

Long-term carbon storage in a semi-natural British woodland

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By

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Abstract

Atmospheric levels of CO₂ are currently 395 ppm (dry air mole fraction measured at Mauna Loa, Hawaii), their highest concentration in 420,000 years. Forests play a major role in the global carbon (C) cycle by taking up inorganic C as CO₂ through photosynthesis, converting it to organic compounds (biomass), and either storing it in living and dead organic matter (above and below ground: including trees, dead wood, litter, and soil) or returning it to the atmosphere by respiration, decay or fire. Globally, forests cover around 4.1 billion ha of the Earth's surface and are estimated to contain up to 80% of all aboveground C and around 40% of all belowground (soils, litter, roots) terrestrial C. Forest C stocks have been reported to be increasing over the past 50 years in Europe and over the past 17 years in the United States. However, national forest inventories used to provide these data are often biased towards managed plantations, thereby leaving a knowledge gap regarding the dynamics of unmanaged, semi-natural forests. There are significant uncertainties about changes in C flux through time and the relative contributions of drivers such as land use, climate and atmospheric CO_2 . Decomposition of tree root C represents a potentially large C flux and contribution to the soil C sink when the input of dead and decaying root tissue, and root exudates, are greater than the output from respiration of roots, their symbionts, and the soil decomposer organisms. Therefore, quantifying decomposition rates and identifying primary controls of root decomposition are important for evaluating ecosystem function and possible responses to environmental change. This thesis explores long-term C dynamics in Lady Park Wood (LPW), an ancient semi-natural woodland situated in the counties of Monmouthshire and Gloucestershire, UK. We calculated changing tree biomass C stocks in LPW from 1945 to 2010. Separate estimates of tree biomass C, soil C and dead wood C were obtained to verify how C is apportioned among these types of forests. We used the dynamic vegetation model LPJ-GUESS to explore the likely contributions of temperature, CO₂ and management to forest C stocks in this region during the last 65 years. A 30 month field experiment was conducted in LPW using oak roots of different diameter classes (<2 mm, 2-5 mm and 5-10 mm) in decomposition bags. These were buried in two locations: one with bare ground and

one with the soil covered by ground layer vegetation, in order to quantify root decomposition rates. Lastly, we utilised long-term monitoring data from 2 other semi-natural woodlands in the UK to investigate whether LPW is a typical representation of live biomass C storage in these types of woodland. We then compared C storage in semi-natural forests with C storage in plantations and managed forests to see which type of forest stores the most C.

Between 1945 and 2010, tree biomass (including roots) carbon stocks in LPW approximately doubled in the old-growth stands, (increasing from 8.92 kg C m⁻² (0.025-quantile 7.21 k C m⁻², 0.975-quantile 10.19 kg C m⁻²) to 17.50 kg C m⁻² (0.025quantile 14.09 kg C m⁻², 0.975-quantile 20.24 kg C m⁻²)), and between 1977 and 2002 increased by almost 50% in the young-growth stands (from 6.30 kg C m^{-2} (0.025-quantile 5.39 kg C m⁻², 0.975-quantile 7.23 kg C m⁻²) to 9.21 kg C m⁻² (0.025quantile 7.72 kg C m⁻², 0.975-quantile 10.65 kg C m⁻²)). In the old-growth stands 60% (0.025-quantile 54%, 0.975-quantile 64%) of carbon was stored in tree biomass, 38% (0.025-quantile 34%, 0.975-quantile 43%) was stored in soil and 2% (0.025-quantile 1%, 0.975-quantile 4%) stored in coarse woody debris. In contrast, storage of carbon in the young-growth stands was allocated almost equally between tree biomass (53%, 0.025-quantile 48%, 0.975-quantile 57%) and soil (43%, 0.025-quantile 39%, 0.975-quantile 47%), with 4% (0.025-quantile 2%, 0.975quantile 7%) stored in coarse woody debris. Results from LPJ-GUESS suggest that release from management was the major driver of carbon storage but CO₂ also had a pronounced effect. Relatively little of the observed increase in carbon stocks was attributable to increased temperature. Similarly, little evidence of a temperature effect was found on root decomposition rates. Mean loss rates of roots buried in the location with ground vegetation were significantly higher than those of roots buried in the bare ground site. Large roots (5-10 mm) decomposed faster than medium (2-5 mm) or fine roots (<2 mm) over the first 18 months.

A typical unthinned Sitka spruce plantation in the UK sequesters carbon faster than semi-natural forests, having accumulated 16 kg C m⁻² by the end of its 60 year rotation, compared to Lady Park Wood which accumulated just 9.31 kg C m⁻² over a 65 year period. However, semi-natural forests comprise much greater carbon stores

over the long term. A time average equilibrium storage value (mean taken across the harvesting cycle) for unthinned Sitka spruce stands is 7.4 kg C m⁻², whereas the mean storage value for semi-natural woodlands in this study is 17.5 kg C m⁻². Although an increase in tree biomass carbon is consistent with European syntheses, this study suggests that semi-natural old-growth stands are storing more carbon than typical plantations, with tree biomass the most important compartment for carbon stores. There is clear evidence to suggest that semi-natural woodland may be an important and underestimated carbon stock in the UK.

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1 Introduction

1.1 Overview and rationale

The global carbon (C) cycle involves the C in and circulating between the three active reservoirs: the atmosphere, the ocean, and the terrestrial system including various stocks, such as forests and organic C found in soils (Figure 1.1). Forests play a major role in the global C cycle by taking up inorganic C as CO₂ through photosynthesis, converting it to organic compounds (biomass), and returning it to the atmosphere by respiration, decay or fire (Figure 1.2) (Post et al. 1990).



Figure 1.1: The global carbon cycles for the 1990s. Main annual fluxes are shown in Gt C y^{-1} and reservoir sizes in Gt C. Pre-industrial 'natural' fluxes in black and 'anthropogenic' fluxes in grey (from IPCC, 2007c).



Figure 1.2: Main pathways for C flux into the forest (Black arrows; C sink) and out of the forest (Black outline arrows; C source). Above-ground biomass (stemwood, branchwood, bark, foliage and seeds), below-ground biomass (coarse roots, fine roots and stumps), and soil organic C all constitute C stocks (redrawn from Forestry Commission, www.forestry.gov.uk/website/forestresearch.nsf/ByUnique/INFD-62NBUH).

Globally, forests cover around 4.1 billion ha of the earth's surface and are estimated to contain up to 80 % of all aboveground C and around 40 % of all belowground terrestrial C (Dixon et al. 1994). The world's forests store ~ 289 gigatonnes (Gt) of C in biomass alone, although between 2005 and 2010 C stocks decreased by ~ 0.5 Gt annually due to a reduction in forest area (FAO, 2010). Between 2000 and 2010 13 million hectares of forest were lost through conversion to other uses or natural causes (FAO, 2010). As a consequence of deforestation and forest degradation large amounts of CO₂ are released into the atmosphere. CO₂ is a

potent greenhouse gas (GHG) and a primary component of anthropogenic emissions. The global concentration of atmospheric CO₂ has increased from a preindustrial value of ~ 280 parts per million (ppm) in 1750 (IPCC, 2007) to 395 ppm at the end of September 2014 (Tans and Keeling, 2014). Initially, this increase was mainly caused by anthropogenic release of C to the atmosphere from deforestation and other land use change activities (Le Quéré et al. 2013). This means forests have a significant role in the global C cycle, especially with regard to mitigating CO₂ emissions, and the ability to accurately measure the standing stock of C stored in forests is becoming increasingly important (Brown, 2002). The Kyoto Protocol, linked to the United Nations Framework Convention on Climate Change (UNFCCC), is an international agreement which commits participating countries to internationally binding emission reduction targets. As part of the Protocol, countries must report detailed information about changes in C stocks and GHG emissions pertaining to sources and removal by sinks from land use, land use change and forestry (LULUCF) activities. When the net uptake of CO₂ from photosynthesis is greater than respiration the forest is acting as a 'sink', i.e. there is a net flux of C into the ecosystem. When C is lost from the forest, i.e. through disturbance, then it becomes a 'source'. The terms 'sink' and 'source' imply a net flux of C (in units of mass/time, g C y-1, or mass/(area*time), g C $m^{-2} y^{-1}$) into or out of the ecosystem, whilst the term 'stocks' refers to a store of C (in units of mass, g C, or mass/area, g C m⁻²).

Increase of tree C stocks has been estimated at 1.7 kg C m⁻² for Europe over the past 50 years (Ciais et al. 2008) and at 0.5 kg C m⁻² for the United States over the past 17 years (Pan et al. 2011). The mostly likely reasons for these increases in C stocks are increased forest area (Kauppi et al. 2006) due to new planting, on former agricultural land or formerly grazed upland habitats, and natural succession following land abandonment and depopulation; increased live C store per unit area, because of reduced levels of forest grazing and recovery from forest degradation (Rautiainen et al. 2009); nitrogen deposition (Magnani et al. 2007); climatic change and increasing CO₂ concentration (Bellasen et al. 2011). However, disentangling the drivers of these increases can be difficult.

Forest area in the UK is ~ 3 million ha (~ 1.6 million ha coniferous and ~ 1.5 million ha broadleaved) which equals 13% of land area (Forestry Commission, 2014). Since 1990 new forest area has been planted at rates between 16,000 and 21,000 ha y^{-1} , with afforestation rates in 2000 being ~ 7,000 ha y^{-1} of conifers and 10,000 ha y^{-1} of broadleaves (Milne et al. 2000). The majority of forest area in the UK is of plantation origin, with approximately 1,516,000 ha (7%) covered by conifer plantations (Norman, 2009) and, as of 1990, 600,000 ha of broadleaved plantations (Cannell and Dewar, 1995). Only 2% (535,000 ha) of land cover is ancient seminatural woodland (Spencer and Kirby, 1992) which means that forest inventories may not fully capture the dynamics of these unmanaged, mixed woodland areas (Harmon, 2010). Little is known about C budgets in these woodlands and detailed long-term data on their C dynamics are rather scarce. Unmanaged forests are thought to store more C than plantations (Thornley and Cannell, 2000; Liao et al. 2010) so are likely to be important for long term C storage, not only because forests can act as C sinks until high ages (Schulze et al. 2000; Luyssaert et al. 2008) but also because preservation of old growth natural forests, with large C pools, has a large effect on the C cycle (Schulze et al. 2000).

Compiling a C budget involves quantifying C pools and flux in the forest. The main C pools are live biomass (stemwood, branchwood, bark, foliage, coarse roots and fine roots), soil organic C (SOC), and dead wood biomass. C budgets for forest ecosystems can be calculated in a variety of ways, for example forest inventories, remote sensing, eddy covariance technique, and process-based modelling (Turner et al. 1995; Baldochii, 2003; Bellassen et al. 2011; Le Toan et al. 2004) and can often involve several different methods (Goodale et al. 2002; de Wit et al. 2006; Sitch et al. 2007). Stocks of C in live biomass are regularly calculated using inventory data, which includes details of tree species and diameter at breast height (dbh) measurements (Gimmi et al. 2009). Allometric equations are then used to calculate tree biomass from the dbh measurements (Jenkins et al. 2004). Ciais et al. (2008) reported a live biomass pool of ~4 kg C m⁻² for broadleaved European forests in 2000 using inventory data, and suggested a potential maximum C stock of 17 kg C m⁻².

Remote sensing procedures, which collect information on above-ground forest biomass, are often used as an alternative to methods based on field measurements as they can obtain reasonably accurate information, at less cost, over large areas (Vicharnakorn et al. 2014). Airborne and satellite sensors can map surface variables such as land cover type and leaf area index, which are then used with process based models to quantify fluxes of C (Turner et al. 2004). The C flux can also be inferred from the change in C pools over time, i.e. the net C accumulation or loss of C from the live biomass pool, and can be calculated as the change in the C pool over the time period, divided by the number of years in the time period (Turner et al. 1995). A direct measurement of CO_2 fluxes between the atmosphere and forest vegetation can be measured using the eddy covariance technique, which measures the covariance between fluctuations in vertical wind velocity and CO_2 mixing ratio (Baldocchi, 2003). Using this method, Thomas et al. (2011) estimated net ecosystem production (NEP, net gain or loss of C from an ecosystem) for an ancient broadleaved, deciduous UK woodland to be 0.12 kg C m⁻² y⁻¹.

The soil C pool is frequently measured using direct field methods, i.e. field sampling and laboratory measurement (Vanguelova et al. 2013). Vanguelova et al. (2013) reported forest soils of the UK to range between 10.8 and 44.8 kg C m⁻² (80 cm depth). C dynamic simulation models can be used to estimate C stock in soils under present land use if field methods are not able to be implemented (FAO, 2004). The Yasso dynamic soil C model, which calculates C pools of litter and soil organic matter, and annual changes in these pools, consists of five decomposition compartments and two woody litter compartments, the dynamics of which are controlled by physical and chemical characteristics of litter and climate (Liski et al. 2006).

Data from forest inventories, remote sensing and eddy covariance methods are often used to test and develop dynamic global vegetation models (DGVMs). LPJ-GUESS (Smith et al. 2001; Sitch et al. 2003) is a process based dynamic vegetation model that uses an individual gap-model approach (Prentice et al. 1993) and can be used to study regional changes on a decennial-centennial timescale. Few attempts have been made to reconstruct regional long-term dynamics of forest C stocks based on historical data (Gimmi et al. 2009; Gingrich et al. 2007) and C modellers are generally not acquainted with long-term monitoring data sets of forest biomass. Comparing simulated C stock estimates from LPJ-GUESS to long-term reconstructed data is one way to examine how well the model can match historical patterns of C pools. Gimmi et al. (2009) calculated C pools in a Swiss mountain forest and found that the potential maximum vegetation C (19 kg C m⁻²) simulated by LPJ-GUESS underestimated historical C stocks in 1975 (20.2 kg C m⁻²), which they explain could be due to the inability of models to grasp peak values and their tendency to generalise. Keith et al. (2009) suggest that process-based models may underestimate C accumulation because of the assumption that C exchange reaches an equilibrium. However, if model reliability can be established the model can then be used to identify possible drivers of change of historical C stocks and to predict future C stocks under different climatic scenarios.

Globally, surface temperatures show a warming of 0.85°C from 1880 to 2012 and this temperature increase is likely to exceed 1.5°C by the end of the 21st century (IPCC, 2013). The amount of CO_2 in the atmosphere is predicted to reach between 541 and 970 ppm by 2100 (Prentice et al. 2001). Whilst is it generally accepted that the increase in atmospheric CO₂ is altering the climate system, it remains unclear whether forests will sequester more C in response to the increase in CO₂ or whether limitations posed by nutrients, temperature and precipitation will limit the effect (Beedlow et al. 2004). Free air CO₂ enrichment (FACE) experiments show enhanced photosynthesis in plants (Norby et al. 2005; Sholtis et al. 2003) and a meta-analysis of FACE experiments by Ainsworth and Long (2005) found increased biomass production in trees. However, data from FACE experiments are limited due to a number of factors, including bias towards young forests, small numbers of sites for each ecosystem, and durations of 10 years or less (Leakey et al. 2012). In a mature deciduous forest, Körner et al. (2005) found that although there was an immediate and sustained increase in C flux through the forest in response to elevated CO₂, the trees did not accrete more biomass C in the stems. Although Norby et al. (2002) found increased net primary production (NPP) led to an increase in wood increment in the first year, in subsequent years the extra C was allocated

to the production of leaves and fine roots. Fine root biomass production and standing crop have been shown to double under enhanced CO₂ (Iversen et al. 2008) meaning that extra C can be stored in the mineral soil (Jastrow et al. 2005). Consequently, tree root C represents a potentially large C flux and soil C sink, and quantifying root decomposition rates and identifying primary controls of root decomposition are important for evaluating ecosystem function (Harmon et al. 1999) and its possible response to environmental change.

Forests constitute a major terrestrial C store, which is highly dynamic and responsive to changes in management, climate and atmospheric CO₂ among other factors (Pan et al. 2011). Understanding the drivers behind the recent increase of C stocks (Ciais et al. 2008; Bellassen et al, 2011) is important for preservation of current C stocks and management policies. Regional long-term forest data are extremely rare (Gimmi et al. 2009) and can be used to create C budgets and to explore C dynamics through time. This knowledge provides useful information that can be used to improve models of terrestrial C cycles (Friedlingstein et al. 2006) and can be applied when considering future changes in C stocks.

1.2 Thesis aims and objectives

The major aim of this thesis is to reconstruct long-term live biomass C dynamics for a semi-natural deciduous woodland in the UK. Little is known about C budgets in semi-natural woodlands, therefore forest inventories may not fully capture the dynamics of these types of woodland. Lady Park Wood (LPW) was designated as an unmanaged nature reserve in 1944 and has the longest and most detailed records available from British semi-natural woodlands. Separate estimates of tree, soil and dead wood C stocks will be obtained to verify how C is allocated in this type of woodland. The dynamic vegetation model LPJ-GUESS will be used to simulate live biomass C stock estimates in LPW for comparison with reconstructed historical data to establish model reliability. LPJ-GUESS can then be used to explore possible drivers of C stock change and to allow future C storage scenarios in LPW under different climate scenarios to be tested. A root decomposition study, commencing in December 2010 for 2 ½ years, will enable us to quantify root decomposition rates in a semi-natural woodland. Lastly, we will utilise long-term monitoring data from 2 other semi-natural woodlands in the UK to investigate whether LPW is a good representation of live biomass C storage in these types of woodland. These data can then be compared to C storage in plantations and managed forests to see which type of forest is storing the most C.

The following specific questions will be addressed:

- How have C stocks changed in a British semi-natural deciduous woodland over the past 60 years?
- How is C apportioned in a British semi-natural deciduous woodland?
- What are the main drivers of C stock changes?
- What is the potential future C storage at LPW under different climate scenarios?
- How quickly do roots breakdown, thereby transferring C to the soil C pool and the atmosphere, and nutrients to the soil?
- How does the temporal variation of C stocks in a semi-natural forest differ from those of a plantation forest?
- Which type of forest (semi-natural, managed or plantation) stores the most live biomass C?

1.3 Status of manuscripts

Chapter 2: Hale K, Spencer M, Peterken GF, Mountford EP, Bradshaw RHW. Rapid carbon accumulation within an unmanaged, mixed, temperate forest. Manuscript submitted to Functional Ecology: rejected with resubmission invited. Current status: undergoing revision with view to resubmit.

Author contribution:

Hale K – Main author responsible for data collection, biomass calculations, statistical analysis, figure and table presentation, and manuscript preparation.

Spencer M – Discussion, assistance with statistical analysis, and detailed manuscript review.

Peterken GF – Manuscript review.

Mountford EP – Provision of long-term monitoring data and manuscript review.

Bradshaw RHW – Discussion and detailed manuscript review.

Chapter 3: Allen KA, Lehsten V, Hale K, Bradshaw RHW. Past and future drivers of a neglected carbon sink in European temperate forest. Manuscript submitted to Global Change Biology: to be published subject to minor changes. Current status: undergoing changes to be resubmitted by 15th January 2015.

Author contribution:

Allen KA – Main author responsible for model runs, figure presentation, and manuscript preparation.

Lehsten V – Discussion and help with model runs.

Hale K – Responsible for historical data calculations, data collection, discussion, and manuscript review.

Bradshaw RHW – Discussion and detailed manuscript review.

Chapter 4: Hale K, Spencer M, Bradshaw RHW. Effects of temperature and ground vegetation on decomposition rates of oak roots in an unmanaged, temperate woodland. Manuscript.

Author contribution:

Hale K – main author responsible for data collection and processing, statistical analysis, figure presentation, and manuscript preparation.

Spencer M – Assistance with statistical analysis, discussion, and detailed manuscript review.

Bradshaw RHW – Discussion and detailed manuscript review.

Chapter 5: Hale K, Spencer M, Bradshaw RHW. Climate change mitigation by carbon sequestration: Semi-natural unmanaged forests or plantations? Manuscript.

Author contribution:

Hale K – main author responsible for data collection and processing, figure presentation and manuscript preparation.

Spencer M – Discussion and detailed manuscript review.

Bradshaw RHW – Discussion and detailed review.

1.3.1 Authors overall contributions

The author was present and assisted with all field work that took place in Lady Park Wood during 2010, 2011, 2012 and 2013, along with help from Richard Bradshaw, Matt Spencer, Kath Allen, Gina Bradshaw and Mike O'Connor (University of Liverpool, UK). The author was responsible for the preparation of all samples and all lab work, apart from C:N analysis, which was run by Sabena Blackbird (University of Liverpool, UK). All statistical work in R was conducted by the author with assistance from Matt Spencer. LPJ-GUESS model runs were made by Kath Allen. Data analysis, interpretation, figure presentation, and manuscript preparation was the responsibility of the author, with the exception of chapter 3, whereby following a period of ill health, Kath Allen became the lead author.

2 Rapid carbon accumulation within an unmanaged, mixed, temperate woodland

2.1 Abstract

Forest carbon (C) stocks have been reported to be increasing over the past 50 years in Europe and over the past 17 years in the United States. National forest inventories used to provide these data give some indication of forest C dynamics but may leave a knowledge gap regarding the dynamics of unmanaged, seminatural forests. We calculated changing tree biomass C stocks for a mixed, unmanaged, semi-natural woodland containing stands of 2 different ages; c. 70 years (young-growth) and c. 100-135 years (old-growth). The old-growth stands have been untouched since 1902, are dominated by trees dating from 1800-1900, and contain transects that have been monitored since 1945. The young-growth stands were clear felled in 1943 and have grown up naturally since then. Transects in the young-growth stands have been monitored since 1977. Separate estimates of tree C, soil C and dead wood C were obtained to verify how C is apportioned in these types of forests. Between 1945 and 2010, tree biomass C stocks approximately doubled in the old-growth stands, (increasing from 8.92 kg C m⁻² to 17.50 kg C m⁻²), and between 1977 and 2002 increased by almost 50% in the young-growth stands (from 6.30 kg C m⁻² to 9.25 kg C m⁻²). In the old-growth stands 60% of C is stored in tree biomass, 38% is stored in soil and 2% stored in coarse woody debris. In contrast, storage of C in the young-growth stands is allocated almost equally between tree biomass (53%) and soil (43%), with 4% stored in coarse woody debris. Although an increase in tree biomass C is consistent with the European synthesis, this study suggests that semi-natural old-growth stands are storing more C than typical plantations, with tree biomass the most important

compartment for C stores. Therefore if management is to be shifted from biomass production to C storage, due consideration should be given to the role of unmanaged, old growth forests.

2.2 Introduction

Forests comprise a large terrestrial C sink, but one which is highly dynamic and responsive to changes in management, climate and atmospheric CO_2 among other factors (Pan et al. 2011). Sequestered forest C has recently increased at global and continental scales. For example, Ciais et al (2008) estimated a 1.7 kg C m⁻² increase over the past 50 years in Europe and Pan et al (2011) estimated a 0.5 kg C m⁻² over the past 17 years in the United States and 0.2 kg C m⁻² globally. The most favoured hypotheses for these increased forest C stocks are increased forest area (Kauppi et al. 2006) due to new planting, on former agricultural land or formerly grazed upland habitats; increased growing volume per unit area as a successional process following reduced levels of forest grazing and recovery from forest degradation (Rautiainen et al. 2009); climatic change, nitrogen deposition and increasing atmospheric CO_2 concentration (Pan et al. 2009) but these hypotheses are hard to evaluate fully using existing data.

Forest area in Europe has been increasing since at least 1950, with estimates ranging from 5% (Ciais et al, 2008) to as much as 30% increase (Gold et al. 2006). Reasons for this disagreement include changing definitions of forest, data incompatibility from different countries, inventories that tend to focus on plantation areas and differing estimates derived from field and remotely sensed data. The increase in forest area in the United States is much smaller by comparison at just 0.5% between 1953 and 2007 (Rautiainen et al. 2011).

Growing volume per unit area has also been increasing since 1950, both in Europe and in America (Rautiainen et al. 2011). Estimates for Europe vary from a doubling of volume to just minor increases (Ciais et al. 2008; Gold et al. 2006). In America, growing volume per unit area has been estimated to have increased by 51% between 1953 and 2007 (Rautiainen et al. 2011). Recovery from previous forest exploitation has led to an increase in timber volume and biomass, which primarily drives development of forest C stocks (Rautiainen et al. 2009). In European managed forests, increasing volume is primarily due to increased stand density (a higher number of trees present) rather than a large increase in tree diameters (Linder and Östlund, 1998). Biomass-density relationships in trees related to selfthinning and succession have received considerable theoretical and empirical study. Weiner & Freckleton (2010) state how total standing biomass initially increases in proportion to density during a succession following disturbance or release from management. Biomass in many systems then levels off and finally can remain constant, as trees increase in size leaving space for fewer individuals. This course of events may be described by a negative relationship between mean tree size and total community biomass, where average tree size has been predicted to scale as the -3/2 (Reineke 1933; Westoby 1984) or -4/3 (Enquist et al. 1998) power of maximum population density, dependent on the underlying conceptual model adopted. Linked to these relationships is the concept of a 'constant final yield', although this has only been experimentally demonstrated in annual plants (Weiner & Freckleton 2010). A study of a natural mixed forest in New Zealand showed a shift in the cause of death from competitive self-thinning in the small-stem phase to exogenous disturbance in the large-stem phase resulting in a changing biomassdensity distribution over time (Coomes et al. 2003). These authors suggest that biomass-density plots might be a useful method for detecting potential impacts of climate change and exogenous disturbance factors. Smith (1969) already suggested that old growth forests continued to sequester C and Luyssaert et al. (2008) showed that older stands with a smaller number of large individuals can obtain the highest amounts of biomass, gained over centuries, with a potential upper limit of between 50 and 70 kg C m⁻² (Luyssaert et al. 2008). Keith et al. (2009) reported even greater forest biomass figures.

Atmospheric CO_2 has increased from ~316 ppm in 1959 to ~394 ppm in 2012 (Tans and Keeling, 2014). This increase in CO_2 often leads to the assumption that forests will increase C sequestration rates in response. Studies show that the increasing levels of CO₂ can increase photosynthesis in plants, at least in the short term (Norby et al. 2005; Sholtis et al. 2004), but it is unclear whether the increase in net primary productivity (NPP) will lead to an increase in biomass, and therefore in C stocks, or simply to an increase in turnover rates of leaves or roots (Norby et al. 2002; Körner et al. 2005). Magnani et al. (2007) propose that the increase in forest C sequestration is more likely to be a consequence of N deposition. The initial increase in NPP seen in some studies, due to increasing CO₂, has been seen to decline over time due to N limitation (Norby et al. 2010). Data about CO₂ fertilisation from free-air CO₂ enrichment (FACE) experiments are still limited due to a number of factors, including bias towards young forests, small numbers of sites for each ecosystem and durations of 10 years or less (Leakey et al. 2012). Ecosystem modellers have demonstrated the potential influence of the recent increase in atmospheric CO₂ on net ecosystem productivity of European forests (Bellassen et al. 2011).

Simulation models can be used to evaluate the contributions of the various mechanisms that influence C dynamics in forests. Kaplan et al. (2012) drove the LPJ dynamic vegetation model with reconstructed climate, land-use and CO₂ concentrations to explore the effects of land-use and climate change on the European C cycle over the past 500 years. They found that land-use change was the primary control on the C budget for this time period with deforestation chiefly contributing to a net loss of C until the 1950's, when the trend was reversed and C accumulation began. They estimate that European forests retain the potential to absorb significant quantities of C at the present day, although coupled climate-carbon cycle models suggest that future climates will reduce the efficiency of the global forests to absorb C because of drought, heat stress and wildfire (Mackey et al. 2013).

Detailed long-term data on forest C dynamics are rather scarce. National forest inventories give some indication of forest C dynamics during the last few decades (e.g. Hu and Wang, 2008; Gingrich et al. 2007), but may not fully capture the dynamics of unmanaged, mixed woodland areas (Harmon, 2010). Long-term monitoring of permanent plots and transects in unmanaged, close to natural, forest

is a rather neglected source of information. These studies provide data on aboveground tree biomass (Peterken and Mountford, 1995). There also appears to be very limited data regarding soil C content and dynamics even though soil C pools are thought to account for as much as 50-60% of C stored in temperate forest systems (Dixon et al. 1994). Current estimates for European forest soils range from between 1.13 and 12.63 kg C m⁻² (Baritz et al. 2010). Liski et al (2002) showed that litter production is related to forest biomass suggesting that unmanaged, old growth forests might be large C sinks.

2.3 Aims

Here we calculate changing C stocks over a 65 year period for a mixed, unmanaged woodland, on the border of England and Wales, to distinguish between forest area and forest density effects, and to explore possible explanatory drivers behind the increase in C stocks. We obtain separate estimates of the tree, soil and dead wood C stocks, to verify how C is allocated, and to investigate whether the soils are storing a high percentage of total ecosystem C. We examine which of the hypotheses outlined above, describing possible mechanisms accounting for recent increases in forest C storage, are tenable.

2.4 Material and methods

2.4.1 Study site

This study took place in Lady Park Wood (51°49′N, 2°39′W) (Figure 2.1), an ancient semi-natural woodland, situated 3 km north east of Monmouth on the southern bank of the River Wye at 30-190 m elevation. Long-term climatic data are available from the Ross-On-Wye weather station (approx. 11 km from the woods). Mean annual precipitation for the period 1971-2000 was 706.2 mm and mean annual temperature was 10.2°C.



Figure 2.1: (a) Location of Lady Park Wood and (b) the distribution of old-growth (clear) and young-growth (stippled) stands, the location of cliffs, and the position of the transects studied (I-VI in this study) (from Peterken and Jones, 1987).

For centuries Lady Park Wood was treated as coppice/coppice-with-standards but was designated as an unmanaged nature reserve in 1944. The reserve covers 35.2 ha, of which 14 ha are known as old-growth stands that were practically untouched by fellings which took place in 1943 (Peterken and Jones, 1987). The remaining 21 ha were clear felled in 1943 and are referred to as young-growth stands (Peterken and Jones, 1989). Although the more mature stand qualifies as old-growth for several reasons: it has been well stocked with standing dead trees since 1976, canopy height and basal area have oscillated around a ceiling achieved by 1976 and the volume of coarse woody debris in the 1990's was similar to volumes found in temperate deciduous 'virgin' forests and USA old-growth, here the terms old-growth and young-growth are used following Peterken and Jones (1987; 1989) criteria. The underlying bedrock is limestone and the main species present are beech (*Fagus sylvatica*), oak (*Quercus petraea*), ash (*Fraxinus excelsior*), lime (*Tilia*)

cordata, T. platyphyllos), wych elm (*Ulmus glabra*) and birch (*Betula pendula, B. pubescens*). The soils range from skeletal rendzinas on the steep slopes (32°) to thin organic loams on the plateau fringe to deeper, lighter loams (derived from river borne deposits) on the gentler mid and low slopes. Transects I – VI (Figure 2.1), (used in this study) were established in 1944, consist of a mixture of old- and young-growth areas and were placed as roughly parallel lines, at equal intervals through the wood (Peterken and Jones, 1987). Each transect is 20 m wide, with length varying from 180 m to 330 m. Old-growth transects were recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010. Young-growth transects were recorded in 1977, 1993 and 2002 (Peterken and Jones, 1989).

2.4.2 Tree biomass C

The reconstruction of tree biomass C dynamics in Lady Park Wood (LPW) was based on unpublished data supplied by Ed Mountford. This comprised measurements of the location, species and diameter of all trees achieving \geq 1.3m height within the monitoring transects. The data for standing C crop were calculated using all trees with a DBH (diameter at breast height) \geq 6.5cm throughout the study. All stems attaining this size were included on multi-stemmed individuals. Tree measurements were converted to above and below ground biomass using European speciesspecific (where possible) allometric regression equations (Table 2.1) (Zianis et al. 2005). It should be noted that the root to shoot ratio (i.e. the ratio RT:AB) for Betula pendula, Fagus sylvatica, and Quercus petraea increases with DBH. As a consequence the root to shoot ratio increases with tree/stand age. This fact is contrary to results of some other authors where the root to shoot ratio decreases with tree/stand age (Cairns et al. 1997; Genet et al. 2009). Where European equations were not available, equations from a North American database (Jenkins et al. 2004) were used. Where there were no species-specific equations available, then appropriate Forestry Commission equations from the 'Carbon assessment protocol' (Jenkins et al., 2010) were substituted. Finally, C content was calculated from total biomass. All calculations involved Monte Carlo uncertainty analysis, as
described in the supporting information (Appendix 1). To compare growth rates between time periods in a way that standardises for the different lengths of time between observations, a mean discrete-time annual growth rate *R* (growth rate for short) was calculated. As growth is likely to be multiplicative, the ratio of carbon $c(t_2)$ at some time t_2 to carbon $c(t_1)$ at time t_1 (where times are measured in years) is a natural measure of the amount of growth. To express this on a one-year time scale we take the $1/(t_2-t_1)$ power. Thus we obtain the mean annual growth rate $R = \left(\frac{c(t_2)}{c(t_1)}\right)^{\left(\frac{1}{t_2-t_1}\right)}$. Note that *R* is a dimensionless quantity and therefore has no

units. C stocks at the two points are related by $c(t_2) = c(t_1)R^{t_2-t_1}$. Values of *R* less than 1 indicate decreases in C stocks, and values greater than 1 indicate increases.

Species	Component	Equation	а	b	С	Units (biomass, dbh)	Equation no.	Reference
Acer campestre	AB	log10biomass=a+b*(log10(dbh^c))	2.2151	2.4209	1	kg, cm	-	Whittaker et al. 1974
Acer campestre	RT	log10biomass=a+b*(log10(dbh^c))	1.7368	2.2006	1	kg, cm	-	Whittaker et al. 1974
Betula pendula	AB	AB=a*dbh^b	0.00087	2.28639	-	kg, mm	31	Zianis et al. 2005
Betula pendula	RT	log10RT=a*log10(dbh)+b	2.3547	-1.3	-	kg, cm	36	Zianis et al. 2005
Fagus sylvatica	AB	AB=a*dbh^b	0.453	2.139	-	kg, cm	88	Zianis et al. 2005
Fagus sylvatica	RT	log10RT=a+b*log10(dbh)	-2	2.7	-	kg, cm	120	Zianis et al. 2005
Fraxinus excelsior	AB	lnAB=a+b*ln(dbh)	-2.4598	2.4882	-	kg, cm	134	Zianis et al. 2005
Fraxinus excelsior	RT	RT=(a*dbh^b)*1000	0.000149	2.12	-	kg, cm	5.3.3	Jenkins et al. 2010
Quercus petraea	AB	lnAB=a+b*ln(dbh)	-0.883	2.14	-	kg, cm	600	Zianis et al. 2005
Quercus petraea	RT	log10RT=a+b*log10(dbh)	-1.56	2.44	-	kg, cm	598	Zianis et al. 2005
Tilia cordata	AB	lnAB=a+b*ln(dbh)	-2.6788	2.4542	-	kg, cm	607	Zianis et al. 2005
Tilia cordata	RT	RT=(a*dbh^b)*1000	0.000149	2.12	-	kg, cm	5.3.3	Jenkins et al. 2010
Ulmus glabra	Stem wood	log10biomass=a+b*(log10(dbh^c))	2.9529	2.1032	1	g, in	2551	Jenkins et al. 2004
Ulmus glabra	Stem bark	log10biomass=a+b*(log10(dbh^c))	2.264	1.9642	1	g, in	2553	Jenkins et al. 2004
Ulmus glabra	Branches	log10biomass=a+b*(log10(dbh^c))	2.5173	2.3507	1	g, in	2556	Jenkins et al. 2004
Ulmus glabra	Foliage	log10biomass=a+b*(log10(dbh^c))	2.1373	1.7043	1	g, in	2557	Jenkins et al. 2004
Ulmus glabra	RT	RT=(a*dbh^b)*1000	0.000149	2.12	-	kg, cm	5.3.3	Jenkins et al. 2010

Table 2.1 Equations used for main tree species: WT = Whole tree biomass, AB = Aboveground biomass, RT = Belowground biomass; letters (a, b, c) refer to parameters obtained from original sources for regression equations, equation numbers refer to original sources; dbh = diameter at breast height; biomass is on left hand side for both the equations and the units.

2.4.3 Soil C

Soil samples were collected in December 2011 using a 2 cm diameter gouge corer. Six soil cores were taken from each transect, three from the old-growth section and three from the young-growth section, except transect 6, where only three cores were taken because this transect contained only young-growth. Cores were taken at random locations within each transect section. Each core was taken to the greatest possible depth and divided into layers: 0-10 cm (Upper), 10-20 cm (Second), 20-30 cm (Third) and > 30 cm (Fourth). Following collection soil samples were placed in sealed plastic bags, returned to the laboratory and stored in a refrigerator overnight. 5ml soil samples were mixed with 40ml double distilled water, stirred and left to settle for 1 hour before measuring pH with a Hanna HI9025 hand held pH meter (Hanna Instruments Ltd., Bedfordshire). Samples were frozen for 24hrs before being freeze dried, weighed and ground into a fine powder using a pestle and mortar. Soil C concentrations were determined with a Carlo Erba NC2500 analyser (CE Instruments Ltd., Wigan, UK), which uses a process known as 'Dynamic Flash Combustion'. C concentration is then measured from the gas passing through the thermal conductivity detector (TCD). The analyser was calibrated with High Organic Sediment OAS (Organic Analytical Standard) prior to the samples being run. Following calibration, four High Organic Sediments (with certified values of 6.72 %C) were run as controls, giving a result of 6.72 %C +/- 0.2. Bulk density was calculated by dividing dry weight by sample volume. Soil C stocks were calculated per unit area in each layer (g C cm⁻²) using C stocks (g C cm⁻³) multiplied by depth of layer. C stocks in full core depth are the sum of C stocks per unit area in each layer. Monte Carlo uncertainty analysis was carried out as described in the supporting information (Appendix 1).

2.4.5 Dead wood C

To account not only for amount of coarse woody debris (CWD) currently at the study site, but also how the amount of CWD has changed over time, the same method of line-intercept sampling was used as in a previous study (Kirby, 1992).

Line-intersect sampling comprises setting down a transect line of known length in a stand of trees and counting all dead logs, branches and trunks that are greater than 5 cm in diameter where they cross the transect line. Using this method, the length of the fallen dead wood can be estimated using the formula (Warren and Olsen, 1964; Van Wagner, 1968; Brown, 1974):

 $L = (\pi \ 10^4 \ N) \ / \ (2 \ /),$

where:

L = total length of fallen wood per hectare (m). The conversion factor of 10⁴ changes the results to metres per hectare instead of per metre square;

N = number of intersections;

I = transect length (m).

Using random sampling and a transect length of 25m, 10 transects were taken in the old-growth stands and 20 in the young-growth stands. All dead wood stems were measured at the point of interception with the transect line and assigned to a diameter class (6-10 cm, 11-20 cm or 20+ cm). Assuming a circular cross section for all logs, the lengths of dead wood stems were then converted to volumes using the formula:

 $V=I\,\pi\,d^2\,/\,4,$

where:

V = volume of dead wood for each diameter class (m³ ha⁻¹);

I = length of dead wood for each diameter class (m ha⁻¹);

d = mean diameter for each diameter class (m).

The sum of the volumes for each diameter class equals the volume of dead wood (m³) per hectare.

To convert the volume of CWD to C stocks a value for wood density is needed. According to Merganičová and Merganič (2010) the decay process must be taken into account so that C stocks in CWD are not overestimated. We therefore assigned each piece of dead wood to one of five decay categories: recently dead, weakly decayed, medium decayed, very decayed and almost decomposed. These decay categories have dry wood density values of 0.63, 0.57, 0.5, 0.51 and 0.22 g cm⁻³ respectively (Paletto and Tosi, 2010). Decay categories were recorded for a sample of dead wood transects, each 25 m long, within the permanent transects at our study site. Data from old-growth transects and young-growth transects were pooled due to the small amount of data. No C stocks or decay categories were reported in the previous dead wood survey, only the volume of CWD, so proportions of CWD in each decay category were calculated from the sample and applied to both the previous survey and our survey. The volume of CWD was then converted to C stocks using the formula (Merganičová and Merganič, 2010):

 $C = 10 V \rho c$,

where:

C = carbon stock of CWD (Kg C ha⁻¹)

V = wood volume of CWD (m⁻³ ha⁻¹)

 ρ = wood density of CWD (g cm⁻³)

c = carbon concentration in percentage of dry mass (50%). We assumed the same percentage as living biomass C concentration as Weggler et al (2012) report that C concentration does not change with decay class. Monte Carlo uncertainty analysis was carried out as described in the supporting information (Appendix 1).

2.5 Results

2.5.1 Tree biomass C

Since recording began, carbon stocks in the older growth stands have approximately doubled, going from 8.92 kg C m⁻² (0.025-quantile 7.21 kg C m⁻², 0.975-quantile 10.19 kg C m⁻²) in 1945 to 17.50 kg C m⁻² (0.025-quantile 14.09 kg C m⁻², 0.975-

quantile 20.24 kg C m⁻²) in 2010, and carbon stocks in the younger growth stands have increased by almost 50%, from 6.30 kg C m⁻² (0.025-quantile 5.39 kg C m⁻², 0.975-quantile 7.23 kg C m⁻²) in 1977 to 9.21 kg C m⁻² (0.025-quantile 7.72 kg C m⁻², 0.975-quantile 10.65 kg C m⁻²) in 2002 (Figure 2.2). This gives a net accumulation of 8.58 kg C m⁻² (0.025-quantile 6.76 kg C m⁻², 0.975-quantile 10.18 kg C m⁻²) in the older growth stands over a 65 year period and a net accumulation of 2.91 kg C m^{-2} (0.025-quantile 2.16 kg C m⁻², 0.975-quantile 3.63 kg C m⁻²) in the younger growth stands over a 25 year period. The mean estimated carbon stocks increased between any two sequential monitoring years in both older and younger growth stands, except for a decrease of 0.78 kg C m⁻² (0.025-quantile -1.17 kg C m⁻², 0.975-quantile -0.37 kg C m⁻²) between 1977 and 1983 in older growth stands. The mean discretetime annual growth rate R in older growth stands had mean estimates between 1.006 and 1.021 for all time periods except 1977-1983, where it was 0.991 (0.025quantile 0.986, 0.975-quantile 0.996). The fastest growth rate in the older growth stands (1.02, 0.025-quantile 1.017, 0.975-quantile 1.024) occurred between 1945 and 1955. The two time periods in younger growth stands had growth rates of 1.018 (0.025-quantile 1.025, 0.975-quantile 1.021) and 1.011 (0.025-quantile 1.007, 0.975-quantile 1.015) respectively. In other words, the rate of increase in tree biomass C was similar between older and younger growth.



Figure 2.2: Change in tree C stock (kg C m⁻²) for old-growth stands (1945-2010) and young-growth stands (1977-2002). Symbols are mean estimates, and vertical bars extend from 0.025-quantile to 0.975-quantile. Other studies (Pan et al. 2011; Nabuurs et al. 2003; Gimmi et al. 2009; Hu and Wang, 2008) added for comparison of changing C stocks over time.

2.5.2 Soil C

The depth to the parent material of soil cores sampled ranged from 5 cm on the steep slopes, to 54 cm on the mid slopes. Mean estimates of C storage from individual cores (over the full core depth) ranged from 2.04 kg C m⁻² (0.025-quantile 1.93 kg C m⁻², 0.975-quantile 2.16 kg C m⁻²) to 35.00 kg C m⁻² (0.025-quantile 34.31 kg C m⁻², 0.975-quantile 35.71 kg C m⁻²), highlighting the substantial variability within these forest soils. More C is stored in the upper layer (0-10 cm) of both the old- growth and young-growth stands (Figure 2.3) and generally decreases by layer. However, the old-growth stands appear to store more C below 30 cm depth, compared to the young-growth stands.



Figure 2.3: Soil C content (kg C m⁻²) by layer (1: 0-10cm, 2: 10-20 cm, 3: 20-30 cm, 4: >30 cm) for (a) old-growth and (b) young-growth stands.

In a biplot of % soil C, depth, pH and bulk density (Figure 2.4), there was little correlation between pH and the other variables. However, bulk density and depth appear strongly correlated, whilst depth and bulk density are both negatively correlated with soil C. None of the samples appear as obvious groups or clusters and no variables seem to point towards a specific group of samples. In other words, the data do not suggest systematic differences in soil properties between transects, or between young and old-growth.



Figure 2.4: Biplot of the first two principal components of natural log of percentage soil C (logC), depth, pH and natural log bulk density (logbulk), labelled by transect number and coloured black for old-growth and blue for young-growth. Arrows indicate the loading of each variable on the first two principle components, and the cosine of the angle between any two arrows approximates the correlation between the corresponding variables. The percentage of variation explained by the first two principal components is 82.5%.

Old-growth stands had more soil C per unit area than young-growth stands (oldgrowth mean estimate 11.03 kg C m⁻², 0.025-quantile 10.76 kg C m⁻², 0.975-quantile 11.27 kg C m⁻²; young-growth mean estimate 7.43 kg C m⁻², 0.025-quantile 7.22 kg C m², 0.975-quantile 7.64 kg C m-2), although this difference was mostly driven by a small number of old-growth cores with unusually high soil C. In the old-growth, 70% of C (0.025-quantile 68%, 0.975-quantile 71%) was stored in the top 20cm, while in the young-growth the top 20cm stored 81% of C (0.025-quantile 80%, 0.975quantile 83%).

2.5.3 Dead wood C

The amount of C currently being stored in CWD is 0.63 kg C m⁻² (0.025-quantile 0.27 kg C m⁻², 0.975-quantile 1.20 kg C m⁻²) in the old-growth stands and 0.75 kg C m⁻² (0.025-quantile 0.37 kg C m⁻², 0.975-quantile 1.22 kg C m⁻²) in the young-growth stands (Table 2.2). In 1992, the corresponding figures were 0.93 kg C m-2 (0.025-quantile 0.34 kg C m⁻², 0.975-quantile 1.86 kg C m⁻²) in the old-growth stands and 0.61 kg C m⁻² (0.025-quantile 0.22 kg C m⁻², 0.975-quantile 1.42 kg C m⁻²) in the young-growth stands. The uncertainty on changes between 1992 and 2011 is too large to say whether there has been an increase or a decrease in dead wood (old-growth stands mean change -0.30 kg C m⁻², 0.025-quantile -1.09 kg C m⁻², 0.975-quantile 0.34 kg C m⁻²; young-growth stands mean change 0.14 kg C m⁻², 0.025-quantile -0.52 kg C m⁻², 0.975-quantile 0.63 kg C m⁻²).

Lady Park Wood	This study, 2011			Kirby, 1992		
	YG	OG		YG	OG	
Stand Age:	66 yrs	100-135 yrs		46 yrs	80-115 yrs	
No. of transects (25m):	20	10		10	10	
Mean number of						
intersections per						
25m transect:	5.6	3.7		4.8	5.8	
Standard error:	0.8	0.9		0.8	1.8	
Number of intersections						
stem diameter (cm)						
6 - 10:	65	19		38	35	
11 - 20:	42	15		9	19	
20+	5	3		1	4	
Estimated length of						
dead wood (m/ha):	3325	2377		3110	3662	
0.025- and 0.975-quantiles:	(2740, 3895)	(1596, 3189)		(2214, 4070)	(2666, 4718)	
Estimated volume of						
dead wood (m ³ /ha):	33	28		27	41	
0.025- and 0.975-quantiles:	(24, 43)	(15, 44)		(12, 54)	(21, 71)	
-2	0.75	0.62		0.64	0.02	
C stock (kg C m ⁻):	0.75	0.63		0.61	0.93	
0.025- and 0.975-quantiles:	(0.37, 1.22)	(0.27, 1.20)		(0.22, 1.42)	(0.34, 1.86)	
Number of snags in ten transects	7	3		10	6	

Table 2.2: Line intercept sampling results for current study (2011) compared to previous study (1992) in old-growth (OG) and young-growth (YG) stands.

2.6 Discussion

2.6.1 Tree biomass C

The rapid increase in C storage in living trees during recent decades is clear, both in this study and in European syntheses (Ciais et al. 2008, Pan et al. 2011, Nabuurs et al. 2003). Although the old-growth and young-growth stands in this study have been increasing at similar rates, they are storing vastly different amounts of C. This

is due to the differing treatments they received in 1943, when the young- growth stands were clear felled (and the timber extracted to aid the war effort), whilst the old-growth stands have been mostly untouched since 1870, save for light thinnings in 1902 and probably the 1920's (Peterken and Jones, 1987).

The old-growth stands (as of 2010) are currently storing almost twice as much C as the young-growth stands (as of 2002), and as of 2010 had a 66% chance of exceeding the potential maximum C stocks for temperate, deciduous forest of 17 kg C m⁻² reported by Ciais et al. (2008). Old growth stands are often assumed to be in a steady state but evidence suggests that they will grow steadily, possibly for centuries, until set back by disturbance (Luyssaert et al. 2008). The dip after 1976 was due to a major drought, which greatly, but temporarily increased CWD to levels recorded in old-growth forests in N. America (Green and Peterken, 1997). The Swiss mountain forest (Figure 2.2), with similar values to our old-growth stands, reached 20.2 kg C m⁻² in 1975 but has since declined to 18 kg C m⁻² due to two severe windthrow events and bark beetle damage. The main tree species in LPW can probably live for 200 -500 years, yet few individuals are over 200 years due to past felling (Peterken and Jones, 1987).

Most studies available for comparison (Figure 2.2) show the amount of C stored in forested areas as being similar to the amount stored in the LPW young-growth stands. European and U.S. forests had very low growing volume per unit area around 1950 due to the large scale fellings that took place across western, central and eastern Europe during and after World War II (Vilén et al. 2012) and to earlier periods of extensive forest harvest in the U.S. (Turner et al. 1995). Although similar histories makes the increase in C storage in the young-growth stands comparable to the rest of European forests, our study site has shown no increase in forest area, as has been suggested for European forests (Kauppi et al. 2006). As increased forest area was not a factor in LPW, the increase must have been driven by an increase in growing volume per unit area.

Possible factors behind an increase in growing volume per unit area include successional dynamics and changes in disturbance regime, climate, CO₂ fertilisation and N deposition (Pan et al. 2011; Boisvenue and Running, 2006; Goodale et al. 2002). The recent large increase in C storage in the old-growth stands (1.42 kg C $\rm m^{-2}$ (0.025-quantile 0.88 kg C m⁻², 0.975-quantile 2.02 kg C m⁻²) between 2000 and 2010) may reflect tree growth and a consequent reduction in stand density (number of trees per ha), which has fallen from 384 trees/ha in 1977 to 287 trees/ha in 2010. Following suggestions from Weiner & Freckleton (2010), we plotted our data to compare plot trajectories with a -3/2 power relationship between mean biomass and stem density to detect the importance of factors other than successional self-thinning on forest biomass (Figure 2.5). As described in previous forest studies (Westoby 1984, White et al. 2007, Weiner & Freckleton 2010), we find that most of the transects rarely exceed the -3/2 power slope and generally lie within the bounds of possible size-density relationships suggested by White (1985: Fig 2.5, grey lines). Where the slope is steeper than -3/2, it is during an early successional stage following disturbance (e.g. younger 2, older 3). The transects with higher biomass do run together, parallel to a -3/2 slope and the rate of biomass increase in transect 'older 4' with the maximum biomass values does slow in recent years suggesting that a final yield value is being approached. This value may have exceeded the 17 kg C m⁻² (Fig 2.5, black line) reported for European temperate deciduous forest by Ciais et al. (2008). The curves show various trajectories dependent on disturbance history as proposed by Coomes et al. (2003). Westoby (1984) and Zeide (1987) presented evidence for how various factors such as soil fertility affected the properties of the thinning lines in biomass-density plots and we might anticipate variation in climate, CO₂ fertilisation and N deposition to influence our data when plotted in this way, although it would need controlled experiments to separate out the effects of these different drivers in Lady Park Wood. Exploration of the relative importance of these factors by comparing C measurements with experiments using a climate-driven dynamic vegetation-model indicated that release from former management and CO₂ fertilisation were the dominant factors (Chapter 3).



Figure 2.5: Logarithm (base 10) of mean tree biomass (kg, mean over transect of mean biomasses from uncertainty analysis, including both aboveground and belowground tree biomass) against logarithm (base 10) of number of stems per metre squared. Filled symbols: old-growth. Open symbols: young-growth. Arrows connect consecutive observations on the same transect. Small black dots on arrows indicate 1-year intervals (assuming constant proportional rates of change between observations), so that closely-spaced dots indicate slow change, and widely-spaced dots rapid change. Black line: constant total biomass equivalent to 17 kg C m⁻², assuming mean tree C content 48.8%. Grey lines: lines with slope -3/2, and intercept values $log_{10}(3.2)$ and $log_{10}(100)$, delimiting the boundaries of possible size-density relationships suggested by White (1985, p. 306).

2.6.2 Soil C

Soil carbon stocks in LPW were highly variable but well within the range reported from other studies. In the BioSoil soil survey (which measured soil properties from 167 plots throughout Great Britain) Vanguelova et al. (2013) reported total amounts of soil carbon stores as 10.8 kg C m^{-2} for rendzinas and 15.2 kg C m^{-2} for brown earths. These amounts are similar to the mean estimate for carbon stores in the old-growth stands (11.03 kg C m^{-2}) at LPW, however the young-growth stands are storing considerably less (7.43 kg C m^{-2}). This difference is mostly driven by a small number of old-growth cores with unusually high soil carbon. Such a wide range of values results from the complexity and number of factors that can affect soil carbon stores, for example, climate, soil (type, texture, and depth), topography, dominant trees species and management (Lal, 2005). Both the old- and younggrowth stands share the same management history until 1943 when the younggrowth stands were clear cut. The higher level of disturbance resulting from clear cutting can cause loss of soil carbon due to an increased rate of detritus decomposition and a change in microclimate (Bhatti et al. 2002). Covington (1980) produced a curve demonstrating that in the 20 years following clear cutting the forest floor decreased by over 50% (4.5 kg/m⁻²), which he attributed to rapid decomposition and reduced leaf and wood litter fall. However, other studies suggest either slower decomposition in the clear cuts (Blair and Crossley, 1988) or show no evidence that litter decomposes faster in clear cuts than in adjacent forests (Prescott et al. 2000). Currie et al. (2002) report that leaf litter is reduced for less than a decade and that canopy closure, along with leaf production, occurs quickly, within 8 years. Although the canopy in the young-growth stands was largely closed by 1955 (Peterken and Jones, 1989), it is possible that the disturbance meant that some soil carbon was lost or at the very least that soil carbon accumulation was arrested for a while. Schulp et al. (2008) suggest that organic carbon stores mainly develop in the upper layer in the first decades after disturbance and that if the stand is undisturbed for longer periods, the carbon will be transferred to deeper layers. This could explain why the old-growth stands store more carbon below 30 cm depth compared to the young-growth stands. The soils in this study are storing similar percentages of soil carbon in the top 20 cm (70% in the oldgrowth stands and 81% in the young-growth) to the rendzina soils in the BioSoil survey (Vanguelova et al. 2013), which stored 75% in the top 20 cm. However, the old-growth stands store a similar amount of carbon, as well as a similar percentage stored in the top 20 cm, to amounts reported in Vanguelova et al. (2013) whereas the young-growth stands store less carbon overall with a greater percentage being stored in the top 20 cm. This suggests that over time, if undisturbed, more carbon may be transferred to the deeper layers and therefore the amount of carbon being stored in the young-growth stands could increase.

2.6.3 Total ecosystem C (TEC)

C is apportioned differently in the different aged stands at LPW. Currently, 60% (0.025-quantile 54%, 0.975-quantile 64%) of C in the old-growth stands is stored in live biomass, 38% (0.025-guantile 34%, 0.975-guantile 43%) is stored in soil and 2% (0.025-quantile 1%, 0.975-quantile 4%) is stored in CWD. In contrast, storage of C in the young-growth stands is apportioned almost equally between live biomass (53%, 0.025-quantile 48%, 0.975-quantile 57%) and soil (43%, 0.025-quantile 39%, 0.975quantile 47%) and 4% (0.025-quantile 2%, 0.975-quantile 7%) is stored in CWD. Although soil C storage is low in LPW compared with the national average, it is the high amount of tree biomass C being stored that causes soil C to account for less than two-fifths of TEC in the old-growth stands. Soils in LPW do not account for anywhere near the 60% of TEC that Pan et al (2011) report for European temperate forests. However, Pan et al (2011) suggested that whilst tree biomass C had risen between 1990 and 2007, soil C had stayed roughly the same, meaning the proportion of C stored in tree biomass rose by 3% and the proportion of C in soil decreased by 3%. Nabuurs et al. (2003) suggested that the European annual C sink was almost equal between tree biomass and soil compartments until the 1970's, after which the tree biomass portion increased rapidly and by the 1990's accounted for 68%. Therefore it seems likely that as forests age, and tree biomass increases, there is a shift away from the soil compartment storing the majority of TEC.

What we found is mainly consistent with the European synthesis, in that tree biomass C has been increasing over the last fifty years. However the fine spatial resolution of our study yielded new insights. Far more C is being stored in tree biomass than in the soils in the old-growth stands, soils in the old-growth stands store more carbon than soils in the young-growth stands, and the soil store accounts for less than 50% TEC in both the old-growth and young-growth stands. C increase in this study is all attributable to an increase in volume per unit area and is primarily driven by recovery from former forest exploitation prior to 1944. While the rate of biomass increase in the most heavily stocked transect is slowing, C stocks are still increasing. Pan-European data also showed an increase in forest area, meaning Europe had a smaller increase in volume per unit area than LPW. The old-growth stands are storing a substantial amount of C and even the young-growth stands (of similar age to European forests) are storing more C than the amounts reported by Ciais et al. (2008) or Pan et al. (2011), with the potential to store more. This study suggests that tree biomass C can become the most important compartment for C storage, as forests age and tree biomass C increases faster than soil C. Therefore, if C storage is to be given as much emphasis as biomass production then due consideration should be given to the role of unmanaged, oldgrowth forests which contain larger trees than are found in forests managed for timber. Analysis of changing biomass-density relationships through time was not sufficiently sensitive to detect potential influence from climate change, CO2 fertilisation or N deposition. The influence of these factors can be more effectively explored using dynamic ecosystem modelling.

3 Past and Future Drivers of a Neglected Carbon Sink in European Temperate Forest

3.1 Abstract

Forests are major carbon (C) stores on a global scale but there are significant uncertainties about changes in C flux through time and the relative contributions of drivers such as land-use, climate and atmospheric CO2. We used the dynamic vegetation model LPJ-GUESS to test the relative influence of CO₂ increase, temperature increase and management on carbon storage in living biomass in an unmanaged European temperate deciduous forest. The model agreed well with living biomass reconstructed from forest surveys and maximum biomass values from other studies. High-resolution climate data from both historical records and general circulation models was used to force the model and was manipulated for some simulations to allow relative contributions of individual drivers to be assessed. Release from management was the major driver of carbon storage for most of the historical period while CO_2 took over as the most important driver in the last 20 years. Relatively little of the observed historical increase in carbon stocks was attributable to increased temperature. Future simulations using IPCC RCP4.5 and RCP8.5 scenarios indicated that carbon stocks could increase by as much as 3 kg C m⁻² by the end of the century, which is likely to be driven by CO_2 increase. This study suggests that unmanaged semi-natural woodland in Europe can be a major potential carbon sink that has been previously underestimated. Increasing the area of unmanaged forest would provide carbon sink services during recovery from timber extraction, while long-term protection would ensure carbon stocks are maintained.

3.2 Introduction

Forests globally provide a substantial and important C store but significant uncertainties exist about the changes in C flux through time (Erb et al. 2013; Mackey et al. 2013). Over the last 300 years, US forests have switched from being a C source to a C sink (Birdsey et al. 2006) and this is also likely to have occurred in China and Europe because of reforestation and reduction of intensive land-use practices, which are returning C to forest ecosystems (Erb et al. 2013; Mackey et al. 2013). Indeed Mackey et al. (2013) estimate that global terrestrial ecosystems currently act as a net C sink, as forest regrowth in the developed-world more than compensates for the effects of deforestation in developing countries. Estimates for recent changes in C fluxes are available at global (Pan et al. 2011) and regional (Birdsey et al., 2006; Ciais et al. 2008) scales, but uncertainty remains about the drivers of these changes, which may include reduced management, CO₂ fertilisation, nitrogen availability and climatic influence on photosynthesis and respiration. Bellassen et al. (2011) used a dynamic vegetation model to suggest that CO₂ fertilisation and climate change were the dominant influences on C stocks in European forests between AD 1950 and 2000, while Erb et al. (2013) stressed the role of management relaxation. The relationship between these drivers of C flux in terrestrial ecosystems is likely to have shifted through the recent past and will continue to do so in future.

Increased forest C stocks in the recent past are commonly reported and have been estimated at 1.7 kg C m⁻² in the last 50 years in Europe (Ciais et al. 2008) and 0.5 kg C m⁻² in the last 17 years in the United States (Pan et al. 2011). This is most commonly attributed to increased forest density due to recovery from more intense management (Rautiainen et al. 2011; Erb et al. 2013), or changes in atmospheric composition or climate (e.g. Bellassen et al. 2011; Mackey et al. 2013). A meta-analysis of free-air CO₂ enrichment (FACE) experiments revealed that elevated CO₂ resulted in larger plants, with greater allocation to wood and increased biomass production in trees (Ainsworth & Long, 2005). The effect of climate warming is less clear, as C stocks may be increased in some regions through extended growing

seasons due to increased temperature, but may also be reduced by negative effects on plant growth through drying or heat stress (Mackey et al. 2013).

The capacity to store C in vegetation is ultimately limited, although the maximum will change with prevailing environmental conditions. Ciais et al. (2008) suggested a potential maximum C stock of 17 kg C m⁻² for broad-leaved forests (14-15 kg C m⁻² for forests in general) using managed forest data, although such inventory data may underestimate the true C carrying capacity significantly (Keith et al. 2009). A review of global and European datasets revealed that most forests are below or close to this suggested maximum, but some forests already store considerably more (Chapter 5). These may be primary forests which are under-represented in the data used by Ciais et al. (2008), but it is possible that as a forest recovers from management, it may exceed its theoretical maximum until self-thinning processes restore equilibrium densities (Shugart, 1998). Therefore, as most UK forest is recovering from some form of timber extraction, these elevated levels may still subside to a long-term maximum.

Native temperate deciduous forests account for 36.7% of European forest cover and 12.8% (1.2 x 10^8 ha) of European land area (Schuck et al. 2002). Most of this forest is managed or experiencing the effects of management legacy (e.g. Erb et al. 2013) and only 26% of Europe's forest is now primary forest (FAO, 2010). Unmanaged forest has the potential to store more C as living biomass than forest experiencing current or recent timber extraction, although it is not clear by how much. Keith et al. (2009) reported biomass data from mature and older forests to be 2-3 times the temperate biome default values (from forest inventory data) used to inform climate change mitigation policies (IPCC, 2003). Better understanding of the role of management in determining C flux in forests, and how it relates to other drivers such as atmospheric CO₂ fertilisation and climatic change is clearly crucial for guiding policy to optimise C storage.

3.3 Aims

Here we use long-term monitoring data from a European, temperate, semi-natural, deciduous forest to reconstruct C storage in living biomass. This forest has been unmanaged since 1945 and as such represents an important contrast to studies of plantations and managed forests. We compared output from the dynamic vegetation model LPJ-GUESS with long-term monitoring data to establish reliability of simulated C stock estimates. We then used the model to explore the sensitivity of forest C stocks in this region to temperature, precipitation, CO₂ and management. Simulation results were compared to estimate the relative contribution of different variables to C fluxes during the last 65 years. Only living biomass (above- and below-ground) was considered; C stored in soils and dead biomass was omitted. The nitrogen cycle is not represented in LPJ-GUESS and therefore N fertilisation could not be considered.

3.4 Materials and methods

3.4.1 Site description and data collection

Lady Park Wood is an ancient, semi-natural woodland in the UK (51°49'N, 2°39'W; 30-190m elevation), which was coppiced for centuries but designated an unmanaged nature reserve in 1945. The main species present are beech (*Fagus sylvatica* L.), oak (*Quercus petraea* (Matt.) Liebl.), ash (*Fraxinus excelsior* L.), lime (*Tilia cordata* Mill., *T. platyphyllos* Scop.), wych elm (*Ulmus glabra* Huds.) and birch (*Betula pendula* Roth). The reserve covers 35.2 ha, of which 14 ha (old-growth stands) have experienced no management since c. 1900 when approximately 50% of tree biomass was removed (Peterken & Jones, 1987). Species proportions in these stands are around 50% beech, 20% oak, 20% ash, 8% lime, and 1% each of elm and birch. The oldest trees are c. 220 years and these stands have been well stocked with standing dead trees since 1976 when many were killed by drought. Canopy height and basal area have oscillated around a ceiling achieved by 1976 and the volume of coarse woody debris in the 1990's was similar to temperate

deciduous 'virgin' forests and USA old-growth forests. The remaining 21 ha (younggrowth stands) were virtually clear-felled in 1943 (Peterken & Jones, 1989). Species proportions in these stands are around 30% beech, 24% birch, 15% each of ash, oak and lime, and 1% elm.

Transects were established in old- and young-growth areas in 1944. Old-growth transects were recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010 and young-growth transects in 1977, 1993 and 2002 (details in Peterken & Jones, 1987; 1989). These long-term monitoring data (Mountford, E. unpub) provide location, species and diameter of all trees achieving \geq 1.3 m height. Allometric regression equations were used to calculate above-ground biomass in order to reconstruct long-term C dynamics (Chapter 2).

3.4.2 The LPJ-GUESS model

LPJ-GUESS (Smith et al. 2001) is a dynamic vegetation model that uses a gap modelling approach (Shugart, 1984; Prentice et al. 1993; Bugmann, 2001). Various plant functional types (representing groups of species with similar functional traits) and species can be simulated (hereafter PFT refers to both PFTs and species) (Hickler et al. 2004). Bioclimatic limits (Prentice et al. 1992; Sykes et al. 1996) are used to define the climate space in which each PFT may occur. Biophysical and physiological processes are represented mechanistically, using the formulations given in Sitch et al. (2003) for LPJ-DGVM, which uses an area-averaged representation of vegetation structure. In contrast, LPJ-GUESS simulates vegetation as age cohorts of different species, competing for light and water on replicate patches (100 in the present study). The model is driven by short-wave radiation (photosynthetically active light), temperature, precipitation, and CO₂ concentration of the air. Soil conditions modify the water uptake of the plant. CO₂ influences assimilation rate following the Farquar et al. (1980) approach.

Twenty-two PFTs and species were modelled including the major tree and shrub species plus a group comprising grasses and herbaceous plants, which compete

with trees for resources. Bioclimatic limits determine whether plants establish and whether they die in cold spells (for details and species specific parameters see Hickler et al. 2012). Each PFT also has a specific drought tolerance, characterised by its water uptake rate. Summergreen species require varying periods of chilling to induce budburst (Murray et al. 1989). Cohort establishment and mortality are modelled as stochastic processes within each patch. In addition, stochastic patchdestroying disturbances, representing processes such as herbivory and storm damage, result in all vegetation in a patch being transferred to the patch's litter pool and occur with an annual probability of 1/500.

3.4.3 Model forcing and simulation protocol

To equilibrate initial vegetation and carbon pools with climate at the beginning of the study period, the model was first "spun-up" for 1000 years using climate data for the period 1901-1930 cycled repeatedly and the 1901 CO₂ value. The study period then ran from 1901 to 2005. Temperature, precipitation and short-wave radiation data for 1901-2005 were taken from the WATCH dataset (Weedon et al., 2011). Both WFD (1901-1978) and WFDEI (1979-2005) were used to cover the study period and a bias correction was applied to the WFD data to create a continuous dataset. Locally measured daily temperature and precipitation data were also available from Ross on Wye (11 km from site) for years 1961 to 2005 (UK Meteorological Office). These data were used in place of the WATCH dataset for the available years and the WATCH dataset was further bias corrected using these local data (see supplementary material for method: Appendix 2). Missing values in the local station climate data were interpolated using a linear relationship ($r^2 = 0.94$, P < 0.0001) with data from Preston Wynne (34km from site). Atmospheric CO₂ was taken from the RCP Concentration Calculation & Data Group (Meinshausen et al., 2011). Simulations using modifications of these data are described below.

To project future carbon pools, temperature, precipitation and short-wave radiation for the period 2006-2100 were calculated to represent the IPCC

representative concentration pathways (RCP) 4.5 and 8.5, which project an approximate 40% increase in atmospheric CO₂ from 2006-2100 or a 250% increase respectively. These scenarios were chosen as they represent the two extremes of global temperature increase by 2100, within the range given by the IPCC AR5 report (Stocker et al., 2013) for both stabilisation scenarios (RCP4.5 and RCP6.0) and high greenhouse gas emission scenarios (RCP8.5). The RCP2.5 is considered highly unlikely and the derived climate data is not yet available. The two chosen scenarios are to some extent comparable to the AR4 SRES scenarios B1 and A2. Climate projections for the period were taken from CORDEX (Coordinated Regional Climate Downscaling; http://www.euro-cordex.net/) using data downscaled to high resolution (11' longitude / latitude). We used downscaled climate data for the grid cell containing Lady Park Wood from the CMIP5 ensemble general circulation models (GCMs) HadGEM, MPI, IPSL and CNRM. These were the only models for which downscaled data at high resolution for RCPs 4.5 and 8.5 were available. Anomalies for each month in each future year were calculated as the difference between the future month mean and the climatology (monthly mean across all years 1970-2005) for each climate variable. Daily data for the relevant climate variable from the period 1970-2005 were cycled through repeatedly to provide a baseline for future climate, maintaining intra-annual variation, and anomalies were applied to these data. A significant increasing trend was identified in the station temperature data, however, and this trend was removed before applying anomalies. For further details see supplementary material (Appendix 2).

3.4.3.1 Comparison of monitoring data with model output

Vegetation dynamics in Lady Park Wood were simulated in LPJ-GUESS for the period 1901-2000; firstly without simulated clearance, to represent the C carrying capacity of the forest in a "natural" state with no history of anthropogenic disturbance or management. This hypothetical simulation provides a baseline against which C stocks under other real or modelled conditions can be compared and is referred to as "no-clearance" throughout. The clear-felling (100% biomass

removal) that took place in the young-growth areas of Lady Park wood in 1943 and the partial felling (50%) of old-growth stands in 1901 were then simulated. These results were compared with observed old- and young-growth biomass data.

3.4.3.2 Relative effects of climate, CO2 and management

Using the old-growth simulation as a baseline, simulations with no-clearance, with detrended temperature throughout and detrended CO₂ throughout were then compared. This allowed consideration of how different C storage would have been if each observed effect had not been present. As no trend in precipitation was identified in the weather data, the effect of precipitation could not be examined, but cannot have been a driver of the observed biomass increase.

3.4.3.3 Extreme weather

Different climate variables are related strongly to each other; for example, years with higher than average summer temperatures are likely to have decreased precipitation. Hence, when investigating the effect of temperature, changing temperature alone in the driving data would be an oversimplification. The extreme climate experiments assessed the effect of climate factors by replicating years in which those factors were unusually pronounced (e.g. dry years). Local weather data was ranked in terms of temperature or precipitation levels and the top five warmest, coldest, wettest and driest years were extracted and cycled through repeatedly to simulate an extreme climate. By using real daily data from these top ranking years, the relationship between temperature and precipitation was preserved. Radiation data were not available for the site, therefore CRU data were used throughout. Clearance was not simulated here in order to focus on the effects of climate.

3.4.3.4 Future projections

The potential for C storage as biomass towards the end of this century was projected using climate data representing IPCC AR5 scenarios RCP4.5 and RCP8.5. The model was run to 2100, using the end of the no-clearance and young-growth simulations as starting points, the old-growth simulation was not used as its end point in 2000 was very similar to the no-clearance simulation.

3.5 Results

3.5.1 Comparison to data

Measured C stocks increased in old-growth unmanaged stands by 8.5 kg m⁻² over 65 years and in young-growth stands by 9 kg m⁻² over 59 years (Figure 3.1; see Chapter 2 for more details), compared to simulated C stocks which increased by 4.31 kg C m⁻² in old-growth stands and by 8.89 kg C m⁻² in the young-growth stands. Simulations of the partial clearance in 1901 and clear felling in 1943 agree relatively well with these data, with observed values falling within the limits. By the year 2000, simulated C mass in old-growth stands approaches the values of the no-clearance simulation, suggesting recovery from timber extraction is almost complete. The model correctly identified the major tree species (*Fagus, Quercus, Fraxinus, Tilia, Ulmus and Betula*) but tended to overestimate *Quercus* abundance and underestimate *Fagus, Fraxinus* and *Tilia*. This may indicate that some model parameterisations were sub-optimal for local conditions, although models can never perfectly recreate observed conditions due the random effects on vegetation establishment in multi species mixtures.

3.5.2 Relative effects of climate, CO₂ and management

The no clearance simulation represents the C carrying capacity of Lady park wood if no management had ever been applied. C storage was greater in the no clearance than in the old-growth simulation, although the difference decreased through time. The size of the difference between these simulations suggests that, for most of the study period, management legacy is likely to be the most important factor determining C stored in living biomass (Figure 3.2), and has a large but decreasing negative effect on C mass as the forest recovers from past felling. According to the model simulations, CO₂ has an increasingly large positive effect as atmospheric levels rise, indicated by reduced C mass when CO₂ is detrended. Indeed by the end of the period, the positive effect of CO₂ is larger than the negative effect of management legacy. These simulations suggest that the increase in forest biomass observed over the last century is more likely to be attributable to CO₂ fertilisation than to warmer conditions in Lady Park Wood.

3.5.3 Effects of extreme climate conditions

Figure 3.3 compares the extreme climate simulations to that without climate manipulation (all without clearance) (Table 3.2). Under dry conditions C stored as living biomass is reduced, whereas under wet conditions biomass production does a little better than under actual climate. However, biomass production was also greatly suppressed under warm conditions.



Figure 3.1: Observed biomass in old- (open circles) and young-growth (filled circles) at Lady Park Wood and LPJ-GUESS output representing C mass under various past management conditions (lines represent mean values): 50% clearance of all tree species in 1901 representing the old-growth stands (dashed); total clearance in 1943 representing young-growth stands (dotted); and no clearance representing the potential C carrying capacity or 'natural' state with a mosaic of age cohorts and no anthropogenic disturbance (solid). Shaded regions represent the standard error of mean values. Vertical bars on data points extend from 0.025-quantile to 0.975-quantile.

Simulation	1960 Cmass (kg C m ⁻²)	Δ Cmass (kg C m ⁻²)	1980 Cmass (kg C m ⁻²)	Δ Cmass (kg C m ⁻²)	2000 Cmass (kg C m ⁻²)	Δ Cmass (kg C m ⁻²)
Observed temperature & CO_2 with 50% clearance in 1901	12.87 ± 7.18	0	13.93 ± 6.48	0	15.63 ± 6.36	0
Detrended CO ₂	12.17 ± 7.00	-0.7	13.21 ± 6.31	-0.72	13.67 ± 6.10	-1.96
Detrended temperature	13.56 ± 7.30	0.69	14.73 ± 6.62	0.8	16.01 ± 6.78	0.33
No-clearance	16.68 ± 7.64	3.81	16.62 ± 7.27	2.69	16.97 ± 7.74	1.34

Table 3.1: Projected carbon mass values in 1960, 1980 and 2000 (mean \pm SD). The simulation using observed conditions represents old-growth conditions as a baseline. Δ Cmass shows the difference between each modified condition and that baseline. The biggest driver of C mass at each time point is highlighted in bold text.



Figure 3.2: LPJ-GUESS output showing the effect on stored C of removing single variables relative to observed conditions in old-growth stands (i.e. 50% tree clearance in 1901, increasing temperature and CO₂; solid line). The effect of management was removed by running the model without simulated clearance (long dashes). CO2 was detrended by using 1901 levels throughout (short dashes). Temperature was detrended using a linear regression (dotted line; see text). Lines represent means of 500 replicate patches and shaded areas represent standard error.



Figure 3.3: Effects of extreme weather conditions on stored C simulated by LPJ-GUESS using local weather data from the most extreme five years in terms of high/low temperature and high/low rainfall. Shaded areas on LPJ-GUESS output represent 95% confidence intervals.

Top 5	Mean temp Mar-Sept (°C)	Mean prec May-July (mm)	Years	
Warmest	13.70	1.07	1989, 1990, 1995, 1997, 1999	
Driest	12.98	0.89	1975, 1976, 1978, 1984, 1995	
Coldest	11.57	1.83	1962, 1965, 1972, 1974, 1986	
Wettest	12.18	2.60	1967, 1968, 1969, 1985, 1993	

Table 3.2: Summary of weather conditions during top ranking years for mean temperature (March to September) and precipitation (May to July). Climate data from these years were used to produce figure 3.3.



Figure 3.4: Future projections of C mass in Lady Park Wood using the RCP4.5 (left) and RCP8.5 (right) climate models. The starting point for future projections was the no-clearance simulation (top) and new growth simulation (bottom). Lines represent means of 500 replicate patches and shaded areas represent standard error.

3.5.4 Future C storage

During the period 2006 to 2100, C stocks were projected to either maintain approximately 2005 levels or increase by up to 3 kg C m⁻² in the simulations with no historical clearance. Projected C stored as living biomass in the young-growth stands increased rapidly to approach simulated levels without historical clearance and, in some cases, continued to rise by up to 4 kg C m⁻² (Fig 3.4). There are some

consistent differences between GCM's but the overall trends are very similar in most cases. Regardless of clearance history or GCM the difference between the two RCPs is small.

3.6 Discussion

Monitoring data reveal that, since release from management, the old-growth stands in Lady Park Wood have approximately doubled their C storage as living biomass (Figure 3.1). Furthermore, greater biomass appears to be possible and still rising (old-growth stands in 2010 = 17.50 kg C m⁻². This already exceeds the 17 kg C m⁻² maximum potential biomass suggested by Ciais et al. (2008) for European broad-leaved forest, although it may be within the range of natural variability. Previous estimates of current C sequestration have been based mostly on inventories of commercial forests in the European temperate zone and are lower than the values we report from this unmanaged area, which may still be at the lower end of the UK range. In the New Forest, for example, a value of 28 kg C m⁻² has been recorded (Mountford, unpub). The potential range of C in above-ground living biomass for American, Chinese and Australasian temperate forest given by Keith et al. (2009) (c. 15-38 kg C m⁻²) therefore also seems accurate for European forest, even under sub-optimal conditions.

The no-clearance simulations represent the potential C carrying capacity as living biomass in Lady Park Wood if no management had ever been applied. At around 17 kg C m⁻², it is similar to the suggested max of 17 kg C m⁻² for broad-leaved forest (Ciais et al. 2008). Future projections in the no-clearance stands showed either stability at 2005 levels or an increase towards the end of the century of up to 3 kg C m⁻² (Figure 3.4). However, the timescale is relatively short for forest dynamics and longer projections would be required to determine where C levels might stabilise in the long term.

According to these simulations management had the greatest effect on C stocks throughout most of the study period (Table 3.1 Figure 3.2). However, towards the end of the study period, CO₂ has taken over as the bigger driver. This has a parallel

with Erb et al.'s (2013) work in Austria, where a shift from management to 'climate and management' was identified as the major driver of mean annual increment during the latter part of the 20th century, although they did not distinguish CO₂ from climate. Relatively little of the observed increase in C stocks was attributable to climatic change, once the effects of increasing CO₂ and management were removed.

Climate manipulation experiments demonstrated that increased temperature (and associated rainfall reduction) had negative effects on C storage even though warmer conditions have been proposed to stimulate net primary productivity at northern latitudes (e.g. Zaehle et al. 2007) and this can also be demonstrated by manipulating temperature or precipitation in isolation (Appendix 2). While less precipitation will clearly cause water limitation, increased temperatures can also cause water stress by increasing demand for water. Furthermore, assimilation is inhibited in LPJ-GUESS by a negative effect of temperature on light use efficiency above 5°C, which has been demonstrated experimentally (Farquhar et al. 1980; Haxeltine & Prentice, 1996). A negative effect of increased temperature might be rather unusual in a European context, since most temperate broad-leaved forests occur in areas with a continental climate and therefore more pronounced temperature seasonality and longer winters. Under these conditions, an increase in temperature would extend the growing season, allowing more photosynthesis and therefore productivity. However, at Lady Park Wood the climate is oceanic, therefore the growing season could be only marginally extended as temperatures are generally above the photosynthesis threshold already. Any positive effect on winter net primary productivity would be outweighed by a decrease over summer, when increased temperature would increase water demand and reduce light-use efficiency. At other locations with a more continental climate a higher annual temperature may result in increased productivity.

C mass in old-growth stands was approaching "natural" levels by 2005, which indicates an approximate 100-year recovery time from 50% clearance. Recovery from 100% clearance might be expected to take significantly longer, but Figure 3.4 shows projected recovery times of 110-140 years. Therefore, intensively-managed

forest stands may recover relatively quickly if released from management. This is likely to be driven by increased CO_2 levels rather than associated warming (Figure 3.2). In the simulations of "natural" forest without historical clearance, forecasts of C stocks for the next century based on the two climate models are qualitatively similar over the first decades, while in the latter period they differ in detail, one showing relatively little change to a slow, steady increase of up to 3 kg C m⁻².

This study was confined to living biomass carbon stocks, which are closely related to soil and dead biomass carbon stocks. Currently in Lady Park Wood, 29% of carbon stocks are in the soil and 3% in coarse woody debris within the old growth stands and 46% and 5% respectively in the young growth stands (Hale, 2015). These values are rather low compared with other sites in the UK because of the thin soil cover on the steeply sloping site (Vanguelova *et al.*, 2013).

Previous European estimates of carbon storage as biomass have been far lower than the values we report from this unmanaged area, where both model and data approach the potential maximum stock estimated from old forest data and yield tables (Ciais et al. 2008). However, this potential maximum is likely to be site dependent and is significantly exceeded in other old growth deciduous forests in the UK (Hale, 2015). Native temperate deciduous forests cover a significant amount of European land area (12.8% or 1.2 x 10⁸ ha) (Shuck et al. 2002) but are mostly managed for some level of timber extraction. Nabuurs *et al.* (2013) reported that European forests are approaching equilibrium with the current level of management and thus the carbon sink effect is declining.

This study suggests that forests released from management can provide a major carbon sink during the recovery phase, as suggested by Erb *et al.* (2013) and Mackey *et al.* (2013). Consequently, the contribution of European native deciduous forests to recent carbon sequestration is likely to be significant when total ecosystem carbon is considered and this contribution has almost certainly been underestimated in the UK for the latest Global Forest Resources Assessment, where observations from plantations predominated (FRA, 2010; Hale, 2015). However, there are strict environmental limits on the carbon carrying capacity of a degraded
forest and further limits on the degree to which that can be restored. The ultimate value of these areas for carbon mitigation therefore lies in their long-term preservation, rather than their current sink status (Mackey et al. 2013). Therefore increasing the area of neglected or unmanaged semi-natural woodland in Europe will help to maximise the positive effect of CO₂ fertilisation on their carbon sink status and mitigate any negative effect due to associated climate warming. Protecting these areas in the long-term will ensure carbon stocks are maintained and that a return to source behaviour does not occur.

4 Effects of temperature and ground vegetation on decomposition rates of oak roots in an unmanaged, temperate woodland.

4.1 Abstract

The decomposition of roots is one of the most important processes in forest ecosystems, transferring significant amounts of organic matter and nutrients into the soil. Quantifying decomposition rates and identifying primary controls of root decomposition are important for evaluating ecosystem function and its response to environmental change. We conducted a 30 month field experiment using oak roots of different diameter classes (<2 mm, 2-5 mm and 5-10 mm) in decomposition bags, which were buried at two locations, one with bare ground and one with soil supporting ground layer vegetation. A TinyTag data logger, that recorded minimum and maximum temperature every 30 minutes, was buried alongside each litterbag plot. Every 6 months litterbags were removed and the mass loss calculated. Roots were also analysed for percentage carbon (C) and nitrogen (N). Mean mass loss rates of roots buried in the location with ground vegetation were significantly higher than those of roots buried in the location of bare ground. Large roots (5-10 mm) decomposed faster than medium (2-5 mm) or fine roots (<2 mm) over the first 18 months. We found little evidence of a temperature effect, nor did we find any difference between initial C:N ratio in the different diameter classes. C:N ratio dropped quickly in the large diameter class and remained lower than the other diameter classes throughout the study. Our data suggest that root diameter class and type of ground cover may exert important influences on dead root decomposition rates in Lady Park Wood.

4.2 Introduction

Within the biogeochemical cycle of forest ecosystems, the decomposition of litter and roots is one of the most important processes, transferring significant amounts of organic matter and nutrients into the soil. Temperate forests are thought to contain 2.1 - 2.2 kg C m⁻² of tree root C, with 10 - 20% of that C being stored in fine roots (Brunner & Godbold, 2007). As tree root C is retained in soils more efficiently than aboveground C inputs (Schmidt et al. 2011), decomposition of tree root C represents a potentially large C flux and soil C sink. Consequently, quantifying decomposition rates and identifying primary controls of root decomposition are important for evaluating ecosystem function (Harmon et al. 1999) and its possible response to environmental change.

Significant uncertainty still exists regarding the factors (and their interactions) that control root decomposition dynamics. Rates of mass loss have been explained by initial litter chemistry, i.e. C:N ratio, root Ca concentration, N concentration (Silver and Miya 2001; Parton et al. 2007), N as a limiting factor (Lin et al 2010), environmental variables (soil temperature, soil moisture and soil nutrient content) (Solly et al. 2014), C quality (Sun et al. 2103; Chen et al. 2002) and microbial community composition (Brant et al. 2006).

Root diameter is another possible regulating factor in decay rates, with larger diameter roots thought to decompose more slowly than smaller diameter roots, due to the longer period necessary for fungal colonisation and the increasing proportions of resistant organic substrates (Berg, 1984; Harmon et al. 1986). However, Fahey et al. (1988) found that the lignin fraction was higher in very fine roots (<0.6mm) than in small roots (0.6mm – 10mm) and the proportion of non-structural carbohydrates was lower. As initial mass loss primarily comes from the non-structural fraction (McClaugherty et al. 1984) it might be anticipated that larger roots, with a higher proportion of non-structural carbohydrates, would decay faster initially. Yet there appears to be no consistent pattern in decay rates of small or large roots (Camiré et al. 1991; McClaugherty et al. 1984; Berg, 1984; Olajuyigbe et al. 2012). Root diameter has also been linked to C and N concentrations. Gordon

and Jackson (2000) found that C concentrations increased with root diameter, whereas N concentrations decreased. Pregitzer et al. (2002) also found N concentrations decreased as root order increased (mean root diameter decreases with increase in order) but did not find any correlation between diameter and C concentration. Root order is a way to describe root architecture and begins with primary roots (first-order) then increases sequentially with each branch from the proximal to the distal portions of the root system (Pregitzer et al. 1997). This decrease in N concentration in roots with increased diameter leads to them having a higher C:N ratio (Pregitzer et al. 2002). A lower C:N ratio (15-20) is favourable for rapid microbial utilisation, and therefore faster decay rates (Pregitzer et al. 1997). Indeed, Silver and Miya (2001) reported a strong negative correlation between root decay rate and initial C:N ratios on a global scale. Along with a lower C:N ratio, very fine roots also lack secondary (wood) development in all temperate tree species (Fan and Guo, 2010) and are therefore expected to decompose faster. However, some studies show that very fine roots decompose slower than larger diameter roots in spite of these traits (Sun et al. 2013; Sun et al. 2012; McClaugherty et al. 1984).

Temperature has also been found to be a controlling factor in decomposition rates (Berg et al. 1998; Solly et al. 2014), possibly due to temperature being one of the most important drivers of enzyme activities (Wallenstein et al. 2011). Increasing temperature is found to enhance enzyme activities (Chen et al. 2000; McClaugherty and Linkins, 1990) and Baldrian et al. (2013) found that in a temperate forest the highest enzyme activities were in the warm season. Therefore if a temperature effect is present we would expect decomposition rates to be higher in warmer periods.

The microbial community, which secretes the degradative enzymes, is determined by the initial chemical composition of the litter (Baldrian and Štursová, 2011). Through changes in litter quality, plant species can affect decomposition by influencing nutrient cycling, thus possibly overriding temperature effects (Hobbie, 1992). Enzyme activities in forest soils have been shown to have seasonal patterns, related to labile C and N availability for microbes (i.e. peak rates in spring related to root exudates and peak rates in autumn related to input of fresh litter), which can alter microbial community composition (Kaiser et al. 2010). Significant activity of microbes has also been shown to continue over the winter period due to the availability of substrate C following litterfall in October (Kähkönen et al. 2001). This suggests that, although there may be a temperature effect, the availability of resources, i.e. C and N, could be more important (Bardgett et al. 2005). As plant exudates represent a high quality C source for microbes (Bartlett et al. 2005) and have been shown to increase the abundance and activity of microbes and fauna in the rhizosphere (Ostle et al. 2003), we hypothesise that roots buried in soil supporting ground-layer vegetation will decompose faster than roots buried under bare ground.

4.3 Aims

In this study we examined the effect of C:N ratio, soil temperature and ground vegetation on the decomposition of different sized oak roots (<2, 2-5 and 5-10 mm diameter) over a 2 ½ year period. Our specific objectives were to (1) determine whether the presence of ground vegetation would affect root decomposition; (2) explore the relationship between initial C:N ratio and decomposition rates, and (3) investigate effects of temperature on decomposition. We also collated literature data on root decomposition and calculated decomposition rates to compare with rates in this study.

4.4 Materials and methods

4.4.1 Site description

This study took place in Lady Park Wood (51°49'N, 2°39'W), an ancient semi-natural woodland, situated at 30 – 190 m elevation on the southern bank of the River Wye, 3km north east of Monmouth. The woodland covers 35.2 ha and was designated as an unmanaged nature reserve in 1944. Soils in the study area are acid silty clay loam brown earths, derived from old red sandstone drift, and they support old-

growth beech-ash-oak-lime woodland (Ed Mountford, unpublished data). The area chosen for the experiment was under a mixed canopy, with bare ground occurring beneath the larger beech trees. Limestone bedrock is present throughout the woodland. The study ran from November 2010 until July 2013. Thirty-year (1981-2010) mean annual temperature at local weather station Ross-On-Wye was 10.5°C and mean annual precipitation was 733.5mm (http://www.metoffice.gov.uk/climate/uk/averages/19812010/sites/ross on wye. html, accessed 30 September 2014).

4.4.2 Litterbag experiment

Oak roots of a variety of sizes were collected in November 2010. Roots were rinsed, sorted into diameter classes (<2 mm, 2-5 mm and 5-10 mm), and air dried for 2 weeks. Samples were then weighed and \sim 7 g of roots were placed into 10 cm x 10 cm litter bags (nylon, 1 mm mesh). Each litterbag contained roots from each diameter class. Two plots were chosen in the older growth stands (dominated by trees dating from 1800-1900 (Peterken and Jones, 1987)), that differed in ground cover, with one having a selection of ground vegetation present (grasses, brambles and bracken) (Fig. 4.1a) and the other having bare ground (Fig. 4.1b). Fifteen litterbags were buried at each plot by carefully removing the litter layer, laying the bags out in rows on the mineral soil, and replacing the litter layer. At each plot a Tinytag data logger, buried at the same depth as the litter bags, collected soil temperature data every 30 minutes for the duration of the study. To compare above- and below-ground temperature a TinyTag data logger was hung from the closest tree to each plot in the final year of the experiment. Three litterbags were collected from each plot at six monthly intervals. Collected bags were returned to the laboratory, where they were washed, dried at 65°C for 48 hours, and weighed.



Figure 4.1: Litterbag plots in (a) vegetated ground and (b) bare ground.

4.4.3 C:N analysis

Roots were ground into a fine powder using a coffee grinder. C and N concentrations were determined with a Carlo Erba NC2500 analyser (CE Instruments Ltd., Wigan, UK), which uses a process known as 'Dynamic Flash Combustion' whereby the sample, under a continuous flow of helium, reacts with a measured amount of oxygen, at temperatures as high as 1800°C, in order that complete sample combustion takes place (Révész et al. 2012: 3). Resulting combustion gases are then separated and C and N can be measured using a thermal conductivity detector. The analyser was calibrated with a Chitin standard (with certified values of 45.07% +/- 0.22 for C and 6.88% +/- 0.1 for N) prior to the samples being run. Following calibration, two unknown Chitin samples were run as controls, giving a result of 45.07% +/- 0.05 for C and 6.88% +/- 0.01 for N.

4.4.4 Collation of literature data

We collated literature data on root decomposition. Our main source was Silver & Miya's (2001) global data set. Other relevant sources were found from Web of Science searches using search terms such as 'root decomposition'. Sources were

used if they contained data for percentage mass remaining to allow us to calculate a mean loss rate (as described below) for similar time periods in all studies.

4.4.5 Statistical analysis

All root decomposition constants (k, years⁻¹) (this study and others) were calculated in R, version 2.14.0 (R Development Core Team, 2011), as minus the natural log of proportion remaining (weight at the end of the time period divided by weight at the start) divided by the time period (k=-ln(x/x₀)/t (where x is final mass (g), x₀ is initial mass (g), and t is time in years)) (Olson, 1963).

The data were processed using a general linear model with post-hoc analysis done using Tukey tests, in SPSS v20 for Windows. The main and interaction effects of root diameter class, type of ground cover (bare or vegetated), time since start of experiment, mean soil temperature since start of experiment, and C:N ratio on mean loss rates were examined.

4.5 Results

4.5.1 Temperature data

There was much greater variability in daily air temperatures than in daily soil temperatures (Figure 4.2). The maximum recorded difference between daily minimum and maximum air temperatures was 16°C, whereas for soil temperatures it was 7.1°C. Air temperatures generally had a higher daily maximum temperature than the soil maximum temperature and a lower minimum temperature than the soil minimum temperature, thus the soil environment appears buffered against extreme temperatures. For a short period in January 2013 the maximum soil temperatures (around 2.5°C) became warmer than the maximum air temperatures, which had fallen to around -3°C. The soil temperature never dropped below freezing in the entire study period.



Figure 4.2: Daily maximum and minimum temperatures recorded for the air and soil at the (a) bare plot and (b) vegetated plot. Air temperatures were recorded from June 2012 to July 2012 and soil temperatures from November 2010 to July 2013.

4.5.2 Mass loss and mean loss rates

The effect of diameter class depended on time (F(8,50)=3.35, P=0.004). In the first 6 months mass loss was greatest in large roots, which had a mean overall loss (bare and vegetated plots combined) of 21.5% compared to 12.5% for medium roots and 10.5% for fine roots (Figure 4.3). By 24 months the mean overall loss from fine roots (41%) was almost the same as for the large roots (43%), whilst medium roots had lost slightly less (35%). The difference between bare and vegetated plots also depended on time (F(3,50)=7.23, P<0.0005). At 6 months the mean respective mass losses from roots in bare and vegetated ground were 20% and 23% for large roots, 12% and 13% for medium roots, and 9% and 12% for fine roots. By 24 months the difference between the mean respective mass losses from roots in bare and vegetated ground were 30% and 39% for medium roots, and 40% and 42% for fine roots) had grown considerably for large and medium roots, but had stayed similar for fine roots. Mean loss rates of roots placed in bare ground (F(1,50)=45.91, P<0.0005).

There was also a significant effect of root diameter class on mean loss rates (F(2,50)=28.9, P<0.0005) with a significant difference between large and medium roots (P<0.0005) and between large and fine roots (P<0.0005) but no significant difference between medium and fine roots (P=0.981) (post-hoc Tukey tests). There was little evidence of an interaction between type of ground cover and diameter class (F(2,50)=2.675, P=0.079), and no interaction between type of ground cover, diameter class and time since start (F(6,50)=0.637, P=0.7). There was little evidence for an effect of temperature on mean loss rates (F(1,75)=2, P=0.161) (Figure 4.4).

We found no striking differences between our mean loss rates and those from other studies (Figure 4.5, Table 4.1). The mean proportion lost after 1 year was 24.1%. Rates were higher and more variable for short time periods, with less variation between rates as time progresses.



Figure 4.3: Percentage of mass remaining for roots during 30 months of decomposition in bare ground and 24 months of decomposition in vegetated ground for (a) large roots, (b) medium roots, and (c) fine roots. Each point represents a diameter class from a single litter bag.



Figure 4.4: Mean root decomposition rate k (y⁻¹) versus mean temperature (°C) for full period that litterbags were in the ground, 0-6, 0-12, 0-18, 0-24, 0-30 months, for large, medium, and fine roots in (a) bare ground and (b) vegetated ground.

	k rates (y ⁻¹) for various time periods (years) (months in brackets)												
Size	Species	Position	0.25 (3)	0.32 (4)	0.42 (5)	0.5 (6)	1 (12)	1.27 (15)	1.5 (18)	2 (24)	2.25 (27)	2.5 (30)	Reference
Mean *	Alder	15 cm depth		0.85			0.4	0.5					Camiré et al. 1991
Mean *	Poplar	15 cm depth		1			0.42	0.38					Camiré et al. 1991
< 0.5 mm	Not specified	Litter Layer			0.36		0.36						Burke & Raynal, 1994
< 0.5 mm	Not specified	10 cm depth			0.22		0.74						Burke & Raynal, 1994
0.5 mm - 1.5 mm	Not specified	Litter Layer			0.55		0.2						Burke & Raynal, 1994
0.5 mm - 1.5 mm	Not specified	10 cm depth			0.8		0.31						Burke & Raynal, 1994
1.5 mm - 3 mm	Not specified	Litter Layer			0.28		0.22						Burke & Raynal, 1994
1.5 mm - 3 mm	Not specified	10 cm depth			0.42		0.43						Burke & Raynal, 1994
0 - 0.5 mm	Hardwoods	Forest floor			0.15		0.13						McClaugherty et al. 1982
0 - 0.5 mm	Hardwoods	Mineral soil			0.3		0.12						McClaugherty et al. 1982
0.5 - 3 mm	Hardwoods	Forest floor			0.34		0.26						McClaugherty et al. 1982
0.5 - 3 mm	Hardwoods	Mineral soil			0.05		0.16						McClaugherty et al. 1982
0 - 0.5 mm	Hardwoods	Forest floor/A horizon**					0.14			0.05		0.07	McClaugherty et al. 1984
0.5 - 3 mm	Hardwoods	Forest floor/A horizon**					0.29			0.2		0.14	McClaugherty et al. 1984
< 2 mm	Sitka spruce	0 - 10 cm	0.42			0.33	0.19		0.17	0.15	0.14		Olajuyigbe et al. 2012
< 2 mm	Sitka spruce	10 - 20 cm	0.7			0.28	0.19		0.15	0.16	0.16		Olajuyigbe et al. 2012
2 - 10 mm	Sitka spruce	0 -10 cm	0.33			0.19	0.16		0.09	0.12	0.09		Olajuyigbe et al. 2012
2 - 10 mm	Sitka spruce	10 - 20 cm	0.25			0.26	0.11		0.12	0.12	0.12		Olajuyigbe et al. 2012

* Mean of all sizes (< 2 mm, 2 - 5 mm and 5 - 10 mm)

**Litter bags were placed in the same horizon that the roots were collected from.

Table 4.1: k rates (y⁻¹) from other sources for various time periods, along with root size, species, position and original reference information.



Figure 4.5: Comparison of mean root decomposition rates k (y⁻¹) for different time periods (years) between this and other studies.

4.5.3 C:N ratios

C:N ratios decreased over time for all diameter classes, with large roots generally having a lower C:N ratio for all time periods (Fig. 4.6). There was little evidence for an effect of root diameter class on initial C:N ratios (F(1,3)=0.521, P=0.639). There was little evidence of a relationship between C:N ratio at the time of removal from ground and mean loss rate up to that point (F(1,75)=2.13, P=0.149). There was, however, a significant effect of root diameter class on C:N ratio at the time of removal from the ground (F(2,62)=31.29, P<0.0005), with large roots having a significantly lower C:N ratio (post-hoc Tukey tests showed a significant difference between large and medium roots (P<0.0005) and between large and fine roots (P<0.0005) but no significant difference between medium and fine roots (P=0.641).



Figure 4.6: C:N ratios at time of removal from ground for large, medium and fine roots in bare ground (circles) and vegetated ground (diamonds). Initial C:N ratios for large, medium and fine roots (squares) are shown at time 0. Each point represents a diameter class from a single litter bag.

4.6 Discussion

4.6.1 Effects of diameter class and C:N ratio on decomposition rates

Diameter had a significant influence on the rate of decomposition, with large roots decomposing faster than medium or fine roots in the first 18 months. Silver and Miya's (2001) global review found that large diameter roots (>5 mm) decomposed much slower than smaller diameter roots. However, Camiré et al (1991) had mixed results, with the smallest alder roots (0-2 mm) decomposing slower than the medium (2-5 mm) and large (5-10 mm) alder roots. Other studies have also reported very fine roots (<0.5 mm) decomposing slower than larger roots (Sun et al. 2013; McClaugherty et al. 1984), so there appears to be no consistent pattern with regards to root diameter and rate of decomposition.

There was no difference in initial C:N ratio between our diameter classes. This differs from Gordon and Jackson (2000) who found that C concentrations increased with diameter class. The difference in C concentrations, and therefore C:N ratios, has been shown to explain a large amount of the variability in decay rates (Silver and Miya, 2001). Despite there being no initial difference in C:N ratio between our diameter classes, the C:N ratio of large roots fell rapidly and they continued to have lower C:N ratios than fine or medium roots throughout the study period. Lower C:N ratios are much more favourable for decomposition (Pregitzer et al. 1997), which might suggest a reason why our large roots decomposed faster. Mao et al. (2011) found that roots with higher N concentration and lower C:N ratios decomposed faster, possibly due to the stimulation of microbial growth. However, very fine roots have also been shown to decompose slower than larger roots, despite their lower C:N ratios (Sun et al. 2013). Our results showed that at 24 months, decomposition rates were similar for large and fine roots yet the C:N ratio was still much lower in the large roots. C:N ratios can only tell us how much C is present in relation to N, not what type of C is present. It is possible that the large roots in this study had a higher proportion of total non-structural carbohydrates (TNC), and lower proportion of lignin, than the fine roots, as reported by Fahey et al. (1988). Singh and Srivastava (1986) also found that the concentration of TNC increased with root diameter (the largest roots were 8mm diameter), with these roots acting as important carbohydrate storage organs. As the initial mass loss is made up of mostly TNC (McClaugherty et al. 1984) this might explain the initial rapid decay rates of our larger roots, which then slowed down to a rate similar to our fine and medium roots.

4.6.2 Effects of ground layer vegetation

Roots buried in soil supporting ground layer vegetation decomposed significantly faster than roots buried under bare ground. By 18 months, roots buried under vegetated ground had lost on average 20% more mass than roots buried under bare ground (all diameter classes). Microbial decomposition processes are largely controlled by substrate quality and availability of labile C (Koranda et al. 2013). A

seasonal pattern of microbial processes has been observed in temperate forest ecosystems, which is related to seasonal variation in resource availability (belowground C exudation during the growing season and litterfall in autumn) (Kaiser et al. 2010). Plant root exudates, a high quality nutrient source, can stimulate microbial growth and activity in the rhizosphere (Bardgett et al. 2005). It is likely that the vegetated plot received a larger amount of these root exudates than the bare plot throughout the growing season, therefore creating a higher level of biological activity and possibly promoting faster root decomposition. Although roots buried at the vegetated plot consistently lost mass faster, for the first 12 months the difference in decomposition between bare and vegetated plots was relatively small but became much more noticeable at 18 months. Initially, mass loss for roots buried at both plots probably came from TNC, which supplies easily accessible energy for microbes (Sun et al. 2013), thus the addition of plant root exudates at the vegetated plot perhaps only provided an advantage once the easily accessible TNC had been depleted (Fontaine et al. 2003).

Enzyme distribution is highly heterogeneous and can be affected by numerous factors, e.g. variation in microbial biomass, soil moisture and effect of individual trees (Baldrian, 2014). Our plot containing bare ground was situated next to a large beech tree. Beech trees produce low quality litter (high lignin and low N content) that can affect organic layers, pH levels and base status (Aubert et al. 2013). Beech trees, known as ecosystem engineers, create an acid environment suitable for themselves (Kooijman and Cammeraat, 2010) and this can produce a shift in microbial communities to ones with lower N requirements (Kooijman et al. 2008). On the other hand, the vegetated plot likely produced conditions favouring faster decomposition. Vegetation present at the site was largely grass. Soils of grasslands have been shown to have higher moisture content, higher microbial biomass content and higher pH values than forest soils (Solly et al. 2014). Fine roots of grasses have a rapid turnover due to the high proportion of production allocated to fine root biomass (Stewart and Frank, 2008) and decompose faster than tree roots (Silver and Miya, 2001; Solly et al. 2014). Although both plots are on forest soils it is probable that the vegetation present has influenced the soil in a similar way as grasslands, albeit on a much smaller scale. Therefore, it is possible that enzyme distribution differed between our two plots and this may be an additional reason for a difference in decomposition rates. Our results were consistent with the hypothesis that decomposition would be faster in soil supporting ground-level vegetation. However, an observational study with only two plots cannot provide a definitive test. Observations from multiple plots would provide stronger evidence, but could not show definitively that ground vegetation was causing faster root decay. Experimental manipulation could provide a definitive answer, but would be difficult and time-consuming. For example, one could remove ground vegetation from a series of plots, while leaving others as controls, wait for existing roots from the manipulated plots to decay, and then bury litter bags.

4.6.3 Carbon respiration calculations

Mean root necromass (monthly measurements taken over a year) in a mixed hardwood forest was reported to be 288 g m⁻² (Powell and Day, 1991) and C respiration from dead roots in a mid-successional oak- maple-birch forest was reported to be 110 g C m⁻² y⁻¹ (Nadelhoffer et al. 2004). A simple way to calculate the total amount of carbon respired per litter bag over the course of the experiment is to assume a constant proportional decay rate for dead roots, calculated as $k = (\ln m_0 - \ln m_t)/t = 0.254 \text{ y}^{-1}$, where $m_0 = 7.15 \text{ g}$ and $m_t = 4.3 \text{ g}$ are the initial and final dry masses respectively, and t = 2 years is the total time. Under this assumption, it can be shown that the total amount of carbon respired per litter bag is $\frac{a}{k}(m_0 - m_t) = 4.28 \text{ g}$ C, where a = 110 / 288 = 0.38 g C g⁻¹ y⁻¹ is the amount of carbon respired per gram of dead roots per year, based on the data above. It is likely that this somewhat overestimates the true amount of carbon respired, because, as noted above, decay rates tended to be fastest early in the experiment, which will reduce the mean dead root mass over the whole time period.

4.6.4 General comments

Through their ability to produce a wide range of extracellular enzymes, soil fungi and bacteria carry out a variety of decomposition processes (Baldrian et al. 2011). Spatial distributions of soil enzymes are affected by, among other things, effects of individual trees, plant roots, variation in microbial biomass and actual soil moisture, meaning that enzyme distribution, and therefore decomposition rates, are almost certainly highly dynamic (Baldrian, 2014). Temperature has been shown to increase enzyme activity during the warm period of the year (Baldrian et al. 2013) and indeed Berg et al. (1998) reported the average temperature of July as one of the controlling factors of decomposition. However, in our study, temperature appeared to be relatively unimportant, probably due to recorded temperatures approaching a long-term mean which results in decreasing variability in this explanatory variable. Many complex factors affect enzyme temperature sensitivity (Wallenstein et al. 2011), with temperature sensitivity thought to increase with increasing molecular complexity of the substrate (Davidson and Janssens, 2006). Also of critical importance are substrate concentration and the affinity of the enzyme for the substrate (Davidson and Janssens, 2006). Microbial community composition has been shown to have a strong relationship with enzyme activities over the seasonal cycle, with the main substrate for decomposition being soil organic matter in the summer, but plant litter in the autumn (Kaiser et al. 2010), and different microbial communities operating during winter and summer (Bardgett et al. 2005). Therefore it is possible that these seasonal changes override any temperature effects.

All studies showed comparable decomposition rates, with data coming from a young Sitka spruce forest and young plantations as well as from mixed deciduous forests. The fastest decomposition rates occurred in the first 6 months then rates fell. This can possibly be explained by the two-phased pattern of decomposition that McClaugherty et al. (1984) suggested, with the first phase being a period of rapid loss dominated by the loss of soluble compounds, and the second phase a period of much slower loss. How long the initial rapid phase lasted would depend on the initial amount of soluble compounds contained in the roots.

The mean dry mass loss for our roots was 2.85 g over 2 years. We do not know how much of this loss was C so we cannot directly compare this figure to the 4.28 g C respiration associated with root decomposition. However it does suggest that more C was respired than was lost from our decomposing roots. This could be due to the priming effect, whereby a greater availability of energy from the input of fresh organic matter leads to an increase in soil organic matter (SOM) degrading populations, which accelerates SOM mineralisation (Fontaine et al. 2003). This shows how important soils are in C release. Soils in temperate forests of Central Europe store approximately 6.5 kg C m⁻² with a flux of 0.44 kg C m⁻² y⁻¹ from plant litter (20% from coarse roots and 20% from fine roots) to soils (Brunner and Godbold, 2007). C from root litter has a turnover time of 5 – 10 years (Gaudinski et al. 2000). Our study site has a soil C pool of approximately 7.72 kg C m⁻² compared to 18.11 kg C m⁻² (older growth) and 8.15 kg C m⁻² (younger growth) in the tree C pool (Chapter 2).

In conclusion, our data suggest that root diameter class and type of ground cover exert the most important influence on dead root decomposition rates in Lady Park Wood. However we cannot definitively state that the ground vegetation caused faster decomposition rates and would need further experimental manipulation studies to confirm our hypothesis. We found little evidence of a temperature effect on decomposition rates nor did we find any difference between initial C:N ratio in the different diameter classes. C:N ratio dropped quickly in the large diameter class and remained lower than the other diameter classes throughout the study period. Further studies could include examining root C quality in the different diameter classes of oak roots as higher amounts of TNC might explain faster initial decomposition rates, especially noticeable in our large diameter class. Decomposition rates of all studies were generally fastest in the first 6 months and then declined as time progressed.

5 Climate change mitigation by carbon sequestration: Semi-natural unmanaged forests or plantations?

5.1 Abstract

Atmospheric levels of CO₂ are currently 395 ppm, the highest amount in the past 420,000 years, and any associated climate change will be largely irreversible for at least 1000 years. Forest plantations are often proposed as a measure to mitigate climate change due to their ability to sequester carbon (C) in wood and soils. The majority of forest area in the UK is of plantation origin, with over half covered by conifer plantations managed for timber production. Only 535,000 ha of ancient semi-natural woodland remain in the UK and little is known about C budgets in these woodlands. Forest inventories may not fully capture the dynamics of these unmanaged mixed woodland areas. Here we utilise long term monitoring data from 3 semi-natural woodlands to compare C dynamics and storage with a typical Sikta spruce plantation. We also compare C storage between differently managed European forests. A typical unthinned Sitka spruce plantation in the UK sequesters C faster than semi-natural forests, having accumulated 16 kg C m⁻² by the end of its 60 year rotation, compared to Lady Park Wood which accumulated 9.31 kg C $\mathrm{m^{\text{-2}}}$ over a 65 year period. However, semi-natural forests comprise much greater C stores over the long term. A time averaged equilibrium storage value for unthinned Sitka spruce stands is 7.4 kg C m⁻², whereas the mean storage value for semi-natural woodlands in this study is 17.5 kg C m⁻². There is clear evidence to suggest that semi-natural woodland may be an important and underestimated C stock in the UK.

5.2 Introduction

Forests are thought to contain up to 80% of all aboveground and up to 40% of all belowground terrestrial C (Dixon, 1994) and therefore play an important role in the global C cycle. Through photosynthesis, C is captured from the atmosphere and converted to forest biomass or emitted back to the atmosphere during respiration and decomposition (Percy et al. 2003). Since the industrial era, atmospheric CO₂ has risen from ~280 ppm to 395 ppm (Tans and Keeling, 2014), the highest amount in the past 420,000 years (Prentice et al. 2001). The burning of fossil fuels for energy and accelerated land clearance have both contributed to this significant increase in atmospheric CO₂ (Mackey et al. 2013), which will have long lasting effects. Between a quarter and a third of the CO₂ emitted could remain in the atmosphere for millennia (Inman, 2008) and any associated climate change will be largely irreversible for at least 1000 years, even after emissions cease (Solomon et al. 2009). In an attempt to reduce emissions the Kyoto protocol was negotiated. Linked to the United Nations Framework Convention on Climate Change (UNFCCC), the Kyoto protocol is an international agreement which commits participating countries to internationally binding emission reduction targets. The protocol also suggests that increasing C sink strength through afforestation or reforestation will reduce atmospheric CO₂ and consequently forests, through their ability to sequester C, are now increasingly recognised for their mitigation potential. The term 'sink' refers to a net flux (in units of mass/time, g C y^{-1} , or mass/(area*time), g C $m^{-2} y^{-1}$) of C into the ecosystem, whilst the term 'stocks' refers to a store of C (in units of mass, g C, or mass/area, g C m⁻²).

5.2.1 Types of forest/forest management

When considering forests for their climate change mitigation potential, a frequently proposed solution is to use plantations to sequester C in wood and soils (Jackson and Schlesinger, 2004; Winjum and Schroeder, 1997). A definition of plantation forests is given by FAO (2003) as "planted forests that have been established and are (intensively) managed for commercial production of wood and non-wood forest

products, or to provide a specific environmental service (e.g. erosion control, landslide stabilization, windbreaks etc.)". Between 2000 and 2005, 3 million ha of plantations per year were established globally, of which three quarters were for productive functions and one quarter for protective functions (FAO, 2006). As there are different levels of forest management and a range of silvicultural practices with different objectives (FAO, 2003) here we refer to planted forest as forest plantations when they fit the same criteria as Evans (2008), i.e. they are readily distinguished as artificial by possessing features of uniformity, shape and intensity of management. Winjum and Schroeder (1997) suggest that plantations can provide a significant contribution to global C storage, with a store of ~11.8 Pg in 1990 and a sink of 0.78 Pg C y⁻¹. Concerns are often raised about plantations for their lack of biodiversity (Brockerhoff et al. 2008), the assumption that native forest has been destroyed to establish plantations and concern over environmental damage (Sedjo, 1999). However, there are ways to conserve biodiversity in plantations, often with small changes to management practices (Hartley, 2002) and the expanding of plantation area, which is expected to exceed 200 million ha by 2050, means less pressure on remaining natural forests (Evans, 2008). Furthermore, most plantations are established on former agricultural lands and are seldom an important cause of deforestation (Sedjo, 1999).

Forest management is defined by FAO (2003) as "the process of planning and implementing practices for stewardship and use of the forest aimed at fulfilling relevant ecological, economic and social functions of the forest". Forest management can range from high intensive even-aged forestry (plantations) to medium-combined objective forestry, whereby individual objectives are maximised in separate areas, to low-close to nature forestry, where timber can be harvested and extracted but some standing and fallen dead wood has to remain in the forest (Duncker et al. 2012). Due to the range of management practices across Europe forests provide a wide variety of services, including timber, biomass for bioenergy, habitat functions, recreation, and regulation of water, erosion and air quality (Hengeveld et al. 2012). Nearly 90% of forests in industrialised countries have a formal or informal management plan in place (Nabuurs et al. 2007) but there is often confusion surrounding the definition of a forest management plan. For

example, the FAO (2003) suggests that an unmanaged forest has no management decisions, planning or interventions implemented, but this does not necessarily mean a forest is unmanaged. Indeed a management objective can be to have an unmanaged nature reserve (Duncker et al. 2012). In this paper our reference to managed forests means they are managed for production of timber or biomass, generally on a less intensive, more sustainable level than plantations.

Semi-natural forests are neither undisturbed by man nor are they plantations, but represent managed forests modified by man through silviculture and assisted regeneration (FAO, 2002). They usually consist of predominantly native trees which over time take on a number of natural characteristics and key elements of native ecosystems, e.g. enriched species diversity, random spacing and layered canopy (FAO, 2003). Semi-natural forests have a higher level of biodiversity than plantations, which is a key component of sustainable forest management (Rollinson, 2003). When these forests are left unmanaged, or managed as natural reserves, they will eventually take on old-growth characteristics, with the occurrence of large, old trees and dead and decaying wood (Humphrey, 2005). There has been a long accepted theory that natural forests reach a balance between storage and emissions of CO₂ and are therefore in equilibrium (Odum, 1969). More recently this theory has been challenged as new findings suggest that natural forests continue to sequester C even when mature (Luyssaert et al. 2008; Keith et al. 2009; Carey et al. 2001). Bellassen and Luyssaert (2014) propose that higher atmospheric CO₂ concentrations and nitrogen emissions may be responsible for the continual C sink behaviour in mature forests. Although the Kyoto protocol favours young forest stands for sequestering C, Sculze et al. (2000) argue that natural old growth stands allow more C to enter a permanent C pool so preserving these types of forests will have a greater effect on the carbon cycle.

5.2.2 Trade-offs of forest management

Over the past 50 years the objectives of forest management have widened from a main goal of timber production to one of sustainable forest management, whereby all goods and services of the forest should be taken into account (Farrell et al. 2000). This means managing forests for biodiversity, along with regulating, supporting, cultural and provisional services (Hicks et al. 2014). Most recently, following the Kyoto protocol, the emphasis has been on sustainably managing forests for C sequestration, with the IPCC (2007b) suggesting that a long term sustainable forest management strategy which maintains or increases C stocks whilst producing an annual yield of timber or energy will give the largest sustained mitigation benefit. Clearly, focusing on certain management objectives will have an effect on the other services a forest can provide. Managing a forest for a high timber yield, enhancing biodiversity or focusing on maximum C stocks will inevitably involve trade-offs between the various management goals (Carnus et al. 2006; Thornley and Cannell, 2000). Even within the management goal of climate change mitigation there is a possible trade-off between managing a forest for C sequestration or for providing biomass for bioenergy (Zanchi et al. 2010). Therefore, quantifying C stocks and sequestration in different pools in forests under varying management regimes can lead to a greater understanding of the trade-offs involved.

There is still much confusion surrounding the role that forests can play in enhancing and maintaining C sequestration due, in part, to the reporting of a mixture of stocks and fluxes (that are often confused) and the inclusion of different C pools in different studies (Nabuurs and Schelhaas, 2002). Understanding the many integrated C pools and their interactions are therefore important. These include not only the on-site living/dead forest C pools but also the wood product C pool, which contains the C in wood taken from the forest at harvest (Cannell and Milne, 1995), and the substitution effect, whereby fossil fuel emissions are displaced, i.e. wood is burnt in place of fossil fuels or products displace more energy intensive materials, such as steel or concrete (Lippke et al. 2012).

5.2.3 Forests in the UK

Forest area in the UK is 3.14 million ha (~ 1.6 million ha coniferous and ~ 1.5 million ha broadleaved) which equals 13% of land area (Forestry Commission, 2014). The majority of forest area in the UK is of plantation origin, with approximately 1,516,000 ha (7%) covered by conifer plantations of which the primary purpose is timber production (Norman, 2009). Since 1945 predominant conifer planting has been of *Picea sitchensis* (Sitka spruce) and *Pinus contorta* (Lodgepole pine), which share similar C storage characteristics (Cannell and Dewar, 1995). As of 1990 there were 600,000 ha of broadleaved plantations in Britain (Cannell and Dewar, 1995) with new forest area being planted at rates of between 16,000 and 21,000 ha y⁻¹ (afforestation rates in 2000 were ~7000 ha y⁻¹ of conifers and 10,000 ha y⁻¹ of broadleaved) (Milne et al. 2000). More recent afforestation (2013-2014) is at a similar rate for broadleaved (10,900 ha y⁻¹) but much lower for coniferous planting (2,200 ha y⁻¹) (Forestry Commission, 2014).

Almost 40% of ancient semi-natural woodlands were converted into plantations (which mostly contained non-native conifer species) between 1930 and 1980 (Thompson et al. 2003). Ancient woodland (land that has remained as woodland since 1600 AD, regardless of whether it has been felled periodically as part of a management cycle) covers 535,000 ha of Great Britain, with 83% of ancient woodland fragments having areas less than 20 ha (Spencer and Kirby, 1992). This means that forest inventories may not fully capture the dynamics of these unmanaged, mixed woodland areas (Harmon, 2010). Little is known about carbon budgets in these woodlands and detailed long-term data on their carbon dynamics are rather scarce. Unmanaged forests are thought to store more C than plantations (Liao et al. 2010) so are likely to be important for long term C storage, not only because forests can act as C sinks until high ages (Schulze et al. 2000; Luyssaert et al. 2008) but also because preservation of old growth natural forests, with large C pools, can have a large effect on the C cycle (Schulze et al. 2000).

5.3 Aims

Here we utilise long term monitoring data from 3 semi-natural woodlands in the UK to investigate living biomass C dynamics and storage in these types of woodland. We also compare C storage in a typical *Picea sitchensis* (Sitka spruce) plantation with C storage in semi-natural woodlands to see which stores the most C. Data are used from plots in 2 Welsh forests within 1 mile of each other; one forest is a broadleaved semi-natural woodland and the other a conifer plantation, to enable further comparison of C storage between the different types of forest. Finally, the data from semi-natural woodlands are compared to data from sustainably managed forests to allow a comparison of C storage in a range of forests with different management styles.

5.4 Methods

5.4.1 UK study sites

Lady Park Wood, Denny Wood and Clairinsh Wood were selected for study because they are semi-natural, unmanaged woodlands with long-term monitoring data available (Peterken and Jones, 1987; Mountford and Peterken, 2003; Mountford, 2000). Although they are all unmanaged with regards to wood production, Denny Wood and Clairinsh Wood receive some light management for public safety, i.e. removal of trees or branches that pose a risk. At Denny Wood this is due to a camp site that was established in the open wood close to the northern end of the Denny Wood transect (Mountford et al. 1999). Clairinsh Wood is also managed for control of deer to prevent damage and aid natural regeneration (Mountford, 2000). The data from two Welsh forests were used to enable a comparison between a seminatural broadleaved forest (Big Covert) and a typical plantation forest, whereby the close proximity of the forests to one another means that climatic conditions and local soil and rock types are similar for each forest.

5.4.1.1 Lady Park Wood

Lady Park Wood (51°49'N, 2°39'W; 30-190m elevation) is an ancient, semi-natural woodland that was managed for centuries as coppice/coppice with standards but was designated as an unmanaged nature reserve in 1944. It is situated 3 km north east of Monmouth on the southern bank of the River Wye. The reserve covers 35.2 ha, of which 14 ha are known as old-growth stands that were untouched by fellings that took place in 1943 and are dominated by trees dating from 1800-1900 (Peterken and Jones, 1987). The remaining 21 ha were virtually clear felled in 1943 and are referred to as young-growth stands (Peterken and Jones, 1989). Main species present are beech (*Fagus sylvatica*), oak (*Quercus petraea*), ash (*Fraxinus excelsior*), lime (*Tilia cordata, T. platyphyllos*), wych elm (*Ulmus glabra*) and birch (*Betula pendula, B. pubescens*). Transects consisting of a mixture of old- and young-growth areas were established in 1944. Old-growth transects were recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010 and young-growth transects in 1977, 1993 and 2002.

5.4.1.2 Denny Wood

Denny Wood Inclosure (50°51.5′N, 1°32.5′W) is an ancient, mixed deciduous woodpasture with beech (*Fagus sylvatica*) and pedunculate oak (*Quercus robur*) the main species present. It was managed as unenclosed wood pasture, a mixture of woodland and open land (a traditional form of management whereby the woodland was accessible to both deer and domestic stock and wood was harvested and renewed by pollarding) until the late 19th century (Forestry Commission, 2008). Denny Wood is located in the New Forest National Park, 2 miles east of Lyndhurst within Hampshire County. In 1870 part of the wood was fenced into the Denny Inclosure and in 1952 the Forestry Commission designated all the remaining old beech-oak forest (23 ha) in the Inclosure as a Forest Nature Reserve, but this was later reduced to a 100m wide strip (Mountford et al. 1999). The enclosed transect (1000 m x 20 m) was set up in the 1950s and was recorded in 1959, 1964, 1984, 1988 and 1996 (Mountford, 2004).

5.4.1.3 Clairinsh Wood

Clairinsh Wood (56.1° N, 4.6° W), is an ancient, semi-natural oak woodland that was managed as coppice with standards until the last cutting in 1913. Clairinsh is a 6 ha island located in the southern part of Loch Lomond National Nature Reserve (NNR), Central Scotland. The main species present are oak (*Quercus petraea, Quercus robur*) and birch (*Betula pubescens*) (Mountford, 2000). Two transects were set up in 1961, both 10 m wide (increased to 20 m in 1986) with lengths of 174 m and 362 m, and were recorded in 1961, 1986 and 1998 (Mountford, 2004).

5.4.1.4 Big Covert Wood and plantation forest, Clwyd

Big Covert is a broadleaved forest area of approximately 160 ha (53°07′N, 3°11′W). The predominant species are beech (*Fagus sylvatica*), oak (*Quercus petraea*) and birch (*Betula pendula*). The plantation forest (53°07′N, 3°10′W) is a typical conifer plantation (~ 52 ha) comprised almost entirely of Sitka spruce (*Picea sitchensis*) and Eastern hemlock (*Tsuga canadensis*), with a small amount of European larch (*Larix decidua*) (Maddox, 2014). Both forests are situated within the Clwydian Range Area of Outstanding Natural Beauty (AONB). Data was collected from five 20 m² plots in each forest in 2014 (Maddox, 2014).

5.4.2 Tree biomass C calculations

The reconstructions of long-term tree biomass C dynamics in Lady Park Wood, Denny Wood and Clairinsh Wood were based on unpublished data supplied by Ed Mountford (JNCC, personal communication). This comprised measurements of the location, species and diameter of all trees achieving \geq 1.3 m height within the monitoring transects.

Calculations for tree biomass C in the Welsh forests were based on unpublished data supplied by Alex Maddox (Maddox, 2014). These data included plot number, species, height and diameter of all trees ≥5 cm diameter within each plot. Tree core

data were also supplied, which included species from each plot and the amount of growth measured over the last 10 years (cm).

Tree measurements (dbh \ge 6.5 cm) were converted to above ground biomass using European species-specific (where possible) allometric regression equations (Zianis et al. 2005). Where European equations were not available, equations from a North American database (Jenkins et al. 2004) were used. Where there were no speciesspecific equations available, then appropriate Forestry Commission equations from the 'Carbon assessment protocol' (Jenkins et al., 2010) were substituted. Finally, C content was calculated from total biomass where a C content of 50% was assumed (Pettersen, 1984). To calculate the amount of tree C storage in 2003 for the Welsh forests the average growth per species for the last ten years was subtracted from the original dbh measurements. Allometric equations were then used on the new dbh measurements. This may introduce some error as it makes the assumption that no large trees have died/the plantation has not been thinned in the last ten years.

5.4.3 Extracting data on land types and C distributions

Figures 2 – 4, showing distribution of C in vegetation, main land cover groups and soil C, from Milne and Brown (1997) were saved as jpg images. For each figure ImageJ (Rasband, 2014) was used to calculate the area of Great Britain allocated to each category. The area (square km) was then plotted against the categories for each figure to look at the area of each land type in Great Britain and the distributions of vegetation and soil C.

5.4.4 Comparing plantation and managed forest data

The Sitka spruce plantation data came from model output (Dewar and Cannell, 1992) over a 70 year period and therefore has no real dates attached to it. For comparison with our semi-natural long-term monitoring data it was decided to give the plantation data a starting date of 1943. This coincides with the clearance of the young-growth stands in Lady Park Wood, where regeneration has been entirely

natural since then, and allows a comparison of different types of forest management from the same starting point.

The sustainably managed forest data (Bruckman et al. 2011; Ostrogović, 2013) come from chronosequence studies which have a space for time substitution. The Austrian data (Bruckman et al. 2011) come from stands ranging from 1 year to 91 years old and the Croatian data (Ostrogović, 2013) from stands between 5 years and 168 years old. Technically these data do not follow one stand through time, but in order to compare C storage in all forest types the chronosequence data have been added to the graph as if they were sequential data. A date of 1845 was chosen for the start of the sequence in order to make it comparable to LPW, where the old-growth stands are dominated by trees dating from 1800-1900. The Austrian data has a smaller age range of stands and was added to the graph with a starting year of 1901. This was the final year that LPW old-growth stands received management, when 50% of the biomass was removed. As the Austrian data comes from sustainably managed forests, where biomass is never fully removed, this should also enable a reasonable comparison.

5.5 Results

5.5.1 UK land cover and distribution of vegetation and soil C

Grasslands and agriculture are the most dominant land types in Great Britain with each having around 30% of the land cover (Figure 5.1). Woodland accounts for 11% of the land cover in 1997 (although that figure has since increased to 13% (Forestry Commission, 2014)).

The distribution of vegetation C and soil C are strongly right skewed (Figure 5.2) with most areas having very low vegetation C. Only 6% of land area has > 1 kg C m⁻² in vegetation, so all forests (semi-natural, managed and plantations) in this study are in the 94th percentile for vegetation C in Great Britain. Around 50% of land area has between 0 and 20 kg C m⁻² stored in soil. Soils in general tend to store considerably more C than vegetation does (Scharlemann et al. 2014), hence the soil

C histogram has categories comprising ranges of 20 kg C m⁻² up to > 100 kg C m⁻², whereas the vegetation C categories are 100 times smaller. In forests however, especially more mature forests, vegetation C can often reach much higher amounts than soil C.



Figure 5.1: Area of different types of land in Great Britain (data from Milne and Brown, 1997).



Figure 5.2: Distribution of amounts of (a) vegetation C and (b) soil C in Great Britain (Data from Milne and Brown, 1997).

5.5.2 Comparison of tree C storage in different types of UK forest

Denny Wood and the Big Covert forest are storing the highest amount of tree C (Figure 5.3), with Denny Wood storing 21.97 kg C m⁻² at the last recording in 1996 and the Big Covert storing 23.74 kg C m⁻² in 2013. By the end of its rotation, the typical Sitka spruce unthinned plantation had accumulated nearly twice as much tree C as the LPW young-growth stands (16 and 8.15 kg C m⁻² respectively) over the same period of time, although it fell short of storing as much as the old-growth stands (18.11 kg C m⁻²). Clairinsh Wood was storing a similar amount to the typical unthinned plantation (15.32 kg C m⁻²) at the last recording in 1998 and the conifer plantation in Clwyd (11.86 kg C m⁻²). All woodlands have been acting as C sinks apart from Denny Wood.



Figure 5.3: Amount of tree C stored in semi-natural forests (black lines), in a plantation forest, Clwyd (black dashed line) and in a typical Sitka spruce plantation with yield class 14, 2m initial spacing (from Dewar and Cannell, 1992) (grey lines) in the UK.

5.5.3 Comparison of tree C storage between sustainably managed oak forests and semi-natural forests in Europe

Even when comparing semi-natural forests with sustainably managed forests Denny Wood is still storing the greatest amount of tree C (21.97 kg C m⁻²) (Figure 5.4). The next highest C storage is in the managed Croatian forest, with the 108 year old stands storing 20.49 kg C m⁻². As the stands in this forest get older they store less C; 19.66 kg C m⁻² in the 138 year old stands and 12.69 kg C m⁻² in the 168 year old stands. The 68 year old stands are storing 16.6 kg C m⁻², which is less than the LPW old-growth stands but more than double the LPW young-growth stands, which were storing 8.11 kg C m⁻² after approximately 60 years.

The Austrian coppice with standards (CS) forest stores more C than the Austrian high forest (HF), which is initially due to the standards present in the very young CS stands (Bruckman et al. 2011). The Austrian HF has the highest amount of C in the 74 year old stands (9.75 kg C m⁻²) which is more than LPW young-growth stands but nowhere near the amount of tree C stored in the other semi-natural forests, whereas the Austrian CS surpassed the amount of C stored in Clairinsh Wood (15.32 kg C m⁻²) in its 50 year old stands (16.3 kg C m⁻²).

None of the sustainably managed stands reached tree C stores as high as Denny Wood and only the 108 and 138 year old Croatian stands achieved tree C stores higher than LPW old-growth stands. The 50 year old Austrian CS stand, along with some Croatian stands, stored more tree C than Clairinsh Wood. Most of the sustainably managed forest stands stored more tree C than LPW young-growth stands.



Figure 5.4: Comparison of tree C stores between European temperate, semi-natural forests (black lines) and sustainably managed forests (grey lines). Sustainably managed forest data comes from chronosequence studies (Ostrogović, 2013; Bruckman et al. 2011) but has been added to graph as sequential data to allow comparison (see method section for full details).

5.6 Discussion

Semi-natural old-growth forest in the UK may store a large amount of C per unit area. Out of all the forests, Denny Woods reached the highest C stocks of 28.01 kg C m⁻² in 1964. Denny Woods, the Big Covert and LPW old-growth stands have all surpassed the maximum potential C stocks (17 kg C m⁻²) suggested by Ciais et al. (2008). Keith et al. (2009) reported an average amount of 37.7 kg C m⁻² for aboveground living biomass in cool temperate moist forests, which might suggest the UK semi-natural forests have a much higher C carrying capacity than the amounts they currently store. It is likely that recovery from past management histories of browsing and selective felling is not complete yet. Substantial increases in C storage should occur as forests recover from past human disturbance (Merino et al. 2007). Odum's (1969) theory that forests reach an equilibrium, i.e. respiration increases
with forest age and eventually equals gross primary production (GPP), proposes that forests have a limit to the amount of C they can store. Recently these views have been challenged by evidence that suggests old growth forests continue to accumulate C for centuries (Luyssaert et al. 2008). Indeed Stephenson et al. (2014) report that large old trees actively fix large amounts of C, in some cases as much as is contained in a medium sized tree, each year and should not just be thought of as old C stores. However, our results clearly show that C stocks in Denny Wood have been declining since 1964. Watt (1947) concluded there was a cycle of change in all communities which consisted of a building up stage (upgrade) where the balance was positive and a breaking down stage (downgrade) where the balance was negative. Studies frequently show an age related decline in growth and biomass accumulation in forests after they have reached a peak but in contrast to Odum (1969), Ryan et al. (1997) report that the decline in net primary productivity (NPP) is driven by a decrease in GPP, along with a decrease in respiration. However, Luyssaert et al (2008) suggest there is not always a decline in productivity in oldgrowth forests as when large old trees are lost through mortality there are usually new recruits waiting to take over and maintain productivity, which happens on a shorter timescale than the CO₂ release from the dead wood (which can take decades to decompose). In Denny Wood, tree mortality due to stem exclusion and disturbance (storms in 1987 and 1990, drought in 1976) has resulted in canopy gaps extending to 30% of the transect area (Mountford et al. 1999). Despite this opening of the canopy, heavy browsing by deer and ponies has prevented regeneration from taking place since 1964 (Mountford and Peterken, 2003) and therefore productivity has been declining. In an experiment conducted in old-growth forests in Minnesota, White (2012) found that whole tree biomass in plots protected from browsing increased at a rate twice that of unprotected plots and therefore forests subject to high browsing pressure may be limited in their capacity to store C.

Compared to semi-natural forests, a typical unthinned Sitka spruce plantation in the UK may store a similar amount of C (16 kg C m⁻²) at the end of its 60 year rotation. This C is accumulated more quickly than in a semi-natural forest as LPW old-growth stands accumulated 9.31 kg C m⁻² over a 65 year period. However, as any further growth in the plantation is limited by clearfelling at the end of each rotation, the 16

kg C m⁻² is not a permanent store of C. A time-averaged equilibrium value of storage for unthinned stands is given as 7.4 kg C m⁻² (Dewar and Cannell, 1992), which means that over the long term plantations store less than half the amount of C stored in semi-natural forests.

Dead wood is an important component of forest ecosystems yet it is often underestimated or ignored as a C store (Brown, 2002). Although live C stores in Denny Wood have been declining since 1964, the C is being transferred to the dead C pool. As large dead trees can persist for decades to centuries, the dead wood pool has the potential to store large amounts of C (Harmon and Hua, 1991). In 1991, Denny Wood Inclosure had a coarse woody debris (CWD) volume of 273 m³ ha⁻¹, an extremely high amount of dead wood, comparable to amounts reported from oldgrowth stands in NE America (Christensen et al. 2005). This translates to a large C pool (>3 kg C m^{-2}) and is more than 3 times the amount present in LPW at that time. Maximum input of woody debris occurs after a disturbance when none of the formerly live material is removed (Harmon, 2009). Kirby et al. (1998) found that managed forests contained much less dead wood than unmanaged forests (less than 20 m³ ha⁻¹). Reduction of CWD accounts for one third of the difference between C stores in a plantation and in an old-growth forest (Harmon et al. 1990). McGarvey et al. (2014) suggest that the dead wood C pool is likely an important future C store that will help to maintain the sink capacity of forests for many decades. However, as this pool is either missing from or greatly reduced in managed forests or plantations it is unlikely to amount to much of a C store/sink in these types of forest.

Forest soils are an important C store which can comprise as much as 60 % of the total ecosystem C in temperate forests (Dixon et al. 1994). In a meta-analysis, using a paired site design, Liao et al. (2010) compared C stock between plantations and natural forests and found that soil C stock was 32 % lower in plantations than in natural forests (10.4 ± 1 and 12.9 ± 1.4 kg C m⁻² respectively). This analysis also showed fine root biomass to be 66 % lower in plantations (Liao et al. 2010). Fine root turnover is a major source of input to the soil C pool; with more root derived C being retained in soils than above-ground inputs of leaves or needles (Schmidt et al.

2011), therefore it is unsurprising that both fine root biomass and soil C stock were lower in the plantation forests. Bradley et al. (2005) reported woodland soil C stocks for England, Scotland and Wales as 17, 33 and 20 kg C m⁻² respectively, with the high values in Scotland being due to the high percentage of C reported for peat soils. These results come from calculations using soil type and land use data. The BioSoil soil survey (a comprehensive survey of soils in Great Britain) found that C content varied with soil depth and type, rather than type of management, with deep peats and peaty gleys containing the most C and rankers and rendzinas the least (Vanguelova et al. 2013). Much of the plantation forest cover in Scotland has been established on peaty gley soils; 590,000 ha on shallow peat soils and 150,000 ha on deep peat soils, where C stocks can average as much as 35 and 51 kg C m⁻² respectively for the top 1 m of soil (Morison et al. 2010). However, drainage and drying of peat to improve aeration, and lowering of the water table under a maturing stand, can cause an increase in the rates of oxidation, meaning any benefit from C sequestration in tree biomass may be lost (Zerva and Mencuccini, 2005). Although a disproportionate amount of forest plantations in the UK are found on peaty gleys, generally they have been planted on infertile, poor quality soils (Vanguelova et al. 2006). An equilibrium storage value of 8.3 kg C m⁻² is given by Dewar and Cannell (1992) for soils in a typical Sitka spruce plantation, a much lower amount than that found in the soils of forested peatlands. Although Vanguelova et al. (2013) found higher C stores under conifers compared to broadleaves, conifer sites tend to have larger amounts of less decomposed plant C in the organic layers, which are quickly lost following fire or erosion, whereas broadleaved forests tend to store a higher fraction of C in deeper layers of mineral soil which are more protected (Gleixner et al. 2009). Broadleaved forests have also been noted to have no effect on soil C stocks when planted onto pasture or forest land, whereas conifers significantly reduced soil C (Guo and Gifford, 2002).

Forest fragmentation, due to human land use, is leading to a greater proportion of edge habitat (the interface between forested and non-forested ecosystems or between two forests of contrasting composition or structure) meaning that more of the forest ecosystem may be experiencing 'edge effects' (Harper et al. 2005). In England, 74 % of all woodland is within 100 m of the forest edge and 45 % of

ancient woodland is within 60 m of the nearest edge (Riutta et al. 2014). 'Edge effects' are ecological responses that vary with distance from edge (Ries et al. 2004). Some of these edge effects, such as altered microclimate, temperature, moisture, wind, and light intensity (Murcia, 1995) have the potential to affect C storage. Chen et al. (1992) found that live tree biomass reduced near the edge of an old-growth Douglas-Fir forest due to high rates of tree mortality related to high wind velocities. Dantas de Paula et al. (2011) reported that interior forest plots retained almost 3 times more C than edge and fragmented plots in old-growth Atlantic forest because large stems (>70 cm) and tall trees (> 31 m height) were rare in edge or fragmented plots, which suggests that only a small percentage of the land has the full C storage potential. In a British semi-natural ancient woodland, dead wood decomposition rates at the edge of the forest were found to be almost half that of decomposition rates 100 m into the forest, meaning edge effects could have a significant impact on decomposition and the C cycle (Crockatt and Bebber, 2014). The interior habitat differs from the edge habitat in that it is usually cooler, moister and more uniform (Murcia, 1995) and often supports different species richness (Gehlhausen et al. 2000) and assemblages (Ozanne et al. 2000). Edge effects can occur from up to 30 m to > 240 m into the forest (Chen et al. 1995) so woodland needs to be of a certain size to have an interior habitat. Ancient woodland in Britain is highly fragmented, with 83 % of sites in England and Wales being <20 ha (Spencer and Kirby, 1992). Some species require large areas of intact forests to sustain populations, such as the capercaillie in Scotland, which require up to 300 ha of suitable forest habitat (Kortland, 2003). The age of the stand is also important, with edge and generalist species being found in young-growth stands and more specialised species found in old-growth stands (Peterken et al. 1992). Humphrey (2005) suggests that Britain's plantations can play a role in reducing fragmentation of semi-natural old-growth forests by allowing small patches of plantations to develop an old-growth structure, which can happen within 20-70 years. Not only would this create substantial areas of new habitat for late successional species, old-growth Sitka spruce - western hemlock forests of the Pacific Northwest have been shown to contain 90-150 kg m⁻² of living biomass, compared to 20 kg m⁻² of living biomass in a 50 year old Sitka spruce plantation in

Britain (Peterken et al. 1992). This means that areas of old-growth plantation would be likely to have much higher C stocks in living biomass than a typical plantation.

In conclusion, there is clear evidence that semi-natural woodland may be an important C store in the UK. Cannell and Milne (1995) reported C stocks in the vegetation of forests and woodlands of Britain as 91.9 million t C, with broadleaved woodlands storing 53.5 million t C (46.8 % of total C in all vegetation). The UK Global Forest Resources Assessment (FRA, 2010) reported a value of 136 million t C in living biomass for all forests in the UK. Ancient semi-natural woodlands account for 535,000 ha in Britain (Spencer and Kirby, 1992), so taking the mean C stock value for the semi-natural woodlands in this study (17.5 kg C m⁻²/175 t C ha⁻¹) means that ancient semi-natural woodlands could be storing as much as 93.6 million t C in living biomass (more than the total value reported by Cannell and Milne (1995)). Given that these types of woodland represent less than a fifth of British forests it would seem that they have been vastly underestimated as C stocks/sinks and store much more C than the younger plantation forests.

6 Conclusions

6.1 Conclusions

The work conducted for this thesis explores long-term C dynamics in Lady Park Wood, a British semi-natural deciduous woodland. Over the past 65 years C stocks have steadily increased in both the old- and young-growth stands, with C stocks more than doubling in the old-growth stands. Although rates of increase are similar for old- and young-growth stands, the old-growth stands are storing more than twice the amount of the young-growth stands. Disturbance, either anthropogenic or natural, will impact the amount of C being stored by a forest. The young-growth stands were clear-felled in 1943 and have taken 60 years to recover C stocks in the live biomass. A drought in 1976 had a significant impact on beech populations, with many large, mature beech trees being killed immediately (Peterken and Mountford, 1996) causing the noticeable decrease in C stocks in the old-growth stands. The difference between the disturbances being that following the anthropogenic disturbance, i.e. clear felling, the C is removed from the forest, whereas following the natural disturbance, i.e. drought, the C passes from the live pool to the dead wood pool. C stocks in the old-growth stands had recovered from the drought within 15 years, less time than is taken for large dead trees to break down. Recovery from disturbances can lead to substantial increases in C storage.

C is apportioned differently in the different aged stands at LPW. Due to the much larger live biomass C stocks in the old-growth stands, this pool represents 68% of the TEC, with 29% being stored in soil and 3% in CWD. In contrast, storage of C in the young-growth stands is apportioned almost equally between live biomass and soil (49% and 46% respectively), with 5% stored in CWD. Soil in LPW stored less C than expected, possibly due to the amount of shallow soils present, and the amount of C did not differ significantly between old- and young-growth stands. Therefore, it seems that as forests age, tree biomass increases and stores proportionally more of the TEC than the soil compartment.

Simulations of the partial clearance in 1901 and clear-felling in 1943, run using LPJ-GUESS, agree relatively well with C stocks in LPW calculated using historical data, although the data from the old-growth stands overshoots the model output in recent years. Though the model correctly identified the major tree species, it overestimated Quercus abundance and underestimated Fagus and Tilia. Ecosystem models are unlikely to recreate observed conditions perfectly due to their relative simplicity and their underlying assumptions that include for example no systematic browsing effects. Using a no-clearance simulation, to represent the carbon carrying capacity of LPW if no management had ever been applied, reveals that release from management is the main driver behind the increase in C stocks over most of the study period. However the influence of CO₂ on carbon stocks grows in importance as atmospheric concentrations increase and by the end of the period the positive effect of CO₂ is larger than the effect of management legacy. There was very little effect on carbon stocks attributable to temperature; in fact climate manipulation experiments demonstrated that increased temperature had negative effects on carbon storage because of increased respiration and the negative effect of temperature on light use efficiency above 5°C (Haxeltine and Prentice, 1996). During the period 2000 to 2100, projected carbon stored as living biomass in the young-growth stands increased rapidly to reach simulated levels without historical clearance. Calculated C stocks are higher than simulated C stocks in the old-growth stands by the end of the study period and although there is a predicted slow steady increase of 1 to 2 kg C m⁻² (based on IPCC A2 and B1 scenarios) the model simulations never quite reach the amount of calculated C stocks. This could be because process-based models of forest growth and C storage are based on the assumption that stands are even aged and that C exchange reaches an equilibrium (Keith et al. 2009). However as this assumption has recently been challenged (Luyssaert et al. 2008) it is possible that sometimes these models underestimate productivity and therefore C accumulation. Model simulations show that the future scenarios with past disturbance (1943 clearance) accumulate more C than the future scenarios with no clearance. Keith et al (2009) also found that the highest C stocks were found in areas experiencing past partial stand replacement, although it is unclear whether that includes a large amount of dead wood C stocks or not.

Much less is known about C dynamics below ground, i.e. root decomposition and turnover, as roots are hidden from view, occur in an environment that must be disturbed as part of any study, and require much time and effort to measure them. As a result, the contribution of decomposing roots to the C pool is often ignored (Olajuyigbe et al. 2012). Here we gained some insights into the decomposition of oak roots in a semi-natural deciduous woodland. Our data suggest that root diameter class and type of ground cover exert the most important influence on dead root decomposition rates in LPW. Large roots (5-10 mm) decomposed faster than medium (2-5 mm) or fine (<2 mm) roots over the first 18 months and mean loss rates for roots buried in the location with abundant ground vegetation were significantly higher than those for roots buried in the location with bare ground. We found little evidence of a temperature effect, possibly due to buffering effects of the soil on temperature. There was much greater variability in air temperature than in daily soil temperature. Air temperatures generally had a higher daily maximum temperature than the soil maximum temperature and a lower daily minimum temperature than the soil minimum temperature. Thus the soil environment appears buffered against extreme temperatures. For a short period in January 2013 the maximum daily soil temperatures (around 2.5°C) became warmer than the maximum daily air temperatures, which had fallen to around -3°C. In contrast to the air temperature the soil temperature never dropped below freezing in the entire study period. The mean percentage of mass lost from the roots after 1 year was 24.1 % and there were no striking differences between our mean loss rates and those from other studies. Rates were higher and more variable for short time periods, most likely due to the initial amount of soluble compounds the roots contained, with less variation as time progressed. Using available data from studies on root necromass and C respiration from dead roots (Powell and Day, 1991; Nadelhoffer et al. 2004) allowed us to estimate the amount of C respired per litter bag over 2 years (4.28 g C). The mean dry mass loss for our roots was 2.85 g over 2 years. We do not know how much of this loss was C so we cannot directly compare this figure to the 4.28 g C respiration associated with root decomposition. However it does suggest that more C was respired than was lost by physical means from our decomposing roots, possibly due to the priming effect, whereby a greater availability of energy from the input of fresh organic matter leads to an increase in soil organic matter (SOM) degrading populations, which accelerates SOM mineralisation (Fontaine et al. 2003). This shows how important soils are in C release.

The majority of forest area in the UK is of plantation origin, with less than a fifth being ancient semi-natural woodland. However, it is possible that this much smaller amount of woodland could contribute a large, previously unaccounted for, proportion of the C budget in the UK. Although a typical Sitka spruce plantation in the UK sequesters C faster (16 kg C m⁻² by the end of its 60 year rotation) than semi-natural forests (9.31 kg C m⁻² over a 65 year period in LPW), it will store much less C over the long term (7.4 kg C m⁻² compared with 17.5 kg C m⁻²). Taking the mean C storage value for the semi-natural woodlands in this study (17.5 kg C m⁻²) means that ancient semi-natural woodlands could be storing as much as 93.6 million t C, which is more than the value reported by Cannell and Milne (1995) (91.9 million t C) for total C stocks in the vegetation of forests and woodlands in the UK. Given that these types of woodland represent less than a fifth of British forests it would seem that they have been vastly underestimated as C stocks/sinks and store much more C than the younger plantation forests.

6.2 Concluding remarks

The findings in this thesis highlight the value of long-term field based site measurements in distinguishing forest C stocks/dynamics. Through these findings we can see how C stocks change over time and the impact that disturbance can have on C stocks. This knowledge helps up to quantify current C stocks and also anticipate a range of future dynamics. They have shown C stocks in ancient semi-natural woodlands in the UK to be higher than the potential maximum of 17 kg C m² suggested by Ciais et al. (2008). Although the full C storage potential of these ancient semi-natural woodlands is not well understood, the high C stocks obtained

at Denny Wood provide a reasonable estimate of a possible upper limit of these types of woodland, meaning that they could act as C sinks (as well as large C stores) for many years to come. More importantly, they have highlighted that ancient semi-natural woodlands may be an underestimated and neglected C sink/store in the UK.

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Appendix 1

Monte Carlo uncertainty analysis

Tree carbon

We used the following algorithm to estimate the uncertainty in tree carbon. R code is available from the authors on request.

For each replicate:

Draw a percentage carbon content

For each species:

Draw allometric coefficients

For each individual:

Draw diameter

Draw biomass

Multiply biomass by proportional carbon content to get tree

carbon

Add up tree carbon over all individuals and divide by transect area to get tree carbon per unit area

Carbon content

Thomas and Martin (2012a) synthesize data on carbon content in trees. In their raw data (Thomas and Martin 2012b), temperate and boreal angiosperm stem wood (n = 54) had a sample mean proportional carbon content of 48.8% and a sample standard deviation of 2.1%, and can be roughly approximated by a normal distribution. We used the same percentage carbon content for other tissues, because the relationship between carbon content in stems and other tissues is approximately 1:1 (Thomas and Martin 2012a, p. 341). We treated carbon content as constant across species because few of the major species at our site were represented in the database.

Allometric coefficients

Few of our sources for allometric equations used to estimate biomass from diameter at breast height (dbh) reported all the necessary information on uncertainty. However, for *Fagus sylvatica*, the dominant species at our site, Cienciala et al (2005) provided raw data on total aboveground biomass and dbh
(their table 2). We obtained the covariance matrix of estimated parameters from these data for both linear regression on log-transformed data and nonlinear leastsquares on untransformed data. For each species, we chose either the linear or the nonlinear covariance matrix, depending on which form of allometric equation was fitted. To include the effects of sample size on uncertainty in parameters, we scaled the selected covariance matrix by $20/n_a$, where 20 is the sample size in Cienciala et al (2005) and n_a is the sample size in the species. Where sample sizes were not reported, we set n_a to 20. We sampled parameter estimates for each species from multivariate normal distributions with mean vectors given by the reported parameter estimates for the species, and covariance matrices as described above.

Diameter

In our raw data, there was a mixture of measurements of dbh and girth at breast height in different years. We assumed that measurement error in dbh did not depend on whether dbh or girth was originally measured. From 10 replicate measurements using a tape measure of girth at breast height on each of 5 trees, we estimated that the measurement error in girth was approximately normally distributed with mean 0 and standard deviation 0.18 cm. We converted reported dbh to circumference assuming a circular cross-section, added a measurement error drawn from a normal distribution with mean 0 and standard deviation 0.18, and converted back to a simulated dbh.

Biomass

Given a simulated dbh and sampled allometric coefficients, we used the appropriate allometric equation for each species to estimate predicted biomass of each tree component. We then added a simulated normally-distributed residual to this prediction. Where the residual standard deviation was not reported, we used the values obtained from the Cienciala et al (2005) data, for either linear or nonlinear least-squares as appropriate. Since nonlinear least-squares implicitly assumes normally-distributed residuals on the original scale, negative biomasses are possible for small tree components under this method (but not under a linear model on the log scale). We truncated these to zero. This will not have a major effect because truncation only occurs for small trees, which make little contribution

to biomass. We summed the simulated biomasses across all components for each tree.

Tree carbon per unit area

When calculating tree carbon per unit area, we treated transect area as known precisely enough that there was no uncertainty in whether each tree was inside or outside the transect.

Dead wood carbon

We used the following algorithm to estimate uncertainty in dead wood carbon: For each replicate:

Draw a percentage carbon content Draw a set of decay class probabilities

Draw a set of dry densities for decay classes

Draw diameters for each piece of dead wood and put into diameter classes

Calculate mean diameter for each diameter class

For each dead wood transect:

For each diameter class

Draw a length of dead wood intersecting the transect

Calculate volume from length and mean diameter

Calculate carbon content, summing over decay classes

Sum over diameter classes

Calculate mean over transects for each stand age

Carbon content

As explained in the main text, we assumed that the distribution of carbon content was the same for dead wood as for tree biomass (and the same sequence of values for carbon content was used in each replicate of the dead wood algorithm as in each replicate of the tree carbon algorithm).

Decay class probabilities

We had decay class assignments for a total of 36 pieces of dead wood. We used a non-parametric bootstrap on these data to sample from the distribution of decay

class probabilities. Because this was a fairly small sample, we calculated pooled decay class probabilities over transects and stand ages.

Dry densities

We obtained data on dry density by decay class from Paletto and Tosi (2010), who reported means and standard deviations in their Table V. In the absence of detailed information on the distributions of these, we assumed dry densities were independently normally distributed.

Diameters

We assumed that the same measurement error distribution applied to dead wood as described above for tree diameters. When calculating volume from length, we used the mean diameter for each diameter class, because individual diameter measurements were not available for the 1992 data.

Length of dead wood

There is no general formula for the uncertainty in length of intersections from line transect sampling (Paletto and Tosi 2010). We therefore calculated the mean estimated intersection length over all dead wood transects within each of the six forest transects, separately for each stand age and diameter class. We also calculated a pooled standard deviation of intersection length over all forest transects, stand ages and diameter classes (we used a pooled estimate because the sample s were small and showed little evidence of systematic differences in variability). For each dead wood transect and diameter class, we drew a dead wood length from a normal distribution with the appropriate mean and the pooled standard deviation (truncating at zero if the sampled length was negative). For the 1992 data, we had only the total number of intersections over 10 transects for each stand age, so we drew a dead wood length from a normal distribution with this total as the mean, and standard deviation $1/\sqrt{10}$ times the pooled standard deviation for a single transect.

Soil carbon

We used the following algorithm to estimate uncertainty in soil carbon: For each replicate:

For each core layer in each core in each transect: Draw true depth of layer Draw percentage carbon in layer

Calculate carbon content in layer

Sum over layers

Take mean over cores within stand ages

True depth of layer

We assumed that two processes contribute to differences between true depth and measured depth. First, loss or compaction may mean that the apparent depth of the layer differs from the true depth. Second, the apparent depth was only measured to the nearest centimetre.

We had no quantitative information on the amount of loss or compaction that might have occurred. However, we believe that losses of more than 1 cm³ from a layer would have led to rejection of the layer. In the absence of information on compaction, we assume that apparent depth had a symmetrical triangular distribution with mode at the measured depth, minimum equal to measured depth – 1/3.5708 (equivalent to loss of 1 cm³) and maximum equal to measured depth + 1/3.5708 (equivalent to compaction leading to an extra 1 cm³ being included). The constant 3.5708 is the ratio between depth of a layer and volume in cm³ (assumed known exactly, from the shape of the corer).

We measured depth to the nearest cm. We therefore assumed that true depth had a uniform distribution with minimum equal to apparent depth – 0.5 cm, and maximum equal to apparent depth + 0.5 cm.

Percentage carbon in layer

The elemental analyser used to quantify percentage carbon was calibrated against known standards every morning. The calibration gives a standard deviation of 0.17%. We assumed that true percentage carbon had a normal distribution with mean equal to measured percentage carbon, and standard deviation 0.17%.

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Appendix 2

Bias correction:

Temperature and radiation

For the overlapping period in two datasets, a linear model was fitted to the relationship between daily values from each dataset, using the dataset to be bias corrected as the explanatory variable. The coefficients from this model were then applied to daily values in the non-overlapping part of the dataset to be bias corrected.

Precipitation

For the overlapping period in two datasets, the monthly mean value across all years (climatology) was calculated for each dataset. Values for the reference dataset were then divided by values for the dataset to be bias corrected, to give proportional differences for each month. Daily values in the non-overlapping part of the dataset to be bias corrected were then multiplied by these differences.



Figure S1

Top panel: De-trending

Temperature was de-trended by fitting a linear model (blue line) to annual means (red bars) for each month separately. This example uses temperatures for May. The difference between the predicted monthly mean and each daily value was then calculated (sum of daily variation: red arrows and monthly variation: blue arrows) and added to the predicted monthly mean for 1961 (blue dot), thereby maintaining intra-annual variability. Left panel shows data before de-trending and right panel shows data after. It should be noted that while the top panel shows a truncated range of years, the linear models were fitted to all years in the local station dataset (1961-2005).

Bottom panel: Calculating anomalies

The mean of daily values (black dots) across years 1970-2005 was calculated for each month separately to generate a climatology (blue line). This example uses temperatures for May. Monthly anomalies (blue arrows) in each future year were calculated as the difference between the future month mean (red bars) and the climatology (blue line, dashed in future years) for each climate variable. For temperature (shown here) this was calculated by subtracting the climatology from the future monthly mean (delta change method). For precipitation and radiation this was calculated by dividing the future mean by the climatology (multiplicative relative anomalies). These anomalies were then added to or multiplied by the relevant daily values to give future climate daily data.



Year



Figure S2

The effect on carbon storage of changing either temperature (above) or precipitation (below) in isolation. Temperature was modified by adding or subtracting degrees to each daily climate value, whereas precipitation was changed multiplicatively since it is a zero based variable.