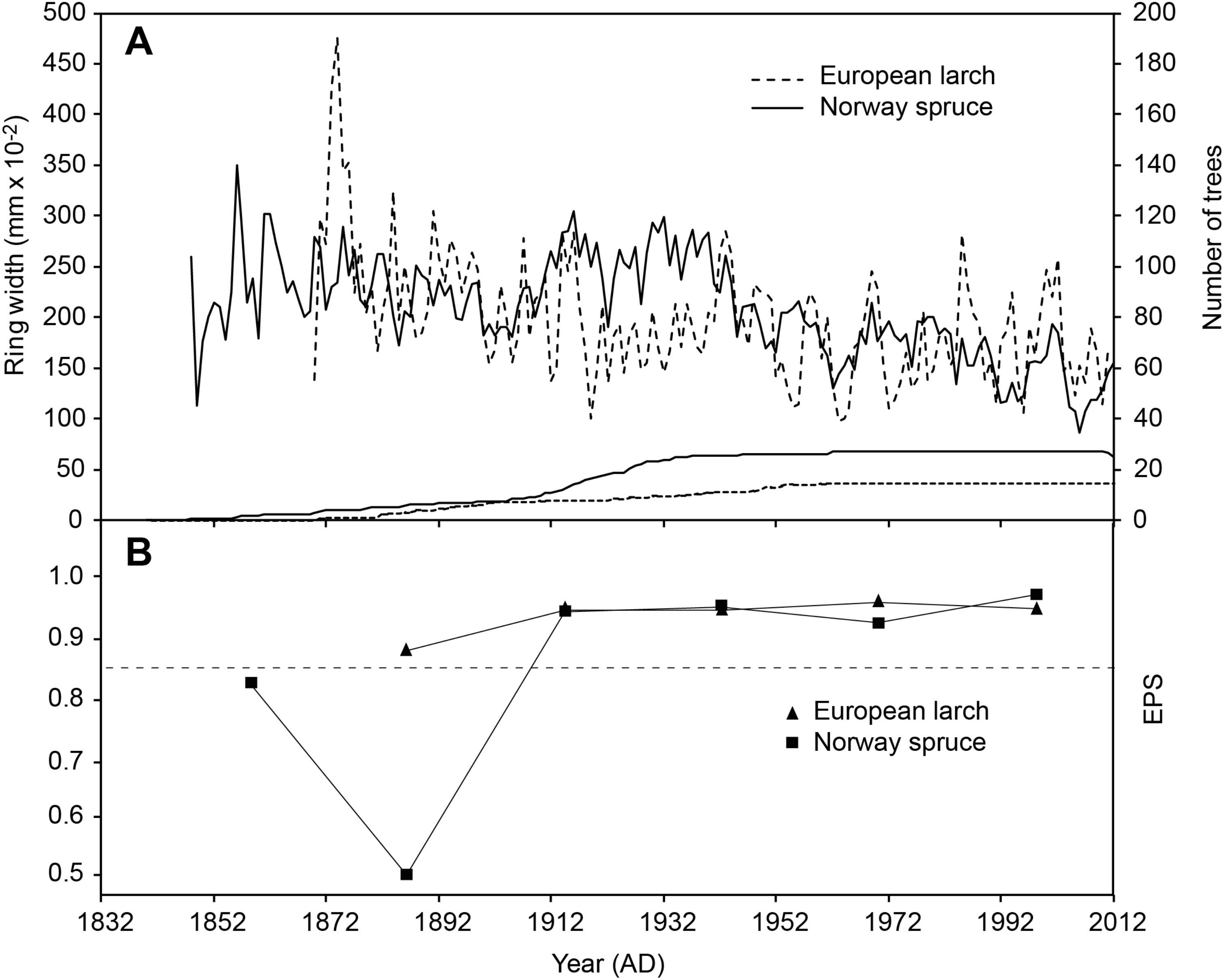
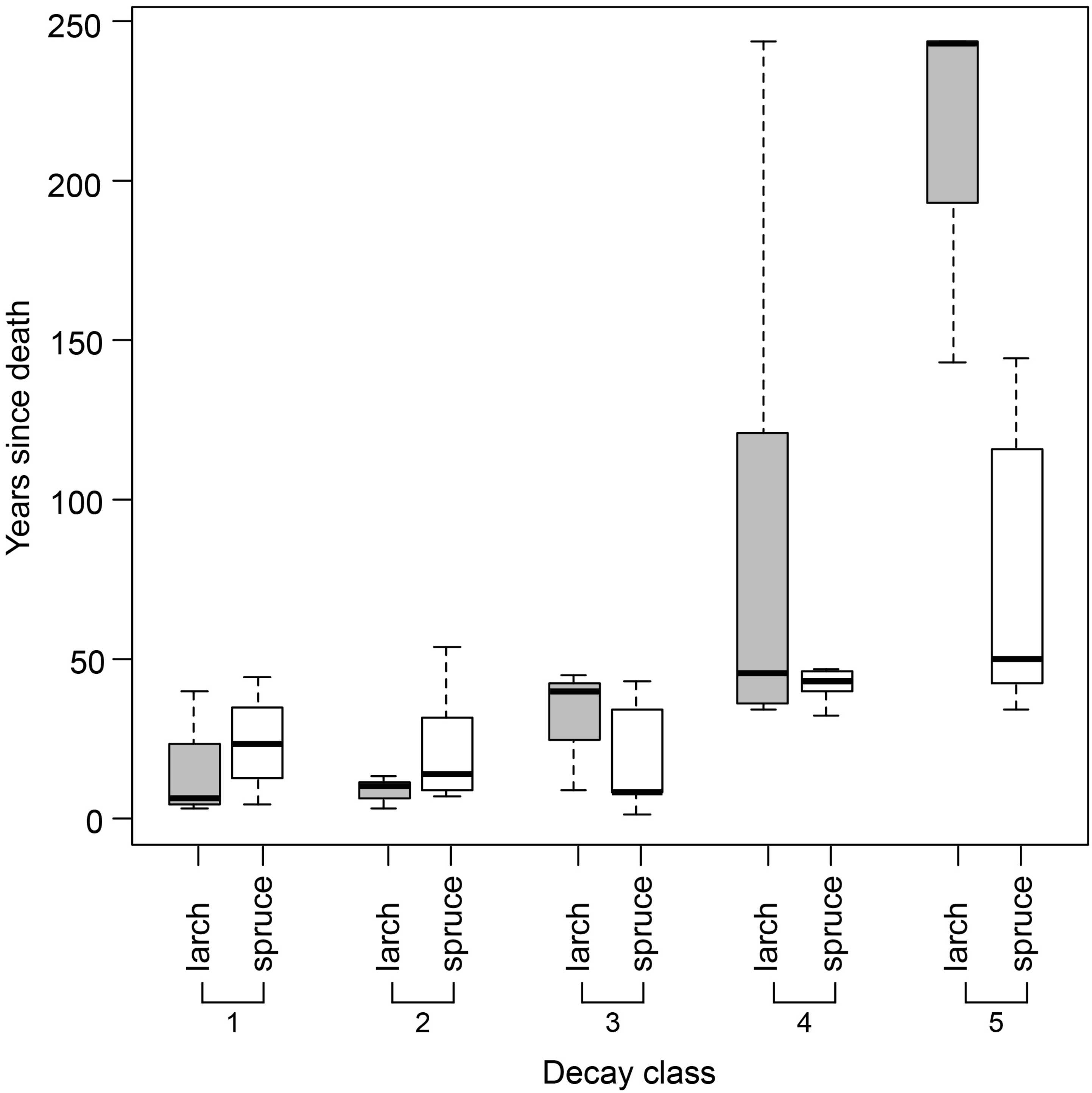


Fig. 3



A
European larch
Norway spruce
Ring width (mm x 10-2)
Number of trees
500
450
400
350
300
250
200
150
100
50
0
200
180
160
140
120
100
80
60
40
20
0
B
European larch
Norway spruce
EPS
1.0
0.9
0.8
0.7
0.6
0.5
1832
1852
1872
1892
1912
1932
1952
1972
1992
2012
Year (AD)

Fig. 4



250
200
150
100
50
0
Years since death
larch
spruce
1
2
3
4
5
Decay class

Fig. 5

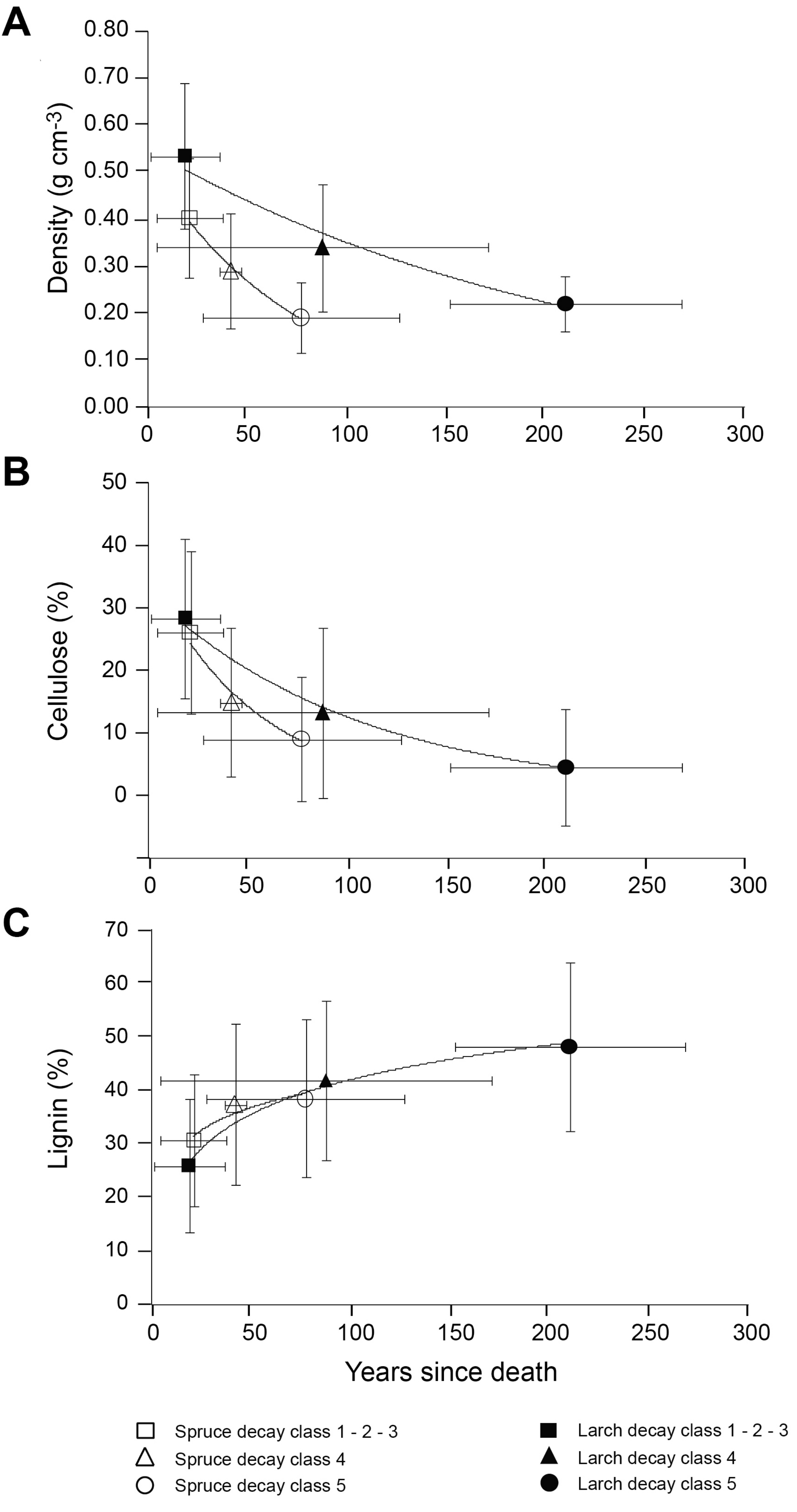
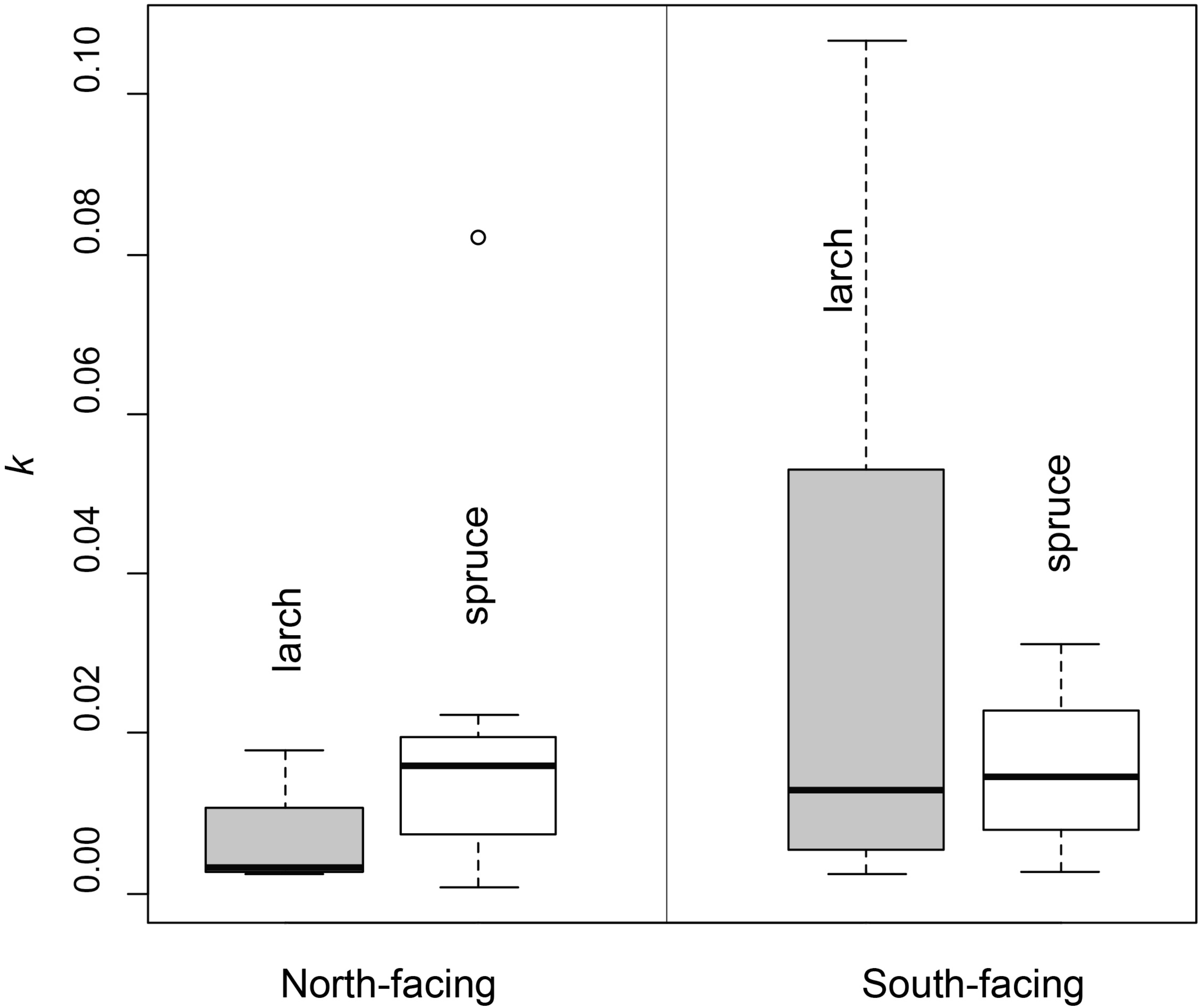
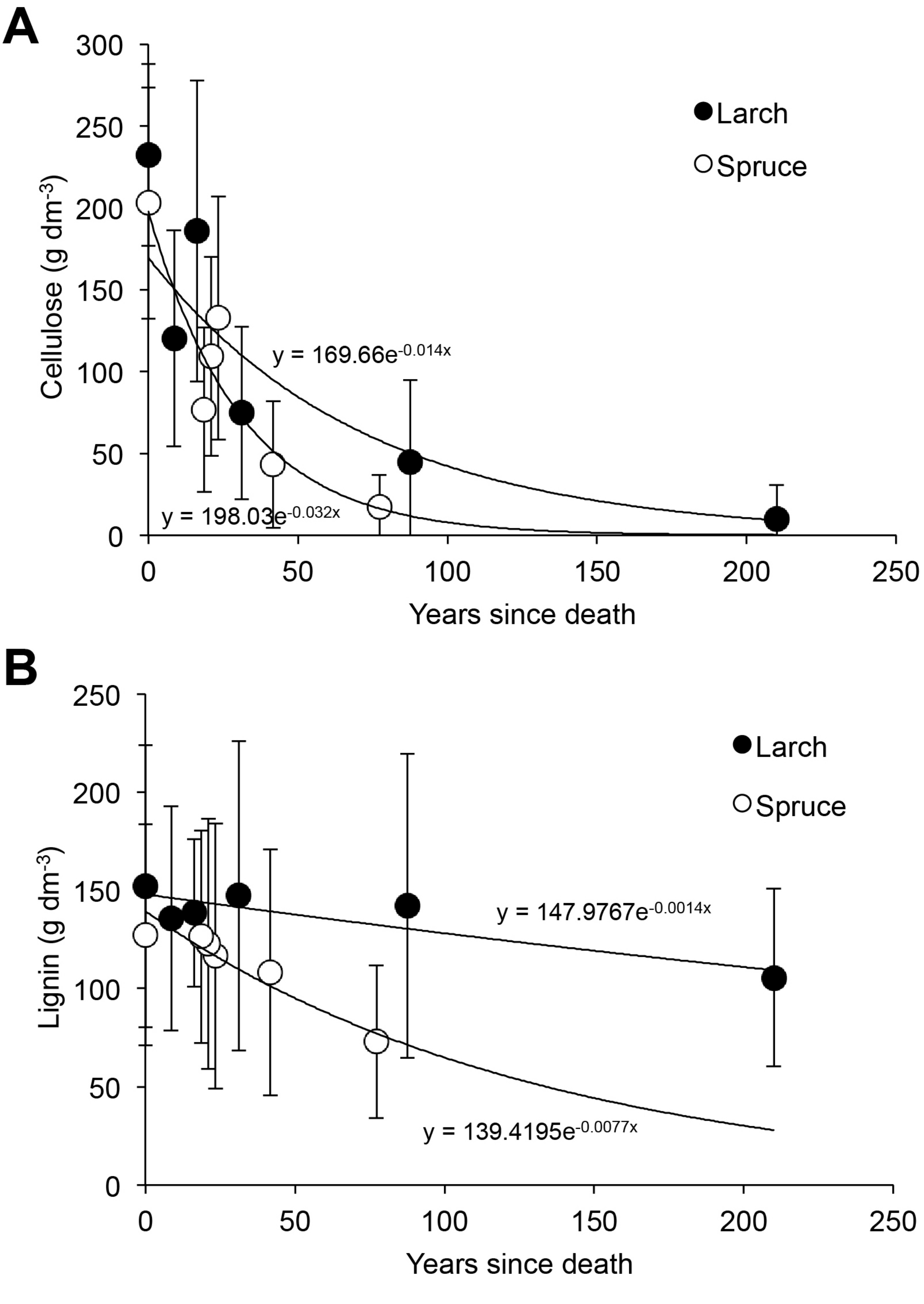

A
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Density (g cm-3)
0
50
100
150
200
250
300
B
50
40
30
20
10
0
Cellulose (%)
0
50
100
150
200
250
300
C
70
60
50
40
30
20
10
0
Lignin (%)
0
50
100
150
200
250
300
Years since death
Spruce decay class 1 - 2 - 3
Spruce decay class 4
Spruce decay class 5
Larch decay class 1 - 2 - 3
Larch decay class 4
Larch decay class 5

Fig. 6



0.10
0.08
0.06
0.04
0.02
0.00
k
larch
spruce
larch
spruce
North-facing
South-facing

Fig. 7



A
Cellulose (g dm-3)
300
250
200
150
100
50
0
Larch
Spruce
y = 169.66e-0.014x
y = 198.03e-0.032x
0
50
100
150
200
250
Years since death
B
Lignin (g dm-3)
250
200
150
100
50
0
Larch
Spruce
y = 147.9767e-0.0014x
y = 139.4195e-0.0077x
0
50
100
150
200
250
Years since death