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***Effects of climate on deadwood decomposition dynamics and
interaction with the soil in Apennine and Alpine beech
forests***

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*Life is short. Forgive quickly, Kiss slowly, Love truly, Laugh uncontrollably.
And never regret anything that made you smile, or cry.*
S. Bambarén

Trees are Earth's endless effort to speak to the listening heaven.
R. Tagore

*Let's take our hearts for a walk in the woods
and listen to the magic whispers of old trees.*
Author Unknown

Adopt the pace of nature: her secret is patience.
R. W. Emerson

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Abstract

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Forests contribute to the sequestration of organic C and a key issue in C cycling in forest ecosystems can be linked to deadwood dynamics. Deadwood and litter act as important linkages between forest productivity and current community, an ecosystem processes. In forest ecosystems, coarse woody debris (CWD) influences the nutrient cycling, humus formation, carbon storage, fire frequency, water cycling and it represents also a habitat for many organisms. While a broad range of literature about CWD decay (above-ground) already exists, mechanisms describing the incorporation of the woody necromass into humus forms are rather poorly investigated.

The objectives of this thesis are focused on providing a deeper understanding of deadwood decay processes in forest ecosystems located in the Mediterranean and Alpine montane areas. Moreover, this research project investigates the relationship between deadwood decay, altitude and exposure, exploring the decomposition timing in Apennine and Alpine forests, with the main aim to deeper understand the deadwood decay processes in these climatic contexts.

In detail, the organic matter integration into the soil was investigated, focusing on the CWD decay and its incorporation in the soil organic matter (SOM) through the analysis of the wood biochemical compounds and soil chemical composition.

A climosequence approach was used to investigate the decay processes, comparing along sites located on north- and south-facing slopes, at different elevations. An accurate sampling configuration and experimental procedure was set up: at each site of the climosequence, a field experiment using soil mesocosms (PVC tubes with deadwood inside) was tested. Data were collected in Apennine (*Fagus sylvatica*) and Alpine (*Picea abies*) forest types, in order to assess the variation of chemical and biochemical compounds in CWD during the decay progression. Lignin and cellulose amounts were quantified in 5 different decay stages of CWD in the Alpine sites (*Picea abies* and *Larix decidua*).

Results showed that CWD decompose differently between Alps and Apennines, depending on the tree species, climate factors and soil composition. In detail, CWD of *Fagus sylvatica* decays very fast, while CWD decay progression of *Picea abies* is lower, as demonstrated by the analysis of lignin and cellulose in the different 5 decay stages.

In conclusion, these results represent a contribution to the knowledge on CWD decay progression in Mediterranean and Subalpine forest ecosystems. However, further studies are needed to deeper explore the factors influencing the deadwood decay rates, in order to clarify the role of deadwood in contributing to the overall forest functioning at different scales.

Key words

Deadwood, mountain forests, decay progression, lignin, cellulose, soil.

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List of Appendices

Papers I-III

- I. Fravolini, G., Egli, M., Derungs, C., Cherubini, P., Ascher-Jenull, J., Gómez-Brandón, M., Bardelli T., Tognetti R., Lombardi F., Marchetti, M. (2016). Soil attributes and microclimate are important drivers of initial deadwood decay in sub-alpine Norway spruce forests. **Publ.** - Science of The Total Environment, 569, 1064-1076.
- II. Fravolini G., Egli M., Ascher-jenull J., Arfaioli P., Tognetti R., Cherubini P., Lombardi F., Marchetti M. Quantifying decomposition in coarse woody debris in Mediterranean mountain forests. - **Subm.**
- III. Petrillo M., Cherubini P., Fravolini G., Ascher J., Schärer M., Synal H.-A., Bertoldi D., Camin F., Larcher R., Egli M. (2016): "Time since death and decay rate constants of Norway spruce and European larch deadwood in subalpine forests determined using dendrochronology and radiocarbon dating. **Publ.** - Biogeosciences, 13, 1537–1552, www.biogeosciences.net/13/1537/2016/ doi:10.5194/bg-13-1537-2016

Extended Abstract

This PhD thesis dealt with CWD decay and integration into the soil of *Fagus sylvatica* forests, in the Apennines (Majella Mt.) and Italian Alps (Val di Rabbi, Val di Sole), and on how climate affects the CWD decay in subalpine natural forests, analysing the decay rates and the relationship between lignin/cellulose decay and soil properties.

Deadwood is an important component in the functioning of forest ecosystems and their structure, as it is relevant for biodiversity, trophic chains, forest natural regeneration, nutrient cycles and overall carbon storage (Harmon et al., 1986; Franklin et al., 1987; Jonsson and Kruys, 2001; Laiho and Prescott, 2004; Luyssaert et al., 2008; Russel et al., 2015). A special contribution to the maintenance of forest functions is provided by CWD (coarse woody debris) residues of living trees in a forest ecosystem including whole fallen trees, fallen branches, and pieces of fragmented wood, stumps and standing dead trees (snags) (Zhou et al., 2007).

Field soil-warming experiments (e.g. Rustad et al., 2001; Melillo et al., 2002; Eliasson, 2005; Allison et al., 2010; Ågren, 2010; Budge et al., 2011) have provided evidences of the particular sensitivity of litter decomposition to temperature. Consequently, a need exists to explore more in detail the interplay between soils, forests, deadwood and climate particularly in mountain areas (Egli et al., 2006; Ascher et al., 2012).

The decay rate of CWD is affected by several factors such as the ratio of bark to wood, tree species, log diameter (or the geometry in general; MacMillan, 1988; Van der Wal et al., 2007), contact with the forest floor (Ganjugunte et al., 2004), soil type (van der Wal et al., 2007), and others. The negative exponential time model is the most commonly used to estimate the decrease in density of CWD (Naesset, 1999; Chen et al., 2005). Although the decay rate of CWD as a function of climate is basic information for understanding the cycle of carbon and nutrients, only scarce data is available. Several studies have been done in the North-Western Pacific in the U.S. and Canada (Harmon et al., 1986; Daniels et al., 1997; Campbell and Laroque, 2007) while our knowledge about decay rates of different tree species in European forest ecosystems is limited to few experimental and field studies (Naesset, 1999; Storaunet and Rolstad, 2002; Lombardi et al., 2008; Herrmann and Bauhus, 2012) or rough estimations and modelling (Storaunet, 2004; Mäkinen et al., 2006).

Recently, more information on deadwood chemistry (even in Europe) as a function of decay stage in temperate to subalpine environments is available (cf. Lombardi et al.,

2008; Petrillo et al., 2015). The relation to the factor time is, however, in most cases completely missing and only in rare cases some estimates are presented (e.g. Petrillo et al., 2016). Detailed information on carbon stored in deadwood and its relationships with different decay stages are required by national forest and carbon sink inventories to understand deadwood dynamics and the impact on microhabitats with a changing climate. These relationships are expected to vary with disturbance regime and forest type.

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

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

(single-negative-exponential model), where x_t is the density or mass of deadwood at a given time, and x_0 is the initial density or mass (Jenny et al., 1949; Olson, 1963).

To unravel the decay behaviour of these compounds, a multiple-exponential model can be applied (Means et al., 1985; Mackensen et al., 2003), with the general form:

$$x = x_1 e^{-k_1 t} + x_2 e^{-k_2 t} \dots + x_n e^{-k_n t}$$

(2)

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

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

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

Experimental Procedure

In this PhD thesis an experimental procedure was set up: at each site of the climosequence, a field experiment using soil mesocosms was set up. The design of the mesocosms in the field followed Maestrini et al. (2014). Mesocosms (10.2 cm diam., 20 cm long PVC tubes) were inserted (summer 2014) into the soil and then normed wood blocks were added. The mesocosms were placed >1 m from large trees and >0.5 m from the adjacent mesocosms. Coarse woody debris having a uniform size was added to the soil mesocosms (with 3 replicates for each time step and site). Because the size and geometry of CWD can strongly influence the decay mechanisms (Van der Wal et al., 2007), wood blocks, having the dimension of 2 cm x 5 cm x 5 cm, from the same *Fagus sylvatica* tree were prepared. All wood blocks were placed on top of the soil and within the mesocosms. The CWD wood blocks were sampled after 8, 16 and 52 weeks; always with 3 replicates. The weight (density) and cellulose and lignin were recorded for these blocks.

The wood cellulose extraction method begins weighing powdered samples into Teflon pockets (10 mg). The first step is the washing of samples in 5% NaOH (Sodium hydroxide) solution for two times at 60°C. Then samples are washed with 7% NaClO₂ (Sodium chlorite) solution and 96% CH₃COOH (acetic acid; until pH is between 4-5) at 60 °C for three times. This method eliminates lignin in the wood samples.

The method for extracting lignin from wood is a long procedure that begins with extracting water-soluble compounds. It means that 80 °C ultrapure water is added to the samples, mixed well and stirred for 3 times. After drying the procedure goes on with extracting ethanol soluble compounds. So ethanol is added to all samples and mixed well, centrifuged for three times. After that the samples with ethanol are filtered with paper filters. Then 72% Sulphuric acid (H₂SO₄) is added in each sample also with ultrapure water and put into the autoclave at 120 °C. This solution is then filtered in ceramic crucibles. The lignin is measured in the crucibles (difference of weight gives Klason lignin; Klason, 1893) and in the bottles that collect the discarded solution of the samples (ASL, Acid Soluble Lignin; Klason, 1893).

The pH in the soil was measured through the Metrohm 620 pH-meter, while the carbonates were analysed using NaOH (Sodium hydroxide) and HCl (Chloridric acid) till the samples became pink.

Soil pH (H₂O) was determined using a soil:solution ratio of 1:10. Particle size-distribution of the <2 mm fraction was determined as weight percentage (USDA scale) using the sieve-and-pipette method with prior oxidation of organic matter by hypochlorite (NaClO) (Patruno et al., 1997).

Determination of the main physical properties

The cellulose was analysed as follows:

$$\text{Cell \%} = (\text{mg of cellulose} * 100) / \text{mg of wood}$$

Where cell mg of cellulose refers to weighed material in the Teflon bag after the whole process, and mg of wood to wood weighed in the Teflon bag before the cellulose extraction process (10 mg ca.).

The lignin extraction follows this formula:

$$(((a-b)-(c-b))/d)*100$$

Where a is the dry sample weighed in ceramic (mg), b is the ceramic tare, c is the ceramic weight after incineration (550°C) and d is the weight of the sample at the beginning of the extraction (300 mg ca.).

Table 1. Some typical characteristics of the soils (mesocosms) on the Apennines (1.a) and on the Alps (1.b).

a) Apennines

Site	Exposure	pH (H ₂ O)	Moisture (g)	Sand (%) 500-250 um	Sand (%) 250-53 um	Silt (%) 53-2 um	Clay (%) < 2 um
S1	south	7.11	20,339	0,938	2,411	8,824	6,174
S2	south	7.15	15,639	1,805	7,619	6,861	2,214
S3	south	6.48	28,325	1,045	2,207	3,273	0,739
S4	south	6.61	24,78	1,331	5,832	6,78	2,053
N6	north	6.38	19,317	0,867	5,09	8,132	3,501
N7	north	6.95	23,752	2,458	7,598	13,46	4,962
N8	north	7.31	18,676	4,316	9,376	17,14	7,217
N9	north	7.2	20,824	1,757	17,89	5,700	5,013

b) Alps

Site	Exposure	Sand (%)	Silt (%)	Clay (%)	pH (H ₂ O)	Moisture (g)
N01	north	57	28	16	5.27	30.8

N02	north	41	39	20	4.54	42.3
N03	north	52	26	22	4.39	47.9
N04	north	62	24	14	5.61	58.0
S06	south	57	29	13	5.76	33.9
S07	south	41	47	12	5.62	13.3
S08	south	62	23	15	5.46	34.0
S09	south	47	29	24	5.25	45.8

The following table shows decay constants, using Equation and Regression Approach. The decay rate constants for beech CWD were estimated on the basis of the mass loss within the observation period using a single negative exponential model and an exponential regression approach. Both approaches yielded comparable values. Over time, the detectable changes in wood mass and cellulose (less in lignin) appear to be significant. Accordingly, the decay constants vary from 0.21 to a maximum of 0.49 y^{-1} (Table 7). The average k -values for CWD (mass loss per year) were in the range of 0.32 to 0.43 y^{-1} , depending on the calculation procedure and exposure.

Table 2. CWD, cellulose and lignin decay constants k (y^{-1}) based on a) equation 1, b) the regression approach on the Apennines (2.a) and on the Alps (2.b). N= north-facing sites, S= south-facing sites.

a) Apennines

Sites	S1	S2	S3	S4	Average S	N6	N7	N8	N9	Average N	Average all
CWD											
a)	0,29	0,25	0,36	0,42	0,33	0,46	0,41	0,37	0,49	0,43	0,38
b)	0,27	0,21	0,38	0,43	0,32	0,41	0,32	0,44	0,48	0,41	0,37
Cellulose											
a)	1,022	1,08	0,71	1,26	1,02	1,42	1,096	1,19	1,25	1,24	1,13
b)	0,975	1,051	0,742	1,321	1,022	1,034	1,107	1,189	0,853	1,046	1,034
Lignin											
a)	0,082	0,054	0,12	0,21	0,12	0,33	0,28	0,19	0,35	0,29	0,204
b)	0,059	0,015	0,15	0,22	0,112	0,292	0,191	0,299	0,44	0,306	0,209

b) Alps

Sites	N1	N2	N3	N4	Average N	S6	S7	S8	S9	Average S	Average all
CWD											
a)	0.080	0.036	-0.006	0.003	0.031	0.028	0.020	-0.009	0.145	0.046	0.039
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	0.096	0.131	0.103	0.101	0.042	0.011	0.029	0.393	0.119	0.110
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	0.035	0.030	-0.028	0.003	-0.018	-0.071	-0.047	0.130	-0.002	0.001
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.

Statistical analysis

All statistical analyses were performed using the software IBM SPSS Statistics 21. The distribution of each population was tested using the Shapiro Wilk normality-test. If the result of the normality test was positive, parametric comparison methods were then adopted through a t-test or an analysis of variance (ANOVA). Otherwise, non-parametric comparison tests were applied, i.e the Mann-Whitney (U-test) and the Kruskal-Wallis test. These tests were used to see if differences between north- and south-facing sites or along the altitudinal gradient exist with respect to the decay rates (mass losses) of deadwood, cellulose or lignin. For the correlation analyses, the Spearman rank correlation coefficient was used with non-normally distributed data. The correlation analyses were applied to detect how the decay rates relate to (micro)climatic conditions and soil parameters.

All statistical tests were carried out using a level of significance of $p < 0.05$.

Table 3. Relationships (Spearman rank correlation coefficients) of a) decay constants of cellulose and CWD and b) mass of cellulose, CWD and lignin with environmental and soil parameters on the Apennines (3.a) and on the Alps (3.b). * $p < 0.05$, ** $p < 0.01$

a) Apennines

	k CWD	k Lign	pH	Inorg C	Org C	N	MAP	MAAT	Moist
a) decay constants									
k Cell	0.25	0.29	0.04	0.05	0.001	-0.23	0.03	0.19	0.01
k CWD		0.84**	-0.11	-0.14	0.11	0.16	-0.37*	0.62**	0.10
k Lign			-0.22	-0.12	0.14	0.26	-0.20	0.55**	0.13
pH				0.80**	-0.71**	-0.12	-0.24	0.31	-0.09
Inorg C					-0.74**	0.16	-0.01	0.18	-0.16
Org C						0.06	0.25	-0.29	0.26
N								0.11	-0.20
MAP								-0.83**	-0.22
MAAT									0.12
Moist									
	M CWD	M Lig	pH	Inorg C	Org C	N	MAP	MAAT	Moist

218	b) Mass									
219	M Cell	0.73**	0.45*	0.17	-0.17	-0.04	-0.65**	0.03	-0.06	-0.12
220	M CWD		0.76**	-0.08	-0.35*	0.13	-0.50**	0.31	-0.54**	-0.24
221	M Lig			-0.19	-0.37*	0.16	-0.30	0.23	-0.36*	-0.17
<i>k Cell (decay constant of cellulose), k CWD (decay constant of CWD), k Lign (decay constant of lignin), M CWD (mass of CWD), M Cell (Mass of cellulose), M Lig (Mass of lignin), Inorg C (inorganic carbon content), Org C (organic carbon content), N (nitrogen content), MAP (mean annual precipitation), MAAT (mean annual air temperature), Moist (soil moisture content).</i>										

222	b) Alps									
		k CWD	MAP	MAST	pH	MAAT	Moist	Clay	Silt	Sand
	a) decay constants									
	k Cell	0.46*	0.43*	-0.26	-0.45*	-0.52**	0.49*	0.61**	-0.05	-0.11
	k CWD		0.01	0.18	-0.05	-0.03	-0.03	0.23	0.14	-0.09
	MAP			-0.68**	-0.29	-0.73**	0.78**	0.39	-0.42*	0.17
	MAST				0.48*	0.81**	-0.88**	-0.41*	0.74**	-0.47*
	pH					0.62**	-0.48*	-0.91**	0.11	0.32
	MAAT						-0.88**	-0.60**	0.40	-0.11
	Moist							0.52**	-0.49*	0.26
	Clay								-0.14	-0.21
	Silt									-0.88**
		M CWD	M Lig	MAP	MAST	pH	MAAT	Moist	Clay	Silt
	b) Mass									
	M Cell	0.80**	0.66**	-0.43*	0.26	0.45*	0.52**	-0.49*	-0.61**	0.05
	M CWD		0.86**	-0.28	0.01	0.33	0.29	-0.22	-0.48*	-0.16
	M Lig			-0.22	0.05	0.42*	0.26	-0.26	-0.56**	-0.14
223	<i>k Cell (decay constant of cellulose), k CWD (decay constant of CWD), M CWD (mass of CWD), M Cell (Mass of cellulose), M Lig (Mass of lignin), MAP (mean annual precipitation), MAST (mean annual soil temperature), MAAT (mean annual air temperature), Moist (soil moisture content)</i>									

226

227 In Table 3 and 4 the amount of cellulose and lignin is not displayed as a concentration
228 value but as a mass — obtained by multiplying the concentration of cellulose and lignin
229 with the CWD mass.

230

231 **Table 4.** Comparison of variables in South- and North-facing sites (using Mann-Whitney Test)
232 on Apennines (a) and Alps (b).

233 a) Apennines

	North	South
<i>k cell</i>	1,28	1,02
<i>k lign</i>	0,27	0,12
<i>k CWD</i>	0,43	0,33
<i>M cell</i>	3,03	3,30
<i>M lign</i>	3,28	3,58
<i>M CWD</i>	10,42	11,80

b) Alps

	North	South
<i>k cell</i>	0,91	0,094
<i>K lign</i>	0,691	0,092
<i>K CWD</i>	0,737	0,303
<i>M cell</i>	0,91	0,094
<i>M lign</i>	0,691	0,092
<i>M CWD</i>	0,988	0,095

k cell (decay constant of cellulose), *k lign* (decay constant of lignin), *k CWD* (decay constant of CWD), *M CWD* (mass of CWD), *M cell* (Mass of cellulose), *M lign* (Mass of lignin), North (North-facing sites), South (South-facing sites).

On the Apennines, already after 8 weeks, the lignin content of the dead wood increased compared to the fresh wood. The cellulose analysis, however, showed a slight decreasing trend (not always statistically significant), both for the north and the south exposure. On the Alps, decay seems to be slower and, in most cases, the amount of cellulose decreased with time while no significant variations were found for lignin. The decay rate of cellulose not only correlates with climatic parameters such as annual precipitation or mean annual temperature, but also with soil parameters such as pH and soil moisture in all the sites. Especially at the highest altitudes this decreasing trend was best expressed. The highest sites are the coolest and also have enough moisture during the dry summer months. The amount of lignin does not seem to be affected by climatic parameters. In addition, lignin significantly correlated with soil parameters such as inorganic C, on the Apennines, and pH and soil texture, on the Alps. This correlation analysis evidences the important role of soil parameters in the complex CWD decay process. Despite all these potential ambiguities, our field experimental approach confirms the fast decay rates of beech CWD in subalpine environments compared to

spruce. At the local scale (our investigation areas) - besides air temperature and annual precipitation - also soil moisture influences the decay dynamics. However, not all wood components react similarly. Cellulose is decaying much faster than lignin or the bulk CWD. Consequently, particularly good correlations of cellulose with environmental and soil parameters can be detected. The slower decay of lignin compared to cellulose suggests that lignin is an important long-term stock of organic carbon, providing the presence of a stable background source for the forest soil.

Introduction

In Europe, forests occupy about 160 million ha (35% of the EU's land area). They are home for the largest number of species on the continent and provide important environmental functions, such as the conservation of biodiversity and the protection of water and soil. The forests as CO₂ sinks gained the highest global political significance in relation to climate change and implementation of the Kyoto Protocol. The atmospheric concentration of CO₂ has increased from 280 ppm in 1750 to 367 ppm in 1999 (31%). About half of the anthropogenic CO₂ emissions between 1750 and 2011 have occurred in the last 40 years (high confidence) (IPCC 2014). More recently, it reached constantly a new record: 400 ppm. In November 2015, the Met Office (United Kingdom's national weather service) predicted that mean concentrations of atmospheric CO₂ in May 2016 would reach 407.57 ppm, with a 0.5 ppm margin of error. In fact, they reached 407.7. In October 2016, NOAA (U.S. National Oceanic and Atmospheric Administration) measured 401.57 ppm in Mauna Loa, Hawaii. The UN's Intergovernmental Panel on Climate Change (IPCC) says that CO₂ concentrations must be stabilized at 450 ppm to have a fair chance of avoiding global warming above 2 °C, which could carry catastrophic consequences. Today's CO₂ concentration has not been exceeded during the past 420,000 years and likely not during the past 20 million years. The rate of increase over the past century is unprecedented, at least during the past 20,000 years (IPCC, 2001). The principal climate forcing, defined as an imposed change of planetary energy balance, is increasing carbon dioxide (CO₂) from fossil fuel emissions, much of which will remain in the atmosphere for millennia (Hansen et al 2013), and from deforestation (IPCC, 2001). The emission of CO₂ concentration from industries, burning of fossil fuels and deforestation causes GHGs (green house gases). Hence, forests in terms of agroforestry, plantation, reforestation has been suggested as one of the most appropriate land management systems for mitigating atmospheric CO₂ through photosynthesis process (Alemu 2014). Forest ecosystems also contribute to store more than 80% of all terrestrial aboveground C and more than 70% of all SOC (Soil Organic Carbon) (Alemu 2014).

Total anthropogenic GHG (greenhouse gases) emissions have continued to increase over 1970 to 2010 with larger absolute increases between 2000 and 2010, despite a growing number of climate change mitigation policies. Emissions of CO₂ from fossil fuel combustion and industrial processes contributed about 78% of the total GHG

emissions increase from 1970 to 2010, with a similar percentage contribution for the increase during the period 2000 to 2010 (high confidence) (IPCC 2014).

Terrestrial ecosystems return carbon to the atmosphere by respiration, decay and fires (Post et al., 1990). The terrestrial carbon reservoir is actually a collection of carbon pools with a wide range of net primary production rates, respiration rates and carbon turnover times (Post et al., 1990). The total net primary production of terrestrial vegetation has been estimated in 1983 by Olson and his colleagues at 62 gigatons per year. This is assumed to be approximately balanced, over a period of several years, by an equivalent return of carbon to the atmosphere from decomposition of litter and soil organic matter (Olson et al., 1983; Post et al., 1990). The return flow comes from two pools of “dead” organic matter: the detritus/decomposer pool, made up of litter and decomposers at the soil surface, and the active soil carbon pool, which consists of that fraction of the carbon in soils, and the associated decomposer organisms, that are in relatively active exchange with the atmosphere (Post et al., 1990). The turnover time of carbon in the detritus/decomposer pool can range from less than a year in moist tropical forests to decades in cold, dry boreal forests (Post et al., 1990).

The IPCC (Gitay et al., 2002), SEC (2006) and the EU Soil Thematic Strategy (COM (2006)231) identified, among others, the following information needs:

- Understanding of the response of biodiversity to changes in climatic factors and other pressure
- Closing the gaps in knowledge about soil processes and strengthening the foundation for policies.
- Knowledge and concepts on how mountainous landscapes, including the soil system, in the Mediterranean to high-mountain areas may change under conditions of fast to accelerated external (climatic) forcing.

Mountainous ecosystems are likely to be especially sensitive to changing environmental conditions, including global warming, acid deposition or nutrient cycling (Theurillat et al., 1998). Landscape, climate, society and infrastructure in the mountainous areas are changing at high rates (Haeberli et al., 2007). Mountainous areas are a complex system, in which different features influence each other while reacting with different intensities and time frames to changing environmental conditions. Unfavorable or threatening

processes need to be prevented or mitigated, in order to preserve the possibility of sustainable development.

It is defined an ecologically sustainable forest management (ESFM) as forest management that perpetuates ecosystem integrity while providing wood and nonwood products; where ecosystem integrity means the maintenance of forest structural complexity, species diversity and composition, and ecological processes and functions within the bounds of normal disturbance regimes (Lindenmayer et al 2012).

The amounts and patterns of deadwood are therefore being increasingly used, both as an index of current ecosystem health and as a means of setting standards for sustainable forest management (Albrecht, 1991; Kohl, 1996; Tomppo, 1996).

Deadwood in forest ecosystems

Deadwood is a key indicator for assessing policy and management impacts on forest biodiversity (Verkerk et al 2011).

Deadwood is an important component in the functioning of forest ecosystems and their structure, as it is relevant for biodiversity, trophic chains, forest natural regeneration, nutrient cycles and overall carbon storage (Harmon et al., 1986; Franklin et al., 1987; Jonsson and Kruys, 2001; Laiho and Prescott, 2004; Luyssaert et al., 2008; Russel et al., 2015). A special contribution to the maintenance of forest functions is provided by CWD (coarse woody debris) residues of living trees in a forest ecosystem including whole fallen trees, fallen branches, and pieces of fragmented wood, stumps and standing dead trees (snags) (Zhou et al., 2007). The decomposition of woody debris has an important influence on carbon (C) retention in forest ecosystems (Yatskov et al. 2003). Woody debris is also an important long-term nutrient storage (Harmon et al. 1986) and is widely regarded as an important structural element for the provision of biodiversity (Christensen et al. 2005). Low levels of woody debris are considered to be a major factor causing the decrease in biodiversity in European forests (Schuck et al. 2004; Christensen et al. 2005; Assmann et al. 2007; Böhl and Brändli 2007; von Oheimb et al. 2007).

The amount of woody debris is normally much lower in managed forests than in unmanaged old-growth forests: most of the large-sized harvestable timber is extracted from managed forests. The remaining trees produce woody debris consisting of twigs

and branches (Christensen et al. 2005). In Germany, branches and twigs have not been used as firewood for several decades. As a result, fine woody debris (FWD) is readily available in most forests (Röhrig 1991). However, the high number of endangered species of saproxylic fauna (Berg et al. 1995; Binot et al. 1998; Ranius and Fahrig 2006; Franc et al. 2007) requiring woody debris to survive, suggests that the availability of coarse woody debris (CWD) in managed forests is insufficient (Muller-Using and Bartsch, 2009). A certain level of CWD storage is a requirement for close-to-nature forest management (Pommerening and Murphy 2004) and certification (FSC 2008; PEFC 2008) of forests. Timber harvesting forests should function as links in a woody debris habitat network (Scherzinger 1996; Ammer and Utschick 2004). However, management concepts to achieve goals for European forests have not yet been developed, because the factors influencing the quantity, quality, and dynamics of woody debris are not sufficiently identified. Therefore, current models for CWD dynamics in Europe (Rademacher and Winter 2003 for beech; Ranius et al. 2003 for spruce) cannot be widely applied (Muller-Using and Bartsch, 2009).

Deadwood cycling is the process of components of wood (carbon, minerals, moisture, and so on) in the forest ecosystem through the processes of death, decomposition, and uptake. The changes of trees, which are the most significant structural features of forests, during this process affect many other forest components and functions (Maser et al. 1979; Maser and Trappe 1984; Maser et al. 1988; Hammond 1991). The amount of CWD in any stand is a function of mortality agents, site conditions and exposure, and decay mechanisms and rates (Harmon and Hua 1991). CWD biomass in some coniferous ecosystems may exceed the total biomass of many deciduous ecosystems (Spies and Cline 1988). Decay classification for CWD has been described by Maser et al. (1988). The total volume or biomass of CWD varies with ecological condition (Spies and Cline 1988; Lofroth, unpublished data). The substantial stocks of woody debris (WD) – forested ecosystems constitute as much as 50% of total C in the terrestrial biosphere (Malhi 2002) and WD represents up to 20% of the total in old-growth forests (Delaney et al. 1998) – and its ecological importance have stimulated studies on various aspects of their role in ecosystem processes (see reviews by Harmon & Sexton 1996; Wirth et al. 2009).

Brewer (1993) reported that CWD in plots in some SBS (sub-boreal spruce) stands ranged from 37 to 384 m³/ha. Mean volumes for all stand conditions and ages were 44.1

m³/ha in the SBSdk (dry-cool) subzone and 159.2 m³/ha in the SBSmc (moist-cold) subzone (Lofroth, unpublished data). The driest sites had the lowest biomass and moist sites the greatest in Douglas-fir forests of Washington and Oregon (Spies et al. 1988). Within mature stands in the SBSmc (moist-cold) subzone, CWD volumes were lowest in xeric ecosystems (Dry Pine: 36.2 m³/ha and highest in moist ecosystems (Devil's Club: 268.4 m³/ha (Lofroth, unpublished data). Mean volumes of CWD in mature stands by natural disturbance type (Province of British Columbia 1995) and biogeoclimatic zone ranged from a low of 60 m³/ha in the Boreal Black and White Spruce Zone in *ecosystems with frequent stand-initiating events* (NDT3) (Province of British Columbia 1995) to a high of 390 m³/ha in the Coastal Western Hemlock Zone in *ecosystems with rare stand-initiating events* (NDT1) (Lofroth, unpublished data). Benson and Schlieter (1979) reported that CWD volumes were 210 m³/ha in dry-site Douglas-fir stands, but as much as 560 m³/ha in grand fir stands.

CWD volumes also vary with successional stages. Mean volumes across a range of moisture and nutrient regimes in the SBSmc (moist-cold) subzone were high in early successional stages (herb/shrub) (174.2 m³/ha), declined to a low of 58.2 m³/ha in young forest successional stages, and were highest in old-growth stands (261.5 m³/ha) (Lofroth, unpublished data). Spies et al. (1988) reported that amounts of CWD were high in the youngest successional stages, were lowest in 60-80-year-old forests, and were high in old stands (< 500 years). After 500 years CWD amounts declined to an intermediate level. Spies and Franklin (1988) reported that CWD input might be low in young stands because of the small size of dead and dying stems. Volumes in these stands are often high, however, due to residual CWD from the previous stand. The amount of this residual CWD depends on the disturbance agent causing the change in succession. In stands where succession has been retarded by natural catastrophic events (windthrow, fire, etc.), it can be significant. Spies *et al.* (1988) suggest that the nature and the timing of disturbance play a key role in CWD dynamics. Human-caused changes (such as logging) will usually result in conditions different than those that may have initiated the original stand. In these circumstances, the amount of CWD, as with standing dead trees, may not be indicative of natural dynamics within ecosystems.

The rates of input and decay also vary with ecological site conditions and stand age, and between tree species (Sollins 1982; Spies and Franklin 1988). Sollins (1982) reported that although there was considerable variability in the data, the highest values for CWD

biomass were reported from old-growth stands. Harmon et al. (1987) reported that decay rates of logs might vary with microclimate, size, substrate, and species of log. Mattson et al. (1987) reported that decay rates varied by as much as tenfold between tree species. They also reported that aspect was an important factor in determining decay rates, and that logs suspended above the ground decayed at slower rates than those on the ground. Keenan et al. (1993) attribute large accumulations of CWD in western red cedar and western hemlock stands on Vancouver Island to slow decomposition rates, high rates of input following windstorms, and the large size and decay resistance of western redcedar. Abbott and Crossley (1982) reported that in chestnut oak (*Quercus prinus*) stands, decomposition was influenced by moisture and temperature and was inversely related to the diameter of the material.

Deadwood quantities are normally much lower in managed forests than in unmanaged old-growth forests, as most of the large-sized harvestable timber is extracted (Green and Peterken, 1997; Kirby et al., 1998; Odor and Standovar, 2001; Winter and Nowak, 2001). In addition, deadwood in managed stands typically consists only of small twigs and branches and short stumps, with few large logs or snags found (Kruys et al., 1999). In the interest of sustainable forestry and biodiversity conservation, efforts are being made to increase deadwood levels in managed forests (e.g. Hodge and Peterken, 1998; Harmon, 2001). In Europe, the volume of standing and fallen deadwood is one of nine pan-European indicators for sustainable forest management (criterion 4: maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems) (MCPFE, 2003).

In central and southern Europe deadwood has received less attention (Bretz Guby and Dobbartin, 1996; Marage and Lemperiere, 2005; Motta et al., 2006; Lombardi et al., 2008) and human pressure has affected forest dynamics since prehistoric times (Farrell et al., 2000; Motta and Nola, 2001; Winter et al., 2010). In this context, quantity and quality of coarse woody debris (CWD) are regarded as important structural indicators of naturalness and biodiversity (Corona et al., 2003; MCPFE, 2003; Jönsson and Jonsson, 2007), providing information on the intensity of past human disturbances and closeness to oldgrowth condition (Stokland, 2001; Woodall and Nagel, 2006).

The public attitude towards forests and forestry has dramatically changed (Castagneri et al., 2010). Past management was concentrated on what was being extracted from the forest, whereas current management emphasizes what is being left (Kohm and Franklin,

1997). In the past, CWD was routinely removed in an attempt to limit fuel loading (thereby minimizing wildfires) and make replanting easier. Also, because of the slow rate at which CWD decayed, its role in nutrient cycling, and therefore its importance, was not well understood (Triska and Cromack 1979).

Deadwood as indicator of biodiversity

Climate is projected to affect all aspects of ecosystems functioning and biodiversity, and their ability to provide services (The Millennium Assessment, 2005); however, the projected changes have to take into account the impacts from other past, present and future human activities (Gitay et al., 2002). Below-ground diversity is difficult to quantify but it is assumed to surpass above-ground plant and animal diversity (Wall et al., 2010). Climate change is expected to affect individual organisms, populations, species distributions and ecosystem composition and function through increases in temperature and changes in precipitation. The data and models needed to project the extent and nature of future ecosystem changes and changes in the geographical distribution of species are incomplete, meaning that these effects can only be partially quantified (Gitay et al., 2002).

Precipitation and temperature influence vegetation and consequently soil properties by affecting type and rates of chemical, mineralogical, biological, and physical processes. Field experiments about soil warming (e.g. Rustad et al., 2001; Melillo et al., 2002; Eliasson et al., 2005; Allison et al., 2010; Ågren, 2010; Budge et al., 2011) have provided evidences about the temperature sensitivity of decomposition. Deadwood is an important component in forest ecosystems, and despite its ecological role has been recognized widely for a long time (Haapannen 1965; Elton, 1966), only recently, research has focused on its role in ecosystems. Deadwood has become a structural key factor (Larsson 2001) and an indicator in the assessment of biodiversity and naturalness of forest systems (McComb and Lindenmayer, 1999; Skogstyrelsen, 2001).

Wood decomposition rate and dynamics, like for other types of litter, are virtually entirely determined by the interactions between (1) wood quality and (2) the composition, abundance and activity of decomposer communities (Cadisch and Giller 1997). However, these interactions are strongly controlled by abiotic drivers, which determine the growth performance of the trees and thereby the properties of their woody

debris (Cornelissen et al., 2012). Moreover, these abiotic drivers also control the moisture and temperature regime of the deadwood as well as the decomposer activity and community. Micro-organisms, particularly fungi and invertebrates, are the main agents of wood decay (Kaarik 1974). The structural and chemical traits of deadwood, inherited from the traits of living trees, are also major drivers of wood decomposition and these traits vary greatly among tree species (Chave et al. 2009; Cornwell et al. 2009; Weedon et al. 2009; Zanne and Falster 2010).

Deadwood and litter act as important linkages between recent productivity and current community, and ecosystem processes (Anderson et al., 2009). The increasing interest in the quantity and properties of coarse woody debris and litter is relevant both to maintaining biodiversity and to global C dynamics (Kueppers et al., 2004). Dying and dead trees are valuable habitats (providing food, shelter and breeding conditions, etc.) for a large number of rare and threatened species: saproxylic insects, invertebrates, fungi, lichens, bryophytes, birds and mammals (Harmon et al., 1986; Ódor and Standovár, 2001; Humphrey et al., 2002; Ódor et al., 2006).

Although wood degrading organisms largely differ in preference of substrate and/or abiotic conditions, most of them share the need for oxygen and water. This makes wood moisture content an important driver of wood decomposition (Cornelissen et al., 2012). Below a wood moisture content of 20%, most fungi are inactive while wood moisture content of 80–100% restricts enzymatic activity of fungi due to lack of oxygen (Tsoumis, 1991; Zabel and Morrell, 1992; Schmidt, 2006).

It has been demonstrated that advanced decay stages of CWD can leach significant quantities of organic matter and dissolved organic carbon into the soil (Zalamea et al., 2007), that soil chemical characteristics can be altered under its influence, increasing calcium, magnesium, and total N concentrations (Kappes et al., 2007), as well as decreasing soil pH (Spears and Lajtha, 2004).

In spite of its demonstrated importance in forest ecosystems, it is not well understood how CWD could affect abiotic and biotic characteristics in its sphere of influence (Gonzalez et al., 2013). Some authors have suggested that soil contact accelerates CWD decomposition (Naesset, 1999; Garrett et al., 2010), but the feedback on soil biotic activity from CWD presence is not clear.

One of the principal legacies of CWD in forest ecosystems is its persistence in time and its slow decomposition (Harmon et al., 1986), which allows for the development of long-term interactions between CWD and soil (Gonzalez et al., 2013).

To a greater or lesser degree, depending on the moisture and temperature regimes of an ecosystem, deadwood may add a significant amount of organic matter to the soil, provide habitat for decomposer organisms, retain moisture through dry periods, providing a refuge for ectomycorrhizal roots and their associated soil organisms, provide a site for asymbiotic or associative nitrogen-fixing bacteria, represent a capital pool of nutrients for the ecosystem, provide a site for the regeneration of conifers and contribute to soil acidification and podsolization (Stevens 1997).

All size classes of decaying pieces of wood contribute to the long-term accumulation of organic matter because the lignin and humus of well-decayed wood are high in carbon constituents (Maser et al. 1988). It improves the moisture-carrying capacity and structure of the soil. To protect the productive potential of a forest soil, a continuous supply of organic materials must be maintained (FAO 2005). Also ectomycorrhizal activity has been found to be essential to the healthy growth of conifers.

This activity is a moisture-dependent phenomenon (Harvey et al. 1983). Both diameter and state of decay affect the ability of down wood to hold moisture. All size classes of decaying wood act as a moisture store and provide refugia for tree roots and ectomycorrhizal fungi during dry periods; however, the larger pieces can hold more water and are therefore more effective at holding moisture and acting as refugia through long, dry spells (Stevens 1997). When moisture returns to the site, it is a much faster process to reinvade the organic layer of soil with ectomycorrhizal root tips when refugia are scattered throughout the forest floor. Wood is only a moderate source of nutrients, but usually occurs in sufficient volumes to be a significant source of moisture (Harvey et al. 1986). Deadwood can also contribute to nutrient storage. This includes the nutrients accumulated in the woody bole, large branches, roots and stumps during tree growth and the nutrients added from litterfall and throughfall (rain falling through the forest canopy) being intercepted by a down log rather than falling on the forest floor (Stevens 1997). If the nutrients are added faster than they are leached out by rain, the result is positive nutrient storage. As the wood decays, the nutrients are added to the available pool. Mechanisms for removing the nutrients from deadwood and adding them to the available pool vary. Harmon et al. (1994) found that during early stages of

decomposition, fungal sporocarps (mushrooms) growing on decaying logs increased the concentrations of nitrogen, potassium and phosphorous 38, 115 and 136 times, respectively, over the concentrations found in the logs (Lombardi, 2013). When these mushrooms fall off the logs and decay, they are returning nutrients from the downed wood into the available nutrient pool. Arthropods and earthworms digest the complex, organic molecules in down deadwood with the help of micro-organisms in their digestive systems, and return the nutrients to the forest in their frass (Stevens 1997). Thus, deadwood can be a reliable and steady source of nutrients over more than 100 years. When coarse woody debris is added to the ecosystem at regular intervals and is well distributed, it represents a long-term source of nutrients (Lombardi et al., 2013).

Moreover, deadwood is also useful for the health of the soil. Soil health is a result of the myriad of biological organisms and interactions that are a part of the forest ecosystem we call soil. This involves soil arthropods, fungi, bacteria, animal waste and among other things, decaying wood. There are many more species and interactions than we currently know, but the strategy for assembling available nutrients into parts of a forest ecosystem is present in all natural forests. These pieces and processes may differ between ecosystems, depending on both biotic and abiotic components available.

Deadwood provides also a structural link with the previous stand in some natural disturbance types, and as such provides continuity of habitat for some species (Hansen et al. 1991). Carey and Johnson (1995) reported that along with understorey vegetation, CWD is the most important habitat factor for small mammals. Healthy small mammal populations help to sustain the ecological processes in which they are an integral part (e.g., the dispersal of seeds and mycorrhizal fungi spores, the maintenance of healthy predator populations, and the control of potentially harmful invertebrate populations). Arthropods are one of the most diverse groups of animals and one of the least understood. Soil microarthropods, although largely unidentified, are the most important arthropods in terms of their impact on nutrient cycling. Groups of them associated with deadwood have been shown to increase the availability and suitability of organic particles for decomposer communities (Norton 1990), and contribute to nutrient cycling and soil formation (Behan-Pelletier 1993; Setälä and Marshall 1994).

Moreover, many species of nonvascular plants and fungi are associated with deadwood. The diversity of these species is related to the diversity of substrates, including a variety of decay stages, and has been linked to forest health (Amaranthus et al. 1994; Crites and

Dale 1995). Variability in piece size contributes to this diversity. Some bryophytes and fungi are restricted to very large pieces (Soderstrom 1988). Deadwood is also important in the geomorphology of terrestrial ecosystems, due to the physical properties of large pieces of wood. Upland sources of deadwood contribute to slope stability, soil surface stability, prevention of erosion and control of storm surface runoff. Particularly, where there is a significant slope, deadwood may play a role in soil stabilization, controlling the flow of water, soil and litter across the forest floor. Material in any decay class, lying across the slope, will reduce soil movement down-slope. Larger pieces collect more material on their upslope side, creating a substrate for invertebrate and small mammal burrowing (Maser et al. 1988) and higher decomposition rates for the debris.

Finally, deadwood plays also a wider role by storing carbon to mitigate global warming as efficiently as many young timber plantations (WWF 2004). As the reality of climate change is widely recognised, carbon sequestration (the storing of carbon in ecosystems) is gaining attention as one way of reducing greenhouses gases. Major forest carbon pools include trees, under-storey vegetation, deadwood, litter, and soil. Deadwood is important as it is both a store and source of carbon but is generally the least studied of the carbon pools (WWF 2004). This will now change because national carbon inventories are required under the Kyoto Protocol of the 1992 United Nations Framework Convention on Climate Change (Woldendorp et al. 2002). Initial discussion on carbon storage focused on fast-growing rotations of exotic plantations. Deadwood itself releases carbon to the atmosphere – becoming a carbon source – during microbial respiration from decomposer organisms (WWF 2004). But in ecosystems in cool climates, microbial activity is restricted and decomposition very slow, so that deadwood tends to act as a long-term storage site. Much of the carbon in long-lived and slow decaying trees, such as Scots pine, can remain sequestered for over a thousand years. Dead trees and old-growth forests are therefore usually better carbon stores than the new forests, which replace them (WWF 2004).

Deadwood is an important and often neglected component of many terrestrial ecosystems (Harmon et al., 1986; Sturtevant et al., 1997; Chen et al., 2001; Rock and Badeck, 2004). Changes in the wood have been decisive influence on plant communities that colonize this substrate. The quantity and wood decay rate in a forest depends on many factors such as temperature, humidity, solar radiation, the specific composition of tree species, structure, age of the population, the spatial structure, the

type and frequency of natural and anthropogenic disturbances. Wood is therefore an important and irreplaceable driving force of biodiversity, which helps to increase the complexity, and with it the stability of forest ecosystems (Dudley and Vallauri 2004).

Deadwood decay processes

The causal factors governing wood decomposition are still poorly understood (Cornwell et al. 2009). The decomposer community, climate, position of the tree (standing or down), and chemical and physical properties of the wood are known to influence the decay rates (Mackensen et al. 2003). Climatic factors determine the temperature and moisture regimes in the woody material. These affect the biological activity of the decomposing organisms.

This effect is apparent in the generally positive relationship between mean annual temperatures and decay rates, when the differences in tree species-specific decay resistance are taken into account (Alban and Pastor 1993, Chambers et al. 2000, Yatskov et al. 2003, Laiho and Prescott 2004). On a stand scale, the dynamics of deadwood, i.e. fluctuations in its volume and quality, are determined by tree mortality and decomposition over time (Grove 2002, Jonsson et al. 2005). When the weakening stress factors are taken into account, tree death can be a lengthy process.

Deadwood is an important component in the functioning of forest ecosystems, as it plays an important role in biodiversity, trophic chains, forest natural regeneration, nutrient cycles and overall carbon storage (Harmon et al., 1986; Franklin et al., 1987; Jonsson and Kruys, 2001; Laiho and Prescott, 2004; Luyssaert et al., 2008). The role of deadwood on biodiversity conservation of forest ecosystems is widely recognised. Interest on deadwood has increased in the last years, and forest management policy regards deadwood as indicator of sustainable forest management (Castagneri et al., 2010). Coarse woody debris (CWD) is the residue of living trees in forest ecosystems including whole fallen trees, fallen branches, and pieces of fragmented wood, stumps and standing dead trees (snags) (Li et al., 2007). It comes from natural tree mortality, disease and insects, as well as catastrophic events such as fires, storms and floods. Also fire creates deadwood directly or by making trees more susceptible to wind, disease, or insect damage. Insects and disease can cause tree death directly or weaken a tree,

thereby contributing to its death and eventual fall to the forest floor (Lombardi et al. 2008).

CWD serves a variety of essential functions in forest ecosystems. It provides sites for seed germination (Harmon *et al.* 1986 & 1989; Graham and Cromack 1982; Gray and Spies 1997; Xu 1998), serves as reservoirs during droughts (Deng *et al.* 2002; Harmon and Sexton 1995; Zhao *et al.* 2002), and provides habitats for many forest animals (Rabe *et al.* 1998; Timothy and Mark 2004; Torgersen and Bull 1995) and microbes (Amaranthus *et al.* 1994).

Decomposition of the organic matter is largely a biological process that occurs naturally; it is the process whereby the complex organic structure of biological material such as wood is reduced to its mineral form (Li et al., 2007). Its speed is determined by three major factors: soil organisms, the physical environment and the quality of the organic matter (Brussaard, 1994). In the decomposition process, different products are released: carbon dioxide (CO₂), energy, water, plant nutrients and resynthesized organic carbon compounds. Successive decomposition of dead material and modified organic matter results in the formation of a more complex organic matter called humus (Juma, 1998). Humus affects soil properties. As it slowly decomposes, it colours the soil darker; increases soil aggregation and aggregate stability; increases the CEC (the ability to attract and retain nutrients); and contributes N, P and other nutrients.

Soil organisms, including micro-organisms, use soil organic matter as food and, as they break down the organic matter, any excess nutrients (N, P and S) are released into the soil in forms that plants can use (mineralization). The waste products produced by micro-organisms are also soil organic matter. This waste material is less decomposable than the original plant and animal material, but it can be used by a large number of organisms (FAO 2005). By breaking down carbon structures and rebuilding new ones or storing the C into their own biomass, soil biota plays the most important role in nutrient cycling processes and, thus, in the ability of a soil to provide the crop with sufficient nutrients to harvest a healthy product. The organic matter content, especially the more stable humus, increases the capacity to store water and store (sequester) C from the atmosphere (FAO 2005).

The decomposition or depletion of CWD involves many different biological and physical processes (Harmon *et al.* 1986; Golladay and Webster 1988). Generally, fine

deadwood material forms a richer habitat for fungi like morels, and cup fungi (Nordén et al. 2004). Due to its high amount of lignin, deadwood is difficult to decay (Floudas et al 2012). Under natural conditions, only fungi substantially decompose deadwood. With their ability to use a battery of secreted oxidoreductases and hydrolases (wood decomposition enzymes), they are considered as the primary wood decomposers and among them are the only organisms, which are able to decompose lignin (Cornelissen et al. 2012, Stokland et al. 2012, Purahong et al. 2014, Kubartva et al. 2015, Persoh et al. 2015). Diverse bacteria also colonize deadwood and form at least commensal interactions with wood-inhabiting fungi, for example, by providing additional nitrogen (de Boer et al. 2005, Hoppe et al. 2005, Hoppe et al. 2015). However, due to their limited ability to decompose polymeric lignocelluloses, bacteria are thought to play only a minor role in wood decomposition (Cornelissen et al. 2012). Elsewhere, research shows that small logs and branches do not decay in the same way as large trunks, so that necessary habitat types will not occur (Yee et al. 2001). The process of deadwood recycling can sometimes take hundreds of years to complete and includes three main phases (Speight 1989).

The dynamics of the mass of deadwood on a site are affected by decay processes and material transfer processes. The first stage of decay processes is the fragmentation. It is the breaking up of deadwood into smaller particles. This occurs as insects chew the wood, as vertebrates forage for insects in decaying wood, when partially or fully decayed snags fall, and when decayed wood is disturbed by falling trees, wind, rain or other physical disturbances. Leaching, collapse and settling, and seasoning are all aspects of fragmentation (Lombardi, 2007). Leaching (water percolating through the log) dissolves soluble materials. It is less important in early decay classes as most of the material in these classes is not soluble. As the decay process proceeds, decomposers change the polymers into soluble material and leaching becomes more important (Stevens 1997). In addition, in later decay classes, as fragmentation begins, the importance of leaching increases as the surface-to-volume ratio increases. As the tree decays, the internal structure becomes weak and settling occurs. This usually increases the contact of the log with the ground, which can increase the activity of microbes, invertebrates and vertebrates at the soil-log interface where there is likely to be increased moisture retention and access for the above organisms (Stevens 1997). During the decay processes, seasoning characterize deadwood. It refers to a series of changes, including a decrease in moisture, shrinkage and the formation of cracks that increase

access to microbes. Initially, it can harden the outside of a log and reduce its susceptibility to fragmentation and interior moisture losses (Lombardi et al., 2013).

Decay rates of CWD are related to microbial activity, air temperature, moisture availability and substrate quality (Edmonds et al., 1986; Harmon et al., 1995). Warmer and moister conditions within openings created by clearcuts have been shown to increase the rates of decomposition of the residual organic matter (Bormann et al., 1974; Prescott, 2002).

Contradicting results may be explained in part by the varied methodologies employed or by the different climates in which the studies were performed. In moisture-limited regions, respiration would be expected to increase with moisture. Whereas, in the relatively wet forests of the Pacific Northwest, dryer conditions promote higher respiration and decomposition rates (Progar et al., 2000). Nearly all studies show an interactive effect of temperature and moisture on decay dynamics. A number of other variables including wood characteristics such as density, nutrient content, decay resistance, and type (log, stump or root) may influence the decomposition as much as the environmental factors surrounding the wood, but few of these have been evaluated.

The moisture content of CWD has previously been identified as a key variable affecting decomposition (Progar et al., 2000) with the strongest effects exhibited at low and high moisture extremes (Chambers et al., 2001; Wang et al., 2002). High moisture inhibits decay by obstructing fungal growth and/or limiting available oxygen, both of which result in lower respiration rates (Rayner and Boddy, 1988; Progar et al., 2000).

Woody debris decay rates have recently received much attention because of the need to quantify temporal changes in forest carbon stocks (Fraver et al. 2013). Decay rates, which may differ among species and regions (Mackensen et al. 2003, Yatskov et al. 2003, Mäkinen et al. 2006), eventually determine the rate of quality change and the persistence of deadwood in forest ecosystems (Aakala 2011).

Accurate deadwood density estimates are essential for evaluating ecosystem biomass and carbon stocks (Seedre et al. 2013). Published decay rates, available for many species, are commonly used to characterize deadwood biomass and carbon depletion. Deadwood biomass is one of the five terrestrial carbon pools that are relevant for the estimation of carbon stocks and carbon stock changes under the UNFCCC and the Kyoto Protocol (IPCC Guidelines for National Greenhouse Gas Inventories) (Di Cosmo

et al., 2013). However, decay rates are often derived from reductions in wood density through time, which when used to model biomass and carbon depletion are known to underestimate rate loss because they fail to account for volume reduction (changes in log shape) as decay progresses (Fraver et al. 2013). The decay rate can be estimated by relating the time since death to the density loss or mass loss of deadwood during a given time period (e.g. Busse, 1994; Melin et al., 2009). The decay rate is commonly expressed through a decay constant k , which indicates the density loss or mass loss per year. This constant is derived from a decay model (Harmon et al., 1986), which can be most simply expressed by the equation

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

(single-negative-exponential model), where x_t is the density or mass of deadwood at a given time and x_0 is the initial density or mass (Jenny et al., 1949; Olson, 1963). Other decay models have also been developed that take wood decomposition into account (reviewed by Mackensen et al., 2003). Several authors (Minderman, 1968; Wider and Lang, 1982; Means et al., 1985) consider the different wood components, e.g. bark, sapwood, heartwood, and chemical compounds, and combine them in multiple-exponential equations. Other authors (e.g. Harmon et al., 1986) consider the time elapsed from the death of a standing tree to the moment when it falls and comes in contact with the forest floor (lag-time models). In several environments, e.g. on dry mountain slopes, the time lag between death and contact with the forest floor can last for almost the entire decay process (Kueppers et al., 2004). A few models take not only the losses due to heterotrophic respiration and leaching into account but also losses due to fragmentation (Mackensen et al., 2003).

Recently, more information on deadwood chemistry (even in Europe) as a function of decay stage in temperate to subalpine environments is available (cf. Lombardi et al., 2008; Petrillo et al., 2015). The relation to the factor time is, however, in most cases completely missing and only in rare cases some estimates are presented (e.g. Petrillo et al., 2016). Detailed information on carbon stored in deadwood and its relationships with different decay stages are required by national forest and carbon sink inventories to help understanding deadwood dynamics and the impact on microhabitats with a changing climate. These relationships are expected to vary with disturbance regime and forest type.

Until now, a number of methods to determine the decay rate have been used:

(1) Long-term studies provide the most reliable results (Stone et al., 1998; Müller-Using and Bartsch, 2009; Anderson et al., 2009).

(2) Decay rate can be estimated from the ratio of deadwood mass inputs to the pool of deadwood (Bond-Lamberty & Gower, 2008).

(3) Chronosequences use historic windfall, fire, wave regeneration, or harvest events. Relating the density or mass of logs to the time they have been undergoing decay determines the decay rate (e.g., Busse, 1994; Melin et al., 2009).

(4) Because of the naturally high variability of snags through time and across the landscape, the sampling intensity must be high to achieve reliable results. A practical, cost-effective, reliable method based on remote sensing techniques.

Determination of mass loss is the most common method used to investigate decay processes (Christensen 1977; Grier 1978; Sollins 1982; Harmon et al. 1987; Arthur and Fahey 1990; Arthur et al. 1993; Mackensen et al. 2003). Wood density has also been used to describe decay processes (Arthur et al. 1993; Schwarze et al. 1999; Schäfer 2002), as it is easy to determine and the initial values within a species do not vary greatly (Sollins et al. 1987; Frangi et al. 1997; Mackensen et al. 2003). Christensen (1984) showed a direct relationship between mass loss and relative density. A prerequisite for this is that mass loss is only due to leaching and biochemical decay. The patterns of density and volume loss indicate, however, that in the decay of beech CWD, fragmentation is not a negligible process. As the presented functions show, mean density decreases only in the first 12 years of decomposition while volume loss continues linear during the whole decomposition process. Additional studies of leaching (Kuehne et al. 2008) and CO₂-emission (Müller-Using and Bartsch 2008) of the same logs showed a difference between carbon loss by this processes and that calculated by mass loss of CWD.

In coniferous forests in Oregon fragmentation has been reported to account for half of the mass loss (Harmon and Hua 1991), usually the part of fragmentation seems about 30% for this type of climate (MacMillan 1988; Harmon and Hua 1991). Harmon et al. (2000) concluded in a comparative study of the decay rate constants of mass, volume and density of pine, spruce, and birch woody debris in northwestern Russia that the

mass decreases more strongly than the density. The change in density due to disintegration of the stem was not taken into account in these studies (Laiho and Prescott 2004), and thus fragmentation was underestimated. The fragmented mass was not included in the estimation of woody debris storage, because the fragmented pieces could not be found and were amalgamated into the humus layer. The smaller the dimension of woody debris, the earlier the process occurred.

While a broad range of literature about CWD decay (above-ground) exists (see e.g. Zell et al., 2009), mechanisms of the incorporation of the trunk necromass into the humus of the soil (Kueppers et al., 2004) are rather poorly investigated (van der Wal et al., 2007). To link processes in the soils, biochemical analyses (e.g. cellulose and lignin) coupled with dendrochronological analyses should provide useful information (e.g. Lombardi et al., 2008).

In an early attempt to determine decay rates for Southern European forests, Lombardi et al. (2008) applied methods commonly used in North America, focusing on dendrochronological techniques. They found that time-since-natural-death of silver fir and beech stumps in Central Italy only roughly indicates decay rates because decay processes only fully start when the tree falls to the forest floor and not the year of tree death, which can be assessed by dendrochronological methods. It was noticed that the typical morphological analysis carried out in the field (Hunter 1990) is insufficient to describe the wood decay progression in these forest ecosystems. As proposed by several authors (Bütler et al. 2007; Saunders et al. 2011) wood density, carbon, nitrogen and phosphorous contents, and lignin and cellulose concentrations may be used to better assess decay patterns of coarse woody debris correlated with specific site characteristics, such as soil and air microclimatic conditions (Lombardi et al. 2013). Lombardi et al. (2008) demonstrated that time since death and decay class were inconsistently related and the structural characteristics of logs did not always reflect the length of time they had been dead (see also Daniels et al. 1997). Stumps could also derive from living trees that started to decay in the heartwood many years before the overall tree death (Cherubini et al. 2002). On the other hand, the features of a stump could erroneously indicate advanced stages of decay, and mask recent tree death. However, decay classes described in the field through visual assessment reflect the decay progression of wood and the sequence of organisms that decompose the wood on

the forest floor rather clearly. Questions remain on deadwood behaviour as chemical pool within forest ecosystems (Lombardi et al. 2013).

Although the decay rate of CWD as a function of climate is basic information for understanding the cycle of carbon and nutrients, only scarce data is available. A recent work has demonstrated that climate alone failed to predict wood decomposition rates at regional scales, while local-scale factors were found to be much more important for explaining most of the variation (Bradford et al. 2014). Other studies indicate that substratum (e.g. litter) quality may be more important than climate in controlling decomposition rates across different biomes (Cornwell et al. 2008, Weedon et al. 2009, Bradford et al. 2014). Deadwood characterizations in the Southern parts of Europe are largely missing for the most commonly occurring forest types and the knowledge is quite low, particularly at Mediterranean latitudes. Several studies have been done in the North-Western Pacific in the U.S. and Canada (Harmon et al., 1986; Daniels et al., 1997; Campbell and Laroque, 2007) while our knowledge about decay rates of different tree species in European forest ecosystems is limited to few experimental and field studies (Naesset, 1999; Storaunet and Rolstad, 2002; Lombardi et al., 2008; Herrmann and Bauhus, 2012) or rough estimations and modelling (Storaunet, 2004; Mäkinen et al., 2006). Such studies have shown different patterns of decay in response to climate depending on the species (e.g., wood quality) and site conditions (e.g., faster decay rates at lower latitudes and warmer sites). New methods and tools for the assessment of decay rates in European forests are urgently needed. A recent work has demonstrated that climate alone failed to predict wood decomposition rates at regional scales, while local-scale factors were found to be much more important for explaining most of the variation (Bradford et al. 2014). Other studies indicate that substratum (e.g. litter) quality may be more important than climate in controlling decomposition rates across different biomes (Cornwell et al. 2008, Weedon et al. 2009, Bradford et al 2014).

Mountainous ecosystems are especially sensitive to changing environmental conditions such as global warming, and most mountain area are experiencing environmental degradation. Mountains also represent unique areas for the detection of climate change and the assessment of climate-related impacts.

In mountain forests, deadwood tends to act as a long-term carbon storage site. Deadwood itself releases carbon to the atmosphere – becoming a carbon source – during microbial respiration from decomposer organisms. But in ecosystems in cool climates,

microbial activity is restricted and decomposition very slow, so that deadwood tends to act as a long-term storage site. As the reality of climate change is widely recognised, carbon sequestration is gaining attention as one way of reducing greenhouse gases.

In contrast to North America and the boreal zone of Europe, where natural deadwood levels have been reviewed thoroughly (Harmon et al., 1986; Siitonen, 2001), there is no such review for the beech and mixed-beech forests of temperate Europe, in which *Fagus sylvatica* L. is a dominant or co-dominant tree. Consequently, a need exists to explore more in detail the interplay between soils, forests, deadwood and climate particularly in Alpine (Egli et al., 2006; Ascher et al., 2012) and Mediterranean areas.

European beech is one of the most important European trees, not only because of its expected role in the face of climate change, but also as a frequent species in forest reserves, national parks and the NATURA 2000 network. For such areas, naturalness and biodiversity conservation are significant issues, in which the presence of deadwood plays an important role. To manage deadwood in forests, one needs to know how the residence time of coarse woody debris is influenced by the environment (Privetivy et al., 2016). Because beech forests are widespread and represent the potential natural vegetation of many areas in Central Europe (Czajkowski et al. 2006; Bolte et al. 2007), information about the decay dynamic are of particular interest for these forests. The study by Christensen et al. (2005) offers an indication of what guidelines for a sustainable woody debris management might include, but it also demonstrates the limited basic knowledge on decay dynamics of beech woody debris.

Moreover, most studies examining the decomposition of CWD of Norway spruce have concentrated on the above-ground biomass (e.g. Shorohova et al., 2008). Regarding gymnosperm, specifically the lignin, N and P content seem to play a role (Weedon et al., 2009). Because the spatial distribution of CWD is highly heterogeneous, only few quantitative data about its long-term decay dynamics are available for European alpine and subalpine forests. Decay models in Europe have, therefore, rarely been parameterised using empirically derived decay constants.

In the field, the different stages of CWD decomposition are often described by so-called decay classes (as defined by Hunter, 1990) through a visual assessment of the wood status (Lombardi et al., 2013). In a previous study, Petrillo et al. (2015) demonstrated that the Hunter classification is particularly suitable for describing changes in the physical–chemical characteristics of European larch (*Larix decidua* Mill.) and Norway

spruce (*Picea abies* (L.) Karst.) deadwood in alpine environments. An improved knowledge of the decay progression of deadwood and the factors affecting these changes is important for maintaining long-term sustainability of soils, to help conservation, and to evaluate the role of deadwood in carbon storage and to preserve microhabitat occurrence.

State-of-the-Art

Climate is projected to affect all aspects of ecosystems functioning and biodiversity, and their ability to provide services (The Millennium Assessment, 2005); however, the projected changes have to take into account the impacts from other past, present and future human activities (Gitay et al., 2002). Below-ground diversity is difficult to quantify but it is assumed to surpass above-ground plant and animal diversity (Wall et al., 2010). Climate change is expected to affect individual organisms, populations, species distributions and ecosystem composition and function through increases in temperature and changes in precipitation. The data and models needed to project the extent and nature of future ecosystem changes and changes in the geographical distribution of species are incomplete, meaning that these effects can only be partially quantified (Gitay et al., 2002).

The IPCC (Gitay et al., 2002), SEC (2006) and the EU Soil Thematic Strategy (COM (2006)231) identified, among others, the following information needs:

- Understanding of the response of biodiversity to changes in climatic factors and other pressure
- Closing the gaps in knowledge about soil processes and strengthening the foundation for policies.
- Clarifying how mountainous landscapes, including the soil system, in the Mediterranean to high-mountain areas may change under conditions of fast to accelerated external (climatic) forcing.

Mountainous ecosystems are likely to be especially sensitive to changing environmental conditions, such as global warming, acid deposition or nutrient cycling (Theurillat et al., 1998). Landscape, climate, society and infrastructure in the mountainous areas are changing at high rates (Haeberli et al., 2007). Mountainous areas are a complex system, in which different features influence each other while reacting with different intensities and time frames to changing environmental conditions. Unfavourable or threatening processes need to be prevented or mitigated in order to preserve the possibility of sustainable development.

Precipitation and temperature influence vegetation and consequently soil properties by affecting type and rates of chemical, mineralogical, biological, and physical processes. Field experiments about soil warming (e.g. Rustad et al., 2001; Melillo et al., 2002;

Eliasson et al., 2005; Allison et al., 2010; Ågren, 2010; Budge et al., 2011) have provided evidences about the temperature sensitivity of decomposition. Deadwood and litter act as important linkages between recent productivity and current community, and ecosystem processes (Anderson et al., 2009). The increasing interest in the quantity and properties of coarse woody debris and litter is relevant both to maintaining biodiversity and to global C dynamics (Kueppers et al., 2004). Dying and dead trees are valuable habitats (providing food, shelter and breeding conditions, etc.) for a large number of rare and threatened species: saproxylic insects, invertebrates, fungi, lichens, bryophytes, birds and mammals (Harmon et al., 1986; Ódor and Standovár, 2001; Humphrey et al., 2002; Ódor et al., 2006). Consequently, a need exists to understand more in detail the interplay between soils, forests, deadwood and climate in Apennine areas. While a broad range of literature about CWD decay (above-ground) exists (see e.g. Zell et al., 2009), mechanisms of the incorporation of the trunk necromass into humus forms (Kueppers et al., 2004) are rather poorly investigated (van der Wal et al., 2007).

Thesis Aims and Questions

This thesis is a contribution to the knowledge on deadwood dynamics in mountain forests of Italy. In the past years, other studies and projects were realized, aiming to understand the role and decay of deadwood in Italian forest ecosystems.

The realized study focused on *Fagus sylvatica* forests, in the Apennines and on *Picea abies*, in the Italian Alps, where ecosystems are sensitive to climate warming. Since deadwood can be a substantial fraction of stored carbon in forest ecosystems, CWD decay rates may be sensitive to climate warming. However, the mechanisms of the decay and incorporation of CWD into the soil and its relation to humus formation and climate are poorly understood. Data and models are strongly needed to quantify future changes in ecosystem processes.

The main objective of this thesis focuses on the integration of plant organic matter into the soil: the decomposition of coarse woody debris (CWD) and its incorporation into the soil organic matter (SOM), through the biological activity of the topsoil. Moreover, the general aim is linked to the following: understand the functional links between climate, degraded CWD and soil properties, evaluating their effects on the stabilisation of SOM.

The main research questions are: 1) What time scales are involved in CWD decay and integration into the soil? 2) How does climate affect the CWD decay in temperate and subalpine natural forests?

Sites along a climosequence were investigated. The selected study areas are located (1) on the central Apennines, in an altitudinal range from 1000 m to 1650 m a.s.l., (2) on the Italian Alps where the altitude varies from 1100 m to 2200 m a.s.l. Moreover, at each site, two altitudinal transect were selected, considering the north- and south-facing slope.

The studies in this thesis were realized in the context of the DecApp project (abbreviated title of a project focused on *Fagus sylvatica* deadwood decay on montane forests on the Italian Apennines), and related to the international DecAlp (dealing with decay on the Alps) project, that dealt with wood decay mechanisms in Alpine forest soils, soil organisms and humus forms and their relation to climate change. The results of this project regarded a conifer species, *Picea abies*. Thus, the DecApp project helped to build up an integrated model of CWD decay mechanisms, comparing coniferous

(DecAlp project) and broadleaved species (DecApp project), and enabled to estimate the effects of a warmer climate on decay processes in subalpine area.

The project was focused only on semi-natural forest ecosystems of subalpine sites along an altitudinal gradient (climosequence). The climosequence approach furnished precious insight into the effects of climate on CWD decay. The above-mentioned linear approach is not absolute because several feedback processes exist, such as the duration of CWD conservation and their interrelation to humus forms. The objectives, hypotheses, research plan and methods aim at understanding: a) the main processes in each of the studied compartment and b) the interrelations between them.

Furthermore, the project tested the following hypotheses:

- On the Alps, CWD decay products will not or only to a very low degree affect the stable organic matter fraction due to already existing strong organic-mineral associations (Favilli et al., 2008). CWD will only affect the labile fractions, especially on north-facing sites.

- On the Apennines, CWD decay should be quite fast because of warm conditions, and, moreover, moisture conditions on the north exposure should influence positively decay process.

- Decay of deciduous species on the Apennines is expected to be faster than conifer species on the Alps.

Summary of papers

European beech is one of the most important European trees, not only because of its expected role in the face of climate change, but also as a frequent species in forest reserves, national parks and the NATURA 2000 network (Privetivy et al., 2016). For such areas, naturalness and biodiversity conservation are significant issues, in which the presence of deadwood plays an important role. To manage deadwood in forests, one needs to know how the residence time of coarse woody debris is influenced by the environment.

Study areas

The studies in this thesis were conducted in two different geographical zones. All the papers were realized in Italian context, respectively I and III on the Alps (Trentino region) and paper II on the Apennines (Abruzzo region). Both in Trentino and Abruzzo, to assess the contribution of climate, decomposition processes were studied at sites with different constellations: a) exposure: north and south exposure; b) altitude (toposequence).

Sites along two climosequences were investigated: one north- and one south-facing. The climosequence includes sites from 1000 m asl up to 2400 m asl on the Alps and from 1000 to 1650 m asl on the Apennines.

Particularly, paper II was realized in an Italian National Park founded in 1991, Parco Nazionale della Majella (fig. 1b). The area of the Majella National Park (740.95 km²), especially the Majella Mount, has been subject to a major international geoscientific research Project Task Force Majella from 1998 up to 2005. Majella Mount (called *Padre dei Monti* - Mountains' Father - by Pliny the Elder and *Montagna Madre* - Mother Mountain - by the people of Abruzzi) is a high, imposing, wild mountain group, which is part of the world heritage of National Parks. This National Park is unique for several factors, such as its geographical position, harshness, extension, and climatic changes. It also includes widelands with peculiar wilderness features, the most precious and rare part of the biodiversity national heritage, important not only at a European, but also at a world level. Our 8 sites were located in *Fagus sylvatica* natural forests. Altitude range went from 1000 to 1650 m asl; 4 sites were located in Feudo d'Ugni and 4 in Orfento Valley. In these sites climate is temperate and precipitation range is usually between 800 and 1000 mm.

Paper I and III were conducted in Trentino region, particularly in Val di Rabbi and Val di Sole (fig. 1a). This area was chosen due to its situation in between a rather warm Insubric and a cold Alpine climate and the existing and well-established network (including the good collaboration with local authorities). All sites have a natural coniferous forest, a natural forest that is usually dominated by a *Piceetum montanum* and a *Larici-Pinetum*. The selected areas are in dry inner-Alpine valleys. The climate of the valleys ranges from temperate to alpine (above the timberline), the mean annual temperature from 8.2 °C at the valley floor to about 0 °C at 2400 m a.s.l., and the mean

annual precipitation from approximately 800 to 1300 mm (Sboarina and Cescatti, 2004). Furthermore, an already existing large dataset (soil profiles, chemical and mineralogical data, GIS datasets) serves as the basis for the planned investigations.

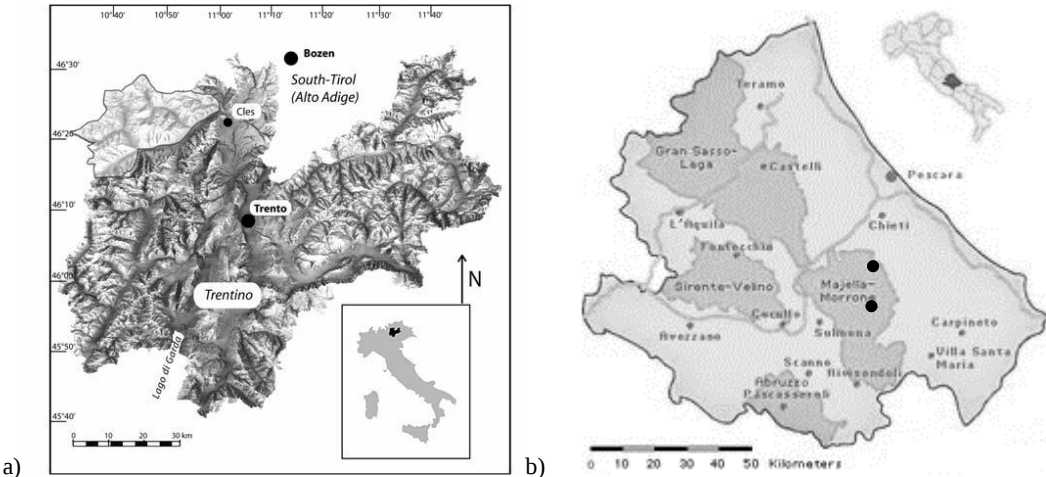


Fig.1. Location of the investigation areas: a) Alps, in Trentino (Paper I and III) and b) Apennines, in Abruzzo (Paper II).

Climate and soil parameters are main drivers of the slow decay of Norway spruce in sub-alpine forests (Paper I)

How the decay rate of deadwood is affected by climate is basic information for understanding the C-cycle and other nutrients. Deadwood chemistry has recently been studied as a function of decay stage in temperate to subalpine environments (Lombardi et al., 2008; Petrillo et al., 2015), but only exceptionally related to time (Petrillo et al., 2016). To better assess deadwood decay processes, analysing wood density, carbon, nitrogen, phosphorous contents, as well as lignin and cellulose concentrations have been proposed (Bütler et al., 2007; Saunders et al., 2011).

The purpose of this paper was to collect data about deadwood decay from temperate and subalpine forests on the Alps. The study was conducted at 8 different sites, in Trentino region, northern Italy, chosen to represent a typical mountain climate. To assess the contribution of climate, the decay processes were studied at sites with different exposures (north- vs south-facing), and altitudes (toposequence). Eight sites were selected along two climosequences: one north-facing and one south-facing ranging from 1200 m a.s.l. up to 2000 m a.s.l. (with 4 sites, pairs on each, resulting in a total of 8

sites). At each climosequence site, a field experiment using soil mesocosms; the mesocosms design was set up as described by Bird and Torn (2006) and by Maestrini et al. (2014). Some 10.2 cm diam., 25 cm long PVC tubes were inserted into the soil prior to the addition of the substrates. The soil and the CWD were sampled after 12, 25, 52 and 104 weeks; each having 3 replicates.

Decay experiments using standardised wood blocks of local *Picea abies* informed about the rate dynamics as a function of climate. Because the size and geometry of CWD can strongly influence the decay mechanisms (Van der Wal et al., 2007), wood blocks, having the dimension of 2 cm x 5 cm x 5 cm, from the same *Picea abies* tree were prepared. After 12, 25, 52 and 104 weeks (T1, T2, T3, T4) three replicates were removed and analysed for the carbon, cellulose and lignin content and for the isotopic ratio of C and N.

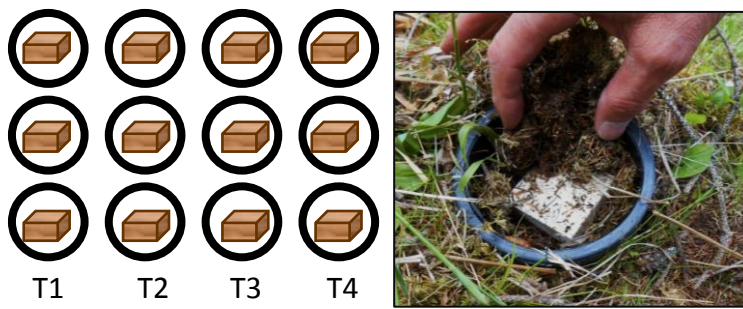


Figure 2: Wood blocks experiment; the replicates were placed into “mesocosms” (i.e. tubes opened on top and bottom, firmly inserted in the soil).

The negative exponential model of time is the most commonly used to estimate the decline in density of logs and CWD (Naesset, 1999; Chen et al., 2005). The decay rate can be estimated by relating the time-since-death to the density loss or mass loss of deadwood during a given time period (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 et al., 1986), which can be most simply expressed by the equation in the single-negative-exponential model:

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

where x_t is the density or mass of deadwood at a given time (t), and x_0 is the initial mass (Jenny et al., 1949; Olson, 1963) or density. The mass is a more reliable parameter because density may underestimate deadwood decay rates. In this investigation, we used

the mass of the wood blocks. Individual decay rates were determined on the basis of total mass losses of deadwood, cellulose and lignin.

To unravel the decay behaviour of these compounds, a multiple-exponential model can be applied (Means et al., 1985; Mackensen et al., 2003), with the general form:

$$x = x_1 e^{-k_1 t} + x_2 e^{-k_2 t} \dots + x_{1n} e^{-k_n t} \quad (2)$$

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

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

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

Table 1. 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 × dry weight of wood block), M_{lign} (Mass of lignin = concentration × 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)

Results revealed that decay rates of *Picea abies* deadwood in Alpine environments seem to be low. Although we used an experimental approach over a rather short time period with relatively small wood blocks, the detected decay rates could be compared moderately well to average values observed for the same species at other sites in Europe. It seems that local scale factors, such as soil parameters and topographic properties, are important and distinctly influence the decay dynamics of deadwood and its components (e.g soil moisture and clay content). In Alpine areas, it seems that

topographic exposure (south- vs north-facing sites) also affects decay processes, which are faster on north-facing sites over 1800 m a.s.l. owing to the moister conditions.

The measured decay rates for deadwood in this study were rather similar to those reported by Petrillo et al. (2016), in the same sites, using a chronosequence approach.

Is climate the most important factor on deadwood decomposition in Apennine mountain forests? (Paper II)

Due to its slow decomposition and persistence on the forest floor (Beets et al. 2008), CWD can represent a substantial reservoir of organic carbon and nutrients in many forest ecosystems (Carmona et al. 2002; Currie and Nadelhoffer 2002; Ganjegunte et al. 2004). The past years have seen substantial interest in efficient methods for collecting information on deadwood material (e.g. Stahl et al. 2001; Travaglini et al. 2006a). Recently, more data of deadwood chemistry (even in Europe) as a function of decay stage in temperate to subalpine environments is available (cf. Lombardi et al., 2008; Petrillo et al., 2015). The relation to the factor time is, however, in most cases completely missing and only in rare cases some estimates are presented (e.g. Petrillo et al., 2016).

In this paper we used a field-experimental approach having controlled conditions, mesocosm approach (see Paper I), to study beech wood decay and how fast wood-compounds cellulose and lignin decay in such a temperate environment. The CWD wood blocks were sampled after 8, 16, 52 and 104 weeks (Fig. 2); always with 3 replicates. The weight (density) and cellulose and lignin were recorded for these blocks. The decay rate constants for spruce CWD were estimated on the basis of the mass loss within the observation period using a single negative exponential model and an exponential regression approach. Over this one-year study, wood mass, cellulose and lignin (Figs. 1, 2 and 3) changed a lot. In all the cases the mass of deadwood, lignin and cellulose exhibited a continuous loss.

Results showed that a close and significant relation between the amount of lignin and mean annual average temperature and the amount of deadwood and mean annual precipitations exists and that cellulose, lignin and CWD decayed significantly ($p < 0.05$) faster at the north-facing sites.

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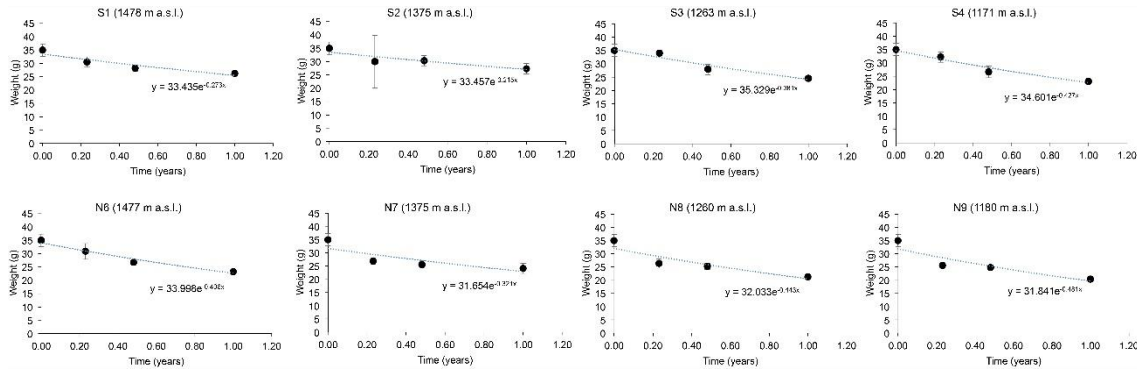


Fig. 2. Deadwood blocks Weight loss during the one-year experiment time.

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

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Until now, various different sampling designs have been used to determine the time since death to estimate the decay rate of deadwood. Dendrochronology can be a helpful tool to determine the year of death, and the technique has been used in several studies to determine the time elapsed since tree-death (Campbell and Laroque, 2007, Lombardi et al., 2008, 2013). Decay models in Europe have, therefore, rarely been parameterised using empirically derived decay constants. In the field, the different stages of CWD decomposition are often described by so-called decay classes (as defined by Hunter, 1990) through a visual assessment of the wood status (Lombardi et al. 2013).

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In this paper the CWD decay dynamics in an Alpine valley in Italy were investigated, using the chronosequence approach and the five-decay class system that is based on a macromorphological assessment. The study area was the same as Paper I, 8 sites in Val di Rabbi and Val di Sole. In spring and summer 2013, wood cores from living trees and cross sections of CWD were taken from all sites. Before sampling, each CWD was first classified relative to the decay stage, using the five-class classification system of Hunter (1990). Tree rings were first counted and then measured using the LINTAB tree-ring-width measurement device (RINNTECH e.K., Heidelberg, Germany), coupled together with a stereomicroscope (Leica, Germany). Most of the CWD samples of the decay classes 1 – 3 could be dendrochronologically dated, but those of decay classes 4 and 5 had to be radiocarbon dated because of the poorly preserved tree rings.

To estimate the decay constants, the average densities in class 1 and in class 5 (the earliest and latest decay stages) were used and the single-negative exponential model of Jenny et al. (1949) applied (eq. 1):

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

where x_t is the density or mass of deadwood at a given time, and x_0 is the initial density or mass (Jenny et al., 1949; Olson, 1963). Equation 1 was then solved for the decay constant k according to equation 2:

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

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

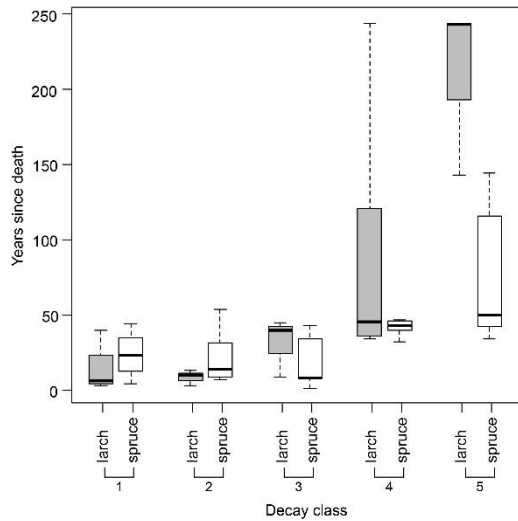


Fig. 3. Calculated decay rate constants (k) as a function of tree species and site exposure.

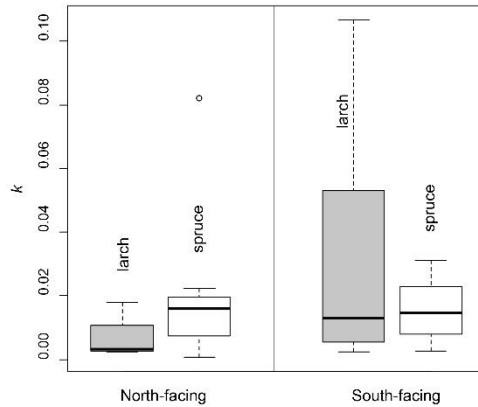


Fig. 4. Box plots of the larch and spruce deadwood age as a function of decay class.

Results showed that the spruce chronology ranged from 1848 to 2012 AD and the larch chronology from 1871 to 2012 AD. About CWD, in the first three decay classes, ages of spruce and larch seemed to be in a similar range: values varied from 1 to 54 years. In decay classes 4 and 5, the average and maximum ages of CWD were usually higher for larch than for spruce; particularly, in decay class 5, the average age of spruce CWD increases to 77 years and the age of larch CWD to 210 years. This showed that larch wood, particularly in the decay classes 4 and 5, is much more resistant to rotting than spruce.

The first 3 decay classes do not seem to reflect the age of the CWD, but taking classes 1 – 3 as one group and relating them to the decay classes 4 and 5, a time trend with increasing decay stage can then be detected. This time trend also closely correlates to the wood density, and the cellulose and lignin content (analysed in Petrillo et al., 2015).

Moreover, using the dating approach (dendrochronology and ^{14}C -dating), the behaviour of cellulose and lignin as a function of time could be assessed. Results demonstrated that lignin in larch may persist particularly long, with a mean residence time of > 100 years.

Conclusions and Future Perspectives

The aim of this study was to investigate the decomposition processes in a montane Mediterranean and in an Alpine ecosystem, and specifically to assess changes in chemical variables (lignin, cellulose, carbon and nitrogen content) in deadwood during the decomposition process, in relation to climate and to the species.

Results showed how lignin degraded slowly in comparison with cellulose and differences between species were observed. Microclimate conditions may influence the decay progression. Water availability, micro-topography and incoming radiation are factors that influence the high variability of decomposition patterns (Lombardi et al., 2013).

CWD and cellulose decay rates were higher at the north facing sites both in Alps and Apennines. Although north-facing sites are thermally less favourable compared to the south-facing sites, decay rates seemed to be higher. These differences should, therefore, be better explained by moisture availability. At the south-facing sites, evapotranspiration is higher (annual precipitation is the same as at north-facing sites) giving rise to drier conditions and a subsequent limited wood degradation.

The hypothesis that the deciduous species on Apennines would decompose faster than conifer species on Alps was accepted. The slower decay of lignin, compared to cellulose, suggested that lignin could be an important long-term source of soil organic carbon, and that this process could be greatly affected by forest species mixtures. Finally, decomposition processes in the investigated Mediterranean montane forests were definitely faster than in the colder climates of the Alps.

Using a field-experimental approach, it was possible to measure decay rates under controlled conditions. These results highlight the importance of multiple edaphic and topographic factors that control CWD decomposition processes in mountain forest ecosystems, in conjunction with climate. The analysis of CWD dynamics, including decomposition of deadwood, is important for modelling and managing mountain forests and for understanding the contribution to nutrient cycling and carbon balance.

This study showed that soil properties and involved environmental parameters influence decay rates in montane forests on Alps and Apennines. The factors that mostly influence this process (according to statistics) seem to be air temperature and precipitations in

both areas, then moisture into the soil (on Apennines) and soil moisture, soil acidity and grain size (on Alps). Within the framework of this study we could shed more light on some important deadwood decay factors and their interactions, including chemical compounds, soil moisture, soil texture and... Therefore, in these areas, a basis for further research on decay process interactions, dynamics and rates has been established.

This study was focused on the beginning of the decay process and a short-term approach was adopted. For this reason, it will be interesting to extend future studies in a long-term perspective, using more replicates, with the aim to follow the decay progression for several years. Yet, advancement in this analysis can be represented by the comparison of the activities of the microbial communities at the studied forest ecosystems, for a deeper understanding of the processes involved in deadwood decay.

Using a field-experimental approach we were able to measure decay rates under controlled conditions. These results highlight the importance of multiple edaphic and topographic factors that control CWD decomposition processes in mountain forest ecosystems, in conjunction with climate. The analysis of CWD dynamics, including input and decomposition of deadwood, is important for modelling and managing mountain forests and their projections after disturbances, and for understanding the contribution to nutrient cycling and carbon balance.

In this study, we showed that site-specific conditions (e.g. texture) influence ground conditions (e.g. soil moisture). Moisture conditions are essential for many soil processes (including allocation of soil carbon). To obtain a more detailed picture, however, it would be necessary to monitor soil conditions, when soil is in contact with deadwood, in the long term in order to accurately describe the interaction of deadwood decay processes and site-specific conditions.

A large empirical dataset based on chemical and physical data was obtained. The chemical and physical data can now be conveniently integrated in deadwood decay modelling to understand the decay processes related to subalpine environments in more detail, and to provide a predicting framework for decomposition processes under changing climate conditions.

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