University of Reading

Exploring the role of deadwood in the forest soil carbon cycle

Thesis submitted for the degree of Doctor of Philosophy

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DECLARATION

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Victoria Shannon

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Abstract

Deadwood is an important part of forest ecosystems, holding ~5% of global forest carbon, and providing other ecosystem services such as habitat for biodiversity, natural flood management, and production of woodfuel. Threshold volumes of deadwood, usually >20 m^3 ha^{-1}, are aimed for, to help preserve biodiversity. The carbon stocks held in deadwood are now included as a pool to report in carbon inventories such as the Global Forest Resource Assessment. However, the exact contribution of deadwood from woodlands in Great Britain is unknown, with estimates of carbon stocks being based on simplistic calculations, assuming all deadwood is uniform and that volumes do not change over time. Additionally, there is little research into how volumes and carbon stocks vary between factors such as woodland type, origin, and management.

In this work, we aimed to quantify the effects of these factors and ascertain how this compares to other forest floor materials. We also aimed to identify whether significant fluxes of dissolved organic carbon (DOC) were released from deadwood during decomposition, and whether this 'primed' soil microbes. This was carried out from plot scale experiments to national scale using data from the National Forest Inventory.

We conclude that across GB, an average deadwood volume of 26 m^3 ha^{-1} occurred. However, this significantly differed between countries in GB, woodland type, and management practices. Carbon stocks were calculated with wood density and carbon concentrations specific to tree species and decay class, which proved to significantly differ when compared to the standard calculation used for national reporting. Changes to wood density significantly affected the overall carbon stocks reported, while carbon concentration did not. It is possible deadwood provides a significant source of DOC into underlying soil, producing as much DOC per g material as leaf litter, though overall fluxes depend on the volume of deadwood present. The fate of DOC released by deadwood is currently unknown as there is no evidence that it causes a priming effect on soil microbes, and further study is required to ascertain whether deadwood derived DOC is strongly minerally-associated, or recalcitrant.

Contents

Glossary of acronyms

BL - Broadleaf

C - Carbon

C/N – Soil carbon to nitrogen ratio

CH_4 – Methane

CO_2 – Carbon dioxide

CON - Coniferous

CWD – Coarse woody debris

DBH – Diameter at breast height

DOC – Dissolved organic carbon

DOM – Dissolved organic matter

ECN – Environmental change network

FLII - Forest Level II Intensive Monitoring Network

FWD – Fine woody debris

GPP – gross primary production

LD – Lying deadwood

MBL – Mixed broadleaf

MC – Mixed coniferous

NFI – National Forest Inventory

NPP – Net primary production

S - Stumps

SD – Standing deadwood

SOC – Soil organic carbon

SOM – Soil organic matter

TOC – Total organic carbon

WEOC – Water extractable organic carbon

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1 Introduction

1.1 Overview

Forests are important parts of the global carbon cycle, with carbon stored in many different pools that include living and dead organic matter. As trees die, either wholly or in part, they become part of the deadwood pool, and thus, so will the carbon contained within. While living trees absorb CO_2 from the atmosphere during photosynthesis, dead and decaying wood will release carbon during decomposition. This has potential to be released into the atmosphere as CO_2 or CH_4, or into the surrounding soils as dissolved organic carbon (DOC). There are many factors that may influence the decomposition of deadwood (section 1.3.5), and as such the rate and amount of carbon released by deadwood. Comparatively little is known about the deadwood carbon pool and further work is needed to improve estimates of stocks, and whether carbon is transferred from the deadwood pool into soils.

Forests make up nearly a third of total global land cover, with a total area of 4.06 billion hectares (ha) (FAO, 2020a), of which 25% (1.02 billion ha) are held in Europe (including Siberia) according to the FAO. Within this land area there is a living biomass of 606 Gt globally, of which 110 Gt is held within these European forests. This land forms a substantial carbon pool. Terrestrial ecosystems hold an estimated 3170 Pg (1 Pg = 10^{15} g) of carbon globally (Jansson *et al.*, 2010), split between soil (79%), plant biomass (18%) and microbial biomass (3%). Of this total terrestrial pool, it is estimated 861 ± 66 Pg (~27%) are held within forests (Pan *et al.*, 2011), with 44% in the soil and 56% in above ground biomass. The UK contributes around 1095 Mt (1 Mt = 10^{12} g) carbon to this forest pool (Forest Research, 2021). The partitioning of this carbon held within forests will vary by country, though on a global level it is believed that 42-44% of organic carbon is held in living biomass: 44-45% is held in soils; 5-6% is held in litter, and the remaining 4-8% is held in deadwood (Pan *et al.*, 2011; FAO, 2020a). The UK however, holds a far larger proportion in forest soils, at an estimated 69%, while above and below-ground biomass hold 23%, litter ~5%, and deadwood holds the remaining ~4% (Forest Research, 2021).

The size of forest carbon pools will vary with forest age and type, but other factors, such as climate, soil type or management, can influence the carbon stocks of an ecosystem (Dar and Sundarapandian, 2015). In a large forest soil carbon evaluation (Vanguelova *et al.*, 2013), it was found that organic soils held the greatest carbon stock (448 t carbon ha^{-1}) with organo-mineral and mineral soils holding less (321 t ha^{-1} and 108-155 t ha^{-1} respectively). Keith *et al.*

(2009) found that cool temperatures and high precipitation favour carbon accumulation due to rates of primary production that exceed those of decomposition. Dar & Sundarapandian (2015) concluded that coniferous forest has a greater potential for carbon storage than broadleaved forest. Broadleaved species typically hold less than 10 t carbon ha^{-1} in their litter pools (Takahashi *et al.*, 2010) whereas conifers may hold 19.4 t carbon ha^{-1} (Yoneda, 1982). How species, soil types and climate affect deadwood stocks is poorly understood, and further research is needed.

With the increasing importance of mitigating climate change, it is necessary to monitor carbon pools and their changes over time. International agreements, such as the United Nations Framework Convention on Climate Change (UNFCCC; United Nations, 1992), adopted in 1994, Kyoto Protocol (United Nations, 1998), Land Use, Land-use Change and Forestry (LULUCF), REDD+, and the Paris Agreement (United Nations, 2015), have been created in an effort to unify a global response. These agreements were created to commit countries to reduce greenhouse gas emissions, or broadly limit global warming to below 2°C. As part of this, periodic reports are required, which include the carbon stocks held in forests. While forest carbon stocks have generally received a lot of scientific attention, the deadwood pool is often overlooked, or combined into the litter pool, with living biomass receiving the most attention. The Global Forest Resource Assessment found that many countries did not report a deadwood carbon stock, with only 78/193 countries and territories including it in their reporting (FAO, 2020b), and others, such as the Intergovernmental Panel on Climate Change (IPCC) guidelines, only include deadwood as an optional pool to report. This has led to some uncertainty over the size of the deadwood specific carbon pool and work is needed to clarify its size.

1.2 Aims and objectives of PhD

Aim: This PhD aims to (i) evaluate to the role of deadwood in the forest carbon cycle in terms of its direct contribution to overall stocks and indirect contribution to below ground soil carbon storage, and ii) how deadwood volumes and carbon stocks are influenced by woodland management and policy; (iii) understand how factors like tree species, cause of tree death, and management practices affect deadwood volumes and carbon stocks.

Objectives

1. Assess how local, national, regional, and international policies affect deadwood management in the UK **(aim ii)**

2. Explore the influence of forest management on forest floor materials and DOC dynamics in soils **(aims i and ii)**
3. Assess how forest type (coniferous and broadleaf) and stand age influences soil carbon under deadwood **(aim i)**
4. Evaluate carbon stocks in deadwood across the UK with respect to woodland types, state of decay and forest management **(aim iii)**

Key scientific concepts underpinning these aims and objectives are explained below in section 1.3. Each objective addressed is presented as a research paper, as outlined in section 1.4, and presented in subsequent thesis chapters. Two of the chapters have been published in peer reviewed journals: Hollands *et al*. (2022) in Science of The Total Environment, and Shannon *et al*. (2021) in the European Journal of Forest Research.

1.3 Key concepts

1.3.1 Forest carbon cycle

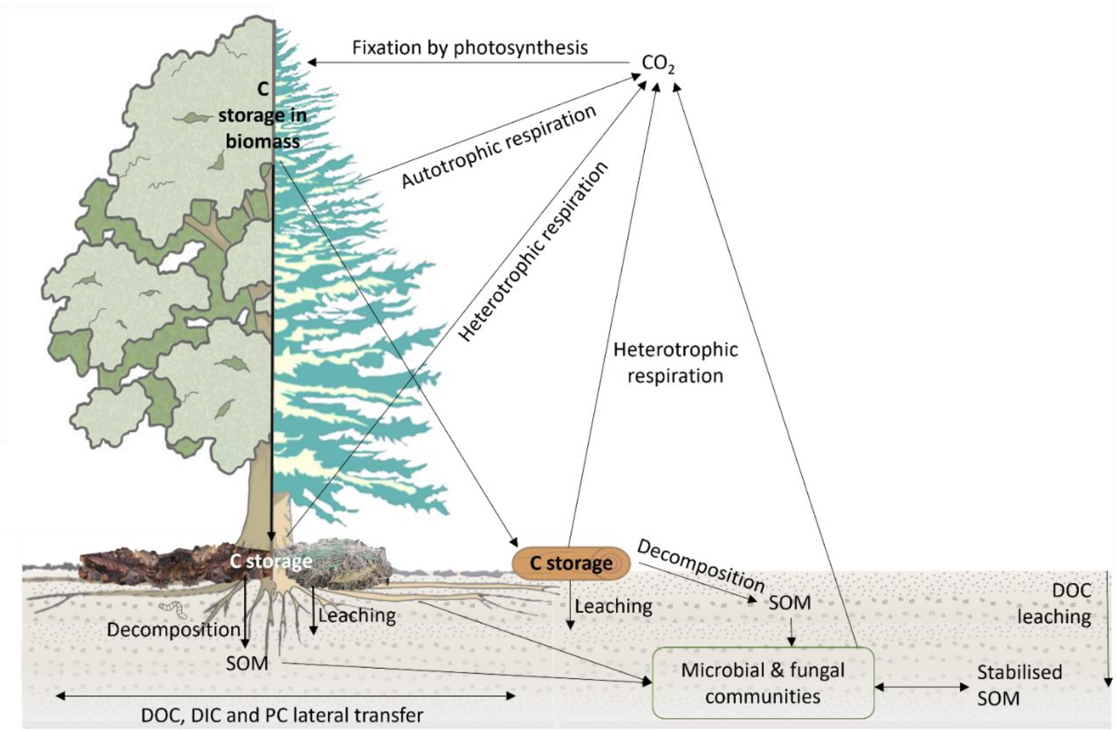


Figure 1-1 - schematic of the forest carbon cycle. DOC = dissolved organic carbon; DIC = dissolved inorganic carbon; PC = particulate carbon; SOM = soil organic matter.

Carbon accumulates in forests due to an imbalance between inputs and outputs (Figure 1-1). The carbon stock is usually partitioned into above- and below-ground biomass, deadwood, litter, and soil carbon. Above-ground biomass includes all living biomass such as stems, bark, and foliage. Below-ground biomass includes all living fine and coarse roots that are under the soil surface. Estimates have suggested that up to 30% of tree carbon is held in the root biomass (Kast and Berrill, 2016). Photosynthesis by plants takes in atmospheric carbon in the form of CO_2 which is then converted into glucose and oxygen. The total amount of CO_2 fixed by plants in this way is used to calculate gross primary production (GPP). It is usually estimated that 50% of tree biomass comprises of carbon (Martin and Thomas, 2011; Thomas and Martin, 2012) but values are known to vary slightly amongst tree organ (e.g. leaf, stem or root), tree species and forest types. For instance, Thomas & Martin (2012) found that in temperate/boreal forests, angiosperms were comprised of 48.8% carbon whilst conifers were 50.8% C. Similarly, in a global synthesis of 315 studies, Ma *et al*. (2017), identified the carbon content of coniferous stems to be 50.48%, while deciduous and evergreen broadleaves were 47.69% and 47.78%, respectively. A proportion of this carbon will be lost to the atmosphere during autotrophic respiration, by plant roots (Hogberg *et al.*, 2005) or foliar and woody tissue respiration, and some carbon will be fixed in plant biomass where it is converted into various biomolecules i.e. cellulose or starch. The carbon fixed in plant biomass is a measure of net primary production (NPP).

Organic compounds may then be released into the soil from living plant roots through root turnover and rhizodeposition (Wang *et al.*, 2006). Microbial decomposition of exudate components and other products of root turnover occurs through the production of microbial enzymes (Renella *et al.*, 2006). These enzymes can biochemically break down complex organic compounds and release CO_2 back into the atmosphere in the process of soil heterotrophic respiration, with the residual of NPP less heterotrophic respiration termed net ecosystem production (NEP). The soil heterotrophic respiration process is largely controlled by environmental factors such as soil temperature and moisture (Scott-Denton, 2003). Plant carbon can be transferred to the soil from plant matter, usually as soil organic matter (SOM) and this may be through a range of processes such as litterfall, fruiting, herbivory, rhizodeposition or plant death. Litterfall contributions to the carbon cycle will vary by species, with most deciduous broadleaf species having pulses of high litterfall in the autumn while evergreen conifers have a lower, more continuous input. While broadleaf litter has been found to have a lower C% than conifers (Morison *et al.*, 2012), its mean carbon stock (t CO_2 ha^{-1}) is larger, due to a higher density of litter found. Broadleaf litter generally decomposes faster than conifer litter, and organic matter is incorporated into upper soil layers.

NEP may be calculated by measuring changes in carbon stocks over time and is used to assess the net accumulation of carbon by ecosystems. SOM may persist for millennia (Schmidt *et al.*, 2011) or its carbon may be released back into the atmosphere during soil respiration. SOM in soil may become protected from decomposition either physically, chemically, or biochemically. Physical protection occurs where SOM becomes enclosed by aggregates within the soil and is thus inaccessible to soil microbes (Goh, 2004). Chemical stabilisation occurs where SOM chemically binds to minerals within the soil (Six *et al.*, 2002). SOM may be inherently biochemically stabilised where its constituents are primarily recalcitrant compounds such as lignin (von Luetzow *et al.*, 2006). Carbon may also be lost from the soil through the leaching of dissolved organic carbon (DOC) into groundwater (Kindler *et al.*, 2011) or by loss of particulate organic matter (POC) through erosion.

Fresh inputs of organic matter into the soil may have a 'priming effect' on soil microbes whereby the increase in availability of labile carbon leads to increased rates of microbial activity and therefore enzymatic activity (Fontaine, Mariotti and Abbadie, 2003; Kuzyakov, 2010; Beverly and Franklin, 2015) which in turn results in increased decomposition of native SOM. Microbes and invertebrates use organic matter from coarse woody debris (CWD) for their metabolism (Swift, 1973) and several studies have found that DOC levels beneath woody debris are significantly higher than beneath adjacent litter layers (Spears *et al.*, 2003; Hafner, Groffman and Mitchell, 2005; Kahl *et al.*, 2012; Yurkov *et al.*, 2012). This ranges from three times as much (Spears *et al.*, 2003) to ten times as much (Hafner, Groffman and Mitchell, 2005). Inputs of deadwood could potentially cause a priming effect, yet research is needed to verify this process.

1.3.2 Deadwood definitions and importance

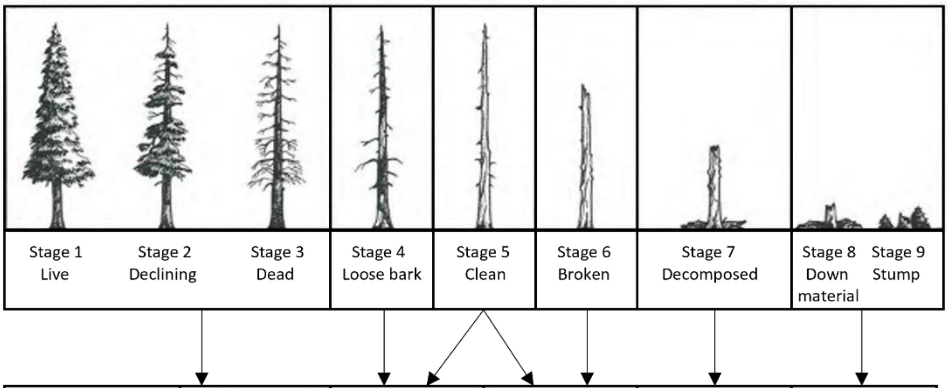
Trees are not only beneficial as carbon stores and for biodiversity when they are living, but also once they have died. Deadwood may be defined as sections of non-living wood, that may or may not occur attached to a living tree, and may be found on land or in water courses (Stokland, Siitonen and Jonsson, 2012). There are three main classifications of deadwood (Figure 1-2): standing dead trees (also called snags), stumps, and lying deadwood (often referred to as coarse woody debris; CWD). Standing dead trees and stumps may include coarse roots below ground. Lying deadwood may be branches or whole trees that have fallen to the ground.

Size of debris is important for classification, with different organisations and nationalities using various thresholds. For instance, CWD definitions vastly differ between studies, with some measuring debris with a diameter >2.5 cm (Peterken, 1996), between 7 and 12 cm (Weggler *et al.*, 2012) or >15 cm (Threlfall, Law and Peacock, 2019). However, a diameter between 7 and 10 cm is most common. For instance, the European BioSoil deadwood protocols (Durrant *et al.*, 2011), include CWD as woody debris with a diameter >10 cm and FWD as debris <10 cm diameter. It has also been proposed that a separate classification for fine (FWD) and very fine (VFWD) woody debris should be used (Kuffer and Senn-Irlet, 2005b), whereby VFWD has a diameter <5 cm and FWD has a diameter 5-9 cm, though other studies may include these smaller debris as part of the litterfall. In a study by Norden *et al*. (2004) in a temperate forest, 46% of deadwood sampled was FWD with a diameter between 1-10 cm, 22% were between 10-20 cm and 32% were >20 cm. Similar results were seen by Ruiz-Peinado *et al*. (2016) in a Mediterranean forest, where FWD (2-7 cm diameter) contributed between 90-98% of deadwood C. This suggests that studies which do not include a FWD class will be underestimating the volume of deadwood present.

This lack of consistency in definitions may cause difficulties when assessing deadwood distribution. For instance, using the larger, 15 cm threshold, would lead to deadwood being disregarded during field surveys and could lead to underreporting of volumes. This has been found in a study by Bohl & Brandli (2007) whereby using different definitions changed their assessment of whether target threshold volumes had been met. For this thesis, the definitions of deadwood as used by the National Forest Inventory of Great Britain (NFI) will be followed. These define lying deadwood as having a diameter ≥7 cm. Stumps must still be rooted to the ground and be ≤1.3 m tall with a minimum diameter of 4 cm. Standing trees must also be rooted, over 4 cm in diameter but taller than 1.3 m.

Figure 1-2 - examples of deadwood types. a – lying deadwood; b – stump; c – standing dead tree

Debris of all sizes can be further classified based on stage of decay (Hunter, 1990) (Figure 1-3), ranging from early decay at stage 1 to late stage decay in class 5 and stage 9. This is broadly split by standing dead trees, stumps and lying deadwood, whereby standing dead trees may be at decay stages 3 – 7, stumps at stages 8 or 9 and lying deadwood classified as decay class 1 – 5.



Decay class	1	2	3	4	5
Bark	Intact	Intact	Trace	Absent	Absent
Twigs < 3 cm	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft, blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Colour of wood	Original colour	Original colour	Original colour to faded	Light to faded brown or yellow	Faded to light yellow or grey
Portion of log on ground	Log elevated on support points	Log elevated but sagging slightly	Log is sagging near ground	All of log on ground	All of log on ground

Figure 1-3 - Classification of deadwood decay stages as described by Hunter (1990)

Deadwood at all stages of decay will host a range of biodiversity, including many endangered species and legislation now includes deadwood as a habitat that must be preserved for conservation. For instance, saproxylic invertebrates such as the Stag beetle (*Lucanus cervus*), and birds like the Lesser spotted woodpecker (*Dendrocopos minor* subsp. *comminutus*), which use deadwood as a habitat, are protected as UK Biodiversity Action Plan (UK BAP) priority species. In order to help conserve biodiversity and encourage diversity of species, it is aimed for deadwood to be present in a non-uniform dispersal; with all stages of decay and of all types to be present. Individual logs may create a continuum of decay, whereby different ends are at different stages (Kuffer and Senn-Irlet, 2005a). This creates habitat for both early and late stage decomposer species (Heilmann-Clausen and Christensen, 2003).

Target volumes of deadwood are created to help conservation, with suggestions that forest management now leave deadwood *in situ*. It is thought that 20 – 30 m^3 ha^{-1} is the minimum required to help maintain biodiversity in boreal and temperate forests (Dudley and Vallauri, 2004; Müller and Bütler, 2010). However, current volumes often fall below this threshold, with volumes of standing and lying deadwood ranging between 8 m^3 ha^{-1} in northern Europe and 20 m^3 ha^{-1} in central and western Europe (Pelyukh, Paletto and Zahvoyska, 2019).

1.3.3 Deadwood decomposition and soil carbon pool

The deadwood present in a forest will decompose over time, as it is broken down by various microorganisms and fungi, until its carbon is emitted to the atmosphere or leached to the soil (Błońska *et al.*, 2019). As wood decomposes, its density lowers, and it begins to break apart. The breakdown of deadwood can lead to the release of carbon in several forms, such as CO_2, CH_4 and DOC, but eventually the majority of CWD are thought to be converted to soil organic matter and the nutrient content is returned to the soil (Zhou *et al.*, 2007). In the initial stages of decomposition, few soluble materials are produced but as decomposition continues, microbes break down polymers into soluble forms that can be leached (Zhou *et al.*, 2007). While deadwood is known to emit significant amounts of CO_2 during decomposition (Covey *et al.*, 2016), Galicia *et al*. (2015) concluded that because CWD can decay very slowly it may represent a long-term sink for atmospheric CO_2.

CH_4 outputs have been found to be highest from large logs in the early stages of decay (Covey *et al.*, 2016). This may be a result of larger stores of carbon being held in larger logs or may be linked to moisture content of logs. It has been found that increased moisture content slows diffusion of gas through wood (Covey *et al.*, 2016) and so debris with higher moisture contents will release CH_4 more slowly. Other research has suggested that moisture content of debris is initially low in early stage decay and increases as water is reabsorbed in late decay (Pichler *et al.*, 2012). It may also be expected that methane emissions are higher from early stages of decay as by the later stages of decay, the majority of carbon has already been lost. Fungi that produce enzymes which split cellulose and lignin have been found to form an initial link in a trophic chain leading to methanogenic archaea (Mukhin and Voronin, 2009) and so the presence of fungi is directly linked to the production of CH_4.

Fungi are believed to be the main decomposers of deadwood. Of the fungi, basidiomycetes are the main decomposition-causing group but some ascomycetes can also cause decay (Schwarze, Engels and Mattheck, 2000). Ascomycetes may be particularly prevalent on deadwood that is not overgrown by a bryophyte layer as seen in a study by Moroni *et al*. (2015). They found that basidiomycetes were only present on deadwood sections that were not overgrown. Fungal community assemblies on deadwood are believed to be driven by a combination of tree species and decay stage (Jonsson, Edman and Jonsson, 2008; Küffer *et al.*, 2008). Identification of these communities is usually through identification of fruitbodies but this is not always possible (Baldrian *et al.*, 2016). Wood decomposing fungi can largely be split into three groups: brown rot fungi, white rot fungi and soft rot fungi. Other fungi, such as yeast, have been found to be positively influenced by the presence of decaying logs (Yurkov *et al.*, 2012) but their association with deadwood is not widely studied.

Brown rot fungi are primarily involved in the breakdown of celluloses and hemicelluloses (Stokland, Siitonen and Jonsson, 2012) and are most commonly found in conifers and boreal forests (Hoppe *et al.*, 2016). They initially degrade holocellulose and lignin components of cell walls using a Fenton reaction; a non-enzymatic oxidative process (Arantes, Jellison and Goodell, 2012) which relies on a constant supply of oxygen in order to decompose substrates and this leads brown rot fungi to favour drier environments. This mechanism opens gaps in the wood cell wall which allows access by the enzymes which are subsequently secreted. Cellulose degradation is usually carried out by endoglucanases and β-glucosidases. Brown rot fungi has a characteristic cracked appearance and brown colouring which is caused by the remaining lignin in the wood it decomposes (Stokland, Siitonen and Jonsson, 2012).

White rot fungi are primarily basidiomycetes responsible for most wood decomposition in temperate and tropical forests and will colonise both coniferous and broadleaved species (Hibbett and Donoghue, 2001). They are capable of breaking down lignin as well as cellulose and hemicellulose. Lignin degradation is usually carried out through the production of lignin peroxidases which can cleave the aromatic rings and degradation may be either simultaneous or through selective lignin degradation. After initial decomposition by selective lignin degradation, hemicellulose and cellulose will be degraded and this forms pockets of cells with a honeycomb like appearance. Wood being decomposed by white rot fungi is characterised by a loose, pale structure that spans a large surface area. The enzymes involved in lignin degradation require a constant supply of O_2 in order to function so white rot fungi is rare in wet environments (Hoppe *et al.*, 2016).

Soft rot fungi are primarily ascomycetes species that break down cellulose and hemicellulose although some can degrade lignin. Soft rot leaves wood darkened with a spongy texture. As soft rot fungi are not constrained by a constant need for O_2, they are more commonly found in wet habitats where the growth of white rot and brown rot are inhibited (Purahong, 2014). They can also occur buried in soil but are outcompeted by basidiomycetes when they establish.

Bacteria may also decompose wood and do so using a range of mechanisms or through forming commensal relationships with fungi (Purahong *et al.*, 2016). However, this is limited as bacterial decomposition in soils occurs more slowly than with fungi so bacteria are often outcompeted (Stokland, Siitonen and Jonsson, 2012).

The wider biodiversity present in a habitat may play an important role in the decomposition of deadwood. Li *et al*. (2007) found that fungi only began decaying heartwood after wood-boring invertebrates bore through the wood surface and allowed spores access. Other research has found that invertebrate entry into CWD can facilitate faster decomposition (Barker, 2008). Current management practices aim to conserve deadwood for its biodiversity values, and this may have knock-on effects for its decomposition. While many wood-boring species in temperate forests are not decomposers, and as such do not alter the degradability of wood, they can facilitate access for decomposing species. However, research has also found that some invertebrates, such as *Leptura rubra* and *Ptilinus pectinicornis*, are capable of producing endoglucanases which have been found in salivary extracts (Martin, 1983) and are known to break down cellulose. Some fungus growing termites and wasp larvae may also acquire the ability to digest cellulose via the ingestion of fungal enzymes. In US temperate forests, ants have been found to have an inhibitory effect on decomposition of woody debris (Warren II and Bradford, 2012). This was thought to be in part due to predation of ants on termites which consume woody debris but also through secretion of antimicrobial compounds (Zettler *et al.*, 2002) which inhibits fungal decay. While termites are not present in UK forests, it may be that native ants are also producing antimicrobial compounds that can inhibit decomposition. Other evidence suggests the possibility of lignin degradation in insect guts (Geib *et al.*, 2008) though the mechanism behind this is uncertain. It is believed that it may be due to a soft rot fungi found in the gut.

1.3.4 Composition of wood

The composition and structure of wood is known to influence the rates and mechanics of decomposition and can broadly be split between conifers (gymnosperms) and broadleaves (generally angiosperms). The structure of angiosperm and gymnosperm wood is known to differ (Harmon *et al.*, 1986; Meerts, 2002) with gymnosperm wood containing less living tissue than angiosperms and gymnosperms typically having a lower wood density than angiosperms. Angiosperm wood contains both tracheids and vessels whilst gymnosperms contain only tracheids. This may lend to higher rates of decomposition being found in angiosperms as nutrients and decomposable materials, such as sugars, are more readily available and accessible. Wood density not only differs by species type, but also stage of decay, with wood in advanced stages of decay having a lower density (Paletto and Tosi, 2010; Harmon, Woodall and Sexton, 2011; Vanguelova, Moffat and Morison, 2016; Moreira, Gregoire and do Couto, 2019; Stakėnas *et al.*, 2020). In the calculation of carbon stocks in deadwood, the GB NFI assumes all deadwood has a density of 0.45 ODT m^3, though this may lead to over or under estimating carbon stocks. Studies are now working to assess species specific, and deadwood type specific densities across a range of decay classes. Additionally to the differences seen between decay classes, stumps and standing dead trees tend to have a higher density than lying deadwood (Di Cosmo *et al.*, 2013).

The three main components of wood are cellulose, comprising 40-50% dry wood weight in both conifers and broadleaves; hemicellulose, at 25-30% and 25-40% dry wood weight in conifers and broadleaves respectively and lignin, making up 25-35% and 18-25% in conifers and broadleaves respectively (Figure 1-4) (Stokland, Siitonen and Jonsson, 2012). Lignin consists of a complex chain of aromatics and the irregular bonds holding units together make it hard to decompose. In a study by Fravolini *et al*. (2016), no change was detected in the concentration of lignin released from deadwood over a two-year period. This was thought to be either due to a lag period in establishment of decomposers or indicative of the slow decomposition of lignin. In a study by Lombardi *et al*. (2013), lignin content remained stable until late stage decay and was only seen to decline in decay class 4-5 for *F. sylvatica* and decay class 5 for *Abies alba*. In contrast, both cellulose and hemicellulose are carbohydrates with a simpler structure and are easier to break down. Zhou *et al*. (2007) found that coniferous species decomposed slower than broadleaved. This was due to the higher lignin content in conifers compared with broadleaves, which contained more sugars, starch and protein.

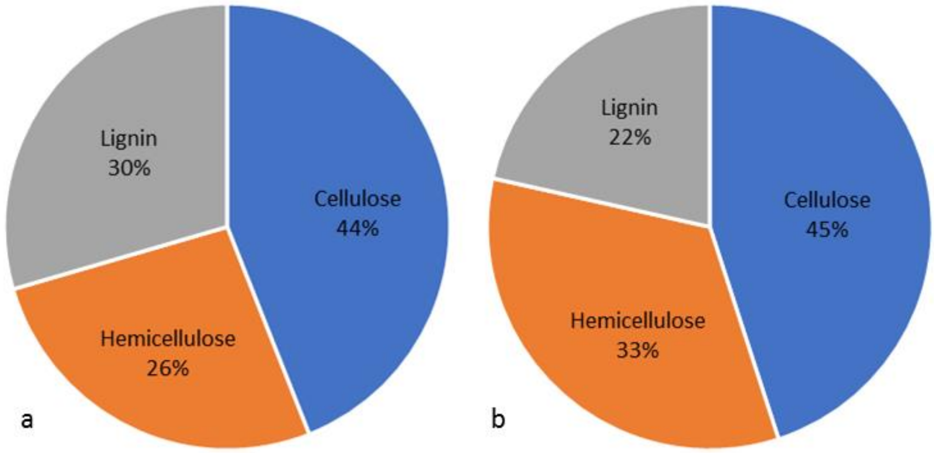


Figure 1-4 – comparison of average coniferous (a) & broadleaved (b) wood composition. Derived from data from Stokland *et al*. (2012)

1.3.5 Factors affecting decomposition and deadwood carbon stocks

There are many biotic and abiotic factors that influence the degradation of deadwood. Soil parameters such as pH and moisture content may play a crucial role, however few studies have been carried out to examine this. Fravolini *et al*. (2016) state that fungi prefer acidic conditions, high soil moisture and clay content. Baldrian *et al*. (2016) found that pH generally decreased during decomposition creating more acidic substrates and these favourable conditions may influence the presence or abundance of fungi which in turn effects the rate of decomposition. Similarly, temperature has been found to have a significant effect on the degradation of deadwood (Berbeco, Melillo and Orians, 2012). In a study by Berbeco *et al*. (2012), it was seen that an increase of 5^{o}C significantly increased the concentration of lignin released from FWD and could lead to an increase of 211 – 456 carbon g m^2 being released over 2 years. Under current climate warming scenarios, this may have implications for the long term decomposition of deadwood. However, other studies have found that although FWD decomposes faster than CWD, FWD carbon stocks may be less affected by a warming climate (Woodall and Liknes, 2008). In the study by Woodall & Liknes (2008), latitude was used as a surrogate for temperature with the effect of decreasing latitude decreasing carbon stocks. FWD carbon stocks showed a weaker relationship with latitude than CWD and so it is possible an increase in temperature will have less effect on the decomposition of FWD than CWD.

Debris size can influence the number of fungal species that are found (Kuffer and Senn-Irlet, 2005b; Blaser *et al.*, 2013) whereby larger debris hold more species. If the presence of more species has a link to decomposition, this could have implications for studies that only look at CWD. Fungi colonies can persist for five to eight years on large logs with a diameter over 30cm (Jonsson, Edman and Jonsson, 2008) which on average is two years longer than found for colonies on smaller logs. However, this may be because larger logs take longer to decompose and so the habitat is present for longer. Ascomycetes species have been found to strongly associate with FWD. In a study by (Norden, Ryberg, *et al.*, 2004), 75% of ascomycetes species found were exclusive to FWD. As ascomycetes are known to be the primary cause of soft rot and are capable of degrading cellulose, hemicellulose and lignin, it may be that this association affects the decomposition that occurs. Decay class may also affect the fungi present and decomposition rates. In contrast to leaf litter decay, fungal biomass is found to be highest during late stage decomposition rather than early stages (Baldrian *et al.*, 2016). Fungal species richness has also been found to increase with increasing decay class (Hoppe *et al.*, 2016).

The proximity of deadwood to the soil may also impact rates of decomposition. Bryophyte colonisation while deadwood is on the soil surface creates an antimicrobial barrier that begins to slow decomposition (Hagemann *et al.*, 2010). Over time, debris is buried in the organic layer of soil where it is kept at a cool, constant temperature and with high moisture content and low oxygen levels (Zeng, 2008). Low decomposition rates occur here due to the antimicrobial conditions (Hagemann *et al.*, 2010) and buried wood has been found to persist for 250 – 500 years (Moroni, Hagemann and Beilman, 2010). Due to this, it has been suggested that carbon sequestration could be maximised through the burial of logs (Zeng, 2008). Buried wood is more commonly reported in coniferous forests that are associated with a dominant bryophyte layer (Moroni *et al.*, 2015) and quantities often range between 100 – 400 m^3 ha^{-1}. Additionally, the cause of tree death could influence the amount, and degradation, of deadwood found. Potentially, trees that have been suffering ill health could be decaying well before they are in contact with the soil, and thus decompose quickly. In contrast, healthy trees that have been killed by other means, such as extreme weather events or felled by management, are likely to be in an undegraded or very low decay class, and so take longer to fully decompose.

Forest management has a large influence on the amount of deadwood in a forest, and subsequently influences the carbon stocks held. Traditionally, management has removed deadwood for aesthetic or health and safety reasons, leading to lower volumes (Peterken, 1996), though it is now recommended to be left *in situ* (Forestry Commission, 2017). Increasing the amount of deadwood present will ultimately lead to an increase in carbon stored in the deadwood pool, though this is currently unquantified at an accurate level.

1.4 Thesis outline

Chapter 2: The impact of woodland management policies regarding deadwood on biodiversity and regulating services in the UK

Chapter 2 addresses objective 1, to assess how local, national, regional and international policies affect deadwood management in UK. This work is based on a literature review.

Historically, deadwood has been removed by forest management for aesthetic reasons, because it might pose an obstruction to access, or because it could be a possible source of pests or disease (Dudley and Vallauri, 2004). In recent years, volumes of deadwood have been used as indicators of biodiversity, with volumes of 20-30 m^3 aimed for as a minimum conservation threshold (Dudley and Vallauri, 2004; Müller and Bütler, 2010), particularly for saproxylic invertebrates. Additionally, there are other environmental benefits to leaving deadwood *in situ* or moving to other locations within the woodland, such as providing materials to support types of natural flood management like leaky barriers in surface runoff pathways or channels. The introduction of policies, such as the Kyoto protocol (United Nations, 1998) have identified deadwood as a forest carbon pool that requires reporting. However, there are no clear, deadwood specific policies and so management can have conflicting priorities regarding removing deadwood or leaving it *in situ*. This review paper aims to identify and collate key policies involved in deadwood management, on a local, national and international scale to assess how it affects UK woodland management. We aim to integrate information on policies regarding both deadwood volumes and carbon inventories into a single resource.

This paper is in preparation to be submitted for peer review in Forest Ecology and Management.

Chapter 3: Field sites

Chapter 3 presents a detailed background to the field sites and data sets used in the following results chapters.

Chapter 4: The impact of forest management on dissolved organic carbon in soils in a temperate Oak woodland

Chapter 4 addresses objective 2, to explore the influence of forest management on forest floor materials and DOC dynamics in soils. This work combined long-term monitoring data with a field survey from a single temperate woodland, Alice Holt Research Forest.

In a previous study analysing long-term data by Sawicka (2015), an unmanaged plot in the lowland oak forest at Alice Holt Forest, South East England, was found to have twice the median DOC compared to a neighbouring, managed plot that underwent regular thinning and deadwood removal. It was hypothesised that the presence of deadwood was the cause of this increase in soil DOC and other studies have found a similar increase in soil DOC where deadwood is present (Hafner, Groffman and Mitchell, 2005; Bantle *et al.*, 2014). Deadwood, along with forest floor vegetation and leaf litter, was assessed as a source of DOC and compared against background levels in various soil horizons. The carbon stocks in each of these pools was also calculated, to assess the contribution of deadwood relative to other forest floor materials and forest soils.

This chapter has been published in Science of the Total Environment (Hollands *et al.*, 2022). Analysis of long-term monitoring data presented in the paper was from Sawicka (2015), who is co-author. The field and lab work was originally carried out as a dissertation project by Reading University BSc student Claire Hollands, supported by co-authors from the University of Reading and Forest Research, who supervise this PhD, Joanna Clark and Elena Vanguelova, and with help from Sue Benham. The data produced was subsequently re-analysed and the paper was independently written following Holland's graduation by Shannon, her supervisors, and collaborators. However, the BSc student, Hollands, has been submitted as lead author, with Shannon as second and corresponding author. Work in this paper underpinned the ideas submitted to the NERC iCASE funding application for this PhD, hence publication of this work was considered crucial for the thesis.

Chapter 5: The contribution of deadwood to soil carbon dynamics in contrasting temperate forest ecosystems

Chapter 5 addresses objective 3, to assess how forest type (coniferous and broadleaf) and stand age influence soil carbon under deadwood. This work represents a combined field survey and laboratory analysis at two Forest Research sites: Alice Holt and Kielder.

In the research by Hollands (2022), it was discovered that deadwood produces 44-53 mg g^{-1} DOC, equivalent to leaf litter (46-49 mg g^{-1}), which was significantly more than fresh vegetation or soils. This paper (Chapter 5) aimed to further explore this relationship using two contrasting woodlands: upland Sitka spruce and lowland oak forest, to identify whether a deadwood effect occurs in both forest types. The quantity and quality of DOC in soils produced by deadwood and plots with only leaf litter was assessed. We aimed to identify the effect that additional DOC produced by deadwood may have on surrounding soil activities, hypothesising that a priming effect may occur. Priming effects are defined as an increase in microbial activity, caused by fresh inputs of labile carbon, leading to increased rates of decomposition of organic matter (Fontaine, Mariotti and Abbadie, 2003; Beverly and Franklin, 2015).

This work has been published in the European Journal of Forest Research (Shannon *et al.*, 2021). This study was led by Shannon, who designed the method, carried out work, analysis and led the write up of the paper, with design, analysis and write up supported by her supervisors/co-authors.

Chapter 6: Impacts of stand type, management, and cause of tree mortality on deadwood carbon stocks in Great Britain from the Natural Forest Inventory (2009-2015)

Chapter 6 addresses objective 4, to evaluate carbon stocks in deadwood with respect to forest types, state of decay and forest management. This paper presents an analysis of the NFI data set and focuses on plot scale data.

Previous estimates of the UK deadwood carbon stock have been based on the principle that all deadwood has a uniform wood density. For this chapter (6), we have applied a specific wood density by decay class and species type to determine carbon stocks in deadwood across GB. As previously seen in Chapter 4, woodland management can influence carbon stocks in forest floor materials. In this chapter, we assess the effect of different woodland management practices on deadwood volumes and carbon stocks, and how this is distributed between forest and deadwood types. Additionally, we assess how cause of tree death impacts volumes and carbon stocks of standing deadwood and identify whether certain causes are more prevalent.

This paper is in preparation to be submitted for peer review, subject to agreement with the NFI team. The design, analysis and write up has been led by Shannon, with main support on design, analysis and write up from Vanguelova and Morison and additional support from Shaw and Clark with design, write up and presentation.

Chapter 7: Upscaling NFI plot data to national level inventories: challenges and results

Chapter 7 addresses objective 4, to evaluate carbon stocks in deadwood with respect to forest types, state of decay and forest management. This paper focuses on analysis of the NFI data set, upscaling the plot scale data from Chapter 6 to present national scale stock estimates.

In the latest UK estimates (Forest Research, 2020), a density of 0.45 ODT m^3 is assumed for all types of deadwood; concluding that there is 40.6 million tonnes carbon held within UK deadwood. However, we know that wood density varies depending on state of decay and type of tree (broadleaf or conifer). In a large, UK study, wood density was found to vary from between 0.16 -0.57 g cm^3 in broadleaves and 0.21 - 0.49 g cm^3 in conifers, reducing as wood decayed (Vanguelova *et al.*, 2013). Using the results from Chapter 6, we upscaled volumes and carbon stocks to a national level to calculate total volumes and carbon stocks in GB. We also assessed how volumes of deadwood were distributed between countries in the UK. We explore the role of different methods in estimation of national scale stock estimates and discuss some of the challenges in upscaling NFI data.

This paper is in preparation. Submission for peer review is subject to agreement with the NFI team. There has been much discussion about different methods which could be used and the need to align with the published national statistics. The work is an important part of Shannon's PhD research training and so is presented as a standalone chapter here in the PhD thesis. The design, analysis and write up has been led by Shannon, with main support on design, analysis and write up from Vanguelova and Morison and additional support from Shaw and Clark with design, write up and presentation.

Chapter 8: Discussion and conclusion

Chapter 8 brings together the key findings from each of the chapters presented, to examine the advance in knowledge made by this thesis to understand the role of deadwood in forest carbon dynamics. Key findings, limitations and further research needs are presented.

2 The impact of woodland management policies regarding deadwood on biodiversity and regulating ecosystem services in the UK

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2.1 Abstract

Deadwood is an important, though often overlooked, part of forest ecosystems, which may be regulated and utilised as part of biodiversity conservation, woodfuel and timber production, forest health management, and regulating ecosystem services of climate mitigation through carbon sequestration and natural flood management. Retention of deadwood may be suggested to benefit biodiversity, carbon storage and as a method of natural flood management. Alternatively, deadwood may require removal to protect forest health or for the provision of woodfuel and timber. Additionally, there are instances where both retention and removal are desired, such as increasing biodiversity and carbon storage in timber plantations. Despite this, policy and guidelines involving deadwood are vague and often only address one or two of these five forest ecosystem services, with a minimal focus on deadwood itself.

We review the role of deadwood in each of main forest ecosystem services and assess the various policies and forest guidance involved in deadwood regulation, from a global to regional scale. We identify where these are conflicting or synergistic and the impact they have on deadwood retention. We further discuss the methods used to calculate deadwood volumes and carbon stocks for reporting and review the direct effects of woodland management on these to create an accessible deadwood management resource for forest managers. We conclude that policy across all five ecosystem services recommends deadwood retention, in varying amounts, unless there is an immediate danger to forest health. We suggest future policy addresses multiple ecosystem services to provide comprehensive guidance to forest managers.

2.2 Introduction

Dead and decaying wood, or deadwood, is a key component of forest ecosystems. Deadwood provides a habitat for plants, fungi and invertebrates, many of which are endangered or rare (Ashwood *et al.*, 2019), and which form the basis of complex food chains (Hunter, 1990). A proportion of woodland carbon (C) stocks is held in deadwood, with Pan *et al*. (2011) estimating that deadwood accounts for 8% (73 ± 6 Pg) of the world's forest carbon. Deadwood can provide a supply of woody material into stream and river networks to support the creation of natural dams that can slow the flow of water, providing natural flood management (Thomas and Nisbet, 2012). Therefore, deadwood supports forest biodiversity and regulating ecosystem services provided by woodlands.

Yet, deadwood has historically been removed by woodland management. This is usually for aesthetic reasons or to make the environment safe where there is public access, prevention of pests and disease, removal of obstacles to management or the view that it is a wasted resource (Dudley and Vallauri, 2004; Evans, 2021). For instance, pests, such as bark beetles, are known to inhabit dying and dead wood and pose a risk to surrounding trees, carrying diseases such as Dutch Elm Disease, prompting the removal of deadwood for sanitary reasons, especially in commercial plantations (Evans, 2021). This has led to snags, late stage decay and large diameter deadwood becoming rare in managed woodland (Thompson, Vehkaoja and Nummi, 2016). However, these can provide important habitat for a number of species.

These differences between woodland management aims have led to contrasting policies surrounding deadwood management practices. Guidelines and practice guides that focus on biodiversity conservation advocate leaving deadwood in situ and actively 'enriching' deadwood stocks through felling or ring barking to create standing dead trees (Humphrey *et al.*, 2002), whereas guidelines for timber production sometimes recommend deadwood removal to support forest health and maintenance (e.g. FAO Guide to implementation of phytosanitary standards in forestry), or to use brash as a source of woodfuel for bioenergy (Moffat, Jones and Mason, 2006). Recommendations for regulating services like carbon sequestration or natural flood management are less clear and poorly connected to wider management practices. This can lead to seemingly conflicting advice for forest managers.

The aim of this review is to identify the key policies affecting deadwood management in the UK to evaluate the synergies and trade-offs between timber production, biodiversity conservation, and regulating ecosystem services of climate mitigation through carbon sequestration and natural flood management.

2.3 Definitions of deadwood

Deadwood (also referred to as woody debris) is formed through the death of all or part of a tree and may occur on land or in streams and rivers (Stokland, Siitonen and Jonsson, 2012). This may take the form of dead branches that are attached to a living trunk, entire dead trees still standing or sections of dead wood that have fallen to the forest floor and also includes stumps or coarse roots below ground (see Figure *2-1*). Deadwood is often split into two main classes: coarse woody debris (CWD), which is usually described as having a diameter >10 cm, and fine woody debris (FWD) with a diameter <10 cm. Dead trees may be classified as either standing dead trees (SDT or snags) or lying dead trees (LDT or logs) and are composed of the whole tree rather than a single branch. However, the threshold to classify CWD and FWD varies between studies. For instance, Peterken (1996) used a minimum diameter of 2.5cm to classify CWD whereas the Swiss National Inventory classifies 'smaller woody debris' as between 7 and 12 cm (Weggler *et al.*, 2012). Kuffer and Senn-Irlet (2005b) proposed the introduction of very fine woody debris (VFWD) as the classification of debris with a diameter <5 cm and FWD was then used to classify debris with a diameter of 5 - 9 cm. However, in line with the deadwood assessment protocols used in the European BioSoil project (Durrant *et al.*, 2011), for this review CWD will be defined as woody debris with a diameter >10 cm and FWD as debris <10 cm diameter. These diverse definitions make comparison between studies difficult as they may be including very different sizes of debris.

Most studies focus on CWD with little being published on FWD or VFWD. Despite this, FWD can contribute a high proportion of total deadwood volume with an estimated 46% being FWD in temperate forests (Norden, Gotmark, *et al.*, 2004). In a study by Ruiz-Peinado *et al*. (2016), FWD was found to contribute 90% of deadwood carbon in an unthinned stand of Scots pine (Pinus sylvestris) in Spain and 98% in a moderately thinned stand. Kuffer and Senn-Irlet (2005b) found that VFWD had much greater fungal species diversity than either FWD or CWD but debris of this small size are rarely studied. However, management often only removes CWD and standing dead trees which may lead to an accumulation of smaller debris in forests. As such, the value of studying smaller debris should not be overlooked.

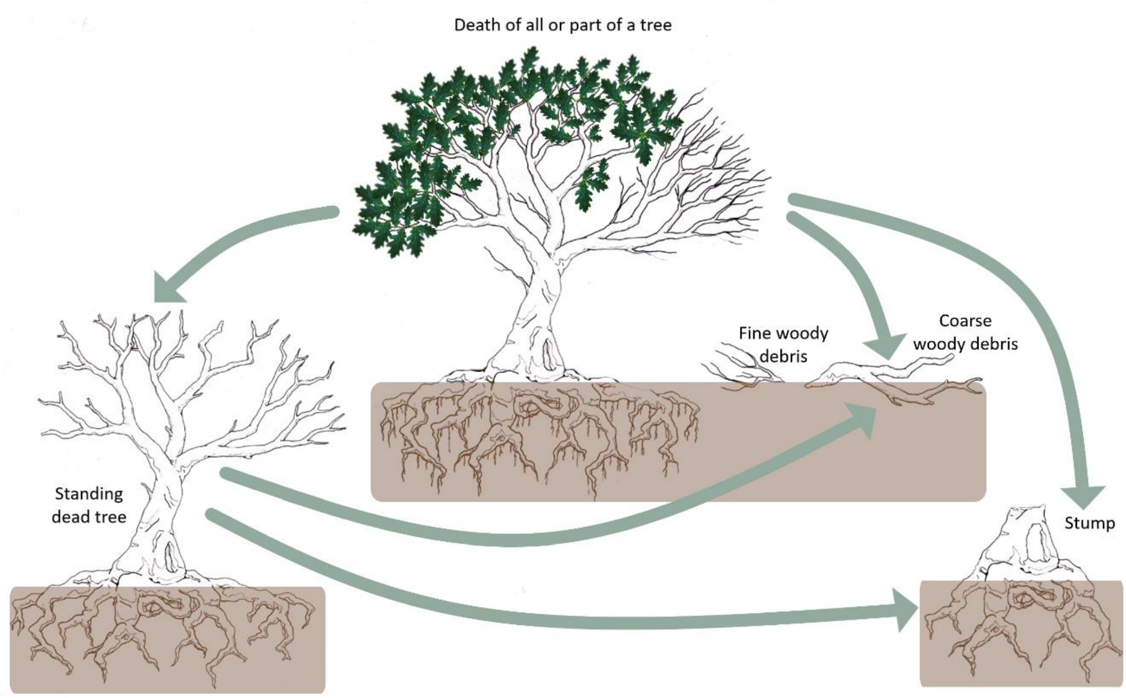

Figure 2-1 – examples of different types of deadwood and transitions between types

Deadwood is also defined by its state of decay (Figure 2-2) as described by Maser *et al*. (1979) and Hunter (1990). Stage of decay is assessed based on field observations, with woody debris often ranked on a scale of one to five (Maser *et al*, 1979; Hunter, 1990) and standing trees and stumps on a scale of one to nine. For standing trees, death is presumed to occur at stage three, before the bark loosens (stage four), branches snap off (stage five), and the stem breaks (stage six). Stage seven indicates a decayed stem with stages eight and nine being stumps.

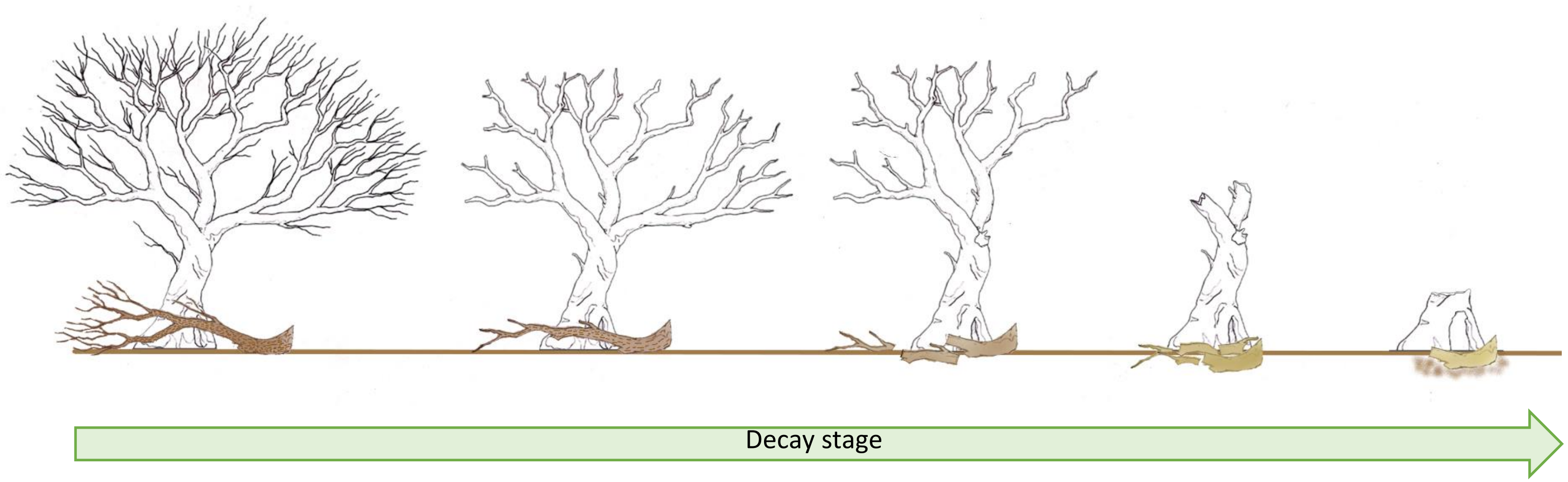

Figure 2-2 – examples of increasing decay stage from freshly dead wood (left) to advanced decay (right)

Woody debris on the ground begin at stage one as freshly dead wood before losing small twigs (stage two), bark (stage three), and the texture turning soft (stage four) and powdery (stage five).

Deadwood volume is often used to form threshold targets for preservation of biodiversity, particularly for saproxylic invertebrates. However, other studies suggest that volume alone may not provide adequate indication of saproxylic biodiversity, and a diversity of wood species and locations is required. In a meta-analysis by Lassauce *et al*. (2011), it was found that while species richness of saproxylic organisms and deadwood volume were correlated, it was not strongly so. They suggested that other factors, such as decay class, when coupled with deadwood volume may help better predict biodiversity.

2.4 Policy and guidelines

2.4.1 Scale and accountability

Deadwood is included as part of many different policies and guidelines, although most only briefly refer to deadwood directly. At a global level, policy created to combat climate change, such as the Kyoto Protocol, have included deadwood as a carbon pool that requires national reporting. Other global standards created by non-governmental organisations, such as the Programme for the Endorsement of Forest Certification (PEFC), created a global benchmark that is then translated to a national level (PEFC UK Certification Scheme), though the objectives are similar. At national levels, governments may create specific woodland management policy which will affect deadwood management, which can be general or specific to a region or site. These are often translated into practical guidance documents for managers which include more in-depth advice on deadwood management or standalone deadwood practice guides e.g. Humphrey & Bailey (2012). A synthesis of policy, guidelines and guidance which include deadwood is presented in Table 2-1, giving examples from international, to national (UK) and country or regional within the UK.

Table 2-1 – Summary of policy, guidelines, guidance and practices and their scale of remit. ✓ implies that deadwood is monitored or general guidance is given, + that deadwood retention is advised, - that deadwood removal is advised in certain situations

Scale	Policy	Biodiversity	Carbon sequestration emissions and climate change	Flood management	Forest health management	Fuel and fibre production
Global	LULUCF section of the United Nations Framework Convention on Climate Change (IPCC, 2003)		✓			
	Kyoto Protocol (1998)		✓			
	Programme for the Endorsement of Forest Certification (PEFC) Sustainability Benchmarks (2018)	+			-	
	FAO Guide to implementation of phytosanitary standards in forestry (2011)				-	
European	The Pan-European Ministerial Conference on the Protection of Forests in Europe (MCPFE) State of Europe's Forests (2020)	✓	✓			
	Forest Stewardship Council (FSC) certification (2021)	+				
	EU Biodiversity Strategy (2011)	+				
National: UK	UK Forestry Standard (Forestry Commission, 2017)	+		+		
	Climate Change Act (2008)		✓			
	Guidance on site selection for brash removal (2009a)	+	✓			-
	Stump Harvesting: Interim Guidance on Site Selection and Good Practice (2009b)	+	✓	+	-	-
	Whole Tree Harvesting: A guide to good practice (1997)	+				+
	Protecting the Environment during Mechanised Harvesting Operations (2005)					+

	Scottish Forestry Strategy (SFS) implementation plans (2020)	✓	✓			
	UK FSC/United Kingdom Woodland Assurance Scheme (UKWAS) (2016)	+			-	
	PEFC UK Certification Scheme for Sustainable Forest Management (2016)	✓				
	Natural flood management guidance: Woody dams, deflectors and diverters (2016)			+		
	Practice Guide entitled: Managing deadwood in forests and woodlands (2012)	✓				
Devolved – England, Scotland, Northern Ireland	Practice guide entitled: Achieving diversity in Scotland's forest landscapes (2012)	+			-	
	Deadwood summary guidance for FES staff (Kortland, 2016)	+				
	Practice guide entitled: Scottish Invertebrate Habitat Management (2011)	+				
	Forest Resilience Guide 1: Improving the structural diversity of Welsh woodlands (2017)	✓				-
Regional and site specific	Practice note: Managing Brash on Conifer Clearfell Sites (2006)		✓		+	
	Practice guide series: The Management of Semi-natural Woodlands (1994)	+				
	UK Biodiversity Action Plans (1994)	+				
	Species and habitats listed under the EU Habitats Directive (Directive 92/43/EEC (1992)	+				
	Woodland management plans	✓	✓	✓	✓	✓

2.4.2 Biodiversity: Forest processes and policy

Lying deadwood increases the heterogeneity of forest floors which provides a range of habitats and helps sustain diversity of species. Chemical changes that occur during decomposition, coupled with the fact that logs do not decompose equally along a length, helps create the wide variety of niches that lead to a high level of diversity (Kuffer and Senn-Irlet, 2005a). For instance, a single log may comprise different decay classes and so offer habitat for both early and late stage decomposer species (Heilmann-Clausen and Christensen, 2003). In the study by Heilmann-Clausen & Christensen (2003), it was found that decay classes 3 and 4 were significantly more diverse than decay classes 1 and 5. These authors also found that log length and surface area was more important for diversity than debris diameter. However, as with many other studies, this only looked at CWD so these findings may not be true for FWD or VFWD. Deadwood also provides nursery sites which aid seedling establishment (Fukasawa, 2012). UKBAP priority species such as the Stag Beetle (*Lucanus cervus*) and Violet Click Beetle (*Limoniscus violaceus*) are strongly associated with deadwood for their reproduction and so the habitat must be conserved by law. Other species, such as cavity nesting birds, rely on dead or decaying wood in order to build nests (Hodge and Peterken, 1998) and a loss of deadwood habitat may lead to a decline in populations.

Separate policies exist to conserve biodiversity, and these make up the majority of policies and guidance documents that involve deadwood (Table 2-1). In woodlands, deadwood is often used as an indicator for biodiversity, particularly for invertebrates, with a greater volume of deadwood indicating larger levels of biodiversity. The UK Forestry Standard (UKFS) was created to outline the UK government's approach towards sustainable forestry. Deadwood is included in the criteria for the 'maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems'. In this, it is advised that management avoids a uniform distribution of deadwood whilst leaving a proportion of standing and fallen deadwood *in situ*. A recommended volume of $20m^3$ per hectare is given, however, there is no requirement for volumes to be measured in order to comply with UKFS Requirements for Forests and Biodiversity. Volumes of no less than ~20 m^3 ha^{-1} are often cited as the threshold volume required for biodiversity (Dudley and Vallauri, 2004; Humphrey and Bailey, 2012; UKWAS, 2018), though higher volumes of <100 m^3 ha^{-1} should be expected in semi-natural woodlands (Humphrey *et al.*, 2002). However, guidance on deadwood retention does not always apply in instances where tree health is endangered e.g. *Heterobasidion annosum* infection in stumps. In such cases, it may be necessary to remove deadwood, at the risk of reducing biodiversity.

Other policies, such as Forest Europe (previously the Ministerial Conference on the Protection of Forests in Europe), also list deadwood as an indicator of forest biodiversity and provide volume thresholds for managed and unmanaged woodlands across different species compositions. They recommend that the volumes of lying and standing deadwood in forested land are periodically monitored to assess the levels of diversity, particularly saproxylic invertebrates. This may be inferred through the use of National Forest Inventories which measure deadwood volumes.

2.4.3 Climate change policy: Forest processes and policy

Forests are an important part of the global carbon cycle, covering around 1/3 of land surface globally (FAO, 2020b), and holding ~27% (861 Pg) of terrestrial carbon stocks (Pan *et al.*, 2011) in their soils, biomass, litter and deadwood. Carbon may be lost from deadwood through decomposition, as either CO_2 or CH_4 emitted into the atmosphere or as dissolved organic carbon or incorporated into the soil organic matter.

International agreements are increasingly being used to reduce climate change through the creation of target limits to emissions or incentives to limit greenhouse gas emissions, such as CO_2 and CH_4. The Kyoto Protocol was created in 1997 as part of the UN Framework Convention on Climate Change (UNFCC) and subsequently the 2015 Paris Agreement aims to limit global warming to below 2°C compared to pre-industrial levels. These agreements, require national carbon inventories to be carried out annually and for all parties to annually report emissions and efforts to curb them. Carbon inventories often split forests into four main categories: carbon in above-ground biomass, below-ground biomass, soil carbon, carbon in litter and/or deadwood, with not all reports differentiating between the litter and deadwood carbon pools.

Many countries carry out National Forest Inventories (NFIs) which aim to collate information, such as forest area, composition and biodiversity of a nation's forests and carbon storage is now included as a measurement. Forest inventories date back to the early 20th century and have historically been carried out in order to collate information on the productive function of forests (Chirici *et al.*, 2012). However, previous inventories have excluded deadwood as a carbon pool. The introduction of the Land Use, Land-use Change and Forestry (LULUCF) section of the Kyoto Protocol requires that deadwood carbon pools are now reported. Forest inventories were updated in the late 20th century to report on a wider range of goods and services and many now include a deadwood component. However, deadwood is still a seldom reported pool of carbon in scientific literature and NFIs focus on carbon in living biomass or the soil. For instance, the Global Forest Resource Assessment (FRA) reports deadwood carbon stocks for only 78 out of 193 countries (FAO, 2020b).

The Woodland Carbon Code (WCC) has been created in the UK as a voluntary standard that afforestation projects can join in an effort to mitigate carbon emissions. The Code requires that any woodlands created are sustainably managed to a national standard and that estimates of carbon sequestration through the planting are made. As part of this, litter and deadwood are included as a carbon pool to be measured during the calculation of baseline carbon stocks. However, it is assumed that these stocks will stay constant over time.

2.4.4 Natural flood management: Forest processes and policies

Deadwood may also have benefits for environments outside of forests, such as contributing to Natural Flood Management (NFM), where it is typically referred to as 'coarse woody debris' or 'large woody debris'. NFM seeks to reduce flood risk by restoring and emulating natural processes that act to store and slow flood runoff within catchments (Ngai *et al.*, 2017). This can involve a wide range of land management-based interventions from changing soil management practices to re-meandering rivers. Woodland creation is potentially a very effective NFM measure due to the ability of trees to enhance canopy evaporation, improve soil infiltration, and create hydraulic roughness (Nisbet and Thomas, 2021). Deadwood can make an important contribution to the latter, accounting for as much as 98% of flow resistance within wooded river channels (Dixon, 2013).

Floodplain and riparian woodland contribute most to hydraulic roughness as the lack of management that typifies these woodlands promotes diversity in woodland form and structure, allowing deadwood to accumulate over time. Deadwood is most effective in slowing runoff when located within or along runoff pathways, where there is greater contact with flowing water (Nisbet *et al.*, 2011). Individual pieces of deadwood can deflect and divert shallow flood flows, but deadwood is most effective where it collects to form leaky dams that promote water ponding and flood storage.

Leaky woody dams form naturally as deadwood is supplied to the river by riparian woodland but have traditionally been actively removed by river managers to avoid issues with angling or washout blocking downstream structures and causing flooding. This has led to a deficit of deadwood in rivers and, in recent years, to efforts to restore leaky woody dams by felling bankside trees or installing structures, including securing these into place to reduce the risk of washout (Environment Agency, 2018). Older, more decomposed deadwood is less stable and more likely to fail at high flows, so installed dams may need active management to maintain effectiveness.

Studies are increasingly demonstrating the potential for deadwood and leaky woody dams to contribute to NFM. Although the effects are site specific and greatly influenced by the number and location of dams, they have been shown to reduce flood peaks and delay the progression of the flood wave (Ngai *et al.*, 2017). Impacts are greatest at the reach scale, with measurements showing a reduction in local peak discharge of up to 27% (Norbury *et al.*, 2021) and an increase in flood wave travel time of over 100 minutes (Gregory, Gurnell and Hill, 1985). Modelling predicts that these effects can extend to a catchment scale, where a network of leaky woody dams could reduce downstream flood velocity by 2.1 m s^{-1} (Thomas and Nisbet, 2012) and flood peaks by up to 19% (Dixon *et al.*, 2016).

Deadwood in rivers provides other ecosystem services including carbon storage, improved water quality and biodiversity (Short *et al.*, 2019; Seddon *et al.*, 2020). It exerts a major influence on channel formation and floodplain geomorphology, creating complex and dynamic freshwater habitats that benefit a range of aquatic life (Grabowski *et al.*, 2019).

The ecological and NFM benefits of retaining deadwood in rivers is now widely recognised and accepted by water regulators and fishery groups. The UK Forestry Standard (Forestry Commission, 2017) promotes the creation and management of native riparian woodland buffers along watercourses to provide a source of deadwood and leaf litter, as well as shade and shelter. Felled brash should be kept away from buffer areas but the retention of coarse woody debris and formation of leaky woody dams is favoured where the washout of these do not pose a significant risk of blocking downstream structures. Separate guidance has been produced to assess and manage the potential hazards of using leaky woody dams for NFM in the UK (ADEPT, 2019).

2.4.5 Woodfuel and timber production

Woodlands worldwide have long been used as a naturally regenerating resource, providing timber and woodfuel alongside their regulatory and cultural benefits. The species grown in managed plantations will reflect the intended use of wood, with most coniferous woodlands in the UK having a plantation origin. Wood grown for timber holds a higher value when there is a substantial fraction that is straight, knot, branch and shoot free and with a wide diameter. To achieve this, management may implement thinning, which provides remaining trees with increased availability of nutrients, water and light (Kerr and Haufe, 2011), or pruning to reduce knot formation. These activities may create deadwood, as outlined in section 2.5, below.

Demand for woodfuel has been increasing over recent years (Forest Research, 2021), due to an increase in the use of wood for heating and energy production. Nearly all wood, including low quality timber can be used as woodfuel, offering an opportunity for plantations to retain low timber quality trees and implement less intensive management practices. However, guides, such as the guidance on site selection for brash removal (2009a), cover nutrient sustainability of soils, acidity, carbon, water, physical damage but not biodiversity and other ecosystem services which deadwood benefits.

Certification schemes such as PEFC and Forestry Stewardship Council (FSC) have been created to ensure timber is produced and processed in a responsible and sustainable manner by demonstrating good management practices compared against a standard. The UK government Timber Procurement Policy (TPP) stipulates that any timber used by the government's estate must be sustainable, as defined by their guidelines to meet criteria similar to certification. To achieve this, forest management must be able to prove that harm to ecosystems is minimised through protection of soil, water and biodiversity (TPP section 5.b) and biodiversity is maintained (TPP section 8), whilst also ensuring the health of the forest (TPP section 7) (Defra, 2013). As of 2021, 44% of UK woodland (1.41 million ha) is certified (Forest Research, 2021).

2.5 Management practices

2.5.1 Deadwood management

Global policies, such as the Kyoto Protocol, are translated into national legislation, such as the Climate Change Act 2008 (Table 2-1). This is then used to inform guidance practices which will be implemented by forest management. Deadwood management practices will differ depending on the aim of the forest and the benefits and disadvantages of each practice have been discussed in papers such as Vítková *et al*. (2018). Forests that are managed for timber or fuel production are likely to undergo more intensive management than those that are managed solely for biodiversity, for instance, and lead to varying amounts of deadwood production (Table 2-2). Typical management practices include thinning (removing trees to reduce density), coppicing (cutting trees to ground level to encourage new growth), and clearfelling (felling an entire stand of trees) with certified woodlands carrying out management according to their certifying body (Table 2-1). Woodlands that are managed for purposes other than timber production are likely to still be managed in some way. In some cases, conservation management may include measures to actively create deadwood habitats for saproxylic species through activities such as ring barking, or girdling, (Agnew and Rao, 2014) whereby the bark is removed around the circumference of a trunk or branch to kill the upper portions. Management practices, such as coppicing which produce deadwood can benefit invertebrate populations. Timber and brash created through coppicing or felling may be left *in situ* for biodiversity needs, turned into dead hedging, or removed and turned into woodfuel.

Table 2-2 – Woodland management categories and their potential to create deadwood

Woodland management categories	**Deadwood generation potential**	**Description**
Natural reserves, ancient semi-natural woodlands, native pinewoods	High	Lack of forest management allows a high generation and retention of deadwood.
Riparian woodland/buffers along watercourses	High	Riparian woodlands are a main source of inputs of large woody debris into watercourses, which has beneficial impacts for many species, including fish, as well as a method of flood prevention.
Plantations on ancient woodland sites (PAWS) with high ecological potential	High	PAWS enclosed by other semi-natural woodlands, that may host protected species, will reduce management impacts.
Wood pasture / open grown trees	Medium	Trees in wood pastures are able to grow large side branches due to lack of competition for light.

		The crowns of open grown trees retrench with the highest branches dying.
Minimum intervention areas of broadleaved woodlands, PAWS, long-established plantation origin woods (LEPOs), long-term retentions, low impact silvicultural systems (LISS) coupes.	Medium	Areas with reduced management which allows some retention of deadwood.
All other stands i.e. stands where timber production is the priority	Low	Stands where thinning and clearfelling operations are carried out may leave little deadwood, particularly if brash is removed.
Stands managed for tree health control reasons, e.g. stump harvesting to eliminate pest / disease.	Low	Where pest and disease occur, deadwood, particularly stumps, are sometimes removed to limit the spread.

Current UK management practice guides (Table 2-1) aim to maintain healthy forests while incorporating deadwood as a habitat (Humphrey and Bailey, 2012). This may be through identifying areas with high ecological value and limiting management or retaining a portion of fallen deadwood. For example, fallen deadwood that is presenting an obstacle may be moved or piled into one area rather than being completely removed from the forest. In some instances, artificially creating a deadwood environment, through felling or injuring existing trees, may be carried out to create habitat or aid the continuation of habitat corridors (Cathrine and Amphlett, 2011). Thinning practices in managed forests may also result in the production of deadwood as debris or stumps (Duvall and Grigal, 1999). Using a chronosequence approach, Duvall & Grigal (1999) found that the amount of CWD in forests was high immediately following thinning and amounts produced increased with stand age due to older trees being larger. Other natural disturbances such as storm damage and wind throw may create additional deadwood.

Large variability in the response of deadwood to management has been seen but carbon pools in deadwood generally show a declining trend in forests under intensive management (Kalies, Haubensak and Finkral, 2016). Using regression modelling, Duvall & Grigal (1999) estimated that managed forests reached 90% of their asymptote deadwood volume after 100 to 125 years in contrast to an unmanaged forest that required 900 to 1200 years, because of the higher volume of deadwood that is expected to be found in an unmanaged forest.

In a natural, unmanaged forest, deadwood of all decay stages would be present forming a diverse array of habitats. However, management will often remove deadwood in a non-uniform way. For instance, Siitonen (2001) found that large diameter trees with advanced decay were most commonly removed whilst CWD were less affected. The UK Forestry Standard suggests that a proportion of standing and lying deadwood is left *in situ* and well linked with other deadwood habitat in order to preserve diversity and protect habitat. A diversity of deadwood sizes is known to be necessary to maintain saproxylic biodiversity (Brin *et al.*, 2011) and so it is important to retain different size debris at different stages of decay.

Many currently unmanaged forests will have been managed in the past and may still be influenced by previous practices. Blaser *et al*. (2013) found that managed *Fagus sylvatica* plots in Germany contained higher levels of deadwood than presently unmanaged plots, which they attributed to the recent cessation of management practices only 10 to 30 years prior to the study, while it takes 200 to 300 years before the mortality of *F. sylvatica* increases to the levels seen pre-management.

2.6 Policy evaluation and measurement tools

2.6.1 Carbon stocks

In order to evaluate trends in woodland carbon, the carbon pools in woodlands are regularly evaluated and reported as shown in Table 2-1. Deadwood has been estimated to contribute 8% (73 ± 6 Pg) of the world's forest carbon stock across all biomes, and in temperate forests it represents 14% (Pan *et al.*, 2011). The amount of carbon held in deadwood is calculated by determining the biomass and then multiplying this by the carbon fraction (%), generally assuming the carbon fraction of wood is 50%. However, recent work is aiming to identify more specific carbon fractions (Ma *et al.*, 2017; Martin *et al.*, 2021), as it is acknowledged that carbon content is slightly larger in conifers than broadleaves, and increases with decay class (Martin *et al.*, 2021). The implication of more specific carbon fractions on overall deadwood stocks is unclear, and further work is needed to evaluate this. Research has shown that a lower deadwood input into soil results in a smaller soil carbon pool (Zeng, 2008). Carbon held in tree material has the potential to be released as CO_2 or leached as DOC during decomposition of plant material (Hollands *et al.*, 2022), so it is important to evaluate the stocks that are held and fluxes that are released. Deadwood carbon stocks are influenced by the volume of deadwood present.

2.6.2 Deadwood volumes

Assessment of deadwood volumes is necessary, not only as an indicator of biodiversity, but also for calculating carbon stocks. Deadwood biomass is calculated as the product of wood density and volume. The abundance of deadwood can be impacted by woodland management activities (Table 2-3). The UK Woodland Assurance Standard suggests that a minimum of 20 m^3 ha^{-1} or 5-10% of the average standing volume of deadwood are left *in situ*. In the UK Humphrey *et al*. (2002) suggest that values over 100 m^3 ha^{-1} are approaching the more natural levels of an undisturbed environment but a managed wood will average 30 - 50 m^3 ha^{-1}. They state that in UK native pinewoods and old pine plantations, snags are more abundant than logs. This difference in snag and log abundance may be due to a variety of factors, such as tree species or climate, but in most woodlands will be affected by management. In a natural, temperate European beech forest, an average CWD volume of 130 m^3 ha^{-1} was found (Hahn and Christensen, 2005). The study by Hahn & Christensen (2005) found that decaying logs were typically more abundant than snags with snag volumes ranging from 1 - 282 m^3 ha^{-1} (average 39 m^3 ha^{-1}) and log volumes ranging from 3 - 456 m^3 ha^{-1} (average 94 m^3 ha^{-1}). However, other research suggests lower values, particularly in managed woods (Table 2-3). In a UK study based on the BioSoil survey network, deadwood volume was calculated at 10.45 m^3 ha^{-1} in conifer plots compared with 5.61 m^3 ha^{-1} for broadleaves (Vanguelova, Moffat and Morison, 2016). Muller and Butler (2010) recommend volumes of 20 - 30 m^3 ha^{-1} for boreal coniferous forests and it is likely this volume will also help maintain biodiversity in temperate forests (Dudley and Vallauri, 2004). The use of policy to encourage greater deadwood volumes will benefit biodiversity, as at present many managed woodlands hold a volume below the recommended threshold. However, there are currently very few instances where a quantified volume is included in policy, providing woodland managers with little guidance on the quantity to aim for. Implementation of thresholds for specific circumstances may aid woodland managers to make informed decisions regarding deadwood retention. For instance, areas of minimum intervention may be expected to hold larger deadwood volumes than those with intensive management (Crane, 2020). However, management practices, such as thinning, create deadwood (Hollands *et al.*, 2022) and if this was left *in situ* it could support higher volumes.

2.7 Conclusions

The benefits of deadwood range from increasing forest biodiversity, storing carbon and acting as a natural protection to flooding. There are 26 policies and guidance documents from global to national scale that affect the management of deadwood in the UK. The general consensus of these policies is to retain deadwood *in situ*, unless there is an immediate threat to woodland or public health. Management can create deadwood, and thus enhance biodiversity and carbon storage, or remove it, which has the effect of reducing carbon stocks and have a potential negative impact on biodiversity. National policies, such as the UKFS which recommend a minimum target volume of deadwood for the preservation of biodiversity, may also aid climate change mitigation as deadwood acts as a carbon pool. Presently, few policies link the five key uses and benefits of deadwood: biodiversity, carbon storage, flood management, forest health management, and fuel and fibre production, and instead offer guidance on only one or two aspects e.g. biodiversity and carbon storage. Specific guidance on deadwood retention in woodlands that are managed for fuel or fibre, and the volumes that are achievable, would clarify best practice for managers. Further updates to policy would benefit from research exploring the transfer of carbon from deadwood to the surrounding environment e.g. soils and groundwater, to assess the impact this has.

2.8 Acknowledgements

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Table 2-3- A synthesis of studies on deadwood biomass, volumes, and carbon stocks in temperate woodlands under differing management practices.

Study region	**Tree spp.**	**Management**	**Debris classification (diameter)**	**Mean deadwood biomass (Mg ha^{-1})**	**Mean deadwood volume (m^3 ha^{-1})**	**Carbon stocks (Mg ha^{-1})**	**Reference**
Spain	*Pinus sylvestris*	Unthinned (U) Moderate (M) Heavy thinning (HT)	CWD ≥ 7 cm FWD 2 ≤ 7 cm	266.1 ± 7.4 (U) 206.9 ± 2.6 (M) 177.8 ± 4.3 (HT)	474.5 ± 8.9 (U) 375.6 ± 5.0 (M) 321 ± 7.6 (HT)	13.5 (U) 15.9 (M) 21.3 (HT)	(Ruiz-Peinado *et al.*, 2016)
Italy	Data collected at a national scale from the Italian National Forest Inventory	Unspecified	CWD ≥ 9.5 cm FWD 2.5 ≤ 9.5 cm	-	-	Ranging between 0.3 (Poplar plantation) - 8.2 (Chestnut)	(Gasparini and di Cosmo, 2015)
New Zealand	Combinations of *Nothofagus,* broadleaved & coniferous indigenous forest	Managed for conservation (including dead biomass): no deadwood can be removed	CWD ≥ 10 cm	54 ± 2	158 ± 6	-	(Richardson *et al.*, 2009)
New Zealand	*Pinus radiata* & *Pinus nigra* plantations	Woody debris in streams: Pre-harvest (Pre), Harvest (H), Post-harvest (Post)	Small debris: 1 ≤ 9 cm large debris: >10 cm	-	Pre: 105 ± 42 H: 147 ± 84 Post: 289 ± 100	-	(Baillie, Cummins and Kimberley, 1999)
Ireland	*Picea sitchensis*	Thinning in 1985, 1991, 1998	CWD ≥ 7 cm	-	2 – 6	12.103 (1985) 13.154 (1991) 5.140 (1998)	(Tobin *et al.*, 2007)
Germany	*Fagus sylvatica; Quercus petraea; Picea abies*	Unthinned (U) Thinned (T)	CWD ≥ 7 cm	-	64 - 165 (U) ~30 (T)	11 - 30 (U) 4 - 6 (T)	(Krueger, Schulz and Borken, 2017)

Turkey	*Abies nordmanniana* subsp. *Equi-trojani*	Managed by selection silviculture. GA – old uneven-aged stands, trees with large DBH. GB – young uneven-aged stands, trees with small DBH. GC – even-aged stands, trees with middle-large DBH. GD – uneven-aged stands, trees with small & large DBH.	Small (0-40cm), large (40+ cm)	-	Small: 7.95 (GA), 3.38 (GB), 4.48 (GC), 4.77 (GD). Large: 10.33 (GA), 0 (GB), 0.84 (GC), 3.76 (GD).	-	(Topacoglu *et al.*, 2017)
Poland	*P. sylvestris (~50%), Quercus spp., A. glutinosa*	Managed until the end of the 20th century: clear-cutting in pine & mixed forests ; group selection in deciduous. From the start of the 21st century: group selection, group shelterwood, minimal clear-cutting	CWD ≥ 10 cm	-	3.4 (snags) 3.5 (logs)	-	(Kapusta *et al.*, 2020)
Switzerla nd	Data collected at a national scale from the	Silvicultural interventions: 1) <10 years ago 2) 11-20	Sum of: CWD ≥ 7 cm and standing	-	1) 26.85 ± 1.81 2) 20.57 ± 2.19 3) 25.82 ± 3.52 4) 32.26 ± 4.72	-	(Böhl and Brändli, 2007)

	Swiss National Forest Inventory	3) 21-30 4) >30 years					
France	Broadleaf species varying by site	Stand types of: Coppice with standards (CWS); High forest (HF); Coppice (C) Management of: 1) improvement; 2) Overstory removal; 3) clearcut	Sum of: FWD 4 ≤ 7 cm and CWD > 7 cm	CWS 1: 9.75 CWS 1: 5.27 HF 2: 3.71 HF 2: 5.80 CWS 2: 6.68 C 3: 10.29 CWS 3: 13.21 CWS 3: 5.84 HF 2: 3.69	-	-	(Bessaad, Bilger and Korboulewsky, 2021)

3 Study sites and long-term monitoring data

3.1 Introduction

This chapter presents contextual background information about the field sites used in the thesis across different spatial scales. Sections 3.2.1-3 outline the Alice Holt field site where long-term monitoring and supporting lab work, as outlined in Chapter 4, was carried out, stimulating hypotheses about the role of deadwood on the soil carbon cycle. Section 3.2.3 and 3.3.1 outline the chronosequences used for additional field sampling at Alice Holt (Broadleaf) and Kielder (Conifer), respectively, used for Chapter 5. Section 3.4 outlines the national scale monitoring programme carried out by the National Forest Inventory teams that forms the bases of Chapters 6 and 7.

3.2 Alice Holt Forest

The Alice Holt Forest sites (51° 9' N, 0° 52' W), in Surrey, south east England (Figure 3-1), are dominated by lowland oak forest (mainly *Quercus robur*, L.) on surface water gleys (Pelo-stagnogley). The site is regularly managed and undergoes thinning activities. Elevation is 80 m with monthly average air temperatures between 4.7 and 17.6°C with an annual mean of 10.5°C, and mean annual precipitation of 634 mm. The full site history is described in detail in Pitman *et al*. (2014).

3.2.1 Alice Holt: Environmental Change Network

The Environmental Change Network (ECN) was first established in 1992 to provide long-term monitoring of freshwater and terrestrial ecosystems and includes 12 terrestrial sites, 17 lake sites and 29 river sites. This includes a terrestrial site at Alice Holt Forest, where soil, soil water and deposition chemistry data are routinely collected, along with information on site biology. Soil solutions are collected fortnightly, with measurements including pH, conductivity, TOC, total N and various elements. A full description of the measurements taken, and their frequency, is described by Benham (2008).

The Alice Holt ECN plot is lowland, on a gentle slope, and dominated by oak with occasional ash (*Fraxinus excelsior*). It has been unmanaged since 1992, though was previously thinned every 20-25 years. As a result, there is dense tree cover at the site, with little to no vegetation in the shrub layer.

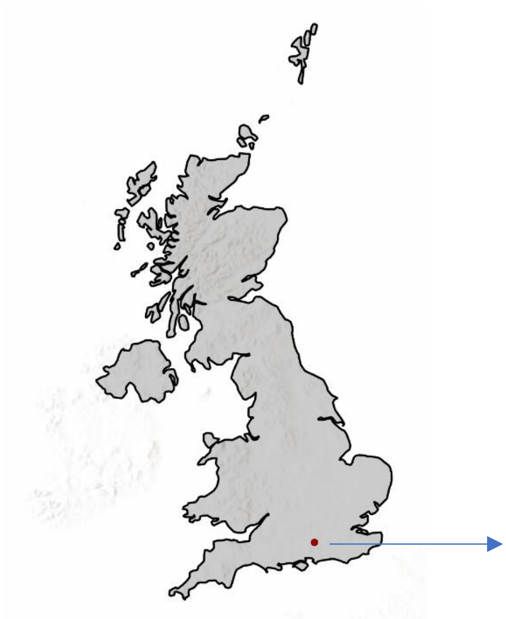

Figure 3-1 – Location of the Alice Holt Forest and chronosequence sample plots. The FLII and ECN plots are used in long-term monitoring and follow up lab work. The plots identified as Young, Mid or Old form the chronosequence.

3.2.2 Alice Holt: Forest Level II Intensive Monitoring Network

Alice Holt Forest also hosts a Forest Level II Intensive Monitoring Network (FLII) site, adjacent to the ECN site. The FLII network was set up as a long-term monitoring programme which is part of the European ICP network. This was set up to monitor crown condition over time, and to investigate the impacts of air pollution, climate change and other stressors. There are over 800 plots established throughout Europe, with 20 situated in the UK. The Alice Holt site was established in 1994, with measurements taken including soil and soil solution chemistry, atmospheric deposition, meteorology, biology and crown condition. Between 1995-2006, soil solutions were collected fortnightly, though from 2007 this was reduced to monthly. The forest undergoes regular thinning at 5-10 year intervals, which has lessened the density of the tree canopy and allowed vegetation in the shrub layer to establish. Full details of measurements are described by Vanguelova *et al*. (2007).

3.2.3 Alice Holt chronosequence

The Alice Holt chronosequence consists of nine plots, all occurring over the same soil types (Figure 3-1). Stand ages of these plots are classified as: young (~30 years old), middle age (~70 years old) and old (~180 years old). Three stands per age group are used.

3.3 Kielder Forest

Kielder Forest is an upland Sitka spruce (*Picea sitchensis* (Bong.), Carr.) plantation in Northumberland, north east England (55° 15' N, 2° 23' W) (Figure 3-2), over peaty gley soils and deep peat (histosol). It undergoes regular management, including thinning. Elevation across the forest ranges between 240 m and 365 m, with monthly average air temperatures ranging between 3 and 14.8°C with an annual mean of 8.3°C, and precipitation of 759 mm. The site history is described in detail in Vanguelova *et al*. (2019).

3.3.1 Kielder chronosequence

The chronosequence used at Kielder consists of nine plots, as located in Figure 3-2, with three plots per each age group. Stands are uniform and the ages are classified as: young (~10-20 years old), middle age (20-40 years old) and old (40-60 years old). The majority of plots are in their second rotation (i.e. second crop) since afforestation.

Figure 3-2 – Location of Kielder Forest and the chronosequence sample plots

3.4 National Forest Inventory data

The GB National Forest Inventory (NFI) is split into two projects: A main woodland inventory and a small woodland and trees survey. For the purpose of this thesis, the main woodland inventory data will be used.

For the main woodland inventory, woodland is defined as an area ≥ 0.5 ha, with a width ≥ 20 m and crown/canopy cover ≥ 20% or the potential to achieve this (Forestry Commission, 2016). Assessments are carried out every 5 years, beginning in 2009. The dataset used for this thesis is from the 1st NFI cycle, with surveying carried out between 2009-2015. During surveying, ~15,000 one-hectare sample squares are selected across Britain, with 66% allocated on a systematic grid and 33% on a random basis.

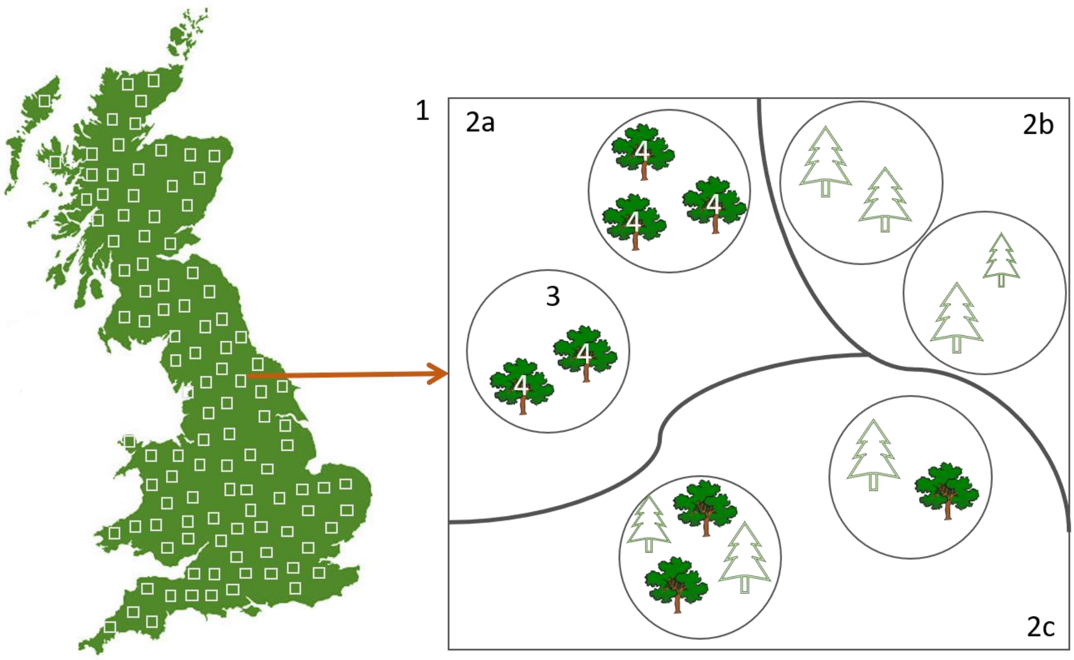

Figure 3-3 - NFI sampling strategy where 1 = a 1 ha ‘square’; 2 = a ‘section’, a homogenous area of woodland; 3 = a ‘plot’, a circular plot with a planimetric area of 0.01 ha; 4 = ‘tree’, individual trees within a plot.

Within each 1 ha square, field surveyors split woodland into homogenous sections of ≥ 0.05 ha. Homogenous sections too small to map are identified as ‘component groups’ and attached to the most similar section of a square. Within each section two, 0.01 ha circular plots, are assessed (Figure 3-3). A single 10 m transect is used at every plot to assess lying deadwood. Assessments are carried out at the section or plot levels:

1. Whole Section Plots – where there are < 40 standing measurable stems within a section (and any associated sample RAS[1] up to 21 m from the square boundary) then all measurable stems are assessed. Some assessments (e.g. stumps) are based around a point randomly located within the section.

2. Circular plots – if there are ≥ 40 standing measurable stems (live and dead) within a section (and any associated sample RAS where applicable), circular plots are used to gain a representative sample of the section. All circular plots measured have a 5.64 m horizontal

[1] Relevant adjacent stands (RAS) are areas of NFI tree cover outside the sample squares, which cross the squares boundary.

radius (0.01 ha planimetric area). In the case of sections < 0.6 ha, two plots are used, whilst for sections ≥ 0.6 ha there are three plots.

Deadwood assessments are undertaken at the section, plot and tree level. At a section level, a visual estimate is made for lying and standing deadwood, as low, medium, high, not applicable or none. At a plot level, assessment is carried out to include the following information for the three types of deadwood: lying, standing and stumps.

Lying deadwood is classified as dead, woody material from trees that has not been processed e.g. branches or stem-wood; ≥ 7 cm in diameter. One 10 m transect per plot is used where all intersecting deadwood is measured and the attributes outlined in Table 3-1 are recorded. Standing deadwood is classified as a dead tree whereby all stems have died and a DBH ≥ 4 cm is found. Stumps are classified as part of a tree stem that still has roots attached to the ground; ≤ 1.3 m in height; no visible live shoots; with a minimum diameter of 4 cm. Two different methodologies are used to assess stumps: the nearest stump to each plot centre/point is measured and mapped (at tree level); remaining stumps are visually assessed and tallied into size classes at a plot/section level.

Table 3-1 – NFI data provided per each deadwood type

	Deadwood type		
	Lying	**Standing**	**Stumps**
Species category	N/A	Measured to a species level	Measured at a high level as either conifer or broadleaf
Diameter	An *in situ* measurement. Must be ≥ 7 cm.	An *in situ* measurement of DBH. Must be ≥ 4 cm.	An *in situ* measurement. Must be ≥ 4 cm.
Height	Measured as length	A visual estimate is provided	An *in situ* measure. Must be ≤ 1.3 m.
Decay class	Measured on a scale of 1-5 (Hunter, 1990). 1 being the lowest decay and 5 the most advanced.	Measured on a scale of 3-7	Measured as either 8 (a fresh stump, still fairly solid) or 9 (an older, partially or almost fully rotted) stump.
Windblow or windsnapped	Evidence of windblow	Evidence of windsnap	N/A
Cause of death	N/A	Broken down into 16 categories.	An assessment of whether the stump is coppiced or not
Number of samples	N/A	A count of the number sampled	A count of the number sampled

Additional information has been provided at a section level, including planting year, silvicultural systems, manual interventions and the area they cover.

4 Management impacts on the dissolved organic carbon release from deadwood, ground vegetation and forest floor in a temperate Oak woodland

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4.1 Abstract

The forest floor is often considered the most important source of dissolved organic carbon (DOC) in forest soils, yet little is known about the relative contribution from different forest floor layers, understorey vegetation and deadwood. Here, we determine the carbon stocks and potential DOC production from forest materials: deadwood, ground vegetation, leaf litter, the fermentation layer and top mineral soil (Ah horizon), and further assess the impact of management. Our research is based on long-term monitoring plots in a temperate deciduous woodland, with one set of plots actively managed by thinning, understorey scrub and deadwood removal, and another set that were not managed in 23 years. We examined long-term data and a spatial survey of forest materials to estimate the relative carbon stocks and concentrations and fluxes of DOC released from these different pools. Long-term soil water monitoring revealed a large difference in median DOC concentrations between the unmanaged (43.8 mg L^{-1}) and managed (18.4 mg L^{-1}) sets of plots at 10 cm depth over six years, with the median DOC concentration over twice as high in the unmanaged plots. In our spatial survey, a significantly larger cumulative flux of DOC was released from the unmanaged than the managed site, with 295.5 and 230.3 g m^{-2}, respectively. Whilst deadwood and leaf litter released the greatest amount of DOC per unit mass, when volume of the material was considered, leaf litter contributed most to DOC flux, with deadwood contributing least. Likewise, there were significant differences in the carbon stocks held by different forest materials that were dependent on site. Vegetation and the fermentation layer held more carbon in the managed site than unmanaged, while the opposite occurred in deadwood and the Ah horizon. These findings indicate that management affects the allocation of carbon stored and DOC released between different forest materials.

Keywords

DOC, carbon cycling, broadleaf woodland, soil, management

4.2 Introduction

The global forest carbon (C) stock is estimated at 861 ± 66 Pg (Pan *et al.*, 2011) (1 Pg = 10^{15} g) of which 119 ± 6 Pg are held in temperate forests and 878 Mt C (1 Mt = 10^{12} g) are found in UK woodlands (Morison *et al.*, 2012). Carbon enters the terrestrial carbon cycle via photosynthesis; it is then cycled through the living biomass which on average accounts for 42-44% of organic C, before being transferred to the soil which contains on average 44-45% of forest C stocks (Pan *et al.*, 2011; FAO, 2020a), while the remaining carbon is held in litter (5-6%) and deadwood (4-8%). However, this partitioning varies nationally, with UK forests holding approximately 5% of their carbon stocks in litter and deadwood, 18% in standing trees, and 76% in soil (Morison *et al*., 2012).

Dissolved organic carbon (DOC) is produced during the decomposition of organic material and is transported between carbon pools through hydrological processes such as leaching from the forest floor to the mineral soil (Kolka, Weishampel and Froberg, 2008) An estimated 17% of the annual C input from litter leaches into mineral soils as DOC (Michalzik *et al.*, 2001). The composition of DOC depends on the composition of organic material, which impacts its turnover time and therefore the soil's ability to sequester carbon in the long-term (Aitkenhead and McDowell, 2000). The forest floor, woody debris and ground vegetation are considered to be important sources of DOC and contain various substrates which contribute differing amounts of DOC of varying complexity. Park *et al*. (2002) investigated the impact of resource availability on DOC production over 98 days and determined that leaf litter was the most important source of DOC in deciduous woodlands followed by fresh wood litter (<1 year old). Other studies have found the amount of DOC released from litter to decrease significantly over time, indicating a large labile pool of DOC that can be consumed as a substrate for biological activity (Moore and Dalva, 2001; Don and Kalbitz, 2005). Over the course of a year, deadwood has been found to produce 10x as much DOC as litter (Hafner, Groffman and Mitchell, 2005), and between 3-20x as much DOC as throughfall (Hafner, Groffman and Mitchell, 2005; Bantle *et al.*, 2014). Overall, these studies show that the production of DOC beneath deadwood could be significant in relation to other forest floor materials but the relative magnitude of the contributions of deadwood, forest ground vegetation, and forest floors as sources of DOC-derived carbon fluxes into soils are not always in agreement between studies and therefore require further characterization.

Deadwood is defined as the non-living woody biomass not contained in litter and can be either standing, lying on the ground, or in the soil (FAO, 2010). It has many functions within the forest, it is a key indicator of forest biodiversity (MCPFE Liaison Unit and UNECE/FAO, 2003; Humphrey and Bailey, 2012); it influences stand dynamics (Hodge and Peterken, 1998); it has a protective role in stabilizing slopes (Stevens, 1997); and is also an important carbon pool (Pan *et al.*, 2011; Morison *et al.*, 2012; FAO, 2020b). However, it is one of the least studied carbon pools and is often not included in forest carbon models or inventories despite being a potentially significant store of carbon. Deadwood is often classified as coarse woody debris (CWD) with a diameter greater than 10 cm; fine woody debris (FWD) with a diameter less than 10 cm or as snags or stumps (Working Group on Forest Biodiversity, 2004). It may be further classified according to stage of decay following the classification by Hunter (1990). Under this classification , decay classes range from class 1 (least decomposed; intact texture with bark present) to class 5 (largely decomposed, bark is absent, powdery texture). The degree to which deadwood has decomposed will determine the biomass of the deadwood and thus the amount of carbon available for leaching. It has been determined that wood at a later stage of decay releases more DOC but over a longer period of time (Bantle *et al.*, 2014). Therefore, forest management that decreases the amount of deadwood within a forest could reduce the amount of DOC within the soil. The aim of this work is to test the hypothesis that management practices, particularly forest thinning and the removal of woody debris created during harvesting, reduce the DOC fluxes into soil water. Our specific objectives are to: (1) determine whether management has altered DOC concentrations in long-term monitoring data; (2) determine the impact of management on the carbon stocks of forest material; (3) evaluate the dominant sources of DOC between different forest materials.

4.3 Materials and methods

4.3.1 Site information

Alice Holt Forest is a semi-natural ancient woodland located on the Surrey-Hampshire border, UK (51° 9′ N, 0° 52′ W). Plots under different management within Alice Holt Forest were used: an environmental change network (ECN) plot and a Forest Level II Intensive Monitoring Network (FLII) plot (Figure 3-1). Both of these have undergone regular monitoring, that includes soil chemistry and atmospheric pollution, since the mid-1990s. The ECN and FLII sites are dominated by 75 year old oak (*Quercus robur*) with occasional ash (*Fraxinus excelsior*) occurring on Gault Clay overlain by poorly draining surface-water gleys. Soil properties (Ah Horizon) for the ECN and FLII sites, respectively, are as follows: organic carbon content (5.6% and 2.7%); pH_{water} (4.4 and 5.4); sand (%): silt (%): clay (%) (~9:50:40 and ~4:44:52) (Benham, Vanguelova and Pitman, 2012; Vanguelova, Moffat and Morison, 2016). Site elevation ranges from 110-125m and the climate is temperate with a mean annual temperature of 10.8°C and mean annual precipitation of 833mm. The forest has historically been thinned at intervals of 20-25 years; however, the ECN site has been unmanaged since 1992. Woody debris, created by self-thinning of subdominant or diseased trees which die and fall, are not removed from the site. By contrast, the FLII site is still managed with practices which include tree thinning and scrub layer removal. Harvesting material is removed from the plot by management i.e., the main trunk and lop and top along with any dead trees as part of the thinning process, however deadwood which falls from the canopy to the forest floor (mainly, but not exclusively, fine material) is left *in situ*. Management that took place at the FLII site during the long-term monitoring (section 4.3.2) and sampling (section 4.3.3) campaigns was as follows: thinning of oak (2005) and scrub removal (2010), where hazel bushes were cut down and debris removed. Sampling took place two years before the next management for scrub removal (in 2017).

Figure 4-1 - The ECN site (left) is presently unmanaged whilst the FLII site (right) still undergoes regular management.

4.3.2 Long-term monitoring

The initial ECN measurement protocols were developed by an expert group in the late 1980s (Morecroft *et al.*, 2009) and a detailed series of protocols (Sykes and Lane, 1996) were published. Some protocols have been revised in light of experience, but most methods remain essentially unchanged, allowing robust comparisons across time. The assessment of forest condition under the United Nations Economic Commission for Europe (UNECE) and EU Level I and Level II long-term forest monitoring programmes constitutes one of the world's largest bio-monitoring networks (Vanguelova *et al.*, 2007). Plot establishment and instrumentation follow standardised monitoring protocols, as created by the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests, 2006). In this study, we use the long-term soil water monitoring data collected every two weeks at both sites between 2002 and 2010. Long-term soil water monitoring at the ECN site stopped in 2010 due to funding restrictions. Both networks use the same type of tension samplers (PRENART SuperQuartz soil water samplers, Prenart Equipment Aps, Denmark) and measure soil water chemistry at two similar depths with 6 replicate samplers at each depth. At Alice Holt, the ECN shallow and deep soil solution samplers are located in the Ah and Btg horizons. The FLII shallow and deep soil solution samplers are located in the Ah and Bcg horizons. Shallow and deep samplers are located at 10 and 50 cm depth, respectively. Soil water was sampled at two different locations within the FLII plot to better capture the site variability. Measurements from the ECN shallow plots and FLII deep plots were only available from 2004 – 2010. Soil water samples were filtered through a 0.45 µm membrane filter and analysed for dissolved organic carbon (DOC) by Thermal Catalytic Oxidation using a Thermalox^{TM} Analyzer (Analytical Sciences UK, Cambridge, UK; pH < 5.5, therefore Total Dissolved C = Total DOC).

4.3.3 Sampling for deadwood, vegetation, forest floor and soil

Deadwood sampling was carried out using the BioSoil (2004) protocols. This was carried out in November 2015, during peak litter fall and the autumn seasonal peak in DOC concentrations. Three circular plots with an area of 400 m^2 were randomly selected to survey deadwood at both the ECN and FLII sites. Within each 400 m^2 area, all deadwood debris found were recorded, including stumps and lying coarse and fine woody debris. The length (cm) and diameter (cm) of each deadwood piece were recorded along with decay class 1-5 following the guidelines presented by Hunter (1990) to enable the deadwood biomass and carbon stock to be estimated.

A sample of deadwood from each decay class was collected from each plot for further laboratory analysis, though decay class five was absent from one FLII plot. A total of 15 deadwood samples were collected from the ECN and 14 from the FLII. Within each circular plot, three quadrats measuring 0.25 x 0.25 m were randomly sampled. Fresh ground vegetation, leaf litter (L), fermentation (F) layer and the top 5cm of the Ah mineral soil horizon were collected individually by excavating the quadrats. The three quadrat samples per plot were then pooled to produce a composite sample per plot to estimate the mass of each type of forest material. It was impractical to sample on the same spatial scale for both deadwood and forest floor materials due to the irregular coverage of deadwood and large quantities of forest materials.

Moisture content (%) was determined from subsamples of each collected forest material through the mass lost after oven drying at 105°C overnight. The mass of deadwood per decay class was then calculated using:

$$Biomass = Density\ x\ Volume$$

Using the wood density (g cm^{-3}) values from Vanguelova *et al*. (2016).

Subsequently carbon stocks were calculated as follows:

$$Carbon\ stock = Biomass\ x\ carbon\ fraction$$

Where carbon fraction is presumed as the standard value of 50%, as per the IPCC Good Practice Guidance for Land Use, Land-Use Change and Forestry (Penman *et al.*, 2003).

Carbon content of ground vegetation, litter and the fermentation layer was determined as 50% of the mass per quadrat (Penman *et al*., 2003). Organic carbon concentrations of 5.6% (ECN site; Benham *et al*., 2012) and 2.7% (FLII site, Vanguelova (unpublished results)) as determined by combustion C:N analyser were used for C stock calculations for the Ah horizon. All carbon stock measurements were upscaled to Mg C ha^{-1}.

4.3.4 Dissolved organic carbon

A water extract was taken from all samples (deadwood in each decay class 1-5, vegetation, litter, F layer, Ah horizon) of the spatial survey using a ratio of 1:10 as 10 g wet sample to 100 mL deionised water. Material from each of the plots per site (n=3) was homogenised and cut in to ~1cm pieces prior to sub-sampling for extraction. Samples were placed on a rotary shaker for 24 hours at 180 rpm before centrifuging at 3500 rpm for ten minutes and pre-filtering through Whatman GF/A filter papers using vacuum filtration. Samples were centrifuged at 1300 rpm for a further 15 minutes before filtering through 0.45 µm cellulose nitrate filter paper.

DOC concentration for these samples was determined using a Shimadzu TOC Analyser. DOC release per unit mass of each source (mg g^{-1}) was scaled up to estimate the potential DOC flux from the forest floor (g m^{-2}).

4.3.5 Statistical analysis

Long-term trends in DOC were analysed using the statistical environment R v. 2.13.2 to 3.1.2. The data were tested for normality using Shapiro-Wilk and homogeneity of variances using Flinger-Killeen. Where these were not met, data was analysed using the non-parametric Kruskal-Wallis analysis of variance test.

Statistical analysis of data from the forest material survey was mainly carried out using the Statsmodels module in Python (Seabold and Perktold, 2010). Data were tested for normality of residuals using the Jarque-Bera test and for heteroscedasticity using the Breusch-Pagan test. Raw (non-transformed) data failed to meet either normality or equality of variances or both, likely due to the large range in the size of the actual mean values and variances. We therefore performed Robust (to unequal variance) type III Two-Way ANOVA to identify if site (ECN, FLII) or forest material type (deadwood, fresh vegetation, leaf litter, fermentation layer, Ah soil horizon) affected C stocks and DOC flux results. Data were Box-Cox transformed: $(Y^{\lambda}-1)/\lambda$ where λ was chosen so as to minimise the p-value testing normality of residuals (using Jarque-Bera). Significant differences were accepted at $p<0.05$. Where the Two-Way ANOVA identified a significant main effect, post-hoc comparisons were made using the Games-Howell Method and 95% Confidence in Minitab 18. In the case of a significant site × forest material type interaction, paired t-tests (Minitab 18; equal variances not assumed) were used to examine the effect of site within each forest material type.

Cumulative fluxes of DOC were assessed using Welch's two sample t-test assuming unequal variance.

4.4 Results

4.4.1 Long-term trends in soil water DOC at ECN and FLII sites

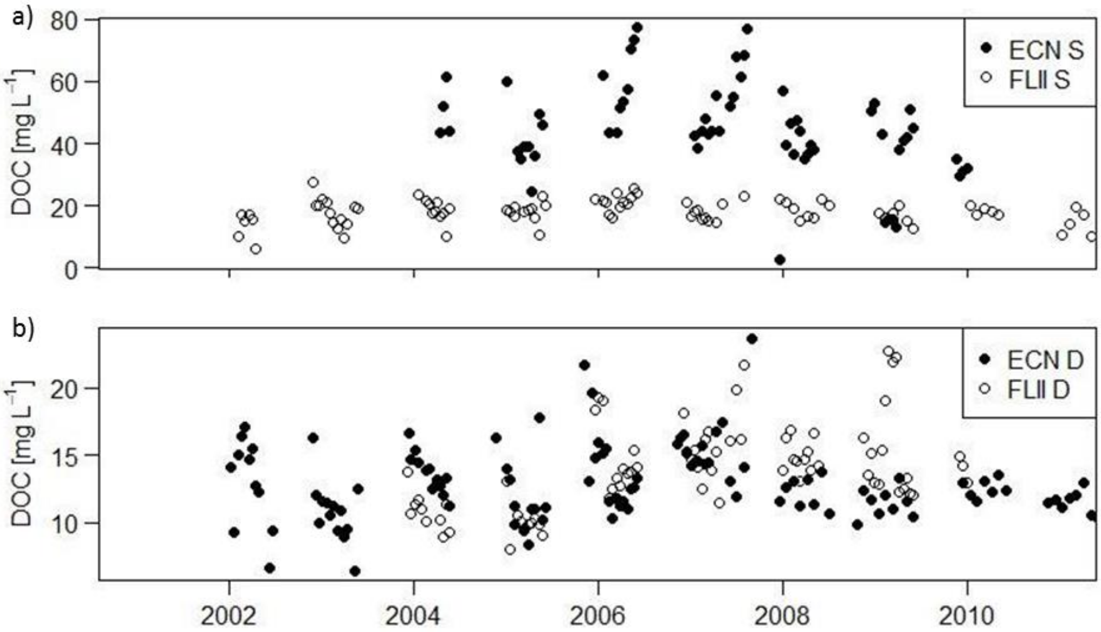

Figure 4-2 - ECN and FLII time series of soil water DOC concentrations from (a)* shallow (S) samplers in the upper plot and (b) deep (D) samplers in the lower plot. Solid dots represent the ECN data and hollow dots represent the FLII data.

Long-term soil water monitoring data shows consistently higher DOC concentrations within the ECN plot compared to the FLII plot, which was particularly evident at shallow depths (Figure 4-2 a). From 2002 to 2010, median DOC concentrations in the ECN plot were 2.4 times higher than FLII ($p<0.00001$) in the shallow samplers, with concentrations of 43.8 mg L^{-1} and 18.4 mg L^{-1}, respectively (Figure 4-3). ECN shallow samplers also displayed a greater range in values from 2.67 – 77.3 mg L^{-1}, compared to 6.42-27.6 mg L^{-1} in FLII samplers. Median values in the deep samplers were also significantly higher in ECN than FLII (13.8 mg L^{-1} and 12.4 mg L^{-1}, respectively, $p<0.01$), although the difference was less (1.1 times higher) (Figure 4-3). Gaps in the time series for both monitoring programmes exist during the summer months in each year due to low soil moisture restricting sample collection.

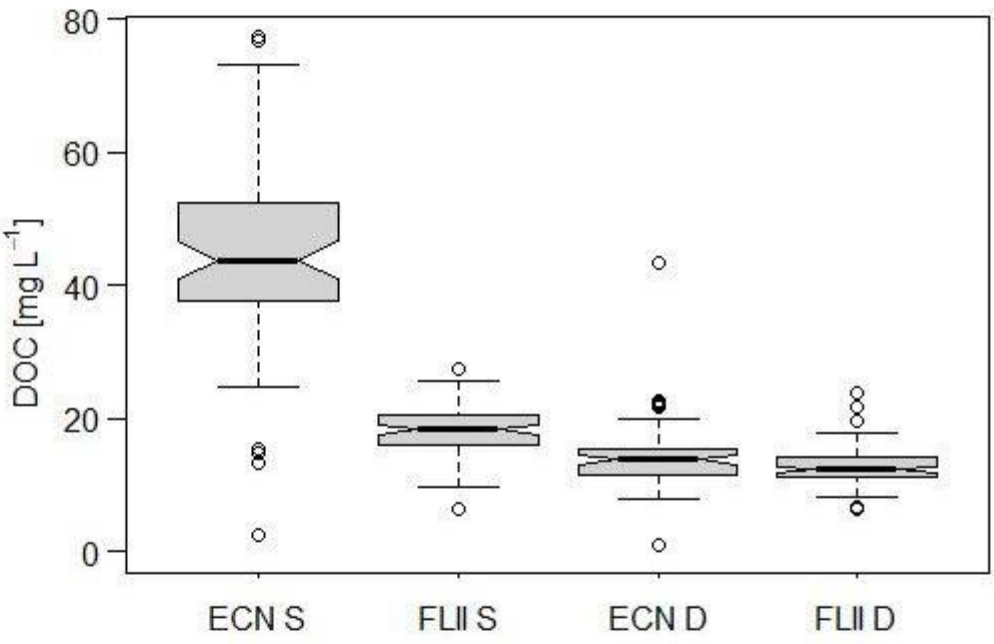

Figure 4-3 - Comparison of the long term median (2002-2011) of soil water DOC concentrations at ECN and FLII sites. Letters "S" and "D" denote shallow and deep samplers, respectively. Kruskal Wallis-test indicates that shallow soil DOC from the ECN and FLII plots significantly differ ($p<0.00001$). Deep soil DOC was also found to significantly differ between the two plots ($p=0.01$).

4.4.2 Survey of mass, C stocks and DOC production for forest floor materials

4.4.2.1 Deadwood, vegetation, litter, F layer and Ah horizon

Examining the effect of forest material type and site on the mass (kg m^{-2}) of forest materials using two-way ANOVA revealed that mass differed significantly between material types (d.f. = 4; F = 129.2; $p<0.001$), with the greatest mass associated with the Ah soil layer followed by the F layer (Table 4-1). With vegetation, deadwood contributed lower mass than all other materials. Whilst mass of forest materials did not differ overall between management sites (d.f. = 1; F = 0.298; p = 0. 591), there was a significant interaction with material type (d.f. = 4; F = 10.56; $p<0.001$) such that a larger density of the Ah soil horizon and deadwood was found in the ECN plot whilst a greater mass of vegetation and F layer was present at the FLII plot (Table 4-1).

Two-way ANOVA revealed that total carbon stocks (Mg C ha^{-1}) held in forest material did not differ between the sites (F = 1.56; p = 0.226) but depended on material type (F = 38.56;

$p<0.001$) and the interaction between material type and site ($F = 19.13$; $p<0.001$). Overall, deadwood and the Ah horizon held greater carbon stocks in the unmanaged ECN site than the managed FLII site. In contrast, the F layer and vegetation held significantly greater stocks in the managed FLII than unmanaged ECN site (Table 4-1). Notably, deadwood stocks are over four times lower in the managed FLII plot than the unmanaged ECN plots, while vegetation stocks are over three times larger.

Table 4-1 - Mean mass ± SE (kg m^{-2}) and carbon stock (Mg C ha^{-1}) for each source material at the ECN and FLII sites (n=3). Total is the cumulative total of all sources. Material types that do not share a lowercase grouping letter are significantly different ($p<0.05$) according to Games-Howell pairwise comparisons. Means within each material type that share an uppercase letter are not significantly different ($p>0.05$; paired t test). Values in parenthesis are the coefficient of variation (%).

Material type	**Mass (kg m^{-2})**			**Carbon stock (Mg C ha^{-1})**		
	ECN	**FLII**	**Games-Howell group**	**ECN**	**FLII**	**Games-Howell group**
Deadwood	0.480 ± 0.129 $(46.5)^{A}$	0.100 ± 0.040 $(68.7)^{B}$	d	2.29 ± 0.620 $(46.9)^{A}$	0.481 ± 0.192 $(68.9)^{B}$	c
Vegetation	0.489 ± 0.040 $(14.2)^{B}$	1.67 ± 0.275 $(28.4)^{A}$	cd	2.26 ± 0.187 $(14.4)^{B}$	7.86 ± 1.29 $(28.4)^{A}$	bc
Litter	3.10 ± 1.07 $(59.9)^{A}$	1.82 ± 0.122 $(11.5)^{A}$	c	14.3 ± 4.93 $(59.5)^{A}$	8.45 ± 0.594 $(12.2)^{A}$	b
F layer	4.61 ± 0.960 $(36.1)^{B}$	7.86 ± 0.428 $(9.4)^{A}$	b	21.6 ± 4.58 $(36.7)^{B}$	37.1 ± 1.92 $(9.0)^{A}$	a
Ah horizon	18.8 ± 2.58 $(23.8)^{A}$	11.9 ± 0.633 $(9.2)^{B}$	a	10.2 ± 1.41 $(24.0)^{A}$	3.11 ± 0.166 $(9.3)^{B}$	b
Total	27.43 ± 2.60^{A}	23.37 ± 1.31^{A}		50.68 ± 1.59^{A}	57.02 ± 2.31^{A}	

4.4.2.3 Inventory of deadwood by decay class

According to the survey of deadwood volumes within the 400 m^2 plots, a larger volume of deadwood was found at the ECN site with the average total, when scaled to a per hectare basis, of 21.2 ± 6.3 m^3 ha^{-1} and 4.1 ± 1.6 m^3 ha^{-1} for the ECN and FLII sites, respectively. Robust ANOVA on Box-Cox-transformed data revealed that decay class significantly affected deadwood biomass (d.f. = 4; F = 3.68; p = 0.022) and deadwood C stocks (F = 3.68; p = 0.022). The largest quantities of deadwood per m^2 were found in decay classes 3 and 4 for both plots (Table 4-2), with a maximum of 0.242 ± 0.171 kg m^{-2} for the ECN site (decay class 4) and a maximum of 0.0501 ± 0.0242 kg m^{-2} for the FLII site (decay class 3). There was no overall significant effect of site on deadwood biomass (d.f. = 1; F = 1.49; p = 0.237) or C stock (F = 1.44; p = 0.245) and no significant site * decay class interaction (d.f. = 4; F = 0.105; p = 0.980 for both biomass and C stock).

Table 4-2 - Mean biomass ± SE (kg m^{-2}) and carbon stocks (Mg C ha^{-1}) of each deadwood decay class at the ECN and FLII plots, n=3 per group. Games Howell groups that do not share a letter are significantly different (p<0.05). Values in parenthesis are the coefficient of variation (%).

Deadwood	**Biomass (kg m^{-2})**			**Carbon stock (Mg C ha^{-1})**		
decay class	**ECN**	**FLII**	**Games-Howell group**	**ECN**	**FLII**	**Games-Howell group**
1	0.017 ± 0.015 (151.7)	0.005 ± 0.002 (71.6)	bc	0.080 ± 0.070 (151.5)	0.022 ± 0.009 (71.5)	bc
2	0.018 ± 0.005 (51.7)	0.013 ± 0.009 (113.9)	abc	0.086 ± 0.026 (51.8)	0.064 ± 0.042 (113.7)	abc
3	0.199 ± 0.113 (97.8)	0.050 ± 0.024 (83.8)	a	0.949 ± 0.539 (98.3)	0.242 ± 0.117 (84.1)	a
4	0.242 ± 0.171 (122.3)	0.029 ± 0.011 (63.5)	ab	1.154 ± 0.817 (122.7)	0.142 ± 0.052 (63.6)	ab
5	0.004 ± 0.0002 (9.8)	0.003 ± 0.003 (131.0)	c	0.017 ± 0.001 (10.0)	0.016 ± 0.015 (131.2)	c

4.4.2.4 Forest floor materials as sources of DOC

Analysis indicated that stage of deadwood decay did not significantly affect the production of DOC (p = 0.096). Therefore, for the subsequent analysis, all decay classes have been pooled into one class, 'deadwood', and robust two-way ANOVA used to analyse the effect of forest material: deadwood, fresh vegetation, leaf litter, F layer, Ah horizon, and site: ECN and FLII.

The mean amount of DOC released from each source ranged from 2.92-52.78 mg g^{-1}, with the lowest concentrations in the FLII Ah horizon and highest in the ECN deadwood, respectively (Figure 4-4). Two-way ANOVA found that significant differences occurred between forest material sources of DOC (F = 95.11; p<0.001) but not sites (F = 0.22; p = 0.643). Deadwood and litter produced significantly (p<0.05) more DOC mg g^{-1} than the vegetation, F layer and Ah horizon (Figure 4-4). No significant interaction was found between site and source (F = 1.10; p = 0.368).

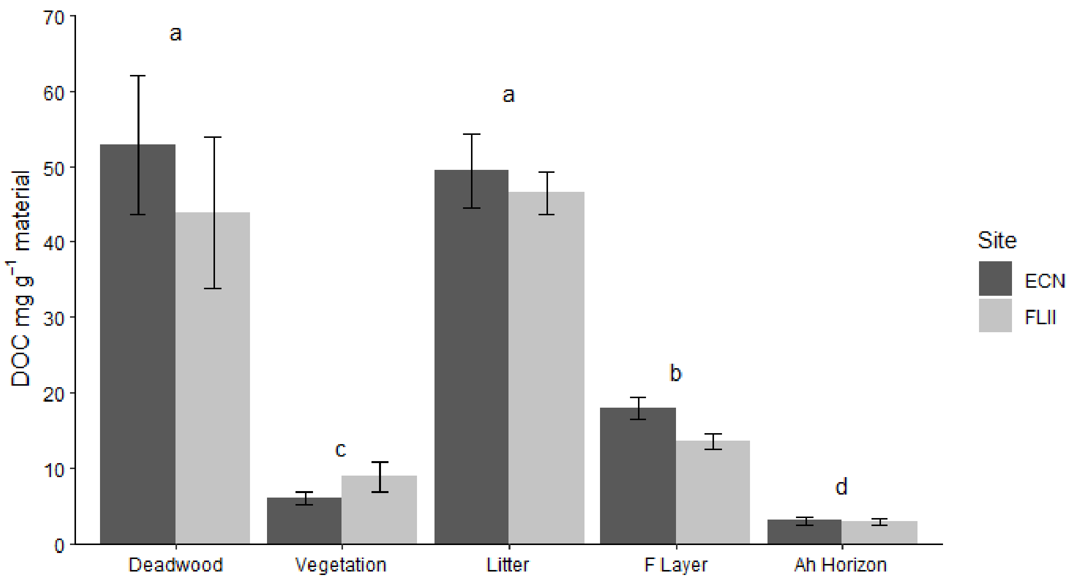

Figure 4-4 - The influence of site and material type on DOC concentrations (mg g^{-1} material). Data are mean ±1SE (n=3, except deadwood n=15). Material types that do not share a letter are significantly different (p<0.05; Games-Howell method on Box-Cox transformed data).

The largest DOC flux per unit area (132.6 ± 31.0 g m^{-2}) was found in the ECN litter samples whilst the least was found in deadwood at the FLII plot (0.763 ± 0.297 g m^{-2}) (Figure 4-5). By contrast to the DOC produced per unit mass (mg g^{-1}), the DOC produced per area (g m^{-2}) was lower from deadwood sources because of the lower volume on the forest floor (Figure 4-5). Two-way ANOVA found no overall significant effect of site on DOC g m^{-2} (F = 0.24; p = 0.627) but a significant effect of material type (F = 98.89; p<0.001) and a significant interaction between site and source ($F = 14.21$; $p<0.001$), such that vegetation contributed more DOC g m^{-2} in FLII plots but the Ah horizon contributed more in the ECN plots.

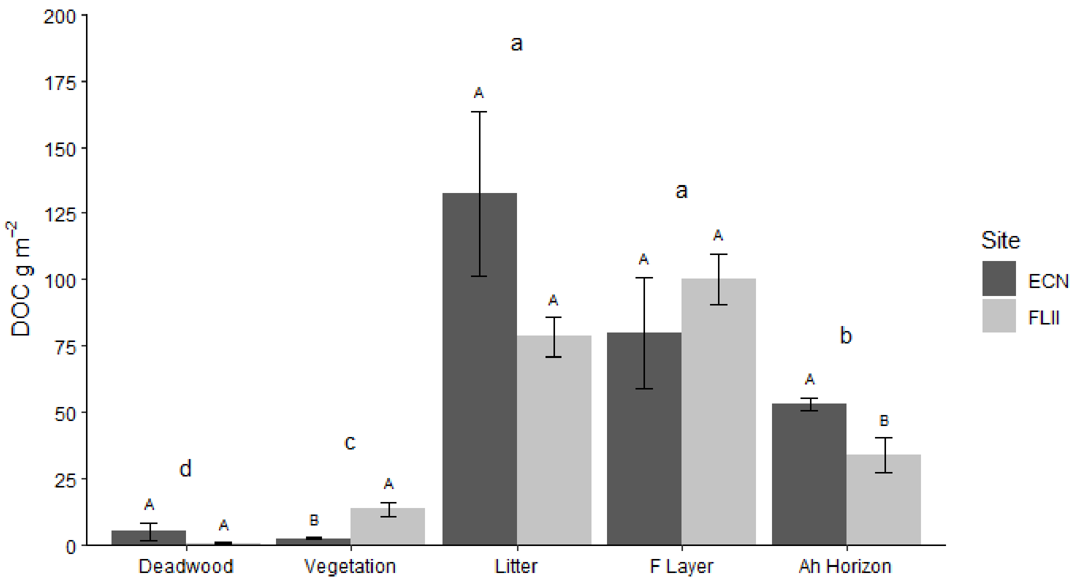

Figure 4-5 - The influence of site and material type on DOC fluxes (g m^{-2}). Data are mean ±1SE (n=3, except deadwood n=15). Material types across sites that do not share a lower-case letter are significantly different ($p<0.05$; Games-Howell method). Sites within each material type that do not share an upper-case letter differ significantly ($p<0.05$; two sample t-test).

The cumulative DOC flux from all sources was higher in the ECN than the FLII site, measuring 295.5 and 230.3 g m^{-2}, respectively (Figure 4-6). Results of a Welch two sample t-test found that the flux from the ECN was significantly larger than that of the FLII ($p = 0.02$).

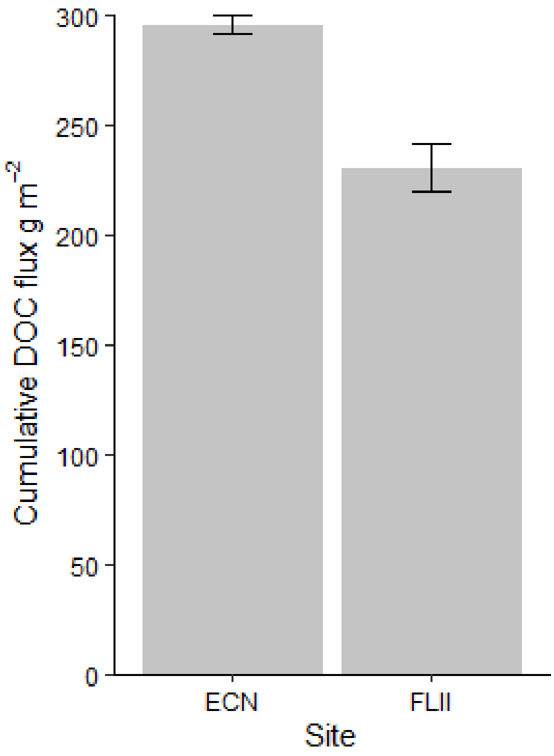

Figure 4-6 - Cumulative flux of DOC (g m^{-2}) from forest floor materials at sites under different management. The ECN is unmanaged whilst the FLII is managed. Welch two sample t-test found a significant difference between sites (p=0.02)

4.5 Discussion

The long-term monitoring data revealed that forestry management practices may have a large impact on DOC concentrations and export. We found larger quantities of DOC in shallow soil at the unmanaged ECN site, whereby the annual median was twice that of the managed FLII site. The larger quantity of DOC found in the shallow soils than in deep soils is consistent with other research that has found DOC quantities reduce with depth (Michalzik *et al.*, 2001; Wu, Clarke and Mulder, 2010; Kaiser and Kalbitz, 2012; Lv and Liang, 2012). DOC is largely produced in the upper, organic soil layers and associated litter. DOC that leaches into deeper, mineral soil layers is more susceptible to removal by adsorption or decomposition (Michalzik *et al.*, 2001) and given the high clay content of the mineral soils under both sites, adsorption of DOC to soil mineral particles is very likely. The difference in DOC quantity between the ECN and FLII sites might be attributed to management effects on the quantity of forest materials as sources of DOC, as further discussed below. It is also possible that management effects on the water balance, for example, tree thinning (causing less canopy interception of rainfall and reduced evapotranspiration) enhanced leaching losses of DOC at the FLII site leading to reduced DOC concentrations in pore water.

4.5.1 Impact of management on the quantity of forest material

A greater mass of litter, F layer and Ah horizon per unit area was seen than deadwood and vegetation. This would be expected as both leaf litter and organic and mineral soil horizons have a larger spatial extent in comparison to deadwood and ground cover vegetation due to almost continuous, rather than patchy, ground coverage. Differing management may also affect the inputs from these sources. Although not significant due to high variability between plots at the ECN site, the unmanaged ECN plots consistently had greater quantities of leaf litter on the forest floor which could be a result of a denser tree cover in comparison to the FLII site which undergoes thinning. The presence of a shrub layer in the ECN plots, which is not periodically removed by management like the FLII plots, may also contribute to the greater amounts of leaf litter. This has been found in other studies, whereby management, specifically thinning, significantly reduced litterfall (Henneron *et al.*, 2018). In addition, the FLII site has more open canopy due to management than the ECN site, so canopy water interception is smaller and thus higher water and light input to the forest floor could speed the decomposition rate of leaf litter. In addition, the greater light input to the forest floor at the FLII site enables the herb layer to establish which is consistent with the finding that all FLII plots had greater vegetative mass.

Typical values of fallen deadwood volumes in temperate, unmanaged forests range from 50 $m^3\ ha^{-1}$ (Hodge and Peterken, 1998) to 165 $m^3\ ha^{-1}$ (Krueger, Schulz and Borken, 2017). By contrast, managed woodlands can exhibit deadwood volumes ranging from as low as 2 $m^3\ ha^{-1}$ (Tobin *et al.*, 2007) to 30 $m^3\ ha^{-1}$ (Krueger, Schulz and Borken, 2017), largely due to its removal (Powers *et al.*, 2012). In the managed FLII site, deadwood volumes were low (4.1 $m^3\ ha^{-1}$) but fell within the range cited by other literature. However, in the unmanaged ECN site, deadwood volumes averaged 21.2 $m^3\ ha^{-1}$ which would fall below cited volumes in other studies. This may be as a result of the historical management undertaken at the ECN site. As management only ended in 1992 at the ECN site, it may be that the deadwood volumes have not reached a level that would be seen in pristine woodland. The volume of deadwood present in forests is dependent on forest stand dynamics and management practices. As the intensity of forest management increases, the amount of deadwood per hectare decreases (Green and Peterken, 1997; Hodge and Peterken, 1998; Paletto *et al.*, 2014). It is not surprising, therefore, given the management history, that the managed FLII site had a smaller biomass of deadwood than the unmanaged ECN site. Tree thinning carried out in the FLII site will have reduced the rate of tree mortality and so resulted in decreased deadwood production whilst the production of deadwood in the ECN site is more dependent on disturbance events. Instances of thinning will have created pulses of deadwood inputs to the forest floor, leading to certain decay classes being more common. For instance, immediately after thinning, deadwood at a lower stage of decay will be more prevalent than later stages of decay (Thibault and Moreau, 2016).

The amounts of vegetation, deadwood and litter at each site will have influenced the formation of the F layer and Ah horizon. The F layer is a mix of organic matter at different stages of decomposition which lies on top of the soil (Trimble and Lull, 1956); the Ah horizon is the surface mineral soil consisting of organic material mixed with parent material. Soil organisms digest and incorporate organic matter from forest floor materials into underlying soil (Boyle and Powers, 2013). There is evidence of high density earthworm populations in Alice Holt forest soils with some even found within the deadwood itself (Ashwood *et al.*, 2019). This will have contributed to the transfer of organic matter from the forest floor materials to the soil. At FLII, the trend for a smaller biomass and therefore C stock of litter might indicate lower total inputs from the thinned canopy, as previously discussed. However, the quantity and distribution of organic material between the litter, F layer and (as measured C) in the Ah horizon will depend not only on quantity of input via litter fall, but also subsequent decomposition and redistribution processes. The reduced C stock in the FLII Ah horizon also reflects a lower soil bulk density at this site (in addition to a lower C concentration). The greater biomass and C for the F layer matching the lower C stock for the Ah horizon at FLII might indicate less soil incorporation of organic material from the F layer, if bioturbation activity is reduced at the managed site. However, quantification of process rates (e.g. litterfall, decomposition, bioturbation activity) is required in order to understand the basis of differences in mass and C stocks of forest floor materials between the two sites.

While total mass was largest at the ECN site, it was not significantly larger than at the FLII site, and the high variability in mass of individual materials (coefficients of variation were large: > 30% for many of the materials and approaching 70% for deadwood at the FLII site) may have masked any effect of management. The high variability seen in our results is common in forest floor material (Cools and De Vos, 2013), and other research has similarly found that management effects were hidden by large variability (Bouriaud *et al.*, 2019). Larger scale sampling may help to clarify this effect.

4.5.2 Dominant sources of DOC between different forest materials and the impacts of management

As expected, the amount of DOC produced per g of material for each source did not vary with management (Figure 4-4). Both sites were part of the same semi-natural woodland and so the quality (as a DOC source) of material between the sites may not vary substantially, only the quantity. Even though the C content of the Ah horizons differed between sites, this did not result in between-site differences in DOC production when considered on a mg g^{-1} basis (Figure 4-4). Therefore, the amount of DOC produced per m^2 varied between sources of forest floor material as a result of differences in quantity not quality. While management did not significantly affect DOC amounts per area (g m^{-2}) when examined as a main effect across all the individual sources (Figure 4-5), the cumulative flux of DOC in the ECN was higher than that of the FLII (Figure 4-6), as also seen by our long-term monitoring (Figure 4-2, Figure 4-3). Other research has also found that carbon pools of unmanaged forests are larger than similar, managed forests (Chatterjee, Vance and Tinker, 2009; Schulze *et al.*, 2009; Krug, Koehl and Kownatzki, 2012). Although vegetation and the Ah horizon did differ as sources of DOC (g m^{-2}) with respect to management, reflecting the differences in their quantities between the sites, the large variability in DOC production per source may have masked management as a main effect in our study. Additionally, long-term management was similar at both sites prior to monitoring, with the ECN plot only being unmanaged over the last 20 years. It is likely that the time-span required to evaluate an unmanaged forest is longer than this, and for some studies has been defined as an absence of management for 250 years (Knohl *et al.*, 2003; Wirth, 2009). The use of further long-term monitoring would help to clarify how the time since management effects forest carbon stocks and fluxes.

Leaf litter produced a substantial amount of DOC both per gram of material, and per m^2. The amount of DOC produced from leaf litter is notably higher at the ECN site as a result of larger litter inputs. This is possibly due to management practices resulting in a denser tree canopy in comparison to the FLII site. However, leaf litter will only provide inputs to the soil for a short period of time and will not be present all year round. The rate of leaf litter decomposition has been found to be high at Alice Holt forest with 74% decomposition over a year (Benham *et al.*, 2012). Fresh leaf litter releases the largest amount of DOC with the flux declining as leaf litter decays (Don and Kalbitz, 2005). In contrast to leaf litter, deadwood decays more slowly (Didion *et al.*, 2014) due to the greater content and structure of polymers, such as lignin, found in wood (Zhou *et al.*, 2007). Full decomposition may take 3-750 years (Harmon *et al.*, 2020), depending on the size and diameter of individual logs (Currie *et al.*, 2002). Thus, deadwood has the potential to form a long-term source of DOC in comparison to the short, seasonal pulses provided by litter. Deadwood produced less DOC per m^2 than the Ah horizon, F layer and leaf litter due to its patchy spatial distribution. However, along with litter, it released the most DOC per unit mass. Bantle *et al*. (2014) considered the patchy distribution of deadwood to cause "hotspots" of DOC input into the forest soil. These hotspots could increase their spatial coverage with time under management practices that enable deadwood accumulation and so provide a greater input of DOC over the long-term (Spears and Lajtha, 2004). DOC production per gram of material indicated that deadwood provides a far larger input of DOC to the soil than either the Ah horizon or vegetation (Figure 4-4). Similar results were found by Kahl *et al*. (2012) who identified greater fluxes of DOC from logs than the forest floor. Studies have found that the amount of DOC released from deadwood increased as samples decayed (Hafner, Groffman and Mitchell, 2005; Bantle *et al.*, 2014).

The DOC released from forest floor materials and upper, organic soil layers during decomposition can translocate into deeper, mineral soil horizons (Michalzik *et al*., 2001). The quantity of DOC found in the Ah horizon has been found to be largely due to amounts leaching from litter rather than in-situ production (Peichl *et al.*, 2007). Our results broadly show this pattern (Figure 4-5), with litter producing 2.3-2.5 x more DOC g m^{-2} than the Ah horizon in the FLII and ECN, respectively. Where there were greater quantities of DOC produced by litter in the ECN site, we also found larger quantities in the Ah horizon than in the FLII. Long term repeated soil sampling has determined an accumulation of C within the topsoil mineral Ah horizon in the ECN site (Benham *et al*., 2012) which also confirms the continuous input of carbon from the forest floor layer to top mineral soil and the capacity of clay rich mineral topsoil to capture C. Here we have considered forest floor materials as sources of DOC production for translocation to underlying soil but also acknowledge that the activities of living woody and herbaceous vegetation (e.g. root exudation and turnover) might also contribute to DOC concentrations differentially, depending on management.

4.6 Conclusions: has management altered the flux of DOC into soil waters?

The results of long-term forest monitoring indicate that there is a difference in the DOC production between the two sites under different managements, with the annual median at the unmanaged ECN being twice that of the managed FLII. We examined forest organic materials that are thought to release DOC that is transported into soil waters by leaching. The results of our field study also show that a significantly larger total DOC flux is produced in the

ECN site (295.5 g m^{-2}) compared to the FLII site (230.3 g m^{-2}). Whilst no significant differences were found in the total forest organic material mass or carbon stocks between different managements, significant differences were found between different forest floor materials that were dependent on management. Likewise, with DOC release, the flux depended on forest material and management. Management affects the allocation of carbon between different forest organic materials and DOC fluxes. This study has identified that the quantity and type of material has a great potential to influence the amount of DOC in the soil. Whilst in our study the overall volume of deadwood was fairly low, and thus contribution of deadwood to DOC per m^2 was lower than for other organic sources, in forests with greater deadwood volumes, substantial amounts of DOC may be produced. Management practices, such as tree thinning and the removal of woody debris created by harvesting, may be influencing the amounts of DOC found in forest soil water. Further studies are required across a range of sites and intensity and longevity of management to confirm whether management is affecting DOC in soil water by influencing the composition of forest materials. More work is needed to understand how litter and deadwood contribute to Ah horizon material and DOC through this indirect pathway.

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5 The contribution of deadwood to soil carbon dynamics in contrasting temperate forest ecosystems

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5.1 Abstract

Deadwood forms a significant carbon pool in forest systems and is a potential source of dissolved organic carbon (DOC) input to soil, yet little is known about how deadwood effects forest soil carbon cycling. Deadwood DOC inputs to soil may be retained through sorption or may prime microbial decomposition of existing organic matter to produce additional DOC. To determine impacts of deadwood on soil C cycling, we analysed surface soil from beneath deadwood or leaf litter only, along chronosequences of stands of lowland oak and upland Sitka spruce. The concentration and quality (by optical indices) of water-extracted soil DOC (water-extractable organic carbon; WEOC), i*n situ* decomposition 'tea bag index' (TBI) parameters and enzymatic potential assays (β-D-cellubiosidase, β-glucosidase, β-xylosidase, leucine aminopeptidase, phosphatase, phenol oxidase) were determined. Presence of deadwood significantly ($p<0.05$) increased WEOC concentration (~1.5 - ~1.75 times) in the mineral oak soil but had no effect on WEOC in spruce soils, potentially because spruce deadwood DOC inputs were masked by a high background of WEOC (1168 mg kg^{-1} soil) and/or were not retained through mineral sorption in the highly organic (~90% SOM) soil. TBI and enzyme evidence suggested that deadwood-derived DOC did not impact existing forest carbon pools via microbial priming, possibly due to the more humified/aromatic quality of DOC produced (humification index of 0.75 and 0.65 for deadwood and leaf litter WEOC, respectively). Forest carbon budgets, particularly those for mineral soils, may underestimate the quantity of DOC if derived from soil monitoring that does not include a deadwood component.

Keywords

Coarse woody debris, dissolved organic carbon, forest soils, microbial priming

Declarations

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5.2 Introduction

Forests are acknowledged as large and important carbon (C) sinks, storing carbon in soils and both living and dead biomass. Globally, forests are estimated to hold 861 ± 66 Pg C, of which 119 ± 6 Pg are accounted for by temperate forest ecosystems (Pan *et al.*, 2011). The amount of carbon stored in forest soils and biomass varies with forest type. Pan *et al*. (2011) state that tropical forests hold 56% of carbon in biomass with only 32% in the soil whereas boreal and temperate forests may hold 20% and 37% in biomass and 60% and 49% in soil, respectively. The remaining carbon is held within litter and deadwood and Pan *et al*. (2011) estimated that 8% (73 ± 6 Pg) of the world's forest C is held in deadwood. In the UK, forests store up to 1Pg C (Morison *et al*. 2012), of which 74% is held within the soils down to 1 m depth (Vanguelova *et al.*, 2013). The remaining 26% C is split between tree biomass (22%) and litter and deadwood (4%) (Morison *et al*. 2012). The stock of C in deadwood alone in the UK represents 3.5% of the total forest C storage, with almost twice the amount per unit area in conifer (2.36 t C ha^{-1}) when compared to broadleaved forests (1.24 t C ha^{-1}) (Vanguelova *et al*. *in-press*). Deadwood may be present in the form of standing or lying dead trees or as stumps, with standing and lying deadwood categorised into decay classes for inventory purposes (Hunter 1990). For example, for lying deadwood, the decay classes range from 1 (least decomposed; intact bark, texture and structure) to 5 (most decomposed; bark absent, powdery texture and structure collapsed) (Hunter 1990). Currently about 50% of the deadwood in the UK is in a less degraded state, at less than 10% decay or decay class 2, and the rest in different decay classes (Vanguelova *et al*. *in-press*).

Initiation of the decomposition of wood is thought to be primarily carried out by fungi (Schwarze, Engels and Mattheck, 2000) and occurs slowly, as the lignin content of wood provides a physical barrier to the enzymatic decomposition of non-lignin macromolecules, and, as such, it can take decades before a tree is fully decomposed (Russell *et al.*, 2014). Research has shown that most conifers are slower to decay than broadleaved species (Weedon *et al.*, 2009; Shorohova and Kapitsa, 2014; Herrmann, Kahl and Bauhus, 2015), partially due to the greater amounts of lignin, waxes, lipids, and resins found in coniferous wood (Zhou *et al.*, 2007; Lukac and Godbold, 2011). Wood decay begins immediately following the death of cells. After the action of lignin peroxidases or polyphenol oxidases (Janusz *et al.*, 2017), the resulting depolymerisation of lignin structures allows easier access for extracellular hydrolytic enzymes that are responsible for the depolymerization of polymers such as cellulose and hemicellulose (Li *et al.*, 2018). These depolymerization reactions produce lower molecular weight compounds with increased solubility and initial bioavailability; deadwood-derived dissolved organic carbon (DOC) may enter underlying soil via leaching (Wambsganss, Stutz and Lang, 2017; Piaszczyk, Lasota and Błońska, 2019), contributing to the soil DOC pool and undergoing subsequent fates, e.g. microbial metabolism including respiration to, or driving production of, greenhouse gases (CO_2, CH_4, N_2O) or stabilization (Wambsganss, Stutz and Lang, 2017) through interaction with soil minerals (Guggenberger and Kaiser, 2003), depending on its quality. The flux of DOC released by deadwood (44 – 53 mg per g material) has been found to be comparable to leaf litter (47 – 49 mg per g material) and is significantly greater than forest vegetation and the upper soil layers (3 – 18 mg per g material) (Hollands *et al*. 2022).

Although we know that deadwood forms a significant pool of C in forest systems, and previous studies have shown that soil DOC concentrations are elevated in forest systems with deadwood when compared to those without (Spears and Lajtha, 2004; Hafner and Groffman, 2005; Kahl *et al.*, 2012; Stutz *et al.*, 2019; Minnich *et al.*, 2021; Hollands *et al.*, 2022), it is less clear what effects the presence of deadwood has on forest soil C cycle processes and how this varies in contrasting forests. It is not clear if the reported elevations in soil DOC concentrations are a result of solely the input and subsequent stabilization of deadwood decomposition derived DOC, or, if inputs of deadwood DOC promote the release of DOC from existing soil organic matter (SOM) (Minnich *et al*. 2021). On the one hand, deadwood-derived DOC might be stabilized in soil as a result of either: (i) chemical protection from decomposition through association with mineral phases; (ii) physical protection through sequestration within soil structure; or, (iii) biochemical protection through inherent or acquired structural recalcitrance (Six *et al.*, 2002; von Luetzow *et al.*, 2006; Piaszczyk, Blonska and Lasota, 2019). On the other hand, deadwood DOC components may prime decomposition of, or release DOC from, existing SOM pools through: (i) stimulation of microbial activity and as such enzymatic activity (Fontaine, Mariotti and Abbadie, 2003; Gonzalez-Polo, Fernandez-Souto and Austin, 2013; Beverly and Franklin, 2015; Minnich *et al.*, 2021) which in turn primes increased depolymerisation of, and release of DOC from, native soil organic matter; or (ii) abiotic liberation of native dissolved organic compounds from protective associations with minerals (Keiluweit *et al.*, 2015). As previously mentioned, deadwood varies with respect to the stage of wood decomposition, or decay class. Wood decay class is known to influence subsequent rates of deadwood decomposition (Tobin *et al.*, 2007; Olajuyigbe *et al.*, 2011; Stutz *et al.*, 2019). Wood in the late stages of decay hosts a greater primary decomposer microbial biomass (Küffer *et al.*, 2008; Baldrian *et al.*, 2016). Increased microbial and fungal biomass in and under deadwood (Peršoh and Borken, 2017) may lead to larger DOC and CO_2 fluxes being produced, and therefore potentially enhance impacts on the soil DOC pool and C cycling processes. Wood composition will also influence the rates of decay, with wood from conifers (‘softwoods’) and broadleaves (‘hardwoods’) decaying at different rates (Herrmann, Kahl and Bauhus, 2015), and likely producing different quality and lability of DOC.

Soil properties, such as soil texture and type, pH and moisture will affect the amount of organic matter held in soils (Matus, 2021) and influence the rate of decomposition processes that may release DOC. Silt and clay content in soils may capture and stabilize organic compounds through sorption (Six *et al.*, 2002; Villada, 2013; Matus, 2021). Low soil pH and high moisture content inhibit decomposition rates (Hagemann *et al.*, 2010) which may increase SOM accumulation (Keith, Mackey and Lindenmayer, 2009). It is possible that the physical presence of large woody debris on the forest floor may create a localised microclimate, through the shading of soils which will affect temperature, or preventing water and litter reaching the soil. In tropical forests, deadwood has been found to buffer soil temperature, preventing diurnal fluctuations (Zalamea, González and Lodge, 2016). Anoxic conditions can be created through waterlogging of soils and these conditions are known to inhibit decomposition processes (Hagemann *et al*. 2010). However, little research has been carried out into the creation of microclimates under deadwood in temperate forests (Woodall *et al.*, 2020).

Accordingly, the aim of this study is to confirm whether deadwood produces significant inputs of DOC into underlying soil and to identify the effect this has on C cycling. Specific objectives of this study are to: (1) identify whether the presence of lying deadwood influences the amounts of DOC in underlying soil, comparing common hardwood (oak) and softwood (Sitka spruce) species on their typical soil types in Britain; (2) identify the impact of deadwood on soil carbon processes and cycling; and (3) characterize the quality of soil DOC in order to help identify its source and potential lability. We use a combination of traditional measurements (e.g. extracellular enzyme potentials as sensitive indicators of change in decomposition processes) and more novel indices, as applied to forest C studies, to derive decomposition data (the teabag index, (Keuskamp *et al.*, 2013) and to assess the biochemical stability ($SUVA_{254}$, (Hansen *et al.*, 2016) and humification index (HIX, (Ohno, 2002) and source (fluorescence index (FI), (McKnight *et al.*, 2001) of soil DOC.

5.3 Materials and methods

5.3.1 Study sites

Oak woodland and Sitka spruce plantations represent the two most common British forest types. In the UK, oak covers 16.4% of land under broadleaves (Brewer, 2014a) whilst Sitka spruce covers 50.8% of land under conifers (Brewer, 2014b). Two chronosequences (Benham, Vanguelova and Pitman, 2012; Vanguelova *et al.*, 2019) were used: 1) in Alice Holt Forest, Surrey in S.E. England; and, 2) in Kielder Forest, Northumberland in N.E. England to represent a range of tree stand ages and decay classes of deadwood (Table 5-1). The Alice Holt Forest sites (51° 9' N, 0° 52' W) consist of young (~30 years old), middle age (~70 years old) and old (~180 years old) managed lowland oak forest (mainly *Quercus robur*, L.) on surface water gleys (stagnosols). The upper soil profile consists of silty clay in the Ah horizon (7 cm deep) over an Eg horizon (8 cm deep). High rates of decomposition in Alice Holt soils mean that there is no distinct O layer; instead, organic matter is mixed with mineral soil in the upper Ah horizon. The Ah horizon has a bulk density of 704.3 kg m^{-3} and carbon stock of 13.3 t ha^{-1}. The Eg horizon has a bulk density of 968.2 kg m^{-3} and carbon stock of 22.3 t ha^{-1}. Elevation is 80 m with monthly average air temperatures ranging between 4.7 and 17.6°C with an annual mean of 10.5°C and mean annual precipitation of 634 mm. Kielder Forest (55° 15' N, 2° 23' W) consists of uniform, managed young (~10-20 years old), middle age (20-40 years old) and old (40-60 years old) upland Sitka spruce (*Picea sitchensis* (Bong.), Carr.) plantations on peaty gley soils and deep peat (stagnohumic gleys/histosols). The upper soil profile is predominantly organic material, with an O layer (2 cm deep) over the H peat layer (17 cm deep). The O layer has a bulk density of 86 kg m^{-3} and carbon stock of 22.7 t ha^{-1}. The H layer has a bulk density of 157 kg m^{-3} and carbon stock of 114 t ha^{-1}. Elevation ranges between 240 m and 365 m, monthly average air temperatures range between 3 and 14.8°C with an annual mean of 8.3°C, and precipitation of 759 mm. The majority of plots are in their second rotation (i.e. second crop) since afforestation (Table 5-1). At each site three plots of 10 m^2, per chronosequence age group were selected for field measurements and sampling. These age groups contained a range of different sized debris at different stages of decay. The dominant decay stage per age group is shown in Table 5-1, however, other decay classes were present at each plot. Decay class was visually assessed according to the guidelines by Hunter (1990) as decay classes 1 - 5, whereby freshly fallen wood with little to no decay is considered class 1 whilst heavily decayed wood is class 5.

Table 5-1 - Site plot information. Decay class represents the dominant stage of decay found within each age group.

Site	Age group	Age (years)	Rotation	Decay class
Alice Holt Forest (oak)	Young	24-34	-	1-2
	Mid	64-84	-	3
	Old	184+	-	4-5
Kielder Forest (spruce)	Young	12, 18, 19	2nd	1-2
	Mid	20, 30, 31	2nd	3
	Old	46, ~60, 74	1st, 2nd	4-5

5.3.2 Field sampling

At each chronosequence plot, five subplots (~1x1 m^2) where deadwood was present were randomly selected along with five subplots (~1x1 m^2) where no deadwood was present, but only forest leaf litter was. These subplots will be referred to as "deadwood" and "leaf litter" respectively. Deadwood diameters at Alice Holt ranged between 5 – 90 cm, with a mean of 10.8 cm. Two samples of large diameter deadwood (>30 cm diameter) were selected due to an absence of smaller debris. Deadwood diameters at Kielder ranged between 5 – 13.7 cm, with a mean of 7 cm. An average mass of 0.1 kg m^{-2} deadwood (~4.5 m^3 ha^{-1}) was found at Alice Holt (Hollands *et al*. 2022) and ~0.3 kg m^{-2} (~10.5 m^3 ha^{-1}) at Kielder. After removal of the surface litter layer at both the leaf litter and deadwood plots, a soil sample was taken from the top 10 cm of soil from all ten subplots. Soil temperature of the soil surface layer from each of the ten subplots was measured with a handheld probe (Delta-T Devices Ltd., UK). This was repeated over two site visits, the first in June-July and the second in September-October 2017.

5.3.3 Tea Bag Index

A tea bag index (Keuskamp *et al.*, 2013), which exploits the differential in decomposition between green tea (*Camellia sinensis*; fast decomposing) and rooibos tea (*Aspalathus linearis*; slow decomposing) leaves over ca. 3 months, was used to compare decomposition rate and organic matter stabilization potential of soils under deadwood and neighbouring soils where no deadwood was present. Following the protocol of Keuskamp *et al*. (2013), pre-weighed pairs of commercially available Lipton green tea and Lipton rooibos tea bags were buried in June and July 2017 and retrieved in September or October after an incubation of 81-85 days. They were buried 8 cm deep and 15 cm apart, in the soil layer beneath the deadwood and in leaf litter subplots. Following retrieval, tea bags were oven dried at 60°C and external debris removed before weighing. Mass lost between the date of initial burial and retrieval was used to calculate both k, a decomposition rate that measures the turnover time of labile carbon, and S, the stabilisation factor, a measure of the stabilisation potential of organic carbon according to the following equations (Keuskamp *et al.,* 2013).

$$W(t) = a_r e^{-kt} + (1-a_r)$$

$$S = 1 - \left(\frac{a_g}{H_g}\right)$$

Where: W(t) is the weight (g) of rooibos tea remaining after incubation time t (d); a_r = decomposable fraction of rooibos litter (g g^{-1}) as calculated from S and the hydrolysable fraction of rooibos tea (H_r); k = rooibos tea decomposition rate (d^{-1}). S = stabilization factor (unitless); a_g = decomposed fraction of green tea after incubation (g g^{-1}); H_g = hydrolysable fraction of green tea (g g^{-1}). H_g and H_r have been previously determined as 0·842 and 0·552 by Keuskamp *et al.* (2013).

5.3.4 Lab analyses

Soil samples were kept stored at 4°C until analysis. Moisture content of soils were measured gravimetrically as loss of mass on oven heating to 105°C. Soil organic matter (%) was measured through mass loss on ignition at 550°C. Subsamples of soil were oven dried at 105°C for 12 hours prior to grinding with a planetary ball mill (Pulverisette 5, Fritsch, Germany). The total C and N of ground samples was then measured using a Thermo Flash 2000 Carbon and Nitrogen Analyser.

Water extractable carbon was determined by mixing 4.5 g soil in to 45 ml water, at a ratio of 1:10 soil:ultrapure water. These were placed on an end-over-end shaker for 24 hours before pH was measured and the extracts then centrifuged at 3500 rpm for 15 minutes. Extracts were then filtered through Whatman GF/A filter papers before centrifuging at 3500 rpm for a further 15 minutes and vacuum filtering through 0.45 µm cellulose nitrate filter papers. Total organic carbon (TOC; mg L^{-1}) of these filtered solutions was measured using a carbon analyser (Shimadzu TOC-L, Shimadzu Corporation, Japan) as Total Carbon (mg L^{-1}) – Inorganic Carbon (mg L^{-1}). As they had been filtered to 0.45 µm, it is presumed that all TOC measured is DOC. Water extractable organic carbon (WEOC; mg kg^{-1} dry soil) was calculated from the DOC readings to correct for the volume of water used during extraction and dry mass of soils. Quantities of DOC will be referred to as WEOC.

The specific ultraviolet absorbance at 254nm ($SUVA_{254}$) can be used as a proxy measurement for the aromatic content of DOC, with higher $SUVA_{254}$ values indicating a greater aromatic content (Hansen *et al*. 2016). Absorbance of soil solutions was measuring using spectrophotometer (Jenway 5000, Jenway, UK) at wavelength 254 nm. A baseline of ultrapure water was used and blanks run every five samples. $SUVA_{254}$ ($L\ mg\ C^{-1}\ m^{-1}$) was then calculated as:

$$SUVA_{254} = \frac{Absorbance_{254}}{DOC\ (mg\ L^{-1})}\ x\ 100$$

Fluorescence measurements of the soil solutions and enzyme activities were made using a microplate reader (SpectraMax i3x, Molecular Devices, USA). In order to calculate a humification index (HIX), spectra were obtained with an excitation wavelength of 254 nm over the emissions waveband of 300 – 480 nm at increments of 5 nm (Ohno, 2002) and calculated as:

$$HIX = \frac{\sum I_{435\to480}}{\sum I_{300\to345} + \sum I_{435\to480}}$$

where *I* is the detected fluorescence intensity.

A fluorescence index (FI) was calculated using the ratio of wavelengths 470 to 520 nm at excitation 370 nm (McKnight *et al*. 2001).

Enzyme assays to determine potential hydrolytic depolymerase activity rates were selected as follows: carbon cycle - β-D-cellubiosidase (CB; cellulose degradation), β-glucosidase (BG; sugar degradation) and β-xylosidase (XYL, hemicellulose degradation); carbon and nitrogen cycle - Leucine aminopeptidase (LAP, protein degradation); phosphorus cycle - phosphatase (PHOS, phosphorus mineralisation). Phenol oxidase (POX) activity, an important oxidative enzyme involved in lignin depolymerization was also determined.

Microplate fluorometric analysis of CB, BG, XYL, LAP, and PHOS potential activities in soil slurries were determined using the methods of Bell *et al*. (2013). Fluorescence was measured at excitation 365 nm and emission 450 nm after a two-hour incubation at mean field soil temperature (Table 5-2). For all enzyme assays, sodium acetate buffer was used and adjusted to the corresponding site pH (Table 5-2) using glacial acetic acid.

POX activity was measured following the methods of Allison (2012) using L-dihydroxyphenylalanine (L-DOPA) as a substrate. Optimum incubation times were found after reading plates at absorbance 460 nm every 30 minutes for five hours. Final assay plates were incubated at mean field soil temperature (Table 5-2) for 3.5 hours before measurement.

5.3.5 Deadwood DOC extraction

In June 2018, the young and old plots at Alice Holt were revisited (Zhao, 2018) and samples of deadwood (>10 cm diameter) were collected for the extraction of WEOC. Five samples per plot were selected and cut to ~20 cm lengths in the field. These were sealed in plastic bags and transported back to the laboratory for storage at 4°C. Prior to extraction, deadwood samples were cut into 1.5 cm x 1.5 cm x 1.5 cm cubes of centre wood (i.e. cubes were formed by sawing off the outer wood to leave a cube at the centre) and air dried for 15 days. These were then placed in 50 ml centrifuge tubes and 33.75 ml ultrapure water added. Tubes were shaken on an overhead shaker for 24 hours before centrifuging at 3500 rpm for 15 minutes. Supernatants were filtered through Whatman GF/A and then through 0.45 μm cellulose nitrate filter papers. Filtrates were further diluted as 2 ml sample: 4 ml MilliQ water before analysis on an Analytical Sciences liquid CN analyser.

5.3.6 Statistical analyses

Statistical analyses were carried out using R core v 3.5.1 (R Core Team, 2017). Data were tested for normality using Shapiro-Wilk test and equality of variances using Levene's test. Data were $\log_{10}$ transformed where equality of variances was not met. The effect of site, stand age and presence of deadwood were analysed using a general linear model. Significant differences were accepted at $p<0.05$. Means are presented with standard errors. Tukey HSD post-hoc testing was used to identify where significant differences occurred.

5.4 Results

5.4.1 Effects of deadwood on underlying soil properties

Soil properties varied significantly between the two sites, with Kielder being cooler, wetter, and more organic and acidic (Table 5-2). The larger organic matter content (%) at Kielder was reflected in the C (%) measures (43% and 12% C at Kielder and Alice Holt, respectively), and subsequently the surface soil C:N ratio. Presence of deadwood had no effect on soil pH ($p=0.6$), gravimetric soil water content ($p=0.721$), SOM ($p=0.333$) or soil C:N ($p=0.502$). Oak subplots with deadwood had slightly higher % water content but were not found to be statistically significantly different to leaf litter subplots (Table 5-2), whilst deadwood subplots in the spruce forest had marginally lower water content to the leaf litter subplots.

Table 5-2 – Average surface soil properties (0-10 cm depth) from Alice Holt and Kielder Forests ± 1 standard error of the mean, grouped by stand age and presence or absence of deadwood. N= 15 per group. Field soil temperature and moisture were measured at [1] time of tea bag burial (June-July) and [2] time of tea bag retrieval (September-October). Bold values are averages per group presence of deadwood within site). Tukey groupings for the effect of interaction between presence of deadwood and site are shown by superscript letters. Where Tukey groupings are not given, there was no significant presence of deadwood * site interaction term.

		Alice Holt Forest (oak)				**Kielder Forest (spruce)**			
		Young	**Mid**	**Old**	**Mean**	**Young**	**Mid**	**Old**	**Mean**
Field soil	[1]Leaf litter	16.9±0.2	16.6±0.1	16.5±0.1	**16.6±0.1**^{A}	10.7±0.1	10.9±0.1	10.2±0.1	**10.6±0.1**^{C}
temperature	[1]Deadwood	16.3±0.1	16.3±0.1	16.5±0.1	**16.4±0.1**^{B}	10.7±0.1	10.8±0.1	10.2±0.1	**10.6±0.1**^{C}
(°C)	[2]Leaf litter	13.0±0.1	12.5±0.1	12.5±0.1	**12.7±0.0**	9.8±0.0	9.7±0.1	9.1±0.1	**9.5±0.0**
	[2]Deadwood	13.2±0.1	12.5±0.1	12.5±0.1	**12.8±0.1**	9.9±0.0	9.6±0.1	9.1±0.1	**9.5±0.0**
pH	Leaf litter	4.4±0.1	4.2±0.1	4.5±0.1	**4.4±0.1**	3.7±0.1	3.8±0.1	4.1±0.1	**3.9±0.1**
	Deadwood	4.3±0.1	4.4±0.1	4.6±0.2	**4.4±0.1**	3.8±0.1	3.7±0.1	4.0±0.1	**3.9±0.1**
Soil Water	Leaf litter	34.6±1.4	33.2±1.9	33.6±2.4	**33.8±1.1**	73.0±3.3	70.8±1.8	78.4±0.6	**74.0±1.3**
content (%)	Deadwood	36.5±1.4	35.6±3.2	34.3±2.7	**35.4±1.4**	71.6±1.5	69.2±2.2	77.1±1.3	**72.6±1.1**
SOM	Leaf litter	17.0±1.3	19.0±2.7	21.5±2.6	**19.2±1.3**	76.9±6.4	92.7±1.6	93.6±1.2	**87.7±2.5**
(%)	Deadwood	18.9±1.0	26.9±5.0	23.3±3.0	**23.0±2.0**	80.0±3.7	91.9±3.4	90.8±3.2	**87.6±2.1**
C (%)	Leaf litter	10.0±1.2	13.0±2.7	9.9±1.4	**11.0±1.1**	35.5±2.9	46.7±0.3	46.5±0.8	**42.9±1.3**
	Deadwood	12.0±1.3	15.3±2.3	9.4±0.9	**12.2±1.0**	38.3±1.7	46.8±0.5	44.5±1.7	**43.2±1.0**
N (%)	Leaf litter	0.7±0.1	0.8±0.1	0.7±0.1	**0.7±0.1**	1.3±0.1	1.5±0.0	1.7±0.1	**1.5±0.1**
	Deadwood	0.8±0.1	0.9±0.1	0.6±0.0	**0.8±0.1**	1.3±0.1	1.5±0.1	1.6±0.1	**1.5±0.0**
C/N	Leaf litter	14.5±0.4	15.1±0.6	14.2±0.4	**14.6±0.3**	27.8±1.1	31.4±1.0	28.4±1.2	**29.2±0.7**
	Deadwood	15.3±0.6	15.7±0.6	15.4±0.6	**15.5±0.3**	29.0±1.1	30.3±0.7	27.6±1.1	**28.9±0.6**

Stand age affected soil properties across both sites. Soil pH was significantly higher (0.18 - 0.41 units) in old stands than the mid-aged and young stands, at both forests ($p<0.001$). Gravimetric water content was significantly affected by an interaction between site and age ($p=0.013$) whereby at Kielder, old stands were found to hold significantly more water than the mid-aged stand ($p=0.004$), with means of 78 ± 1% and 70 ± 1% respectively. Young stands had a significantly lower organic matter content than old or mid stands ($p<0.001$) at both forests. Soil C:N was also affected by stand age, with mid aged stands having a significantly ($p=0.048$) higher ratio in both forests (Table 5-2).

5.4.2 Effect of deadwood on surface soil WEOC

DOC release from deadwood ranged between 0.55 – 15.45 mg^{-1} g^{-1} air dried wood, with means of 2.45 ± 0.49 mg^{-1} g^{-1} air dried wood and 3.45 ± 0.93 mg^{-1} g^{-1} air dried wood in the old and young plots at Alice Holt, respectively. Age did not significantly affect the amount of DOC released by deadwood ($p=0.33$). Concentrations of Water Extractable Organic Carbon (WEOC) were two to five-fold higher in soils from Kielder Forest than Alice Holt Forest (Figure 5-1), averaging 1168 ± 43 and 353 ± 45 mg kg^{-1} dry soil, respectively. There was a significant interaction between site and presence of deadwood ($p=0.003$), as soils under deadwood in Alice Holt Forest held 1.45 – 1.76 x more WEOC than the corresponding leaf litter soils (Tukey HSD $p<0.001$). However, there was no effect of the presence of deadwood evident in Kielder Forest plots. Stand age also had no significant effect on WEOC quantity ($p=0.900$).

A fluorescence index (FI) can be used to infer the source of DOC in the soil solutions. FI values >1.9 indicate DOC from a microbial origin, such as lysates and extracellular release from bacteria, whilst values <1.4 might indicate an origin from plant material, reflecting contributions from lignin degradation products (McKnight *et al.*, 2001). Soil solutions from Kielder Forest showed a lower FI compared to those from Alice Holt Forest, ranging between 1.07 – 3.31 at Kielder Forest and 1.39 – 4.03 at Alice Holt Forest. Most samples fell within a FI of 1.4-1.9 indicating a mix of origins (Table 5-3). However, for Alice Holt Forest, soil solutions from the young leaf litter stand and the old stands with deadwood had mean FI values of 2.20 and 2.09 respectively, (Table 5-3) which indicates a microbial origin only. Soil solutions from under deadwood in the young stands in Kielder Forest had a mean of 1.36 which indicates WEOC originated from plant material only. Because of the differences between stand ages and sites, a significant three-way interaction was found between site, stand age and presence of deadwood for the fluorescence index (p=0.013). Mean values and the results of Tukey HSD post-hoc testing are shown in Table 5-3.

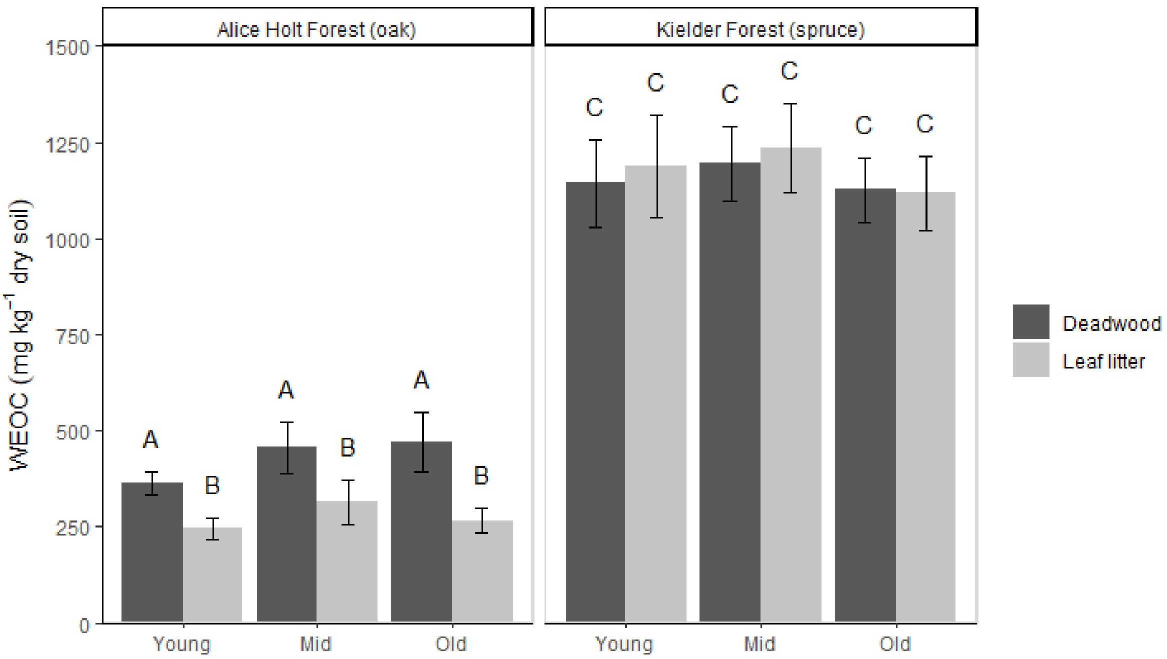

Figure 5-1 – Mean water extractable organic carbon (WEOC) in surface soil from Alice Holt and Kielder forests with or without deadwood, and in different stand age groups. Error bars are ± 1 SE of the mean. N = 15 per group. Groups that do not share a letter are significantly different from one another.

For soil solutions from Alice Holt Forest the mean humification index (HIX) was higher in soils under deadwood than in leaf litter soils (Table 5-3), indicating that soil from under deadwood had a greater degree of humification. Significant interaction was found between site and presence of deadwood (p=0.015) and site and age (p=0.003). The presence of deadwood significantly (p=0.007) increased the HIX value at Alice Holt Forest whilst stand age did not. For Kielder Forest samples, the opposite occurred, whereby presence of deadwood had no significant effect but stand age did (old-mid p=0.035, young-mid p=0.995, young-old p=0.006), with the old stands having a lower HIX value.

The specific ultraviolet absorbance ($SUVA_{254}$) was significantly larger for soil solutions from Alice Holt Forest than Kielder Forest for all sample groups (Table 5-3). Significant interactions were found between site and presence of deadwood (p=0.032) and site and age (p<0.001). Post-hoc testing found that the only significant within-site differences occurred at Kielder Forest between the young stand and the mid (p=0.001) and old stands (p=0.003).

Table 5-3 – Mean optical properties of soil WEOC from Alice Holt and Kielder Forests with or without deadwood, and in different stand age groups. FI – Fluorescence index; HIX – humification index; $SUVA_{254}$ – Specific UV Absorbance at 254nm. Results of Tukey post-hoc testing for the fluorescence index (FI) are shown in lowercase, where a significant three-way interaction occurred. Results of post-hoc testing for HIX and SUVA are shown in uppercase. Groups that do not share a letter are significantly different.

		Alice Holt Forest (oak)				**Kielder Forest (spruce)**			
		Young	**Mid**	**Old**	**Mean**	**Young**	**Mid**	**Old**	**Mean**
FI	Leaf litter	2.20±0.20^{a}	1.74±0.08^{abc}	1.66±0.04^{abc}	**1.87±0.08**	1.52±0.08^{c}	1.53±0.07^{c}	1.64±0.13^{bc}	**1.56±0.05**
	Deadwood	1.80±0.09^{abc}	1.78±0.12^{abc}	2.09±0.19^{ab}	**1.89±0.08**	1.36±0.05^{c}	1.66±0.14^{abc}	1.40±0.04^{c}	**1.48±0.05**
HIX	Leaf litter	0.60±0.04	0.67±0.04	0.68±0.04	**0.65±0.02^{B}**	0.76±0.03	0.72±0.04	0.63±0.05	**0.70±0.02^{AB}**
	Deadwood	0.74±0.03	0.77±0.04	0.76±0.04	**0.75±0.02^{A}**	0.74±0.04	0.74±0.04	0.60±0.05	**0.70±0.03^{AB}**
$SUVA_{254}$	Leaf litter	4.62±0.13	4.90±0.12	4.73±0.11	**4.75±0.07^{A}**	4.49±0.33	3.47±0.20	3.56±0.18	**3.85±0.16^{B}**
(L mg C^{-1} m^{-1})	Deadwood	4.84±0.06	5.29±0.24	5.26±0.28	**5.13±0.13^{A}**	4.12±0.14	3.48±0.26	3.54±0.18	**3.72±0.12^{B}**

5.4.3 Effect of deadwood on tea bag index parameters

The stabilisation factor of soils (S) and decomposition rate (k) derived from the tea bag index method was up to twofold higher in soils from Kielder Forest than those from Alice Holt Forest, with a significant interaction between site and age ($p<0.04$), (Figure 5-2). The presence of deadwood did not influence either S ($p=0.763$) or k ($p=0.720$). Within Kielder Forest samples, the old stands had a significantly higher S than the mid stands, with mean values of 0.47 ± 0.04 and 0.28 ± 0.02 ($p<0.001$), respectively (Appendix Table 10-1). Little variation occurred with the mean decomposition rates derived from the tea bag index (k) between samples (Figure 5-2).

It should also be noted that whilst a large number of tea bag pairs were buried (n=90 pairs per site), 21 pairs were discounted due to holes and 26 produced negative k values, which were discounted from analysis (Appendix Table 10-2 and Discussion in Chapter 10.1).

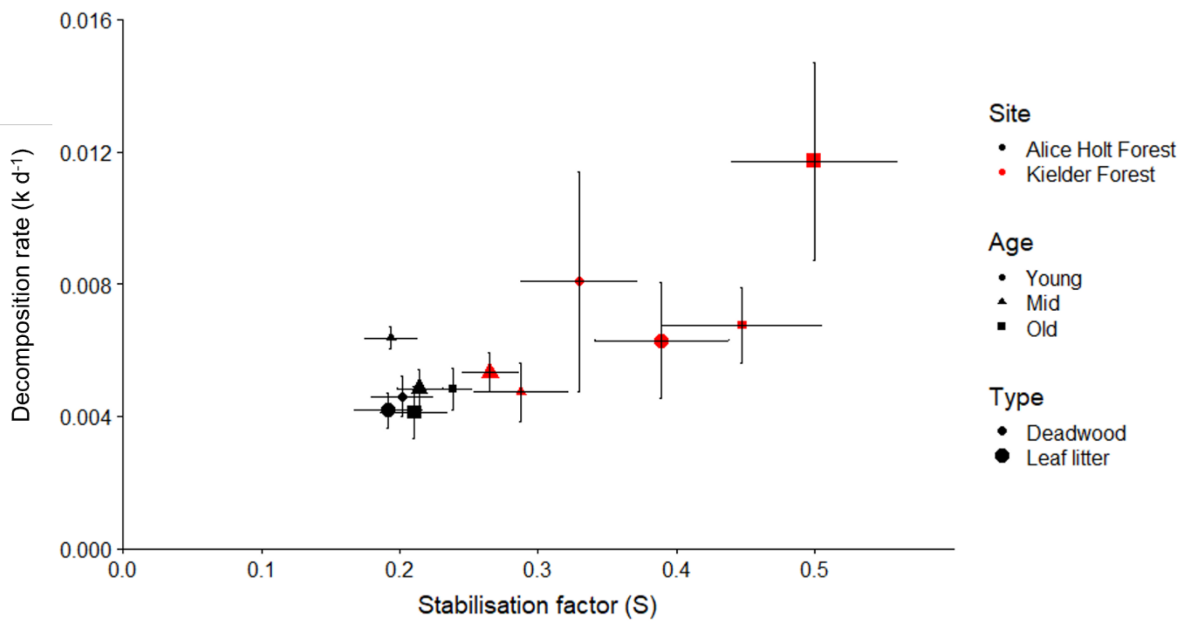

Figure 5-2 - Average values for the stabilisation factor (S) and decomposition rate (k, d^{-1}) derived from the tea bag index method, in either leaf litter soils or soils under deadwood in stands of different ages at Alice Holt and Kielder Forests. Bars show ± 1 standard error of the mean.

5.4.4 Effect of deadwood on soil enzyme activity potential

Enzyme activity rates were highly variable between soil samples (large s.e.m, Figure 5-3). However, a clear site difference occurred, whereby soil suspensions from Kielder Forest showed significantly higher enzyme activity rates than those from Alice Holt Forest. This site difference ranged from between 1.2 x (β-D-cellubiosidase young plots with only leaf litter) to 19.3 x

(Leucine aminopeptidase young plots with only leaf litter). Means are presented in Appendix Table 10-3. However, the presence of deadwood did not appear to stimulate an increase in enzyme activity at either forest, nor in different aged stands. There was no apparent link between DOC origin and enzyme activity rates.

Stand age significantly affected the carbon cycling enzymes β-glucosidase ($p=0.002$) and marginally β-D-cellubiosidase ($p=0.076$) and β-xylosidase ($p=0.074$). A significant interaction was found between site and age for β-D-cellubiosidase ($p=0.041$) but not β-xylosidase ($p=0.093$). A significant interaction between site, presence of deadwood and stand age was found for β-glucosidase ($p=0.011$). For each of these enzymes, activity rates peaked in the mid aged stands in both Alice Holt and Kielder Forests. For these three enzymes, at Alice Holt Forest, the average activity rates were between 1.1 and 1.5 times higher in the mid age stands than in young or old stands, whilst at Kielder Forest the rates varied between 1.3 – 2.4 times higher in mid aged stands than young and old. A significant interaction also occurred between site and stand age for phosphatase activity ($p=0.010$). Site and stand age effects on enzyme potentials are discussed in the Appendix Chapter 10.1.

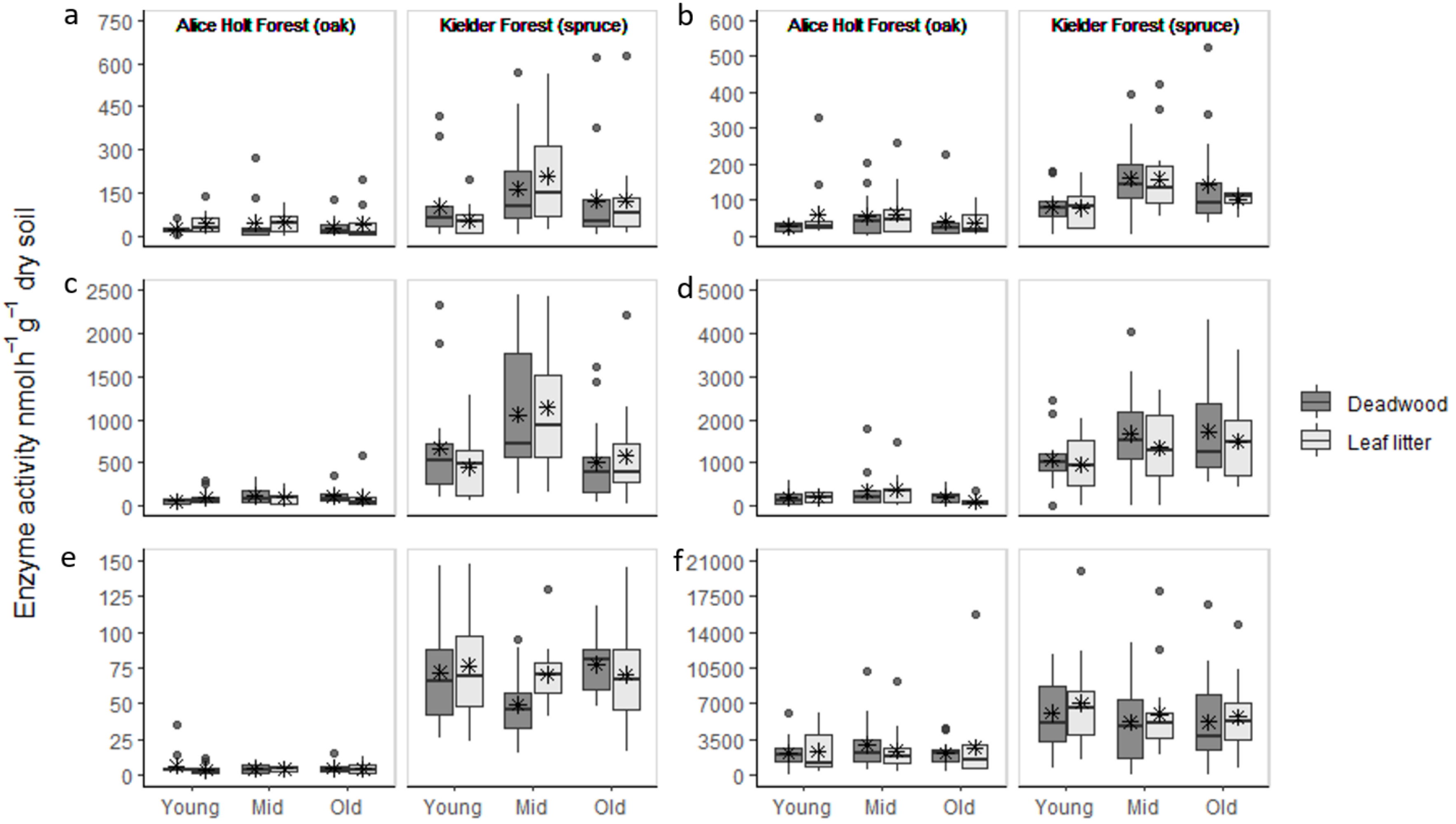

Figure 5-3 - potential enzyme activities in soils at Alice Holt and Kielder forests, with and without deadwood, and in different stand age groups: a: β-D-cellubiosidase, b: β-xylosidase, c: β-glucosidase, d: Phosphatase, e: Leucine aminopeptidase, f: Phenol oxidase. Data are * = mean, – = median, • = outliers defined as outside of the range of plot whiskers, ± = plot whiskers to show Q1 - 1.5*IQR or Q3 + 1.5*IQR. Mean values and results of statistical tests can be found in Table 10-3 of the supplementary material

5.5 Discussion

5.5.1 Soil properties in contrasting forest systems

In order to examine the contribution of deadwood to soil carbon dynamics, we chose to sample soils from stands in a lowland oak forest (Alice Holt) and an upland Sitka spruce forest (Kielder) as forest sites that contrast but also represent the dominant broadleaf and coniferous forest cover in the UK, covering 16.4% (Brewer, 2014a) and 50.8% (Brewer, 2014b) of forested land, respectively.

There was a clear difference in the soil and WEOC properties between Kielder and Alice Holt Forests, with significant differences occurring between sites for all measures except the HIX. Comparison of soil properties (Table 5-2) between the two sites reflected the soil classifications of peaty gleys/deep peat and surface water gleys at Kielder and Alice Holt, respectively. The cooler and wetter conditions at Kielder, combined with low pH, inhibit decomposition rates (Hagemann *et al*., 2010) and favour SOM accumulation (Keith, Mackey and Lindenmayer, 2009) at this site. Our finding that WEOC concentrations were substantially higher at Kielder (1168 mg C kg^{-1} soil) than Alice Holt (353 mg C kg^{-1} soil) (Figure 5-1) most likely reflected the SOM content as a substantial source of soluble carbon (Morison *et al*. 2012).

5.5.2 Deadwood influence on concentrations of soil water extractable organic carbon

It was expected that deadwood would provide a source of DOC into underlying soil. Out of all of the soil properties studied, the clearest effects of deadwood were seen in soil WEOC, albeit in a site-dependent manner. For the surface soils under oak at Alice Holt Forest, WEOC concentrations were significantly (between 1.45 and 1.76 times) higher for soils under deadwood when compared to soils without deadwood. However, a deadwood effect on WEOC was not observed in soils from the spruce stands in Kielder Forest. Our finding of greater quantities of WEOC under deadwood at Alice Holt is in accordance with other research that has found that concentrations of soil DOC increase in forests over mineral soils where deadwood is present (Spears and Lajtha, 2004; Hafner, Groffman and Mitchell, 2005; Kahl *et al.*, 2012), with increases of up to nine-fold when compared to soils with leaf litter only (Hafner, Groffman and Mitchell, 2005). The organic nature of the peaty-gley Kielder Forest soils may explain why no difference was seen between WEOC in leaf litter soils and soils below deadwood whereas a difference was seen between them in the mineral soils at Alice Holt Forest. In Kielder Forest, where % organic matter averages 77-94%, the input of DOC by deadwood is likely to be masked by such high levels of existing SOM as a significant source of WEOC. In contrast, at Alice Holt

Forest, where % organic matter averages 17-27% in topsoil, additional DOC inputs from deadwood may be more easily detectable. In addition, the soil type may have played a role in the retention of deadwood-derived DOC at Alice Holt with lower permeability of the surface water gley leading to reduced potential for leaching losses to lower soil depths. Furthermore, the high silt (particle size 0.063-0.002 mm) and clay (particle size <0.002 mm) content (69% and 10% in volume, respectively; Villada 2013) of the sampled A horizon at Alice Holt may have promoted retention of DOC via mineral sorption. The potential for physical protection of DOC through sorption to soil minerals would be, in comparison, limited in the peat soils at Kielder (Schmidt *et al.*, 2011). As a result of the field sampling design, the decay class of deadwood that was sampled within each stand was nested within stand age, reflecting the dominant stage of decay found for each stand age. We initially hypothesized that the effects of deadwood on the soil DOC pool might depend on stand age (decay class) due to differences in DOC fluxes from wood at different stages of decay. Wood in the late stages of decay, i.e. the old stands, is thought to hold a larger fungal and microbial biomass (Küffer *et al.*, 2008; Baldrian *et al.*, 2016) which has potential to increase rates of decomposition (Peršoh and Borken, 2017). However, this was not seen in our results as the deadwood effect on WEOC was of similar magnitude at Alice Holt, irrespective of stand age ($p=0.900$).

5.5.3 Deadwood influence on soil C cycle processes linked to WEOC concentration and quality

Microbial priming occurs when fresh inputs of organic matter into the soil, and the subsequent increase in available labile carbon, leads to increased rates of microbial activity stimulating the decomposition of already stored C in the system (Fontaine, Mariotti and Abbadie, 2003; Beverly and Franklin, 2015). It was possible that the additional inputs of C from deadwood might prime depolymerization of existing SOM pools (Peršoh and Borken, 2017; Minnich *et al.*, 2021), potentially leading to increased WEOC through DOC production. If deadwood DOC-induced microbial priming was occurring in our forest soils, we might expect to find an enhanced decomposition rate, seen in the TBI results, and enhanced potential enzyme activity in the soil under deadwood. In a previous, long-term experiment at Kielder, higher mineralisation and loss of C was found when brash (branches and litter) was left *in situ* compared to sites where it was removed, suggesting a likely priming effect (Vanguelova *et al.*, 2010). It is evident at Alice Holt that WEOC concentrations are elevated under deadwood, however, there is no indication through analysis of extracellular enzyme activity or the TBI that this additional soluble C is priming microbial decomposition or the production of extracellular enzymes involved in decomposition. One possible explanation for the lack of a deadwood effect on decomposition is that the k parameter in the TBI may not be sensitive to priming effects since k is estimated from the decomposition of added rooibos tea litter (Keuskamp *et al*. 2013), which in itself represents an input of fresh organic matter, rather than pre-existing SOM. The lack of an effect of the increased WEOC beneath deadwood on potential enzyme activity might relate to the quality of deadwood DOC inputs, as discussed below.

Optical methods are commonly used to assess the quality of DOC in surface waters, and their potential application to the study of carbon cycling in soils, through characterization of the WEOC, could add to interpretation with respect to the impact of the 'extra' WEOC in soils under the influence of deadwood at Alice Holt. As previously explained (section 2.4 & 3.2), $SUVA_{254}$ (Hansen *et al.*, 2016) and a HIX (Ohno, 2002) provide a measurement of the aromatic content and degree of humification of WEOC, whereby larger values indicate a larger aromatic content with increased levels of humification related with higher levels of aromatic C (Zech *et al.*, 1997; Ji *et al.*, 2015). The HIX indicated a greater level of humification and aromaticity, and potentially stability of WEOC, for Alice Holt soils under deadwood (HIX = 0.75) compared to those under leaf litter only (HIX = 0.65). Consistent with this deadwood signature in soil WEOC, Bantle *et al*. (2014) have shown both *Quercus* sp. and *Picea abies* - derived DOM to be a more significant source of humified material (HIX = 9.3 and 7.5, respectively) than throughfall (HIX = 3.8). $SUVA_{254}$ also suggested stronger aromaticity for WEOC underneath deadwood although statistical evidence for this was weaker. Among the many factors suggested to influence the size and direction of priming effects, the chemical structure of soluble C inputs has been shown to be important (Di Lonardo *et al.*, 2017). Aromatic compounds (e.g. vanillic acid) have been shown to induce the most pronounced priming effects when compared to non-aromatics (e.g. saccharides) on an energy content basis, possibly because they resemble compounds present in more stable SOM (Di Lonardo *et al*. 2017). In contrast, the aromatic compounds catechin and caffeic acid (a key intermediate in the biosynthesis of lignin) have been shown to have no effect on potential enzyme activity (Zwetsloot *et al.*, 2020). Due to the relatively energy-poor nature of these aromatic monomers, greater concentrations are needed to produce effects on a carbon concentration equivalent basis (Di Lonardo *et al*. 2017) and therefore it is possible that the aromatic enrichment of the WEOC pool under deadwood at Alice Holt, as suggested by HIX and $SUVA_{254}$, was not of sufficient magnitude to produce detectable effects on corresponding enzyme potentials.

An alternative mechanism to microbial priming by which inputs of soluble organic matter might impact on soil organic matter pools has been suggested. This involves the mobilization and solubilization of organic C previously intimately associated with reactive mineral phases through dissolution and metal chelating reactions mediated by inputs of organic compounds that are ligands with metal complexing activities (Keiluweit *et al.*, 2015). If this mechanism was in operation in the Alice Holt soils, the ‘extra’ WEOC under deadwood would be of both deadwood and soil organic matter origin. The origin of WEOC, as inferred from the FI of ~1.9 indicated that the WEOC was a mixture of both microbial and plant origin (McKnight *et al*. 2001) but this did not differ between soils from under deadwood and those under only leaf litter. Whether deadwood-derived DOC contains compounds that are more active as ligands in mobilizing additional soluble C from mineral associations than those in leaf litter-DOC requires further investigation. At this stage it is not possible to conclude if elevated WEOC under deadwood at Alice Holt was solely a consequence of stabilized DOC from deadwood or if abiotic priming also contributed.

5.6 Conclusions

The presence of deadwood significantly elevated (by ~1.5 to ~1.75 times) the concentrations of soil DOC, analysed as WEOC, in the mineral horizon of a surface water gley chronosequence under lowland broadleaf (*Q. robur*) forest. We believe that this increase in WEOC was, at least in part, due to deadwood acting as a significant input of DOC, released as a result of decomposition processes, to the underlying soil, which was subsequently retained through interactions with the soil mineral horizon. In highly organic soils sampled from an upland Sitka spruce chronosequence, effects of deadwood on WEOC were not detectable. This is potentially because inputs of DOC from deadwood were masked by the already high background of WEOC and/or did not persist in soil due to low potential for mineral sorption. There was no evidence, from TBI decomposition parameters or potential extracellular enzyme data, that deadwood-derived DOC impacted other forest carbon pools via microbial priming effects, possibly due to the aromatic quality of DOC produced. It was not possible to determine whether the increased WEOC under deadwood at the lowland oak site was solely due to retention of deadwood-derived DOC, or, if OC solubilized from existing SOC pools via deadwood DOC-mediated abiotic reactions also contributed. At present, the source and impacts on soil C cycling of elevated WEOC associated with leaving deadwood *in situ* requires further characterization. Forest carbon budgets, particularly those for mineral soils, that are only derived from DOC concentrations sampled from under leaf litter may be an underestimation; efforts should be made to include a deadwood component in temporal and spatial monitoring of forest ecosystems.

5.7 Acknowledgements

We would like to thank Anne Dudley, Alice Dibley and Ilse Kamerling for their assistance with lab analyses and Sue Benham, Ed Eaton and Paul Gough for their assistance with field work. Special thanks also go to Yi Zhao for his work on deadwood DOC extraction, both in the field and the lab.

6 Effects of forest stand type, management, and cause of tree mortality on deadwood carbon stocks

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6.1 Abstract

Deadwood forms a significant carbon pool in woodlands and is recommended as a pool to report in forest carbon inventories. However, the exact contribution by deadwood is unknown, and knowledge of how deadwood volumes and carbon stocks are partitioned between different woodland types, deadwood types and decay stages is unknown, with reports often assuming uniform measures of deadwood carbon across Great Britain. Here, we use data collected from the first cycle of the GB National Forest Inventory to calculate the volumes and carbon stocks of deadwood across Great Britain and identify how this is partitioned between 'pure' and mixed woodlands and different decay classes in stumps, standing and lying deadwood. We also assess the effect of woodland management, woodland origin (i.e. ancient woodlands or more recent plantations), and cause of tree death on deadwood volumes and carbon stocks. We determined that woodlands that were classified as ancient semi-natural held significantly more deadwood than those with a non-ancient origin. Deadwood volumes were significantly larger in coniferous than broadleaf woodlands, potentially due to the activities of woodland management, though management as a direct cause of death in coniferous woodlands created smaller volumes of deadwood than abiotic events, diseases and insects. We suggest that woodland management practices may help increase deadwood volumes across Great Britain, provided deadwood is subsequently left *in situ*.

6.2 Introduction

Woodlands have a major role in the carbon cycle due to the large fluxes of carbon between the atmosphere and woodlands, and between the different component carbon stocks. It is estimated that temperate forests hold 119 Pg of carbon, of which the deadwood fraction can form a substantial carbon pool which forms as trees die or wood is damaged. Current global estimates are of 59 Gt deadwood mass, or 4-8% of woodland carbon stocks (Pan *et al.*, 2011; FAO, 2020a). Little is known about deadwood volumes in different woodland types or how different causes of mortality affect deadwood stocks. Carbon held in deadwood may be released during decomposition as CO_2 or leached as dissolved organic carbon (DOC) (Ritter and Saborowski, 2012). Estimates of deadwood volumes, mass and carbon stocks for the UK have varied considerably over the years. For the UK forest resource reporting it was assumed that deadwood biomass per unit area, and consequent carbon stocks, remained unchanged over the past 30 years at 25 t ha^{-1} biomass or 13 t C ha^{-1} (FAO, 2020c). Between 2000-2018, it was estimated that a total of 2.7 million t carbon were held in deadwood in GB forests (Forest Research, 2018), and in 2015, following the national BioSoil survey, 5.49 million t carbon (Vanguelova, Moffat and Morison, 2016). However, this value was substantially updated to 39.3 million t carbon for GB in 2020 (Forest Research, 2020) when estimates of volumes were taken from the current National Forest Inventory (NFI) rather than the earlier National Inventory of Woodland and Trees 1995-1999 (Gilbert, 2007). A detailed evaluation of measured deadwood volume and carbon stocks between 2006-2010 from the national BioSoil survey at 167 plots estimated GB averaged deadwood volume of 8.03 m^3 ha^{-1} and total GB forest deadwood carbon storage of 5.5 Mt. Based on this evaluation, deadwood make 3.5% of total GB forest carbon pool (Vanguelova, Moffat and Morison, 2016).

Carbon pools in woodlands are required to be periodically assessed by the LULUCF section of the United Nations Framework Convention on Climate Change (UNFCCC; United Nations, 1992), and the Kyoto Protocol (United Nations, 1998) and also as part of the REDD+ framework. The Intergovernmental Panel on Climate Change (IPCC) has developed methods and guidelines to provide consistent reporting between countries, though there are still inconsistencies in reported values and deadwood (also referred to as coarse woody debris) is often an optional report. The implementation of a National Forest Inventory in various countries has created some consistency in reporting of living carbon pools, however, the deadwood, litter and soil pools are still omitted by many countries globally. For instance, only 78 of 193 countries are currently reporting deadwood carbon stocks for the Global Forest Resource Assessment (FRA), accounting for 74% of global woodland area. In most cases, deadwood and litter are combined as a single pool, dead organic matter, leaving some uncertainty as to the specific deadwood contribution. While the UK NFI field surveys include a deadwood component, volumes of stumps are currently excluded from NFI reports on woodland condition, leaving uncertainty to their volumes and carbon stores.

The presence and volume of deadwood is likely to vary with tree species, woodland age/origin and management. In the UK, semi-natural woodlands often originate from very old woodlands and are identified by nature conservation agencies as ‘ancient semi-natural woodland’ (ASNW). These are woodlands that consist of locally native species derived from the original woodland cover and have been continuously wooded since at least 1600 (England; Wales) or 1750 in Scotland. It is thought that ~10.8% of UK woodlands are ASNW (Forestry Commission, 2017). A further 13% of UK woodlands are classified as ‘plantations on ancient woodland’ (PAWS); these are non-native species that have been planted in woodland that was once ASNW. Both ASNW and PAWS may undergo management.

Woodland management has often removed deadwood, leading to lower volumes being left *in situ.* For example, lower volumes were found in woodlands that are coppiced, thinned, and clearcut or from which brash is extracted for bioenergy than in natural woods (Peterken, 1996). However, the increasing interest in biodiversity conservation has led to management being advised to leave some deadwood in managed stands because deadwood is not only of interest as a carbon pool as it hosts a diverse range of organisms, many of which are threatened, as either habitat or a food source. The European Habitats Directive (1992) was created to protect threatened species across Europe, including saproxylic species, through the protection of habitats. Where such species are inhabiting deadwood, it is now a legal requirement to protect their habitat. This may involve the conservation of deadwood *in situ* or creation of new deadwood piles. Similarly, in the UK, species such as the Stag Beetle (*Lucanus cervus*), which rely on deadwood at the larval stage, are identified for conservation by the UK Biodiversity Action Plan (UKBAP). In these cases, woodland managers are required to leave deadwood piles *in situ*, and advised to avoid moving unnecessarily (Forestry Commission, 2017). Management should also aim to avoid homogeneity and concentrate on areas of high ecological value to maximise the benefits to biodiversity.

The target volume of deadwood required for conservation varies, with a general consensus within Europe that a threshold of 20 m^3 ha^{-1} non-uniformly organised deadwood per stand is the minimum (The RSPB Conservation Management Advice, no date; Humphrey and Bailey, 2012), with 20-30 or 50 m^3 ha^{-1} the threshold target (Dudley and Vallauri, 2004; Müller and Bütler, 2010; UKWAS, 2018). In some countries more ambitious targets are being implemented by land managers with aims to gradually increase deadwood volumes over the next century. For instance, in the UK wildlife charities such as the RSPB recommend a target of 20-40 m^3 ha^{-1} in the ‘medium term’, reaching 100 m^3 ha^{-1} in 100 years (The RSPB Conservation

Management Advice, no date). Other organisations may introduce more ambitious targets which vary depending on woodland management, with higher targets (40-100 m^3 ha^{-1}) suggested in semi-natural woodland compared to those that are managed (20-40 m^3 ha^{-1}) in the UK (Humphrey *et al.*, 2002).

Despite this interest, little work has been carried out to identify the abundance of deadwood, and the factors associated with its creation and removal. Therefore, the aim of this study is to evaluate the amounts of deadwood and its contribution to carbon stocks within GB woodlands. The specific objectives of this paper are to use data from the National Forest Inventory to:

1. Calculate deadwood volumes and their associated carbon stocks within the main woodland types and 'origins' in Great Britain
2. Investigate the effect of woodland management practices on deadwood volumes and carbon stocks
3. Determine whether the cause of tree death assessed in the NFI has an impact on deadwood volumes and carbon stocks

6.3 Methods

6.3.1 Study sites & measurements

Data was collected in the first cycle of the GB National Forest Inventory programme over the years 2009-2015. Full protocols are explained in the NFI survey manual (Forestry Commission, 2016); a summary of these methods is presented here. Field surveys were carried out at 15,633 randomly selected one-hectare sample sites across Great Britain (Figure 6-1). Sites cover temperate climates in the south and east, maritime to the west and more boreal climate at higher altitudes in north Scotland. Mean annual temperature in lowlands range from 7°C in the Shetlands (Scotland) to 11°C in Cornwall (south west England) and mean annual precipitation ranges from 500 mm in eastern England to 4000 mm in the western Scottish Highlands.

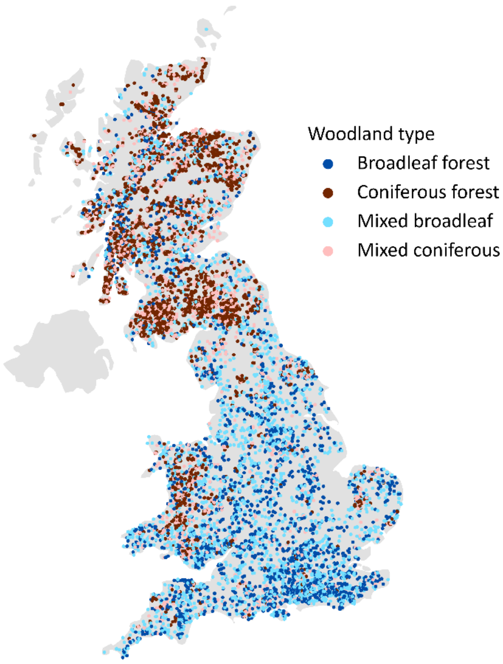


Figure 6-1 – National Forest Inventory data sample plot locations in Great Britain split by woodland type

Woodlands included in sampling must cover a minimum of 0.5 hectares with a width of 20 m and 20% tree canopy cover or have the potential to achieve this (in order to include areas recently planted or harvested). Woodland types were assessed based on the proportion of species present. 'Pure' broadleaf and coniferous woodland contained >80% broadleaf or conifer species, while mixed broadleaved or mixed conifer woodlands were those with between 50% and 80% broadleaf or conifer species, respectively (Forestry Commission, 2016). Each 1 ha sample site was subdivided into homogeneous area sections for data recording according to the stands and species present.

Field measurements taken included the tree species present, their area and their condition as well as individual tree measurements and any observable management practices. Deadwood was classified during surveying into standing dead trees, lying deadwood and stumps during surveying and measurements of height and diameter were taken to calculate volumes of deadwood present, where deadwood is defined by the NFI working protocol as follows:

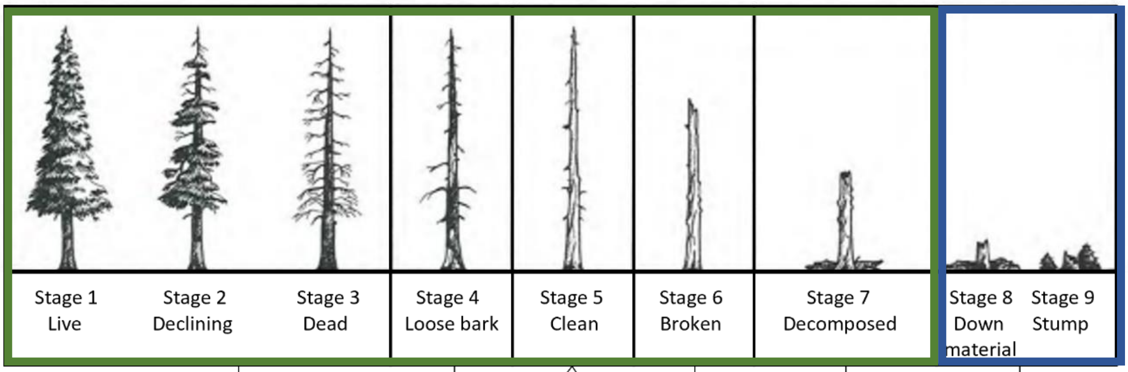
Lying deadwood (LD) – dead, woody material from trees that has not been processed e.g. branches or stem-wood; ≥ 7 cm in diameter

Stumps (S) - part of a tree stem that still has roots attached to the ground; ≤ 1.3 m in height; no visible live shoots; minimum diameter of 4 cm

Standing deadwood (SD) - all dead stems ≥ 4 cm diameter at breast height (DBH)

In each sampling section, three 10 m transects are used to assess lying deadwood, along which every occurrence of lying deadwood that intersects the transect is recorded. Total numbers of stumps are recorded per entire sections and two sample stumps are measured. All standing deadwood samples are recorded and measured.

The decay class classification as described by Hunter (1990) was used to assign a standardised classification, 'decay stage', of standing dead trees and stumps to a lying debris equivalent (Figure 6-2), ranging from decay stage 1 to 5. For the purpose of analysis, standing decay class 5 was included in decay stage 3.



Decay stage	1	2	3	4	5
Bark	Intact	Intact	Trace	Absent	Absent
Twigs < 3 cm	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft, blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Colour of wood	Original colour	Original colour	Original colour to faded	Light to faded brown or yellow	Faded to light yellow or grey
Portion of log on ground	Log elevated on support points	Log elevated but sagging slightly	Log is sagging near ground	All of log on ground	All of log on ground

Figure 6-2 – Decay stages of deadwood adapted from Hunter (1990). Standing deadwood are highlighted in green, stumps in blue and lying deadwood in yellow. A standardised decay stage is issued on a scale of 1-5.

Further contextual information on site management and cause of death are recorded as part of the survey. These contextual data are based on a combination of *in situ* observations by field surveyors and reports by landowners and therefore may not be 100% accurate, though serve to provide some insight to current practice.

32 management classes are recorded by NFI. A detailed explanation of management definitions is provided in (Table 6-1). For the analysis in this paper, three main management groupings were created by aggregating these management classes into: ‘deadwood specific management’ (deadwood is both created and removed), ‘non-deadwood specific

management' (management occurs that is not directly creating deadwood), and 'not managed' (no evident signs of any management activity).

Table 6-1 – Woodland management practices as described by the NFI. Practices are further grouped depending on the outcome specific to deadwood, as: creation (of deadwood), non-deadwood specific (where deadwood is neither directly created or removed), removal (of deadwood).

Management practice	**Explanation**
Grouping: not managed	
Based on the evidence from the site visit, no management was recorded	
Grouping: deadwood specific	
Brashing	Removal of the lower dead branches, up to about 2 meters, of trees in a stand.
Cleaning	The removal of unwanted broadleaves and woody plants, usually before canopy closure.
Clearfell	Cutting down an entire area of woodland at one time.
Coppicing	Trees that are cut near ground level causing them to produce many small shoots.
Pollarding	A pollard is a tree with branches which have been cut back (above ground level) to the trunk so that it may produce a dense growth of new shoots.
Pruning	Cutting off / back stems.
Thinning once	Thinning – reducing the density of trees in a stand to improve the quality & growth of those that remain.
Thinning more than once	Thinning that has occurred more than once.
Brash removal / mulched / burned	Lying branches and deadwood has been removed, mulched or burnt.
De-stumped	Removal of tree stumps following felling.
Scarified	A method for clearing planting lines by clearing brash and vegetation and leaving the soil bare.
Windrowed	Timber which is pushed into lines for burning during a clearing operation.
Grouping: non-deadwood specific management	
Agroforestry	A combination of agriculture and forestry – trees and shrubs are used with crops and/or livestock.
Conservation	The land is used for conservation.
Draining	The site has open drains dug to drain water.
Fencing – partial or complete	Presence of fencing (wooden or metal).
Game birds	There is evidence that the land is used for game birds e.g. feeders are present.
Grazing	The site is being used for grazing livestock.
Mounded	Site has mounds of earth across it in preparation for planting.
Other	Other activity not included in the groups listed.
Orchard	Consisting of fruit trees.

Ornamental	Sites managed as ornamental areas.
Personal & public recreation	The site is used for recreation.
Planting	A newly planted site.
Ploughed – single mouldboard	Ploughed – the earth from the plough line is all to one side.
Ploughed – double mouldboard	As above but earth is gathered on both sides of plough line.
Ripped	Compacted soil has been broken up to aid seedling survival.
Screening/shelter	Sites used as shelter or screening.
Timber production	The site is being managed for future timber production.
Weeding	A method to remove heather prior to planting.

Additionally, 21 causes of standing tree death were identified during the survey. These have been grouped into six categories for analysis in this paper (Table 6-2). Decay class data was unavailable and so accurate carbon stock calculations could not be carried out. To analyse the effect of different mortality causes on deadwood amounts, five principal tree species for both broadleaf and conifer woodlands were chosen based on stocked GB coverage (Brewer, 2014b, 2014a) from 2012. Broadleaf species were: oak, birch, beech, ash, sycamore. Conifer species were: Sitka spruce, Scots pine, Larches, Lodgepole pine, Norway spruce. Cause of death for these species was assessed and compared with those for less common species considered as a single grouping.

Table 6-2 – Causes of standing tree death as assessed during field surveying. These are grouped into six main categories.

Cause of death groupings	**Specific cause**
Vertebrates	Deer
	Horse
	Mammals: Any mammal that is not clearly identifiable
	Rabbit
	Sheep
	Squirrel
Management	Physical damage during operations
	Ring barking
Pest and disease	Diseases
	Insects
Abiotic	Erosion
	Fire
	Snow
	Water logging
	Wind snap
	Wind throw
Natural mortality	Natural mortality
Not discernible	Unknown cause

The age of stands including standing deadwood at the time of assessment was calculated using the known planting year, where data was available, and used to calculated average deadwood volumes per stand age. Cause of death data was subset for any analysis involving stand ages.

6.3.2 Calculations

Results were determined per section, calculating deadwood volumes per hectare (m^3 ha^{-1}) as:

$$Deadwood\ volume\ (m^3/\ ha^{-1})\ =\ \frac{total\ volume\ of\ sample\ (m^3)}{section\ area\ (ha)}$$

Equation 1

Where the total volume of a sample is calculated as the sum of stem, root and branch volumes as per NFI methods (Forestry Commission, 2018).

Subsequently carbon stocks were calculated as:

$$Carbon\ stocks\ (t\ /\ ha^{-1}) = \frac{Biomass\ (t)\ x\ carbon\ fraction\ (\%)}{section\ area\ (ha)}$$

Equation 2

Whereby

$$Biomass\ (t) = Density\ (g\ cm^{-3})\ x\ Volume\ (m^3)$$

Equation 3

Wood density is known to decrease in later stages of decay (Paletto and Tosi, 2010; Harmon, Woodall and Sexton, 2011; Moreira, Gregoire and do Couto, 2019); as wood rots it becomes hollow or disintegrates and thus density lowers. In recent work, Vanguelova *et al*. (2016) assessed the density of deadwood from a small sample of the four main UK tree species: oak, beech, Scots pine and Sitka spruce as part of the national BioSoil survey. Their results showed that density declined with decay classes 1-5, from 0.39-0.14 g cm^{-3} in conifers and 0.50-0.18 g cm^{-3} in broadleaves. These wood densities (appendix Table 10-4) have been applied to our volumes in order to calculate biomass.

In total, data from 15,629 one-hectare squares were provided, containing 44,814 homogenous sections, leading to 679,152 measurements when split by tree species, deadwood type and decay class. 44 decay class specific entries (0.006%), where deadwood volumes were measured as >250 m^3 during site visits, were assumed implausible and erroneous (appendix Figure 10-1) so removed as outliers from the calculation of means and medians. However, for cause of tree death calculations all data, including volumes over 250 m^3 ha^{-1} were included, to assess the impacts of abiotic events. 5,025 squares (32%) could not be assigned to one of the four woodland types of interest, while 17,654 (39%) sections also could not be assigned to a woodland type. Sections where data were incomplete were discounted (e.g. those that could not be assigned to a woodland type).

After the data cleansing analysis, 10,604 squares and 27,160 sections remained. Total volume data provided for sections was the sum of all deadwood present and ranged between 0-3285 samples per section. To assess data at the 1 ha sample square level, the sum of each deadwood type from all constituent sections was calculated to give deadwood volumes and carbon stocks per hectare.

6.3.3 Additional data

A full dataset of woodland or stand age information was not available for the NFI sample squares at the time of analysis, but as there has been substantial expansion of woodland area in GB over the last century many woodlands are relatively young, which is likely to influence the amount of deadwood present. To provide some information on age, we used information on their historical origin designation. 'Ancient woodland sites' were identified using the open access datasets from England: https://data.gov.uk/dataset/9461f463-c363-4309-ae77-fdcd7e9df7d3/ancient-woodland-england; Scotland: https://gateway.snh.gov.uk/natural-spaces/dataset.jsp?dsid=AWI; and Wales http://lle.gov.wales/catalogue/item/AncientWoodlandInventory2021/?lang=en. From these, sites are identified as ancient semi-natural woodland (ASNW), plantation on ancient woodland sites (PAWS), ancient site of unknown origin (AU), restored ancient woodland site (RAWS), or as non-ancient ('Other'). RAWS are a subset of ASNW, unique to Wales, and have been included in ASNW. Spatial data were analysed using ArcGIS Pro 2.7.0. Direct spatial intersection of NFI woodland locations to the ancient woodland maps was used to identify woodland origin classification, although this is a broad classification and cannot guarantee full accuracy.

6.3.4 Statistical analyses

Data were analysed using R version 4.0.2. Normality of residuals was checked using the Shapiro-Wilk test. Homoscedasticity was assessed using Levene's test. Where these assumptions were not met, data was log transformed and/or classes were aggregated and re-tested.

The first part of the data analysis explored the main factors of interest and their impact on total deadwood volumes and carbon stocks. Woodland origin (ASNW, PAWS, Other), management and cause of tree death (SD only) effects on volumes and carbon stocks were assessed with a general linear model (GLM) with the factors: woodland or tree species type and deadwood type. For these, mixed woodland types were aggregated into either broadleaf or conifer woodlands, whereby species composition was assessed as >50% either broadleaf or conifer. Woodland origin was assessed at a square level, while management type was analysed per section, as differing sections per square may be subjected to differing management. Management was initially assessed with groups of managed vs unmanaged sections, before the management practices were split into the four management groups (Table 6-1). Cause of death in standing trees was analysed by classifying the specific species of each sample as either broadleaf or conifer per section. Carbon stocks were not calculated for cause of tree death as decay classes could not be accurately assigned to each cause of death. Decay class was required in order to assign wood density as per equation 3.

The second part of the data analysis looked in more detail at the type of deadwood, specifically decay stage and class, on overall deadwood volumes (m^3 ha^{-1}) and their associated carbon stocks (t^{-1} C ha^{-1}). For this work, a linear mixed effects model (LMEM) was applied because decay stage and deadwood type could not be controlled and varied on a site by site basis. Due to the differences in climate, topography, and species distribution between England, Scotland and Wales (Figure 6-1), country was included as a factor that may influence deadwood production and decomposition. Therefore, in this analysis, fixed factors were: country and woodland type (BL, Con, MB, MC), and random factors were: decay stage and deadwood type (LD, SD). Deadwood types of SD and S were aggregated into a single group for statistical analysis by LMEM because of unequal distribution of S data. Interaction between country*woodland type and decay stage*deadwood type was assessed.

Tukey post-hoc testing was carried out where significant effects occurred from GLM or LMEM analysis, in order to identify where significant differences between factors occurred.

6.4 Results

6.4.1 Deadwood volumes and carbon stock densities by country

Volumes per individual sections ranged between 0-1591 m^3 ha^{-1}. 19% of squares (2046) recorded no deadwood present. To calculate overall volumes and carbon stocks, sections in each square were summed to produce a total per hectare. Across GB as a single unit, the mean volume of deadwood per hectare (totalled across the three deadwood types) was 26.40±0.40 m^3 ha^{-1}, with a median of 10.07 m^3 ha^{-1}. This reduced to 17.5±0.30 m^3 ha^{-1} when stumps were removed from the total. The mean mass was 6.59±0.10 t ha^{-1}, with a median of 2.52 t ha^{-1}, and this contained an average carbon stock of 3.29±0.05 t C ha^{-1}, with a median of 1.26 t C ha^{-1} (2.36±0.04 t C ha^{-1} when stumps were removed from the total). However, the deadwood volume varied considerably between country, woodland type, and type of deadwood recorded (Figure 6-4). Average volumes across all woodland types were largest in Wales (34.7±1.43 m^3 ha^{-1}), with plots in England and Scotland holding an average of 25.2±0.53 and 25.2±0.60 m^3 ha^{-1}, respectively, when all deadwood type were summed to produce a total deadwood volume. Average carbon stocks were also largest in Wales (4.36±0.18 t ha^{-1}), and similar between England and Scotland, with 3.19±0.07 and 3.07±0.07 t ha^{-1}, respectively.

Results of the statistical analysis (LMEM) found the fixed effects of country ($p < 0.001$), woodland type ($p < 0.001$) and their interaction ($p < 0.001$), significantly affected deadwood volumes and carbon stocks. The random factors, deadwood type ($p = 0.437$) and decay stage ($p = 0.664$), did not significantly affect deadwood volumes or carbon stocks ($p = 0.337$ and 0.719). However, a significant interaction was found between these factors ($p < 0.001$) for both volumes and carbon stocks.

Volumes were largest in coniferous woodlands across all three countries and deadwood types (Figure 6-4), leading to a significant difference between broadleaf and conifer woodlands in all three countries. Mixed conifer woodlands also held significantly more deadwood than mixed broadleaf woodlands in England and Wales, though not in Scotland. In Scotland and Wales coniferous woodlands also held significantly larger carbon stocks than broadleaf woodlands, though this was not seen in England. For lying deadwood, the difference between volumes in broadleaf and coniferous woodlands was minimal (0.4 - 1.7 m^3 ha^{-1}; Wales – Scotland). Standing deadwood (SD) volumes were 1.6-3.3 x larger in coniferous woodlands than broadleaf, while volumes of stumps were between 1.7-7.5 x larger. More lying deadwood (LD) was present in broadleaf (BL) and mixed broadleaf (MBL) woodlands than the other deadwood types, while in English and Welsh coniferous (CON) and mixed coniferous (MC) woodlands stumps were the most prevalent. For lying deadwood, the largest mean volumes were most often found in decay stage 3 (appendix Table 10-5), which was also often the most commonly recorded decay stage (Figure 6-3). The lowest mean volumes for lying deadwood occurred in decay stage 1, which was the least recorded decay stage for lying deadwood (Figure 6-3). Carbon stocks were lowest in either decay stage 1 or 5. For standing deadwood, the largest volumes and carbon stocks were most frequently found in decay stage 1 and reduced in the stage order 2>3>4, which matched the abundance of each decay stage (Figure 6-3). A full table of results regarding volumes and carbon stocks is included in appendix Table 10-5.

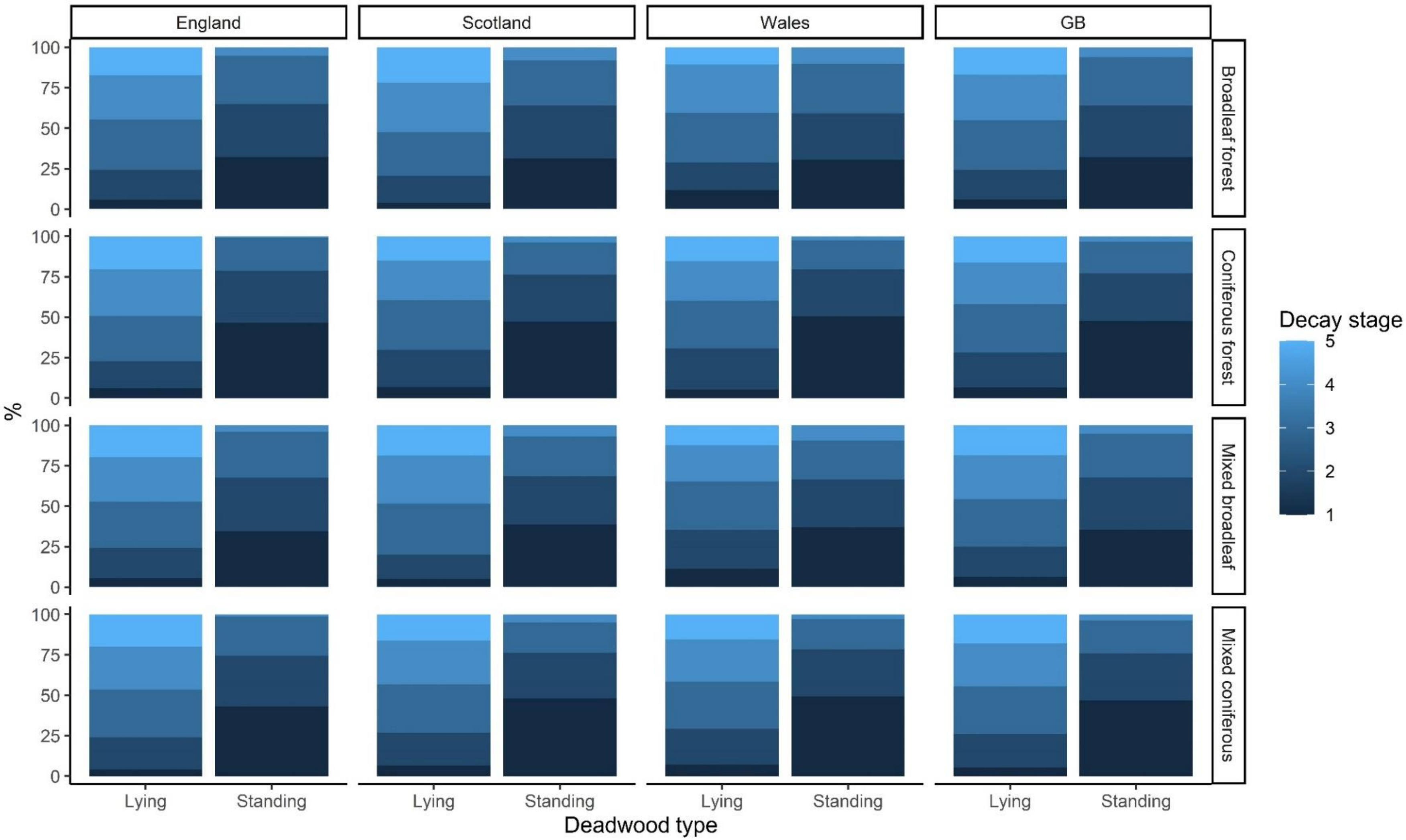


Figure 6-3 - % of number of squares sampled during the NFI with deadwood recorded in each decay class for standing and lying deadwood. Stumps were presumed to all be decay stage 5 and so omitted.

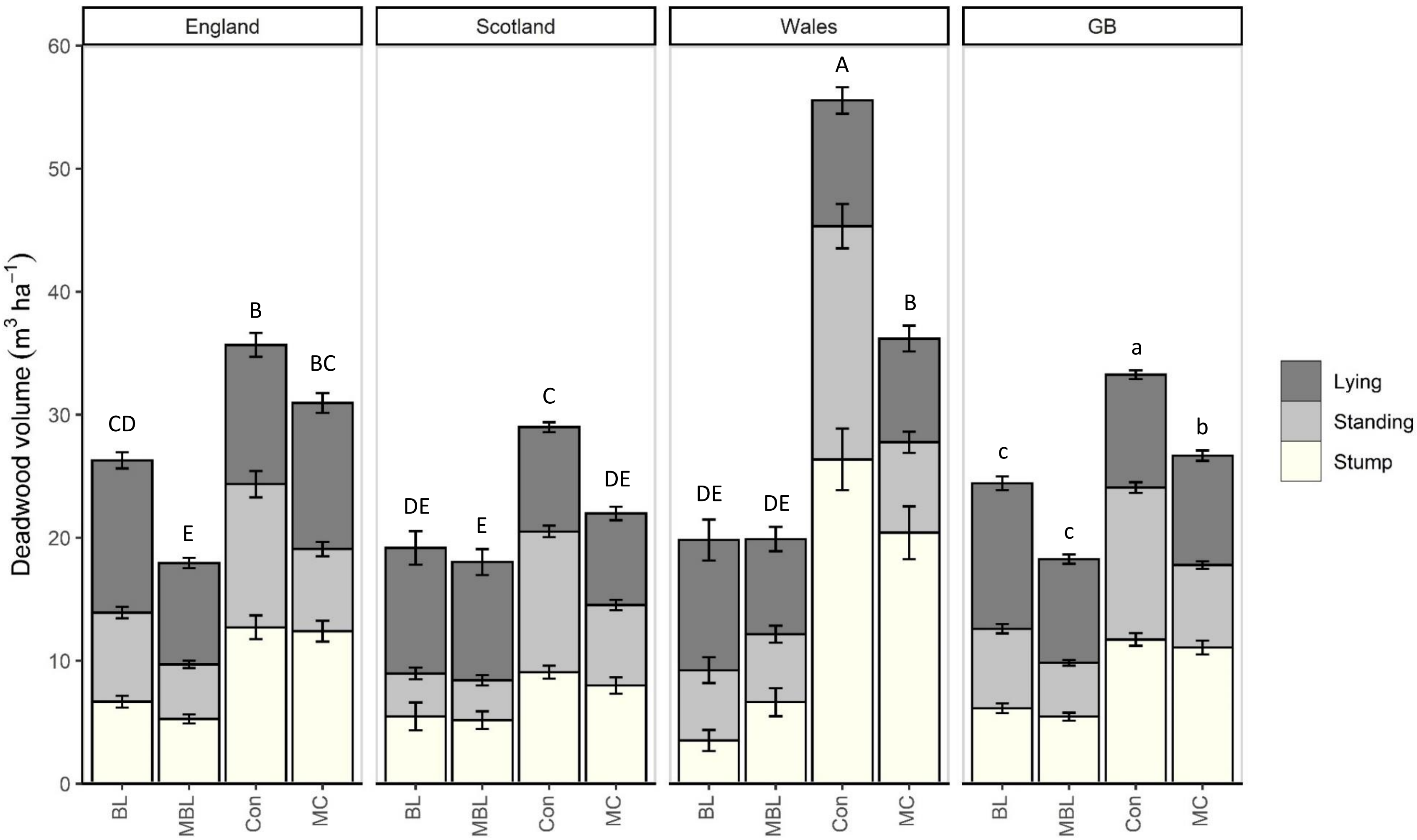


Figure 6-4 – mean volumes of deadwood (m^3 ha^{-1}) in woodlands of Great Britain, split by woodland and deadwood type. Error bars are one standard error of the mean per deadwood type. BL = broadleaf, MBL = mixed broadleaf, CON = coniferous, MC = mixed coniferous. Tukey post-hoc grouping letters for the interaction between country and woodland type on volumes of deadwood are included in capitals. Grouping letters for the effect of woodland type across GB are shown in lower case. Those which do not share a letter are significantly different.

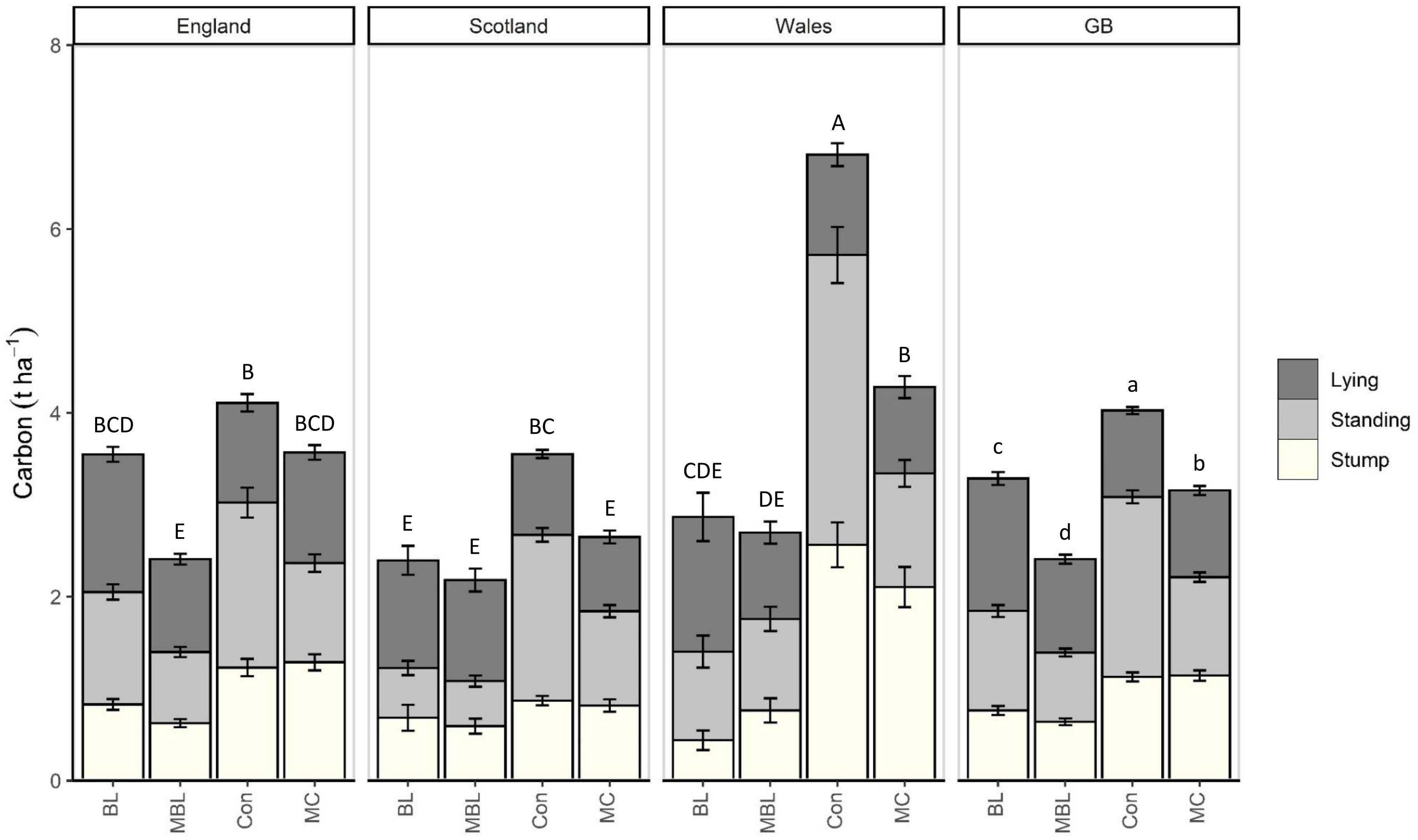


Figure 6-5 – mean carbon stock held in deadwood (t C ha^{-1}) in woodlands of Great Britain, split by woodland and deadwood type. Error bars are one standard error of the mean per deadwood type. BL = broadleaf, MBL = mixed broadleaf, CON = coniferous, MC = mixed coniferous. Tukey post-hoc grouping letters for the interaction between country and woodland type on volumes of deadwood are included in capitals. Grouping letters for the effect of woodland type across GB are shown in lower case. Those which do not share a letter are significantly different.

6.4.2 Woodland origin classification

Results of the statistical analysis (GLM) showed that the origin classification of woodlands significantly affected deadwood volumes ($p < 0.001$), and carbon stocks ($p < 0.001$), with ASNW and PAWS holding more than 'other'. For volumes, a significant interaction occurred between origin classification and deadwood type ($p < 0.001$), though not with woodland type ($p = 0.507$). Three-way interaction between woodland origin, type and deadwood type was insignificant ($p = 0.689$). For carbon stocks, a significant interaction occurred between origin classification and deadwood type ($p < 0.001$), but not woodland type ($p = 0.093$), or three-way interaction ($p = 0.182$).

In BL woodlands, volumes and carbon stocks of LD and SD were largest in ASNW, while stump volumes and carbon stocks were largest in PAWS (Figure 6-6). However, in coniferous woodlands, volumes and carbon stocks were larger in PAWS woodlands for stumps and lying deadwood than in other woodland origin types, while for SD this was found in woodlands with an 'other' origin.

In woodland with an 'other' origin, a significantly lower volume of standing deadwood was found compared to lying. Likewise, in PAWS, the mean volume of standing deadwood was significantly lower than both lying and stumps. In ASNW volumes did not differ between deadwood type. Volumes of lying deadwood were significantly lower in woodland with an 'other' origin than ASNW and PAWS, while volumes of SD did not differ between woodland origins. Stump volumes were significantly higher in PAWS than ASNW and the 'other' origin types. Deadwood carbon stocks in ASNW and PAWS were significantly larger than in the 'other' category. Carbon stocks in lying deadwood and stumps were significantly larger in PAWS than woodlands with an 'other' origin, while SD carbon stocks did not differ between woodland types. Carbon stocks in ASNW and PAWS did not vary by deadwood type, though in woodlands with an 'other' origin, differences were found between all three deadwood types.

9.53% of sites visited were classified as ASNW; 9.46% as PAWS, and 81% as 'other'. Woodland ages were assessed using planting year. In ASNW, woodland ages ranged between 0-311 years, with an average of 35, (35 in broadleaf; 31 in conifer) in PAWS, ages ranged between 0-362 years, with an average of 32 (33 in broadleaf; 31 in conifer), and in 'Other' ages ranged between 0-511 years, with an average of 30 (32 in broadleaf; 26 in conifer). ASNW and PAWS recorded fewer woodlands with no deadwood (13% and 7%, respectively) compared to those with an 'other' origin (21%). A larger proportion of ASNW and PAWS were found in broadleaf

(17.9% & 11.0%) than coniferous woodlands (2.9% & 8.2%), with this difference proving significant ($p < 0.001$) with Pearson's chi-square test of association.

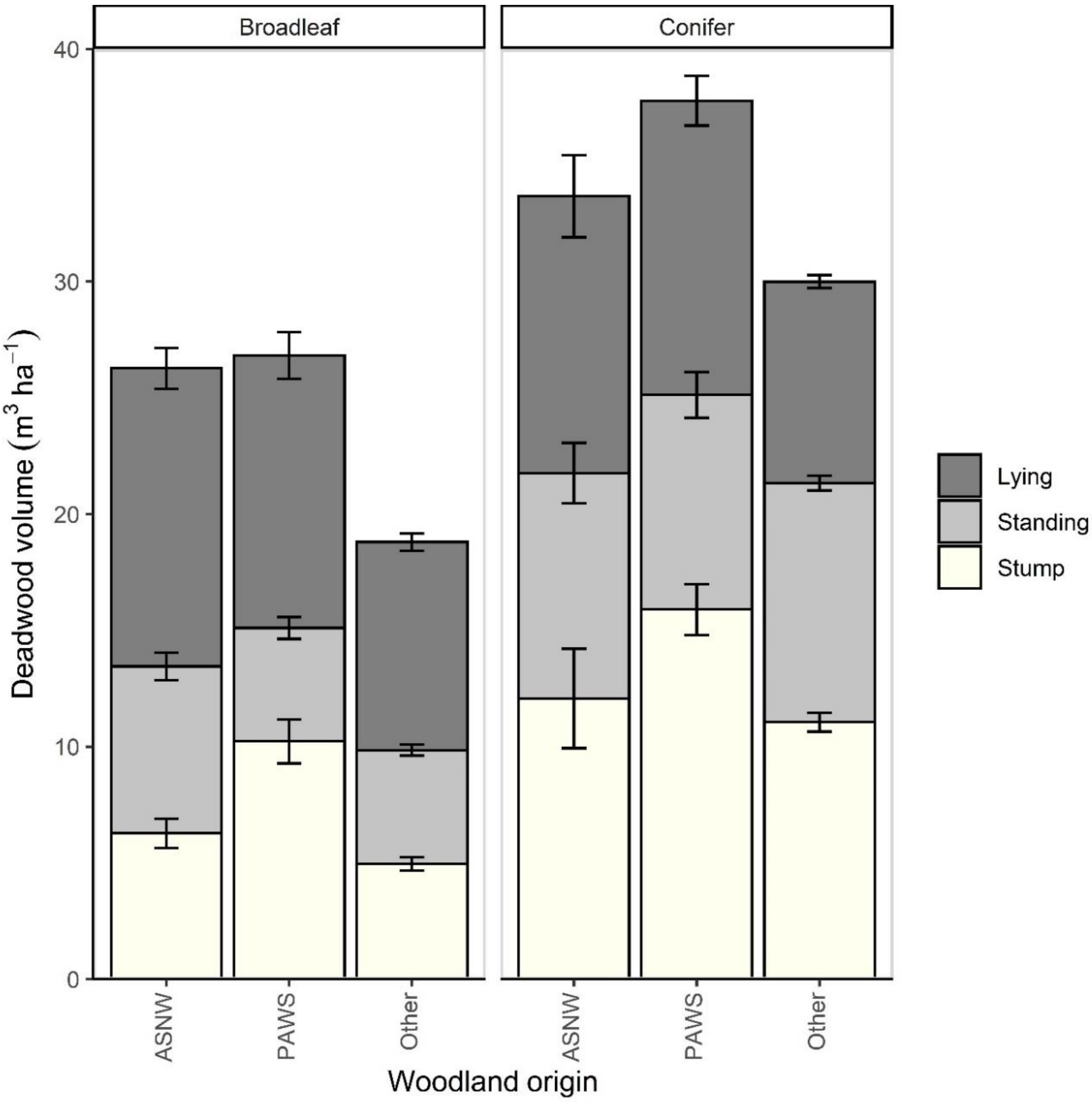


Figure 6-6 – GB deadwood volumes (m^3 ha^{-1}) in broadleaf and conifer woodlands, split by deadwood type in ancient semi-natural woodlands (ASNW), plantations on ancient woodlands (PAWS) and newer, non-ancient woodlands (Other). Mixed broadleaf and conifer woodlands are included in broadleaf and conifer woodlands, respectively. Error bars show one standard error from the mean.

6.4.3 Management effects

Results of the effects of woodland management practices that were evident during the survey on deadwood volumes and carbon stocks were highly variable. There were very few sections where practices were expected to solely remove deadwood, and few where activities might both generate or remove deadwood, so deadwood estimates could not be robustly calculated for these groups. Instead, we have grouped all management that creates or removes deadwood into a single group: deadwood specific management.

Table 6-3 – GB mean deadwood volumes and carbon stocks split by deadwood management type. Data from stands which were classified as either mixed broadleaf or conifer have been amalgamated into broadleaf or conifer, respectively. The number of sections in each management category is included in brackets under carbon stocks for broadleaf and conifers. A full description of management practices included in each group are in Table 6-1. Tukey post-hoc testing letters are given for the significant interactions between management and woodland type (uppercase) and three-way interaction between management, deadwood type and woodland type (lowercase). Groups that do not share a letter are significantly different.

Woodland type	**Deadwood type**	**Management activity type**	**Volumes (m^3 ha^{-1})**	**Carbon stock (t^{-1} C ha^{-1})**
Broadleaf	Lying	Deadwood specific	12.92±0.77^{cd}	1.68±0.11^{abc} (2834)
		Non-dw specific	8.30±0.46^{gh}	1.03±0.06^{fgh} (4416)
		Both	11.21±0.63^{def}	1.46±0.10^{bcde} (2493)
		Not managed	10.43±0.53^{defg}	1.31±0.08^{cdefg} (4682)
	Standing	Deadwood specific	6.30±0.45^{hij}	1.11±0.09^{efgh}
		Non-dw specific	4.56±0.30^{jk}	0.78±0.06^{hij}
		Both	4.91±0.36^{jk}	0.84±0.07^{hij}
		Not managed	5.86±0.32^{ij}	0.99±0.05^{gh}
	Stump	Deadwood specific	10.46±0.87^{defg}	1.16±0.11^{defgh}
		Non-dw specific	2.99±0.23^{k}	0.30±0.02^{l}
		Both	9.56±0.62^{efg}	0.94±0.07^{ghi}
		Not managed	3.97±0.34^{jk}	0.54±0.08^{jkl}
	Total	**Deadwood specific**	**29.68±1.26^{CD}**	**3.94±0.18 (8502)**
		Non-dw specific	**15.84±0.63^{G}**	**2.11±0.09 (13248)**
		Both	**25.68±0.99^{DE}**	**3.25±0.15 (7479)**
		Not managed	**20.27±0.73^{F}**	**2.84±0.12 (14046)**
Conifer	Lying	Deadwood specific	15.92±0.66^{b}	1.74±0.08^{ab} (2617)
		Non-dw specific	5.99±0.32^{ij}	0.65±0.04^{ijk} (4966)
		Both	14.42±0.77^{bc}	1.57±0.12^{abcd} (2869)
		Not managed	10.20±0.63^{defg}	1.02±0.07^{efghi} (2234)
	Standing	Deadwood specific	11.42±0.64^{def}	1.79±0.11^{ab}
		Non-dw specific	12.03±0.43^{cde}	1.92±0.07^{a}
		Both	8.83±0.45^{fgh}	1.44±0.08^{bcde}
		Not managed	12.26±0.68^{cde}	1.94±0.12^{a}
	Stump	Deadwood specific	20.02±0.93^{a}	1.91±0.10^{a}
		Non-dw specific	5.17±0.38^{jk}	0.43±0.04^{kl}
		Both	16.62±0.73^{b}	1.39±0.07^{bcdef}
		Not managed	8.48±0.68^{fghi}	0.79±0.06^{hijk}
	Total	**Deadwood specific**	**47.36±1.35^{A}**	**5.45±0.17 (7851)**
		Non-dw specific	**23.19±0.69^{EF}**	**3.00±0.10 (14898)**
		Both	**39.87±1.19^{B}**	**4.40±0.16 (8607)**
		Not managed	**30.94±1.22^{C}**	**3.76±0.16 (6702)**

Broadleaf woodlands were more likely to not show signs of management, with ~32% of sections ‘not managed’, compared to ~18% in coniferous woodland. When all deadwood types were aggregated into a single group, volumes in both woodland types followed the pattern of declining volumes from ‘deadwood specific’ > ‘both specific and non-deadwood specific’ > ‘not managed’ > ‘non-dw specific’ (Table 6-3). This was the same for carbon stocks in both woodland types.

GLM analysis of managed vs unmanaged sections found a significant difference in the volumes of deadwood ($p = 0.001$), due to the larger volumes of stumps found in managed woodlands (appendix Table 10-6). However, carbon stocks did not significantly differ ($p = 0.135$). When the category of managed was split into different management practices (deadwood specific, non-dw specific, and both), results of the GLM found that management significantly affected both deadwood volumes and carbon stocks ($p < 0.001$), with all combinations of management groups significantly differing. For volumes, a significant interaction was found between management and deadwood type ($p < 0.001$) and woodland type ($p < 0.001$). However, for carbon stocks, only the interaction between management and deadwood type was significant ($p < 0.001$), with the interaction with woodland type being non-significant ($p = 0.088$). A significant three-way interaction between deadwood type, woodland type, and management practices ($p < 0.001$) was found for both volumes and carbon stocks.

Post-hoc testing on the interaction between management and deadwood type showed that where management occurred which involved deadwood specific practices (groups of deadwood specific, deadwood specific & non-dw specific), volumes and carbon stocks of standing deadwood were significantly lower than LD and stumps. However, in woodlands that were not managed, or where only non-deadwood specific management occurred, volumes and carbon stocks of stumps were significantly lower than lying and standing deadwood.

Results of post-hoc tests on the three-way interaction and interaction between management and woodland type are shown in Table 6-3. In broadleaf woodlands, volumes and carbon stocks of lying deadwood were significantly lower where non-deadwood specific management was carried out compared to where deadwood specific and both management types occurred. This was also seen in volumes of LD in coniferous woodlands, where volumes in unmanaged woodlands were also significantly lower than where deadwood specific and ‘both’ management practices occurred. However, for carbon stocks, no difference occurred between non-deadwood specific management and unmanaged woodlands. In both broadleaf and coniferous woodlands, volumes and carbon stocks of stumps were higher where deadwood specific management occurred, compared to unmanaged woodlands and those with non-deadwood specific management. Volumes and carbon stocks of standing deadwood were less impacted by management, with the only significant differences occurring in coniferous woodlands between the group of ‘both’ and non-deadwood specific and unmanaged woodlands. No differences were found between the volumes of SD in broadleaf woodlands.

6.4.4 Cause of death for standing deadwood

For standing deadwood, a cause of tree death was recorded in the NFI survey based on *in situ* observations where possible. Data was analysed at a species level per section. These records were for ~65% (10,073) of all species at a section level, with 35% (5,492) dying from non-discernible causes. Of the samples that had a discernible cause of death, 86-87.7% were attributed to natural mortality in conifer and broadleaf species, respectively. Abiotic events accounted for 5.8% of attributable standing tree deaths in broadleaf species and 11.9% in conifers. Diseases and vertebrate damage were more frequently recorded in broadleaf species (2.5% and 2.8%) than in conifers (0.3% and 0.3%) while management accounted for 1.3% in both broadleaf and conifers. Insect damage was not recorded in broadleaf species and was minimal in conifers, occurring in 0.1% of sections.

Erosion created the largest average volume of deadwood per section (109 m^3 ha^{-1}, Figure 6-8B), although this was only recorded in one woodland, and fire was otherwise the largest abiotic cause of deadwood (37±27 m^3 ha^{-1}). Vertebrate animal damage, particularly squirrels, was attributed as cause of death in as many woodlands as management and pests and disease, although on average vertebrate damaged plots had much smaller standing deadwood volumes. 81% of tree death caused by vertebrates occurred in woodlands aged under 40 years (Table 6-4).

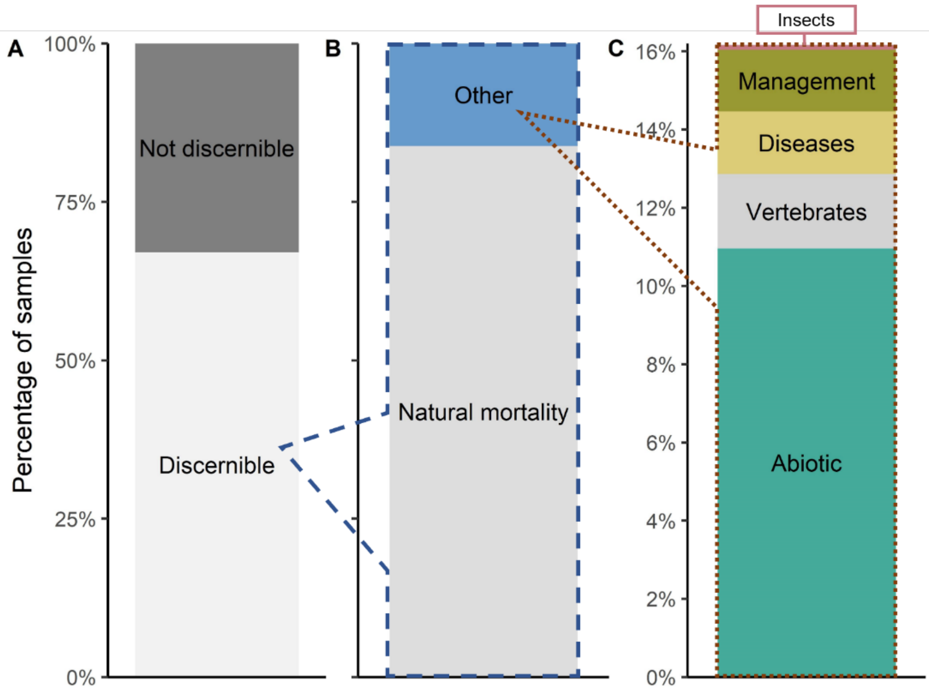


Figure 6-7 – Number of samples at a section level (%) per cause of death. Fig A shows % of those with a discernible cause of death. Fig. B is a breakdown of discernible causes into natural mortality and 'other' causes. Fig. C is a breakdown of the 'other' causes into specific groups.

Results of the GLM analysis with all tree species pooled into groups of either broadleaf or conifer species indicate that cause of tree death significantly affected deadwood volumes ($p < 0.001$). A significant interaction occurred between species type and cause of death ($p < 0.001$). The group of diseases created significantly larger volumes of deadwood than abiotic events, management, natural mortality and vertebrates, but not insects. Abiotic events and management did not create significantly different amounts of deadwood to each other, though created significantly more than natural mortality and vertebrates. The group of insects did not create significantly different volumes of deadwood to any other cause. Results of Tukey post-hoc tests on the interaction between species type and cause of death are shown on Figure 6-8A.

In broadleaf woodlands, abiotic events, diseases and management created significantly larger deadwood volumes than natural mortality and vertebrates (Figure 6-8A). Vertebrates created the least deadwood and did not significantly differ to the volumes created by natural mortality. Insects were only recorded as cause of death in broadleaves in one section, and so volumes did not prove to differ significantly to the other groups. However, where insect damage was recorded, deadwood volumes were larger than diseases (Figure 6-8C). In coniferous woodlands, abiotic events, insects and diseases created significantly more deadwood than management, natural mortality, and vertebrates. Natural mortality, management and vertebrates did not create significantly different volumes of deadwood compared to each other (Figure 6-8A).

When principal species were analysed separately to all other species using GLM, volumes of the broadleaf species ash, beech, and birch did not significantly vary with cause of death (appendix Figure 10-2), nor did volumes of the conifer species lodgepole pine, Scots pine and ‘other conifer spp.’ (appendix Figure 10-3). In broadleaves, oak that died naturally produced more deadwood than the other broadleaf species except ash and beech. In conifer woodlands, Sitka spruce produced more deadwood than Scots pine when it died of natural causes, though volumes did not differ to any other species. Abiotic causes created more deadwood than natural mortality in larches, Sitka spruce, and ‘other broadleaf spp.’. In Sitka spruce, abiotic causes also created larger volumes than management. Pest and disease created larger volumes of deadwood in larches and Norway spruce than abiotic causes, management, natural mortality and, for larches, vertebrate damage.

Table 6-4 – average standing deadwood volumes (m^3 ha^{-1}) split by woodland age at the time of assessment for sections containing standing deadwood. Mixed ages were sections with ages spanning multiple age classes. The number of sections are shown within parentheses. Tukey grouping letters are shown in lowercase. Groups that do not share a letter are significantly different.

Age class (years)	**Deadwood volume (m^3 ha^{-1}) Cause of death**					
	Abiotic	**Management**	**Natural mortality**	**Pest & disease**	**Vertebrates**	**Mean**
0-20	4.00±1.66 (89)	0.22±0.09 (28)	1.12±0.14 (947)	2.58±1.32 (32)	0.48±0.11 (73)	1.32±1.15 (1169)^{d}
21-40	11.62±0.89 (474)	3.43±0.76 (54)	3.85±0.16 (4591)	8.15±2.00 (79)	2.34±0.58 (97)	4.57±0.16 (5295)^{c}
41-60	21.95±1.51 (449)	16.76±4.31 (46)	11.63±0.47 (2598)	37.8±10.7 (41)	4.87±1.79 (25)	13.46±0.48 (3159)^{b}
61-80	29.89±4.39 (94)	40.4±32.5 (8)	10.90±0.92 (644)	29.3±12.8 (11)	3.90±3.40 (5)	13.77±1.04 (762)^{a}
81-100	37.5±11.6 (11)	67.4±34.0 (3)	5.70±1.62 (178)	166±157 (2)	0.77±0.23 (7)	9.79±2.37 (201)^{ab}
101-150	3.64±2.87 (9)	162±126 (3)	13.86±5.24 (111)	11.90 (1)	0.10±0.10 (2)	16.42±5.62 (126)^{ab}
151-200	-	0.50±0.50 (3)	9.92±5.54 (29)	-	0.07 (1)	8.76±4.89 (33)^{abcd}
201+	0.76±0.76 (3)	-	20.0±14.1 (20)	-	-	17.5±12.3 (23)^{abc}

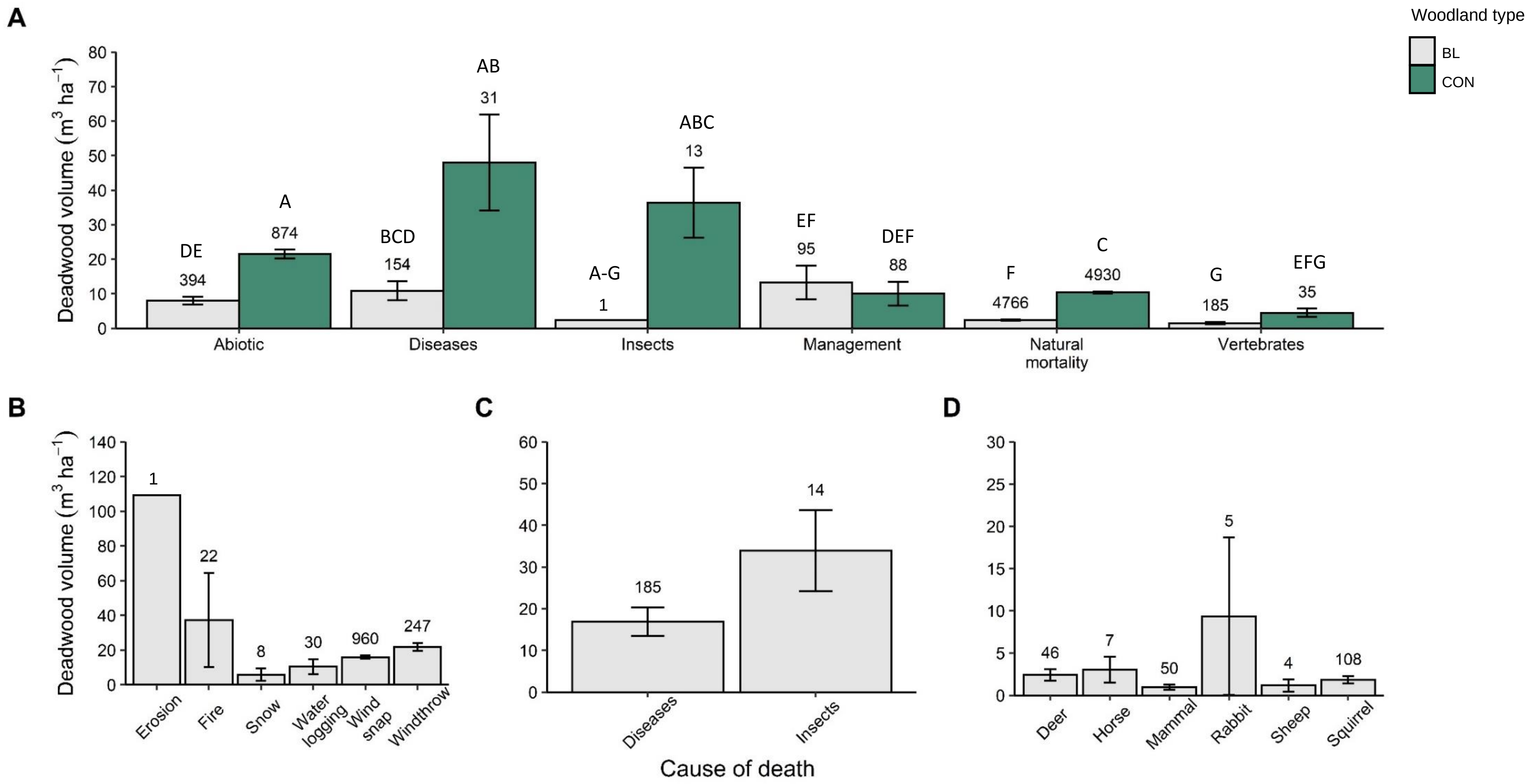


Figure 6-8 – Mean volumes (m^3 ha^{-1}) of standing deadwood by their associated cause of death in GB ± the standard error, where known. Number of sections sampled are included above the error bars. **Fig**. **A**: Volumes are split by tree species type (BL – broadleaf, CON – coniferous) across the main causes of death. In figs. B:D, all species types are pooled. Tukey post-hoc grouping letters are included in capitals. Those which do not share a letter are significantly different. The categories from fig. A of, abiotic events, insect pest and disease and vertebrate pests are split into their constituents to create **fig**. **B,** **C** and **D,** respectively, which are the mean standing deadwood volumes for those sections where that cause was attributed .

6.5 Discussion

6.5.1 Objective 1: Deadwood volumes and carbon stocks

We calculated the mean GB volume of deadwood as 26.40±0.40 m^3 ha^{-1}, holding an average mass of 6.59±0.10 t ha^{-1} and carbon stock of 3.29±0.05 t carbon ha^{-1}. The volume we report is far higher than the European average of 11.5-15.8 m^3 ha^{-1} (Puletti *et al.*, 2019; MCPFE Liaison Unit and UNECE/FAO, 2020) and would account for ~7% of Europe's live growing stock volume, though these averages often discount stumps. The Biosoil survey carried out in GB also found a lower average deadwood volume of 8 m^3 ha^{-1}, though it should be noted that this was calculated across all deadwood types, rather than total volume of all types found in a sample square (Vanguelova, Moffat and Morison, 2016).

In the NFI woodland ecological condition reports (Forestry Commission, 2020), a volume of lying and standing deadwood ≥ 80 m^3 ha^{-1} is considered favourable condition, with 20-80 m^3 ha^{-1} intermediate and 0-19 m^3 ha^{-1} unfavourable. Our finding of 17.50 m^3 ha^{-1} across GB would suggest that woodland is in an unfavourable condition, though it should be noted that this value varied substantially between country and woodland type, ranging between 12.67 m^3 ha^{-1} in English MBL and 29.18 m^3 ha^{-1} in Welsh coniferous woodland.

In the results of our analysis, we established that stumps contributed 25-42% of deadwood volumes across GB, depending on woodland type, and 23-49% of deadwood carbon stocks (appendix Table 10-5), suggesting that omitting stumps from reports leads to a large underestimate. Removal of stumps from the GB total average would lead to a mean volume of ~17.5 m^3 ha^{-1}, comparable to the upper European average. In the NFI woodland ecological condition report (2020), it was estimated that an average 29 m^3 ha^{-1} deadwood (excluding stumps), with a median of 9 m^3 ha^{-1}, occurred across all woodland types. While stumps are often excluded from reports of deadwood volumes, their benefits to biodiversity should not be overlooked, providing an abundant habitat (Blasy and Ellis, 2014), particularly when a variety of sizes are present (Jonsell, Nittérus and Stighäll, 2004; Abrahamsson and Lindbladh, 2006) and other deadwood types are absent.

The assessment for the FAO (2020c) for the UK reports a uniform measure of 25 t ha^{-1} mass of deadwood (13 t C ha^{-1}) which has remained unchanged since 1990. However, our results indicate there is a much lower biomass and carbon stock, reaching a maximum of 3.15 t C ha^{-1} in standing deadwood (SD) of Welsh coniferous woodlands (Figure 6-5). This is due to the use of specific wood densities in our evaluation, assigned for different deadwood decay classes, which will have reduced the mass and carbon stock held in deadwood at later stages of decay. For lying deadwood, decay stages 4 and 5, with the lowest wood density and carbon stock, made up 44% of all samples, while decay stage 1, with a higher density, accounted for ~6% (Figure 6-3). All stumps were presumed to be in a uniform decay stage (Figure 6-2), though this is unlikely to be a true representation of their actual state of decay, and thus potentially under or overestimates the carbon stocks held within. Our results which showed an average deadwood carbon stock of 4.03 t ha^{-1} in conifers, 3.28 t ha^{-1} in broadleaves and 2.41-3.15 t ha^{-1} in mixed woodlands are closer in comparison to those found in the UK BioSoil survey of deadwood, whereby deadwood carbon stocks were measured at 2.36 t ha^{-1} in conifers, 1.24 t ha^{-1} in broadleaves, and 1.23 t ha^{-1} in mixed woodlands (Vanguelova, Moffat and Morison, 2016). The calculation of deadwood carbon stocks in the BioSoil also used specific wood density values, suggesting that future reports for the FAO would benefit from applying a more accurate calculation.

Deadwood volumes were consistently larger in coniferous and mixed conifer (MC) woodlands than in broadleaf and mixed broadleaf (MB, Figure 6-4), with a tendency to hold larger carbon stocks (Figure 6-5). This may be in part due to the substantially larger contribution of SD in coniferous woodlands than in broadleaves, which has been seen in woodlands across Europe (Oettel *et al.*, 2020; Bujoczek, Bujoczek and Zięba, 2021). This is contrary to the assessment for the FAO which assumes deadwood volumes are uniform across all woodland types in the UK and therefore suggests estimates can be improved.

Despite differences in woodland and deadwood types, we found that volumes of deadwood did not significantly differ between decay stages, indicating that within each deadwood type there was a heterogenous mix of wood at different stages of decay. This heterogeneity of decay stages is beneficial to biodiversity, creating varied habitats that can be utilised by different taxa and species (Heilmann-Clausen and Christensen, 2003; Kuffer and Senn-Irlet, 2005a) .

Large volumes of a specific decay class did not always equate to large carbon stocks. For instance, decay class 3 usually produced the largest standing deadwood volumes in broadleaf woodlands. However, the largest carbon stocks were found in decay stage 1. Due to the higher density in deadwood at decay stage 1 compared to more decayed stages (appendix Table 10-4, Vanguelova *et al*., 2016), the lowest carbon stocks were most often found in lying deadwood at decay stage 5. It is well established that wood density is generally higher in broadleaved species than conifers, certainly in the tree species growing in Britain, when undecayed. Wood density clearly decreases with advancing stages of decay (Paletto and Tosi, 2010; Harmon, Woodall and Sexton, 2011; Moreira, Gregoire and do Couto, 2019), thus, less mass (and carbon stocks) are present in late decay stages than in early stages. It should be noted that the densities used for calculating mass (and thus carbon stocks) were calculated using standing deadwood only (Vanguelova, Moffat and Morison, 2016). While it is acknowledged that the density of wood from lying deadwood and stumps will differ (Paletto and Tosi, 2010; Teodosiu and Bouriaud, 2012; Seedre *et al.*, 2013), there is a lack of literature that can provide exact values. Future studies would benefit from using more exact densities for different decay classes of lying deadwood and for stumps, and to examine if there are differences between species.

A large proportion (19%) of squares recorded no deadwood present. This may have been in part due to the classifications used (diameter ≥7 cm for LD) which omitted smaller lying debris from surveying. Fine woody debris, generally classified as debris with a diameter ≤ 7 cm, are often discounted from field studies due to time constraints. However, in a study of the French NFI, it was found that using a 7 cm diameter threshold disregarded ~40% of deadwood volume (Teissier du Cros and Lopez, 2009). Including some measure of fine woody debris would be beneficial to further studies, though there are challenges in the implementation.

Our ‘origin’ classification of woodlands as ASNW or PAWS relied on the accuracy of spatial datasets derived from maps which were difficult in places to interpret and may have under-represented the number of woodlands classified as either ASNW or PAWS. It was expected that ASNW would hold greater volumes of deadwood than PAWS and other origin woodlands, as the latter would be dominated by woodlands created within the last century. While ASNW held significantly more deadwood than those with an ‘other’ origin, they did not differ to PAWS, and the average age of ASNW (35 years) was only 5 years older than those with an ‘other’ origin. Age of woodland stands varied between broadleaf and conifer, reflecting the slower growing speed of broadleaf species compared to conifers. Broadleaf species managed for timber are thus less likely to have undergone management than conifers during the same time span as they are slower to reach maturity. The larger volumes found in coniferous woodlands than broadleaf is consistent with our findings on overall volumes (Figure 6-4). The differences seen in volumes between deadwood types in different woodland origins may reflect different management practices occurring with significantly more stumps found in PAWS, which are managed plantations. Conifer species are most often grown in managed plantations, with only three species of conifer native to the UK and tend to be found in Scotland where the climate is cooler and wetter (Figure 6-1). Low temperatures and wet, anoxic conditions are known to inhibit decomposition (Hagemann *et al*., 2010). The greater volume of stumps and standing deadwood in the coniferous woodlands may be due to management practices occurring in plantations and during PAWS restoration processes. In our assessment of woodland origin, it was found that significantly less coniferous woodlands occurred in ASNW and PAWS, suggesting that coniferous woodlands were predominantly new, non-native plantations.

6.5.2 Objectives 2 & 3: Influences on deadwood volumes

Distribution of woodland types surveyed for the NFI (Figure 6-1) showed a clear divide, with broadleaf woodlands dominating England, and conifers dominating Scotland which is cooler and wetter than England. Subsequently, there were differences in the deadwood volumes and carbon stocks between the countries (Figure 6-4, Figure 6-5), particularly for conifer stands, where both volumes and carbon stocks were much larger in Wales. In coniferous and mixed coniferous Welsh woodlands, stumps contributed 47% and 56% of the total volume, respectively, which was larger than the total volume of deadwood in Welsh broadleaf and mixed broadleaf woodlands. These differences can be attributed to the different mix of species and age classes between countries, which reflects both climate and topography differences and consequent choice of species, and also history of woodland creation. For example, there is a smaller proportion of standing timber volume in Sitka spruce stands in Wales than in Scotland, less in pine species, but more in larch species (55%, 7%, and 16% respectively, compared to 62%, 22% and 8%, (Ditchburn, 2012). Age classes of stands differ too; in England and Wales the proportion of standing conifer volume in the 41-60 year age class is similar (53% and 51%, respectively) , but in Scotland it’s 36%, with 50% in the younger 21-40 year age class (compared to 23% and 35% in England and Wales, respectively).

Presence of woodland management had a clear effect on deadwood volumes, and thus carbon stocks. Woodlands where deadwood specific management practices, such as thinning, coppicing and brashing, were carried out held on average 46-53% more deadwood than sites that were not managed, though this varied considerably with type of deadwood. Volumes of stumps increased by 136-163% in woodlands where deadwood specific management occurred, compared to those that were not managed (Table 6-3) while volumes of standing deadwood in coniferous woodlands reduced by 7%. Timing of site visits could have influenced this, as most of the deadwood removal activities occur post felling. It has been presumed that forest management reduces the amount of deadwood present, and managers now seek to increase the amounts of deadwood to help reduce loss of biodiversity. With many species, particularly saproxylic organisms, relying on deadwood as either a food source or habitat, target volumes have been introduced. The UK Forestry Standard (Forestry Commission, 2017) suggests leaving a proportion of fallen deadwood *in situ,* while volumes of 20 - 50 m^3 ha^{-1} non-uniformly dispersed have been suggested by others (Dudley and Vallauri, 2004; Müller and Bütler, 2010; Humphrey and Bailey, 2012; UKWAS, 2018). Our results suggest that management practices, particularly those that directly involve deadwood creation (Table 6-3), can be beneficial in reaching these targets, provided deadwood is not subsequently removed.

Retention or removal of deadwood in managed forests will vary depending on the aims and needs of forest managers. With the increasing demand for woodfuel as a form of bioenergy (Forest Research, 2021), more deadwood may be removed, as nearly all wood is usable as woodfuel. However, the benefits to biodiversity that are provided by deadwood are recognised by schemes such as the Programme for the Endorsement of Forest Certification (PEFC) which recommend a proportion of deadwood is left *in situ* (PEFC UK, 2016). Deadwood may also be beneficial in improving nutrient-poor soils, as it releases nutrients during decomposition (Humphrey *et al.*, 2002). Nutrient release has been found to be significantly larger in later stages of decay (Lasota *et al.*, 2018), and as deadwood may take decades to fully decompose (Vrška *et al.*, 2015), it will require long-term deadwood retention by management for such benefits to accrue. These conflicting priorities will likely lead to changes in the proportions of deadwood that are found in managed woodlands over the next few years, and further assessments would help to clarify whether deadwood volumes change over time.

Woodlands may also be managed for other reasons, such as public recreation, or as ornamental areas and for game birds (Table 6-1), and deadwood is more likely to removed where it impedes access or poses a health and safety risk (Humphrey *et al.*, 2002). The increasing awareness of deadwood as a priority habitat for saproxylic species (Brin *et al.*, 2011; Forestry Commission, 2017), many of which are endangered, may lead to increasing volumes of deadwood found in such woodlands, though this would need to be assessed over future NFI surveys.

Deadwood volumes in broadleaf and conifer woodlands were differently affected by causes of death (Figure 6-8A). While woodland management can indirectly influence volumes of deadwood, as previously discussed, in coniferous woodlands management as a direct cause of death produced less deadwood than abiotic events, disease and insects, though did not differ to natural mortality of vertebrate damage.

The largest volumes of SD were created by insects and diseases and the lowest by vertebrates (Figure 6-8A). However, occurrence varied hugely between groups (Figure 6-8). Natural mortality was the most common cause of death recorded, at 86-88%, while insects were the least common (Figure 6-7). Of the vertebrates, squirrels have received particular attention as the cause of tree damage (Peden, 2020). Our results indicated that squirrel damage as an attributable cause of death was more prevalent than all other vertebrates and insects. However, the volume of deadwood produced was smaller than most of these other causes and this may be due to squirrel preference for young trees. Trees between the ages of 11-60 showed the greatest amount of squirrel damage in the work by Peden (2020). Woodland age may be an important factor in determining the amount of deadwood produced by different causes of tree death (Table 6-4). In research by Ruel *et al*. (2000) it was found that the windspeed required to break or overturn a tree reduced with tree age, suggesting that mature and old age stands are more susceptible to abiotic damage such as windthrow and windsnap. In our results deadwood volumes significantly increased with age until ~80 years, while ~60% of the standing deadwood sampled occurred in woodlands under the age of 40. However, this may not only be due to the susceptibility of older trees to damage such as windthrow. Young trees have less biomass, and as such will produce smaller volumes of deadwood compared to older, mature trees.

While some causes of death, such as damage by rabbits (Figure 6-8D), or erosion (Figure 6-8B) create large volumes of deadwood at a section level, they are rare events and presumably have less of an impact at a national level than more widespread occurrences such as disease. Other factors, like topography and climate may also influence causes of tree death and subsequently impact on the volumes of deadwood created. It is predicted that the abundance of aphids and other insects that cause tree damage will increase in Britain due to climate change (Wainhouse and Inward, 2016). Aphid infestations have been found to increase the litterfall from conifers (Pitman, Vanguelova and Benham, 2010) which may potentially increase deadwood production. Should this occur, it is likely that larger volumes of deadwood will be found on a national scale.

It should be noted that the data recorded for cause of death was based on *in situ* observations and so some causes, such as damage by specific organisms, may have been harder to discern in the field. The NFI protocol (Forestry Commission, 2016) has been updated since the 1st cycle to include more observations that can identify a cause of damage to trees (Peden, 2020). The use of 2nd and 3rd cycle NFI data would help to clarify the impact of different causes of death.

6.6 Conclusion

The occurrence of deadwood in GB woodlands is highly variable with many factors influencing the quantity of deadwood present at a site, and consequent carbon stocks. There were differences in mean volumes and carbon stocks between the three countries, particularly in coniferous woodlands, which we attribute to different species composition, age class mixes and climate. While mean volumes were similar to previous estimates by the NFI ecological condition report (2020) the estimated carbon stocks were -75% than values reported to the FAO (2020c), because of the use of decay stage-adjusted density values. Coniferous woodlands held larger volumes than broadleaf woodlands, notably due to larger volumes of standing deadwood and stumps, and thus held larger carbon stocks. Woodland management and the causes of tree death were found to significantly influence the volumes of deadwood and should be considered when planning deadwood management. Management that creates deadwood may be a key tool in increasing overall deadwood volumes across GB and thus may be an important tool for biodiversity conservation.

6.7 Acknowledgements

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7 Upscaling deadwood volumes and carbon stocks from the National Forest Inventory (2009-2015) in Great Britain

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7.1 Abstract

Inventories of woodland carbon, such as those in the Kyoto protocol, are implemented to assess changes in forest carbon pools over time, and deadwood is now included as an optional pool to report. Calculation of carbon pools in deadwood relies on measures of wood density and carbon concentration, and upscaling to national totals requires knowledge of the overall area of woodlands across Great Britain (GB). However, current protocols employ a simplistic calculation, whereby a standard wood density and carbon concentration are applied to calculate carbon stocks. In GB, reports of woodland area are limited to broadleaf and conifer woodlands, and are inaccurate where mixed woodlands are included, with ~25% of woodlands mapped by the National Forest Inventory (NFI) as an unknown type. Here, we calculate the total deadwood volume and carbon stock in broadleaf and conifer woodlands across GB over the years 2011, 2015 and 2019, using data from the National Forest Inventory. We assess how the calculation of GB deadwood volumes and carbon stocks can be improved through the use of wood densities and carbon concentrations specific to tree species division and stage of decay. We conclude that deadwood volumes did not significantly change between 2011 – 2019, though significantly differed between woodland and deadwood type. The use of specific carbon concentrations did not affect overall carbon stocks, while specific wood densities did. We suggest that calculations of deadwood carbon stocks for reporting include the use of specific wood densities. Accurate reporting of woodland area for mixed woodlands would further improve reports of deadwood volumes and carbon stocks.

7.2 Introduction

Globally it is estimated that deadwood holds 8% of woodland carbon stocks (Pan *et al.*, 2011) at 73 Pg, with 0.04 Pg found in deadwood in Great Britain (GB) (Forest Research, 2021). National Inventories of woodland carbon pools are required for carbon emission reporting by the LULUCF sector of the United Nations Framework Convention on Climate Change (United Nations, 1992), and the Kyoto Protocol (1998). As part of this, deadwood has been included as a carbon pool that needs regular assessment (United Nations, 1998). Regular assessment is required to assess changes in woodland carbon pools, due to changes in forest management and natural lifecycles of woodlands.

National stocks are calculated by estimating the plot level stocks of deadwood from measurements of volume, wood density and carbon content and then upscaling these values by woodland area. The UK National Forest Inventory (NFI) was first implemented in 2009 (Forestry Commission, 2016), following an update to the forest inventories of Great Britain which have been carried out since 1924. It aims to assess the current state of woodlands within the United Kingdom and includes many assessments of woodland condition and management. The NFI provides detailed data on deadwood volume across the UK, however carbon content is not monitored and so estimates are required. Deadwood volume and carbon stock estimates have uncertainties associated with their measurements due to the natural variability between tree species, decay classes, deadwood type, cause of wood death and age of woodlands. For instance, deadwood found in young woodland (0-20 years) produced significantly smaller volumes (1.32 m^3 ha^{-1}) than woodlands aged between 21-150 years (4.57 – 16.42 m^3 ha^{-1}; Chapter 6). In addition, different ways of reporting and mapping woodland create further uncertainty in woodland area, with substantial differences between those reported by Forestry Statistics (Forest Research, 2019) and the National Forest Inventory open access data (Figure 7-1). Therefore, further work is needed to explore the impact on estimates of carbon content and area of overall national level stock estimates.

It is assumed, for the purpose of national statistics reports (Forest Research, 2019) that all deadwood is uniform, having the same density and holding the same carbon concentration (50%). Previous work has shown that wood density changes with stage of decay and between tree species division (Paletto and Tosi, 2010; Harmon, Woodall and Sexton, 2011; Vanguelova, Moffat and Morison, 2016; Moreira, Gregoire and do Couto, 2019). Various studies have also addressed the difference in carbon between varying tree species. It has been found in temperate forests that angiosperms have lower carbon content than conifers (Thomas and Martin, 2012), measuring 48.8% and 50.8% respectively. Similar results have been found by the IPCC (2006) (48% in broadleaves; 51% in conifers) and Ma *et al*. (2017) (47.7-47.8% in broadleaves; 50.5% in conifers). While these changes may only have small implications on individual measurements, the effect can be much greater when used at a national or global scale. In a study by Ma *et al*. (2017), it was identified that by changing the standard carbon fraction of 50% by 1%, a difference of 7 Pg carbon was found in the global vegetative carbon stock. In a recent study by Martin *et al*. (2021), it was found that using specific carbon concentrations when calculating carbon stocks in tropical deadwood led to a ~3 Pg difference compared to using the standard 50%. It was also evident that carbon concentrations differed with the decay stage of deadwood, with a tendency to increase as decay advanced, and also with coniferous species holding a higher carbon concentration than broadleaf species. It is currently estimated that 1.6 Gt (1.6 Pg) of carbon are held within European deadwood (excl. Russia) (FAO, 2020b), half that of the estimated change in tropical deadwood when using specific concentrations.

In order to assess the contribution of Great Britain to these global pools, it is necessary to upscale the measures of volumes and carbon stocks using current woodland areas for each nation. However, this relies on accurate reports of woodland area. Woodlands can be split into broadleaf, conifer (>80% broadleaf / conifer species in an area), or mixed broadleaf / conifer (>50% broadleaf / conifer species in an area), as defined by the NFI (Forestry Commission, 2016). Total woodland areas for these woodland types have been provided by the NFI (Forestry Commission, 2011; Forest Research, 2021) since 2011. Open access maps are created by interpreting woodland boundaries from colour aerial orthophotographic imagery, which is split into woodland categories and interpreted open areas. However, the data provided (discounting interpreted open areas) includes a category of 'other woodland' whereby the specific woodland type could not be identified. The area of 'other woodland' has been increasing steadily since 2011 (Figure 7-1) and so upscaling using these split woodland areas would be highly inaccurate. While the area assessed as broadleaf has remained roughly constant, area of conifer woodland has been decreasing though it is not known whether this is an accurate assessment of changes in woodland management due to the large amount of unknown woodlands reported. An alternative source of UK woodland area is provided by the Forestry Statistics reports; however, these do not include a measure of mixed woodland area (Forest Research, 2019), with these woodlands instead being included as part of either broadleaf or conifer. This allows a preliminary calculation of upscaling, though does not provide any measure of the deadwood present in mixed woodlands. In a report of deadwood from the Swiss National Forest Inventory, mixed broadleaf and conifer woodlands were found to hold more deadwood than pure broadleaf or conifer woodlands (Böhl and Brändli, 2007), while in Chapter 6 we also found significant differences in the volumes of deadwood between mixed and pure woodlands, indicating that mixed woodlands are a valuable inclusion to deadwood reports. Methods have been created to harmonise the calculation of deadwood volumes from National Forest Inventories globally (Rondeux *et al.*, 2012), though calculations of deadwood carbon stocks have received less attention.

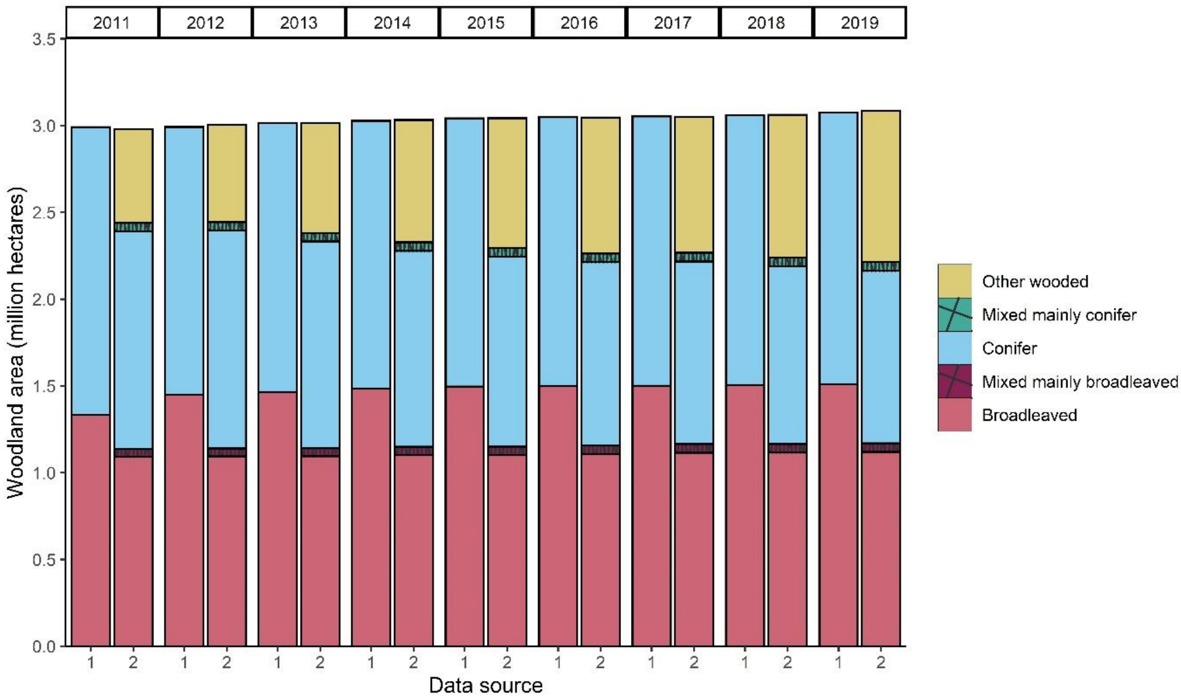

Figure 7-1 – comparison of GB woodland area (million hectares) between 1: published Forestry Statistics and 2: NFI woodland map metadata, split by woodland type

Given the importance of accurate estimates of national scale carbon pools, it is important to better understand the degree to which different methodologies affect the final output. Including specific values in the calculations of upscaled values (e.g. wood density, carbon concentrations and woodland area), rather than using standard values (Forest Research, 2019), will help to improve the accuracy of volumes and carbon stocks reported. Therefore, the aim of this study is to calculate the total volume of deadwood in GB, along with carbon stocks. The specific objectives of this paper are to:Table 7-1

1. Calculate the total volume and carbon stocks of deadwood in Great Britain
2. Determine how these totals are affected by estimates of woodland area
3. Investigate the effect of using specific carbon concentrations and wood densities on overall carbon stocks measured in deadwood

7.3 Methods

7.3.1 NFI data set

Data were collected as part of the first cycle of NFI measurements between 2009-2015, including measurements of volume (m^3) from lying deadwood (dead stems with a diameter ≥ 7 cm). standing deadwood (a rooted dead tree stem ≥ 1.3 m tall with a diameter at breast height of ≥ 4 cm), and stumps (a rooted dead tree stem ≤ 1.3 m tall with diameter ≥ 4 cm). Protocols for NFI measurements are described in detail in Chapter 3.4 and Chapter 6.3. Here, we explain the relevant details for the analysis carried out on upscaling and changes to carbon concentrations.

7.3.2 Deadwood volumes

Calculations of deadwood volumes ($m^3\ ha^{-1}$) were first determined as the sum of the volume (m^3) from all decay classes (m^3) per deadwood type in a one hectare sample square.

Carbon stocks ($t\ ha^{-1}$) were calculated as the sum of carbon (t) from all decay classes per deadwood type in a one hectare square, whereby carbon (t) was calculated as:

$$Carbon\ stocks\ (t) = Biomass\ (t)\ x\ carbon\ concentration\ (\%)$$

Equation 4

Whereby:

$$Biomass\ (t) = Density\ (g\ cm^{-3})\ x\ Volume\ (m^3)$$

Equation 5

Wood density values were assessed by Vanguelova *et al.* (2016), using four of the main UK tree species: oak, beech, Scots pine and Sitka spruce, as part of the national BioSoil survey and are presented in Table 7-1. For comparison, calculations of carbon stocks were also carried out using the standard value of 0.45 g cm^{-3} (Forest Research, 2019).

Table 7-1 – wood density (g cm^{-3}) in lying deadwood (LD), standing deadwood (SD), and stumps, split into broadleaf or conifer species and by decay class, adapted from Vanguelova *et al* (2016).

	Wood density (g cm^{-3})	
Decay class	**Conifer**	**Broadleaf**
LD 1, SD 3	0.390	0.500
LD 2, SD 4	0.250	0.320
LD 3, SD 5	0.191	0.250
LD 4, SD 6	0.156	0.200
LD 5, SD 7	0.137	0.180
Stumps	0.191	0.250

Carbon concentration was assigned based on the decay stage and species division of each deadwood sample per sample square. Carbon stocks were assessed using the standard 50% and a more specific %, as outlined below (Figure 7-2).

7.3.3 Carbon concentration impact on deadwood stocks estimates

Here we assess the use of specific carbon concentration against the standard 50% to compare deadwood carbon stocks, at a plot level and on a national scale. Carbon concentrations were selected from the supplementary data of the synthesis by Martin *et al*. (2021) and used to calculate mean carbon fractions per species division and decay class (Figure 7-2) for broadleaf and conifer species. Data was filtered to use only the species that were present in the NFI dataset. This led to 11 species of conifer: *A. amabilis, A. grandis, A. procera, P. abies, P. sitchensis, P. contorta, P. radiata, P. sylvestris*, *P. menziesii, T. plicata*; *T. heterophylla;* and six species of broadleaf: *A. glutinosa, A. incana, B. pendula, B. pubescens, F. sylvatica, P. tremula* (Table 7-2).

Table 7-2 – average carbon concentration ± 1 standard error of the mean, split by species and decay class. Raw data was provided in the supplementary data of Martin *et al*. (2021).

Species	**Mean carbon concentration (%)**				
	Decay stage 1	**Decay stage 2**	**Decay stage 3**	**Decay stage 4**	**Decay stage 5**
Alnus glutinosa	49.00	49.30	49.60	49.60	50.20
Alnus incana	48.40	48.30	47.90	49.60	51.30
Betula pendula	48.98 ± 0.61	49.28 ± 0.53	49.15 ± 0.59	50.05 ± 0.47	50.25 ± 0.33
Betula pubescens	47.20	47.70	47.50	48.80	50.10
Fagus sylvatica	47.07 ± 1.25	47.70 ± 0.95	48.27 ± 0.98	48.47 ± 0.81	46.30
Populus tremula	48.00	48.20	48.10	48.40	48.10
Abies amabilis	49.55 ± 0.85	49.80 ± 1.30	-	-	-
Abies grandis	50.40 ± 1.10	49.95 ± 0.95	48.50 ± 0.60	-	-
Abies procera	-	50.70 ± 1.00	51.80 ± 0.80	52.80 ± 0.50	-
Picea abies	48.54 ± 0.31	48.77 ± 0.62	48.48 ± 0.71	50.00 ± 0.86	47.96 ± 2.34
Picea sitchensis	50.70 ± 1.20	51.45 ± 1.15	50.15 ± 0.15	51.25 ± 0.55	50.15 ± 0.35
Pinus contorta	50.98 ± 0.70	51.13 ± 0.65	51.46 ± 0.53	53.80	54.80
Pinus radiata	48.77 ± 0.27	48.77 ± 0.25	47.57 ± 0.78	-	-
Pinus sylvestris	49.73 ± 0.30	50.17 ± 0.54	50.41 ± 0.35	50.63 ± 0.91	50.45 ± 1.05
Pseudotsuga menziesii	50.51 ± 0.89	51.02 ± 1.08	51.53 ± 0.75	54.94 ± 0.94	52.75 ± 1.84
Thuja plicata	48.90 ± 1.47	49.63 ± 1.26	48.38 ± 1.47	50.97 ± 2.17	56.90 ± 1.40
Tsuga heterophylla	50.49 ± 0.88	50.06 ± 0.99	50.86 ± 0.85	52.34 ± 0.97	55.55 ± 1.45

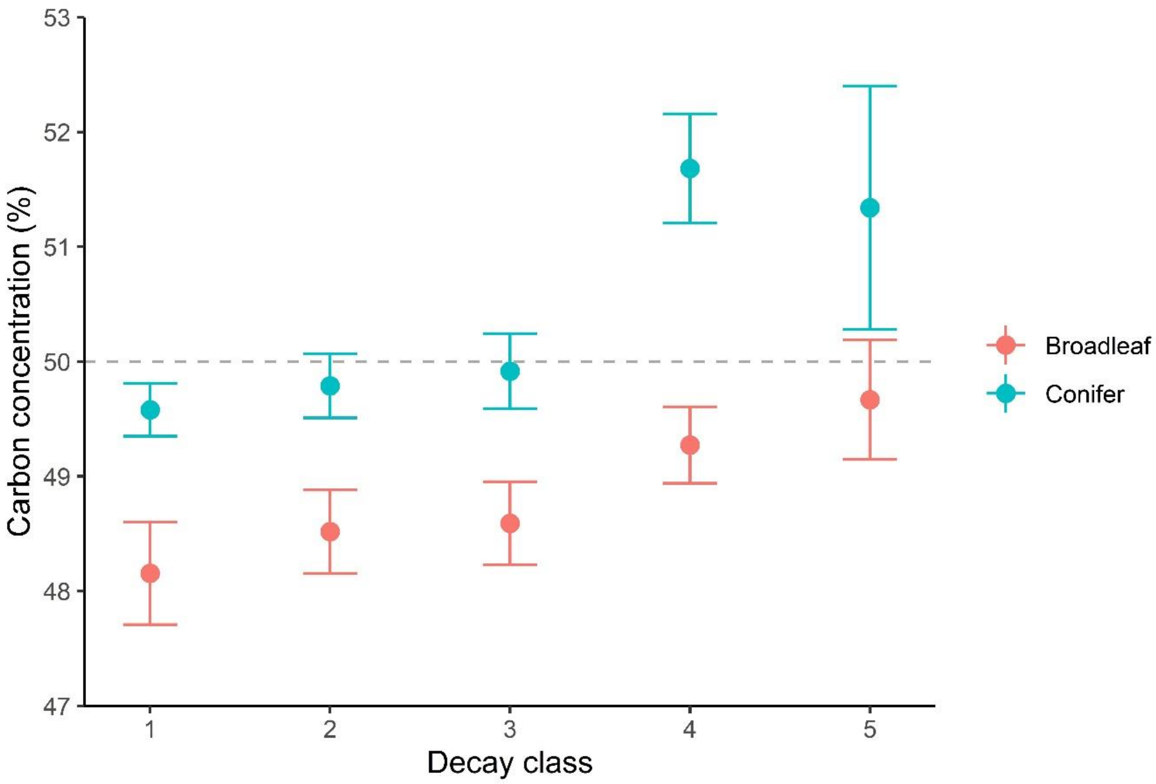

Figure 7-2 – average carbon concentrations in deadwood by decay class, split by species division with margins showing the standard error of the mean. Based on a subset of data from Martin *et al*., 2021. The dashed line shows the standard carbon concentration of 50%.

Subsequently, four combinations of carbon calculation were used:

Standard (Std) - standard wood density of 0.45 g cm^{-3}, standard carbon concentration of 50%

Standard 2 (StWD-SpC) - standard wood density of 0.45 g cm^{-3}, specific carbon concentrations

Standard 3 (SpWD-StdC) - specific wood density, standard carbon concentration of 50%

Specific (Sp) - specific wood density, specific carbon concentrations

The specific carbon concentrations (Figure 7-2) and wood densities (Table 7-1) were applied during the calculation of Equation 4 using the NFI data. A subset of the NFI data was used where the specific species division of deadwood (broadleaf or conifer) could be identified. Samples where species division could not be identified, and a mix of species were present, were discounted as it could not be certain which species the deadwood had been produced by. As such, averages per country and woodland type will differ to those reported in Chapter 6 and those produced for upscaling over the years 2011, 2015 and 2019, where the full NFI dataset was used.

Calculated deadwood volumes that were used as the basis for upscaling using different woodland areas are presented in Table 7-3. Carbon stocks (t ha^{-1}) were analysed using both the standard 50% carbon concentration, and species division and decay class specific values.

7.3.4 Impact of woodland area estimates on upscaled carbon stocks

Due to the large uncertainty using NFI woodland area datasets, whereby ~25% of woodlands in the 2019 woodland data were woodlands of an unknown type (Figure 7-1), areas from Forestry Statistics reports were used for upscaling, with woodlands split into either broadleaf or conifer woodlands.

The average sample square data calculated in Chapter 6 (Table 7-3) was upscaled to national total volumes (m^3) and carbon stocks (t) by multiplying volumes and carbon stocks per hectare by the woodland areas (ha) from the 2011, 2015 and 2019 UK Forestry Statistics (Forestry Commission, 2011, 2015; Forest Research, 2019) (Table 7-4). For this purpose, only categories of broadleaf and coniferous woodland are presented as there are currently no accurate measures of mixed woodland area available (Figure 7-1). Sections identified in the NFI data as mixed woodland were aggregated into either broadleaf or conifer, depending on the majority species (>50%), as the total woodland area remains similar between FR statistics and the NFI open access data (Figure 7-1). Carbon stocks for these were calculated using specific wood density and carbon concentration of 50% (SpWD-StdC).

Table 7-3 – average deadwood volumes and carbon stocks per hectare, split by country, woodland type, and deadwood type, as calculated for broadleaf and conifer woodlands in Chapter 6.

		Volume m^3 ha^{-1}		**Carbon t ha^{-1}**	
		Broadleaf	**Conifer**	**Broadleaf**	**Conifer**
England	Lying	12.38 ± 0.66	11.32 ± 0.96	1.50 ± 0.08	1.08 ± 0.10
	Standing	7.23 ± 0.47	11.63 ± 1.07	1.22 ± 0.08	1.80 ± 0.16
	Stump	6.68 ± 0.48	12.72 ± 0.96	0.83 ± 0.06	1.23 ± 0.09
Scotland	Lying	10.21 ± 1.36	8.48 ± 0.40	1.17 ± 0.16	0.88 ± 0.04
	Standing	3.48 ± 0.48	11.44 ± 0.47	0.54 ± 0.08	1.80 ± 0.08
	Stump	5.48 ± 1.13	9.08 ± 0.53	0.68 ± 0.14	0.87 ± 0.05
Wales	Lying	10.58 ± 1.66	10.22 ± 1.08	1.46 ± 0.26	1.09 ± 0.13
	Standing	5.72 ± 1.05	18.96 ± 1.80	0.97 ± 0.17	3.15 ± 0.30
	Stump	3.52 ± 0.86	26.36 ± 2.51	0.44 ± 0.11	2.57 ± 0.24

Table 7-4 – woodland areas from the Forestry Commission Forestry Statistics (Forestry Commission, 2011, 2015; Forest Research, 2019)

		Woodland area (ha)		
		2011	**2015**	**2019**
England	Broadleaf	886,000	965,000	968,000
	Conifer	411,000	339,000	340,000
	Total	**1,297,000**	**1,304,000**	**1,308,000**
Scotland	Broadleaf	309,000	375,000	385,000
	Conifer	1,081,000	1,057,000	1,072,000
	Total	**1,390,000**	**1,432,000**	**1,457,000**
Wales	Broadleaf	137,000	156,000	158,000
	Conifer	167,000	150,000	152,000
	Total	**304,000**	**306,000**	**310,000**
Total		**2,991,000**	**3,042,000**	**3,075,000**

7.4 Statistical analysis

A general linear model (GLM) was applied to assess whether changes in woodland area over time and the use of standard or specific values during calculations affected deadwood volumes and carbon stocks, with the factors: country, woodland type, deadwood type, and year or measurement type.

7.5 Results

7.5.1 Impact of different carbon concentrations and wood densities on deadwood carbon stocks

Carbon stocks (t ha^{-1}) from the subset NFI dataset were upscaled using woodland areas from 2015 (Table 7-4) to assess the differences between carbon calculation methods on total carbon stocks. This had varying effects, depending on country and woodland type. Using the standard wood density and standard carbon concentration increased overall carbon stocks by 2.5 million t (+69%) in broadleaf woodlands and 4.4 million t (+86%) in coniferous woodlands across GB, compared to using Sp (Table 7-5).

Comparison of carbon concentration effects found in broadleaf woodlands, using specific wood density and a standard carbon concentration increased deadwood carbon in all countries by 2.4-2.8% compared to using specific wood density and specific carbon concentration. In contrast, in coniferous woodlands using Sp had very little impact on overall carbon stocks, showing no change in England and Wales, and a 0.3% increase in Scotland (Table 7-5). Likewise, when Std (with a standard wood density of 0.45 g cm^{-3}) was compared to StWD-SpC, an increase in deadwood carbon of 2.4% was found in broadleaf woodlands in England and Scotland, and 3.6% in Wales. In coniferous woodlands no difference was seen between Std and StWD-SpC in any country.

Change in wood density values had a greater effect on overall carbon stocks than changes in carbon concentration. Using Std (with a standard carbon concentration) instead of SpWD-StdC in broadleaf woodlands increased carbon stocks by 54.1-76.7%, and 83.2-92.0% in coniferous woodlands. When StWD-SpC (with specific carbon concentrations) was compared to Sp, an increase in carbon stocks of 52.8-77.5% was seen in broadleaf woodlands, and 83.8-92% in coniferous woodlands.

Results of the GLM found the use of specific values for wood density and carbon concentration during carbon calculations significant ($p < 0.001$). Post-hoc testing found that using Std and StWD-SpC calculated significantly larger carbon stocks than using either SpWD-StdC and Sp, suggesting that the use of specific wood density significantly changed calculations of carbon stocks.

Table 7-5 – upscaled carbon stocks in deadwood using 2015 woodland areas (Table 7-3) and: a standard wood density and carbon concentration (Std) or specific carbon concentrations (StWD-SpC), specific wood density and standard carbon concentration (SpWD-StdC) or specific carbon concentrations (Sp). Percentage change of the total by country between Std to StWD-SpC, SpWD-StdC and Sp is presented as the 'Change from Std'.

		Carbon stock (millions t)															
Woodland type	**Dead-wood type**	**England**				**Scotland**				**Wales**				**GB**			
		Std	**StWD-SpC**	**SpWD-StdC**	**Sp**	**Std**	**StWD-SpC**	**SpWD-StdC**	**Sp**	**Std**	**StWD-SpC**	**SpWD-StdC**	**Sp**	**Std**	**StWD-SpC**	**SpWD-StdC**	**Sp**
Broadleaf	Lying	1.92	1.88	1.05	1.03	0.65	0.64	0.34	0.33	0.24	0.24	0.14	0.14	2.81	2.76	1.53	1.50
	Standing	1.27	1.24	0.96	0.94	0.30	0.29	0.20	0.20	0.20	0.20	0.16	0.15	1.77	1.73	1.33	1.29
	Stumps	1.07	1.04	0.59	0.57	0.34	0.33	0.18	0.18	0.12	0.12	0.07	0.06	1.53	1.49	0.84	0.82
	Total	4.26	4.16	2.60	2.54	1.29	1.26	0.73	0.71	0.57	0.55	0.37	0.36	6.11	5.98	3.70	3.61
Conifer	Lying	0.68	0.68	0.29	0.29	1.67	1.68	0.76	0.76	0.26	0.26	0.12	0.12	2.60	2.62	1.17	1.18
	Standing	0.72	0.72	0.50	0.50	2.37	2.37	1.66	1.65	0.49	0.49	0.36	0.36	3.59	3.57	2.53	2.51
	Stumps	0.76	0.75	0.32	0.32	1.86	1.86	0.79	0.79	0.68	0.68	0.29	0.29	3.30	3.29	1.41	1.41
	Total	2.15	2.15	1.12	1.12	5.90	5.90	3.22	3.21	1.43	1.43	0.77	0.77	9.49	9.49	5.11	5.09
Total		6.41	6.32	3.72	3.65	7.19	7.17	3.94	3.92	2.00	1.98	1.14	1.13	15.6	15.5	8.81	8.70
Change from Std		-	-1.4%	-42%	-43%	-	-0.3%	-45%	-45%	-	-1.0%	-43%	-44%	-	-0.6%	-44%	-44%

7.5.2 Changes of deadwood volumes and carbon stocks with changes in woodland area over time

When upscaled by woodland area, total deadwood volumes decreased from 87.2 million m^3 in 2011, to 86.7 million m^3 in 2015 (-0.57%), before increasing to 87.6 million m^3 in 2019 (+1.04%) (Table 7-6). Of this ~43-44% was distributed in England, ~43-44% in Scotland, and ~13-14% in Wales. This broadly matched the proportion of GB woodland area in the different countries (43%, 47% and 10%, respectively). Approximately 20% of the sample squares included in the dataset contained no recorded deadwood. Lying deadwood was the most prevalent deadwood type in broadleaf woodlands contributing 47-53% of the total volume, while standing deadwood was the least prevalent in Scotland (18%), and stumps in England and Wales (18-25%) had the lowest volumes. In contrast, in coniferous woodlands lying deadwood contributed the least total volume (18-32%) across all three countries. Standing deadwood had the largest volume in Scotland (40%), and stumps had the largest volume in England and Wales (36-48%). Results of the GLM found that deadwood volumes did not significantly differ with changes in woodland area between 2011, 2015 and 2019 ($p = 0.987$). Interaction between year and country ($p = 0.995$), woodland type ($p = 0.226$), and deadwood type ($p = 0.998$) were all insignificant. However, the main factors, country ($p < 0.001$), woodland type ($p <0.001$), and deadwood type ($p = 0.044$) did significantly affect deadwood volumes, with a significant three-way interaction ($p < 0.001$). In broadleaf woodlands post-hoc testing found no differences between volumes in different deadwood types in Scotland and Wales, while in England greater volumes of lying deadwood were found compared to standing and stumps. In coniferous woodlands, post-hoc tests found no differences in volumes of different deadwood types in England and Wales. However, in Scotland volumes were significantly larger in standing deadwood than lying deadwood and stumps lying.

As carbon concentration was not found to significantly affect the overall carbon stocks calculated, while specific wood densities did, the standard 50% carbon concentration and specific wood densities (SpWD-StdC) were used to calculate the totals presented below.

The total GB carbon stock held in deadwood was estimated to decrease from 10.94 million t in 2011 to 10.93 in 2015 (-0.09%) and then increase to 11.04 in 2019 (+1.01%) (Table 7-7). Distribution of carbon stocks did not always follow the same patterns as volumes. In broadleaf woodlands across GB, lying deadwood held the largest amount of carbon (42-51%), while in England and Wales stumps held the least carbon (15-23%), and in Scotland standing deadwood held the least (22-23%). In coniferous woodlands, standing deadwood held the largest amount of carbon (44-51%) in all countries, while lying deadwood held the least (16-27%) in England and Wales. In Scotland, stumps held the least carbon (24-25%). As with the GLM on volumes, results of the GLM on carbon stocks found the main effects of country, woodland type, and deadwood type significantly affected carbon stocks ($p < 0.001$), while changes in woodland area did not ($p = 0.984$). Interaction between year and country ($p = 0.998$), woodland type ($p = 0.280$), and deadwood type ($p = 0.998$) were all insignificant. A significant interaction occurred between country, woodland type and deadwood type ($p < 0.001$). Broadleaf woodlands in England were found to hold significantly smaller carbon stocks in stumps < standing deadwood < lying deadwood, while no differences between deadwood types were found in Scotland and Wales. In coniferous woodlands, carbon stocks in Scotland were significantly larger in standing deadwood than lying deadwood and stumps, while no differences occurred between carbon stocks in different deadwood types in England and Wales.

Table 7-6 – total volumes (millions m^3) of deadwood in woodlands of different types across Great Britain. Values from Table 7-4 are upscaled using the FC statistics for woodland areas in Table 7-3. Overall totals per country are calculated as the sum of the totals from both woodland types. GB values are the sum of the row (country).

		Volumes (millions m^3)											
Woodland type	**Deadwood type**	**England**			**Scotland**			**Wales**			**GB**		
		2011	**2015**	**2019**	**2011**	**2015**	**2019**	**2011**	**2015**	**2019**	**2011**	**2015**	**2019**
Broadleaf	Lying	11.0	12.0	12.0	3.16	3.83	3.93	1.45	1.65	1.67	15.6	17.4	17.6
	Standing	6.41	6.98	7.00	1.08	1.31	1.34	0.78	0.89	0.90	8.27	9.18	9.25
	Stumps	5.92	6.45	6.47	1.69	2.05	2.11	0.48	0.55	0.56	8.09	9.05	9.13
	Total	**23.3**	**25.4**	**25.5**	**5.93**	**7.19**	**7.38**	**2.72**	**3.09**	**3.13**	**31.9**	**35.7**	**36.0**
Conifer	Lying	4.65	3.84	3.85	9.16	8.96	9.09	1.71	1.53	1.55	15.5	14.3	14.5
	Standing	4.78	3.94	3.95	12.4	12.1	12.3	3.17	2.84	2.88	20.3	18.9	19.1
	Stumps	5.23	4.31	4.33	9.81	9.59	9.73	4.40	3.95	4.01	19.4	17.9	18.1
	Total	**14.7**	**12.1**	**12.1**	**31.3**	**30.6**	**31.1**	**9.23**	**8.33**	**8.44**	**55.3**	**51.1**	**51.6**
Total		**38.0**	**37.5**	**37.6**	**37.3**	**37.8**	**38.5**	**12.0**	**11.4**	**11.6**	**87.2**	**86.7**	**87.6**

Table 7-7 – carbon stocks (millions t) of deadwood in woodlands of different types across Great Britain. Carbon is calculated from the volumes in Table 7-4 using a specific wood density and carbon concentration of 50%. Stocks are upscaled using the FC statistics for woodland areas in Table 7-3. Overall totals per country are calculated as the sum of the totals from both woodland types. GB values are the sum of the row (country).

		Carbon stock (millions t)											
Woodland type	**Deadwood type**	**England**			**Scotland**			**Wales**			**GB**		
		2011	**2015**	**2019**	**2011**	**2015**	**2019**	**2011**	**2015**	**2019**	**2011**	**2015**	**2019**
Broadleaf	Lying	1.33	1.44	1.45	0.36	0.44	0.45	0.20	0.23	0.23	1.89	2.11	2.13
	Standing	1.08	1.18	1.18	0.17	0.20	0.21	0.13	0.15	0.15	1.38	1.53	1.54
	Stumps	0.73	0.80	0.80	0.21	0.26	0.26	0.06	0.07	0.07	1.01	1.12	1.13
	Total	**3.14**	**3.42**	**3.44**	**0.74**	**0.90**	**0.92**	**0.39**	**0.45**	**0.45**	**4.28**	**4.77**	**4.81**
Conifer	Lying	0.45	0.37	0.37	0.95	0.93	0.94	0.18	0.16	0.17	1.58	1.46	1.48
	Standing	0.74	0.61	0.61	1.95	1.91	1.93	0.53	0.47	0.50	3.21	2.99	3.02
	Stumps	0.50	0.42	0.42	0.94	0.92	0.93	0.42	0.38	0.38	1.87	1.71	1.73
	Total	**1.69**	**1.39**	**1.40**	**3.84**	**3.75**	**3.81**	**1.13**	**1.02**	**1.03**	**6.66**	**6.16**	**6.23**
Total SpWD-StdC		**4.83**	**4.82**	**4.83**	**4.58**	**4.65**	**4.73**	**1.52**	**1.46**	**1.48**	**10.94**	**10.93**	**11.04**
Total Std		**8.55**	**8.54**	**8.55**	**8.11**	**8.25**	**8.36**	**2.69**	**2.59**	**2.66**	**19.36**	**19.37**	**19.57**

7.6 Discussion

We estimate a total volume of 87.6 million m^3 of deadwood across GB in 2019 based on the amounts recorded at the time of surveying (2015), within which 11.04 million t of carbon was stored. Our results of total national carbon stocks in deadwood (11.04 million t) are far lower (-72%) than the latest figures released by FR (Forest Research, 2019) which suggest that GB deadwood contributed 39-40 million t of carbon from 2010-2015. However, previously, between 2000-2018, it was estimated that a total of 2.7 million t C were held in GB deadwood (Forest Research, 2018), before the substantial increase (~14 times more) to reported figures in 2019, and results of the national BioSoil survey indicated a total of 5.49 million t carbon held in deadwood (Vanguelova, Moffat and Morison, 2016). Total values were dependent on woodland area and the reduction in volumes and carbon stocks between 2011 and 2015 may be attributed to the decrease in coniferous woodland area (Table 7-3). There is an estimated 1.6 Gt of carbon held within European deadwood (excl. Russia) (FAO, 2020b), of which the UK has been estimated to contribute ~2.4% (Forest Research, 2019). At a global level, deadwood is presumed to hold 4% of the 662 Gt carbon held within woodlands, with 26.48 Gt carbon in deadwood. UK deadwood is thought to hold 0.15% of this (Forest Research, 2019). Using our upscaled carbon stocks would reduce the amount of deadwood carbon contributed by the UK to 0.69% in Europe, and 0.04% globally.

There are several possible reasons why our carbon stock estimates do not match those of the NFI. Volumes > 250 m^3 ha^{-1} were removed from the dataset (Chapter 6) during data cleansing as they were presumed to be outliers, though this accounted for relatively few samples (0.006%) and is unlikely to have significantly lowered averages. Accuracy of data recording for the data set is more likely to have caused an underestimate of volumes and carbon stocks as ~20% of sample squares included in analysis recorded no deadwood. While it is possible that some sites had no deadwood present, it seems erroneous due to the large number of sites visited. Potentially, this is due to deadwood classification requiring a minimum diameter of 7 cm for lying deadwood and 4 cm for standing deadwood and stumps. However, smaller woody debris may account for ~40% deadwood volume (Teissier du Cros and Lopez, 2009). The use of wood densities specific to species and decay class may have had the largest effect as in comparison, the NFI use a standard wood density of 0.45 g cm^{-3}. We found that using SpWD-StdC instead of Std significantly reduced overall carbon stocks by 44% (Table 7-5). Using a standard wood density (Std) in our calculations would have led to an estimated 19.6 million t carbon compared to 11.0 million t carbon (Table 7-7). This would contribute 1.2% of the

European deadwood pool and 0.07% of the global deadwood carbon pool. The variation in specific wood density values (Table 7-1) was larger than the variation in specific carbon concentrations (Figure 7-2) which may be the cause of significant changes in carbon stocks when using specific wood density but not carbon concentrations.

The volume of 87.6 million m^3 of deadwood across GB is equivalent to ~14.5% of the living volume of trees in the UK. There was an estimated 603 million m^3 live volume of trees in the UK as of 2013 (Brewer, 2014a, 2014b), of which 57% was held within conifer and 43% in broadleaf species. Similarly, we found more deadwood in coniferous woodlands (59-63%) than broadleaf woodlands (37-41%) across GB, though this varied between country. In 2015, broadleaf woodland accounted for 74% of wooded area in England, decreasing to 51% in Wales and 26% in Scotland. However, the volume of deadwood was partitioned in broadleaf woodlands as 68% of the English total, 27% in Wales, and 19% in Scotland. The variation in the proportion between live trees and deadwood may be due to management that creates deadwood (Chapter 6). In England and Wales, deadwood in coniferous woodlands was predominantly stumps (36% and ~47.5%), while in Scotland standing deadwood contribute the most volume (~39.5%), which may reflect the high proportion of coniferous woodlands which are managed plantations. Management practices, such as felling and coppicing, can create standing deadwood and stumps, while lying deadwood may be removed for woodfuel (Forest Research, 2021). Management is discussed further in Chapter 6.

Differences in percentage between total deadwood volume and carbon in each country might be due to the use of specific wood densities used for each decay class in the calculation of deadwood carbon. For instance, in 2011 Welsh stumps held ~48% of deadwood volume in stumps, though this only contained 37% of carbon stocks. As density decreases with advancing stages of decay, the amount of carbon calculated also lowers. Therefore, a high volume of deadwood in an advanced stage of decay may still hold less carbon than a lower volume of fresh deadwood.

The availability of accurate data relating to the classification of woodland areas can have a large impact on upscaled values. Upscaling using the area for broadleaf and coniferous woodland provided by the open access NFI data (Figure 7-1) would have discounted ~25% of woodland area (~770,000 hectares in 2019). As such, our total volume calculated for that year would have been an at underestimate at only 65.7 million m^3, with a carbon stock of 8.3 million t. Additionally, no accurate analysis of deadwood in mixed woodlands can be undertaken. While the proportion of mixed woodland appears to remain fairly constant (Figure 7-1), it is not known what proportion of woodland classed as 'other' would consist of mixed woodlands. Areas of mixed woodland are likely to change over time, with monocultures becoming diversified. In the results of Chapter 6, we found that mixed broadleaf and coniferous woodlands held smaller volumes of deadwood and stores of carbon per hectare than non-mixed woodlands, significantly so in coniferous woods. Separating mixed woodlands from non-mixed during upscaling would likely improve the accuracy of estimates and result in lower total amounts of carbon. As of 2015, the UK was one of the least forested countries in Europe, with only 13% of land area being woodland, compared to an average of 38% across Europe (FAO, 2015). However, UK woodland area has been increasing by ~0.5% every five years, and so it can be presumed that future deadwood volumes will be higher, as more woodland is created that can provide inputs. Many coniferous woodlands in the UK are now being converted to mixed woodlands, with broadleaves replacing non-native conifers. In Wales, areas of broadleaf and conifer woodlands were similar in 2015 (51% broadleaf, 49% conifer). Despite this, volumes of deadwood in broadleaf woodlands were ~70.5% lower than in conifer woodlands, with ~56% less carbon held in deadwood (Table 7-6, Table 7-7). This suggests that overall deadwood volumes and carbon stocks will lower as the amount of coniferous woodland decreases. However, it should be noted that there are many factors that will have influenced the amount of deadwood produced, such as topography, climate, occurrence of pest and disease, and woodland management, and so further research would be needed to confirm the effect of woodland diversification on deadwood production. The implementation of guidelines and policy, such as the Habitats Directive (1992) and UK Biodiversity Action Plan, which suggest there are areas where deadwood should be left in situ for species conservation, may further lead to an increase of deadwood volumes, and thus carbon, over time.

The use of specific carbon concentrations in the calculation of deadwood carbon showed minimal impacts on the total carbon stored, with the total amount in GB reducing by ~1.3% when a specific wood density was also used (Table 7-5). The majority of this change came from broadleaf woodlands, where the average specific carbon fraction was 48.8%, compared to 50.5% in coniferous woodlands. Applying this change (-1.3%) to the European total deadwood carbon pool would lead to a decrease of 20.8 million t. For the purpose of reporting national carbon stock inventories, such as for the Kyoto protocol, using a standard carbon concentration will be sufficient, though specific wood density values should be used where possible. These calculations may be further improved by the partitioning of deadwood into standing and lying deadwood. In the study by Martin *et al*. (2021) standing deadwood was found to have a higher carbon fraction than lying deadwood, though not significantly so. Our results were calculated assuming both standing and lying deadwood had the same carbon concentrations, specific to decay class. Including further classification by type of deadwood would likely change the overall totals calculated, with standing deadwood holding more carbon. However, at present, there are few studies that have calculated carbon concentrations in the deadwood species present in the UK NFI so evidence for this is lacking. The use of specific concentrations by decay class is also likely to change results over time, as wood moves into higher decay stages and fresh deadwood is produced.

7.7 Conclusion

We calculated a total GB deadwood volume of 87.6 million m^3 in 2019, holding a total carbon stock of 11.04 million t when specific wood densities and the standard carbon concentration of 50% were used. This was a large decrease (72%) from the carbon stock reported in the UK national statistics (Forest Research, 2019) and may be in part due to the use of specific wood densities which significantly reduced carbon estimates by 44% compared to using a standard value. Changes in carbon concentration did not significantly affect overall carbon stocks. Future reports would benefit from using specific wood densities in calculations of deadwood carbon stocks. Deadwood volumes may decrease with increasing woodland diversification and reports would benefit from including measures of deadwood in mixed woodlands.

8 General discussion and summary

The overall aim of this thesis was to improve our understanding of the contribution of deadwood to the forest carbon pool and cycles. The objectives, as set out in Chapter 1, were addressed in a series of review or primary research papers that make up Chapters 2 and 4-7 of this thesis. In this summary Chapter, the key findings presented in these Chapters will be further discussed, to highlight the key findings and messages, and links between the separate pieces of research, and address the implications and needs for further research. We set the site-based studies carried out in field and lab within the context of our findings from national data sets and analysis, considering issues of scale.

8.1 Aim 1: to evaluate the role of deadwood in the forest carbon cycle in terms of its direct contribution to overall stocks and indirect contribution to below ground soil carbon storage

It is increasingly being acknowledged that deadwood forms a significant carbon pool in forest ecosystems, though accurate reporting of the size of these stocks and the factors that influence them are limited. Globally, deadwood is estimated to contribute 8% (73 Pg) of the world's forest carbon pool (861 Pg) (Pan *et al.*, 2011). According to the latest UK Forestry Statistics report (Forest Research, 2021), which is used for reporting to international organisations such as the Food and Agriculture Organisation of the United Nations (FAO), UK woodlands are thought to hold 1.095 Pg of carbon (0.13% of the global pool), with 0.04 Pg of carbon held in deadwood (3.7% of the UK total). In order to accurately calculate the carbon stocks held in deadwood, it is first necessary to assess the overall volumes and then estimate carbon stocks (Chapters 4, 6 and 7).

Deadwood volumes in Great Britain (GB) were calculated by the National Forest Inventory, which reports an average volume of 29 m^3 ha^{-1} and median of 9 m^3 ha^{-1}, though stumps are excluded from this (Forestry Commission, 2020). The calculations used by the UK to assess overall deadwood carbon stocks assume a uniform density (0.45 g cm^{-3}) and carbon concentration (50%) between all types of deadwood and stages of decay, which may lead to inaccuracies in calculated stocks. We aimed to improve the estimates of GB deadwood volumes and carbon stocks, through the use of more specific calculations to estimate the carbon densities per unit area (Chapter 6) and upscaled estimates for countries within GB (Chapter 7). We determined that across GB, an average volume of 26.4 m^3 ha^{-1} deadwood was found with a median of 10.1 m^3 ha^{-1}, which contained an average carbon stock of 3.3 t ha^{-1} and median of 1.3 t ha^{-1}. The average mass of deadwood was found to be 6.59 t ha^{-1}, far lower (-74%) than 25 t ha^{-1} reported by the FAO (2020c) since the 1990s. However, the volumes we report were within a similar range to the NFI ecological condition report (Forestry Commission, 2020), which measured an average deadwood volume of 29 m^3 ha^{-1} across GB, suggesting inaccuracy with the figures reported to the FAO. Volumes and carbon stocks of deadwood vastly differed in our analysis depending on the type of deadwood (standing, lying or stumps), woodland type (broadleaf, conifer, mixed broadleaf or mixed conifer) and also by country, indicating a climatic and topographic influence (Chapter 6.4.1) which can affect forest productivity.

When upscaled by the total woodland area for GB (Chapter 7), we found that this produced an overall volume of 86.7-87.6 million m^3 between 2011-2019 with a carbon stock of 0.02 Pg (when using a standard wood density of 0.45 g cm^{-3}, and carbon concentration of 50%). This led to a decrease of ~50% the total deadwood carbon pool compared to official reports and suggests that deadwood only contributes 1.8% of UK total woodland carbon. However, the proportion of these values varied depending on woodland type and deadwood type, and overall stocks depended on the wood density and carbon concentration used during carbon calculations, suggesting that using the standard, simplified calculation may lead to overestimates. Changes in carbon concentration alone did not lead to significant changes in the overall carbon stock calculated (~3% difference overall), while changes in wood density, by species division and decay stage, increased estimates by 83-92% in coniferous woodlands and 53-78% in broadleaf woodlands. The use of standard calculations for determination of deadwood carbon stocks is perhaps necessary in countries where national forest inventories do not include detailed data such as decay class by species division e.g. China and Cyprus (Tomppo *et al.*, 2010). However, where this data is available, estimates would greatly benefit from using specific wood density values, applied on a species division level, due to the large difference in total carbon stocks we reported.

Calculation of total deadwood carbon stocks relies on accurate assessments of woodland area. While these were available in GB for broadleaf and conifer woodlands, no up-to-date, accurate measures were available for mixed woodlands. To meet the UK Forestry Standard, it is expected that a single species should not cover more than 75% of a woodland (Forestry Commission, 2017), and with efforts to increase diversification it is likely that the proportion of mixed woodland will increase over time. The proportion of deadwood volume and carbon stocks held in mixed woodland was found to significantly differ from ‘pure’ woodlands and is worthy of inclusion in reports. Thus, efforts to increase the accuracy of woodland area reports are necessary.

Deadwood not only contributes to woodland carbon cycles as a carbon pool, it also releases carbon during decomposition in the forms of dissolved organic carbon (DOC), CO_2 and CH_4, as well as releasing other nutrients (Hafner, Groffman and Mitchell, 2005; Bantle, Borken and Matzner, 2014; Morris *et al.*, 2015), or may be incorporated into the soil as soil organic matter (Zhou *et al.*, 2007).

In Chapter 4, we identified the amount of DOC released by deadwood in comparison to other forest floor materials and determined that per unit mass of material, deadwood produced as much DOC as leaf litter, which was significantly more than vegetation, and the F layer and Ah Horizon of soil (Chapter 4.2.2.3). However, at a larger scale, as the amounts of DOC produced were dependent on the mass of deadwood present, deadwood produced a significantly lower amount of DOC per m^2 than other forest floor materials. The average mass of deadwood found in the specific sites used in Chapter 4 ranged between 1 t ha^{-1} - 4.89 t ha^{-1}, which was lower than the overall average mass of deadwood (6.58 t ha^{-1}) found in GB through analysis of the NFI (Chapter 6). Therefore, it is probable that across GB, the flux of deadwood derived DOC is proportionate to the pool size and therefore larger than the calculated fluxes from the single site studied in Chapter 4.2.2.3. However, it is still unlikely that these fluxes will be as large as those from leaf litter, the F layer and Ah horizon, where masses ranged between 18.2 – 188 t ha^{-1}. To test this, larger and more replicated studies across GB would help to clarify average DOC fluxes from deadwood, leaf litter and different soils to aid comparison with our values. In a long-term study at the site, it was established that consistently larger amounts of DOC were present in shallow soils at the unmanaged plot compared to the managed plot, by ~2.4 times. It was established that the difference in DOC was probably due to management, whereby the managed site underwent thinning and scrub removal during the monitoring period. Thinning reduces litterfall (Henneron 2018) and has been linked to a decrease in deadwood volumes and carbon stocks (Ruiz-Peinado *et al.*, 2016).

The mass and type of material present on the forest floor influences soil formation (Strand *et al.*, 2016) and in turn soil carbon and DOC fluxes (de Vos *et al.*, 2015). In our results from Chapter 5 (Shannon *et al.*, 2021), it was found that soils under deadwood in a coniferous woodland held significantly more DOC than soils under deadwood in a broadleaf woodland (Shannon *et al.*, 2021), which may have been partially due to the marginally higher carbon concentration found in conifer than broadleaf deadwood (IPCC, 2006; Thomas and Martin, 2012; Ma *et al.*, 2017). However, it is likely that this result was confounded by the high organic content in the soils, and specifically the forest floors, sampled at the conifer woodland compared with the broadleaf woodland. The broadleaf woodland selected for this study (Shannon *et al.*, 2021) overlay a mineral soil, whereby it was detected that larger amounts of DOC were present underneath deadwood than in neighbouring control samples with no deadwood. In organic soil horizons, it has been found that microbial activity is the primary factor controlling DOC cycling, whereas in mineral soils, DOC cycling is controlled by adsorption to minerals and soil surfaces (Kalbitz *et al.*, 2000).

Further research should be carried out to clarify the difference in DOC release from broadleaf and conifer deadwood, to ascertain whether the high organic content found in the coniferous woodland masked a 'deadwood effect' that increased soil DOC.

8.2 Aim 2: how are deadwood volumes and carbon stocks influenced by woodland management?

Woodland management practices vary depending on the overall purpose of a woodland, for example woodlands may be managed as commercial plantations or nature reserves, and these are governed by different policies and guidance documents. In Chapter 2, we reviewed the various policies and guidance documents that included deadwood, to identify key recommendations regarding deadwood management over five key forest ecosystem services: biodiversity; carbon sequestration, emissions and climate change; flood management; forest health management, and fuel and fibre production. It was apparent that although many different policies and guidance documents exist (Chapter 2.4.1), very few covered more than one theme. At a global level, this was most evident, with policy focusing on only one or two key areas, e.g. the Programme for the Endorsement of Forest Certification (PEFC) Sustainability Benchmarks (PEFC Council, 2018) included information on deadwood management for biodiversity and forest health management. Recommendations for biodiversity and flood management encouraged the retention or increase of deadwood, while forest health management and fuel and fibre production recommended both retention and removal, depending on the site conditions. There are also instances where specific guidance documents can recommend both the retention and removal of deadwood, such as a guide on stump harvesting (Forest Research, 2009b) or the UK Woodland Assurance Scheme (UKWAS

Support Unit, 2016). This can lead to confusion for woodland managers where there are conflicting priorities.

Policy regarding biodiversity often stipulates that a deadwood volume of >20 m^3 ha^{-1} with non-uniform dispersal is required to provide adequate habitat for reliant species (The RSPB Conservation Management Advice, no date; Humphrey and Bailey, 2012; UKWAS Support Unit, 2016). There are few policies that advocate for deadwood removal, except for use as woodfuel or in instances where it is unsafe to workers or the public or posed a threat to woodland health (Forest Research, 2009b; FAO, 2011). In our analysis of deadwood volumes under different management practices (Chapter 2.8, 4.4.2.1, 6.4.3) it was evident that management can have a large effect on the amounts and type of deadwood present in a woodland. Management activities such as thinning often reduce the amounts of deadwood found (Ruiz-Peinado *et al.*, 2016; Krueger, Schulz and Borken, 2017), and volumes can increase over time following the cessation of management (Böhl and Brändli, 2007).

In our study in Chapter 4 (Hollands *et al.*, 2022), it was found that in a woodland unmanaged for 23 years ~5 times the amount of deadwood was present in comparison to a neighbouring site which underwent thinning and the removal of harvested material. However, in our analysis of the UK NFI data, sites with different management practices that were expected to create or remove deadwood were found to have comparable volumes to woodlands that were not managed (Chapter 6.4.3). This may be due to the majority of sites sampled being managed in ways that could create deadwood (e.g. brashing, coppicing, thinning), rather than removal (e.g. de-stumping, brash removal, scarification), and the timings of site visits whereby it is possible assessments were carried out before the intended removal of deadwood. The average volume of stumps was ~2.4 times larger where management that involved deadwood (both by creation and removal) occurred compared to unmanaged woodlands, likely due to practices such as coppicing and clearfelling. When all deadwood types were summed to produce a total pool, it was found that unmanaged woodlands held a smaller volume of deadwood than those which had undergone management that involved deadwood creation and removal. In these cases, woodlands managed for deadwood had a total volume of 30 m^3 ha^{-1} in broadleaf woodlands and 47 m^3 ha^{-1} in coniferous woodlands, far larger than the 20 m^3 ha^{-1} threshold recommended for biodiversity conservation (The RSPB Conservation Management Advice, no date; Humphrey and Bailey, 2012). It may therefore be presumed that management may be used as a way of increasing the overall volumes of deadwood, provided it is left *in situ*, and thus enhance biodiversity in woodlands. Presence of deadwood may also contribute a source of nutrient and carbon input into the soil (Hafner, Groffman and Mitchell, 2005), a benefit to nutrient-poor soils in managed woodlands.

Management that affects deadwood will therefore affect deadwood carbon stocks, with woodlands that have greater volumes of deadwood holding larger carbon stocks (Hollands et al., 2022; Krueger, Schulz and Borken, 2017).

8.3 Aim 3: understand how factors like tree species, cause of tree death, and management practices affect deadwood volumes and carbon stocks

Deadwood is included as an optional report for carbon inventories such as the Global Forest Resource Assessment (FAO, 2020b) and IPCC guidelines also recommend deadwood as a carbon pool to report (IPCC, 2006). For reporting purposes, in the UK it is generally assumed that all deadwood is uniform, with the same wood density and carbon concentration across all deadwood types and stages of decay (Forestry Commission, 2020). However, it is well established that the carbon content of broadleaf and conifer species differs slightly (IPCC, 2006; Thomas and Martin, 2012; Ma *et al.*, 2017), with carbon concentration measuring ~51% in conifers and ~48% in broadleaves. It has also been found that carbon concentration increases with advancing stage of wood decay (Martin *et al.*, 2021), while wood density decreases substantially (Paletto and Tosi, 2010; Harmon, Woodall and Sexton, 2011; Vanguelova, Moffat and Morison, 2016; Moreira, Gregoire and do Couto, 2019; Stakėnas *et al.*, 2020). Wood density also varies by tree species, with gymnosperms generally having a lower density than angiosperms (Harmon *et al.*, 1986; Meerts, 2002). Using values specific to the species and decay class of the deadwood being assessed may lead to significant differences in the carbon stocks of deadwood being reported. In a study of deadwood in tropical forests, it was found that using a specific carbon concentration during calculations led to a ~3 Pg difference in overall stocks compared to using the standard 50% (Martin *et al.*, 2021).

Stand age may potentially impact deadwood volumes, with older trees achieving a larger size before dying, and thus creating a larger volume of deadwood (Duvall and Grigal, 1999) and potentially holding more carbon. Volumes of deadwood, and subsequently carbon stocks, may also be impacted by cause of tree death. For instance, vertebrates such as the grey squirrel find certain tree species like beech more palatable (Mayle and Broome, 2013) and thus greater amounts of ring barking are seen in these species (Peden, 2020), potentially leading to tree death. However, stand age (differing between 24-84 years in broadleaves and 12-74 years in conifers) did not significantly affect the amount of DOC found under deadwood at either of the sites sampled for Chapter 5 (Shannon *et al.*, 2021), suggesting that factors other than tree age, such as tree species or underlying soil type, may have a larger influence on the amounts of DOC released or measured from deadwood during decomposition.

In the analysis of the NFI dataset in Chapter 6 it was found that conifer woodlands held significantly larger deadwood volumes and carbon stocks than broadleaf woodlands. Similarly, mixed conifer woodlands, where conifer species accounted for >50% of the area covered by trees, held significantly greater volumes of deadwood, and carbon stocks, than mixed broadleaf woodlands. It is possible that this larger volume found in woodlands dominated by conifer species is due to the presence of management, particularly where practices that created stumps were carried out, as discussed in Chapter 8.2. We found that ~32% of broadleaf sites showed no sign of management in comparison to ~18% of conifer sites. The proportion of coniferous to broadleaf woodlands is likely to change over time, with more native broadleaf species being planted, leading to an increase in broadleaf woodland cover by 4-6% between 2011 (Forestry Commission, 2011) to 2019 (Forest Research, 2019). This may lead to changes in deadwood volumes, potentially with the amount of deadwood decreasing due to the increase in broadleaf species, as seen in Chapter 7.5.2 between 2011 and 2015, where changes in woodland area occurred. However, this would require monitoring and could be carried out through the use of 2nd and 3rd cycle NFIs.

8.4 Implications and further research

8.4.1 Guidance on reporting national deadwood statistics

In Chapter 6 we assessed the contribution of deadwood to the total forest carbon pool of Great Britain, using data from the National Forest Inventory. Across GB, we found an average 26.4 m^3 ha^{-1} of deadwood, holding 3.3 t carbon ha^{-1}, and have also included analysis on the amounts contributed by different decay classes, woodland types, management practices and cause of tree death. At present, very few studies have included these factors, and GB measures of deadwood are based on a simplistic calculation of deadwood volume and carbon stocks. The results from Chapter 6 will be of use to reporting bodies, and woodland managers who want to include a deadwood component in woodland carbon reports. The inclusion of these different factors will help others to assess the various factors that influence deadwood. In Chapter 7 we addressed the various issues surrounding upscaling of deadwood volumes and carbon stocks from a plot level to national totals. The issues we found (particularly regarding measures of mixed woodland area) should be addressed by future analysis, as this would help to increase the accuracy of reported results. We found that volumes of deadwood and carbon stocks differed between mixed woodlands and those classified as either broadleaf or conifer and so the inclusion of mixed woodland in upscaled totals would be a valuable addition.

Wood density values had a strong effect on the overall carbon stocks calculated in deadwood (Chapter 7.5.1), proving to significantly decrease the overall stocks by 77% when compared to using a standard density of 0.45 g cm^{-3}. However, the 'specific' values used are based on a relatively small subset of tree species (Vanguelova, Moffat and Morison, 2016) from GB. Further work to identify wood density from a wider range of species which are included in GB NFIs would be beneficial, and assessment of whether this can be applied on a species level rather than species division should be made. At present, it is unknown whether species specific wood densities would change the overall carbon stocks measured in deadwood. The use of specific wood density values in the calculation of deadwood carbon stocks is recommended for future reports as it significantly changes the carbon stocks reported.

8.4.2 Understanding the role of DOC released from deadwood in long-term soil carbon stabilisation

In Chapter 5 (Shannon *et al.*, 2021) we had hypothesised that the additional inputs of DOC into surface soils could create a priming effect on soil microbes (Peršoh and Borken, 2017; Minnich *et al.*, 2021), whereby the increased availability of labile carbon would stimulate microbial activity (Fontaine, Mariotti and Abbadie, 2003; Beverly and Franklin, 2015), and thus decomposition of stored carbon. We discovered that although the presence of deadwood significantly increased concentrations of soil DOC in mineral soils (Chapter 5.4.2), there was no evidence of increased rates of decomposition, either through use of the Tea Bag Index (TBI(Keuskamp *et al.*, 2013) (Chapter 5.4.3) or extracellular enzyme activity (Chapter 5.4.4).

There are many biotic and abiotic factors which are thought to regulate microbial priming of soils such as the amount of soil organic carbon present (Bastida *et al.*, 2019), the chemical structure of 'labile' inputs (Di Lonardo *et al.*, 2017), soil acidity, soil nitrogen availability (Chen *et al.*, 2014), and protection of soil organic matter by aggregates and minerals (Chen *et al.*, 2019). Instead of having a priming effect, results indicate that leaching of DOC from deadwood could be a source of carbon to mineral soils, contributing to a more stable mineral associated carbon pool. Further research is needed to explore this in greater detail.

However, given that it was not possible to unequivocally determine the source (deadwood and/or SOM) of the DOC in the deadwood-influenced mineral soils via the optical and fluorescence-based techniques employed (Shannon *et al.*, 2021), further research could investigate the potential of stable isotopic techniques for source apportionment of DOC and also the CO_2 ultimately respired to quantify the magnitude of any priming. Further research could also assess whether the lack of a priming effect was caused by the unavailability of soil DOC to soil microbes. This may be due to the DOC being either recalcitrant (not labile) or strongly-mineral associated, and thus unavailable to soil microbes. Such research may be conducted using methods such as fractionation (Plaza *et al.*, 2012), or by batch studies whereby a microbial inoculum is added to extracted deadwood and changes in DOC and CO_2 are monitored.

8.5 Conclusions

There are many factors which influence the volumes of deadwood found, and subsequently the carbon stocks held and released from deadwood. Woodland management has been found to lower deadwood volumes, though in the National Forest Inventory some management practices were instead found to create large volumes. Management that creates deadwood could be utilised as a method of increasing deadwood volumes nationally, which would be beneficial to biodiversity as well as providing a nutrient source to soils. While the total volumes of deadwood we report are in accordance with others (Forestry Commission, 2020), carbon stocks are vastly lower than those reported to the FAO (2020c). This is likely due to different wood density values used during the calculation of carbon stocks, implying that accurate reports require the use of specific wood density values by species division and decay stage. Use of a standard carbon concentration in the calculation of carbon stocks is unlikely to significantly affect overall carbon stocks. It is possible that deadwood provides a significant source of DOC into underlying soil, though further work is needed to identify whether this is occurring in woodlands on organic soils as well as those over mineral soils. The fate of the DOC released by deadwood is currently unknown as there is no evidence that it causes a priming effect on soil microbes, and further study is required to ascertain whether deadwood derived DOC is strongly minerally-associated, or recalcitrant.

9 References

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10 Appendices

10.1 Chapter 5 appendix

This supplementary information contains:

- Supplementary Table 10-1 – Means of S (stabilisation factor) and k (decomposition rate) derived through the Tea Bag Index (TBI) for soils under deadwood and under leaf litter only, split by forest and stand age.
- Supplementary Table 10-2 – Numbers of negative k values produced by the TBI, under deadwood or under leaf litter only, per each stand age group at each site.
- Supplementary discussion of Tea Bag Index parameters
- Supplementary Table 10-3- Enzyme activity rates for surface soil samples from Alice Holt and Kielder Forests, grouped by stand age and presence or absence of deadwood.
- Supplementary discussion of enzyme activity rates

Table 10-1 – Means of S (stabilisation factor) and k (decomposition rate, d^{-1}) derived through the Tea Bag Index (TBI) for soils under deadwood and under leaf litter only, split by forest and stand age. Numbers in parentheses = n.

		Alice Holt Forest (oak)				**Kielder Forest (spruce)**			
		Young	**Mid**	**Old**	**Mean**	**Young**	**Mid**	**Old**	**Mean**
S	Leaf litter	0.19 ± 0.02 (14)	0.21 ± 0.02 (12)	0.21 ± 0.02 (13)	**0.21 ± 0.01 (40)**	0.39 ± 0.05 (15)	0.27 ± 0.02 (14)	0.50 ± 0.06 (15)	**0.39 ± 0.03 (44)**
	Deadwood	0.20 ± 0.02 (13)	0.19 ± 0.02 (13)	0.24 ± 0.01 (14)	**0.21 ± 0.01 (39)**	0.33 ± 0.04 (14)	0.29 ± 0.03 (14)	0.45 ± 0.06 (15)	**0.36 ± 0.03 (43)**
	Mean	**0.20 ± 0.02 (27) ^{D}**	**0.20 ± 0.01 (25)^{CD}**	**0.22 ± 0.01 (27)^{CD}**	**0.21 ± 0.01 (79)^{a}**	**0.36 ± 0.03 (29)^{AB}**	**0.28 ± 0.02 (28)^{BC}**	**0.47 ± 0.04 (30)^{A}**	**0.37 ± 0.02 (87)^{b}**
k	Leaf litter	0.004 ± 0.001 (11)	0.005 ± 0.001 (13)	0.004 ± 0.001 (12)	**0.004 ± 0.000 (36)**	0.006 ± 0.002 (11)	0.005 ± 0.001 (13)	0.012 ± 0.003 (10)	**0.008 ± 0.001 (34)**
	Deadwood	0.005 ± 0.001 (14)	0.006 ± 0.000 (14)	0.005 ± 0.001 (11)	**0.005 ± 0.000 (39)**	0.008 ± 0.003 (8)	0.005 ± 0.001 (13)	0.007 ± 0.001 (10)	**0.006 ± 0.001 (31)**
	Mean	**0.004 ± 0.000 (25)^{AB}**	**0.006 ± 0.000 (27)^{AB}**	**0.004 ± 0.001 (23)^{B}**	**0.005 ± 0.000 (75)**	**0.007 ± 0.02 (19)^{AB}**	**0.005 ± 0.001 (26)^{AB}**	**0.009 ± 0.002 (20)^{A}**	**0.007 ± 0.001 (65)**

Table 10-2 – Numbers of negative k values produced by the TBI, under deadwood or under leaf litter only, per each stand age group at each site. The numbers in subscript indicate the order of resulting k rates of decomposition, descending from 1 as the highest.

	Plot age		
	Young	**Mid**	**Old**
Kielder deadwood	5_{2}	1_{9}	4_{3}
Kielder leaf litter	3_{5}	2_{6}	4_{1}
Alice Holt deadwood	0_{10}	1_{4}	3_{8}
Alice Holt leaf litter	2_{11}	1_{7}	0_{12}

Supplementary discussion of Tea Bag Index parameters

A large proportion of our tea bags had to be discounted due to negative k values or holes in the tea bags (Supplementary Table 2). The negative k values may have occurred due to the incubation period being too long or decomposition occurring too quickly. This was particularly noticeable at Kielder, whereby 19 of these negative values occurred. It was apparent that the plots with the greatest k value produced the most negative values. It may be that a shorter incubation time is required in organic soils in order to avoid this in future studies. Whilst we might have expected k to have been lower at Kielder given colder soil temperatures (Supplementary Table 1), it is possible that differences in other environmental (e.g. soil moisture controls on diffusion/aeration) and biological (e.g. enzymatic potential) variables between sites acted to moderate the temperature effects. The higher S factor at Kielder may also be a function of the same environmental and biological conditions that favoured the decomposition rate with concomitant promotion of transformations of labile litter material into novel recalcitrant substances (Prescott. 2010).

Table 10-3 - Enzyme activity rates for surface soil samples from Alice Holt and Kielder Forests, grouped by stand age and presence or absence of deadwood. Site significantly influenced the activity rates of all enzymes (p<0.001), as shown by lowercase superscript. Significant three way interaction was found for β-glucosidase (p=0.011). Numbers in parenthesis = n. Tukey post-hoc grouping letters are shown in capitals for significant interactions.

		Enzyme activity (nmol h^{-1} g^{-1} dry soil)							
		Alice Holt Forest (oak)				**Kielder Forest (spruce)**			
Enzyme		**Young**	**Mid**	**Old**	**Mean**	**Young**	**Mid**	**Old**	**Mean**
β-D-cellubiosidase	Deadwood	22.8 ± 4.66 (10)	45.3 ± 23.3 (12)	29.0 ± 8.85 (14)	**32.7 ± 8.50 (36)**	100.3 ± 31.2 (15)	163.9 ± 41.9 (15)	122.7 ± 42.9 (15)	**129 ± 22.4 (45)**
	Leaf litter	43.6 ± 10.0 (14)	48.8 ± 10.4 (14)	40.6 ± 15.8 (13)	**44.4 ± 6.88 (41)**	52.1 ± 13.6 (15)	207.4 ± 47.5 (14)	121.9 ± 39.5 (15)	**125.3 ± 22.4 (44)**
	Mean	**34.9 ± 6.43 (24)^{BCD}**	**47.2 ± 11.9 (26)^{CD}**	**34.6 ± 8.79 (27)^{D}**	**39.0 ± 5.41 (77)^{a}**	**76.2 ± 17.3 (30)^{BC}**	**184.9 ± 31.2 (29)^{A}**	**122.3 ± 28.7 (30)^{AB}**	**127.2 ± 15.8 (89)^{b}**
β-xylosidase	Deadwood	25.1 ± 4.34 (14)	54.8 ± 17.2 (13)	40.3 ± 16.4 (13)	**39.69 ± 7.90 (40)**	81.2 ± 12.7 (15)	159.6 ± 25.8 (15)	142.3 ± 34.8 (15)	**127.7 ± 15.5 (45)**
	Leaf litter	58.8 ± 22.8 (14)	61.1 ± 18.7 (14)	35.6 ± 9.89 (12)	**52.6 ± 10.6 (40)**	77.8 ± 13.9 (15)	159 ± 27.3 (15)	101.2 ± 6.68 (15)	**112.7 ± 11.4 (45)**
	Mean	**41.9 ± 11.8 (28)**	**58.1 ± 12.5 (27)**	**38.0 ± 9.57 (25)**	**46.2 ± 6.62 (80)^{a}**	**79.5 ± 9.24 (30)**	**159.3 ± 18.4 (30)**	**121.7 ± 17.8 (30)**	**120.2 ± 9.63 (90)^{b}**
β-glucosidase	Deadwood	53.0 ± 8.94 (15)^{C}	119.9 ± 27.0 (15)^{C}	112.5 ± 23.8 (14)^{BC}	**94.7 ± 12.8 (44)**	665 ± 164 (15)^{A}	1056 ± 189 (15)^{A}	503 ± 124 (15)^{AB}	**741.7 ± 97.5 (45)**

	Leaf litter	96.6 ± 22.3 (14)^{C}	99.1 ± 20.6 (15)^{C}	86.6 ± 41.1 (14)^{C}	**94.2 ± 16.4 (43)**	445 ± 96.3 (15)^{AB}	1140 ± 186 (15)^{A}	576 ± 143 (15)^{A}	**720.6 ± 94.3 (45)**
	Mean	**74.0 ± 12.2 (29)**	**109.5 ± 16.8 (30)**	**99.5 ± 23.4 (28)**	**94.5 ± 10.3 (87)^{a}**	**555.2 ± 95.8 (30)**	**1098 ± 131 (30)**	**539.8 ± 93.1 (30)**	**731.1 ± 67.5 (90)^{b}**
Phosphatase	Deadwood	188.4 ± 45.2 (15)	339 ± 114 (15)	201.0 ± 39.5 (15)	**242.7 ± 43.3 (45)**	1067 ± 155 (15)	1673 ± 288 (15)	1724 ± 299 (15)	**1488 ± 151 (45)**
	Leaf litter	188.2 ± 31.5 (15)	360.3 ± 94.4 (15)	96.6 ± 23.1 (15)	**215 ± 37.1 (45)**	947 ± 169 (15)	1343 ± 237 (15)	1488 ± 236 (15)	**1259 ± 127 (45)**
	Mean	**188.3 ± 27.1 (30)^{A}**	**349.6 ± 72.9 (30)^{A}**	**148.8 ± 24.5 (30)^{A}**	**228.9 ± 28.4 (90)^{a}**	**1007 ± 114 (30)^{B}**	**1508 ± 186 (30)^{B}**	**1606 ± 188 (30)^{B}**	**1374 ± 98.9 (90)^{b}**
Leucine aminopeptidase	Deadwood	6.72 ± 2.18 (15)	4.71 ± 0.89 (15)	4.88 ± 1.07 (14)	**5.45 ± 0.86 (44)**	72 ± 9.01 (15)	49.1 ± 6.14 (15)	77.4 ± 5.28 (15)	**66.2 ± 4.35 (45)**
	Leaf litter	3.97 ± 0.83 (15)	4.63 ± 0.74 (15)	4.80 ± 0.99 (15)	**4.47 ± 0.49 (45)**	76.6 ± 9.48 (15)	70.3 ± 5.74 (15)	70.3 ± 8.02 (15)	**72.4 ± 4.48 (45)**
	Mean	**5.35 ± 1.17 (30)**	**4.67 ± 0.57 (30)**	**4.84 ± 0.71 (29)**	**4.95 ± 0.49 (89)^{a}**	**74.3 ± 6.44 (30)**	**59.7 ± 4.57 (30)**	**73.8 ± 4.76 (30)**	**69.3 ± 3.12 (90)^{b}**
Phenol oxidase	Deadwood	2204 ± 395 (15)	2963 ± 663 (15)	2164 ± 332 (14)	**2450 ± 283 (44)**	6112 ± 905 (14)	5219 ± 1167 (13)	5240 ± 1244 (14)	**5531 ± 630 (41)**
	Leaf litter	2342 ± 520 (14)	2381 ± 563 (15)	2738 ± 1042 (14)	**2484 ± 417 (43)**	7062 ± 1276 (14)	6007 ± 1073 (15)	5710 ± 1050 (13)	**6267 ± 648 (42)**
	Mean	**2271 ± 318 (29)**	**2672 ± 431 (30)**	**2451 ± 540 (28)**	**2467 ± 250 (87)^{a}**	**6587 ± 773 (28)**	**5641 ± 779 (28)**	**5466 ± 805 (27)**	**5903 ± 451 (83)^{b}**

Supplementary discussion of enzyme activity rates

Fluorometric and colorimetric enzyme assays can be used to measure the potential for depolymerization of macromolecular SOM and subsequent production of WEOC, though it should be noted that assays do not measure actual *in situ* rates (Wallenstein and Weintraub, 2008) but instead quantify the potential of the soil, at a given time point, to perform an enzyme-catalysed reaction. Soil enzyme activity can be regulated by environmental factors such as nitrogen availability (Fatemi *et al.*, 2016), soil pH (Cenini *et al.*, 2016), soil moisture (Baldrian, 2014) and SOM concentration (Sinsabaugh *et al.*, 2008; Trasar-Cepeda, Leirós and Gil-Sotres, 2008; Štursová and Baldrian, 2011). The potentials measured may reflect the activities of enzymes recently secreted and associated with viable cells at the time of sampling and/or produced in the past and stabilized through associations with the soil matrix (Nannipieri, Trasar-Cepeda and Dick, 2017). In forested settings, additions of nitrogen have been found to both supress hydrolytic enzyme activity (Fatemi et al. 2016) and stimulate it (Sinsabaugh *et al.*, 2005; Gress *et al.*, 2007), implying other factors play a role in activity regulation. In the study by Ullah *et al*. (2019) carbon cycling enzymes, such as β-D-cellubiosidase, β-glucosidase and β-xylosidase, were found to have a positive relationship with the SOC content of soils. This in turn may influence nitrogen cycling enzymes, such as leucine aminopeptidase, which have been found to be influenced by the activity of carbon cycling enzymes. Similar results have also been found in other studies, whereby increases in SOM lead to increased rates of enzyme activity (Sinsabaugh et al. 2008; Štursová and Baldrian 2011). These regulatory factors are likely to have had an impact on the enzyme potential seen in soils from Alice Holt and Kielder, whereby Kielder, with higher SOM% had greater enzyme activity rates.

Age of forest stands was found to affect the activity of the enzymes involved in carbon cycling: β-D-cellubiosidase, β-glucosidase and β-xylosidase. Mid aged stands showed higher rates of activity than both the young and old stands. This was unexpected as late stage decay is known to host a greater fungal biomass (Baldrian *et al.*, 2016) which could be expected to produce a greater output of extracellular enzymes, particularly oxidases (Wu, Cheng and Han, 2019). Decomposition by β-glucosidase is believed to peak in late stages of decay (Rinkes *et al.*, 2013), whilst β-xylosidase occurs during the final stages of hemi-cellulose decomposition. As such, it is surprising that activity rates for both of these enzymes are peaking in the mid-aged stands at both forests. Previous research has found that soil texture, bulk density of the top 20 cm, and soil pH were similar between all chronosequence plots (Ražauskaitė, 2019). We hypothesise that in young stands, C is incorporated into mineral-associated fractions and microaggregates (Ma *et al.*, 2014) and is inaccessible for use by microbes and fungi that are associated with wood decay. However, this would require further testing that was beyond the scope of this experiment. In the mid-aged stands, enough decomposition has occurred that C is available for use and so enzyme activity increases. Additionally, % SOM was found to be lower in young than mid or old aged stands, which may be a cause of the trends in enzyme activity. Thinning activities are also carried out at both Alice Holt Forest and Kielder Forest, usually in ages of stands that correspond to our mid age chronosequences. Thinning can alter the microclimate, decreasing water interception, and also provides a fresh supply of brash to the forest floor. Light thinning has been found to increase the activity of β-glucosidase whilst decreasing phenol oxidase activity (Wu et al. 2019), and this thinning effect may be reflected in our enzyme results.

10.2 Chapter 6 appendix

Table 10-4 – wood density values split by decay class, deadwood type and species division, adapted from Vanguelova et al (2016). LD – lying deadwood, SD – standing deadwood.

	Wood density (g cm^{-3})		
Decay class	**Conifer**	**Broadleaf**	**Mixed**
LD 1, SD 3	0.390	0.500	0.445
LD 2, SD 4	0.250	0.320	0.285
LD 3, SD 5	0.191	0.250	0.221
LD 4, SD 6	0.156	0.200	0.178
LD 5, SD 7	0.137	0.180	0.158
Stumps	0.191	0.250	0.221

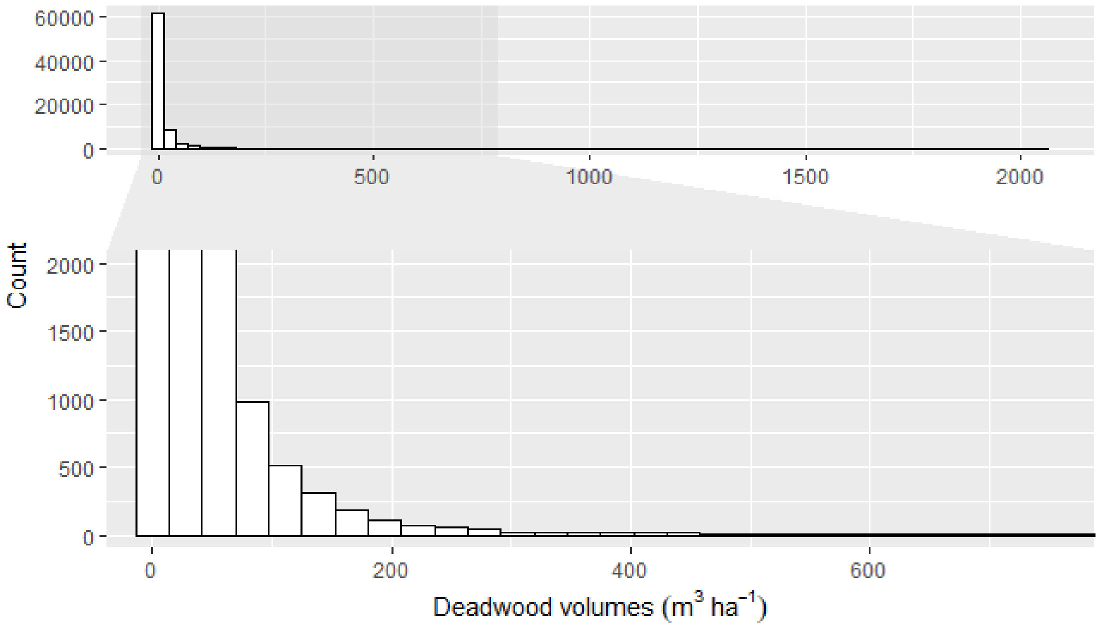

Figure 10-1 – Histogram of deadwood volumes (m^3 ha^{-1}) per sample square. Subsequently, values over 250 m^3 ha^{-1} were removed from analysis.

Table 10-5 - mean volumes (m^3 ha^{-1}) and carbon (t ha^{-1}) in each deadwood type, split by decay stage and woodland type. Totals (Tot) for lying and standing deadwood are presented as the sum of decay classes per each deadwood type. BL – broadleaf, CON – conifer, MB – mixed broadleaf, MC – mixed conifer

Woodland type	Deadwood type		Volume (m^3 ha^{-1})				C stock (t ha^{-1})			
			England	Scotland	Wales	GB	England	Scotland	Wales	GB
BL	Lying	1	0.59 ± 0.11 n=1504	0.12 ± 0.06 n=340	1.72 ± 0.68 n=222	0.63 ± 0.11 n=2066	0.15 ± 0.03	0.03 ± 0.01	0.42 ± 0.16	0.16 ± 0.03
		2	1.82 ± 0.22	1.29 ± 0.36	1.71 ± 0.62	1.72 ± 0.19	0.29 ± 0.04	0.21 ± 0.06	0.27 ± 0.10	0.27 ± 0.03
		3	3.90 ± 0.32	3.31 ± 0.85	3.06 ± 0.66	3.71 ± 0.28	0.48 ± 0.04	0.41 ± 0.11	0.38 ± 0.08	0.46 ± 0.03
		4	3.47 ± 0.37	3.18 ± 0.74	3.09 ± 0.71	3.38 ± 0.30	0.34 ± 0.04	0.32 ± 0.07	0.31 ± 0.07	0.34 ± 0.03
		5	2.61 ± 0.32	2.32 ± 0.58	1.00 ± 0.52	2.39 ± 0.26	0.23 ± 0.03	0.21 ± 0.05	0.09 ± 0.05	0.21 ± 0.02
		Tot	**12.38 ± 0.66**	**10.21 ± 1.36**	**10.58 ± 1.66**	**11.83 ± 0.56**	**1.50 ± 0.08**	**1.17 ± 0.16**	**1.46 ± 0.26**	**1.44 ± 0.07**
	Standing	1	2.46 ± 0.26	0.94 ± 0.24	1.87 ± 0.44	2.15 ± 0.20	0.60 ± 0.06	0.23 ± 0.06	0.46 ± 0.11	0.52 ± 0.05
		2	2.21 ± 0.23	1.00 ± 0.20	1.66 ± 0.52	1.95 ± 0.18	0.34 ± 0.03	0.16 ± 0.03	0.26 ± 0.08	0.30 ± 0.03
		3	2.18 ± 0.27	1.34 ± 0.34	2.03 ± 0.73	2.02 ± 0.22	0.25 ± 0.03	0.14 ± 0.03	0.23 ± 0.09	0.23 ± 0.03
		4	0.39 ± 0.10	0.21 ± 0.08	0.17 ± 0.06	0.33 ± 0.07	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.03 ± 0.01
		Tot	**7.23 ± 0.47**	**3.48 ± 0.48**	**5.72 ± 1.05**	**6.45 ± 0.37**	**1.22 ± 0.08**	**0.54 ± 0.08**	**0.97 ± 0.17**	**1.08 ± 0.06**
	Stump	**5**	**6.68 ± 0.48**	**5.48 ± 1.13**	**3.52 ± 0.86**	**6.14 ± 0.40**	**0.83 ± 0.06**	**0.68 ± 0.14**	**0.44 ± 0.11**	**0.76 ± 0.05**
CON	Lying	1	0.69 ± 0.20 n=653	0.61 ± 0.11 n=2564	0.71 ± 0.32 n=420	0.64 ± 0.09 n=3637	0.14 ± 0.04	0.12 ± 0.02	0.14 ± 0.06	0.13 ± 0.02
		2	1.43 ± 0.28	2.20 ± 0.20	3.36 ± 0.63	2.19 ± 0.17	0.18 ± 0.04	0.28 ± 0.02	0.42 ± 0.08	0.28 ± 0.02
		3	3.82 ± 0.61	2.79 ± 0.21	3.06 ± 0.62	3.00 ± 0.20	0.37 ± 0.06	0.27 ± 0.02	0.29 ± 0.06	0.29 ± 0.02
		4	2.93 ± 0.34	1.70 ± 0.15	2.05 ± 0.42	1.96 ± 0.13	0.23 ± 0.03	0.13 ± 0.01	0.16 ± 0.03	0.15 ± 0.01
		5	2.45 ± 0.40	1.18 ± 0.14	1.04 ± 0.27	1.39 ± 0.13	0.17 ± 0.03	0.08 ± 0.01	0.07 ± 0.02	0.10 ± 0.01
		Tot	**11.32 ± 0.96**	**8.48 ± 0.40**	**10.22 ± 1.08**	**9.19 ± 0.35**	**1.08 ± 0.10**	**0.88 ± 0.04**	**1.09 ± 0.13**	**0.94 ± 0.04**
	Standing	1	5.46 ± 0.56	6.47 ± 0.32	12.74 ± 1.39	7.01 ± 0.30	1.07 ± 0.11	1.26 ± 0.06	2.49 ± 0.27	1.37 ± 0.06
		2	4.44 ± 0.57	2.95 ± 0.20	3.33 ± 0.52	3.26 ± 0.19	0.56 ± 0.07	0.37 ± 0.03	0.42 ± 0.07	0.41 ± 0.02
		3	1.68 ± 0.29	1.81 ± 0.17	2.85 ± 0.57	1.91 ± 0.15	0.15 ± 0.03	0.16 ± 0.01	0.24 ± 0.05	0.17 ± 0.01
		4	0.05 ± 0.04	0.21 ± 0.04	0.04 ± 0.02	0.17 ± 0.03	0.004 ± 0.004	0.01 ± 0.00	0.003 ± 0.001	0.01 ± 0.00
		Tot	**11.63 ± 1.07**	**11.44 ± 0.47**	**18.96 ± 1.80**	**12.34 ± 0.44**	**1.80 ± 0.16**	**1.80 ± 0.08**	**3.15 ± 0.30**	**1.96 ± 0.07**
	Stump	**5**	**12.72 ± 0.96**	**9.08 ± 0.53**	**26.36 ± 2.51**	**11.73 ± 0.51**	**1.23 ± 0.09**	**0.87 ± 0.05**	**2.57 ± 0.24**	**1.13 ± 0.05**

Table 10-5 continued - mean volumes (m^3 ha^{-1}) and carbon (t ha^{-1}) in each deadwood type, split by decay stage and woodland type. Totals (Tot) for lying and standing deadwood are presented as the sum of decay classes per each deadwood type. BL – broadleaf, CON – conifer, MB – mixed broadleaf, MC – mixed conifer

Woodland type	Deadwood type		Volume (m^3 ha^{-1}) England	Scotland	Wales	GB	C stock (t ha^{-1}) England	Scotland	Wales	GB
MBL	Lying	1	0.67 ± 0.16 n=1727	0.31 ± 0.11 n=501	0.89 ± 0.32 n=404	0.64 ± 0.12 n=2632	0.16 ± 0.04	0.07 ± 0.02	0.21 ± 0.08	0.15 ± 0.03
		2	1.32 ± 0.13	1.72 ± 0.54	1.68 ± 0.35	1.45 ± 0.14	0.20 ± 0.02	0.26 ± 0.08	0.25 ± 0.05	0.22 ± 0.02
		3	2.50 ± 0.23	3.30 ± 0.51	2.17 ± 0.38	2.60 ± 0.19	0.30 ± 0.03	0.39 ± 0.06	0.25 ± 0.04	0.31 ± 0.02
		4	2.19 ± 0.20	2.76 ± 0.48	1.78 ± 0.60	2.24 ± 0.18	0.21 ± 0.02	0.26 ± 0.05	0.17 ± 0.06	0.21 ± 0.02
		5	1.56 ± 0.16	1.51 ± 0.41	1.21 ± 0.39	1.50 ± 0.15	0.13 ± 0.01	0.12 ± 0.03	0.11 ± 0.04	0.13 ± 0.01
		Tot	**8.24 ± 0.42**	**9.60 ± 1.05**	**7.73 ± 0.99**	**8.42 ± 0.37**	**1.01 ± 0.06**	**1.10 ± 0.13**	**0.94 ± 0.12**	**1.02 ± 0.05**
	Standing	1	2.04 ± 0.22	1.02 ± 0.15	3.09 ± 0.53	2.00 ± 0.17	0.46 ± 0.05	0.22 ± 0.03	0.69 ± 0.11	0.45 ± 0.04
		2	1.23 ± 0.13	1.16 ± 0.29	1.39 ± 0.27	1.24 ± 0.11	0.19 ± 0.02	0.16 ± 0.04	0.20 ± 0.04	0.18 ± 0.02
		3	1.05 ± 0.11	0.89 ± 0.18	0.83 ± 0.15	0.99 ± 0.08	0.12 ± 0.01	0.10 ± 0.02	0.09 ± 0.01	0.11 ± 0.01
		4	0.11 ± 0.04	0.18 ± 0.06	0.21 ± 0.06	0.14 ± 0.03	0.01 ± 0.00	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.00
		Tot	**4.43 ± 0.29**	**3.24 ± 0.43**	**5.53 ± 0.69**	**4.37 ± 0.23**	**0.77 ± 0.06**	**0.49 ± 0.06**	**1.00 ± 0.12**	**0.75 ± 0.04**
	Stump	**5**	**5.27 ± 0.36**	**5.17 ± 0.72**	**6.63 ± 1.12**	**5.46 ± 0.33**	**0.62 ± 0.04**	**0.59 ± 0.08**	**0.76 ± 0.13**	**0.64 ± 0.04**
MC	Lying	1	0.37 ± 0.12 n=667	0.63 ± 0.20 n=1274	0.46 ± 0.15 n=328	0.53 ± 0.12 n=2269	0.08 ± 0.02	0.13 ± 0.04	0.10 ± 0.03	0.11 ± 0.03
		2	2.32 ± 0.30	1.54 ± 0.23	2.38 ± 0.62	1.89 ± 0.18	0.31 ± 0.04	0.21 ± 0.03	0.32 ± 0.08	0.25 ± 0.02
		3	3.15 ± 0.30	2.14 ± 0.23	2.79 ± 0.65	2.53 ± 0.18	0.33 ± 0.03	0.22 ± 0.02	0.29 ± 0.07	0.26 ± 0.02
		4	3.20 ± 0.35	1.80 ± 0.23	1.93 ± 0.35	2.23 ± 0.17	0.27 ± 0.03	0.15 ± 0.02	0.16 ± 0.03	0.19 ± 0.01
		5	2.83 ± 0.49	1.34 ± 0.25	0.87 ± 0.19	1.71 ± 0.21	0.21 ± 0.04	0.10 ± 0.02	0.06 ± 0.01	0.13 ± 0.02
		Tot	**11.87 ± 0.80**	**7.45 ± 0.56**	**8.43 ± 1.05**	**8.89 ± 0.42**	**1.20 ± 0.08**	**0.81 ± 0.07**	**0.94 ± 0.12**	**0.94 ± 0.05**
	Standing	1	3.52 ± 0.38	3.52 ± 0.28	4.53 ± 0.61	3.67 ± 0.21	0.71 ± 0.08	0.70 ± 0.05	0.91 ± 0.12	0.73 ± 0.04
		2	1.96 ± 0.27	1.66 ± 0.20	2.08 ± 0.37	1.81 ± 0.15	0.26 ± 0.04	0.21 ± 0.03	0.26 ± 0.05	0.23 ± 0.02
		3	1.17 ± 0.16	1.15 ± 0.17	0.69 ± 0.17	1.09 ± 0.11	0.11 ± 0.01	0.10 ± 0.02	0.06 ± 0.02	0.10 ± 0.01
		4	0.02 ± 0.01	0.21 ± 0.05	0.05 ± 0.02	0.13 ± 0.03	0.001 ± 0.001	0.02 ± 0.00	0.004 ± 0.001	0.01 ± 0.00
		Tot	**6.67 ± 0.58**	**6.54 ± 0.42**	**7.34 ± 0.86**	**6.69 ± 0.32**	**1.08 ± 0.09**	**1.03 ± 0.07**	**1.24 ± 0.15**	**1.07 ± 0.05**
	Stump	**5**	**12.41 ± 0.85**	**7.99 ± 0.66**	**20.41 ± 2.14**	**11.08 ± 0.55**	**1.29 ± 0.09**	**0.82 ± 0.07**	**2.11 ± 0.22**	**1.14 ± 0.06**

Table 10-6 - Volumes and carbon stocks per hectare for different deadwood types in plots classified as managed or unmanaged

Woodland type	Deadwood type	Managed?	Volume (m^3 ha^{-1})	Carbon (t ha^{-1})
Broadleaf	Lying	Yes	10.39±0.34	1.33±0.05
		No	10.43±0.53	1.31±0.08
	Standing	Yes	5.15±0.21	0.89±0.04
		No	5.86±0.32	0.99±0.05
	Stump	Yes	6.84±0.32	0.72±0.04
		No	3.97±0.34	0.54±0.08
Conifer	Lying	Yes	10.79±0.31	1.18±0.04
		No	10.20±0.63	1.02±0.07
	Standing	Yes	11.00±0.29	1.76±0.05
		No	12.26±0.68	1.94±0.12
	Stump	Yes	12.03±0.36	1.07±0.04
		No	8.48±0.68	0.79±0.06

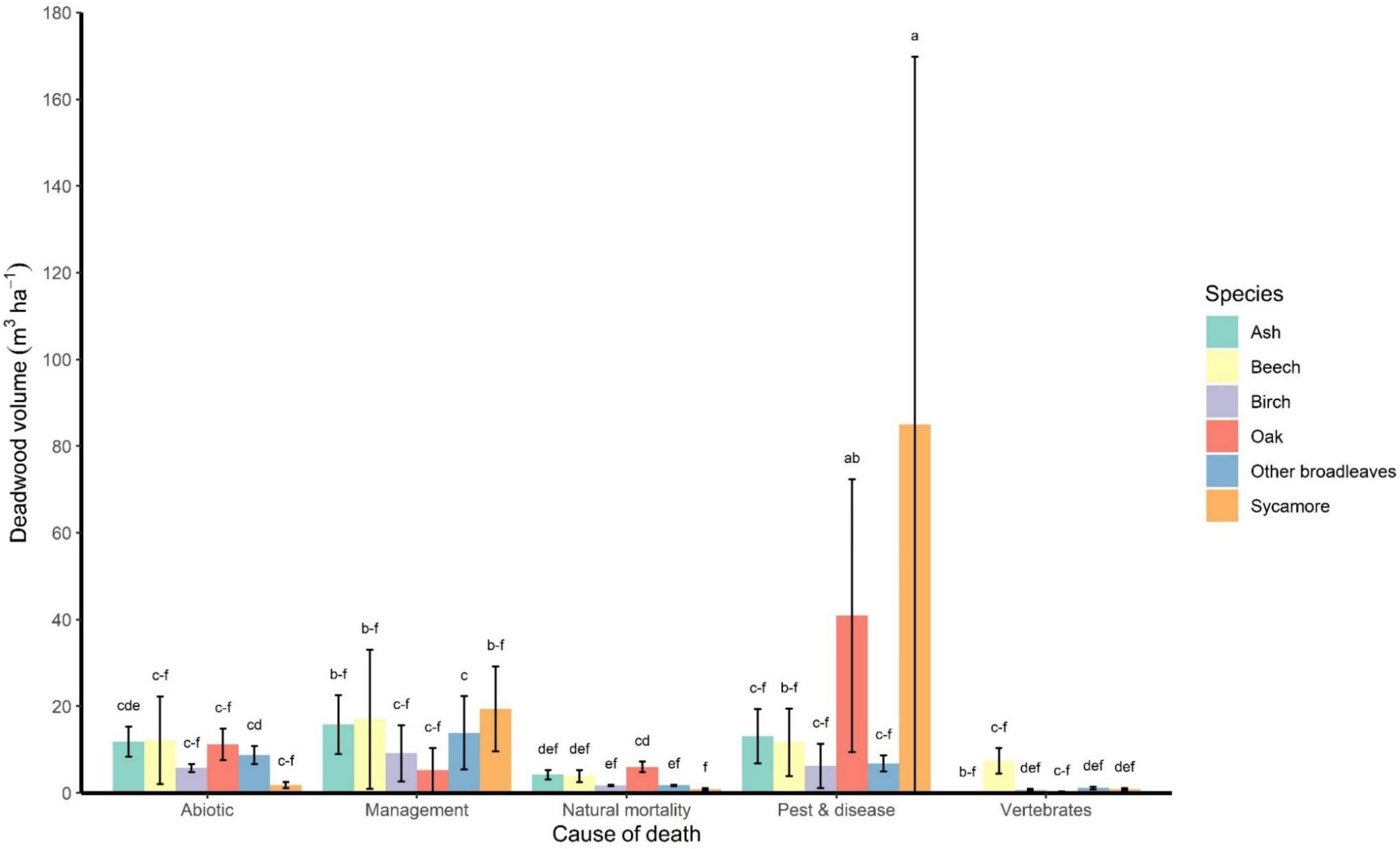

Figure 10-2 – standing deadwood volumes ($m^3\ ha^{-1}$) by principal broadleaf tree species in Great Britain, split by specific cause of tree death. Error bars show one standard error of the mean. Tukey post-hoc grouping letters are shown, with groups not sharing a letter significantly differing.

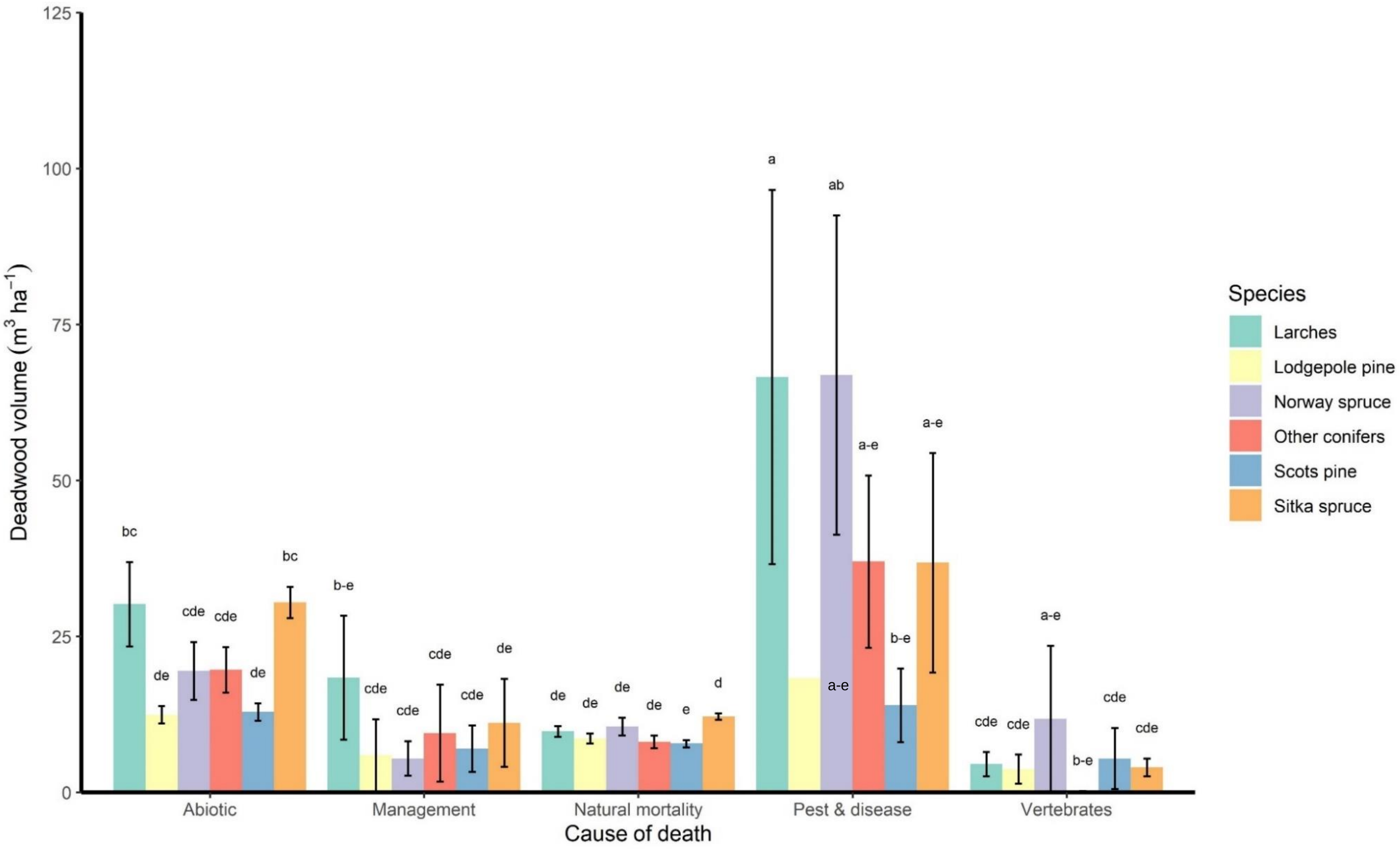

Figure 10-3 - standing deadwood volumes ($m^3\ ha^{-1}$) by principal conifer tree species in Great Britain, split by specific cause of tree death. Error bars show one standard error of the mean. Tukey post-hoc grouping letters are shown, with groups not sharing a letter significantly differing.