Quantifying decay progression of deadwood in Mediterranean mountain forests

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This document is the accepted manuscript version of the following article:
Fravolini, G., Tognetti, R., Lombardi, F., Egli, M., Ascher-Jenull, J., Arfaioli, P., … Marchetti, M. (2018). Quantifying decay progression of deadwood in Mediterranean mountain forests. Forest Ecology and Management, 408, 228-237.
https://doi.org/10.1016/j.foreco.2017.10.031

Abstract

Forests contribute to the sequestration of organic carbon (C). A key role in forest C cycling is played by deadwood. While a broad range of literature on deadwood decay (above-ground) exists, the mechanisms occurring in the transition zone from deadwood to the humus are poorly understood. In particular, scarce information is available on the temporal patterns of wood compounds (such as lignin and cellulose) during decay processes.

Our objective was to provide a deeper understanding on deadwood decay in a Mediterranean montane environment by focussing on semi-natural forests of *Fagus sylvatica* L. (beech). The decay process was studied in a field experiment (in the Majella mountains, Apennine Mountains, Italy) among an altitudinal transect at different climatic conditions. Beech wood blocks (mass, cellulose, lignin) having all an equal in size (5 cm x 5 cm x 2 cm) were placed in soil mesocosms to investigate over one year changes in the overall mass, cellulose and lignin content. The sites were along an altitudinal gradient, reflecting different climatic conditions. The effect of exposure (north- vs. south-facing slopes) was also considered. Deadwood, cellulose and lignin dynamics were related to soil parameters (pH, grain size, moisture, temperature) and climate data. Deadwood decayed very fast and followed an exponential trend. The decay rate constants of the deadwood mass significantly (positively) correlated with air temperature and soil moisture: the lower the temperature, the lower the evapotranspiration, the higher the moisture availability, and the higher the decay rates. Lignin decayed more slowly than cellulose, resulting in average decay rate constants (k) between 0.368 and 0.382 y^{-1}. Soil properties and topographic traits (slope and exposure) strongly influenced the decay processes. At south-facing sites (having an altitude < 1300 m a.s.l., above sea level), decay processes were lower owing, most likely, to drier conditions. The climosequence revealed slower beech deadwood decay processes in south- than north-facing sites of these Mediterranean mountains, owing to the drier conditions. In-field mesocosms were useful to define meaningful indicators of warming-induced changes on the linkages between C storage in beech deadwood and decomposition processes as a function of altitude and exposure.

Key words: Coarse woody debris; beech forests; organic matter; forest soil; Apennines.

Introduction

The importance of deadwood in forest ecosystems is undeniable, not only in terms of biodiversity it provides, but also in terms of carbon sequestration and emission. Within this context, deadwood is recognised as one of the most important functional and structural components of forest ecosystems (Harmon et al., 1986; Paletto et al., 2012; Marzano et al., 2013), and is considered an indicator of biodiversity conservation (Lassauce et al., 2011) and long-term carbon (C) storage, especially in temperate-cold climate environments (Ravindranath and Ostwald, 2008).

Structural characteristics of standing or downed deadwood provide habitats for different species. Habitat provision for organisms such as nesting birds, refuge for rodent species from predation and safe sites for overstory tree regeneration (Harmon and Franklin, 1989; Heinemann and Kitzberger, 2006) have all been revealed as important roles of deadwood in natural temperate forests (Gonzalez et al., 2013). Due to its slow decomposition and persistence on the forest floor (Beets et al., 2008), deadwood represents a substantial reservoir of organic C and nutrients in many forest ecosystems (Carmona et al., 2002; Ganjegunte et al., 2004).

At the ecosystem scale, variations in the deadwood amount are suggested to occur in relation to forest type, species composition, disturbance regime (natural and anthropogenic) and successional stage (Gonzalez et al., 2013). In particular, coarse woody debris (CWD), considered as standing dead trees, downed woody debris, and stumps, is a critical component of forest ecosystems since it retains essential nutrients, stores water, contributes to soil development and conservation, and provides habitat for plants and animals, insects, fungi and bacteria (Harmon et al., 1986). CWD decay and the related nutrient mineralisation create unique conditions of microsite heterogeneity (Campbell and Laroque, 2007; Fravolini et al., 2016). However, the dynamics of C exchange and storage of the CWD pool remain poorly understood (Harmon et al., 1986; Scheller and Mladenoff, 2002).

The decomposition process of CWD can take up decades to several centuries (Lombardi et al., 2012; Petrillo et al., 2016), depending on wood characteristics (tree species, dimensions), climate (temperature and moisture; Woodall and Liknes, 2008) and the position on the ground (i.e., contact with the soil; Radtke and Bolstad, 2004). Most of the available information on decay processes refers to CWD as mass (Russell et al., 2015), and almost no data exists on the temporal behaviour of its chemical components such as lignin or cellulose, especially for Mediterranean mountain forests (Fravolini et al., 2016; Lombardi et al., 2013).

Contrasting results in CWD decay rates can be explained in part by the methodologies employed or by the different climates in which the studies were performed (Forrester et al., 2012). In moisture-limited regions, decay progression would be expected to be slow, whereas, in relatively wet forests and environments, climate conditions should promote higher decomposition rates (Progar et al., 2000; Chambers et al., 2001). In Alpine forests, Fravolini et al. (2016) have shown an interactive effect of temperature and moisture on decay dynamics. A number of other variables, including wood density, debris size, nutrient content and the contact with the soil surface, may influence decomposition dynamics (Mackensen et al., 2003; Shorohova et al., 2008), as much as micro-environmental factors surrounding the wood.

Wood density, that tells how much C the plant allocates into construction costs (Chave et al., 2006), has often been used to describe decay processes (Schwarze et al., 1999; Schäfer, 2002), as being easily measurable (Sollins et al., 1987; Mackensen et al., 2003). This procedure, however, may underestimate decay dynamics (Petrillo et al., 2016) and does not provide quantitative information on the transition phases of chemical components from woody debris to humus form. As proposed by several authors (Lombardi et al., 2013), lignin and cellulose concentrations may be used to better assess decay patterns of CWD associated with specific site characteristics, such as the microclimatic conditions of topsoil and boundary layer.

Among broadleaved species, *Fagus sylvatica* L. (beech) is a dominant or co-dominant tree in European deciduous forests. However, the process of decomposition and the changes in deadwood properties for beech over several stages of decomposition has been rarely addressed (Christensen et al., 2005; Kahl, 2008; Müller-Using and Bartsch, 2009; Herrmann et al., 2015). These studies indicate small differences in wood density between decay classes, and attribute variation in decomposition rates of beech deadwood to the uncertainty over the cause of death. In central European beech forests, decomposition time and debris dimension (and species) are considered the most important information needed to develop regional decomposition model (Herrmann et al., 2015). Although beech represents a major forest type also in Mediterranean mountain ecosystems (Nocentini, 2009), decomposition processes of deadwood in these forests have been poorly addressed so far (Lombardi et al., 2013).

We focused on early dynamics of deadwood decay in Mediterranean montane beech forests, characterised by a temperate climate. Our principal aims were: i) to determine early decomposition stages in wood blocks of beech under controlled conditions in the forest toposoil, and ii) to quantify the decay rates of its main chemical constituents, i.e., lignin and cellulose. In addition, we related deadwood decay progression to major environmental drivers, i.e., climatic conditions (temperature and precipitation), slope aspects (north- vs. south-facing sites) and soil characteristics (chemical and physical traits). We expected that climate forcing was more effective, accelerating decomposition processes of wood blocks, on south- than north-exposed slopes and at lower than higher altitudes.

Material and Methods

Study area

The investigation area is located in the Majella National Park (Abruzzo, central Italy; Fig. 1, Table 1). The National Park, extending approximately 740 km^2, was established in 1991. Four study sites were selected along two climosequences (north vs. south-facing slopes). The altitudinal range of both slopes was between 1170 and about 1480 m above sea level (Table 1).

The climate of the study area ranges mostly from temperate-oceanic to temperate-oceanic with submediterranean characteristics; the mean annual temperature varies from 14 °C at the valley bottom (around 130 m a.s.l.) to about 3 °C above 2000 m a.s.l., with mean annual precipitation ranging from approximately 700 to 1600 mm (CFS meteo data). The geological substrate is carbonate bedrock at all study sites.

The sub-Mediterranean belt between 1000 and 1700 m a.s.l. consists mainly of beech forests, together with downy oak (*Quercus pubescens* Willd., 1805), Turkey oak (*Quercus cerris* L.), different maples (*Acer* spp.), ash species (*Fraxinus* spp.), hop-hornbeam (*Ostrya carpinifolia* Scop.), with the sporadic occurrence of some conifers. The montane area is dominated by almost pure beech semi-natural forests.

Experimental approach

At each site of the climosequence, a field experiment using soil mesocosms was set up, following the procedure given in Fravolini et al. (2016); DACH DecAlp project (https://www.decalp.org). Mesocosms (10.2 cm in diameter, 20 cm long PVC tubes) were inserted (summer 2014) into the soil and placed >1 m from large trees and >0.5 m from the adjacent mesocosms (Fig. 2). Furthermore, normed wood blocks (2 cm x 5 cm x 5 cm), deriving from the same beech tree, were added onto the soil surface of each of the mesocosms. This strategy was used because the size and geometry of deadwood is supposed to strongly influence the decay mechanisms (Van der Wal et al., 2007). The wood blocks (coarse woody debris, CWD) were sampled after 0, 8, 16 and 52 weeks (Fig. 2), always with 3 replicates for each sampling time and study site. The dry mass of these wood blocks was determined by standard methods (48 h in the oven at 105 °C). The fresh weight and dry mass were determined to assess the density and water content of the wood blocks. The initial dry mass (at the start of the experiment) was obtained from the wood blocks at t_0. Afterwards, the blocks were stored at -20 °C until further processing.

Cellulose and lignin extraction

The samples were air-dried at room temperature, cut-milled to 4 mm (Retsch mill), aliquoted into sterile Falcon tubes (50 mL) and stored at 4°C until further processing. Cellulose extraction started with weighing the powdered samples into Teflon pockets (10 mg) (Leavitt and Danzer, 1993; Fravolini et al., 2016). At first, the samples were washed in a 5% NaOH solution, two times at 60 °C. Thereafter, they were washed another three times, using a 7% $NaClO_2$ solution and 96% CH_3COOH at 60 °C, until the pH was in the range between 4 and 5. This procedure extracts lignin from the wood samples. The pockets were dried in the oven at 50 °C; the cellulose content was determined as the difference between the initial weight and that of dried samples.

The total lignin and the Klason lignin, which is insoluble in strong acid (Dence and Lin, 1992), were then measured. The Klason lignin was obtained using a sequential extraction. The method started with the extraction of water-soluble compounds (Dence and Lin, 1992). Ultrapure water (80 °C) was added to 1 g of each sample and stirred 3 times (each time 15 min.). 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 centrifuged again (10 min at 4500 rpm) and the supernatant was discarded. Thereafter, ethanol was again added to the sample and then filtered. The filters were dried over night at 60 °C. In a next step, 3 ml of a 72% H_2SO_4 solution were added to 300 mg of the filter cake, stirred, 84 ml of ultrapure water added, and put into the autoclave for 1 h at 120 °C. This solution was filtered into ceramic crucibles and the liquid evaporated at 110 °C. The weight of the lignin in the crucibles was then measured (Klason lignin). The acid-soluble lignin (ASL; Klason, 1893) in the filtrate was determined at 205 nm using Cary 50 UV-VIS Spectrophotometer; . The total lignin was finally calculated as the sum of the ASL + Klason lignin. The amount of cellulose and lignin is given as mass (concentration of cellulose and lignin × deadwood mass).

Determination of the decay progression

The decay rate can be estimated by the density loss or mass loss of deadwood during a specific 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 expressed by a single-negative-exponential model:

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

where x_t is the density or mass of wood blocks at a given time (t), and x_0 is the initial density or mass (Jenny et al., 1949; Olson, 1963).

Data obtained from a single decay rate constant may not completely reflect the whole decay process. In fact, due to the faster decomposition of cellulose, lignin is relatively enriched. Lignin, however, also decomposes with time. To unravel the decay behaviour of several compounds in wood blocks, a multiple-exponential model can then be applied (Means et al., 1985; Mackensen et al., 2003), using the following equation:

$$x = x_1 e^{-k_1 t} + x_2 e^{-k_2 t} \ldots + x_n e^{-k_n t} \qquad (2)$$

where $x_{1\ldots n}$ are partitioned parameters of the components. From this, the half-life of cellulose or lignin in the CWD can be calculated:

$$t_{1/2} = \frac{\ln(\frac{1}{2})}{-k} \qquad (3)$$

where $t_{1/2}$ is the half-life and k is the decay constant (obtained from the exponential regression curve).

In addition to equation 1, the decay rate constants were estimated on the basis of the mass loss within the observation period, using an exponential regression approach, automatically displaying a decay constant.

Soil parameters

Soil samples were taken from 0 to 5 cm, inside the mesocosms, then air-dried at room temperature and sieved at 2 mm. Soil pH (H_2O) was determined using a soil:solution ratio of 1:10. Total C and N contents were analysed in dried samples, using a CN analyzer (TruSpec CHN; LECO, Michigan, U.S.A.). Particle-size was assessed following the pipette procedure according to Indorante et al. (1990). Soil bulk density was determined according to Grossman and Reinsch (2002). Humus forms were determined in the field, according to Zanella et al. (2011).

Statistical analysis

The statistical analyses were performed using the IBM SPSS Statistics 21 software (IBM, Chicago, IL, USA). The data distribution was tested using a Shapiro Wilk test. If the test indicated a normal distribution of the data, a t-test or an analysis of variance (ANOVA) was then carried out. In the case of non-normal data distribution, the Mann-Whitney (U-test) or Kruskal-Wallis tests were used to detect differences along the altitudinal gradient and, in particular, between the north- and south-facing sites. Considering that some of the datasets showed a non-normal distribution, the Spearman rank correlation coefficient was applied. A correlation analysis was carried out to infer the influence of environmental conditions (soil, climate) on cellulose, lignin and deadwood decay. All the statistical tests were carried out using a level of significance of 0.05.

Results

Decay rates and half-lives

During the one-year study, wood mass, cellulose and lignin changed significantly in all the study sites (Figs. 1, 2 and 3). In all cases, a distinct (wood mass, cellulose and lignin) loss was recorded. The *k*-values of wood blocks, lignin and cellulose were estimated using the single negative exponential model and an exponential regression curve approach from which also a k-value can be derived (Table 3). The two calculation procedures (equation 1 and the regression approach) displayed quite similar results with *k*-values for wood blocks, on average, in the range of 0.368 to

0.382 y^{-1}. Typically, the minimum *k*-value of 0.215 y^{-1} was registered at a south-facing plot and the maximum (0.496 y^{-1}) at a north-facing plot.

The biochemical data of wood blocks are reported in Figures 2 and 3. Also here, both calculation procedures displayed similar values. The average *k*-value for cellulose was between 1.034 and 1.130 y^{-1} and for lignin between 0.205 to 0.210. Consequently, the *k*-values for lignin were considerably lower than for cellulose and wood blocks.

Using the average *k*-values, the half-life was calculated for deadwood, lignin and cellulose. The deadwood half-life varied (as an average) between 1.82 years (single negative exponential model) and 1.88 years (exponential regression curve approach). The half-life for cellulose averaged 0.61 years using the negative exponential model and 0.67 years using the exponential regression approach. For lignin, the calculation of the half-life showed an average between 3.39 (single negative exponential model) and 3.31 (exponential regression curve approach). However, along the altitudinal gradient, the lignin half-life considerably varied (on average) between 1.4 and 55 years; the higher values were found on the south exposure.

Effects of environmental parameters on deadwood decay

Environmental traits and soil data are reported in Tables 1 and 2, respectively. The texture of the soils is predominantly sandy at all the studied sites; all soils exhibit neutral pH conditions.

The *k*-values of cellulose correlated with both climatic parameters, such as mean annual precipitation (MAP) or mean annual air temperature (MAAT). The deadwood *k*-values (Table 4) were related to MAAT, MAP ($p < 0.05$), soil inorganic C, pH, soil moisture and sand content. The lignin *k*-values correlated with MAAT ($p < 0.05$) and, similarly to wood blocks, to MAP, soil inorganic C, pH, moisture and sand content. The cellulose, lignin and wood blocks showed a good correlation with MAAT, soil moisture and inorganic C and sand content.

The Mann-Whitney test indicated that lignin and wood blocks decomposed faster ($p < 0.05$; Table 5) at north-facing sites than at south-facing sites. Lignin and deadwood half-lives were subsequently higher on south facing-sites, reaching values of 26 and 3 years at S2, respectively. On north-facing sites, lignin half-life was between 2 and 4 years while deadwood half-life was less than 2 years. Significant correlations between the amount of lignin and MAAT, deadwood amount, and MAP were found.

The *k*-values, and the mass of wood components (deadwood mass and lignin mass) differed significantly between north- and south-facing sites. The Mann-Whitney test indicated that cellulose, lignin and wood blocks decayed significantly ($p < 0.05$; Table 5) faster on north-facing sites. The lignin half-life was, however, higher at the uppermost south-facing site.

Discussion

Wood decomposition rates

The field mesocosms proved to be very useful in assessing and monitoring the initial phases of deadwood decay in a typical beech forest ecosystem of the Apennines. Although the observation period was short (1 year), the experimental approach carried out under 'standardised' conditions (as far as possible) enabled the derivation of *k*-values for cellulose, lignin and deadwood mass of beech. Both approaches to calculate the *k*-values (single negative exponential model and exponential regression curve approach) gave comparable values.

The range of the measured *k*-values for the deadwood mass varied between 0.215 and 0.481 y^{-1}. The average *k*-values determined in this study (0.368 to 0.382 y^{-1}) were relatively high. Müller-Using and Bartsch (2009) reported for beech trees in Germany *k*-values of 0.35 y^{-1} (mean) for bark and 0.178 y^{-1} for deadwood (1 to 10 cm in diameter). In our study, the mean *k*-values were clearly higher than those reported by Hermann et al. (2015) for beech (0.054 y^{-1}), but closer to *k*-values found by Ricker et al. (2016) in the south-eastern USA for red maple. The high decay rates can be related, among others, to the size of deadwood (Tarasov and Birdsey, 2001); the smaller the size of deadwood, the faster the decomposition rate. Ostrogovic et al. (2015) studied deadwood decay in *Quercus robur* L., *Carpinus betulus* L., *Alnus glutinosa* Gaernt., *Fraxinus angustifolia* L., with a deadwood size between 1 and 7 cm. The overall *k*-values were 0.182 y^{-1} for *Q. robur*. With a smaller diameter, the rates were between 0.189 y^{-1} and 0.217 y^{-1}. The same study gave also changing *k*-values for *C. betulus* with diameter (from 0.292 y^{-1} with diameter to 0.189 y^{-1}). Johnson et al. (2014) reported a mean value of 0.095 y^{-1} (mass, volume) for American beech (*Fagus grandifolia* Ehrh.) and Rock et al. (2008) obtained of 0.07 y^{-1} based on the density approach.

The exponential decay model approach has been widely used in analysing empirical data and modelling decomposition rates (Olson, 1963). However, a constant *k* assumes a constant relative decomposition rate through time and requires that the decaying material can be treated as a homogeneous mass, which may not apply to heterogeneous deadwood organic matter (Cornwell and Weedon, 2014). Indeed, several authors criticised this approach (e.g., Makinen et al., 2006). A time lag may occur for decomposers to become established (Harmon et al., 2000; Hérault et al., 2010), because deadwood and soil initially form a loose system, and decay proceeds slowly for several years, before the rate increases and approximate exponential decay proceeds (Kueppers et al., 2004; Zielonka, 2006; Lombardi et al., 2013). In our approach, beech wood blocks used were in contact with the soil since the very beginning of decay. The single exponential model function nicely described the patterns of initial decomposition stages. If there had been a time lag until establishment of the organisms that are necessary for the wood decay, then the k-values would be even higher (which rather seems unrealistic). The observed trend however gives no reason to assume that such a time lag has occurred. Differences in wood decay between studies can be due to specific site conditions and species-site combinations, in which the decomposition started. In nature, a certain proportion of deadwood may stay upright for many years before it falls on the forest floor (e.g., trees killed by insects). A tree infected by rot fungi may fall down only a few years after its death and is subject to a much faster decay rate (Stouranet and Rolstad, 2002).

Temperature and precipitation were key variables in early stages of deadwood decay (Table 4).

A negative relationship between the decay constant of wood blocks and air temperature was found in our study. Along the climosequence, the cooler the climate the faster was the decay rate of lignin (not significant for cellulose and deadwood). In an Alpine environment, Ascher et al. (2012), using a climosequence approach, found evidences that thermal conditions (exposure and altitude) shape soil traits and the microbial community. In Mediterranean mountain environments, lower air temperatures correlate with a higher soil (lower evaporative demand) and wood moisture, higher moisture availability accelerating the decay of organic matter. Saproxylic organisms, including fungi (being inactive with less than 20% humidity), strongly rely on the availability of woody resource to complete their life-cycle and, in turn, on the moisture content of deadwood (Cornelissen et al., 2012; Fukasawa and Matsuoka, 2015). Together with the mild climate, optimal conditions for a fast wood decay are created. Here, moisture availability was probably regulated more by evaporative demand (temperature) than water supply (precipitation). In addition, the *k*-values of cellulose were not significantly affected by any of the considered explanatory factors.

In-field investigations on the course of decomposition of beech deadwood are scarce (e.g., Ódor et al., 2006; Lombardi et al., 2013), as well as on the process of decomposition at different stages of decay and changes in deadwood properties over time (e.g., Herrmann et al., 2015; Arnstadt et al., 2016). A clear tendency for a rapid initial CWD density loss followed by a stable density phase was a common observation in these studies. Hövemeyer and Schauermann (2003), investigating the decay of fine woody debris in litterbags (diameter 4.3–11.5 cm) in a beech stand on calcareous soil (Gottingen Forest, Lower Saxony, Germany), observed that 40% and 60% of the wood was decomposed under the litter layer after 2 and 6 years, respectively.

Relationships between decay processes and environmental conditions

Wood blocks progressively showed increasing relative mass loss rates, down to 50–60% mass loss, probably because of the progressive loss of initial heartwood resistances over time (Harmon et al., 1986). Several factors may simultaneously account for the increase in relative decomposition rates from early to intermediate stages of decay. First, leaching of constitutive wood compounds increase progressively with the progress of decay phases (e.g., dissolved organic C, polyphenols; Spears and

Lajtha, 2004), as permeability to water and microbial colonization rise, and the highly polymeric wood compounds are degraded into soluble fractions (Harmon et al., 1986). This feature is more pronounced in CWD of high density or in species producing hydrophobic resins (e.g., *Pinus* spp.). Second, as wood decay advances, microbial decomposers gather and accumulate nutrients, limiting microbial growth and activity through a variety of mechanisms (Cornwell et al., 2009). This strong initial nutrient acquisition by microbial decomposers may be progressively reinvested towards lignocellulolytic enzyme production (Sinsabaugh et al., 1993; Weedon et al., 2009). Finally, invertebrate decomposers and microbial activity reduce wood particle size, and the consequently higher surface-to-volume ratio results in faster decomposition (Harmon et al., 1986). Decomposition models can be developed on the basis of species-specific information on decomposition time and debris dimension (Herrmann et al., 2015).

Soil neutral and basic conditions (pH), soil moisture and the grain size (i.e., sand content) were major drivers governing decomposition dynamics in these beech forests. However, not all wood compounds responded similarly, i.e., cellulose decayed much faster than lignin. Besides wood characteristics and climatic conditions, also soil traits may influence deadwood decay dynamics (Liu et al., 2013), although, substrate-related parameters have been rarely taken into account (e.g., van der Wal et al., 2007; Risch et al., 2013). Microbial activity was found higher in the uppermost soil layer, with a reduced soil microbial biomass with increasing soil depth, topsoil being more exposed to shifts in temperature, moisture and organic matter input (Bardelli et al., 2017). Owing to its slower decay rate, lignin can be considered important in stocking organic C in the mid-term and, thus, for ensuring a quite stable background source of organic C in these beech forest soils. Lignin has a higher proportion of C than cellulose (Donnelly et al., 1990), the latter being easily decomposed by microorganisms (Wild et al., 2014). Information on decomposition patterns of foliage and deadwood is still rare. In a simulation and observational exercise in the Swiss Alps, Didion et al. (2014) found remaining C in beech foliage litter after 10 years and in lying dead trees after 14–21 years. In forest C inventories, an accurate estimation of the variability of C pools in litter, deadwood, and soil remains a major challenge.

The decay rates of cellulose, lignin and deadwood (at the end of the experiment) correlated well with the sand content of forest soils. Sand and inorganic C contents of soils, as well as soil moisture levels, are related to weathering processes and water availability. Decay rates in north-facing sites were higher than in south-facing sites (regardless of the altitude), north-facing sites having probably lower evaporative demand. Bardelli et al. (2017), studying bacterial, fungal and archaeal communities degrading soil organic matter, observed altitude- and enzyme-specific exposure effects along a climosequence in the Italian Alps, with microbial biomass and activity being higher in the north-facing slopes, irrespective of the altitude; hydrolytic enzyme activities declined with decreasing soil moisture. The soil moisture content was lower in south-facing sites (between 30 and 40%) than in the north-facing sites (between 40 and 50%), albeit the similar annual precipitation, probably due to higher evaporative demand. We hypothesize that the moister and cooler conditions gave rise to a more marked weathering at north-facing sites. Moisture availability was found to be a stronger driver of decomposition than temperature or precipitation, when considered alone (Liu et al., 2006). Water availability may add to local topography, soil composition and incoming radiation, shaping the spatial and temporal variation in decomposition rates. Indeed, climatic conditions have a strong impact on wood decomposer communities (Hoppe et al., 2016), soil moisture controlling nutrient availability and oxygen diffusion being essential for microbial decomposition (Skopp et al., 1990).

The present study area has a MAAT of 7-8 °C. Mackensen et al. (2003) found that decay rates increase significantly only at a MAAT above 12-13 °C. These authors observed that, independently from tree species and climatic zones, moisture has a large influence on the maximum rate of decay, in line with our results. Fravolini et al. (2016) showed that, in subalpine and alpine environments, soil traits (including moisture, texture, temperature, and exposure) influence the decay dynamics of deadwood and its components. Considering that the dynamics of decay processes depend on climatic conditions and substrate traits (Harmon et al., 1986; Chambers et al., 2000; Mackensen et al., 2003), and that beech forests in Europe grow at sites with relatively low MAAT (Bolte et al., 2007), cooler and moister environmental conditions (favorable to fungal decomposers) may generally result in higher decay rates.

The spatial structure of the decomposition environment influenced to a great deal the variation in initial decay rates of beech wood blocks. In a comparative study on different tree species in North America, Yin (1999) concluded that short-term studies often overestimate the importance of site conditions and wood properties for decay rates. The decay model developed by Yin (1999) showed that, with an increase in temperature of 2 °C in January and July, a decrease in wood density of 9–55% was observed in the first year. Over a period of 100 years, however, the rate of decay increased by only 1-14%. While the importance of wood decay for the global carbon balance is widely recognized, surprisingly little is known about its long-term dynamics and its abiotic and biotic drivers (Freschet et al., 2011). Progress in this field is hindered by the long time-scale inherent to the low decay rates of wood, and methods to assess initial decomposition dynamics in standardized in-field conditions may provide the basis for modelling decomposition trajectories in different species-site combinations.

Conclusions

We found that the decay rates of beech wood blocks in montane temperate environments (Apennines) were relatively high. Though our observations were focused on the initial phases of decomposition of relatively small wood blocks, the measured decay rates were comparable to average values observed for CWD of the same species in other sites across Europe. Moreover, cellulose and lignin decay rates over the observation time frame highlighted clear decay patterns. Local scale factors, including soil properties and slope aspect, were effective in influencing the decay dynamics of beech wood blocks and their components. Air temperature and soil moisture had a strong impact on the decay processes: the lower the temperature, the lower the evaporative demand, the higher the moisture availability, and the higher the decay rates. In these Mediterranean montane forest ecosystems, decay processes were slower in south- than north-facing sites owing to the drier conditions. This climosequence approach, using in-field mesocosms, provided important information on the variation in the initial stage of beech deadwood decay as a function of altitude and exposure. Since time series are needed to assess and model the dynamics of deadwood decomposition, long-term monitoring of decay processes and parameter estimates from empirical investigations are required to extrapolate beyond the spatial and temporal scale of data collection.

Acknowledgments

This research was supported by UNIMOL-DecApp project. We thank the Corpo Forestale dello Stato and the team that helped us during the research: Luciano Schiazza, Mario De Menna, Nino Di Cosmo, Liliana Perfettibile, Zyhra Lakia Shahina, Vincenza Graniglia, Sergio D'Ambrosio, Massimiliano Carboni, Roberto Fracasso. J. Ascher-Jenull was funded by Fonds zur Förderung der wissenschaftlichen Forschung (FWF) Austria (project I989-B16). A special thank goes to Carmen Giancola and Simone Di Benedetto for their support during the experimental set-up. The authors wish to thank the whole DACH-DecAlp project partners. The research is linked to activities conducted within the COST (European Cooperation in Science and Technology) Action CLIMO (Climate-Smart Forestry in Mountain Regions - CA15226) financially supported by the EU Framework Programme for Research and Innovation HORIZON 2020.

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Table 1. Environmental characteristics of the study sites; [a] MAAT = mean annual air temperature, MAP = mean annual precipitation.

Plot ID	Elevation (m a.s.l.)	Coordinates (°)	Slope (°)	MAP[a] (mm y^{-1})	MAAT[a] (°C)	Parent material	Dominating tree species	Land use	Humus forms
South-facing sites									
S01	1478	425356 E; 4666479 N	23	1100	8.1	Cretaceous limestone	*F. sylvatica*	Natural forest	Mull
S02	1375	425108 E; 4466431 N	25	1050	8.8	Cretaceous limestone	*F. sylvatica*	Ex-coppice, natural forest	Mull
S03	1263	424879 E; 4666309 N	20	1000	9.6	Cretaceous limestone	*F. sylvatica*	Ex-coppice, natural forest	Mull
S04	1171	424521 E; 4666367 N	15	950	10.2	Cretaceous limestone	*F. sylvatica*	Ex-coppice, natural forest	Amphimull
North-facing sites									
N06	1477	431401 E; 4665328 N	20	1100	6.1	Cretaceous limestone	*F. sylvatica*	Ex-coppice, natural forest	Mull
N07	1375	430924 E; 4665401 N	30	1050	6.8	Cretaceous limestone	*Fagus sylvatica*	Ex-coppice, high forest	Mull
N08	1260	431751 E; 4665822 N	25	100	7.6	Cretaceous limestone	*F. sylvatica*	Ex-coppice, natural forest	Mull
N09	1180	432326 E; 4666174 N	20	950	8.2	Cretaceous limestone	*F. sylvatica*	Ex-coppice, natural forest	Mull

[a]MAAT = mean annual air temperature, MAP = mean annual precipitation

Table 2. Main chemical and physical characteristics of the soil in the investigated plots (mesocosms; values ± standard deviation)

Plot	Altitude (m a.s.l.)	Depth (cm)	pH (H_2O)	Organic C (%)	Inorganic C (%)	N (%)	Bulk density (g/cm^3)	Sand (%)[1)]	Silt (%)[1)]	Clay (%)[1)]
S1	1478	0 – 5	6.53 (0.94)	22.5 (16.9)	2.95 (0.15)	1.32 (0.80)	0.24 (0.05)	85.0	8.8	6.2
S2	1375	0 – 5	7.33 (0.28)	11.9 (0.7)	3.78 (0.83)	0.85 (0.00)	0.09 (0.03)	90.9	6.9	2.2
S3	1263	0 – 5	6.42 (0.14)	39.6 (4.2)	0.47 (0.00)	2.58 (0.22)	0.10 (0.01)	96.0	3.3	0.7
S4	1171	0 – 5	6.62 (0.20)	30.0 (1.8)	1.62 (0.97)	1.90 (0.09)	0.07 (0.03)	91.2	6.8	2.1
N6	1477	0 – 5	6.57 (0.25)	31.3 (8.2)	0.29 (0.19)	1.81 (0.48)	0.10 (0.04)	88.4	8.1	3.5
N7	1375	0 – 5	6.60 (0.18)	31.4 (3.8)	0.44 (0.30)	1.63 (0.21)	0.27 (0.03)	81.6	13.5	5.0
N8	1260	0 – 5	7.20 (0.17)	10.5 (2.1)	8.37 (0.80)	0.56 (0.14)	0.57 (0.04)	75.6	17.1	7.2
N9	1180	0 – 5	7.18 (0.12)	15.7 (1.1)	3.04 (0.47)	0.93 (0.08)	0.33 (0.07)	89.3	5.7	5.0

Table 3. Wood blocks, cellulose and lignin decay constants, *k*, (y^{-1}) based on a) equation 1, b) the regression approach. N = north-facing sites, S = south-facing sites.

Sites	S1	S2	S3	S4	Average S	N6	N7	N8	N9	Average N
Wood blocks										
a)	0.291	0.249	0.357	0.416	0.328	0.461	0.411	0.374	0.496	0.435
b)	0.273	0.215	0.381	0.427	0.324	0.406	0.321	0.443	0.481	0.413
Cellulose										
a)	1.022	1.086	0.714	1.259	1.020	1.423	1.097	1.190	1.252	1.240
b)	0.975	1.051	0.742	1.321	1.022	1.034	1.107	1.189	0.853	1.046
Lignin										
a)	0.082	0.054	0.125	0.216	0.119	0.334	0.283	0.192	0.351	0.290
b)	0.059	0.015	0.154	0.222	0.113	0.292	0.191	0.299	0.444	0.307

Table 4. Correlations between decay constants of cellulose (*k*-cellulose), lignin (*k*-lignin) and deadwood (*k*-deadwood) and environmental components (climate and soil; n = 24). *p < 0.05, **p < 0.01.

	k cell	k lign	k CWD
MAAT	-0.302	-0.437*	-0.273
MAP	0.032	-0.199	-0.366*
k cell		0.117	0.197
k lign	0.117		0.841**
k CWD	0.197	0.841**	
pH	0.119	-0.054	-0.173
C inorg	-0.021	-0.303	-0.299
C org	-0.111	0.206	0.301
C tot	-0.049	0.253	0.328
N	-0.275	0.077	0.175
Soil bulk density	-0.028	0.29	0.214
Soil moisture	-0.042	-0.158	-0.113
Sand	-0.239	-0.234	-0.036
Silt	0.213	0.071	0.164
Clay	0.182	0.131	0.007

MAAT: mean annual temperature, MAP: mean annual precipitation

Table 5. Decay constant *k* and mass of wood components (at the end of the experiment) in south- vs. north-facing sites. Average/median values are also reported.

	North	South
k cell	1.24/1.29*	1.02/0.98*
k lign	0.29/0.26*	0.12/0.10*
k CWD	0.44/0.43*	0.33/0.32*
M cell	4.42/4.22	4.87/4.59
M lign	6.87/6.86*	8.34/8.46*
M CWD	22.24/22.24*	25.25/25.31*

*Significant differences between north- and south-facing sites ($p<0.05$).

k-cellulose (decay constant of cellulose), *k*-lignin (decay constant of lignin), *k*-deadwood (decay constant of deadwood), M deadwood (mass of CWD in g), M cellulose (Mass of cellulose in g), M lignin (Mass of lignin in g), North (north-facing sites), South (south-facing sites).

Table 6. Data compilation of decay constants of *Fagus sylvatica* L. and other deciduous trees occurring in temperate climates together with some environmental parameters.

Source	CWD type	Details	Decay constant k (y^{-1})	Mean residence time (y)	Geology, parent material or soil	Coordinates	MAAT[1)] (°C)	Precipitation [2)] (mm/a)
Müller-Using and Bartsch (2009)	*Fagus sylvatica* L.	wood >10cm	0.089*	11	podzolic brown earth	Central Germany	7	1032
		bark > 10cm	0.109*	9	podzolic brown earth	Central Germany	7	1032
		wood 1-10cm	0.178*	6	podzolic brown earth	Central Germany	7	1032
		bark 1-10cm	0.350*	3	podzolic brown earth	Central Germany	7	1032
Herrmann et al. (2015)	*Fagus sylvatica* L.		0.054*	19		S- and N-Germany	8.9	878
Ostrogovic et al. (2015)	*Quercus cerris* L.	1-7 cm	0.182*	5			10.6	962
		< 1cm	0.260*	4			10.6	962
	Quercus robur L.	1:d <1 cm; l = 5cm[3)]	0.217*	5	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
		2: d 1-3cm; l = 10cm	0.189*	5	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
		4: d 3-5cm; l = 15cm	0.208*	5	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″,	10.6	962

					E15°0′30″		
	6: d 5-7cm; l = 20cm	0.096*	10	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
Carpinus betulus L.	1:d <1 cm; l = 5cm	0.292*	3	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
	2: d 1-3cm; l = 10cm	0.189*	5	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
	4: d 3-5cm; l = 15cm	0.227*	4	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
	6: d 5-7cm; l = 20cm	0.208*	5	Pseudogley (acidic)	N45°40′36″, E15°40′26″, N45°40′15″, E15°0′30″	10.6	962
Alnus glutinosa (L.) Gaertn., 1790	1:d <1 cm; l = 5cm	0.262*	4	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
	2: d 1-3cm; l = 10cm	0.154*	6	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
	4: d 3-5cm; l = 15cm	0.194*	5	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
	6: d 5-7cm; l = 20cm	0.113*	9	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962

	Fraxinus angustifolia Vahl, 1804	1:d <1 cm; l = 5cm	0.267*	4	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
		2: d 1-3cm; l = 10cm	0.139*	7	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
		4: d 3-5cm; l = 15cm	0.070*	14	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
		6: d 5-7cm; l = 20cm	0.089*	11	Eugley (acidic)	N45°37′10″, E15°41′17″	10.6	962
Johnson et al. (2014)	*Fagus grandifolia* Ehrh.	whole	0.097**	10	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
		wood	0.095**	11	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
		Bark	0.141**	7	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
	Acer saccharum Marshall	whole	0.079**	13	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
		wood	0.076**	13	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
		Bark	0.116**	9	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
	Betula alleghaniensis Britton	whole	0.065**	15	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
		wood	0.064**	16	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
		Bark	0.074**	14	granite, schist, etc	43° 56′ N, 71° 45′ W	5.5	1395
Ricker et al. (2016)	*Acer rubrum* L.	wood	0.676*	1	slightly acidic, unknown	33°46'19.33"N, 80°43'36.55"W	17.6	1220

			0.637*	2	slightly acidic, unknown	33°46'19.33"N, 80°43'36.55"W	17.6	1220
			0.639*	2	slightly acidic, unknown	33°46'19.33"N, 80°43'36.55"W	17.6	1220
			0.649*	2	slightly acidic, unknown	33°46'19.33"N, 80°43'36.55"W	17.6	1220
			0.650*	2	slightly acidic, unknown	33°46'19.33"N, 80°43'36.55"W	17.6	1220
Swift et al. (1976)	Branches of							
	Quercus petraea (Mattuschka) L. and *Q. robur* L.	Canopy	0.088*	11	unknown	Meathop Wood, Cumbria	8.6	952
		Litter	0.067*	15			8.6	952
	Fraxinus excelsior L.	Canopy	0.019*	53			8.6	952
		Litter	0.165*	6			8.6	952
	Betula pendula Roth and *B. pubescens* Ehrh	Canopy	0.130*	8			8.6	952
		Litter	0.148*	7			8.6	952
	Corylus avellana L.	Canopy	0.098*	10			8.6	952
		Litter	0.280"	4			8.6	952
	Total	Canopy	0.084*	12			8.6	952
		Litter	0.171*	6			8.6	952
McMillan (1988)	*Quercus* sp		0.018***	56	unknown	southern Indiana	11	105
	Carya sp		0.035***	29			11	105
	Fagus grandifolia		0.019***	53			11	105
	Acer sp		0.045***	22			11	105

Yoon et al. (2011)	*Q. serrata, C. laxiflora*, and *C. cordata*		0.049***	20	unknown	37°44'46"N, 127°09'01"E	11.3	1365
Freschet et al. (2012)	*Alnus incana*	Stem	0.102****	10	unknown	68°21'N, 18°49'E	1.3	352
	Betula pubescens	Stem	0.054****	19			1.3	353
	Populus tremula	Stem	0.072****	14			1.3	354
	Salix caprea	Stem	0.098****	10			1.3	355
	Sorbus aucuparia	Stem	0.069****	14			1.3	356
This study	*Fagus sylvatica*		0.290*	3	carbonate		8.13	1100
			0.250*	4	carbonate		8.83	1050
			0.360*	3	carbonate		9.59	1000
			0.420*	2	carbonate		10.22	950
			0.460*	2	carbonate		6.13	1100
			0.410*	2	carbonate		6.83	1050
			0.370*	3	carbonate		7.61	1000
			0.490*	2	carbonate		8.18	950
Yamashita et al. (2015)	*Fagus* sp.		0.085***	12	unknown	36°56'N (?), 140°35'E	10.7	1910
Rock et al. (2008)	*Fagus sylvatica*		0.070***	14	acidic, sandy	Northern Germany, Brandenburg	9	570

Measurement technique to determine the decay constant: * mass, **mass, volume, ***density ****density, mass

1) MAAT: mean annual temperature, 2) Precipitation = annual precipitation, 3) d = diameter; l = length

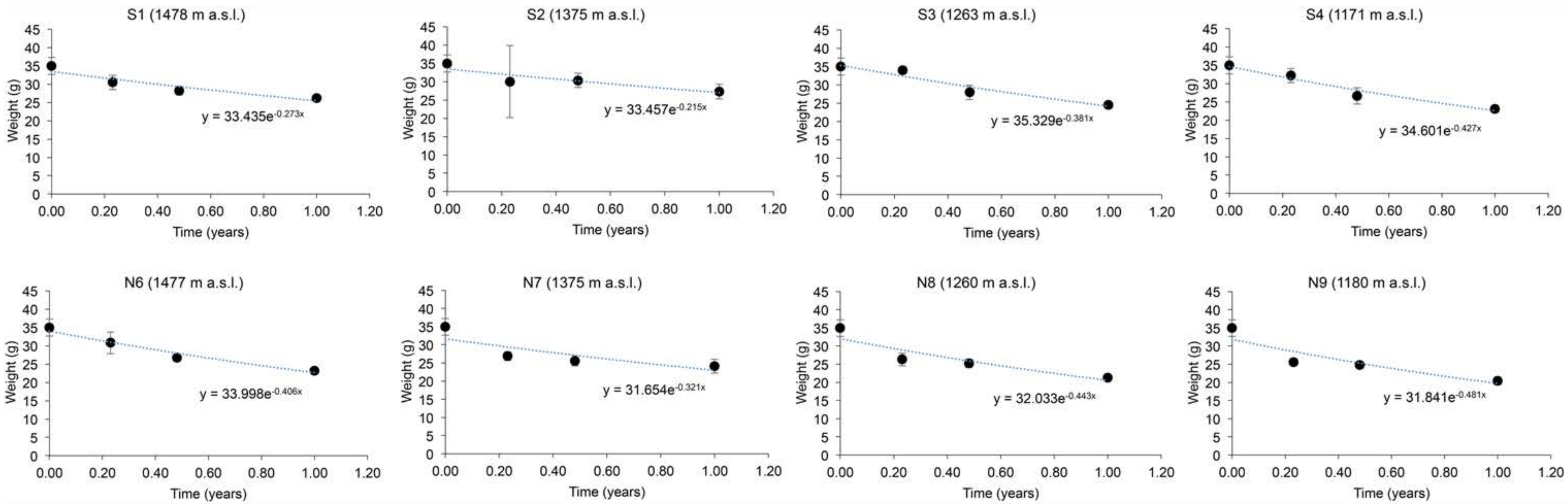
Figure captions

Fig. 1. Amount of dry mass (weight ± standard error) of the wood blocks (placed into mesocosms) as a function of time (0 – 52 weeks), site (altitude) and exposure (north vs. south).

Fig. 2. Amount of cellulose (= concentration × dry mass of wood block; weight ± standard error) as a function of time (0 – 52 weeks), site (altitude) and exposure (north vs. south).

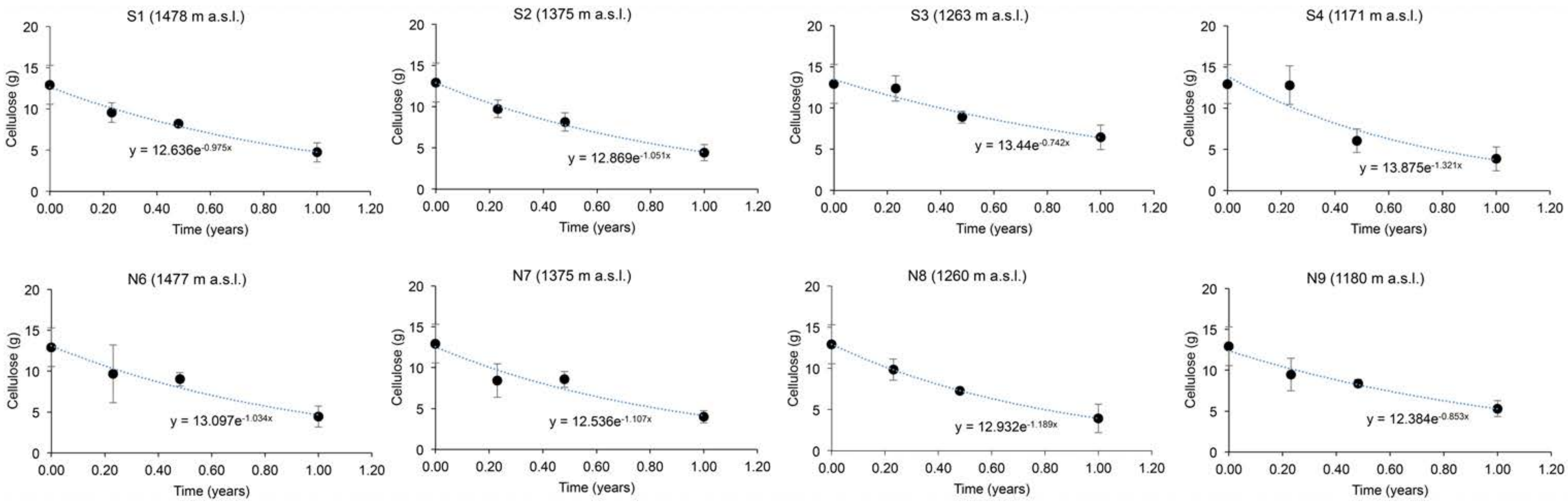
Fig. 3. Amount of lignin (= concentration × dry mass of wood block; weight ± standard error) in the wood blocks as a function of time (0 – 2 years), site (altitude) and exposure (north vs. south).

Fig. 1



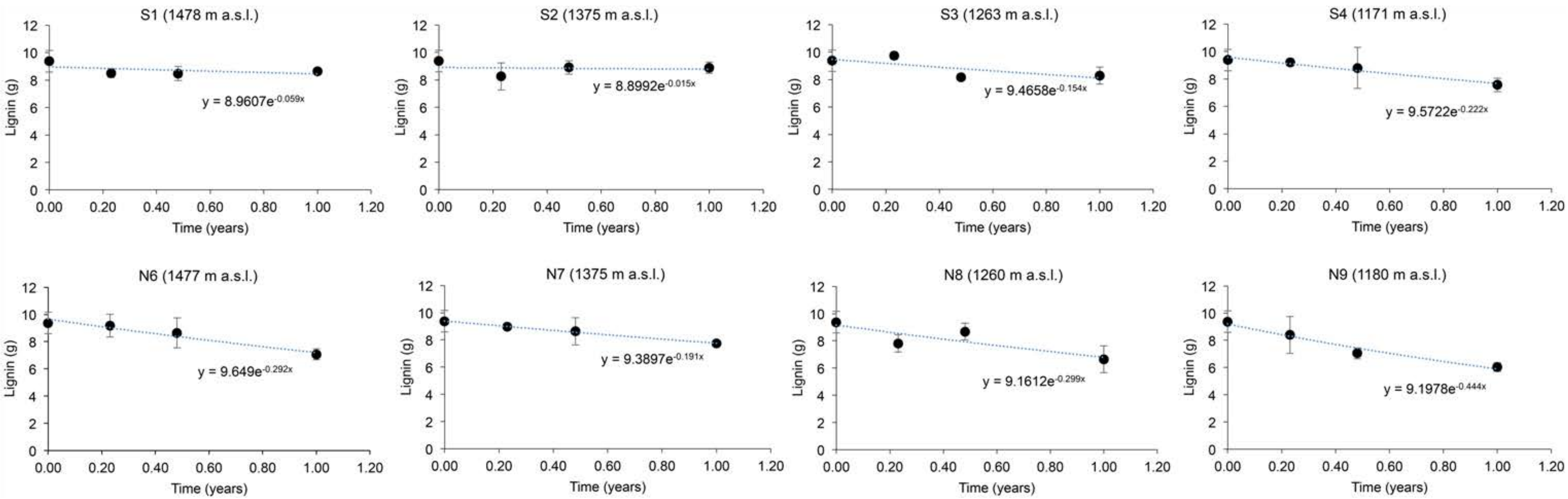
S1 (1478 m a.s.l.)
y = 33.435e-0.273x
S2 (1375 m a.s.l.)
y = 33.457e-0.215x
S3 (1263 m a.s.l.)
y = 35.329e-0.381x
S4 (1171 m a.s.l.)
y = 34.601e-0.427x
N6 (1477 m a.s.l.)
y = 33.998e-0.406x
N7 (1375 m a.s.l.)
y = 31.654e-0.321x
N8 (1260 m a.s.l.)
y = 32.033e-0.443x
N9 (1180 m a.s.l.)
y = 31.841e-0.481x
Weight (g)
Time (years)

Fig. 2



S1 (1478 m a.s.l.)
y = 12.636e-0.975x
S2 (1375 m a.s.l.)
y = 12.869e-1.051x
S3 (1263 m a.s.l.)
y = 13.44e-0.742x
S4 (1171 m a.s.l.)
y = 13.875e-1.321x
N6 (1477 m a.s.l.)
y = 13.097e-1.034x
N7 (1375 m a.s.l.)
y = 12.536e-1.107x
N8 (1260 m a.s.l.)
y = 12.932e-1.189x
N9 (1180 m a.s.l.)
y = 12.384e-0.853x
Cellulose (g)
Time (years)

Fig. 3


S1 (1478 m a.s.l.)
y = 8.9607e-0.059x
S2 (1375 m a.s.l.)
y = 8.8992e-0.015x
S3 (1263 m a.s.l.)
y = 9.4658e-0.154x
S4 (1171 m a.s.l.)
y = 9.5722e-0.222x
N6 (1477 m a.s.l.)
y = 9.649e-0.292x
N7 (1375 m a.s.l.)
y = 9.3897e-0.191x
N8 (1260 m a.s.l.)
y = 9.1612e-0.299x
N9 (1180 m a.s.l.)
y = 9.1978e-0.444x
Lignin (g)
Time (years)