Applied Soil Ecology 123 (2018) 632–645

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Review

What does 'lignoform' really mean?

Dylan Tatti[a,b,*], Vincent Fatton[c], Luna Sartori[d], Jean-Michel Gobat[a], Renée-Claire Le Bayon[a]

[a] Functional Ecology Laboratory, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland
[b] Division of Agriculture, School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Länggasse 85, 3052 Zollikofen, Switzerland
[c] Rue de la Pontaise 14, 1018 Lausanne, Switzerland
[d] Gewässer- und Bodenschutzlabor, Amt für Wasser und Abfall, Canton of Bern, Schermenweg 11, 3014 Bern, Switzerland

ARTICLE INFO

Keywords:
Lignoforms
Humus forms
Deadwood
Coarse woody debris
Fine woody debris

ABSTRACT

Among the many studies devoted to deadwood, very few have considered it in a broader ecosystemic context, especially in relation to the underlying humiferous topsoil. In order to fill this gap, we detail here the concept of lignoforms, humus forms strongly linked to deadwood and mostly ignored by humus forms specialists. After presenting the main characteristics of deadwood, the main actors involved in its life cycle and its important and varied roles in many ecosystems, we explain how to describe and study lignoforms. We also propose new diagnostic horizons for these particular humus forms, as well as a classification system, including an identification key (see Appendix A *Identification key for lignoforms*). Finally, we discuss some important issues pertinent to continuing to improve knowledge of these common but little studied humus forms.

1. Introduction

A growing number of studies about deadwood and its decomposition have been published over the last 30 years (Russell et al., 2015), most of them dealing with the physicochemical properties of deadwood or guidelines for the measurement of woody debris in ecosystems. However, the study of deadwood in a broader ecosystemic context remains relatively untouched (Brändli, 2010), especially when linked to humus systems made of dominant wood under transformation by wood-feeding animals and/or wood-rotting fungi. Such humus forms are currently called lignoforms or hyperlignic parahumus by the European humus forms classification (Jabiol et al., 2013; Zanella et al., 2011). The humus forms classification of British Columbia classifies them as Lignomoder or Lignomor (Green et al., 1993; Klinka et al., 1997), depending on the key influence of fungi and/or bryophytes. More generally, these humus forms have also been referred to as Lignic Folisol by the Canadian soil classification (Soil Classification Working Group, 1998).

The concept of lignoforms still remains broad, encompassing various situations and thus requiring improvement. This contribution is therefore an initial attempt (i) to clarify different concepts evolving around lignoforms, and (ii) to contribute to the system of classification of these atypical humus forms.

2. Characterisation of deadwood

2.1. Categories of deadwood

Deadwood constitutes an important part of forest litter. Its annual input and the quantities lying on the ground have been the subject of many studies (see, e.g. Agee and Huff, 1987; Berg et al., 1993; Brändli, 2010; Elton, 1966; Goodburn and Lorimer, 1998; Kirby et al., 1991; MCPFE, 2007).

In practical terms, deadwood can be subdivided into different categories (Harmon and Sexton, 1996):

(i) **Woody debris** consists of the trunks of dead trees, branches and other parts lying on the ground or at an angle of up to 45° but no longer supported by roots (Waddell, 2002). It is also called logs or lying deadwood (Harmon and Sexton, 1996; Rondeux and Sanchez, 2010). Woody debris can then be further divided (see, e.g. Brown, 1974; Harmon et al., 1986; Harmon and Sexton, 1996) into (ia) **coarse woody debris** (CWD), with a diameter equal to or greater than 10 cm and (ib) **fine woody debris** (FWD), with a diameter smaller than 10 cm.

(ii) **Snags** (or standing dead trees) are short to long vertical pieces of deadwood, standing at an angle of 45° to 90°, still attached to the ground with roots and usually resulting from natural processes (Harmon and Sexton, 1996; Waddell, 2002).

(iii) **Stumps** are short vertical pieces of deadwood, still attached to

* Corresponding author at: Division of Agriculture, School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Länggasse 85, 3052 Zollikofen, Switzerland.
E-mail address: dylan.tatti@bfh.ch (D. Tatti).

http://dx.doi.org/10.1016/j.apsoil.2017.06.037
Received 31 January 2017; Received in revised form 23 June 2017; Accepted 28 June 2017
Available online 23 July 2017
0929-1393/

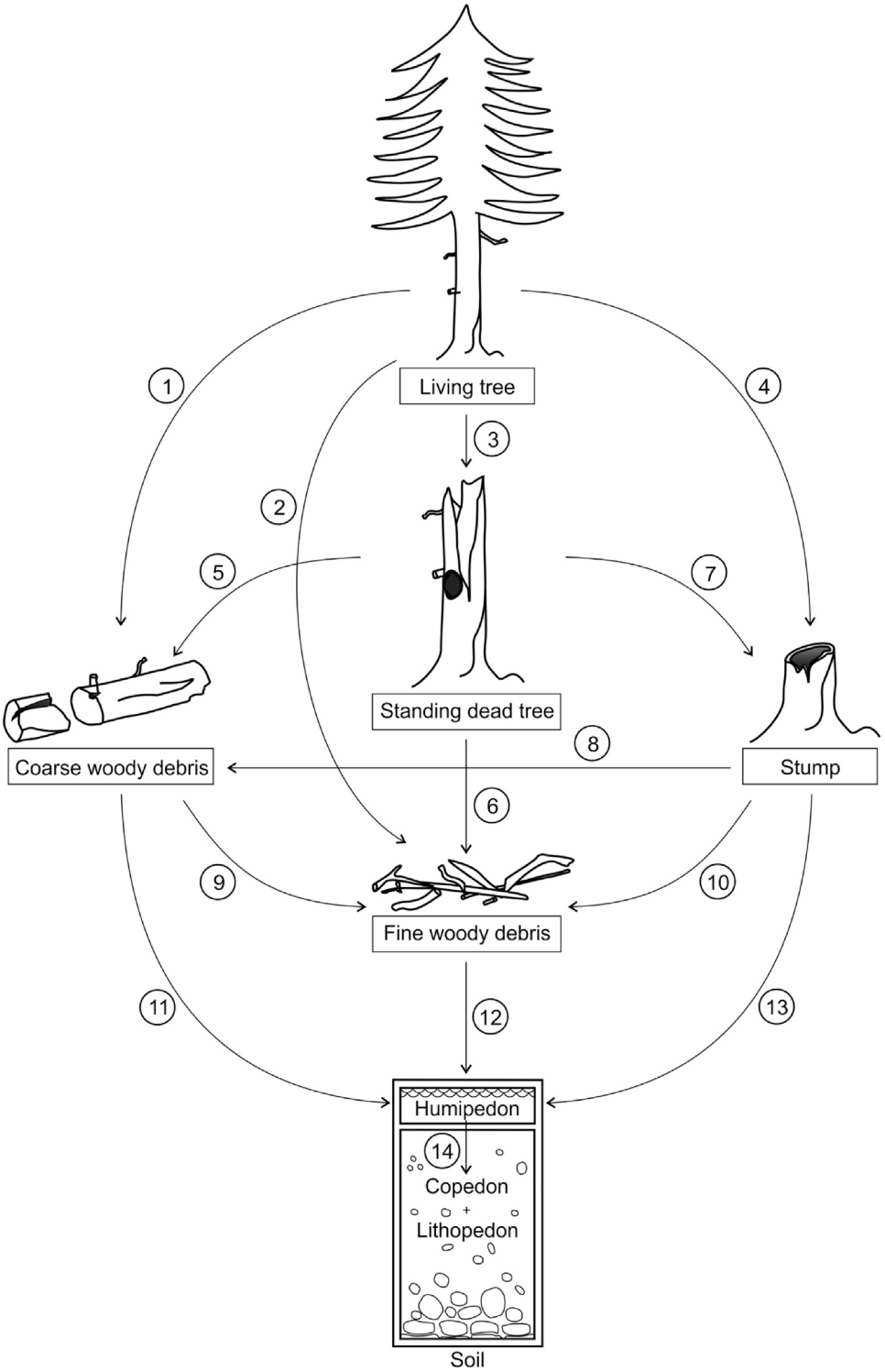


Fig. 1. Links existing between deadwood types and their convergent role in the formation of humus revealed by the humus forms and preceding the formation of soil. Numbers 1 to 14 are related to the numbers shown in Table 1.

the ground with roots and often resulting from the anthropogenic action of cutting (Harmon and Sexton, 1996; Melin et al., 2009).

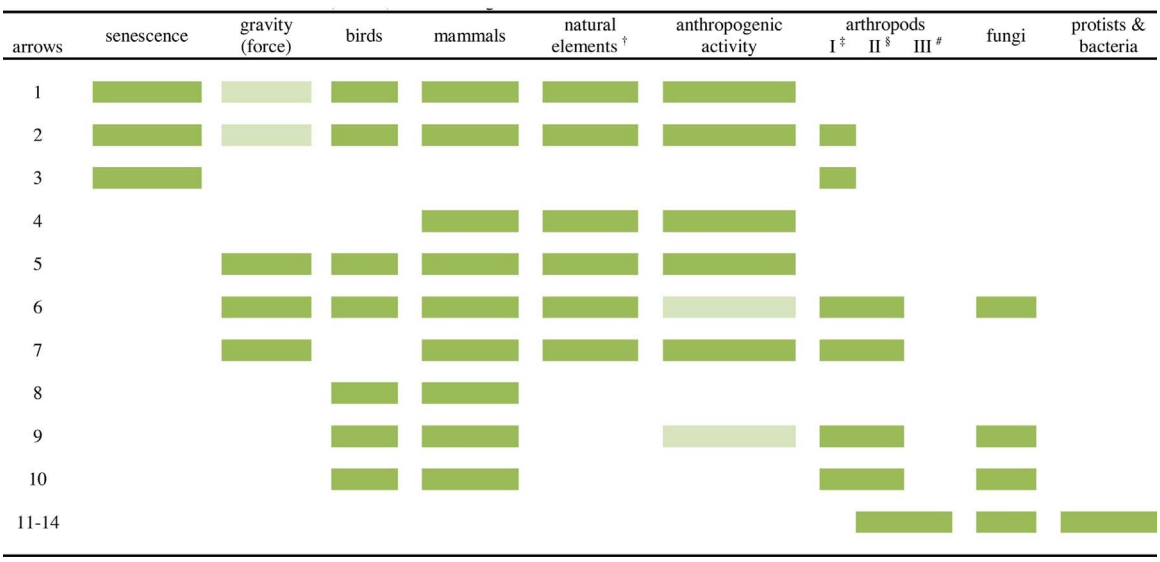
In the two last cases, the root system must be considered independently of the aboveground deadwood because of different decomposition dynamics (Melin et al., 2009).

These different deadwood types can be seen as an interconnected network in which one type can become another, always ending in progressive incorporation into the soil and also eventually in the complete decomposition of deadwood (Bunnell and Houde, 2010; Moroni et al., 2015; Russell et al., 2015). This concept is summarised in Fig. 1. Table 1 shows the actors involved in the links between the different compartments of Fig. 1. Since almost every actor can be found in each link, only the main ones are highlighted here.

2.2. States of decomposition

Deadwood can also be classified in terms of its state of decomposition. Different systems have been established in order to characterise quickly and as objectively as possible the state of decomposition of deadwood. All have subdivided deadwood into different ‘decay classes’.

Table 1
Main actors involved in the links (1 to 14) shown in Fig. 1.(For interpretation of the references to colour in this table legend, the reader is referred to the web version of this article.)



† Storms, lightning, etc.
Arthropods are subdivided into different categories (I, II and III), encompassing various taxonomical levels.
‡ Buprestidae, Cerambycidae, Curculionidae, Scolytinae.
§ Blattodea, Anobiidae, Lymexylidae, Zopheridae, Pantophthalmidae, Tipulidae (genus *Ctenophora*), ants (e.g. *Camponotus* sp.), Megachilidae, Siricidae, Xiphydriidae, xylocopone apids, Cossidae, Hepialidae, Sesiidae.
# Collembola, Acari (Oribatida, Gamasida, …), Diplura, Myriapoda, Isopoda, Lumbricidae, Gastropoda, Coleoptera and Diptera larvae, Termitoidae, Passalidae.
Inspired by Ammer (1991), Bunnell and Houde (2010), Lachat et al. (2014), Maser et al. (1979), Schiegg Pasinelli and Sutter (2000), Siitonen (2001), Stokland et al. (2012) and Ulyshen (2014).

One of the most common systems seems to be that established by Maser et al. (1979), inspired by the previous work of Fogel et al. (1973). This system, initially applied in coniferous forests in the United States, comprises five decay classes based on visual and physical criteria such as the presence or absence of bark or branches, the texture and colour of the wood or the general shape of the trunk. This system has been re-visited and modified by various authors and also extended to hardwood (see, e.g. Keller, 2005; Maser and Trappe, 1984; Ódor and van Hees, 2004; Pyle and Brown, 1998; Woodall and Monleon, 2008). Table 2 shows the main characteristics of these five decay classes.

This common and practical decay class system is a very useful tool (Russell et al., 2015) which can also be used for lignoform descriptions (see § 4.3 *Diagnostic horizons*).

3. Deadwood in ecosystems

3.1. From the falling tree to integration into the soil

3.1.1. Three-stage model

The process running from the arrival of deadwood on the ground until its incorporation into the soil can be roughly subdivided into three stages easily recognisable in the field (on the ground of terrestrial ecosystems) (Bunnell and Houde, 2010; Gobat et al., 2010):

Table 2
The five-decay class system used for the description of woody debris (mainly CWD).

	Decay class				
Log characteristics	1	2	3	4	5
Bark	intact	intact	trace	absent	absent
Twigs (Ø < 3 cm)	present	absent	absent	absent	absent
Texture	intact	intact to partly soft	very few softened portions, hard pieces remaining on large portions of the log	small soft portions of the log easily discernible	soft and powdery (very few portions of the log remain coherent)
Knife test	knife penetrates with great difficulty in the direction of the fibres	knife penetrates with great difficulty in the direction of the fibres	knife penetrates slightly, but only in the direction of the fibres	knife penetrates easily in all directions	(almost) no resistance
Shape	round	round	round	round to oval (elliptical)	oval or elliptical flattened
Colour of wood	original colour	original colour	original colour to faded	light brown to reddish brown or yellowish	faded to light yellow or grey, or red brown to dark brown
Portion of tree on ground	log elevated on support points	log elevated on support points but sagging slightly	log is sagging near ground	all of log on ground	all of log on ground

Adapted from Keller (2005), Maser et al. (1979) and Maser and Trappe (1984).

(i) a **stage of colonisation,** involving the arrival and settlement of various pioneer organisms; this stage extends throughout all processes with the successive arrival of different cohorts (Ulyshen, 2014),

(ii) a **stage of decay,** during which deadwood begins to decompose, thus losing its shape, structure and other original features,

(iii) a **stage of integration** into the soil (co-occurring with the humification processes), occurring more or less rapidly as it is driven by several environmental variables and the type of wood.

It should be noted that this three-stage model does not apply to aquatic ecosystems (e.g. estuaries or lakes) or more specifically, to the wet part of specific terrestrial ecosystems (e.g. black alder (*Alnus glutinosa* (L.) Gaertn.) forests). These processes remain quite unknown in such ecosystems, even if in some cases the accumulation of deadwood can lead to huge amounts of peat partly made of woody material (Moroni et al., 2015).

3.1.2. Influencing factors

The duration and intensity of each of these three stages are driven by and may vary under various factors. Some of them are among the five 'classical' factors of soil development (parent material, climate, topography, biological activity and time) (Jenny, 1941, 1980) and others are more related to woody material:

(a) **Geological substrate**, **soil** (pH, CEC, …) (Berg and McClaugherty, 2014) and **humus forms** (Bocock et al., 1960; Gilbert and Bocock, 1960; Howard and Howard, 1980), but very few studies have been done concerning the effect of these variables on deadwood.
(b) **Climate**, at different spatial and time scales (Russell et al., 2015; Yin, 1999), even if this point remains relatively unknown (Russell et al., 2014).
(c) **Topography** (Beatty and Stone, 1986; Dwyer and Merriam, 1981; McClellan et al., 1990) and **contact surface** between soil and deadwood (Bull et al., 1997).
(d) Living **organisms** responsible for biological transformations, including microbial organisms (Bunnell and Houde, 2010; Ulyshen, 2014).
(e) Type of surrounding **vegetation** (Moroni et al., 2015; Zhang and Liang, 1995).
(f) **Tree/shrub species** and its potential features (age, presence of reaction wood, etc.) (Harmon et al., 2008; Waddell, 2002; Weedon et al., 2009).
(g) Initial **decay stage** of the woody material (Russell et al., 2015).
(h) **Quantity/volume**, **type**, **shape** and **size** of the initial woody material (coarse woody debris, fine woody debris, stumps, snags, etc.) (Harmon et al., 2011; Mackensen et al., 2003; Zell et al., 2009).

The diversity of these variables as well as the lack of specific data, especially concerning point (iii) (see § 3.1.1 *Three-stage model* above) justifies such a simple and flexible 'three-stage' model, which can be applied to various situations.

3.2. Roles of deadwood in ecosystems

Due to its abundance and the multitude of physicochemical changes occurring during its life cycle, deadwood has long been considered as playing important and various roles in many ecosystems (Ammer, 1991; Barnum et al., 1992; Berg and McClaugherty, 2014; Elton and Miller, 1954; Elton, 1966; Graham, 1925; Harmon and Sexton, 1996; Maser et al., 1979; Savely, 1939), among which are:

(a) A contribution to the **structural diversity** of many environments as well as a **protective role for biodiversity** (Bull et al., 1997; Carey and Johnson, 1995; Goodburn and Lorimer, 1998; Lachat et al., 2014; Pyle and Brown, 1998; Siitonen, 2001; Stokland et al., 2012; Woodall and Monleon, 2008), since deadwood can be considered as an annexe of the soil (i.e. as a 'soil dependency') (Delamare-Debouteville, 1951; Gobat et al., 2010).
(b) An important role in the **nutrition of various species** (see Table 1) (Cornwell et al., 2009; Schiegg Pasinelli and Suter, 2000; Sharitz, 1996; Stokland et al., 2012; Ulyshen, 2014) and the important **water reserve** provided by coarse woody debris, especially in decay classes 4 and 5 (Harvey et al., 1979; Lachat et al., 2014).
(c) The stimulation of forest **regeneration** through the creation of favourable environmental conditions (Bolton and D'Amato, 2011; Brändli, 2010; Brown, 1974; Harmon et al., 1986; Zielonka and Piatek, 2004), as well as a beneficial impact on soil quality (erosion, nutrient content, etc.) (Preston et al., 1990).
(d) A role in the **carbon cycle**, (especially concerning the medium-term sequestration of atmospheric carbon dioxide) (Federici et al., 2015; Malmsheimer et al., 2011; Smith et al., 2013; Waddell, 2002) and coarse woody debris acting as preferential sites for **nitrogen fixation** (Hendrickson, 1991; Larsen et al., 1978; Matzek and Vitousek, 2003).
(e) The role of **bioindication** provided by deadwood, especially in the context of conservation projects (Bütler et al., 2004; Kunttu et al., 2015; Müller and Bütler, 2010; Waddell, 2002; Woodall and Monleon, 2008; Woodall and Nagel, 2006).
(f) The use of deadwood as fuel in **bioenergy production** (Sathre and Gustavsson, 2011).
(g) The effect of deadwood on the **behaviour of forest fires** (Arno, 2000).

4. Deadwood and humus forms

4.1. What is it all about?

Despite the importance and the omnipresence of deadwood in ecosystems, the links between deadwood and humiferous topsoil layers remain unexplored (Russell et al., 2015). Better knowledge (morphology, classification, dynamics, etc.) of the humus forms linked to deadwood − the lignoforms − could lead to a better understanding and protection of the various ecosystem services mentioned above (§ *3.2 Roles of deadwood in ecosystems*), especially those related to the carbon cycle (Cotrufo et al., 2011; Federici et al., 2015).

To this end, we attempt here to complement the fundamental concepts of lignoforms recently laid down by the European humus research group (Jabiol et al., 2013; Zanella et al., 2011).

4.2. Field description

4.2.1. General consideration

As for other humus forms, it is essential to describe as precisely as possible the different horizons in order to subsequently understand the essential operating principles of the studied system (Gobat et al., 2010). However, for lignoforms, the usual method of soil description has to be slightly adapted, especially by taking into account the decay stage of the woody material (see Table 2).

4.2.2. Ecological conditions

In addition to the more 'classical' ecological conditions, the shape, dimension and orientation of the woody material must be noted, as well as its angle and degree of contact with the underlying substrate. The wood species and the presence of possible marks, cavities, fire scars and other disturbances must also be taken into account. Any other information that can help to better understand the functioning (present, past and future) of the considered humus form should also be noted (e.g. a stump in close proximity that can indicate the origin of the woody material, a pile of woody debris that can possibly further fuel a buried lignoform, etc.).

A description of the adjacent humus must also be performed in order to better understand the spatio-temporal dynamic of the studied lignoform. A relevé of the surrounding vegetation (including mosses on

Fig. 2. Different tools used for lignoform description.

the bark) should generally also be considered, given the potential influence of the vegetation on the dynamic of deadwood decomposition (Moroni et al., 2015; Zhang and Liang, 1995).

4.2.3. How to open a lignoform profile?

As humus forms with peculiar characteristics (see *inter alia* § *4.3 Diagnostic horizons*), lignoforms require a specific and adapted methodology for their investigation. Below, we explain how to open a lignoform profile and describe it.

A saw, a wood chisel and different types of knifes can be particularly helpful to open a lignoform profile. While handling coarse woody debris, adhesive tape or any other tape should usually be used in order to maintain the physical integrity of the woody material. Special attention must be paid to personal protective equipment and to the safety of others present. It is recommended to wear safety hand gloves, goggles and (steel-toe) boots. In some cases (e.g. huge accumulation of woody debris), the use of a safety helmet is also strongly recommended. In steep terrain, the woody material should to be stabilised to the ground before starting to work. Fig. 2 shows some tools used for lignoform description.

Once the profile is done, all the debris resulting from the mechanical opening (sawdust, etc.) should be carefully removed before starting the description. For coarse woody debris, the description must be performed at the centre of the cut, on one-third of the total diameter (see Figs. 15–28). This selection (one-third) allows, in most cases, the contact area between the woody material and the underlying substrate to be maximised. Sewing pins could be useful to delimit the different horizons (e.g. when taking a photo). Note that different woody horizons can be found in a single piece of coarse woody debris.

4.2.4. Sampling

If necessary, samples can be taken in sections of 5 cm. If more sample material is needed, check that the same horizons are still present. Samples should be carried in resistant bags (sharp pieces of wood can easily perforate flimsy bags). Various analyses can then be performed on the sampling material: pH (Campbell and Bryant, 1941), CHN measurements, colourimetry, etc. On a different spatial scale, the study of thin sections (especially at the interface between deadwood and the underlying substrate) could also give new insights into the dynamic processes (Tian et al., 1997). In the near future, these collected data could be used to better understand these atypical humus forms (see § *5. Conclusion and perspectives*).

4.2.5. Examples of freshly opened lignoform profiles

Figs. 3–6 show some examples of lignoform profiles made of CWD and ready to be described.

4.3. Diagnostic horizons

4.3.1. Woody horizons

Establishing definitions of the humus forms horizons linked to

Fig. 3. Lignoform profile, *Picea abies* (L.) Karst wood.

deadwood is a necessary first step for a better understanding and classification of these atypical humus forms, given that horizons are considered to be the basic functional units of humus forms (Gobat et al., 2010). The decay classes are assessed on the basis of the knife test, the texture and the colour of the deadwood (see Table 2). The threshold of 70% used below is inspired by the values currently used by the European humus forms classification (Jabiol et al., 2013; Zanella et al., 2011). The minimum thickness of any horizon is 3 mm, as previously defined for the 'classical' horizons of humus forms (Zanella et al., 2011). The capital letter W was chosen to refer to the woody horizons. To the best of our knowledge, this letter is not yet used by any of the existing humus forms and soil classification systems.

WL is an organic horizon made of ≥ 70% recognisable woody material (visual cover) not or slightly decomposed (decay class I or II) and almost non-fragmented. The presence of sap is possible.

WF is an organic horizon made of ≥ 70% decomposed woody material (decay class III or IV). This woody material is fragmented or

Fig. 4. Lignoform profile, *Picea abies* (L.) Karst wood.

Fig. 5. Lignoform profile, *Picea abies* (L.) Karst wood.

Fig. 6. Lignoform profile, *Picea abies* (L.) Karst wood.

can easily be fragmented by fingers.

WH is an organic horizon made of ≥ 70% very decomposed woody material (decay class V). The aspect of this material ranges from strongly fragmented to powdery and may still be coherent but can then be easily transformed into powder.

Figs. 7–14 show some examples of different W horizons.

Equivalence with Humusica 2, article 13 is: WL = ligOL; WF = ligOF; WH = ligOH.

4.3.2. Prefixes and suffixes

The prefix '**ω-**' can be added to a 'classical horizon'(OL, OF, OH, A, […]) if it contains 30–70% woody material. '**ω**' can also be used alone if the link with another horizon (OL, OF, OH, A, […]) cannot easily be made. This type of horizon is present most of the time at the interface between a surface WF or WH horizon and the underlying substrate. A lower-case omega 'ω' was chosen instead of 'w' in order to better distinguish it from the capital letter 'W'.

The prefix '**p-**' (for 'pure') can be added to a W horizon if it contains ≥ 90% woody material.

One of the specific features of lignoforms is the presence of W horizons that can possibly be half-buried and half-exposed to open air. If a W horizon is buried at ≥ 50%, it can be considered a **buried** W horizon. Conversely, if a W horizon is buried at < 50%, it can be considered a **surface** (or **unburied**) W horizon. This definition is inspired by the definition of buried wood proposed by Moroni et al. (2015). The suffix '-b' is added to indicate a buried W horizon. A W horizon without the '**-b**' suffix is considered a surface/unburied horizon. The suffix '**-su**' can nevertheless be added to clearly indicate a surface W horizon.

Other suffixes can also be added to characterise more precisely the W horizons. Table 3 summarises the most common among them, as well as the different woody horizons and the prefixes. These suffixes are

Fig. 7. pWL horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 8. pWL horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 9. pWF horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 10. pWF horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 11. WF horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 12. WF horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 13. WH horizon, *Picea abies* (L.) H. Karst. Wood.

Fig. 14. ω- horizon, *Picea abies* (L.) H. Karst. Wood.

Table 3
Woody horizons and their most commonly used prefixes and suffixes.

Categories	Meaning	
Horizons		
WL	organic horizon made of ≥ 70% recognisable woody material (visual cover) not or slightly decomposed (decay class I or II) and almost non-fragmented, possible presence of sap	
WF	organic horizon made of ≥ 70% decomposed woody material (decay class III or IV), woody material fragmented or easily fragmented by fingers	
WH	organic horizon made of ≥ 70% very decomposed woody material (decay class V), aspect of the woody material ranges from strongly fragmented to powdery, may still be coherent but can be easily transformed into powder	
Prefixes		
ω-	can be added to a 'classical horizon' (OL, OF, OH, A, […]) if it contains 30–70% woody material, can also be used alone if the link with another horizon (OL, OF, OH, A, […]) cannot easily be made, this type of horizon is present most of the time at the interface between a surface WF or WH horizon and the underlying substrate	
p-	pure	can be added to a W horizon if it contains ≥ 90% woody material
Suffixes		
-b	buried	W horizon buried at ≥ 50% (the remaining % are exposed to open air)
-c	indurated	indurated W horizon (but non-fossilised)
-cry	cryoturbated	structure of the W horizon clearly affected by cryoturbation
-hr	hemimineral	presence of fossilised indurated wood within the W horizon
-su	surface	W horizon exposed at > 50% to open air (the remaining% are buried)
-z	anthropic	woody material of the W horizon coming from old furniture, pieces of wood planks, sawdust, etc.

mainly inspired by AFES (2009).

If the woody material clearly shows different physicochemical compositions between two horizons (due to different wood species and/or to an anthropic action; e.g. stained or varnished wood), Roman numerals can be used to indicate a discontinuity within the woody material. For example: (I)WL/IIWL/IIWF/[…] (see also Figs. 22 and 25).

4.4. Lignoform classification

4.4.1. A brand new topic

Before trying to establish a system of classification for lignoforms, it is important to keep in mind the two following points: (i) very few studies have been undertaken into the relationships between humus forms and deadwood (Brais and Drouin, 2012; Green et al., 1993; Klinka et al., 1995, 1997; McFee and Stone, 1966; Strukelj et al., 2013), and (ii) the wood of each tree species may respond differently to various environmental variables (Weedon et al., 2009). For example, *Larix decidua* Mill. is usually considered to decompose more slowly than *Picea abies* (L.) H. Karst. (Hobbie et al., 2006), but a recent study showed a similarity in the chemical composition during the overall decomposition process for both species (Petrillo et al., 2015).

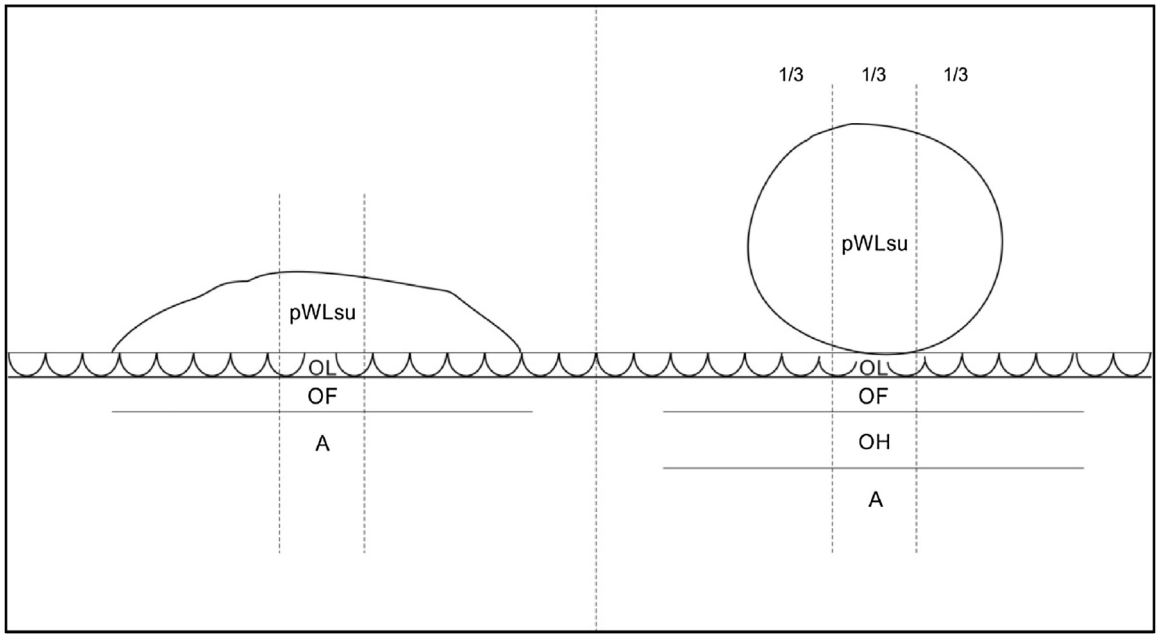
While waiting for more data and a stronger background, the system used for lignoform classification should therefore remain quite simple, but should nevertheless be as close as possible to ecological reality.

The classification of lignoforms is here mainly based on the buried W horizons. Such horizons are a priori more easily subject to horizontal transfers of material and energy with the surrounding environment than a surface W horizon. The system presented here is mainly based on the study of *Picea abies* wood.

Below we present some examples of humus forms with the presence of W horizons. These examples are summarised further in Table 4. Each description is followed by two figures (Figs. 15–28). These figures are not exhaustive but show different possible cases.

Table 4
Overview of the different humus forms linked to deadwood and their horizons.

Horizons	non-lignoform with a W horizon	epiceno	epihebe	epipresby	endodryo	endoglypho	endomalaco	bothrio
WLsu	and/or WLb	possible	possible	possible	possible	possible	possible	–
WFsu	–	and/or WHsu	if present, thickness > WHsu	and/or WHsu	possible	possible	possible	and/or WHsu, in tree cavities, etc.
WHsu	–	and/or WFsu	and/or WFsu	if present, thickness ≥ WHsu	possible	possible	possible	and/or WHsu, in tree cavities, etc.
ω-	possible	–	possible; interface between Wsu and underl. substrate	possible; interface between Wsu and underl. substrate	possible	possible	possible	–
WLb	and/or WLsu	possible	possible	possible	possible	possible	possible	–
WFb	–	–	–	–	present	present, thickness > WHb	and/or WHb	–
WHb	–	–	–	–	–	present	present, thickness ≥ WFb	–
transition between W and other horizons	sharp	sharp	progressive	progressive	(very) progressive	very progressive	very progressive	sharp to very progressive
previous O horizons	quite easily recognisable	quite easily recognisable	recognisable	recognisable	hardly to non-recognisable	non-recognisable	non-recognisable	–



Figs. 15 and 16. Schematic section of fine (left) and coarse (right) woody debris freshly arrived on an already existing humus form (left: Dysmull; right: Eumacroamphi).

These different types of lignoforms are intended to serve as a basis for the description and diagnosis of humus forms linked to deadwood. In complex situations (e.g. with superimposed lignoforms), the diagnosis of a lignoform should be made in the most logical way, depending on the context of the study (see also Humusica 2, article 13 for intergrades toward other humus systems).

4.4.2. Non-lignoform humus forms with a WLsu and/or WLb horizon

This is a humus form with the presence of a continuous WLsu and/or a WLb horizon and/or (more rarely) a 'ω-' horizon. Surface or buried WF and WH horizon are absent. The transition with the other horizons is sharp. The previous O horizons are still quite easily recognisable.

Such a humus form cannot be called a 'true' lignoform, but rather a humus form (e.g. a mesomull) with a WLsu or WLb horizon (see Figs. 15 and 16).

This situation is mainly related to woody material (i.e. WLp horizon) freshly arrived on an already existing humus form. In a general way, the presence of a buried WL horizon can also be mentioned in a lignoform description (for example, **Endodryo**(-lignoform) with a WLb horizon).

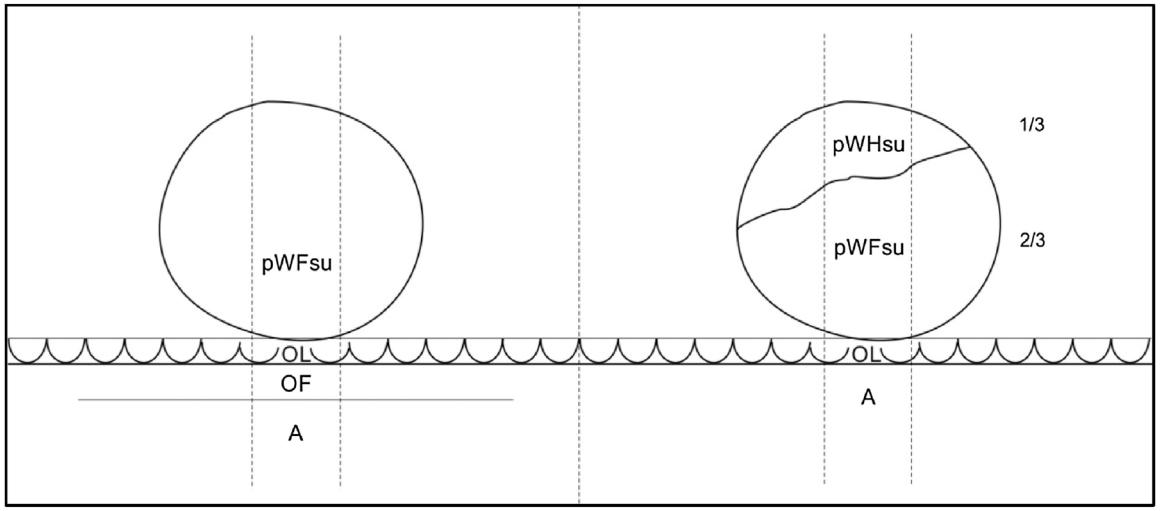
Woody material present in a WL horizon is not altered enough to significantly release components directly into the soil. That kind of horizon will essentially have a physical influence on the underlying substrate.

4.4.3. Distinction between lignoforms and other humus forms

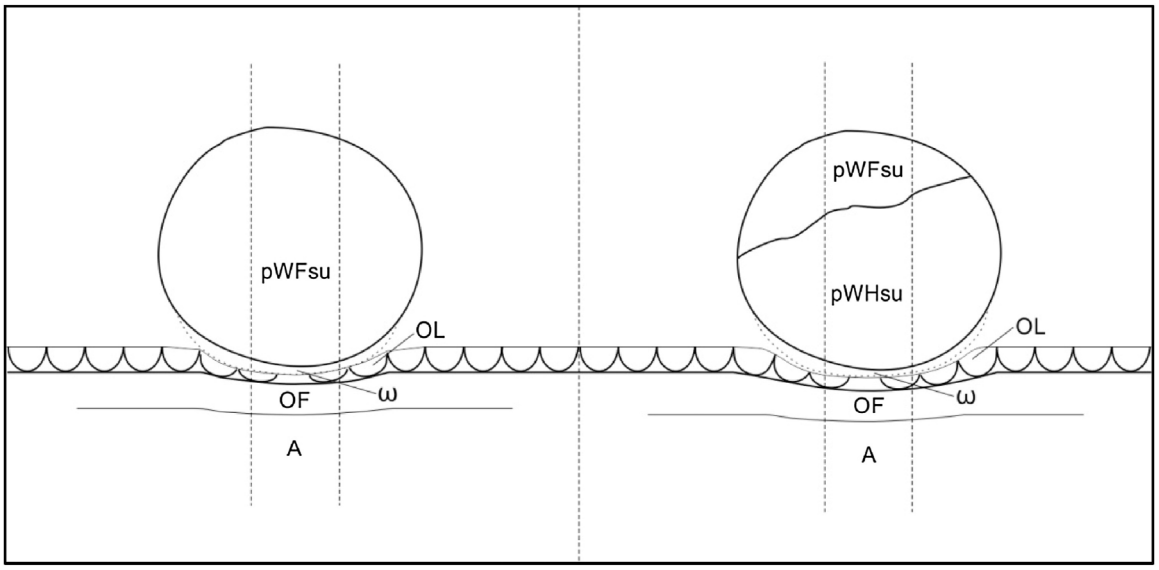
The distinction between a **lignoform** and another humus form can easily be made with the identification of at least a **WF** and/or **WH horizon**. Like the decay progress in such a horizon, various components can be released into the surrounding environment (under the effect of the precipitation, fauna, flora, etc.) (Russell et al., 2015). These components can induce strong modifications in the underlying substrate, which finally lead to the structuration and presence of new horizons (roughly defined as 'lignic forest floor' by Brais and Drouin (2012)), as well as the establishment of an adapted and specific flora and fauna (Bunnell and Houde, 2010; Van der Wal et al., 2013).

4.4.4. Lignoforms

Below are shown the 'true' lignoforms from some real cases observed in the field. These lignoforms are mainly organised according to



Figs. 17 and 18. Schematic sections of two different Epiceno-lignoforms made of coarse woody debris.



Figs. 19 and 20. Schematic sections of an Epihebe-lignoform (left) and an Epipresby-lignoform (right) made of coarse woody debris. A ω horizon is present, acting as a transition between the pWFsu horizon and the underlying (compacted) holorganic horizons.

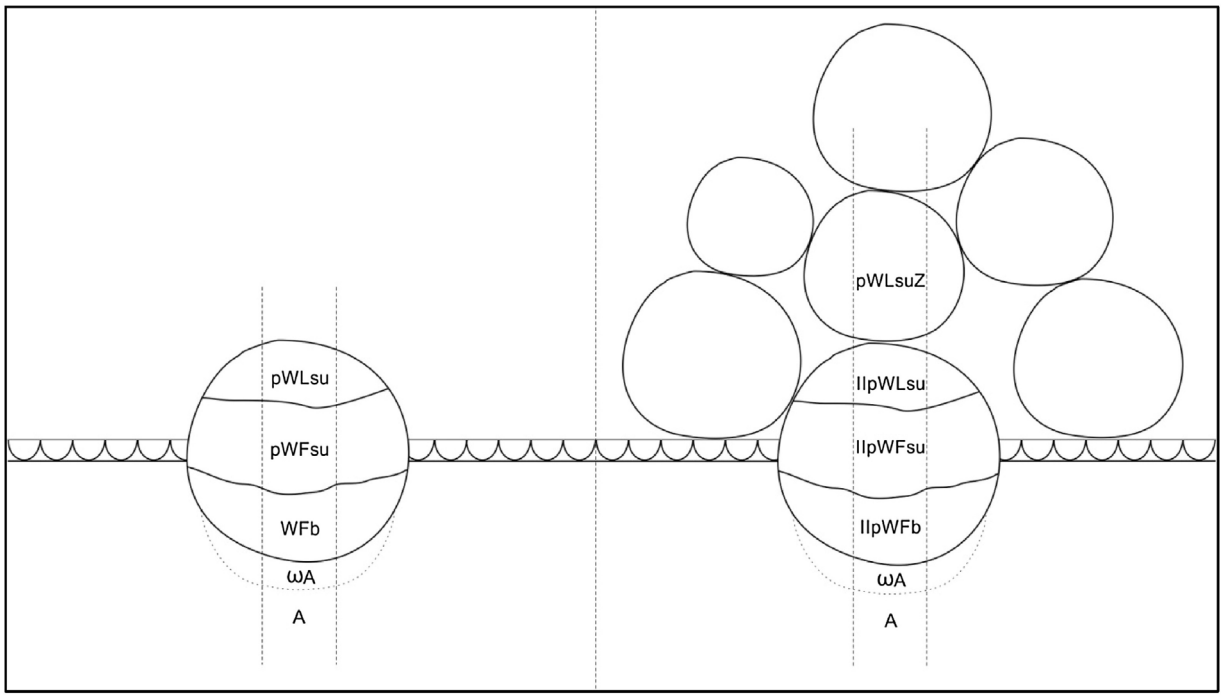
the position of the woody horizons (buried or surface horizons), as well as the presence of and the ratio between the WF and WH horizons.

4.4.4.1. Epiceno(lignoform). This is a humus form with at least a WFsu and/or WHsu horizon and without a buried W horizon. There is a clear and sharp transition between the W horizon and the other horizons and an absence of a 'ω-' horizon at the interface between W horizon and the underlying substrate. The previous O horizons are still quite easily recognisable (see Figs. 17 and 18).

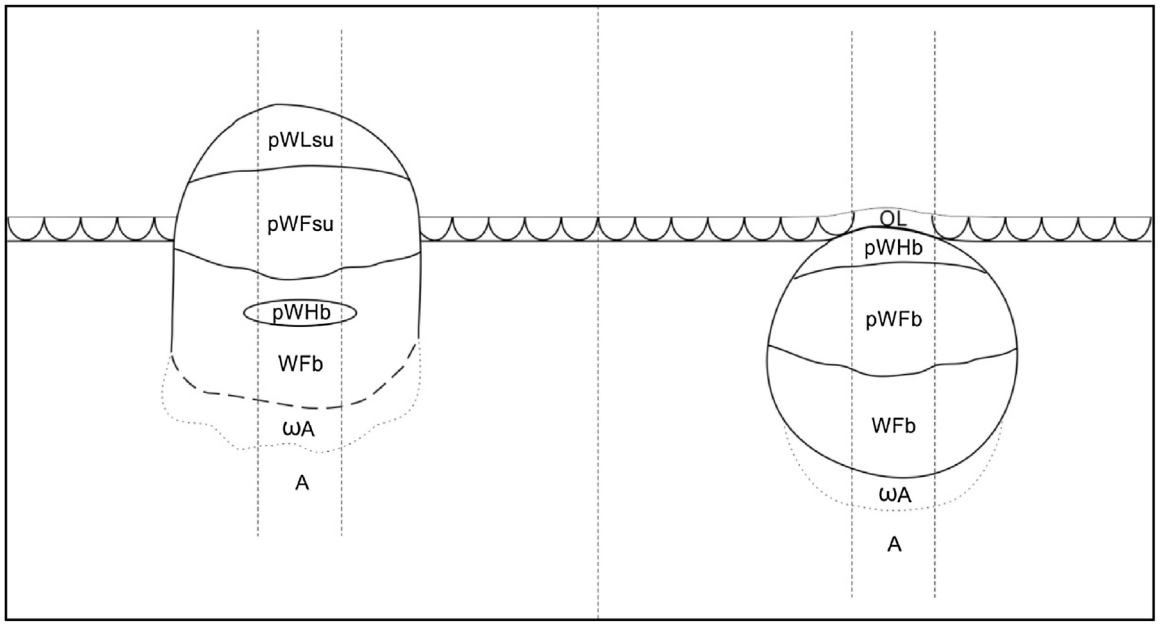
This situation is mainly linked to the arrival of some already decomposed woody material on a new substrate. The absence of 'w' horizon at the transition between the woody material and the underlying substrate, as well as the sharp transition with the other horizons, are indicative of the ex situ degradation of the woody material, which was moved afterwards.

By the special and specific physicochemical composition of wood, a single altered W horizon (WF and/or WH) is already enough to strongly influence the soil and the humus form features and to encourage it progressively in the direction of lignoforms.

4.4.4.2. Epihebe and epipresby(-lignoform). This is a humus form with at least a WFsu and/or WHsu horizon and without a buried W horizon. The transition between the W horizon and the other horizons is not as clear and sharp as in **Epiceno**(-lignoform). The presence of a 'ω-' horizon is located most of the time at the interface between the W horizon(s) and the underlying horizons. The absence of a 'ω' horizon is possible, but in such a case, the transition between WFsu or WHsu and the underlying substrate is progressive (not as sharp as in **Epiceno**



Figs. 21 and 22. Schematic sections of two different Endodryo-lignoforms made of coarse woody debris. The right one presents an accumulation of anthropic woody material, creating thus a discontinuity with the underlying type of wood (signalled here by the Roman numeral 'II').



Figs. 23 and 24. Schematic sections of two different Endoglypho-lignoforms. The left one originates mostly from fine woody debris, the right one is almost completely hidden by the arrival of fresh litter.

(-lignoform)). The previous O horizons are still recognisable but not as easily as in **Epiceno**(-lignoform) (see Figs. 19 and 20).

If the cumulated thickness of WHsu horizon ≥ WFsu, the lignoform is called **Epipresby**(-lignoform).

The surface W horizons begin here to be enough altered in situ (in most cases) to establish a true connection between themselves and the underlying substrate (through the presence of a ω horizon). This facilitates the potential exchanges and movements of organisms between these two compartments (Bunnell and Houde, 2010).

Epihebe(-lignoform) is often linked to a mainly in situ degradation of the woody material, whereas **Epipresby**(-lignoform) corresponds rather to the following of the woody material decay, probably strongly decayed ex situ before its arrival on a new substrate.

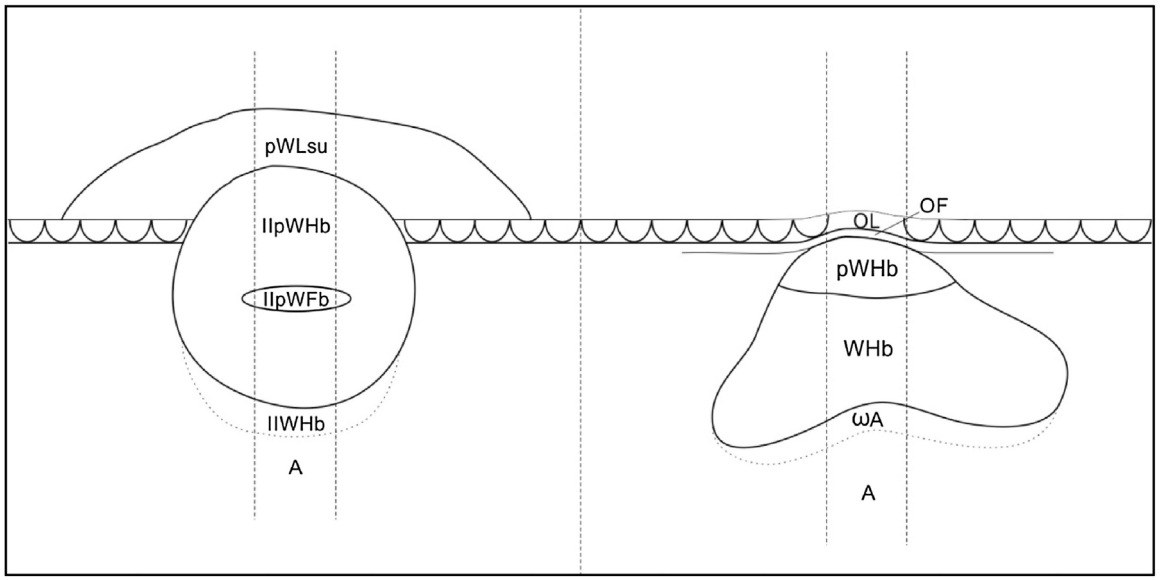
Due to its surface-to-volume ratio and a generally quite low cohesion, a WHsu horizon tends to be more easily leached than a WFsu horizon and may thus influence its surrounding environment more strongly.

4.4.4.3. Endodryo(-lignoform). This is a humus form with the presence of at least one WFb horizon and the absence of a WHb horizon.

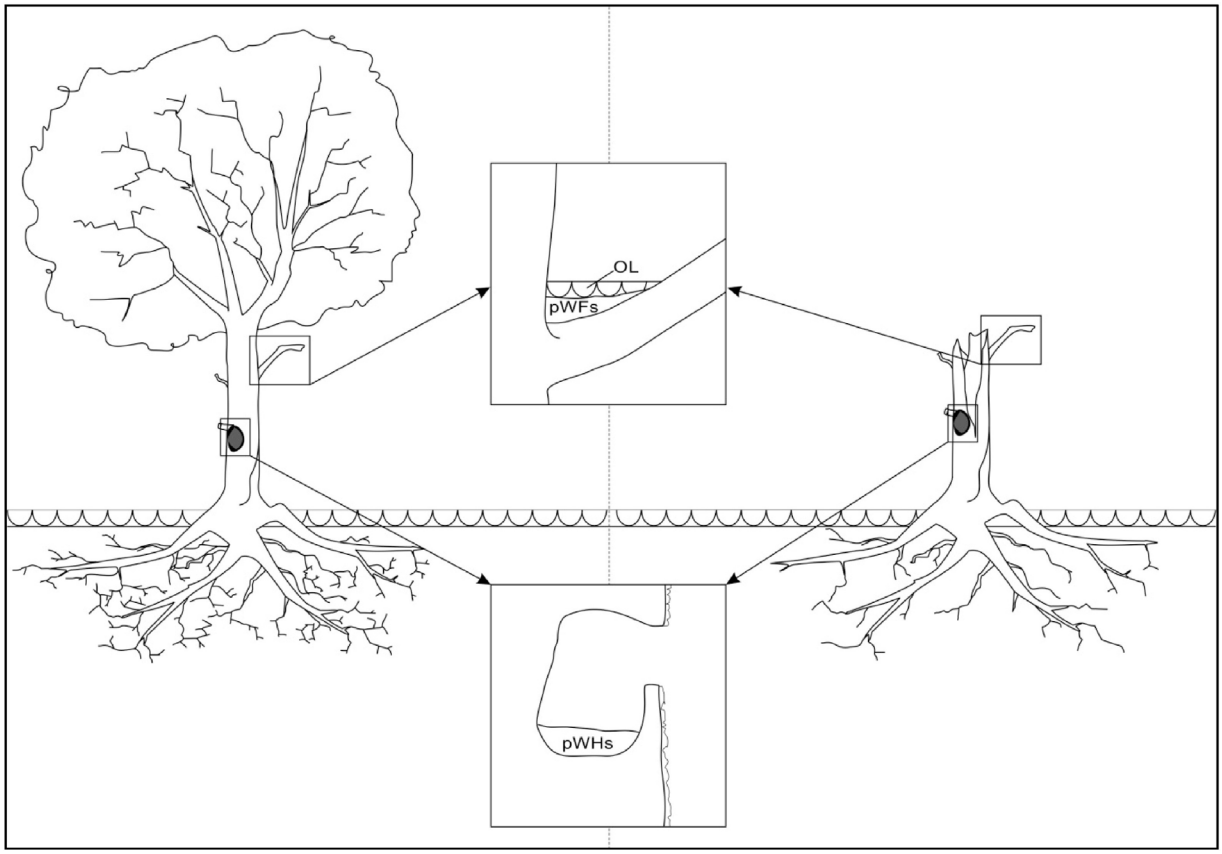
While the characteristic feature of these types of lignoforms is the presence of a buried woody horizon, they could nonetheless have some quite thick surface woody horizons. As this system of classification is mainly based on buried horizons, such surface horizons are not always useful for naming humus forms but they can, however, be noted during the description. Depending on the context of the study, the attribution of a 'double name' to a single lignoform may also be considered (see Figs. 21 and 22).

Although this humus form and **Endoglypho** and **Endomalaco** (-lignoforms) could be linked to a sudden burial of woody material, they are more likely to be the result of a progressive incorporation of woody material under the effect of various factors (see § *3.1.2 Influencing factors*).

Even if all these lignoforms have buried woody horizons, they



Figs. 25 and 26. Schematic sections of two different Endomalaco-lignoforms. The left one originates from coarse woody debris and is covered by the arrival of fresh new material (a discontinuity between these two different types of wood is shown by the Roman numeral 'II'). The right one originates from coarse woody debris and a new OL and OF horizon are already developing on it.



Figs. 27 and 28. Schematic section of two different Bothrio-lignoforms and their position in a living (left) and dying (right) tree. They are located in the hollow of a branch and in the cavity of a tree dug by an animal.

probably have distinct but complementary ecosystemic roles, especially regarding specific flora and fauna, soil quality or even more roles in the carbon cycle (see § *3.2 Roles of deadwood in ecosystems*).

4.4.4.4. Endoglypho(-lignoform). This is a humus form with the presence of continuous WFb and WHb horizons. The thickness of the WFb horizon (or cumulated thicknesses, if several WFb horizons) is greater than the thickness of WHb horizon(s) (see Figs. 23 and 24).

4.4.4.5. Endomalaco(-lignoform). This is a humus form with the presence of at least one WHb horizon. If one or more WFb horizons are also present, the thickness of the WHb horizon (or cumulated thicknesses of WHb horizons) is greater than or equal to the thickness of the WFb horizon(s) (see Figs. 25 and 26).

4.4.4.6. Bothrio(-lignoform). This is a humus form with WFsu and/or WHsu horizons linked to cavities in a living tree or other snag (and thus distinct from **Epiceno**, **Epihebe** and **Epipresby**(-lignoforms)) and clearly delimited in space. Such humus forms are generally located higher than breast height (130 cm) (see Figs. 27 and 28).

Due to its special and protected position, such a lignoform is likely to host very specific flora and fauna (vertebrates and invertebrates), (see e.g. Aubert de La Rüe et al., 1954; Lindo and Winchester, 2007). This type of humus form could be easily related to the concept of suspended soils discussed for example by Paulian (1988) or Gobat et al. (2010).

4.4.5. Overview of the different humus forms linked to deadwood

Table 4 summarises the different humus forms linked to deadwood and their horizons.

Although this information may reflect what is most of the time found in the field, many cases may differ considerably (e.g. buried woody material resulting from a fall from an elevated situation, from a landslide. etc.).

5. Conclusion and prospects

Deadwood has already been the subject of many studies, but these studies have rarely also taken the humiferous topsoil into account (see § *1. Introduction*). Therefore, the way in which deadwood is considered here – i.e. linked to humus forms and more especially to lignoforms – **opens a door to a quite unique field of research**.

Although more data are needed to better understand the spatio-temporal dynamics of lignoforms, the classification established here may be seen as quite universal from a static (non-dynamic) point of view. We believe that this classification provides a valuable and valid tool, particularly since (i) it **can easily be integrated to the already existing habits of pedologists** (horizons, prefixes and suffixes, etc.), (ii) the description performed in the field is self-sufficient but can nevertheless (iii) be complemented by laboratory analyses, and (iv) this system can be considered **universal, since it can be applied and adapted to all cases encountered in the field**. Applying this methodology and classification will initiate a better understanding of these atypical humus forms and their dynamics. Better knowledge of lignoforms will gradually lead to being able to place them in a broad and complex ecosystemic context. This will help **to protect lignoforms and their various ecosystemic services, especially those linked to the carbon cycle**.

As they are fairly recent, the various concepts set out here need to be complemented and clarified with new data acquired through observations and experiments in the field. Here are some research questions, grouped by main topics, the answers to which could prove very informative:

5.1. Time-related processes

- What are the dynamics in space and time (at different scales) of the different humus forms linked to deadwood?
- Is it possible to link different residence times with different types of lignoforms? Such knowledge could be acquired for example by following different CWD from their arrival on an already existing humus form to the establishment of a lignoform, with the progressive incorporation of the woody material into the soil (diachronic approach).

5.2. Environmental factors

- Are there main pathways concerning the creation and evolution of lignoforms? For example, depending on the substrate (e.g. calcareous versus siliceous), on the type of tree (e.g. in temperate climate: hardwood versus coniferous softwood) or on the hardness of the wood?
- To what extent can an already existing humus form influence the establishment and evolution of a lignoform when new woody material arrives?
- What really are the effects of the various environmental factors mentioned in § *3.1.2* (*Influencing factors*) on the creation and evolution of lignoforms?

5.3. Applications and limitations

- What is the role of these different lignoforms in the carbon cycle in terrestrial ecosystems? Do the quantities of carbon stocked in the soil change significantly depending on the tree species, the type of lignoform, etc.?
- With a view to using lignoforms in conservation and other biodiversity monitoring projects: What are the specific flora and fauna linked to each different lignoform?.
- How to deal with 'limit cases'? For example, lignoforms in terrestrial wet places, with the arrival of deadwood on peat, charcoal, etc.

Another point not really considered here is the well-known visible characteristic of the decay structures of deadwood caused by fungi. They are generally distinguished in three types: white rot, brown rot and soft rot (Baldrian, 2008; Kubicek, 2013; Kuhad and Singh, 2013). Only white and brown rot are of great interest for their capacity to deeply decompose deadwood from the sapwood to the heartwood (Van der Wal et al., 2013). These two structures are quite easily recognisable, from bleached, spongy fibres (white rot, affecting mainly hardwood species) to brown, brittle, cube-shaped or powdery pieces of wood (brown rot, affecting mainly softwood species) (Kubicek, 2013). Furthermore, a recent study highlighted a simple method to confirm the presence or absence of these structures, using dilute alkali solubility (DAS) and mass loss measurements (Schilling et al., 2015). Considering the predominant importance of fungi in wood decomposition (Boddy et al., 2008; Cornwell et al., 2009), taking into account these structures as proxies for a type of biotic decomposition process could greatly improve the description of lignoform horizons.

Much **data are needed to provide answers to these questions and to optimise the lignoform classification system**. To this end, the creation of a database would be appropriate. In addition to the macroscopic features observed in the field, this database could also include elements such as the pH of the different horizons, CHN contents, colorimetric data, isotope measurements, images, results of thin sections, etc.

For more information, please see the website of the DACH-DecAlp project: http://www.decalp.org/

Acknowledgements

This research was supported by the Swiss National Science Foundation, DACH-Program, number 205321L_141186. The authors thank all their DecAlp colleagues as well as Elizabeth Steele, Stéphane Burgos, Liv Kellermann, Augusto Zanella, Radu Slobodeanu, Estelle Brüni, Léo Bürgi, Lucie Darbellay, Delphine Desvenoges, Bogdan Favre, Aline Rubeli, Olivia Rusconi, Virginie Trieu and the Stelvio National Park for supporting their fieldwork.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2017.06.037.

References

Ódor, P., van Hees, A.F.M., 2004. Preferences of dead wood inhabiting bryophytes for decay stage, log size and habitat types in Hungarian beech forests. J. Bryol. 26, 79–95.
AFES (Association française pour l'étude du sol) 2009. Référentiel pédologique 2008. Quae, Versailles, http://www.afes.fr/afes/docs/Referentiel_Pedologique_2008.pdf.
Agee, J.K., Huff, M.H., 1987. Fuel succession in a western hemlock douglas-Fir forest. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 17, 697–704.
Ammer, U., 1991. Konsequenzen aus den Ergebnissen der Totholzforschung flit die forstliche Praxis. Forstwissenschaftliches Centralblatt 110, 149–157.
Arno, S.F., 2000. Fire regimes in western forest ecosystems. In: Brown, J.K., Smith, J.K. (Eds.), Wildland Fire in Ecosystems: Effects of Fire on Flora. USDA Forest Service General Technical Report RMRS-42, Ogden, pp. 97–120.
Aubert de La Rüe, E., Bourlière, F., Harroy, J.P., 1954. Tropiques. Horizons de France, Paris.
Bütler, R., Angelstam, P., Ekelund, P., Schlaeffer, R., 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biol. Conserv. 119, 305–318.
Baldrian, P., 2008. Enzymes of saprotrophic basidiomycetes. In: Boddy, L., Frankland, J.C., van West, P. (Eds.), Ecology of Saprotrophic Basidiomycetes. Academic Press, London, pp. 19–41.
Barnum, S.A., Manville, C.J., Tester, J.R., Carmen, W.J., 1992. Path selection by peromyscus-Leucopus in the presence and absence of vegetative cover. J. Mammal. 73, 797–801.
Beatty, S.W., Stone, E.L., 1986. The variety of soil microsites created by tree falls. Can. J. For. Res.-Revue Canadienne De Recherche Forestière. 16, 539–548.
Berg, B., McClaugherty, C., 2014. Plant Litter Decomposition, Humus Formation, Carbon Sequestration. Springer, Heidelberg.
Berg, B., Berg, M., Flower-Ellis, J., Gallardo, A., Johansson, M., Lundmar, J.E., Madeira, M., 1993. Amounts of litterfall in some European coniferous forests. In: Breymeyer, A. (Ed.), Proceedings of SCOPE Seminar. Conference Paper 18. Geography of Carbon Budget Processes in Terrestrial Ecosystems. Szymbark, 17–23 August 1991. pp. 123–146.
Bocock, K.L., Gilbert, O., Capstick, C.K., Twinn, D.C., Waid, J.S., Woodman, M.J., 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types 1. losses in dry weight of oak and ash leaf litter. J. Soil Sci. 11, 1–9.
Boddy, L., Frankland, J.C., van West, P., 2008. Ecology of Saprotrophic Basidiomycetes. Academic Press, London.
Bolton, N.W., D'Amato, A.W., 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota. USA For. Ecol. Manage. 262, 1215–1222.
Inventaire forestier national suisse. Résultats du troisième inventaire 2004–2006. In: Brändli, U.B. (Ed.), Birmensdorf, Institut fédéral de recherches sur la forêt, la neige et le paysage WSL. Office fédéral de l'environnement OFEV, Berne.
Brais, S., Drouin, P., 2012. Interactions between deadwood and soil characteristics in a natural boreal trembling aspen − jack pine stand. Can. J. For. Res.-Revue Canadienne De Recherche Forestière. 42, 1456–1466.
Brown, J.K., 1974. Handbook for Inventorying Downed Woody Material. USDA Forest Service General Technical Report INT-16, Ogden.
Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and Logs Important to Wildlife in the Interior Columbia River Basin. USDA Forest Service General Technical Report PNW-391, Portland.
Bunnell, F.L., Houde, I., 2010. Down wood and biodiversity −implications to forest practices. Environ. Rev. 18, 397–421.
Campbell, W.G., Bryant, S.A., 1941. Determination of pH in wood. Nature 147, 357 (357).
Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-Growth forests. Ecol. Appl. 5, 336–352.
Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? Glob. Change Biol. 15, 2431–2449.
Cotrufo, M.F., Conant, R.T., Paustian, K., 2011. Soil organic matter dynamics: land use, management and global change. Plant Soil 338, 1–3.
Delamare-Debouteville, C., 1951. Microfaune du sol des pays tempérés et tropicaux. Hermann, Paris.
Dwyer, L.M., Merriam, G., 1981. Influence of topographic heterogeneity on deciduous litter decomposition. Oikos 37, 228–237.
Elton, C.S., Miller, R.S., 1954. The ecological survey of animal communities − with a practical system of classifying habitats by structural characters. J. Ecol. 42, 460–496.

Elton, C.S., 1966. Dying and dead wood. The Pattern of Animal Communities. Methuen, London, pp. 279–305.
Federici, S., Tubiello, F.N., Salvatore, M., Jacobs, H., Schmidhuber, J., MacDicken, K., 2015. New estimates of CO2 forest emissions and removals: 1990–2015. For. Ecol. Manage. 352, 89–98.
Fogel, R., Ogawa, M., Trappe, J.M., 1973. Terrestrial Decomposition: a Synopsis. USIBP Coniferous Forest Biome Internal Report 135. University of Washington, Seattle.
Gilbert, O., Bocock, K.L., 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types II. changes in the nitrogen content of oak and ash leaf litter. J. Soil Sci. 11, 10–19.
Gobat, J.M., Aragno, M., Matthey, W., 2010. Le sol vivant: bases de pédologie. biologie des sols Presses polytechniques et universitaires romandes, Lausanne.
Goodburn, J.M., Lorimer, C.G., 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 28, 427–438.
Graham, S.A., 1925. The felled tree trunk as an ecological unit. Ecology 6, 397–411.
Green, R.N., Trowbridge, R.L., Klinka, K., 1993. Towards a taxonomic classification of humus forms. For. Sci. 39, 1–48.
Harmon, M.E., Sexton, J., 1996. Guidelines for Measurement of Woody Detritus in Forest Ecosystems. US Long Term Ecological Research Network, Albuquerque.
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. Adv. Ecol. Res. 15, 133–302.
Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., 2008. Woody Detritus Density and Density Reduction Factors for Tree Species in the United States: a Synthesis. Forest Service General Technical Report NRS-29, Newton Square.
Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., Yatkov, M., 2011. Differences Between Standing and Downed Dead Tree Wood Density Reduction Factors: A Comparison Across Decay Classes and Tree Species. USDA Forest Service Research Paper NRS-15, Newton Square.
Harvey, A.E., Larsen, M.J., Jurgensen, M.F., 1979. Comparative distribution of ectomycorrhizae in soils of 3 western montana forest habitat types. For. Sci. 25, 350–358.
Hendrickson, O.Q., 1991. Abundance and activity of N2-Fixing bacteria in decaying wood. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 21, 1299–1304.
Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288–2297.
Howard, D.M., Howard, P.J.A., 1980. Microbial decomposition of tree and shrub leaf litter 3. effect of species, source of litter, type of soil, and climate on litter decomposition. Oikos 34, 115–124.
Jabiol, B., Zanella, A., Ponge, J.F., Sartori, G., Englisch, M., van Delft, B., de Waal, R., Le Bayon, R.C., 2013. A proposal for including humus forms in the World Reference Base for Soil Resources (WRB-FAO). Geoderma 192, 286–294.
Jenny, H., 1941. Factors of Soil Formation, a System of Quantitative Pedology. McGraw-Hill, New York.
Jenny, H., 1980. The Soil Resource: Origin and Behavior. Springer, New York, Heidelberg.
Schweizerisches Landesforstinventar. Anleitung für die Feldaufnahmen der Erhebung 2004–2007. In: Keller, M. (Ed.), Eidgenössische Forschungsanstalt WSL, Birmensdorf.
Kirby, K.J., Webster, S.D., Antczack, A., 1991. Effects of forest management on stand structure and quality of fallen dead wood: some British and Polish examples. For. Ecol. Manage. 43, 167–174.
Klinka, K., Lavkulich, L.M., Wang, Q., Feller, M.C., 1995. Influence of decaying wood on chemical-Properties of forest floors and surface mineral soils −a pilot-Study. Annales Des Sciences Forestières 52, 523–533.
Klinka, K., Krestov, P., Fons, J., Choumouzis, C., 1997. Towards a Taxonomic Classification of Humus Forms: Third Approximation Scientia Silvica, Extension Series, 9.
Kubicek, C.P., 2013. Fungi and Lignocellulosic Biomass. Wiley-Blackwell, Ames.
Kuhad, R.C., Singh, A. (Eds.), 2013. Biotechnology for Environmental Management and Resource Recovery. Springer, New Delhi, pp. 3–44.
Kunttu, P., Junninen, K., Kouki, J., 2015. Dead wood as an indicator of forest naturalness: a comparison of methods. For. Ecol. Manage. 353, 30–40.
Lachat, T., Brang, P., Bolliger, M., Bollmann, K., Brändli, U.B., Bütler, R., Herrmann, S., Schneider, O., Wermelinger, B., 2014. Bois mort en forêt −Formation, importance et conservation. Institut fédéral de recherche WSL Notice pour le praticien n°52, 12.
Larsen, M.J., Jurgensen, M.F., Harvey, A.E., 1978. N2 fixation associated with wood decayed by some common fungi in western montana. Can. J. Fo. Res.-Revue Canadienne De Recherche Forestière 8, 341–345.
Lindo, Z., Winchester, N.N., 2007. Oribatid mite communities and foliar litter decomposition in canopy suspended soils and forest floor habitats of western redcedar forests Vancouver Island, Canada. Soil Bio. Biochem. 39, 2957–2966.
Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 129, 981–992.
MCPFE (Ministerial Conference on the Protection of Forests in Europe) (Ed.), 2007. State of Europe's Forests 2007. The MCPFE Report on Sustainable Forest Management in Europe. MCPFE Liaison Unit, Warsaw.
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, 27–37.
Malmsheimer, R.W., Bowyer, J.L., Fried, J.S., Gee, E., Izlar, R.L., Miner, R.A., Munn, I.A., Oneil, E., Stewart, W.C., 2011. Managing forests because carbon matters integrating energy, products, and land management policy. J. For. 109, 7–48.
The Seen and Unseen World of the Fallen Tree. In: Maser, C., Trappe, J.M. (Eds.), USDA Forest Service General Technical Report PNW-164, Portland.
Maser, C., Anderson, R., Cromack, K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests, the Blue Mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook 553, pp. 79–85 (Portland).
Matzek, V., Vitousek, P., 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forest. Biotropica 35, 12–19.
McClellan, M.H., Bormann, B.T., Cromack, K., 1990. Cellulose decomposition in southeast alaskan forests − effects of pit and mound microrelief and burial depth. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 20, 1242–1246.
McFee, W.W., Stone, E.L., 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Sci. Soc. Am. J. 30, 513–516.
Melin, Y., Petersson, H., Nordfjell, T., 2009. Decomposition of stump and root systems of Norway spruce in Sweden-A modelling approach. For. Ecol. Manage. 257, 1445–1451.
Moroni, M.T., Morris, D.M., Shaw, C., Stokland, J.N., Harmon, M.E., Fenton, N.J., Merganicova, K., Merganic, J., Okabe, K., Hagemann, U., 2015. Buried wood: a common yet poorly documented form of deadwood. Ecosystems 18, 605–628.
Paulian, R., 1988. Biologie des Coléoptères. Lechevalier, Paris.
Petrillo, M., Cherubini, P., Sartori, G., Abiven, S., Ascher, J., Bertoldi, D., Camin, F., Barbero, A., Larcher, R., Egli, M., 2015. Decomposition of Norway spruce and European larch coarse woody debris (CWD) in relation to different elevation and exposure in an Alpine setting. iForest 9, 154–164. http://dx.doi.org/10.3832/ifor1591-008.
Preston, C.M., Sollins, P., Sayer, B.G., 1990. Changes in organic-Components for fallen logs in old-Growth douglas-Fir forests monitored by C-13 nuclear-Magnetic-Resonance spectroscopy. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 20, 1382–1391.
Pyle, C., Brown, M.M., 1998. A rapid system of decay classification for hardwood logs of the eastern deciduous forest floor. J. Torrey Bot. Soc. 125, 237–245.
Rondeux, J., Sanchez, C., 2010. Review of indicators and field methods for monitoring biodiversity within national forest inventories Core variable: deadwood. Environ. Monit. Assess. 164, 617–630.
Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., Skog, K.E., 2014. Residence times and decay rates of downed woody debris Biomass/Carbon in eastern US forests. Ecosystems 17, 765–777.
Russell, M.B., Fraver, S., Aakala, T., Gove, J.H., Woodall, C.W., D'Amato, A.W., Ducey, M.J., 2015. Quantifying carbon stores and decomposition in dead wood: a review. For. Ecol. Manage. 350, 107–128.
Sathre, R., Gustavsson, L., 2011. Time-dependent climate benefits of using forest residues to substitute fossil fuels. Biomass Bioenergy 35, 2506–2516.
Savely, H.E.J., 1939. Ecological relations of certain animals in dead pine and oak logs. Ecol. Monographs 9, 322–385.
Schiegg Pasinelli, K., Suter, W., 2000. Le bois mort −un habitat. Institut fédéral de recherche WSL (Notice pour le praticien n°33).
Schilling, J.S., Kaffenberger, J.T., Liew, F.J., Song, Z.W., 2015. Signature wood modifications reveal decomposer community history. PLoS One 10, e0120679.
Sharitz, R.R., 1996. Coarse woody debris and woodly seedling recruitment in southeastern forests. In: McMinn, J.W., Crossley, D.A. Jr. (Eds.), Biodiversity and Coarse Woody Debris in Southern Forests. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service General Technical Report SE-94. Asheville. pp. 29–34.
Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.
Smith, J.E., Heath, L.S., Hoover, C.M., 2013. Carbon factors and models for forest carbon estimates for the 2005–2011 National Greenhouse Gas Inventories of the United States. For. Ecol. Manage. 307, 7–19.
Soil Classification Working Group, 1998. The Canadian System of Soil Classification, third ed. NRC Research Press, Ottawa.
Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge.
Strukelj, M., Brais, S., Quideau, S.A., Angers, V.A., Kebli, H., Drapeau, P., Oh, S.W., 2013. Chemical transformations in downed logs and snags of mixed boreal species during decomposition. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 43, 785–798.
Tian, X.J., Takeda, H., Ando, T., 1997. Application of a rapid thin section method for observations on decomposing litter in mor humus form in a subalpine coniferous forest. Ecol. Res. 12, 289–300.
Ulyshen, M.D., 2014. Wood Decomposition as Influenced by Invertebrates. Biological Reviews of the Cambridge Philosophical Society.
Van der Wal, A., Geydan, T.D., Kuyper, T.W., de Boer, W., 2013. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. FEMS Microbiol. Rev. 37, 477–494.
Waddell, K.L., 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecol. Indic. 1, 139–153.
Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol. Lett. 12, 45–56.
Woodall, C.W., Monleon, V.J., 2008. Sampling Protocol, Estimation, and Analysis Procedures for the Down Woody Materials Indicators of the FIA Program. USDA Forest Service General Technical Report NRS-22, Newtown Square.
Woodall, C.W., Nagel, L.M., 2006. Coarse woody type: a new method for analyzing coarse woody debris and forest change. For. Ecol. Manage. 227, 115–121.
Yin, X.W., 1999. The decay of forest woody debris: numerical modelling and implications based on some 300 data cases from North America. Oecologia 121, 81–98.
Zanella, A., Jabiol, B., Ponge, J.F., Sartori, G., de Waal van Delft, B., Graefe, U., Cools, N., Katzensteiner, K., Hager, H., Englisch, M., 2011. A European morpho-functional classification of humus forms. Geoderma 164, 138–145.
Zell, J., Kandler, G., Hanewinkel, M., 2009. Predicting constant decay rates of coarse woody debris-A meta-analysis approach with a mixed model. Ecol. Modell. 220, 904–912.
Zhang, Q., Liang, Y., 1995. Effects of gap size on nutrient release from plant litter decomposition in a natural forest ecosystem. Can. J. For. Res.-Revue Canadienne De Recherche Forestière 25, 1627–1638.
Zielonka, T., Piatek, G., 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra Mountains. Plant Ecol. 172, 63–72.