1 Soil attributes and microclimate are important drivers of initial deadwood decay
2 in sub-alpine Norway spruce forests

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27 **Abstract**

28 Deadwood is known to significantly contribute to global terrestrial carbon stocks and carbon
29 cycling, but its decay dynamics are still not thoroughly understood. Although the chemistry of
30 deadwood has been studied as a function of decay stage in temperate to subalpine environments, it
31 has generally not been related to time. We therefore studied the decay (mass of deadwood, cellulose
32 and lignin) of equal-sized blocks of *Picea abies* wood in soil-mesocosms over two years in the
33 Italian Alps. The 8 sites selected were along an altitudinal sequence, reflecting different climate
34 zones. In addition, the effect of exposure (north- and south-facing slopes) was taken into account.
35 The decay dynamics of the mass of deadwood, cellulose and lignin were related to soil parameters
36 (pH, soil texture, moisture, temperature) and climatic data. The decay rate constants of *Picea abies*
37 deadwood were low (on average between 0.039 and 0.040 y⁻¹) and of lignin close to zero (or not
38 detectable), while cellulose reacted much faster with average decay rate constants between 0.110
39 and 0.117 y⁻¹. Our field experiments showed that local scale factors, such as soil parameters and
40 topographic properties, influenced the decay process: higher soil moisture and clay content along
41 with a lower pH seemed to accelerate wood decay. Interestingly, air temperature negatively
42 correlated with decay rates or positively with the amount of wood components on south-facing
43 sites. It exerted its influence rather on moisture availability, i.e. the lower the temperature the higher
44 the moisture availability. Topographic features were also relevant with generally slower decay
45 processes on south-facing sites than on north-facing sites owing to the drier conditions, the higher
46 pH and the lower weathering state of the soils (less clay minerals). This study highlights the
47 importance of a multifactorial consideration of edaphic parameters to unravel the complex
48 dynamics of initial wood decay.

49

50 **Keywords:** deadwood decay, soil, cellulose, lignin, exposure, Alps

51

52

53 1. Introduction

54 Deadwood and coarse woody debris (CWD) are important components in the functioning of forest
55 ecosystems and their structure, as they are relevant for biodiversity, trophic chains, natural
56 regeneration in forests, nutrient cycles and overall carbon storage (Harmon et al., 1986; Jonsson and
57 Kruys, 2001; Russell et al., 2015). CWD includes fallen trees, fallen branches, pieces of fragmented
58 wood, stumps and standing dead trees (snags) (Zhou et al., 2007). The amount of deadwood varies
59 with forest management. It may comprise up to 160 m³/ha or 40% of the total biomass volume in
60 natural spruce forests (Bobiec 2002; Ranius et al., 2003; Bobiec et al., 2005), but is typically less
61 than 5 % in managed forest stands (MCPFE 2007). Since CWD is relevant for both maintaining
62 biodiversity and understanding global C dynamics (Kueppers et al., 2004; Stokland et al., 2012),
63 quantifying and determining its properties has recently received more attention.

64 The decay rate of deadwood is governed by several factors such as the ratio of bark to wood, the
65 tree species, the log diameter (and the log's geometry in general; MacMillan, 1988; Van der Wal et
66 al., 2007), the contact with the forest floor (Ganjegunte et al., 2004) and the soil type (van der Wal
67 et al., 2007). The decrease in deadwood density over time is usually estimated using a negative
68 exponential model (Naesset, 1999; Chen et al., 2005). The single negative exponential model,
69 particularly for short-term studies, is the one most commonly used to determine and categorise the
70 decomposition rate (e.g., Olson, 1963; Harmon et al., 1986; Laiho and Prescott, 2004). Tobin et al.
71 (2007) showed, however, that the decay constants might vary slightly as a function of decay class.
72 How the decay rate of deadwood is affected by climate is basic information for understanding the
73 C-cycle and other nutrients. However, little data is available, apart from some studies in the North-
74 Western Pacific in the U.S. and Canada (Harmon et al., 1986; Daniels et al., 1997; Campbell and
75 Laroque, 2007), a few experimental and field studies (Naesset, 1999; Storaunet and Rolstad, 2002;
76 Lombardi et al., 2008; Herrmann and Bauhus, 2012) on the decay rates of different tree species in
77 European forest ecosystems and some rough estimates and models (Storaunet, 2004; Mäkinen et al.,
78 2006). Russell et al. (2014) used a modelling approach to estimate the decay constants for 36 tree

79 species common to eastern US forests and were able to show that the decay constants increased
80 from 0.024 y^{-1} (with a mean annual temperature of $< 2.8^{\circ}$) to 0.040 y^{-1} ($\geq 13.7^{\circ}\text{C}$). Furthermore,
81 decay rates have been found (Fersch et al., 2012; Cornelissen et al., 2012) to differ in response to
82 (micro)climate features (e.g., wood moisture), species (e.g., wood quality) and site conditions (e.g.,
83 faster decay rates under warmer conditions).

84 Mountainous ecosystems are particularly sensitive to changing environmental conditions (Mountain
85 Research Initiative EDW Working Group, 2015). New or alternative techniques for assessing the
86 decay rates of deadwood in European forests, particularly in cool mountain regions, are needed to i)
87 obtain more data and ii) overcome difficulties with existing approaches.

88 The often-used chronosequence approach, however, may be criticised since it uses the so-called
89 snap-shot sampling. This may lead to an underestimation of the decay constant k or decay rate in
90 general and an overestimation of the age and the mean residence time of deadwood (Kruys et al.,
91 2002). Furthermore, the dating of deadwood is difficult, particularly for the decay classes 4 and 5
92 (Petrillo et al., 2016) since these are the most advanced decay stages (Hunter, 1990). Alternatively,
93 sites can be revisited and the decay of different deadwood components such as snags and CWD
94 monitored (Russell and Weiskittel, 2012), but this may be skewed by episodic mortality events and
95 uncontrolled conditions. An additional difficulty in determining CWD decay is the fall rate of
96 snags. They can remain upright for several years and decay much more slowly than fallen dead
97 trees (Yatskov et al., 2003). This makes it difficult to determine a clear age trend in decay. The fall
98 rates of snags in Europe are largely unknown and comparisons between tree species are almost
99 impossible, but more data is available from North America, see, e.g. Hilger et al. (2012) and Dixon
100 (2015) for overviews.

101 As deadwood decomposes, its chemical structure and composition change. The type and rate of
102 changes are wood specific and dependent on extrinsic factors, such as climate and others. With
103 time, deadwood becomes incorporated into surface organic soil horizons, where it contributes to the
104 chemical heterogeneity of the forest floor (Strukelj et al., 2013). To better assess deadwood decay

105 processes, the analysis of carbon, nitrogen, phosphorous contents, as well as lignin and cellulose
106 concentrations has been proposed (Bütler et al., 2007; Saunders et al., 2011). Deadwood chemistry
107 has recently been studied as a function of decay stage in temperate to subalpine environments
108 (Lombardi et al., 2008; Strukeli et al., 2013; Petrillo et al., 2015), but only exceptionally related to
109 time (Petrillo et al., 2016). Such information, however, would be necessary to detect how the
110 dynamics of deadwood change with site conditions and climate. Petrillo et al. (2016) showed that
111 the decay of *Picea abies* in Alpine environments is very slow.

112 The following research questions were posed: 1) Can we confirm the very slow decay rates of *Picea*
113 *abies* (L) Karst. as determined by Petrillo et al. (2016) in an Alpine setting (Trentino, Italy) by using
114 a field-experimental approach with controlled conditions?; 2) How fast do the major wood-
115 compounds (cellulose and lignin) in *Picea abies* decay in this cool and humid mountain
116 environment?; 3) How do the decay rates relate to microclimatic conditions and soil parameters? —
117 We hypothesised that Norway spruce wood decay would be very slow but that it might be enhanced
118 under moister (atmosphere and soil) and warmer conditions. We furthermore assumed that cellulose
119 should decay relatively fast and that probably only small changes would be detectable for lignin.

120

121 **2. Study area**

122 Sites in Trentino (Val di Rabbi and Val di Sole, northern Italy) in the European Alps (Fig. 1, Table
123 1) were chosen to represent a typical mountain climate. The sites were particularly suitable because
124 a comprehensive database about their soils was available and that they belong to an already existing
125 observation network (Egli et al., 2006). To assess the contribution of climate, the decay processes
126 were studied at sites with different a) exposures (north- vs south-facing), and b) altitudes
127 (toposequence). Eight sites were selected along two climosequences: one north-facing and one
128 south-facing ranging from 1200 m a.s.l. up to 2000 m a.s.l. (with 4 sites, pairs on each, resulting in
129 a total of 8 sites).

130 The climate of the slope area ranges from subalpine to alpine (above the timberline), the mean

131 annual temperature from 8.2 °C at the valley floor (about 750 m a.s.l.) to about 0 °C at 2300 m
132 a.s.l., and the mean annual precipitation from approximately 800 to 1300 mm (Sboarina and
133 Cescatti, 2004). The geological parent material at all sites is paragneiss debris which is acidic. The
134 soil units are Cambisols, Umbrisols and Podzols (WRB: IUSS working group, 2014). Forests are
135 dominated by Norway spruce and at higher altitudes by European larch (Petrillo et al., 2016), with
136 the timberline close to 2000 – 2200 m a.s.l.

137

138 **3. Materials and Methods**

139 *3.1 Experimental set-up*

140 At each site of the climosequence, a field experiment using soil mesocosms was set up as described
141 in Maestrini et al. (2014). A soil mesocosm is an open soil monolith enabling field-experiments
142 under semi-controlled conditions. Mesocosms (10.2 cm diam., 20 cm long PVC tubes) were
143 inserted in the summer of 2012 into the natural soil one year prior to the addition of the wood
144 blocks at a distance of >1 m from large trees and >0.5 m from the adjacent mesocosms, leaving at
145 the surface a border of about 1 cm (Fig. 2). Since the size and geometry of deadwood can strongly
146 influence the decay mechanisms (Van der Wal et al., 2007), wood blocks of the same *Picea abies*
147 tree were prepared having a uniform size of 2 cm x 5 cm x 5 cm. These wood blocks were added to
148 the soil mesocosms and directly placed on top of the soil with three replicate mesocosms for each
149 time step installed on each of the 8 study sites. The wood blocks were, thus, in contact with the soil
150 surface from the very beginning of the experiment. The deadwood blocks were sampled after 12
151 (t1), 25 (t2), 52 (t3) and 104 weeks (t4) (Fig. 2), resulting in a total of 96 samples (including the 3
152 replicates), with five wood blocks (for chemical analyses) kept as controls for t0 and 50 wood
153 blocks for weight and density control (t0). The wood blocks were collected (with lab-gloves),
154 placed in plastic bags, and transported in cool-boxes to the laboratory. They were then air-dried at
155 room temperature, cut-milled to 4 mm (Retsch mill), aliquoted into sterile Falcon tubes (50 mL) and
156 stored at 4°C until further processing.

157 The dry weight of the wood blocks that were used in the mesocosms was determined by standard
158 methods (48 h in the oven at 105°C). The fresh weight and dry weight were determined to assess the
159 density and water content of the wood blocks. The initial dry weight (at the start of the experiment)
160 was obtained from the wood blocks at t0 (n = 50).

161

162 *3.2 Cellulose and lignin extraction*

163 For the wood cellulose extraction, the powdered samples were first weighed and 10mg placed in
164 Teflon bags (Leavitt and Danzer, 1993). They were washed then in 5% NaOH solution, twice at
165 60°C, and again three times using a 7% NaClO₂ solution and 96% CH₃COOH at 60 °C to ensure the
166 pH was between 4 and 5. This procedure extracts lignin from the samples. The bags were dried in
167 the oven at 50 °C and the cellulose content determined as the difference between the initial weight
168 and dried samples.

169 Both the total lignin and the so-called Klason lignin, which is insoluble in strong acid (Dence and
170 Lin, 1992), were determined. The Klason lignin was obtained in a sequential extraction where first
171 the water-soluble compounds were extracted (Dence and Lin, 1992). Ultrapure water (80 °C) was
172 then added to 1 g of each sample and stirred 3 times for 15 min. After centrifuging for 10 min at
173 4500 rpm, the samples were dried in the oven at 80 °C, washed three times with 5 ml of ethanol and
174 then centrifuged again for 10 min at 4500 rpm. The supernatant was discarded before adding
175 ethanol again and filtering the sample. The filters were dried over night at 60 °C. Afterwards, 3 mL
176 of a 72% sulphuric acid (H₂SO₄) solution were added to 300 mg of the filter cake. This was stirred
177 with 84 mL of ultrapure water and put into the autoclave for 1 h at 120 °C. The resulting solution
178 was then filtered into ceramic crucibles and the liquid evaporated at 110 °C, before weighing the
179 lignin in the crucibles (Klason lignin). The acid-soluble lignin (ASL; Klason, 1893) in the filtrate
180 was determined using a photometer (Cary 50 conc UV-Visible Spectrophotometer; 205 nm). The
181 total lignin is the sum of the ASL + the Klason lignin; this lignin fraction includes also other
182 recalcitrant compounds, such as tannins, cutin and suberin.

183

184 3.3 Determination of mass losses of deadwood, cellulose and lignin and related decay rates

185 The decay rate can be estimated by relating the time-since-death to the density loss or mass loss of
186 deadwood during a given time period (Busse, 1994; Melin et al., 2009). The decay rate is
187 commonly expressed through a decay constant k , which indicates the density loss or mass loss per
188 year. This constant is derived from a decay model (Harmon et al., 1986), which can be most simply
189 expressed by the equation in the single-negative-exponential model:

$$190 \quad x_t = x_0 e^{-kt} \quad (1)$$

191 where x_t is the density or mass of deadwood at a given time (t), and x_0 is the initial mass (Jenny et
192 al., 1949; Olson, 1963) or density. The mass is a more reliable parameter because density may
193 underestimate deadwood decay rates. In this investigation, we used the mass of the wood blocks.
194 Individual decay rates were determined on the basis of total mass losses of the wood blocks,
195 cellulose and lignin. As previously mentioned, decay rate constants may slightly vary during the
196 whole decay process. Herrmann and Prescott (2008) detected that the decay patterns of pine and
197 spruce were similar with the highest k between 6 and 14 years. The information retrieved from a
198 single decay rate constant may, thus, not fully reflect the whole decomposition process.

199 Due to the faster decomposition of cellulose, lignin is relatively enriched. Lignin, however, also
200 decomposes with time. To unravel the decay behaviour of these compounds, a summation-
201 exponential model can be applied (Means et al., 1985; Mackensen et al., 2003), with the general
202 form:

$$203 \quad x_t = x_1 e^{-k_1 t} + x_2 e^{-k_2 t} \dots + x_n e^{-k_n t} \quad (2)$$

204 where x_t is the mass (or density) of deadwood at a given time, and $x_{1...n}$ are partitioned parameters.
205 Subsequently, the half-life of the deadwood mass, cellulose or lignin could be calculated:

$$206 \quad t_{1/2} = \frac{\ln(1/2)}{-k} \quad (3)$$

207 where $t_{1/2}$ is the half-life and k is the decay constant. In addition to equation 1, the decay rate
208 constants of spruce deadwood were also estimated on the basis of the mass loss within the
209 observation period using an exponential regression approach.

210 Freschet et al. (2012), however, question the use of the negative exponential (although it is very
211 commonly used). Therefore, other regression functions to describe the mass loss of deadwood and
212 its compounds as a function of time were applied and compared to the previously mentioned
213 approaches. This included a linear, a polynomial (2nd order) and two sigmoid functions. The first
214 sigmoid function (sigmoid function 1) is described by an exponential decay model (cf. Lichter,
215 1998):

$$216 \qquad f(t) = a + (b - a)e^{-kt} \qquad (4)$$

217 where a represents an asymptote, b the initial quantity, and k the decay constant. The second
218 (sigmoid function 2) is given by (Lichter, 1998):

$$219 \qquad f(t) = \frac{a}{(1 + e^{b(t-e)})} + d \qquad (5)$$

220 where a = range of the wood property, t = time, b = slope coefficient, c = time (in years) of the
221 maximal rate of change and d = asymptotic value ($t = \infty$).

222

223 *3.4 Soil parameters*

224 The soil temperature was measured close to the mesocosms between July 2013 and June 2014 at 3 h
225 intervals with miniature temperature loggers, iButton® (Schmid et al., 2012), placed 10 cm below
226 the soil surface. Soil pH (H₂O) was determined using a soil:solution ratio of 1:10. Particle size-
227 distribution of the <2 mm fraction was determined as a weight percentage (USDA scale) using the
228 sieve-and-pipette method with prior oxidation of organic matter by hypochlorite (NaClO) (Patruno
229 et al., 1997). Soil clay mineralogical data were available from Egli et al. (2006, 2007).

230

231 3.5 Statistical analysis

232 The statistical analyses were performed using the software IBM SPSS Statistics 21 and R (3.2.3).
233 For visualisation, the ggplot package was used. The data distribution of the mass of cellulose,
234 lignin, deadwood and their corresponding decay constant was tested using the Shapiro Wilk
235 normality-test. If the result of the normality test was positive, parametric comparison methods were
236 then adopted through a t-test or an analysis of variance (ANOVA). Otherwise, two non-parametric
237 comparison tests were applied, the Mann-Whitney (U-test) and the Kruskal-Wallis test. Bonferroni-
238 corrections were considered. These tests were used to see if differences between north- and south-
239 facing sites or along the altitudinal gradient exist with respect to the decay rates (mass losses) of
240 deadwood, cellulose or lignin. To explain the data distribution of cellulose, lignin and deadwood
241 (decay rates and amount), explanatory variables such as altitude, exposure (north vs. south), air
242 temperature, precipitation, soil moisture, soil temperature, soil-pH and grain size were used. For
243 several parameters, however, only one measurement or one series of measurements (altitude,
244 exposure, air temperature, etc.) exist. Instead of a mixed linear modelling, we decided for a
245 particular type of correlation analyses. To avoid autocorrelation, one replicate out of the 3 data
246 points of each site (8) was chosen arbitrarily and correlated to the explanatory variables. By
247 permutation, only one value per site was chosen. For each correlation 3^8 combinations (i.e. a total of
248 6561) were possible. In consequence, a high number of permutations and subsequent correlations
249 could be calculated and the stability of the model tested. We performed 100 correlations for each
250 dependent and explanatory variable and displayed the corresponding standard deviation of the
251 correlation coefficients. The relationship between the explanatory variables and cellulose, lignin
252 and deadwood are shown in cross-plots. This procedure does not allow the calculation of a
253 significance level, but trends could be detected. In addition, a subdivision into south- and north-
254 facing sites was done giving rise to 3^4 permutations.

255

256 4. Results

257 4.1 Decay rates and half-lives

258 Over the two-year study, the detectable changes in wood mass, cellulose and lignin (Figs. 3 – 5)
259 were rather small. In several cases almost no time trend was detectable for lignin (Fig. 5) while the
260 mass of deadwood and cellulose exhibited a continuous loss.

261 Several functions were tested to describe the time trends. The exponential, linear and sigmoid
262 functions often yielded quite comparable results (Table 2). Although some authors criticise the
263 exponential approach, it nonetheless seemed to describe the trends (Table 2, Fig. 6) — in general —
264 slightly better than the other approaches. With respect to the comparability of our results with other
265 publications, it makes even more sense to use this approach.

266 Accordingly, the decay constants of deadwood varied from almost zero to a maximum of 0.145 y^{-1}
267 (Table 3). The average k -values for deadwood were in the range of 0.039 to 0.040 y^{-1} , depending on
268 the calculation procedure and exposure (Table 3). The biochemical data of deadwood are given in
269 Figures 4 and 5. The amount of cellulose and lignin is not displayed as a concentration value but as
270 a mass, obtained by multiplying the concentration of cellulose and lignin with the deadwood mass
271 (Figs. 4 and 5). We obtained the average value of 0.110 y^{-1} for the decay constant of cellulose using
272 the single negative exponential model and 0.117 y^{-1} using the exponential regression approach
273 (Table 3).

274 Using the average k -values, the half-life could be calculated for deadwood and cellulose. The
275 deadwood half-life seemed to vary (as an average) between 17 years (single negative exponential
276 model) and 22 years (regression approach; negative values not considered). In fact, negative k -
277 values are not possible for decaying material, and can be attributed to measurement uncertainties.
278 The half-life for cellulose was on average about 19 years using the negative exponential model and
279 only 8 years using the exponential regression approach. However, along the altitudinal gradient it
280 varied (as an average of the sites) between 2 and 74 years (Table 3). For lignin, the calculation of
281 the k -value and, thus, the half-life was difficult or impossible since the decay rates fluctuated
282 around zero (Table 3).

283

284 *4.2 Effects of selected environmental parameters on deadwood decay*

285 Climatic and pedogenic data are given in Tables 1 and 4. The climate varies from temperate to
286 boreal (according to the classification from Köppen, 1918). The texture of the soils is sandy loam to
287 loam. The comparison of the wood parameters (decay rate constants and amount) cellulose, lignin
288 and deadwood is visualised in Figs. 7 and 8. All soils are acidic with generally more acidic
289 conditions on the north-facing sites.

290 Due to the potential risk of autocorrelation, the replicate values of wood components were used by
291 permutation and related to the explanatory variables exposure (north vs. south), air temperature,
292 precipitation, soil moisture, soil temperature, soil-pH and grain size. For this correlation analysis
293 not only the decay rates but also the amount of cellulose, lignin and deadwood at the end of the
294 experiment were taken into account. The decay rate of cellulose not only correlated with climatic
295 parameters, such as e.g. annual precipitation, but also with soil parameters, such as the clay content.
296 The south-facing sites showed a good relation of the cellulose decay rate to MAP, MAAT, soil
297 moisture, soil-pH and particularly to the clay content (Table 5). The higher the clay and soil water
298 content, the faster is the decay of cellulose. Climate exerted its influence over the mean annual
299 precipitation (the higher this parameter, the higher the decay rate of cellulose) and temperature.
300 With temperature, a negative relationship, however, was found. The cooler the climate the faster is
301 the decay rate of cellulose. This negative relationship seems to be surprising. A lower temperature
302 strongly correlates with an increase in soil moisture. As a consequence, the temperature
303 predominantly seemed to interfere over moisture (the lower the temperature the higher the soil
304 moisture that positively influenced the decay rates). On the north-facing sites, however, no
305 particular correlation between the wood parameters and explanatory variables could be found while
306 conditions are completely overlaid by moisture availability due to the lower thermal conditions.

307 In addition, the decay rate constants of deadwood did not seem to be affected by any of the
308 explanatory factors (Table 5). The lignin decay rate constant was not included in the statistical
309 evaluations since during the observation time the values were around zero.

310 However, when considering the mass of deadwood, cellulose and lignin at the end of the field
311 experiment (i.e., after 2 years), a correlation analysis was rendered possible for all of the wood
312 components. This remaining mass could then be compared to environmental parameters. Using this
313 approach, cellulose showed the same correlations as previously mentioned. At the south-facing sites
314 particularly, a close relation between the amount of cellulose and the explanatory variables MAP,
315 MAAT, soil moisture, soil-pH and the clay content exists. Noteworthy is again the good correlation
316 with the clay content (Table 5). Quite a similar situation could be found for the mass of lignin and
317 deadwood when related to these environmental parameters. Whichever comparison is taken, it
318 seemed that the clay content and the amount of precipitation were key variables for the decay of
319 deadwood.

320 The Mann-Whitney test indicated that cellulose decayed significantly ($p = 0.04$; Table 6) faster at
321 the north-facing sites, apart from the uppermost sites (N4 and S9). The cellulose half-life seemed to
322 be higher on the south-facing sites to about 1800 m a.s.l., reaching in one case a value of as much as
323 118 years. Both the decay rate constant and the amount of cellulose differed significantly between
324 north- and south-facing sites.

325

326

327 **5. Discussion**

328 *5.1 Wood decomposition rates*

329 The mesocosms approach showed that deadwood decays relatively slowly in the Alpine
330 environment we investigated. Although the observation period of 2 years was rather short, the
331 experimental approach, carried out under controlled conditions, enabled the derivation of rate

332 constants for cellulose and deadwood and to recognise relationships between wood parameters and
 333 explanatory (environmental and soil) variables.

334 The measured decay rates for deadwood were rather similar to those reported by Petrillo et al.
 335 (2016) who determined the mean rates for spruce to be in the range of 0.018 to 0.022 y^{-1} using a
 336 chronosequence approach. The average rates determined in this study were between 0.039 and
 337 0.040 y^{-1} , and were also in line with results reported by Herrmann et al. (2015) for Norway spruce
 338 in Central Europe. Decomposition rate constants of lying CWD of *P. abies* and *P. sylvestris* were
 339 0.033 y^{-1} and 0.032 y^{-1} , respectively (Herrmann et al., 2015). One plausible explanation for the
 340 lower rates empirically determined by Petrillo et al. (2016) could be related to the time lag between
 341 the death of a standing tree and its contact with the soil (Kueppers et al., 2004; Zielonka, 2006;
 342 Lombardi et al., 2013; Petrillo et al., 2016). Standing dead trees can remain upright for several years
 343 and therefore decay much more slowly than fallen dead trees (Yatskov et al., 2003). Moreover,
 344 some parts of living trees may start to decompose before dying and therefore decay faster than non-
 345 decayed wood after death (Lombardi et al., 2008).

346 Decay rates are often derived from reductions in wood density through time, which when used to
 347 model biomass and carbon depletion are known to underestimate decay rate loss because they fail to
 348 account for volume reduction (changes in log shape) as decay progresses (Fraver et al., 2013). This
 349 also might explain why Petrillo's et al. (2016) decay rate constants were slightly lower than those in
 350 our and other studies, such as that of Rock et al. (2008).

351 The size of the deadwood also matters to a certain extent during the decay process (Tarasov and
 352 Birdsey, 2001). Usually, the smaller the size of deadwood the faster the decomposition rate. Based
 353 on a chronosequence approach, Tarasov and Birdsey (2001) determined quite similar decay rates
 354 with $k = 0.059 \text{ y}^{-1}$ using *Picea abies* (L.) karst wood pieces having a size of 5 – 20 cm in diameter.
 355 *Picea abies* bark (size < 20 cm) showed decay rates of 0.068 y^{-1} (Shorohova et al., 2008). Owing to
 356 the low k values, the deadwood of this tree species therefore constitutes a long-term carbon pool
 357 and a source of nutrients for biota in mountain forests. Furthermore, the k -values we obtained fit

358 reasonably well with those of Russell et al. (2015). For environments where the mean annual
 359 temperature is $< 8^{\circ}\text{C}$, the decay rate constants are mostly $< 0.06 \text{ y}^{-1}$, and may even be below 0.04 y^{-1}
 360 (Mackensen et al., 2003). The differences between the different experimental studies are probably
 361 also due to the uncertainty over the cause of death and the conditions of the decomposition.
 362 Means et al. (1985) were able to derive k values for cellulose values of $0.0109 - 0.0117 \text{ y}^{-1}$ for
 363 Douglas fir logs (in a cool to temperate climate). Petrillo et al. (2016) determined a decay rate
 364 constant of 0.032 y^{-1} for cellulose for spruce (*Picea abies*) and 0.014 y^{-1} for larch (*Larix decidua*).
 365 The average values of the cellulose decay rate constant in our experiment were in the range of 0.095
 366 and 0.117 y^{-1} . Compared to Petrillo et al. (2016) these values are higher. In contrast to Means et al.
 367 (1985) or Petrillo et al. (2016), contact with the soil was given in our experiment from the outset. In
 368 addition, we used the wood mass to calculate rates that may give rise to higher k values.
 369 No changes in the amount of lignin over the two-year observation period could be detected. This
 370 may be due to two reasons: i) No observed changes might be due to a lag period that passes before
 371 the decay of lignin truly begins. Such lag periods are usually observed for deadwood when the
 372 contact with soil is initially not given (Kueppers et al., 2004; Zielonka, 2006; Lombardi et al.,
 373 2013). In this investigation, this was not the case. Furthermore, the single-exponential model
 374 (Olson, 1963) does not always adequately describe the deadwood decomposition process (Harmon
 375 et al., 2000) due to a time lag required for decomposers to become established (Harmon et al. 2000;
 376 Hérault et al., 2010). In our investigation, this might probably be the case in those situations where
 377 the sigmoid functions better described the measured trend (Table 2, Fig. 6). ii) Lignin decomposes
 378 much slower than cellulose and the overall mass of deadwood. As such, the recorded changes over
 379 time (within these two years) were probably too small to be detected due to the insensitivity of the
 380 methods used. Petrillo et al. (2016) stated that the decay rate constant of lignin is a factor of about 5
 381 – 10 lower than for cellulose (spruce, larch). Accordingly, the results are partially limited due to the
 382 rather short observation period (i.e., 2 years).

383 Nonetheless, our field experimental approach confirmed the very low decay rates of Norway spruce
384 deadwood in Alpine environments, despite all of these potential ambiguities. All in all, lignin seems
385 to decompose very slowly (and almost not detectable over a two-year observation period) whereas
386 cellulose reacts rather fast and gives a well-discernible trend.

387

388 *5.2 Relation of deadwood decay to soil and climatic parameters*

389 Local scale factors do influence the decay dynamics, especially those factors that are related to the
390 soil or the substrate and to the wood itself (Liu et al., 2013). Soil related parameters were only in
391 very rare cases taken into account when measuring the decay rates of deadwood (e.g. Bütler et al.,
392 2007; van der Wal et al., 2007; Risch et al., 2013). The decay dynamics at the local scale of our
393 investigation area were influenced not only by air temperature and annual precipitation, but also by
394 soil acidity (pH), soil moisture and the grain size (i.e., clay content) (Table 5). However, not all of
395 the wood components reacted similarly. In this sense, cellulose decays much faster than lignin or
396 the bulk deadwood. Consequently, the relations of cellulose with environmental and soil parameters
397 could be better tested and were in some cases particularly good. Owing to the slow and almost not
398 detectable decay, lignin is important in stocking organic carbon in the long-term and thus for
399 ensuring a stable background source of organic carbon for the forest soil. This might affect
400 processes of deadwood decay and the formation of humic substances since decomposing organisms
401 react differently to wood cellulose and lignin (Stokland et al., 2012; Lombardi et al., 2013).
402 Cellulose is easily decomposed by (micro)organisms, particularly in coniferous trees with a
403 relatively simple wood structure (Lambert et al., 1980; Laiho and Prescott, 2004). Compounds such
404 as tannins and lignin may, however, restrict microbial colonisation and thus slow down wood
405 decomposition (Baldock et al., 1997). Conifers are generally rather resistant to decay and tend to
406 decompose more uniformly than broadleaves.

407 The mass of cellulose, lignin and deadwood (at the end of the experiment) and the cellulose decay
408 rates correlated well with the clay content of the soils (Figs. 7 and 8; Table 5). Particularly at the

409 south-facing sites, a close relationship of these parameters with explanatory variables indicating
410 moisture (soil moisture, annual precipitation), temperature (mean annual air temperature) and soil
411 pH was evident. As a consequence, soil parameters are not negligible when considering wood
412 decay. Important explanatory variables are consequently the clay content, pH and soil moisture.
413 These parameters are principally related to weathering processes and water availability. The clay
414 content of the soils correlated well with soil-pH ($R = 0.91$, $p < 0.01$; Bonferroni corrections
415 considered). Smectitic compounds (i.e. smectite + interstratified smectite-mica; Table 7), as an
416 important part of the clays, positively correlated with soil moisture ($R = 0.78$, $p < 0.05$) and
417 negatively with pH ($R = -0.81$, $p < 0.01$). The higher the smectite content the higher the moisture
418 content and the lower the pH. Clays have the ability to better retain water and consequently improve
419 water availability that is necessary for decay. Clay minerals are formed in these environments by
420 weathering processes (transformation of primary minerals) that are more intense in cooler
421 environments (Egli et al., 2006, 2010) having a lower pH. In addition, more expanding minerals
422 (smectites) were measured on the cooler north-facing sites (particularly below 2000 m a.s.l.) at the
423 same study sites in previous investigations (Egli et al., 2006, 2007; Table 7). Smectites have the
424 possibility to store water in their interlayers and to collapse after drying. The hydroxy interlayering
425 of clay minerals, which prevents them from expansion, was more evident at south-facing sites
426 (Table 7; Egli et al., 2007). As a consequence, north-facing sites have a greater potential to retain
427 water.

428 A more intense weathering is often related to more acidic conditions. The more acidic, moister and
429 cooler conditions gave rise to a more expressed weathering at the moister north facing sites. More
430 specifically, at the north-facing sites N1 – N3 the clay content (depth 0 – 15 cm) was significantly
431 higher ($18 \pm 2\%$) compared to the south-facing sites S6 – S8 (having $14 \pm 0.9\%$). Furthermore,
432 fungi, the principal decomposers of deadwood (Jacobs and Work, 2012; Stokland et al., 2012;
433 Forrester et al., 2015; Hoppe et al., 2015a, b; van der Wal et al., 2015) prefer more acidic conditions
434 that give rise to an enhanced wood decay. A nutrient-poor, strongly weathered substrate and low pH

435 seems to increase stem rot. According to Heinemann et al. (2015), the frequency of stem rot
436 increased significantly in soils with low pH and cation concentrations in topsoil. Soil acidity is
437 known as a dominant factor affecting the soil microbial community structure (Ascher et al., 2012).
438 The saproxylic food web, and especially the role of fungi, known to act as principal deadwood
439 decomposers/digesters (brown rot-, soft rot-, white rot-) (Jacobs and Work, 2012; Stokland et al.,
440 2012; Forrester et al., 2015; van der Wal et al., 2015), cannot be neglected when addressing the
441 decay/decomposition-dynamics of deadwood. The composition of wood-inhabiting fungal
442 communities is predominantly related to the physico-chemical properties of the deadwood substrate
443 (Hoppe et al., 2015b). These properties seemed to also be governed by extrinsic environmental
444 properties as previously mentioned.

445 Neither deadwood nor any of the wood components showed a strong relationship to soil
446 temperature in our study, despite the fact that Risch et al. (2013) suggested that soil temperature
447 was the main variable to explain the differences in the decay rates of aspen and pine. Herrmann and
448 Bauhus (2012) observed that about 60% of the variation in the CO₂ flux of CWD of *P. abies* was
449 explained by climatic variables (wood moisture and wood temperature) in a lab incubation
450 experiment, whereas more than 90% of CWD respiration of individual *P. abies* logs was explained
451 by temperature in a one-year field experiment. This comparison with other data shows again that
452 moisture availability seems to be a stronger driver for decomposition than temperature alone.

453

454 5.3 Effect of exposure

455 North-facing sites are normally cooler than comparable south-facing sites, but unexpectedly decay
456 rates on north-facing sites seemed to be higher up to an elevation of about 1800 m a.s.l., again most
457 likely due to the different moisture availability. The soil moisture content was significantly lower
458 on the south-facing sites (24.8%±10.6) than on the north-facing sites (38.9%±13.5), but
459 evapotranspiration is higher. The soil conditions are thus drier on south-facing sites, even though
460 annual precipitation is the same as on north-facing sites. Wood degradation is subsequently slow.

461 Shorohova and Kapitsa (2014) found that CWD decomposition was faster on sites with a moderate
462 level of moisture than on dry sites, but CWD decay on wet sites is slow in boreal forests. The decay
463 rate constant of 0.032 y^{-1} for Norway spruce (Shorohova and Kapitsa, 2014) is very similar to our
464 study. The high variability of decomposition rates relates to water availability, local topography,
465 soil composition and incoming radiation. Soil moisture controls nutrient availability and oxygen
466 diffusion required for microbial decomposition (Skopp et al., 1990). Although climatic conditions
467 have a strong impact on the wood decomposer community (Hoppe et al., 2015a,b), Norway spruce
468 is relatively resistant to decay confirming the decay-rates to be tree-species specific.

469

470 **6. Conclusions**

471 From our measurements of decay rates under controlled conditions using a field-experimental
472 approach we found:

- 473 - The decay rates of *Picea abies* deadwood in Alpine environments seem to be low. Although
474 we used an experimental approach over a rather short time period with relatively small wood
475 blocks, the detected decay rates could be compared moderately well to average values
476 observed for the same species at other sites in Europe.
- 477 - Lignin decay rates were difficult to determine and fluctuated (over the observation period)
478 around zero. In contrast, cellulose responded much faster and clear trends could be found.
- 479 - Local scale factors, such as soil parameters and topographic properties, are important and
480 distinctly influence the decay dynamics of deadwood and its components. A higher soil
481 moisture and clay content along with a lower pH – favourable conditions especially for
482 fungal deadwood decomposers – accelerate the decay process. Temperature, interestingly,
483 exerts rather an influence on the decay rates over moisture availability. The cooler the
484 environment, the higher the moisture availability and the higher the decay rates. In contrast
485 to other findings, our observations suggest that a lower temperature positively influenced the
486 decay rates of cellulose.

- In Alpine areas, topographic exposure (south- vs north-facing sites) also affects decay processes, which are slower on south-facing sites below 1800 m a.s.l. owing to the drier conditions.

Although our study was conducted in one specific area of the Alps, the findings can be extrapolated to similar regions. Our results highlight the importance of the multiple edaphic and topographic factors that control deadwood decay processes in mountain forest ecosystems in conjunction with climate. Controlled settings allowed for a better discrimination of the processes involved. Longer-term measurements would be advisable to see if the low decomposition rates, particularly of lignin were due to a lag period. Further analyses of deadwood dynamics, including the input and decomposition of deadwood, are needed to better understand and model mountain forests, and predict their development after disturbances.

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Table 1. Characteristics of the study sites (Egli et al., 2006; Petrillo et al., 2016).

Plot ID	Elevation (m a.s.l.)	Aspect (°N)	Slope (°)	MAP ^a (mm y ⁻¹)	MAAT ^a (°C)	MAST ^a (°C)	Parent material	Dominating tree species	Land use	Soil classification (WRB)
<i>North-facing sites</i>										
N1	1180	340	31	950	5.6	7.3	Paragneiss debris	<i>Picea abies</i>	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
N2	1390	0	28	1000	4.6	6.3	Paragneiss debris	<i>Picea abies</i>	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
N3	1620	0	29	1060	3.5	5.8	Paragneiss debris	<i>Picea abies</i>	Natural forest (ecological forestry)	Chromi-Endoskeletal Cambisol (Dystric)
N4	1930	20	12	1180	1.4	5.0	Paragneiss debris, moraine material	<i>Larix decidua</i>	Originally used as pasture	Episkeletic Podzol
<i>South-facing sites</i>										
S6	1185	160	31	950	7.6–8.6 ^b	8.1	Paragneiss debris	<i>Picea abies</i>	Ex-coppice, natural forest (ecological forestry)	Episkeleti-Endoleptic Cambisol (Chromi-Dystric)
S7	1400	145	33	1000	6.6–7.6 ^b	8.7	Paragneiss debris	<i>Larix decidua</i>	Natural forest (ecological forestry)	Dystri-Endoskeletal Cambisol
S8	1660	210	33	1060	5.5–6.5 ^b	6.0	Paragneiss debris	<i>Picea abies</i>	Natural forest (ecological forestry)	Skeletal Umbrisol
S9	1995	160	25	1180	3.4–4.4 ^b	6.4	Paragneiss debris	<i>Larix decidua</i>	Ex pasture, natural forest	Skeletal Umbrisol

^aMAAT = mean annual air temperature, MAP = mean annual precipitation (Sboarina and Cescatti, 2004); MAST = mean annual soil temperature (at 10 cm depth)

^bthermal favourable conditions on south-facing sites included (according to Ascher et al., 2012)

Table 2. Regression functions tested for the temporal trends of the mass of deadwood and cellulose. Given are the R² values.

Site	Type of function				
	Exponential function	Linear function	Polynomial function (2 nd degree)	Exponential decay model (sigmoid function 1)	Logistic function (sigmoid function 2)
Deadwood					
N1	0.93	0.94	0.98	0.93	0.96
N2	0.28	0.26	0.29	0.27	0.25
N3	0.01	0.00	n.m.	0.00	0.00
N4	0.03	0.03	n.m.	0.03	0.01
S6	0.14	0.14	n.m.	0.16	0.11
S7	0.74	0.78	n.m.	0.52	0.33
S8	0.05	0.04	n.m.	0.04	0.07
S9	0.64	0.61	0.62	0.61	0.62
Cellulose					
N1	0.70	0.69	0.73	0.70	0.45
N2	0.72	0.69	0.69	0.69	0.60
N3	0.66	0.64	0.85	0.62	0.91
N4	0.50	0.53	n.m.	0.56	0.35
S6	0.28	0.30	n.m.	0.31	0.07
S7	0.50	0.50	n.m.	0.32	0.10
S8	0.24	0.25	n.m.	0.26	0.17
S9	0.76	0.75	0.80	0.69	0.92

n.m. not meaningful trends (decrease and later increase with time)

Table 3. Deadwood, cellulose and lignin decay constants k (y^{-1}) based on a) equation 1 ($\pm$ standard error), b) the regression approach (exponential function). N = north-facing sites, S = south-facing sites.

Sites	N1	N2	N3	N4	Average N	S6	S7	S8	S9	Average S	Average all
Deadwood											
a)	0.080 (0.060)	0.036 (0.051)	-0.006 (0.025)*	0.003 (016)	0.031 (0.021)	0.028 (0.027)	0.020 (0.064)	-0.009 (0.034)*	0.145 (0.065)	0.046 (0.028)	0.039 (0.017)
b)	0.071	0.057	0.003	0.021	0.038	0.043	0.021	0.002	0.101	0.042	0.040
Cellulose											
a)	0.072 (0.043)	0.096 (0.067)	0.131 (0.036)	0.103 (0.062)	0.101 (0.024)	0.042 (0.045)	0.011 (0.042)	0.029 (0.032)	0.393 (0.080)	0.119 (0.052)	0.110 (0.028)
b)	0.078	0.128	0.135	0.127	0.117	0.062	0.077	0.052	0.347	0.116	0.117
Lignin											
a)	-0.004 (0.064)*	0.035 (0.029)	0.030 (0.057)	-0.028 (0.059)*	0.003 (0.025)	-0.018 (0.026)*	-0.071 (0.060)*	-0.047 (0.020)*	0.130 (0.005)	-0.002 (0.028)*	0.001 (0.018)
b)	-0.004*	0.092	0.031	-0.007*	0.028	-0.027*	-0.024*	-0.029*	0.089	0.002	0.015

* negative values are not possible for a decay, but are due to measurement uncertainties.

Table 4. Some characteristic physico-chemical properties of the soils at the eight sites (values $\pm$ standard error)

Plot	Sand (%)	Silt (%)	Clay (%)	pH (H ₂ O)	Soil moisture (weight-%)
N01	59 (3)	26 (3)	15 (1)	5.27 (0.02)	30.8 (4.7)
N02	46 (7)	33 (5)	21 (3)	4.54 (0.20)	42.3 (3.6)
N03	51 (8)	31 (3)	18 (9)	4.39 (0.07)	47.9 (2.7)
N04	68 (4)	22 (2)	10 (3)	5.61 (0.07)	58.0 (3.8)
S06	56 (2)	30 (1)	14 (1)	5.76 (0.07)	33.9 (4.2)
S07	53 (6)	34 (6)	13 (0)	5.62 (0.04)	13.3 (1.3)
S08	60 (2)	21 (6)	19 (5)	5.46 (0.10)	34.0 (3.5)
S09	37 (5)	37 (4)	26 (1)	5.25 (0.05)	45.8 (5.1)

Table 5
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Table 5. Average correlation coefficients ($\pm$ SD) obtained by data permutation (replicates) at each site. Decay rates and amount of cellulose (k(cell), Mass(cell)), lignin (Mass(lig)) and deadwood (k(deadwood), Mass(dw)) were related to the explanatory variables annual precipitation (MAP), mean annual soil temperature (MAST), MAAT (mean annual temperature), soil-pH, soil moisture (Moist) and clay content (clay).

	k(cell)		k(deadwood)		Mass(cell)		Mass(lig)		Mass(dw)	
	cor	corSD	cor	corSD	cor	corSD	cor	corSD	cor	corSD
All										
MAP	0.56*	0.17	0.07	0.28	-0.50*	0.20	-0.26	0.27	-0.40	0.26
MAST	-0.25	0.18	0.11	0.36	0.35	0.18	0.15	0.35	0.12	0.27
pH	-0.20	0.24	0.17	0.28	0.22	0.23	0.37	0.25	0.22	0.26
MAAT	-0.37	0.20	-0.03	0.24	0.40	0.20	0.16	0.32	0.21	0.31
Moist	0.41	0.13	0.12	0.26	-0.46	0.17	-0.24	0.35	-0.28	0.29
Clay	0.70*	0.12	0.24	0.35	-0.71*	0.13	-0.62*	0.21	-0.59*	0.20
North										
MAP	0.12	0.54	-0.32	0.53	-0.15	0.57	0.13	0.56	0.18	0.66
MAST	-0.11	0.52	0.39	0.55	0.09	0.56	-0.15	0.60	-0.11	0.63
pH	-0.23	0.52	0.04	0.43	0.18	0.48	0.47	0.49	0.15	0.60
MAAT	-0.18	0.58	0.37	0.47	0.07	0.56	-0.22	0.57	-0.24	0.65
Moist	0.00	0.55	-0.42	0.57	-0.23	0.54	0.21	0.57	0.11	0.63
Clay	0.11	0.49	-0.12	0.43	-0.14	0.52	-0.48	0.51	-0.18	0.58
South										
MAP	0.85*	0.11	0.49	0.43	-0.83*	0.14	-0.69*	0.13	-0.82*	0.10
MAST	-0.47	0.15	-0.15	0.50	0.46	0.19	0.39	0.31	0.40	0.17
pH	-0.78*	0.13	-0.42	0.42	0.77*	0.17	0.63*	0.15	0.76*	0.11
MAAT	-0.82*	0.12	-0.45	0.40	0.82*	0.14	0.68*	0.16	0.83*	0.09
Moist	0.71*	0.10	0.43	0.55	-0.73*	0.11	-0.74*	0.20	-0.62*	0.17
Clay	0.94*	0.06	0.54	0.46	-0.92*	0.06	-0.82*	0.11	-0.91*	0.05

* high ($R \geq 0.5$) and stable ($\text{corSD} \leq 0.20$) correlations

Table 6. Comparison of variables between south- and north-facing sites, and higher and lower sites (using the Mann-Whitney Test). Average/median values are given. Significant differences are indicated with * ($p < 0.05$).

	North ¹⁾	South ¹⁾	Low ¹⁾	High ¹⁾	N1 – N3 ¹⁾	S6 – S8 ¹⁾
k_{cell}	0.101/0.095	0.119/0.034	0.055/0.029	0.164/0.095	0.100/0.096*	0.027/0.012*
$k_{deadwood}$	0.031/0.023	0.046/0.023	0.041/0.023	0.036/0.023	0.037/0.023	0.013/0.006
M_{cell}	8.29/8.28	8.32/9.36	9.061/9.45	7.54/8.28	8.29/8.19*	9.53/9.77*
M_{lign}	6.95/6.82	7.041/7.29	7.19/7.06	6.93/6.85	6.95/6.82	7.041/7.29
$M_{deadwood}$	21.35/21.23	21.55/22.74	22.07/21.75	20.28/21.92	21.14/21.20	23.03/23.23

¹⁾ k_{cell} (decay constant of cellulose), k_{lign} (decay constant of lignin), $k_{deadwood}$ (decay constant of deadwood), $M_{deadwood}$ (mass of deadwood), M_{cell} (mass of cellulose = concentration $\times$ dry weight of wood block), M_{lign} (Mass of lignin = concentration $\times$ dry weight of wood block), North (north-facing sites), South (South-facing sites), Low (sites < 1500 m asl), High (sites > 1500 m asl), N1 – N3 (north-facing sites except the highest site N4), S6 – S8 (south-facing sites except the highest site S9)

Table 7. Relative proportion (sum = 100%) of phyllosilicates (value, ±measurement error) in the clay fraction of the studied soils (according to Egli et al., 2006, 2007)

Plot	Elevation (m a.s.l.)	Smectite– Mica (%)	Smectite (%)	Chlorite (%)	HIV (%)	Vermiculite (%)	Mica (%)	Mica– HIV (%)	Kaolinite (%)
N1	1180	0	3±1	3±1	17±3	7±2	40±6	26±4	5±2
N2	1390	0	25±4	6±2	8±2	22±3	11±2	21±3	7±2
N3	1620	10±2	30±5	0	0	44±7	14±3	0	2±1
N4	1930	0	9±2	4±2	9±2	4±2	41±6	24±4	10±2
S6	1185	0	0	2±1	6±2	1±1	67±9	17±3	7±2
S7	1400	0	0	4±2	10±2	9±2	27±4	41±6	9±2
S8	1660	0	0	6±2	13±2	32±5	15±3	28±5	5±2
S9	1995	0	3±1	2±1	6±2	23±3	22±3	35±5	10±2

HIV = Hydroxy-interlayered vermiculite, Smectite–Mica = interstratified smectite/mica, Mica-HIV = interstratified mica/HIV

Figure captions

Fig. 1. Location of the investigation area in Trentino (Italy).

Fig. 2. Set-up of the experimental plots with wood blocks. For each time segment, three replicates were used. Wood blocks with a uniform shape and size were placed into the ‘mesocosms’ (i.e. open tubes inserted into the soil) on the soil surface and left for the indicated duration (weeks).

Fig. 3. Weight ($\pm$ standard error) of the wood blocks (placed into mesocosms) as a function of time (0 – 2 years), site (altitude) and exposure (north vs south).

Fig. 4. Amount of cellulose (= concentration $\times$ dry weight of wood block; weight $\pm$ standard error) as a function of time (0 – 2 years), site (altitude) and exposure (north vs south).

Fig. 5. Amount of lignin (= concentration $\times$ dry weight of wood block; weight $\pm$ standard error) in the wood blocks as a function of time (0 – 2 years), site (altitude) and exposure (north vs south).

Fig. 6. Comparison of exponential, linear, sigmoid (2 types; sigmoid function 1 (eq. 4) and sigmoid function 2 (eq. 5)) and polynomial (2nd order) best-fit decay model for deadwood (dry weight of wood blocks) and amount of cellulose (concentration $\times$ dry weight of wood block) for site S9.

Fig. 7. Comparison between decay constants of cellulose (k_1 , [y^{-1}]) and deadwood (k_2 , [y^{-1}]) and explanatory variables such as the clay content [%], mean annual temperature MAP [$mm\ y^{-1}$], mean annual soil temperature MAST [$^{\circ}C$], soil-pH, mean annual temperature MAAT [$^{\circ}C$] and soil moisture [%]. The different colours refer to the individual sites.

Fig. 8. Comparison between the mass of cellulose [g], lignin [g] and deadwood [g] at the end of the decay experiment with explanatory variables such as the clay content [%], mean annual temperature MAP [mm y^{-1}], mean annual soil temperature MAST [$^{\circ}\text{C}$], soil-pH, mean annual temperature MAAT [$^{\circ}\text{C}$] and soil moisture [%]. The different colours refer to the individual sites.

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