Estimating the integrated degradation rates of woody debris at the scale of a Mediterranean coastal catchment

François Charles, Joseph Garrigue, Jennifer Coston-Guarini, Jean-Marc Guarini

Revised manuscript STOTEN_D_17741_R3_ with changes NO marked

Title: Estimating the integrated degradation rates of woody debris at the scale of a Mediterranean coastal catchment

François Charles[1*], Joseph Garrigue[2], Jennifer Coston-Guarini[3], Jean-Marc Guarini[3]

[1] Sorbonne Université, UPMC Univ Paris 06, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques (LECOB), Observatoire Océanologique de Banyuls, 66650, Banyuls-sur-Mer, France

Email address: charles@obs-banyuls.fr

*Corresponding author

[2] Réserve Naturelle Nationale de la Forêt de la Massane, Sorbonne Université, UPMC Univ Paris 06, Observatoire Océanologique de Banyuls, 66650, Banyuls-sur-Mer, France

Email address: rnn.massane@espaces-naturels.fr

[3] The Entangled Bank Laboratory, 11 rue Anatole France, 66650 Banyuls sur Mer, France

Email addresses: j.guarini@entangled-bank-lab.org; jm.guarini@entangled-bank-lab.org

Abstract

Woody debris is found in all habitats of the land-sea continuum. While isolated experimental studies of wood degradation exist, few programs have observed the dynamics of wood degradation, in situ across this gradient. Since 2014, we have been conducting a series of long-term observations of wood decay in three characteristic areas of a Mediterranean Sea coastal watershed: forest leaf litter ('Forest'), river bed ('River') and the near-shore marine environment ('Sea'). The study sites are within the Massane River watershed (France) whose headwaters are in a protected beech tree (*Fagus sylvatica*) dominated forest. Branch sections from a recently fallen beech tree and standardized blocks of Norway spruce *(Picea abies*) were installed in all three environments. The proportion of remaining mass and volumetric mass of the individual wood samples were determined periodically over 4.2 years. Regardless of wood type, there were marked differences in the decay dynamics. Mass losses at the Forest and River sites were well-described by continuous negative exponential models. At the Sea site, there was a short latency period followed by rapid degradation for the wood fraction exploited by shipworms; in this case, a Weibull-type function was fitted to the data. Integrated mass loss rates at the coastal location were 6 to 20 times faster than in the other two environments. Our study suggests that the early dynamics of wood degradation in a land-sea meta-ecosystem are dominated by the marine invertebrate community. This means woody debris, once it reaches the sea, is likely to break down rapidly within near shore coastal habitats. These results highlight the need to quantify the mass transport dynamics between local ecosystems.

Keywords: dead wood, decay dynamics, long-term ecological experiments, land-sea connections, coastal Mediterranean Sea

1. Introduction

Increasingly, it is recognized by decision-makers that coastal systems cannot be managed as disconnected from processes happening upstream in the watershed (Gomi et al., 2002). Perturbations in local processes and changes in matter fluxes spread from 'source' to 'recipient' ecosystems (Soininen et al., 2015) through diverse means. Runoff and rivers move dissolved and particulate matter from terrestrial to marine environments. Fluxes can be very important (West et al., 2011) and cross physical barriers that separate adjacent systems (Maser and Sedell, 1994). Moreover, societal pressure for new tools, like carbon-accounting, for mitigating the impacts of different economic activities (Keith et al., 2019) is increasing. This means that interdependencies between terrestrial, aquatic and marine systems must be known and reconciled to parameterize these tools and make them operational.

Four-fifths of Earth's total plant biomass is in forests (Reichstein and Carvalhais, 2019) where the carbon necromass (including a significant proportion of dead wood (Delaney et al., 1998)) exceeds that of the living mass (Pan et al., 2013). In unmanaged forests, most standing and fallen woody debris decompose on annual to decadal time scales (Freschet et al., 2012), although it has been reported to occur on centennial scales (Daniels et al., 1997). Some fraction of this mass is exported from the forest floor by diverse transport mechanisms such as fires, debris flows and water currents (Lancaster et al., 2003). Along the way, wood debris of all sizes participates in the biogeochemical and ecological processes (e.g. Charles et al., 2014; Harmon et al., 1986; Leroux and Loreau, 2008; Polis et al., 1997; Ruiz-Villanueva et al., 2016; Sass, 2009; Shumilova et al., 2019) by providing new habitats, adding nutrients, and altering the geomorphology and flow of waterways.

In marine environments, woody debris makes up a relatively small proportion of inner shelf sediments, but occurs across all river-dominated margins (Bianchi and Allison, 2009; Charles et al., 2014; Hedges et al., 1997; Keil et al., 1998; Rabouille et al., 2008; Tesi et al., 2008). The bulk of this material arrives seasonally and provides communities of estuarine and coastal organisms a complex mixture of organic compounds with different chemical reactivities (Benner et al., 1987). However, most studies are confined to qualitative approaches, focusing only on one typical habitat or considering only the most reactive part(s) of the total input (e.g. dissolved and sub-millimetric suspended particles). Large wood debris, derived from terrestrial plants and transported by rivers, are mostly ignored by marine biogeochemists (Charles et al., 2014; Kandasamy and Nagender Nath, 2016), even if vascular plants have been present on Earth for 450 million years and are recognized globally as significant contributors to marine carbon fluxes and sinks (Cragg et al., 2020).

Quantifying not only the movement (Turowski et al., 2016) but also the rate of degradation of woody debris (Díez et al., 2002; Ruiz-Villanueva et al., 2016) has become an important part of managing risks associated with wood debris (Schmocker and Weitbrecht, 2013; Kramer and Wohl 2016). Whether on land (Fravolini et al., 2018; Freschet et al., 2012; S. Müller-Using and Bartsch, 2009), in rivers (Chauvet and Jean-Louis, 1988; Díez et al., 2002), or at sea (Björdal and Nilsson, 2008; Charles et al., 2016; Fagervold et al., 2012), wood degradation takes place over a wide range of spatial and temporal scales. The degradation is the result of a complex interplay between biological, chemical and physical processes that make up the matter and energy cycles of ecological systems (Bienhold et al., 2013; Björdal and Nilsson, 2008; Cragg et al., 2015; Fravolini et al., 2016; Harmon et al., 1986; Krankina et al., 2002; Spänhoff and Meyer, 2004). For example, accumulations of wood can act as a refuge or substrate, as a food source and/or as a dispersal vector (Carlton et al., 2017; Charles et al., 2020). Woody debris therefore is an important factor in constructing ecological continuity within and between many types of ecosystems.

Developing a synthetic view of wood degradation dynamics over environmental gradients requires better coordination between field experiments and modelling (Kramer and Wohl, 2015). The present study is part of a long term ecological research program designed to address this knowledge gap. The overall objective is to assess the variability and recycling dynamics of dead wood inputs in three connected habitats of a land-sea continuum (Xyloscope Project, CNRS (Centre National de la Recherche Scientifique), funding program: “Ecosphère Continentale et Côtière”). The aim of the present study is: (i) to test if wood decomposition rates have different dynamics in each habitat type and (ii) to investigate if variations in decomposition rates may be attributed to the presence of a particular community. To do this, we have been monitoring (since 2014) the changes in sections of beech, *Fagus sylvatica* L., logs and standardized, reference blocks of Norway spruce, *Picea abies* (L.) H. Karst, placed within three environments connected by a relatively small river that drains a watershed in the foothills of the eastern Pyrenees Mountains. We report here the first comprehensive analysis of observed degradation rates along this continuum, from the forest to the coast.

2. Materials and methods

2. 1 Study site

The study sites are in the catchment area of a small, torrential river, called "La Massane", located in the foothills of the French Eastern Pyrenees (Fig. 1). From its source, 968 m above sea level, the river runs through a protected old-growth beech grove (La Réserve Naturelle Nationale de la Forêt de la Massane, 337 ha), then continues, unimpeded, until it empties into the Gulf of Lions at Argelès-sur-Mer (total stream length is 23 km). The nature reserve has recently been designated a site of scientific interest for the conservation of biodiversity (2021, UNESCO World Heritage List of "Primary and ancient beech forests of the Carpathians and other parts of Europe"). La Massane drains a coastal watershed area of 17.2 km². The watershed is characterized by Mediterranean-type precipitation events. These last for short periods from a few hours to days (Molinié et al., 2012). The Mediterranean climate is characterized by mild wet winters and warm to hot, dry summers (Lionello et al., 2006).

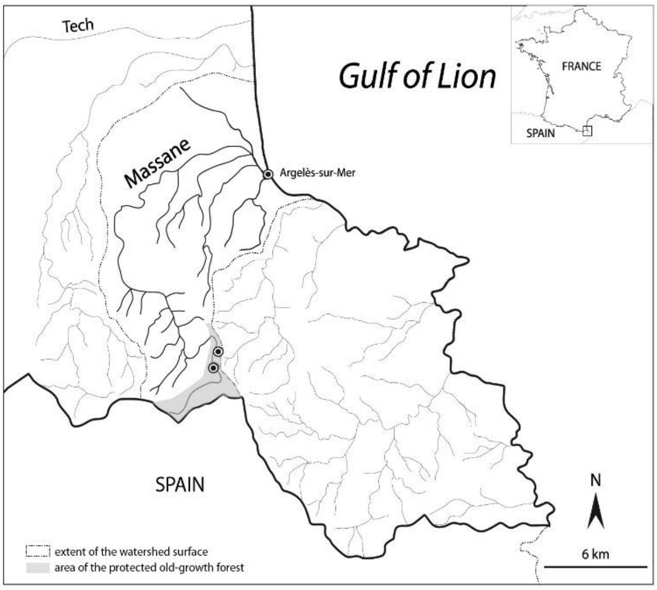


Fig. 1. Geographic location and spatial extent of the watershed. The three considered habitats are indicated by the circles. The Massane Forest Nature Reserve (*Réserve Naturelle Nationale de la Forêt de la Massane*) is indicated in the gray-shaded area, and the dashed line encompasses the watershed of the Massane River.

We selected three different habitats (Fig. 1 and Table 1) for the experiments: the beech leaf litter of the forest floor; a stretch of the river headwaters; and the coastal seawater of the marina at Argelès-sur-Mer at the river mouth. Average interannual water discharge rates at the gaging station ("Mas d'en Tourens"; 8.3 km from the river mouth), range from 0.242 to 0.328 m^3s^{-1} (average, 0.282 m^3s^{-1}, CI 95%, 55 year time series, Water Resources, French Ministry of Ecology, Sustainable Development and Energy, http://www.hydro.eaufrance.fr).

2.2. Experimental set-up

In March 2014, a set of sections (150 mm long) were cut from branches (40.4 ± 5.8 mm in diameter) of a recently fallen beech tree, *F. sylvatica* (L.). Any bark on them was left intact. During the study, we follow the decomposition of two different wood types in three different biotopes. Initially we wished to use a second species of tree present in the Massane Forest Reserve. There are few isolated specimens of yew (*Taxus baccata*) and black pine (*Pinus nigra*) but there were insufficient amounts of suitable fallen material (i.e. from a recently fallen tree with similar characteristics of age, size and condition) available at the time the study was under preparation. Therefore, we decided to use a reference block instead. Test or reference blocks are a common practice in marine wood degradation experiments. A block, or plank shape permits X-ray analyses for the detection and measurement of shipworms (e.g. Steenstrup Kristensen, 1979) and has also been adopted as an ad hoc method for monitoring the presence and activity intensity of shipworms in harbors (e.g. Hill et al., 1927). We elected to use calibrated blocks of Norway spruce, a species that is foreign to the forest but widespread in Europe, and commonly used in general construction, hence readily available in an untreated format. This choice had the advantage of providing the required number of identical samples representative of a gymnosperm species, even if it did not allow any comparison between the two types of wood because of differences in configuration and condition (e.g. branches vs. blocks). Rectangular blocks of sapwood from Norway spruce (*Picea abies* (L.) H. Karst), were manufactured in dimensions of: 150(L) × 34(W) × 34(H) mm (L—

length, W—width, H—height) from untreated, planed boards (2400 × 34 × 34 mm). Both sets of wood samples had surface to volume ratios of 1.1 to 1.3. Each wood piece was drilled (hole diameter: 7 mm) perpendicular to the longest dimension to provide an attachment point, then they were all oven dried at 50 °C ± 5 °C for five days and individually weighed. On 17 April 2014, 60 wood pieces from each species were arranged by sets of 5 along 12, 1 m long rope lines. These were then installed at each of the three field sites (4 lines per site, 20 pieces total). Each line was labelled (1 to 4) and the position of the wood logs (1 to 5) along each line was recorded. Wood pieces were spaced about 15-20 cm apart so that they would not come into contact once the rope was stretched on the ground or submerged in water. We found this arrangement adequately secured the installation of sample sets at each site, and allowed for efficient sample recovery.

In the beech grove, samples were installed on leaf litter among existing woody debris accumulation. Each end of a line was secured by two iron bars driven into the forest ground. Samples immersed in the river were connected by their ends to a steel cable wrapped around a large boulder formation. In the marina of Argelès-sur-Mer, lines were attached to a floating pontoon at one end and weighted at the other in such a way that the lines remained entirely submerged at between 1 to 1.5 m below the water surface.

Air temperature (°C) and precipitation (mm) were recorded by the meteorological station of the *Réserve Naturelle Nationale* of the Massane Forest (42°28'41" N, 3°01'26" E). River water temperature was recorded with a HOBO Pendant® data logger. River flow data are provided by the monitoring program of EauFrance (http://www.eaufrance.fr/). At the Argelès-sur-Mer marina, water temperature and salinity were also measured at each sampling, at 0.6 m below the water surface using a Cond315i conductivity meter (Wissebschaftlich-Technische Werkstätter GmbH, Weilheim, Germany).

2.3 Sample processing

The lines at each site were sampled randomly after varying exposure times, depending on the field site, or the wood type. During recovery, each sample was placed in an individual plastic bag and stored at

−20 °C until processing. Samples were then freeze-dried and blocks gently brushed to clean loose soil particles, leaf litter and epibiota from the surface. Then, each block was individually weighed.

After analysis, all samples collected in the project are stored in a repository under controlled conditions at the Observatoire Océanologique de Banyuls. They can be made available to other researchers for further analysis if desired (contact the corresponding author).

2.4 Data treatment

In this study, wood decay is expressed as the amount of wood remaining after a given time interval. This was calculated as the ratio between the remaining weight of wood and the initial weight of the wood piece. The remaining volume of wood was calculated from the lengths and diameters for the beech branch cylinders, and from the length, width and height for the spruce blocks. The ratio between weight and volume is the change in volumetric mass of a wood piece when the sample was recovered.

Exposure times (Table 1) were different for the Forest and River samples. Thus, differences in degradation rates between sites were tested using an analysis of covariance (ANCOVA) to compare the slopes of linear regressions (Zar, 1984).

Table 1 Position, elevation, description and exposure duration at each of the three habitats

Habitat	WGS 84 coordinates	Elevation (m)	Description	Exposure (year)	Wood type
Forest	42° 29' 34" N 03° 01' 57'' E	698	litter of the beech grove	0; 0.3; 2.1; 3.1; 4 0; 0.3; 0.8; 3.2; 4	Beech Spruce
River	42° 29' 18" N 03° 01' 42" E	648	head of the watershed	0; 0.3; 2.1; 3.1; 4.1 0; 0.3; 2.1; 3.2; 4.2	Beech Spruce
Sea	42° 32' 34" N 03° 03' 08" E	-1	marina at the river mouth	0; 0.3; 0.4; 0.6; 1.1	Both

The Sea samples were all recovered at the same time intervals (Table 1). We compared the effects of the exposure duration on the mass loss of the samples with a one-factor analysis of variance. A Pearson's product-moment correlation was used to test the association between the remaining mass and volumetric mass of the wood blocks in all habitats at the time of sample collection. Coefficient values close to 0 indicate that mass loss is related to volume loss, while values close to 1 indicate that mass loss occurs without significant change in the apparent volume of the wood blocks.

2.5 Modelling the degradation process

Observed decay rates were estimated by fitting the data with either a negative exponential (Equation 1) or Weibull distribution (Equation 2). For samples exposed to the Forest and River conditions, the negative exponential formulation was expressed as:

$$m = m_0 e^{-kt}$$

(1)

where m was the relative mass (dimensionless), t, is the exposure time (year), m0 is the initial mass of the sample, and k is the degradation rate, k (y^{-1}).

The standardized form of the decay rate for Sea samples was a function with three parameters, α_{min}, t_c and c, and of time, t, and was expressed as:

$$m = m_0 \left(\alpha_{min} + (1 - \alpha_{min}) e^{-\left({}^{t}/_{t_c} \right)^c} \right) \qquad (2)$$

where α_{min}, was the minimum fraction of wood remaining (between 0 and 1). The vector {α_{min}, t_c, c} was optimized so that the sum of the squared residuals (RSS) between actual and estimated values was minimized. Equation 2 was fit to the data using the gradient evaluation method from the Python library, SciPy (https://docs.scipy.org/doc/scipy/reference/generated/scipy.optimize.curve_fit.html).

Finally, uncertainty of the parameter estimates in equation (2) was deduced from the variance-covariance matrix computed by bootstrapping (Efron and Tibshirani, 1994). We generated 200 pseudo-replicates by resampling with replacement the centered residuals of the non-linear regression.

3. Results

3.1 Meteorological conditions

Temperatures ranged from 2.8 to 22.2 °C in the forest, and from 0.1 to 17.9 °C in the river water. High rainfall events were recorded at the beginning of the survey in November 2014 and again in March 2015 with 476 and 289 mm, respectively. Episodes of heavy rainfall matched the 5 river flooding events declared; all these occurred between the end of fall and the beginning of spring. The largest flood event occurred on 30 November 2014 and had a maximum instantaneous water discharge of 60 m^3s^{-1} measured at the gaging station. In the marina of Argelès-sur-Mer, water temperature and salinity measured on the sampling dates ranged from 16.0 to 22.8 °C and from 34.9 to 37.4, respectively.

3.2 Wood loss rates

Regardless of wood sample type, there were marked differences in the amount of mass loss, as well as in the dynamics of losses between habitats (Fig 2). All curves decreased monotonically. On the forest floor and in the river, dynamics of degradation were well described by a negative exponential function (Table 2). At Sea, the pattern was different. Initially, the degradation rates were slow, then increase rapidly, then they slow again as the fraction of the wood mass accessible to shipworms decreased.

Table 2 Estimates of the decay rates (k) and the time, in years, needed to reach 50% of mass loss (t_{50}) for the two types of wood exposed to forest and river habitats. Strength (R^2) and statistical significance (*p-value*) of the relationships between the negative exponential model and the observations.

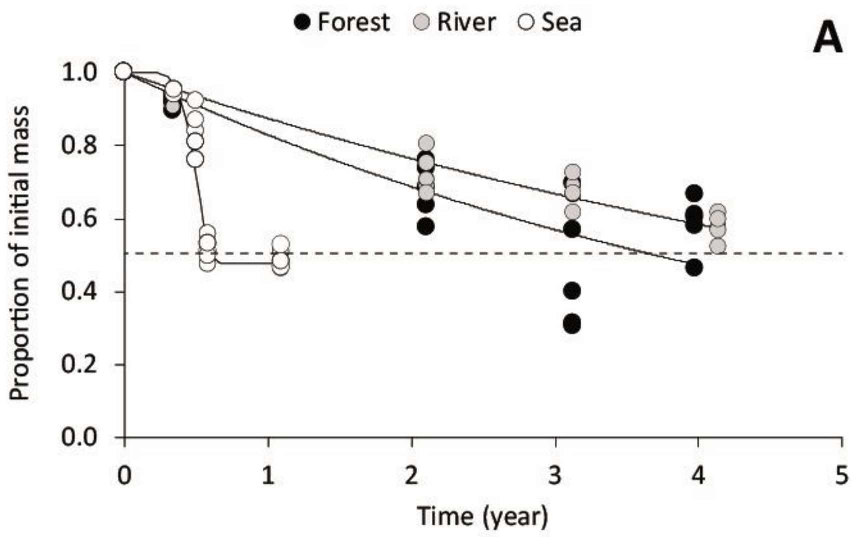
Wood type	Habitat	R^2	*p-value*	k (y^{-1})	SE	t_{50} (y)	t_{50} - range (y)
Beech	Forest	0.6	***	0.187	0.029	3.7	3.3 – 4.5
	River	0.9	***	0.134	0.007	5.2	4.9 – 5.5
Norway spruce	Forest	0.8	***	0.051	0.006	13.6	12.3 – 15.7
	River	0.9	***	0.079	0.006	8.8	8.2 – 9.6

On the forest floor and in the river, spruce decayed more slowly than beech wood (ANCOVA test, $p<0.05$ in both cases). The integrated degradation rate of beech was not significantly different on forest floor and in the river (0.187 y^{-1} and 0.134 y^{-1}, respectively (Table 2); ANCOVA test, $p>0.05$). For spruce, the integrated degradation rate was significantly higher in the river than in the forest (0.079 y^{-1} and 0.051 y^{-1}, respectively (Table 2); ANCOVA test, $p<0.05$).

At the coastal site (Sea), wood mass loss decreased significantly with exposure time (one-way ANOVA, $p<0.001$; Fig. 2). After 1.1 years of exposure the mass of the wood blocks submerged in seawater was halved (Table 3). Beyond this, the wooden blocks were judged too fragile to continue monitoring the degradation process without risking sample loss. Early wood degradation occurred over the first 7 months in seawater for both wood types (Table 3). Degradation was 6 to 9 times slower for beech in the other two conditions (River, Forest) and from 13 to 20 times slower for the spruce blocks, where the integrated degradation rate on the forest floor was by far the slowest (13.6 y^{-1}).

Table 3 Optimized parameters of the curve fitting to the observations made for blocks from both wood types exposed to seawater; $\alpha_{\min}$, proportion of the wood block mass that remained unavailable to wood-borers; t_c, time (in year) required for the borers to consume half of their total consumption; and c, rapidity of mass loss in the vicinity of the inflection point of the fitted curve. Residuals sum of squares (RSS) is given as an estimate of the good of fit; t_{50} is time, in year, needed to reach 50% of the initial mass. SE account for standard errors.

Wood type	$\alpha_{\min}$(SE)	t_c (SE)	c(SE)	RSS	t_{50} (SE)
Beech	0.48(0.01)	0.52(0.01)	6.77(0.99)	0.033	0.61(0.02)
Norway Spruce	0.46(0.01)	0.51(0.01)	4.26(0.31)	0.012	0.64(0.01)



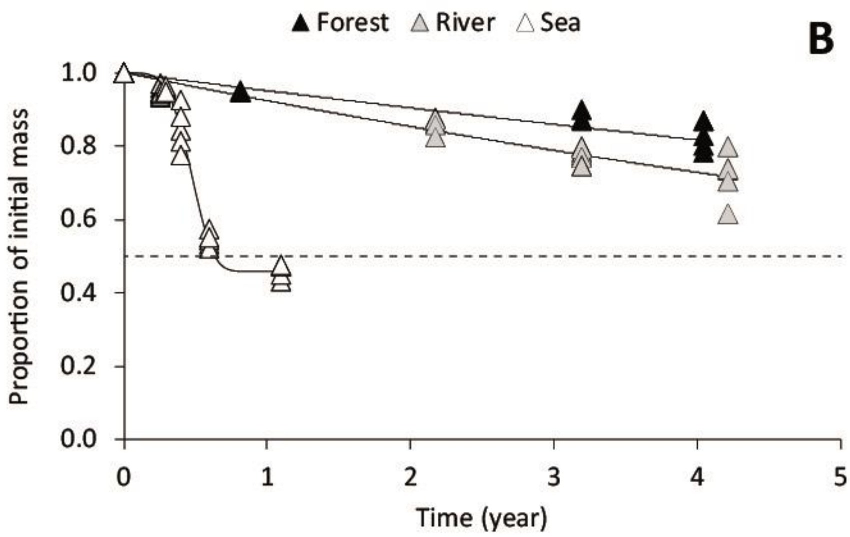


Fig. 2: Degradation observed of wood blocks during the first four years of exposure. Solid lines correspond to the fit of the regression models to the observations for beech cylinders (A) and Norway spruce blocks (B). The horizontal dashed line indicates the proportion equivalent to 50% of the initial wood mass.

3.3 Secondary evidence of the decay process

Visual examination of the samples showed that in forested conditions, the density of fungal hyphae was always much higher on beech logs than on spruce blocks. In the river, the wood samples showed clear signs of erosion (the initially sharp edges were all blunted). The beech samples in the river had completely lost their bark by the second date of sampling. At the other two sites, the percentage of bark at the end of exposure was always greater than 65% of the initial bark coverage (Fig. 3). In the forest, the underside of spruce blocks in direct contact with the soil layer, developed ridges and hollows following the alternating earlywood and latewood layers.

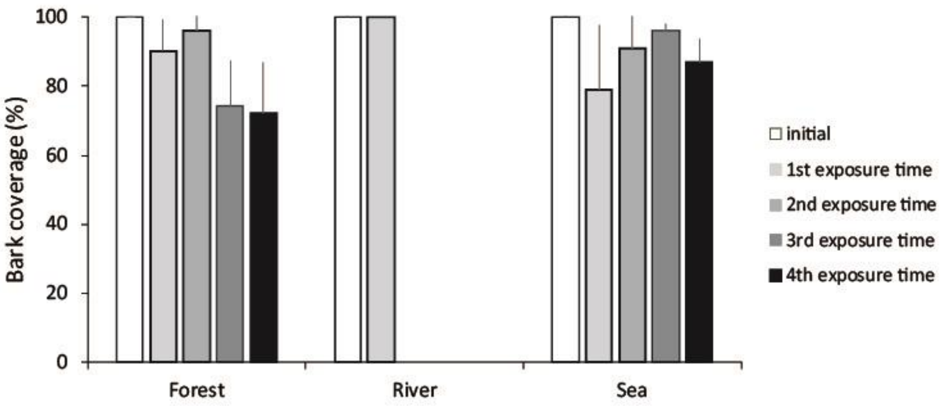


Fig. 3. Relative amount of bark remaining on beech cylinders after each exposure period, in each of the three conditions (Forest, River, Sea). Corresponding exposure times are listed in Table 1.

Wood samples submerged at the marine site had an increasing number of holes with the time of exposure. Beech wood samples only had visible holes where the surface of the wood was not covered with bark. Attacks by shipworms were visible on all sides of the spruce blocks.

Depending on the habitat and wood type, the degree of dependence between mass loss and density of the samples was either close to 0 or close to 1. This suggests that mass loss was either related to volume loss or occurred without significant change in the apparent volume of the wood blocks (Fig. 4 A and B). For beech wood, the correlation was high for samples placed directly on the forest floor (r^2=0.959, n=18, p<0.001) and in the marine conditions (r^2=0.964, n=18, p<0.001) (Fig. 4A). For spruce, the two variables were significantly correlated only for samples at sea (r^2=0.968, n=18, p<0.001) (Fig. 4B). For the remaining conditions, the Pearson's correlation coefficient was between 0.05 for spruce on the forest floor and 0.15 for beech immersed in the river water.

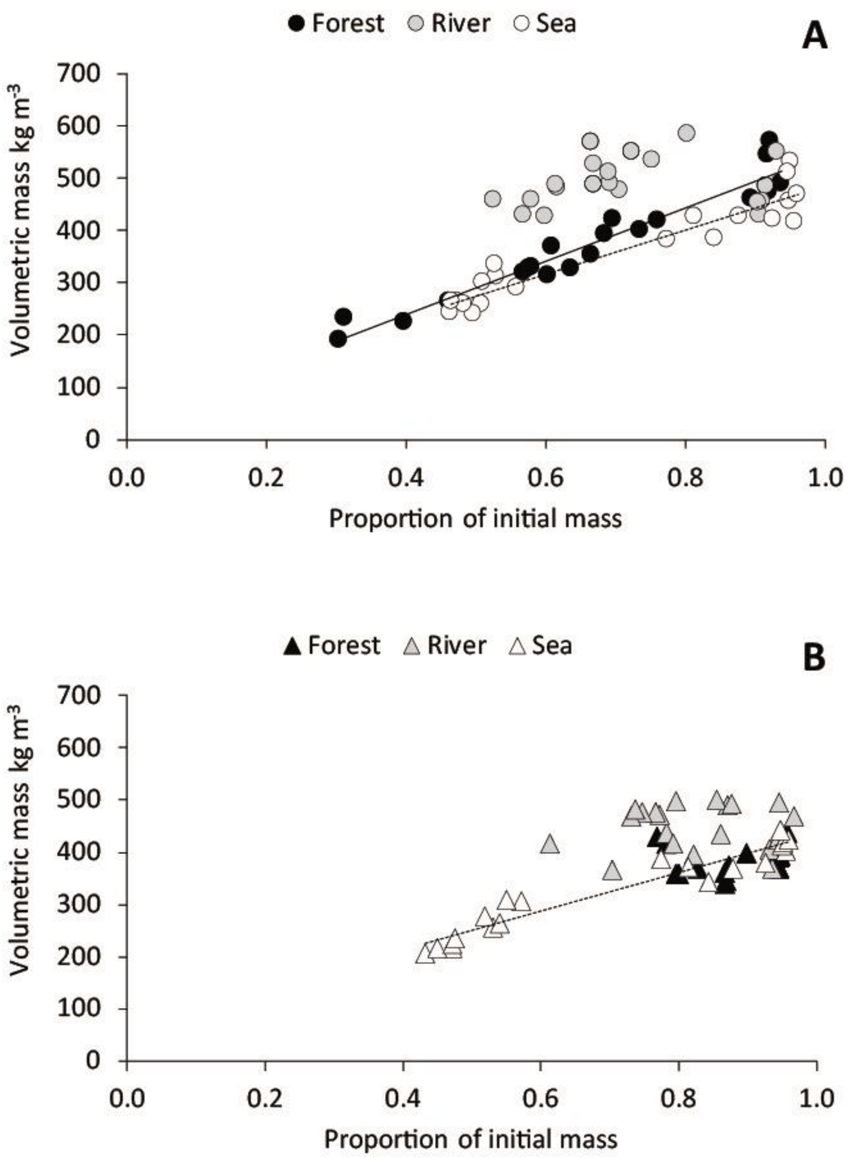


Fig. 4. Relationship between the proportion of remaining wood mass and volumetric mass of beech wood (A) and Norway spruce wood (B) at the time the samples were collected. Straight lines indicate the existence of a significant correlation between the two variables on the Forest floor (solid line) and at the Sea site (dotted line).

4. Discussion

Our multi-year survey of wood degradation suggests the dynamics of wood decomposition differ by up to two orders of magnitude between the three different conditions (Forest, River, Sea) investigated along a land-sea continuum. To the best of our knowledge, only one other similar study (Ferrer et al., 2020) reports on a synoptic comparison of wood recycling kinetics in different habitats of a tropical region. There are very few reports presenting integrated studies on wood production, degradation and transfer from the forest to the coastal sea. Hypothetically, such a study would start by developing a global approach, incorporating progressively processes quantified in all the environments that are crossed by the wood debris, including terrestrial, freshwater and marine biotopes. Quantities of wood transported would be a function of the wood debris mass available when transport processes are active (like flooding events on a river). This makes it important to quantify hydrological conditions as well as biomass production and degradation processes in each of the environments to be represented in a quantitative framework.

4.1 Variability in degradation rate estimates

The most striking result of our study was how much faster wood mass loss occurs under marine conditions, with the presence of shipworms. No difference in degradation rate was detected between the two wood types. In the beech wood samples, shipworms entered on the cut ends and the few places where the bark had disappeared. While the spruce blocks had entry holes on all sides. This suggests there may be variability in substrate colonization by shipworm species but that is undetected by our method. Even if we did not assess the net effect of shipworms on the wood here, the tunneling of these marine bivalves contributed to the nearly 50% of wood mass loss within 7 months. This suggests that wood boring invertebrates degrade wood much faster in the marine environment than has been reported for terrestrial environments (Seibold et al., 2021).

Among the three sites, the Forest samples are the only blocks to have experienced at least two distinct micro-environments because one side is in direct contact with the soil surface, while the other sides are exposed (Tatti et al., 2018). In the sloping, irregular forest floor habitat, not all pieces of wood had strictly identical conditions, especially for humidity. This could account for the dispersion of values for the beech samples. The beech blocks were all covered with fungal hyphae while, by comparison, the surface of the spruce blocks remained nearly bare.

For River-exposed samples, the spruce degraded significantly faster than the Forest samples. However, the difference between them remained small, and decay rates were among the lowest recorded in the study. Conifer species tend to have lower decay rates than angiosperms (Harmon et al., 2020). Compositional differences, like the absence of large vascular vessels, a generally higher proportion of lignin, and a less diverse carbohydrate composition (Pettersen, 1984) may explain why gymnosperm wood decomposes differently than angiosperm wood (Díez et al., 2002; Freschet et al., 2012). Concerning beech wood, our results indicate no significant difference in degradation rates between conditions on the forest floor and in the river water. Nevertheless, the highest mass losses were measured on the forest floor for beech. In the river, loss of mass was more regular and the values for a given exposure duration was less scattered than for samples from the forest floor.

4.2 Decay processes

Mass loss and visual estimates of degradation only provide a non-specific, empirical estimate of wood degradation. In other words, our measurements cannot differentiate between all the ecological, biochemical and physical processes involved. It is thus important to consider what we can learn from the necessity of having to use two different formulations to fit the observations. For observations from the Forest and River sites, decay was described by a negative exponential model, which is a not only a common but also a minimal formulation (Díez et al., 2002; Freschet et al., 2012; Müller-Using and Bartsch, 2009; Spänhoff and Meyer, 2004). This simple linear process suggests that the material decomposes over time at the same relative rate, and hence there is no variation imposed by any external factors, but only a single dependence of the substrate composition and its availability. In the marine environment, the strong non-linearity of the formulation suggests that, on the contrary, there are components involved that are not accounted for (e.g. the shipworm community). The change of relative rate in the decay can be attributed to change in the shipworm community composition, abundance and/or activity rate.

At sea, wood is removed and damaged as shipworms tunnel into and grow within the wood mass, hollowing out the structure from the interior and leaving unchanged the external dimensions. This leads to (for both wood types) a relatively rapid reduction in the mass of wood without an apparent decrease in volume. At the marine site, shipworms are known to occur quickly after the installation of wood samples (Charles et al., 2016). The dynamics of degradation depend on the seasonality of fallen wood production and the timing and frequency of new dead wood arrivals at the coast. In marine environments, there are also fungal and bacterial decomposers present (Björdal and Nilsson, 2008; Ferrer et al., 2020). The effects of these groups are expressed more slowly but probably favored by the increase in the surface-volume ratio resulting from the creation of an extremely dense network of galleries by the bivalves. We cannot exclude the hypothesis that degradation in the other two habitats could eventually catch up, given a longer observation time.

In the river, the volumetric mass of wood blocks did not change significantly during exposure regardless of the type of wood. This does not mean an absence of effect of other processes, but suggests instead that physical processes of erosion on the external edges of the blocks were the main cause. For example, the beech branches quickly lost their bark after the first flood event (November 30, 2014) which was also the largest event over the entire monitoring period. Bark affects the dynamics of wood decomposition in sometimes antagonistic ways, depending on the species, size of the woody debris, and position (Dossa et al., 2018). However, our study does not allow us to draw any important conclusions on this matter. We can only report that the loss of bark into the river accounts for the erosion effect of the water current and suspended materials, while the persistence of bark on samples exposed to the marine environment may have acted as a barrier to shipworms.

Volumetric mass of the beech wood that stayed the longest in the river was on average lower than the rest of the series. It is thus possible that for the beech samples, degradation processes other than surface erosion were active. No similar effect was detectable for the spruce blocks. At the Forest site, the beech wood blocks had a relatively constant volume, while losing mass throughout the study period. Fungi hyphae covered the entire surface of some blocks. The mass of the spruce blocks on the forest floor changed little and few scattered fungal hyphae could be observed on them. The main deterioration factor appeared to be erosion of the block surfaces that were in direct contact with the soil.

4.3 Influence of the experimental context

Studies on wood decay differ in terms of tree species used, size of the wood debris and how they are installed in the environment. The climatic context as well as the species involved are considered particularly important for wood degradation (Edman et al., 2021; Pietsch et al., 2019; Ulyshen, 2016). Our estimated decay rates in each of the three habitats were consistent with data on wood degradation on soil, in riverine water and at sea as reported in the literature dealing with the same tree species under the same latitudes (Charles et al., 2016; Díez et al., 2002; Müller-Using and Bartsch, 2009; Spänhoff and Meyer, 2004). In the comparable synoptic study in a tropical zone, Ferrer et al. (2020) showed that regardless of the habitat conditions, wood decayed at similar rates. Mackensen et al. (2003) reported significant inverse relationships between sample size and decomposition rate. Therefore, Díez et al. (2002) suggested that direct comparison must be limited to similar sizes and types of wood. In other studies, litter bags have been used to monitor the degradation of wood blocks to prevent the material under study from becoming dispersed in the environment. The disadvantage is that these bags partially isolate the sample from the environment (Seibold et al., 2021), thus limiting interactions with biotic and abiotic factors. At the risk of losing the material, we chose not to put any physical barrier between the wood and the environment, which allowed us to monitor all environmental effects (including surface erosion) on the wood.

5. Conclusion

Woody debris transferred to the sea is largely absent from studies of the global carbon (Ciais et al., 2013). Yet, large accumulations of plant and tree remains are visible in many habitats of the land-sea continuum. The fluxes of this pool of organic carbon are considered negligible compared to fluxes of terrestrially derived dissolved and particulate organic carbon (Bianchi, 2011). There are, however, no estimates of the flux, or stock of wood debris discharged into the sea available.

We observed that once woody material reaches the waters of the Mediterranean Sea, the integrated early degradation occurs at rates of 6 to 20 times faster than on the forest floor or when submerged in a river. Counter-intuitively, the results show that although woody debris continues to perform the same ecological functions and ecosystem services as in its source ecosystem where it originates, woody materials in marine environments cannot be considered part of the degradation-resistant organic carbon pool. At the level of the meta-ecosystem, because the location of the fast degradation is different from the location of the wood debris production, our study suggests that the limiting factor of the wood degradation process is the transfer between local ecosystems at the regional scale. The transfer rate between local ecosystems would constrain wood borer community dynamics and diversity. This limitation on the local system highlights how some limiting ecosystem functions and processes may be obscured in large-scale accounting approaches attempting to represent carbon cycles (e.g. Ward et al., 2020).

Acknowledgements

This work was supported by the French CNRS (Centre National de la Recherche Scientifique) through their funding program EC2CO (Ecosphère Continentale et Côtière) with the DEFLAM and XYLOSCOPE projects. We thank the referees whose thoughtful reviews considerably improved the quality of the manuscript.

References

Benner, R., Fogel, M.L., Sprague, E.K., Hodson, R.E., 1987. Depletion of 13C in lignin and its implications for stable carbon isotope studies. Nature 329, 708–710. https://doi.org/10.1038/329708a0

Bianchi, T.S., 2011. The role of terrestrially derived organic carbon in the coastal ocean: A changing paradigm and the priming effect. Proceedings of the National Academy of Sciences 108, 19473–19481. https://doi.org/10.1073/pnas.1017982108

Bianchi, T.S., Allison, M.A., 2009. Large-river delta-front estuaries as natural "recorders" of global environmental change. Proceedings of the National Academy of Sciences 106, 8085–8092. https://doi.org/10.1073/pnas.0812878106

Bienhold, C., Pop Ristova, P., Wenzhöfer, F., Dittmar, T., Boetius, A., 2013. How deep-sea wood falls sustain chemosynthetic life. PLoS ONE 8, e53590. https://doi.org/10.1371/journal.pone.0053590

Björdal, C.G., Nilsson, T., 2008. Reburial of shipwrecks in marine sediments: a long-term study on wood degradation. Journal of Archaeological Science 35, 862–872. https://doi.org/10.1016/j.jas.2007.06.005

Carlton, J.T., Chapman, J.W., Geller, J.B., Miller, J.A., Carlton, D.A., McCuller, M.I., Treneman, N.C., Steves, B.P., Ruiz, G.M., 2017. Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. Science 357, 1402–1406. https://doi.org/10.1126/science.aao1498

Charles, F., Coston-Guarini, J., Guarini, J.-M., Fanfard, S., 2016. Wood decay at sea. Journal of Sea Research 114, 22–25. https://doi.org/10.1016/j.seares.2016.05.002

Charles, F., Coston-Guarini, J., Lantoine, F., Guarini, J.-M., Yücel, M., 2014. Ecogeochemical fate of coarse organic particles in sediments of the Rhône River prodelta. Estuarine, Coastal and Shelf Science 141, 97–103. https://doi.org/10.1016/j.ecss.2014.03.005

Chauvet, E., Jean-Louis, A.-M., 1988. Production de litière de la ripisylve de la Garonne et apport au fleuve. Acta Oecologia, Oecologia Generalis 9, 265–279. https://oatao.univ-toulouse.fr/14392/

Ciais, P., Sabine, C., G. Bala, L. Bopp, V. Brovkin, J. Canadell, A. Chhabra, R. DeFries, J. Galloway, M. Heimann, C. Jones, C. Le Quéré, R.B. Myneni, S. Piao and P. Thornton, 2013. Carbon and other biogeochemical cycles, in: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. https://doi.org/10.1017/CBO9781107415324.015

Cragg, S.M., Beckham, G.T., Bruce, N.C., Bugg, T.D., Distel, D.L., Dupree, P., Etxabe, A.G., Goodell, B.S., Jellison, J., McGeehan, J.E., McQueen-Mason, S.J., Schnorr, K., Walton, P.H., Watts, J.E., Zimmer, M., 2015. Lignocellulose degradation mechanisms across the Tree of Life. Current Opinion in Chemical Biology 29, 108–119. https://doi.org/10.1016/j.cbpa.2015.10.018

Cragg, S.M., Friess, D.A., Gillis, L.G., Trevathan-Tackett, S.M., Terrett, O.M., Watts, J.E.M., Distel, D.L., Dupree, P., 2020. Vascular plants are globally significant contributors to marine carbon fluxes and sinks. Annu. Rev. Mar. Sci. 12, 469–497. https://doi.org/10.1146/annurev-marine-010318-095333

Daniels, L.D., Dobry, J., Klinka, K., Feller, M.C., 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. Can. J. For. Res. 27, 1132–1141. https://doi.org/10.1139/x97-055

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Quintero, N.B., 1998. The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30, 2–11. https://doi.org/10.1111/j.1744-7429.1998.tb00364.x

Díez, J., Elosegi, A., Chauvet, E., Pozo, J., 2002. Breakdown of wood in the Agüera stream: Breakdown of wood. Freshwater Biology 47, 2205–2215. https://doi.org/10.1046/j.1365-2427.2002.00965.x

Dossa, G.G.O., Schaefer, D., Zhang, J.-L., Tao, J.-P., Cao, K.-F., Corlett, R.T., Cunningham, A.B., Xu, J.-C., Cornelissen, J.H.C., Harrison, R.D., 2018. The cover uncovered: Bark control over wood decomposition. J Ecol 106, 2147–2160. https://doi.org/10.1111/1365-2745.12976

Edman, M., Hagos, S., Carlsson, F., 2021. Warming effects on wood decomposition depend on fungal assembly history. J Ecol 109, 1919–1930. https://doi.org/10.1111/1365-2745.13617

Efron, B., Tibshirani, R.J., 1994. An Introduction to the Bootstrap. Chapman and Hall/CRC. https://doi.org/10.1201/9780429246593

Fagervold, S.K., Galand, P.E., Zbinden, M., Gaill, F., Lebaron, P., Palacios, C., 2012. Sunken woods on the ocean floor provide diverse specialized habitats for microorganisms. FEMS Microbiology Ecology 82, 616–628. https://doi.org/10.1111/j.1574-6941.2012.01432.x

Ferrer, A., Heath, K.D., Canam, T., Flores, H.D., Dalling, J.W., 2020. Contribution of fungal and invertebrate communities to wood decay in tropical terrestrial and aquatic habitats. Ecology 101. https://doi.org/10.1002/ecy.3097

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. Science of The Total Environment 569–570, 1064–1076. https://doi.org/10.1016/j.scitotenv.2016.06.167

Fravolini, G., Tognetti, R., Lombardi, F., Egli, M., Ascher-Jenull, J., Arfaioli, P., Bardelli, T., Cherubini, P., Marchetti, M., 2018. Quantifying decay progression of deadwood in Mediterranean mountain forests. Forest Ecology and Management 408, 228–237. https://doi.org/10.1016/j.foreco.2017.10.031

Freschet, G.T., Weedon, J.T., Aerts, R., van Hal, J.R., Cornelissen, J.H.C., 2012. Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition: New method to assess wood decay dynamics and rates. Journal of Ecology 100, 161–170. https://doi.org/10.1111/j.1365-2745.2011.01896.x

Gomi, T., Sidle, R.C., Richardson, J.S., 2002. Understanding processes and downstream linkages of headwater systems. BioScience 52, 905. https://doi.org/10.1641/0006-3568(2002)052[0905:UPADLO]2.0.CO;2

Harmon, M.E., Fasth, B.G., Yatskov, M., Kastendick, D., Rock, J., Woodall, C.W., 2020. Release of coarse woody detritus-related carbon: a synthesis across forest biomes. Carbon Balance Manage 15, 1. https://doi.org/10.1186/s13021-019-0136-6

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems, in: Advances in Ecological Research. Elsevier, pp. 59–234. https://doi.org/10.1016/S0065-2504(03)34002-4

Hedges, J.I., Keil, R.G., Benner, R., 1997. What happens to terrestrial organic matter in the ocean? Organic Geochemistry 27, 195–212. https://doi.org/10.1016/S0146-6380(97)00066-1

Hill, C.L.R., Kofoid, C.A., National Research Council (U.S.), San Francisco Bay Marine Piling Committee., 1927. Marine borers and their relation to marine construction on the Pacific coast, being the final report of the San Francisco Bay Marine Piling Committee, prepared under the direction of the San Francisco Bay Marine Piling Committee, cooperating with the National Research

Council and the American Wood-preservers' Association; C. L. Hill and C. A. Kofold. The Committee, San Francisco, Calif.,. https://doi.org/10.5962/bhl.title.39572

Kandasamy, S., Nagender Nath, B., 2016. Perspectives on the terrestrial organic matter transport and burial along the land-deep sea continuum: Caveats in our understanding of biogeochemical processes and future needs. Front. Mar. Sci. 3. https://doi.org/10.3389/fmars.2016.00259

Keil, R.G., Tsamakis, E., Giddings, J.C., Hedges, J.I., 1998. Biochemical distributions (amino acids, neutral sugars, and lignin phenols) among size-classes of modern marine sediments from the Washington coast. Geochimica et Cosmochimica Acta 62, 1347–1364. https://doi.org/10.1016/S0016-7037(98)00080-5

Keith, H., Vardon, M., Stein, J.A., Lindenmayer, D., 2019. Contribution of native forests to climate change mitigation – A common approach to carbon accounting that aligns results from environmental-economic accounting with rules for emissions reduction. Environmental Science & Policy 93, 189–199. https://doi.org/10.1016/j.envsci.2018.11.001

Kramer, N., Wohl, E., 2015. Driftcretions: The legacy impacts of driftwood on shoreline morphology [WWW Document]. Geophysical Research Letters. https://doi.org/10.1002/2015GL064441

Krankina, O.N., Harmon, M.E., Kukuev, Y.A., Treyfeld, R.F., Kashpor, N.N., Kresnov, V.G., Skudin, V.M., Protasov, N.A., Yatskov, M., Spycher, G., Povarov, E.D., 2002. Coarse woody debris in forest regions of Russia Krankina, Olga N; Harmon, Mark E; Kukuev, Yuri A; Treyfeld, Rudolf F; Kashpor, Nikolai N; Kresnov, Vladimir G; Skudin, Viktor M; Protasov, Nikolai A; Yatskov, Mikhail; Spycher, Gody; Povarov, Ewgeni D (2002). Coarse woody debris in forest regions of Russia. Canadian Journal of Forest Research, 32(5), 768–778. doi:10.1139/x01-110 32, 11. https://doi.org/10.1139/x01-110

Lancaster, S.T., Hayes, S.K., Grant, G.E., 2003. Effects of wood on debris flow runout in small mountain watersheds: effects of wood on debris flow runout. Water Resour. Res. 39. https://doi.org/10.1029/2001WR001227

Leroux, S.J., Loreau, M., 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems: Subsidies and trophic cascades. Ecology Letters 11, 1147–1156. https://doi.org/10.1111/j.1461-0248.2008.01235.x

Lionello, P., Malanotte-Rizzoli, P., Boscolo, R., Alpert, P., Artale, V., Li, L., Luterbacher, J., May, W., Trigo, R., Tsimplis, M., Ulbrich, U., Xoplaki, E., 2006. The Mediterranean climate: An overview of the main characteristics and issues, in: Lionello, P., Malanotte-Rizzoli, P., Boscolo, R. (Eds.), Developments in Earth and Environmental Sciences. Elsevier, pp. 1–26. https://doi.org/10.1016/S1571-9197(06)80003-0

Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris—A review with particular emphasis on Australian tree species. Aust. J. Bot. 51, 27. https://doi.org/10.1071/BT02014

Maser, C., Sedell, J.R., 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans. St. Lucie Press, Delray Beach, FL.

Molinié, G., Ceresetti, D., Anquetin, S., Creutin, J.D., Boudevillain, B., 2012. Rainfall regime of a mountainous Mediterranean region: statistical analysis at short time steps. Journal of Applied Meteorology and Climatology 51, 429–448. https://doi.org/10.1175/2011JAMC2691.1

Müller-Using, S., Bartsch, N., 2009. Decay dynamic of coarse and fine woody debris of a beech (Fagus sylvatica L.) forest in Central Germany. Eur J Forest Res 128, 287–296. https://doi.org/10.1007/s10342-009-0264-8

Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The Structure, Distribution, and Biomass of the World's Forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

Pettersen, R.C., 1984. The chemical composition of wood, in: The Chemistry of Solid Wood, Advances in Chemistry. American Chemical Society, pp. 57–126. https://doi.org/10.1021/ba-1984-0207.ch002

Pietsch, K.A., Eichenberg, D., Nadrowski, K., Bauhus, J., Buscot, F., Purahong, W., Wipfler, B., Wubet, T., Yu, M., Wirth, C., 2019. Wood decomposition is more strongly controlled by temperature than by tree species and decomposer diversity in highly species rich subtropical forests. Oikos 128, 701–715. https://doi.org/10.1111/oik.04879

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. 28, 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

Rabouille, C., Conley, D.J., Dai, M.H., Cai, W.-J., Chen, C.T.A., Lansard, B., Green, R., Yin, K., Harrison, P.J., Dagg, M., McKee, B., 2008. Comparison of hypoxia among four river-dominated ocean margins: The Changjiang (Yangtze), Mississippi, Pearl, and Rhône rivers. Continental Shelf Research 28, 1527–1537. https://doi.org/10.1016/j.csr.2008.01.020

Reichstein, M., Carvalhais, N., 2019. Aspects of forest biomass in the Earth system: Its role and major unknowns. Surv Geophys 40, 693–707. https://doi.org/10.1007/s10712-019-09551-x

Ruiz-Villanueva, V., Piégay, H., Gurnell, A.M., Marston, R.A., Stoffel, M., 2016. Recent advances quantifying the large wood dynamics in river basins: New methods and remaining challenges: Large Wood Dynamics. Rev. Geophys. 54, 611–652. https://doi.org/10.1002/2015RG000514

Sass, G.G., 2009. Coarse Woody Debris in Lakes and Streams, in: Encyclopedia of Inland Waters. Elsevier, pp. 60–69. https://doi.org/10.1016/B978-012370626-3.00221-0

Schmocker, L., Weitbrecht, V., 2013. Driftwood: Risk Analysis and Engineering Measures. J. Hydraul. Eng. 139, 683–695. https://doi.org/10.1061/(ASCE)HY.1943-7900.0000728

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R.S., Birkemoe, T., Boros, G., Brandl, R., Brustel, H., Burton, P.J., Cakpo-Tossou, Y.T., Castro, J., Cateau, E., Cobb, T.P., Farwig, N., Fernández, R.D., Firn, J., Gan, K.S., González, G., Gossner, M.M., Habel, J.C., Hébert, C., Heibl, C., Heikkala, O., Hemp, A., Hemp, C., Hjältén, J., Hotes, S., Kouki, J., Lachat, T., Liu, J., Liu, Y., Luo, Y.-H., Macandog, D.M., Martina, P.E., Mukul, S.A., Nachin, B., Nisbet, K., O'Halloran, J., Oxbrough, A., Pandey, J.N., Pavlíček, T., Pawson, S.M., Rakotondranary, J.S., Ramanamanjato, J.-B., Rossi, L., Schmidl, J., Schulze, M., Seaton, S., Stone, M.J., Stork, N.E., Suran, B., Sverdrup-Thygeson, A., Thorn, S., Thyagarajan, G., Wardlaw, T.J., Weisser, W.W., Yoon, S., Zhang, N., Müller, J., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8

Shumilova, O., Tockner, K., Gurnell, A.M., Langhans, S.D., Righetti, M., Lucía, A., Zarfl, C., 2019. Floating matter: a neglected component of the ecological integrity of rivers. Aquat Sci 81, 25. https://doi.org/10.1007/s00027-019-0619-2

Soininen, J., Bartels, P., Heino, J., Luoto, M., Hillebrand, H., 2015. Toward more integrated ecosystem research in aquatic and terrestrial environments. BioScience 65, 174–182. https://doi.org/10.1093/biosci/biu216

Spänhoff, B., Meyer, E.I., 2004. Breakdown rates of wood in streams. Journal of the North American Benthological Society 23, 189–197. https://doi.org/10.1899/0887-3593(2004)023<0189:BROWIS>2.0.CO;2

Steenstrup Kristensen, E., 1979. Observations on growth and life cycle of the shipworm *Teredo navalis* L. (Bivalvia, mollusca) in the Isefjord, Denmark. Ophelia 18, 235–242. https://doi.org/10.1080/00785326.1979.10425501

Tatti, D., Fatton, V., Sartori, L., Gobat, J.-M., Le Bayon, R.-C., 2018. What does 'lignoform' really mean? Applied Soil Ecology 123, 632–645. https://doi.org/10.1016/j.apsoil.2017.06.037

Tesi, T., Langone, L., Goñi, M.A., Miserocchi, S., Bertasi, F., 2008. Changes in the composition of organic matter from prodeltaic sediments after a large flood event (Po River, Italy). Geochimica et Cosmochimica Acta 72, 2100–2114. https://doi.org/10.1016/j.gca.2008.02.005

Turowski, J.M., Hilton, R.G., Sparkes, R., 2016. Decadal carbon discharge by a mountain stream is dominated by coarse organic matter. Geology 44, 27–30. https://doi.org/10.1130/G37192.1

Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates: Invertebrates and wood decomposition. Biol Rev 91, 70–85. https://doi.org/10.1111/brv.12158

Ward, N.D., Megonigal, J.P., Bond-Lamberty, B., Bailey, V.L., Butman, D., Canuel, E.A., Diefenderfer, H., Ganju, N.K., Goñi, M.A., Graham, E.B., Hopkinson, C.S., Khangaonkar, T., Langley, J.A., McDowell, N.G., Myers-Pigg, A.N., Neumann, R.B., Osburn, C.L., Price, R.M., Rowland, J., Sengupta, A., Simard, M., Thornton, P.E., Tzortziou, M., Vargas, R., Weisenhorn, P.B., Windham-Myers, L., 2020. Representing the function and sensitivity of coastal interfaces in Earth system models. Nat Commun 11, 2458. https://doi.org/10.1038/s41467-020-16236-2

West, A.J., Lin, C.-W., Lin, T.-C., Hilton, R.G., Liu, S.-H., Chang, C.-T., Lin, K.-C., Galy, A., Sparkes, R.B., Hovius, N., 2011. Mobilization and transport of coarse woody debris to the oceans triggered by an extreme tropical storm. Limnol. Oceanogr. 56, 77–85. https://doi.org/10.4319/lo.2011.56.1.0077

Zar, J.H., 1984. Biostatistical analysis, 2nd ed. ed. Prentice-Hall, Englewood Cliffs, N.J.