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Controls on Coarse Wood Decay in Temperate Tree Species: Birth of the LOGLIFE Experiment

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Abstract Dead wood provides a huge terrestrial carbon stock and a habitat to wide-ranging organisms during its decay. Our brief review highlights that, in order to understand environmental change impacts on these functions, we need to quantify the contributions of different interacting biotic and abiotic drivers to wood decomposition. LOGLIFE is a new long-term 'common-garden' experiment to disentangle the effects of species' wood traits and site-related environmental drivers on wood decomposition dynamics and its associated diversity of microbial and invertebrate communities. This experiment is firmly rooted in pioneering experiments under the directorship of Terry Callaghan at Abisko Research Station, Sweden. LOGLIFE features two contrasting forest sites in the Netherlands, each hosting a similar set of coarse logs and branches of 10 tree species. LOGLIFE welcomes other researchers to test further questions concerning coarse wood decay that will also help to optimise forest management in view of carbon sequestration and biodiversity conservation.

Keywords Coarse woody debris · Wood decomposition · Forest · Functional trait · Fungi · Invertebrates

INTRODUCTION

Dead wood plays several paramount roles from local to global scale (Harmon et al. 1986; Cornwell et al. 2009; Wirth et al. 2009; Yin 1999). It is an important component of global biogeochemistry, including nitrogen (N) and phosphorus (P) cycling (e.g. Lindahl et al. 2002; Laiho and Prescott 2004). Most importantly, it represents a substantial, dynamic carbon stock that is generally more resistant to decomposition than other plant litter (Taylor et al. 1991; Cadisch and Giller 1997; Harmon 2009; Freschet et al. 2012a). Accumulation of dead wood on the forest floor can also serve as fuel for fire, which can release massive amounts of carbon to the atmosphere pulse-wise. Both decomposition and fire are major determinants of CO_2 release from the earth surface over decadal time scales (Sitch et al. 2003; Brovkin et al. 2012), with possible implications for global temperature regimes. Apart from its importance for biogeochemical cycling, dead wood in the forest is also a great source of biodiversity (Harmon et al. 1986; Jonsson and Jonsson 2007; Wirth et al. 2009). Northern forests in cool and cold biomes, for instance, support a wealth of wood-rot fungi (Odor et al. 2006; Schmidt 2006; Hottola et al. 2009), vertebrates (Bunnell and Houde 2010), diverse taxa of invertebrates (Grosser 1985; Grove 2002; Castro and Wise 2010; Dechene and Buddle 2010; Janssen et al. 2011; Ulyshen et al. 2011), lichens (Humphrey et al. 2002) and bryophytes (Andersson and Hytteborn 1991; Humphrey et al. 2002). Bacteria are among the first organisms to colonise dead wood and metabolise especially the easily degradable and accessible substrates (Schmidt 2006; De Boer and Van der Wal 2008).

Coarse wood decomposition in temperate and boreal forests has been relatively well studied over several decades (e.g. Harmon et al. 1986; Yin 1999, Harmon 2009). However, we still know little about the relative contributions of the different drivers of wood decomposition rate and dynamics in forest ecosystems (Fig. 1), let alone about recalcitrant soil organic matter formation associated with coarse wood (Harmon 2009). Wood decomposition rate and dynamics, like for other types of litter, are virtually entirely determined by the interactions between (1) wood

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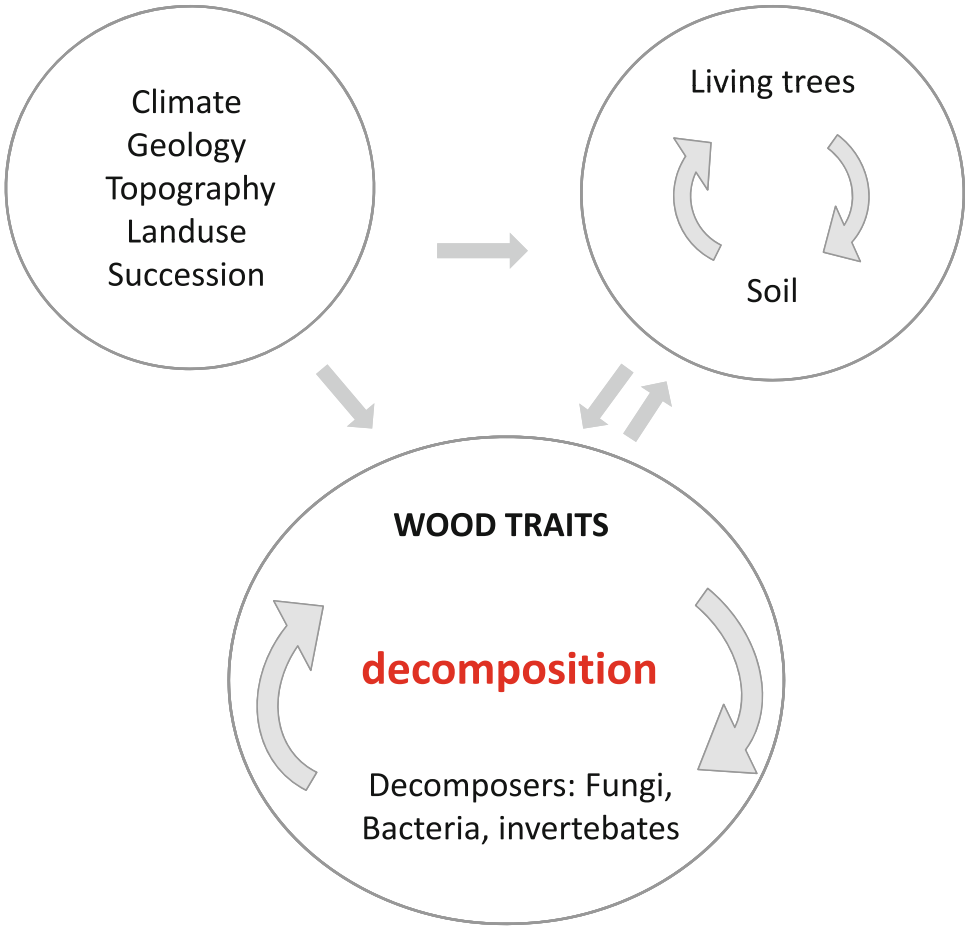

Fig. 1 Drivers of wood decomposition. Wood decomposition is the outcome of multiple interactions between decomposer communities (composition, abundance, activity) and the substrate (structure, chemistry). These interactions largely depend on top–down control from abiotic and biotic factors whose interactions determine the local environment

quality and (2) the composition, abundance and activity of decomposer communities (Cadisch and Giller 1997). However, these interactions are strongly controlled by abiotic drivers, which determine the growth performance of the trees and thereby the properties of their woody debris. Moreover, these abiotic drivers also control the moisture and temperature regime of the dead wood as well as the decomposer activity and community (Fig. 1). The challenge remains to disentangle the relative effects of these different factors on the decomposition of dead wood, and in turn the sequestration of carbon and biodiversity of forests.

WOOD TRAITS AND DECOMPOSITION

The structural and chemical traits of dead wood, inherited from the traits of living trees, are also major drivers of wood decomposition and these traits vary greatly among tree species (Chave et al. 2009; Cornwell et al. 2009; Weedon et al. 2009; Zanne and Falster 2010). However, variability within species as determined by site growing conditions of the trees and trait variation within individual trunks may have important afterlife effects on wood decomposition dynamics too.

Tree Size Matters

Firstly, trees are tall plants that, based on rules of allometry, need trunks of sufficient diameter to support their extensive canopies (Gartner 1995; Enquist and Niklas 2001). Tree species may vary greatly in their maximum stem diameter and it was shown that this trait explains differences in decomposition rate among a wide range of Bolivian tree species (van Geffen et al. 2010). However, the actual diameter of the logs was an even better predictor. In practice, log diameter varies greatly with tree height and age, position within the tree, site conditions and presumably also the genotype of a given species. Therefore, the diameters of logs are usually regarded as a covariate to take into account when testing the effects of other predictors of wood decomposition rates (Harmon et al. 1986; Yin 1999). To tease out the contributions of chemical and structural traits to wood decomposition (see below), it is generally a useful approach to hold diameter constant to the extent possible in interspecific comparisons (Weedon et al. 2009; Freschet et al. 2012c).

Wood Chemistry and Structure

Higher lignin contents and (concomitant) higher dry matter contents tend to make dead wood more recalcitrant to

decomposition (Harmon et al. 1986; Freschet et al. 2012c), while there is also a potentially important role for the micro-structure of the woody cell wall, i.e. the type and share of cellulose, lignin and hemicellulose (Eriksson et al. 1990). However, the specific chemical structure of lignin itself is important too. For instance, lignin is generally more recalcitrant per unit mass for gymnosperms than for angiosperms (Cornwell et al. 2009). Different types of lignin coexist even across closely related species or within the same species and individual plants (Vanholme et al. 2010) and these different chemical types of lignin can lead to substantially different decomposition rates of litters (Talbot et al. 2012). Wood density as such is not regarded as having direct influence on decomposition rates, but may have important indirect effects, e.g. through determining moisture regime of the dead wood. Wood density may also influence whether or not the wood shatters when a tree falls down and thereby provides easy access to decomposers (Cornwell et al. 2009). Also, many dense woods contain less oxygen and high amounts of extractives in their heartwood, making them resistant to decay (Blanchette 1991; Tsoumis 1991).

Wood of species with higher nitrogen content tends to decompose faster (Weedon et al. 2009), which is possibly caused by differential effects of nitrogen on microbial enzyme activities (Zak et al. 2011) and possibly by the N requirements of their decomposers (see below). However, initial N dead wood N content was not a good predictor of decomposition rate among subarctic tree species (Freschet et al. 2012c). Recently initial pH of dead wood has also been shown to be a potentially powerful positive predictor of interspecific variation in decomposition rate, at least in a subarctic flora (Freschet et al. 2012c). The causal relationship between initial wood pH and decomposition rate may relate to organic acids such as tannins, which make wood both acidic and recalcitrant. However, it is important to also consider that most wood rot fungi acidify their wood during decay.

Trait Variability Within Tree Trunks

Also variation in wood traits within tree trunks can determine decomposition rates. Key traits may show strong gradients from the centre to the outside of the xylem and the strength of these gradients varies strongly between tree species. For instance, oaks (*Quercus* spp.) show strong differentiation between reinforced heartwood and sapwood, while birches (*Betula* spp.) do not. Wood outer bark forms a formidable physical (and chemical) barrier to penetration, which can considerably retard decomposer penetration (Käärik 1974; Pearce 1996). However, this protection only prevails as long as wood moisture content stays constant as drying out of the outer wood and bark tissue will lead to crack formation and entrance ports for decomposers. Resistance of wood to decomposition by various decomposers is strongly influenced by moisture content, permeability of the wood and the presence of organic (toxic) substances (Panshin and de Zeeuw 1980; Tsoumis 1991; Schmidt 2006). These factors explain the relatively high decomposition resistance of heartwood in comparison to sapwood, although due to the nature of organic substances in different species also heartwood resistance varies substantially (Hillis 1987; Eriksson et al. 1990). Heartwood formation is a genetically determined process that occurs in many broad-leaved and coniferous species and indicates the transformation of partly living tissue, which is actively involved in water transport and storage, into dead tissue, which is made impermeable and impregnated with—often toxic—organic substances (Panshin and de Zeeuw 1980; Bamber and Fukazawa 1985; Pearce 1996; Taylor et al. 2002; Cornwell et al. 2009).

At smaller scale, the anatomy of different conductive tissues and structures may affect the water holding capacity while it may also affect relative penetrability and accessibility of the wood to fungi. For example, conductive elements (tracheids and vessels) are long cell types orientated longitudinally in stems, which facilitate rapid intra-stem spread by fungi after mortality, although this effect might be (at least partly) counteracted by the cell walls of vessels and tracheids, which are strongly lignified (Barcélo 1997). Parenchyma cells function as storage cells in living trees and are relatively rich in easily decomposable materials including starch and N-rich compounds (Dix and Webster 1995; Gartner 1995), potentially facilitating fast colonisation by micro-organisms. However, the parenchyma cell walls are highly decay-resistant, and as a consequence, parenchyma cells can have a decay-inhibiting effect (Schwartze et al. 2003). Furthermore, thick-walled fibre cells provide mechanical support in stems, so they should be resistant to decomposition. However, the role of variation in the amount of these cell types between or within tree species in driving interspecific variation in wood decay rates remains largely unknown (Cornwell et al. 2009; but see Van Geffen et al. 2010). The spatial configuration of the recalcitrant versus more degradable compounds may also play a role (e.g. Talbot et al. 2012). We still know very little about the relative importance of such anatomical–structural traits compared to overall chemical quality (Cornwell et al. 2009).

Intraspecific Variability Between Sites and Populations

Large, partly predictable, variation exist within the same tree species with respect to wood structure (density; dry matter content) and chemistry (lignin, tannin and other phenolics contents), both within and across classes of wood

diameter (Ursem, Cornelissen and Freschet, unpublished data). Besides genotypic differences between populations, a major source of intraspecific variability in wood traits is caused by the environmental regime as determined by soil properties and microclimate (Sungpalee et al. 2009; Fajardo and Piper 2011). Although, overall, such intraspecific variability tends to be much smaller than interspecific variation, it can certainly be very substantial and we assume it will therefore also lead to important differences in wood decomposability. Quantifying relative contributions of interspecific and intraspecific trait variation to wood decomposability is a high research priority indeed.

DECOMPOSITION AND DECOMPOSER COMMUNITIES

Although wood degrading organisms largely differ in preference of substrate and/or abiotic conditions, most of them share the need for oxygen and water. This makes wood moisture content an important driver of wood decomposition. Below a wood moisture content of 20 %, most fungi are inactive while wood moisture content of 80–100 % restricts enzymatic activity of fungi due to lack of oxygen (Tsoumis 1991; Zabel and Morrell 1992; Schmidt 2006). Some soft-rot fungi are specialised at attacking water saturated wood but their degradation speed is much lower than that of the other two types, the brown rot fungi (specialised in degradation of cellulose) and the white rot fungi (specialised in degradation of cellulose and lignin). Bacteria can also act as real wood degraders and three degradation types have been described: tunnelling bacteria, erosion bacteria and cavitation bacteria (Nilsson and Daniel 1983; Nilsson and Singh 1984). Although their wood processing rate is slow (Klaassen 2008), they can degrade even recalcitrant wood species under limited supply of oxygen and nutrients. Under such conditions, wood degrading bacteria work in consortia of a variety of species and are always ubiquitous (Nilsson and Björdal 2008). Bacteria are also present in wood under decay by rot fungi (De Boer and Van der Wal 2008; Valaskova et al. 2009). Although the direct contribution of these bacteria to wood turnover appears minor, their interactions with wood-rot fungi may be important. For instance, rot fungi may benefit from bacteria if they metabolise toxic intermediates or provide them with a nitrogen source (De Boer and Van der Wal 2008).

Also the occurrence and activity of wood degrading invertebrates is related to abiotic conditions of wood, as well as the presence of concurrent other degraders. Wood diameter has a strong effect on saproxylic (i.e. dead wood inhabiting) invertebrate communities (Grove 2002; Jonsell et al. 2007), because it determines wood moisture content and the pool of available resources. Large-diameter wood pieces also support more and partly specific, fungal species (Kruys and Jonsson 1999; Nordén and Paltto 2001), on which many wood inhabiting invertebrate species depend (Grove 2002). Moreover, wood traits that define resource quality for saproxylic species, such as lignin and nitrogen content, affect decomposer community composition (Irmler et al. 1996; Grove 2002). As wood has a low C/N ratio it is a difficult substrate to degrade because of the N requirements of decomposers for tissue building. Fungi with extensive mycelia may also import N from outside the log when in short supply in the log itself. Initial fungal infection therefore favours subsequent insect degradation. The wood degrading invertebrates can be divided into dry and wet wood borers, which can contribute importantly to biodiversity (Grosser 1985; Grove 2002). The interactions between saproxylic decomposers, especially between fungi and wood-feeding invertebrates, and how these interactions are shaped by wood traits, are still poorly known.

DRIVERS OF DECOMPOSER ACTIVITY

The composition, abundance and activity of all decomposer communities are the fundamental drivers of wood decomposition. However, as mentioned above, they interact with the wood characteristics (see "Wood Traits and Decomposition") and local abiotic and biotic conditions (Fig. 1). Thus, to some extent, the identity and ecological function of the decomposing fungi and saproxylic invertebrates will match the traits of the tree species. Other factors such as placement, soil type and fertility may also play important roles in the colonisation and activity of different decomposing fungi and bacteria, at least in the early phase (Van der Wal et al. 2007). The stochasticity of wood colonisation, i.e. the 'who comes first' effect, may also be an important determinant of community composition and decay activity (Valaskova et al. 2009; Fukami et al. 2010; Dickie et al. 2012).

Temperature and moisture regimes for decomposer communities are determined by a combination of macroclimate, local topography and soil characteristics. Tree species composition determines the physical and chemical properties of forest soils and drives decomposer community composition and abundance (Strickland et al. 2009; Ayres et al. 2009). Forest composition, age distribution and structure also determine the light regime on the forest floor, with obvious consequences for temperature and moisture regimes (Wirth et al. 2009). In the case of dead wood, the relative surface area that is in contact with the soil surface may be very important, the most extreme contrast being that between slow-decomposing standing wood versus downed dead wood with its more favourable moisture

regime and decomposer access (Cornwell et al. 2009; Harmon et al. 2011). Among many others, biotic factors such as throughfall of leachate and insect or fungal transport of resources can also modify resource availability in dead boles. Thereby they contribute to the complex interactions between wood quality and the decomposer communities.

THE CHALLENGE: DISENTANGLING THE INTERACTING EFFECTS OF WOOD TRAITS AND OTHER DRIVERS OF COARSE WOODY DECAY DYNAMICS

Although, as briefly reviewed above, a lot of progress has been made in investigating the controls on coarse wood decomposition rates, important challenges still lie ahead. It is obvious from the above and further studies (Schmidt 2006; Yin 1999; Wall et al. 2008; Freschet et al. 2012b) that the different abiotic and biotic drivers of wood decomposition dynamics interact strongly. Also, different species are found in different environments and this makes it difficult to disentangle the species wood trait effects from the effects of the other drivers. For instance, does dead wood of conifers in boreal forest generally decompose slowly because of specific wood characteristics, harsh climate conditions, the composition and dynamics of the microbial communities, low soil pH and nutrient availability, or a combination thereof? Recently, several research approaches have attempted to single out the contribution of species traits on coarse wood decomposability. Weedon et al. (2009) carried out a global meta-analysis of the currently available studies where decomposition rates of logs of similar diameter of two or more tree species had been reported from the same site (presumably in broadly similar environment). They found strong and consistent species contributions to mass loss and generally slower decomposition of conifer logs compared to those of broad-leaved species within sites. However, it is not yet certain whether these differences might be attributed partly to the fact that the accompanying broad-leaved species, especially in the boreal zone, tend to lack heartwood (e.g. *Betula*; see above) and are therefore more degradable than broad-leaved species in other vegetation belts. Van Geffen et al. (2010) employed a novel approach based on the chronosequence methodology; they derived dead wood mass loss rates of 15 tree species in a Bolivian forest by linking wood density of living trees to that of decaying logs (the proportional decrease in density representing mass loss) and reconstructing the duration of decomposition of each log from tree fall data in forest tree censuses. They found more than an order of magnitude difference between slow and fast decomposing species within the same forest area, i.e. under broadly comparable environmental regimes.

COMMON GARDEN EXPERIMENTS

A relatively easy way to exclude effects of environmental variation in species comparisons for litter decomposability is to use the common garden approach. In this approach, litters of multiple species are incubated simultaneously, in the same litter matrix ('litterbed'), so that mass loss rates can be interpreted directly in terms of species' litter 'decomposability'. After the first study of this kind on leaf litter in a temperate flora (Cornelissen 1996), this common garden approach made some key advances at Abisko Research Station in sub-Arctic Sweden under the guidance and directorship of Terry Callaghan (Quested et al. 2003; Cornelissen et al. 2007; Freschet et al. 2012c) and eventually in many biomes of the world. Together these studies revealed that the range of variation in leaf litter decomposition rates among species within sites worldwide was generally greater than the range of variation of a given litter type across climatic zones from the Arctic to the Tropics (Cornwell et al. 2008). Freschet et al. (2012a) extended this approach to decomposition of dead wood of six sub-Arctic species, again at Abisko Research Station. They successfully applied a new method to derive long-term mass loss dynamics from 2-year experimental incubations. For each species they started with a series of stems of wide-ranging decay stages and the 2-year mass loss vectors of all these stems were connected through a model that optimised the fit of mass loss (dependent variable) versus time (independent variable). As all species were incubated simultaneously in the same 'litterbed', they could reveal large differences in wood decomposability among these subarctic species. They could also predict these differences from interspecific variation in initial lignin content, dry matter content and pH. Although a very promising new method, the limitations of this study were that (1) Freschet et al. (2012c) only included 5 cm diameter stems and branches, i.e. the fine fraction of the coarse wood diameter spectrum; (2) time was modelled rather than absolute; (3) mass loss dynamics at later decay stages were less reliable owing at least partly to disintegration of the stem shape (and volume); (4) intraspecific variation in wood quality as dependent on site properties was not accounted for; and (5) trait by environment interactions could not be included, as there was only one litterbed.

Finally, commercial timber species have also been screened in the laboratory and in 'graveyard tests' for resistance to decay caused by different microorganisms. Although these tests are rather detached from the natural situation, as they do not tend to leave the tree logs in their

natural shape and size and usually involve bark removal, they give a good indication of the specific resistance of the heartwood.

LOGLIFE TO THE RESCUE

As tree species composition is set to change this century as a consequence of climatic and land-use changes (e.g. Koca et al. 2006), we need to understand and quantify better how such species shifts affect ecosystem carbon storage through changing interactions between coarse dead wood decomposability (Cornwell et al. 2009) and environmental regimes; and how these interactions both affect and depend on the biodiversity associated with changes in dead wood quality and decomposition dynamics. Specifically, we need a better handle on (1) disentangling the relative contributions of species variation in dead wood traits and environmental variation on the rate and dynamics of dead wood decomposition by decomposer communities, but also on recalcitrant soil organic matter formation; (2) understanding the roles of functional groups of decomposers, particularly fungi, bacteria and invertebrates, on such interactions; (3) quantifying the relative importance of interspecific variation and site-dependent intraspecific variation of wood traits on decomposability; (4) determining how (1) and, (3) affect community composition and (functional) diversity of various wood-dwelling organisms, such as fungi, bacteria, invertebrate animals and bryophytes; (5) estimating the extent to which interspecific variation in coarse wood decomposability corresponds with that of other tree organs such as branches, twigs, leaves and roots (cf. Freschet et al. 2012a). This is important, as it determines whether trees as a whole promote or inhibit carbon and nutrient cycling through decomposition, or whether turnover rates of different organs cancel out one another to some extent. For instance, if all organs of species A are relatively more easily decomposable compared to those of species B, then replacement of species B by species A in a forest would accelerate the overall turnover of organic matter and thereby of carbon and nutrients.

To deal with these challenges requires a concerted effort of many ecological disciplines and long-term commitment. Below we describe LOGLIFE, which is a large new experiment especially designed and set up by an energetic and multidisciplinary team of scientists to answer these questions concerning wood decomposition directly over a time period of about 15 years. It involves coarse wood, branches, twigs, leaves and probably roots of 10 tree species for starters, each incubated in two 'tree cemeteries' in strongly contrasting temperate forest sites. We describe the current experimental design, setup and sampling protocol as well as add-ons of the main experiment, now and possibly in the future. The aim of putting LOGLIFE on the map early on is to invite other researchers to join with important complementary questions and activities and to inspire others to set up comparable experiments in other ecosystems and biomes so as to obtain more robust insights into what drives wood decomposition worldwide. One such complementary initiative has been set up recently at Tyson Research Center, St. Louis, USA (Amy E. Zanne, pers. comm.)

THE RESEARCH SITES AND SPECIES

We selected two strongly contrasting temperate sites in terms of soil and microclimate, so as to maximise the potential for interactions between tree species and incubation environment. In brief, both sites are in the central part of the Netherlands. The Hollandse Hout site is in East-Flevoland (F), i.e. just below sea level on land claimed from the former Zuiderzee (sea) in the 1960-ies. The young soils in the Hollandse Hout (and in the incubation plot) have formed in marine clay and are calcareous, moist, fertile and close to neutral pH. The trees were extracted (Fig. 2) from monospecific plantations used for commercial forestry. The log incubation plot is a relatively light-open *Populus x canadensis* Moench stand with a luxuriant herb layer dominated by nitrophylic *Urtica dioica* L. and *Galium aparine* L. The plot is situated within a forest reserve for long-term monitoring of spontaneous forest development and has been left unlogged and without other interference since 1995. The other site is located at the Schovenhorst estate (S) in the Veluwe region and hosts postglacial (loamy) sand deposits (elevation approx. 30 m a.s.l.) in which well-drained, acidic podzolic soils of low fertility have formed. Here the trees were also extracted from monospecific forestry plantations. The log incubation plot is a rather light-open *Larix kaempferi* (Lambert) Carrière stand with a low and dense ground layer of predominantly the grass *Deschampsia flexuosa* (L.) Trin. intermingled with mosses and patches of the dwarf shrub *Vaccinium myrtillus* L. These two sites thus represent the two extremes of the major acidity/texture/fertility axis of forests in NW Europe. For details of these sites, incubation plots and their environments see Table 1 and Figs. 3, 4.

From each site 10 individuals per tree species were extracted. In total 10 different species were extracted, of which six broad-leaved and four coniferous species. All species are important in NW European forests or forestry plantations. For broad-leaved *Quercus robur* L. and coniferous *Picea abies* we extracted 10 individuals from each of the two contrasting study sites in order to account for the effects of site growing conditions on intraspecific

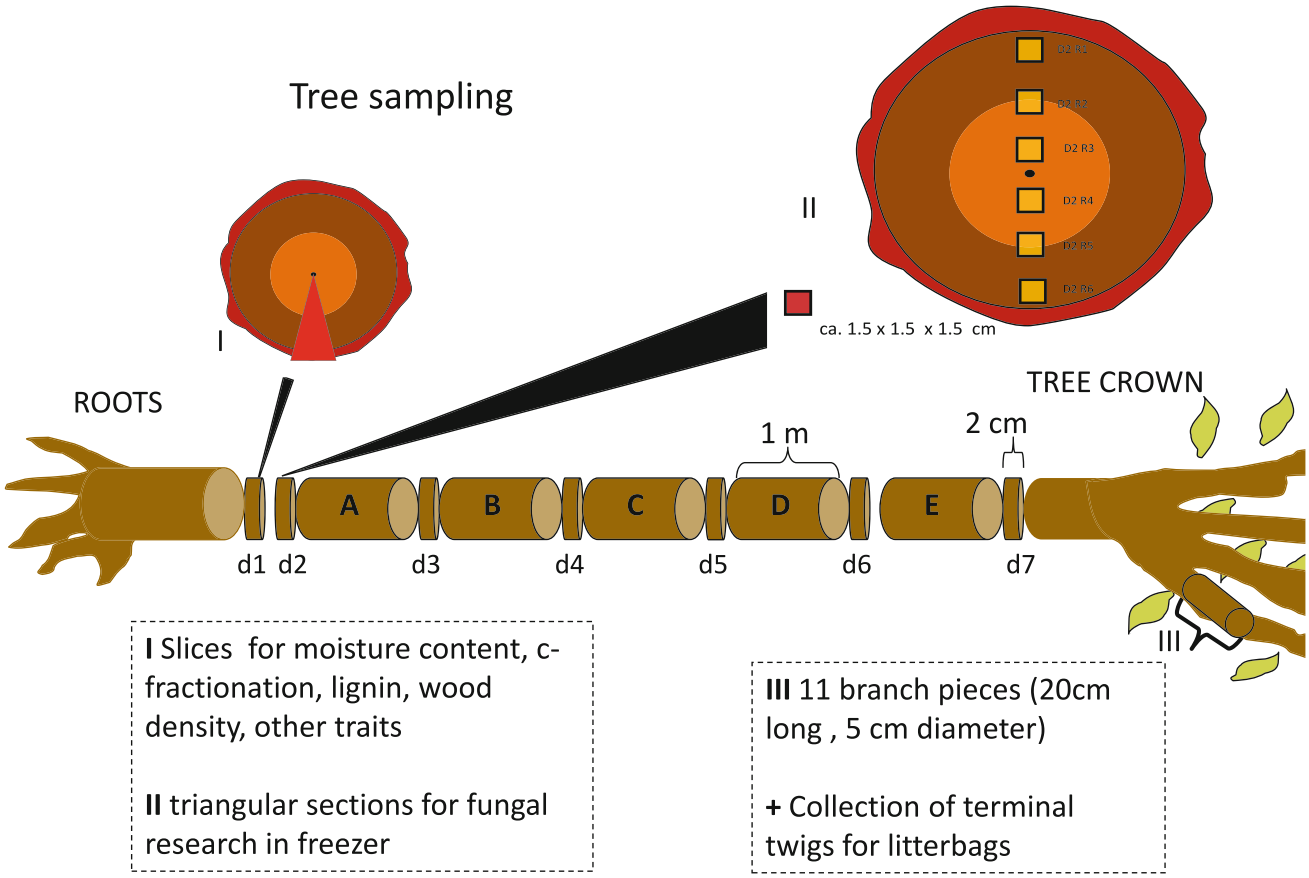

Fig. 2 Sampling design for an individual tree in LOGLIFE. Logs *A–E* are subsamples from the same tree trunk to be harvested in random order for mass loss monitoring over a 15-year period

Table 1 Description of the two LOGLIFE sites in the Netherlands where the trees were extracted and are being incubated

Site	Flevoland–Hollandse Hout—F	Schovenhorst (Veluwe)—S
Coordinates	52.46 N, 5.42 E	52.253 N, 5.626 E
Soil	Calcareous heavy clay	Loamy Sand, well drained
	Luvisol	Podsol
	pH 6.5–7	pH approx. 4
Tree species extracted	Needle-leaved trees	Needle-leaved trees
	Picea abies	***Picea abies***
	Broad-leaved trees	*Abies grandis*
	Quercus robur	*Larix kaempferi*
	Betula pendula	*Pseudotsuga menziesii*
	Fagus sylvatica	Broad-leaved trees
	Fraxinus excelsior	***Quercus robur***
	Populus x canadensis	*Populus tremula*
Incubation plot details	Light-open *Populus x canadensis* stand with dense herbaceous understory of *Urtica dioica* and *Galium aparine* and a substantial moss layer	Light-open *Larix kaempferi* stand with low understory dominated by *Deschampsia flexuosa,* mosses and patches of *Vaccinium myrtillus*

Species in bold typeface were extracted from both sites. All species are being incubated in both sites (see Figs. 3, 4)

variability in wood quality and decomposability. The other eight species were extracted from only one site each (for details see Table 1). These include the broad-leaved *Betula pendula* Roth, *Fagus sylvatica* L., *Fraxinus excelsior* L., *Populus x canadensis*, *Populus tremula* L. and the needle-leaved *Abies grandis* (D. Don) Lindl., *Larix kaempferi* and

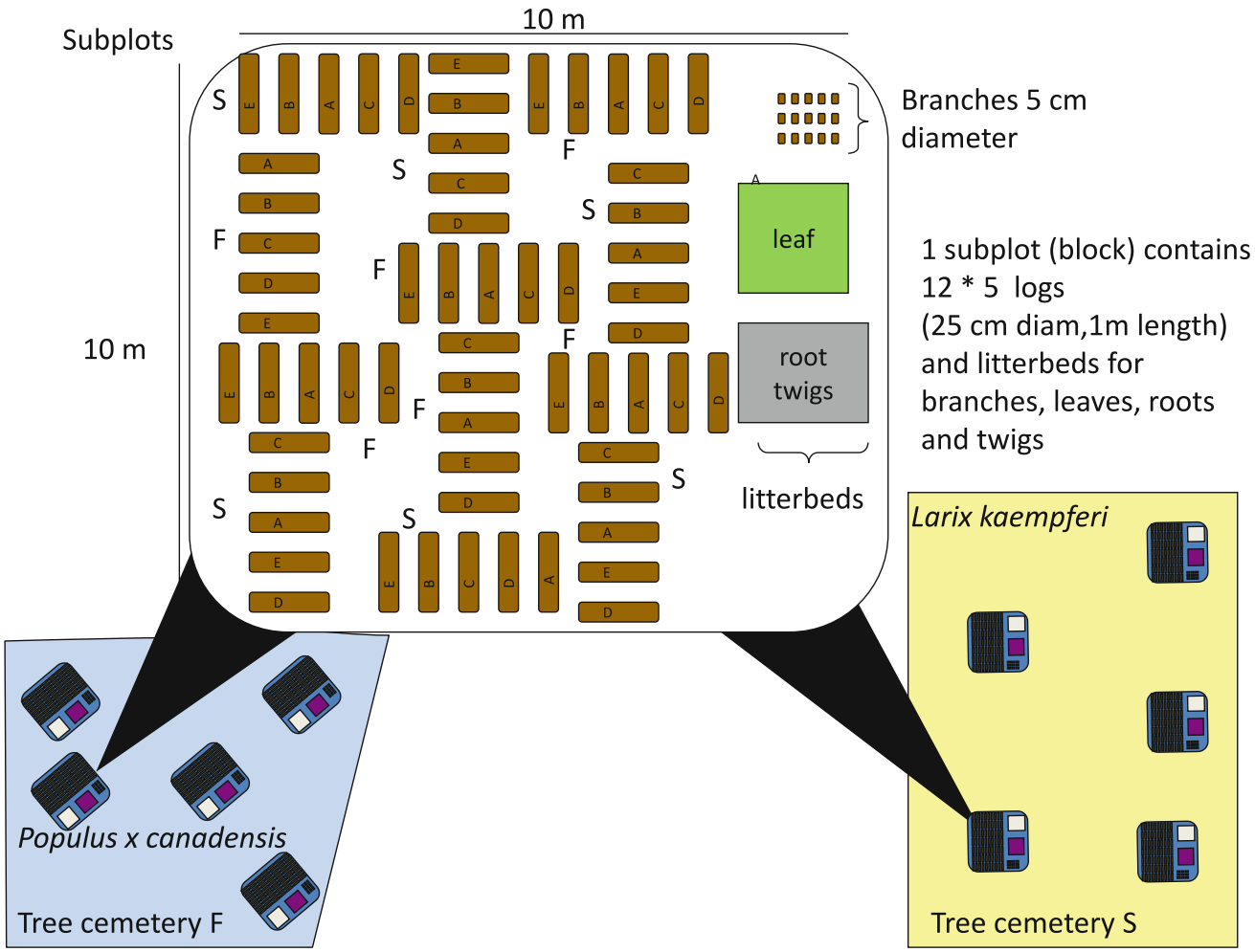

Fig. 3 Experimental design of LOGLIFE

Pseudotsuga menziesii (Mirb.) Franco. Between mid January and mid February 2012 we cut apparently healthy, well developed trees of which the trunk was approximately 25 cm diameter at mid-height and ranged between 22 and 28 cm over at least 5 m (see below). While at a later stage we plan to additionally include logs of naturally senesced trees for comparison, we decided on using living trees because (1) in NW European forests and tree plantations, as in many other forests worldwide, a large proportion of the trees fall down before natural senescence, either owing to major natural disturbances such as wind-throw or soil instability or owing to logging (which generally leaves large coarse wood residues); (2) because defining and standardising the initial, undegraded phase (and finding enough suitable logs) is difficult for trees that have died a natural death through senescence, with possible complications of prior pathogen attack having altered wood quality; (3) they provide a direct link to the functional traits of living trees, and therefore to the ecological roles of the different species.

PREPARATION AND EXPERIMENTAL DESIGN

From each individual tree without symptoms of logging-related wood shattering, we selected and chain-sawed five sections (A–E) each of 1 m length, 25 ± 3 cm diameter and without major side branches from the main trunk, often leaving the bottom and top part of the trunk unsampled (Fig. 2). Adjacent to each end of a stem section (log) a 2-cm thick disk was sawn out for analyses of initial wood traits (Figs. 2, 4a). Typically the five stem sections were adjacent, but in case of major branches, damage or other irregularities some intermediate stem parts were left unsampled. We cut off any thin branches and took the disks to the lab for analyses of bark thickness, width of sapwood/heartwood, moisture content, wood density (fresh and dry mass per volume), chemistry and anatomy across the radius. These traits (1) represent the ecological strategy of the species and provide (2) a baseline for subsequent changes in mass (via wood density), structure and chemistry during the incubations and (3) in the dynamics of

Fig. 4 Images of LOGLIFE preparations and layout. **a** Sawing five logs for long-term incubation and stem disks for analysis of initial wood characteristics. **b** Logs of the coniferous Douglas fir (*Pseudotsuga menziesii*). **c** Subplot (block) in the poplar stand in Flevoland at the start of incubation. Two other subplots are visible in the background. **d** An incubation subplot in the larch stand at the Schovenhorst (Veluwe) site. Photos by J. van Hal and G. T. Freschet

Fig. 4 continued

colonisation and degradation by different decomposers. For the latter, we also cut out and froze a representative pie from the bottom and top disks of each tree (Fig. 2) for analyses of any microbial presence, as a baseline for the development of fungal and bacterial communities during the incubations. From each tree crown we cut out eleven

20-cm long branch sections of 5 ± 0.5 cm diameter: one for initial lab analyses (see above), five for monitoring mass loss (as for the logs of the same individual tree and adjacent to them within plots and blocks) and five for analyses of invertebrate colonisation in LOGLIFE. For *Abies*, *Picea* and *Pseudotsuga* we could only obtain six sections of the right diameter class, and only from the top of the main trunk. We also collected a set of terminal twigs from each crown to be incubated for mass loss analysis adjacent to the logs of the same individual in each incubation plot and block (see below).

We transported the logs to their incubation plot, minimising any damage to the bark, which we considered a key component of the log during subsequent decay. For each species from either site, five individual trees (replicates), each divided in five logs (subsamples), were placed in the Flevoland plot and the other five trees at Schovenhorst, so that each tree individual had its own subplot representing a statistical block (Fig. 3). The five blocks per site measure 12 by 12 m each with minimum distances of 20 m between blocks (Figs. 3, 4c). Logs and big branches already present in the blocks were removed before log placement. Each of the Schovenhorst blocks has a 1.2-m high fence to keep out the wild pigs that are abundant in this area. Thus between 21 and 27 February 2012, 600 logs were placed in their final position in their respective blocks in their respective incubation sites. As the month prior to that had been particularly cold, mostly with subzero temperatures, we exclude the possibility of any decomposition already having commenced before final log placement. Within each block, the logs are positioned on the soil surface 30 cm apart, making good contact with the soil (Fig. 4b–d). The five logs from each individual lie together with the same compass orientation, but the location and orientation of each individual within each block was selected haphazardly (Figs. 3, 4c–d). We opted for the short distances between logs purposefully, as this should facilitate exposure of all logs to a wide array of wood decomposer taxa. Although any two given logs may have different microbial communities in their immediate vicinity, such differences are random at the species level at each site because of the randomised block design. At the same time, the 30 cm distances should be enough to prevent effects of neighbour logs on the microclimate of any given log. An add-on experiment (Box 1) will investigate microbial colonisation effects on logs within and between species explicitly. The 5 cm diameter branch sections and twigs will be placed in the same blocks in autumn 2012, together with leaf litter of the same species collected in the sample plots and perhaps also root litter. We will add coarse logs of 10 more tree species in 2013, two being the same as in 2012 in order to calibrate between start years.

FUTURE SAMPLING

While LOGLIFE will be hospitable to different add-on experiments and analyses testing many further questions (e.g. Box 1), we briefly introduce a minimum sampling and analysis programme for LOGLIFE. We will:

- Monitor mass loss dynamics over approximately 15 years by determining wood density (across the radius from bark to pith) based on (1) wood cores at half-year intervals; (2) harvesting a whole (random) log from each tree at longer time intervals, e.g. subsequently after 2, 4, 7, 10 and 15 years of incubation.

Box 1 LOGLIFE at microscale: subproject on the fungal factor in variation in wood decay

Wood decomposition is strongly influenced by physical and chemical properties of woody species as well as by environmental conditions. These factors form the basis for most predictive forest wood decay models (Müller-Using and Bartsch 2009; Radtke et al. 2009; Yin 1999; Zell et al. 2009). These large-scale models do not account for the variation in wood decay rates at smaller temporal and spatial scales (Onega and Eickmeier 1991; Palviainen et al. 2010; Van der Wal et al. 2007; Woodall 2010). A large fraction of mass (and carbon) loss of woody materials actually takes place during the first decade, for which the predictions of current models have the lowest accuracy (Fahey et al. 2005). This hampers the extrapolation of short-term, site-based measurements to larger temporal and spatial scales, consequently reducing the reliability of carbon sequestration estimates. The reason for this mismatch could be the underlying assumption of current models that community dynamics of decomposing organisms is not important for predicting decay rates, although it is generally acknowledged that the identity and type of rot fungus largely affect the process and rate of wood degradation (Pandey and Pitman 2003; Toljander et al. 2006; McGuire and Treseder 2010)

To investigate how dynamics of wood-rot fungal communities contribute to the prediction of local variation in wood decay rates, we have set up a common garden experiment in which many replicate logs of two tree species (*Larix kaempferi* and *Quercus rubra* L.) were placed within the *Larix kaempferi* stand (see Table 1). For each tree species, 16 (2×2 m) subplots host 9 logs each in random position. The subplots are at least 15 m apart. The logs, 30 cm long and about 20 cm in diameter, were sawn from 8 individual trees for each species. Each year, we will take one wood block of each subplot to the lab for analyses. Since we incubate the wood on the same forest soil, we attempt to minimise the between-subplot variability in abiotic conditions. In this way, and in combination with 16 replicates per time point, we hope we can demonstrate the range of decomposer-related variation in wood-decay. The experiment will run for approx. 10 years and will be of interest to microbiologists, entomologists, biogeochemists and ecologists alike, all of whom we encourage to help us get an integrated understanding of decomposer–wood interactions

- Sample the diversity and dynamics of fungal, bacterial, invertebrate and cryptogam communities associated with wood or bark both non-destructively (e.g. observation of wood beetle holes) and upon log harvest for mass loss analyses.
- Analyse initial wood characteristics hypothesised to be indicative of wood decomposability, including anatomical, structural and chemical traits.
- Describe patterns of decomposition across the log to understand (1) the dynamics of infection (colonisation, interaction between different decomposers) and (2) species-specific differences in resistance to decomposition.
- Quantify the dynamics of chemical constituents of the xylem and the bark, notably lignin, cellulose, mineral nutrients and multiple secondary compounds.
- Monitor soil carbon in different compounds accumulating below the logs of different tree species.

Eventually, we aim to use LOGLIFE results as input for dynamic models of ecosystem-scale carbon pools and fluxes as well as assessments of overall forest biodiversity at the plot scale.

CONCLUSION

Here we have presented LOGLIFE as a new long-term 'common-garden' experiment to disentangle the effects of species' wood traits and site-related environmental drivers on wood decomposition dynamics and its associated diversity of microbial and invertebrate communities. LOGLIFE is also an open research facility for many questions concerning coarse wood decay and warmly welcomes new and exciting additions to the recently initiated programme of experimental and monitoring activities. Together these concerted research activities will further our understanding so as to optimise our forest management in view of carbon sequestration and biodiversity conservation.

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