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

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**Abstract**

Forest carbon stocks have increased in both Europe and North America in recent decades. National forest inventories are often used to indicate recent carbon dynamics, but the data from unmanaged forests are often incomplete. Here we calculate changing biomass carbon stocks for a mixed, unmanaged British woodland with two different management histories: (1) older growth stands untouched since 1902 and (2) younger growth stands clear felled in 1943 but have developed naturally since. Transects in the older growth have been monitored since 1945 and the younger growth since 1977. Separate estimates of tree carbon (C), soil C and dead wood C were obtained to verify how C is apportioned in these stands. Tree biomass C stocks had approximately doubled in the older growth stands since 1945 and 60% of C was stored in tree biomass, 38% was stored in soil and 2% stored in coarse woody debris. This study suggests that natural older growth stands are storing more C than typical managed forests, with tree biomass the most important compartment for C stores. If management is to be shifted from biomass production to increased C stores, due consideration should be given to the role of unmanaged, older growth forests.

Keywords: carbon stocks, soil carbon, dead wood carbon, Lady Park Wood, semi-natural forest, long-term monitoring, permanent transects.

**Introduction**

Forests comprise a large terrestrial carbon store, but one which is highly dynamic and responsive to changes in management, climate and atmospheric CO2 among other factors (Pan et al. 2011). Sequestered forest C has recently increased at global and continental scales. For example, recent estimates of C increase ranged from 1.7 kg C m-2 over the past 50 years in Europe (Ciais et al. 2008) to 0.5 kg C m-2 over the past 17 years in the United States (Pan et al. 2011). The most favoured hypotheses for these increased forest C stores are 1) increased forest area (Dominguez et al. 2015) due to new planting (Ciais et al. 2008) or natural regeneration on abandoned low productivity agricultural land, 2) increased live C store per unit area, because of reduced levels of forest grazing and recovery from forest degradation (Rautiainen et al. 2009), 3) climatic change, nitrogen deposition, and increasing atmospheric CO2 concentration, and 4) low levels of harvesting activity (compared to growth) (Dominguez et al. 2015). However, these hypotheses are hard to evaluate fully using existing data.

Forest area in both Europe and the USA has been increasing since at least 1950 (Gold et al. 2006; Rautiainen et al. 2011). The rates of expansion have been estimated at ca. 8.8% in Europe between 1990 and 2015 (Dominguez et al. 2015) and 0.5% between 1953 and 2007 (Rautiainen et al. 2011) and ca. 2.5% between 1990 and 2015 in the United States (FAO, 2015).

Live C store per unit area (i.e. C within living trees) has also been increasing since 1950, both in Europe and in America (Rautiainen et al. 2011). Estimates for Europe vary from minor increases to a doubling of live C store (Ciais et al. 2008; Gold et al. 2006), and between 1990 and 2015 the live C store increased by ~30% (1.36 kg C m-2; Dominguez et al. 2015). In America, live C store per unit area has been estimated to have increased by 51% between 1953 and 2007 (Rautiainen et al. 2011), which is thought to be due to the recovery of forests following the abandonment of agricultural land (Birdsey et al. 2007) ). A study of forests in Central Europe showed that there was faster tree growth and standing stock accumulation in 2000 compared to 1960, whereas self-thinning remained constant (Pretzsch et al. 2014). Biomass-density relationships in trees related to self-thinning and succession have received considerable theoretical and empirical study. Weiner & Freckleton (2010) discuss 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 and observed to scale as the -3/2 (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 demonstrated experimentally 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 biomass-density 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) had already suggested that old growth forests continued to sequester carbon and Stephenson et al. (2014) showed that large old trees continue to fix large amounts of C compared to smaller trees. Keith et al. (2009) reported an average value of 37.7 kg C m-2 for temperate forests.

Atmospheric CO2 has increased from ~316 ppm in 1959 to ~407 ppm in January 2018 (Tans and Keeling 2015). This increase in CO2 often leads to the assumption that forests will increase carbon sequestration rates in response. Studies show that 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) showed a positive relation between carbon balance and N deposition, although the response to additions of N may be an order of magnitude smaller than suggested (Högberg 2007). 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). McCarthy et al (2010) showed that elevated CO2 could significantly increase the rate of biomass production and the rate of C storage, although NPP enhancement was highly dependent on water and N availability. 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 likely contributions of the various mechanisms that influence the carbon 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 carbon cycle over the past 500 years. They found that land-use change was the primary control on the carbon budget for this time period with deforestation chiefly contributing to a net loss of carbon until the 1950s, when the trend was reversed and carbon 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 carbon 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 are a rather neglected source of information and they usually provide data on 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 m-2 of C (Baritz et al. 2010). Liski et al (2002) showed that litter production is related to forest biomass suggesting that unmanaged, older growth forests might be large C sinks.

In this paper we calculate changing tree 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 stores. We obtain separate estimates of tree, soil and dead wood C stores, to verify how C is allocated, and to investigate whether the soils are storing a high percentage of total ecosystem C. We also examine which of the above hypotheses about the mechanisms of recent increases in forest C storage are tenable.

**Materials and Methods**

***Study site***

This study took place in Lady Park Wood (51˚49′N, 2˚39′W) (45 acres of woodland crossing the border of Gloucestershire, England and Monmouthsire, Wales), 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 approximately 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 1 near here]

For centuries Lady Park Wood was managed as coppice/coppice-with-standards, but was designated as an unmanaged nature reserve in 1944. The reserve covers 35.2 ha; 21 ha were clear felled in 1943 and 14 ha were practically untouched by this felling (Peterken and Jones 1987). These are referred to as younger growth and older growth stands respectively.

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 (Fig. 1) that were used in this study, were established in 1944, and consist of a mixture of older and younger 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. Older growth transects were recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010. Younger growth transects were recorded in 1977, 1993 and 2002 (Peterken and Jones 1989).

***Tree biomass C***

The reconstruction of long-term C dynamics in Lady Park Wood (LPW) is based on long-term monitoring data supplied by Mountford, E. (unpublished) with location, species and diameter of all trees achieving ≥1.3 m height being recorded. Tree mortality was accounted for because measurements were made on living trees. The data for standing C crop were calculated using all trees with a DBH (diameter at breast height) ≥ 6.5 cm throughout the study. Tree measurements were converted to above- and below-ground biomass using European species-specific (where possible) allometric regression equations (Table 1) (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 species-specific equations available, 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. Throughout the results and discussion, we report the 0.025- and 0.975-quantiles of estimated quantities in parentheses.

DBH ranges for the data used to estimate allometric equations (where available) are given in Table A1 (see supporting information). In older growth, few trees were outside these ranges in 1945, but with increasing tree size, by 2010 up to 78% (for *Tilia*) were bigger than the maximum dbh used to estimate allometric equations. In younger growth, up to 70% (for *Betula* in 2002) of trees exceeded the maximum DBH used to estimate allometric equations. Thus, estimates of tree biomass may be affected by extrapolation beyond the range of data used to estimate the allometric equations, but there are few allometry data available for larger trees such as those found in Lady Park Wood.

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 C *c*(*t2*) at some time *t2* to C *c*(*t1*) at time *t1* (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/(*t2-t1*) power. Thus we obtain the mean annual growth rate   
Note that *R* is a dimensionless quantity and therefore has no units. C stocks at the two points are related by . Values of *R* less than 1 indicate a decrease in C stocks, and values greater than 1 indicate an increase. [Table 1 near here]

***Soil Organic C***

Soil samples were collected in December 2011 using a 2 cm diameter open gouge corer. The open corer insured there was negligible soil compression. Sampling in a protected forest restricted samples to small volumes and stones were almost entirely absent from the samples. Six soil cores were taken from each transect, three from the older growth stands and three from the younger growth stands, except transect 6, where only three cores were taken because this transect contained only younger growth. Cores were taken at random locations within each transect section. Each core was taken to the greatest possible depth (parent material) 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. Soil samples (5 ml) were mixed with double distilled water (40 ml), 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 24 h before being freeze dried, weighed and ground into a fine powder using a pestle and mortar. Soil organic C (SOC) concentrations were determined with a Carlo Erba NC2500 analyser (CE Instruments Ltd., Wigan, UK), which uses a process known as ‘Dynamic Flash Combustion’. Carbon 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) before the samples were 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. SOC stocks were calculated per unit area in each layer (g cm-2 of C) using SOC stocks (g cm-3 of C) multiplied by depth of layer. SOC stocks in full core depth are the sum of SOC stocks per unit area in each layer. Monte Carlo uncertainty analysis was carried out as described in the supporting information.

***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, Kirby’s (1992) line-intersect sampling method was used This method sets a transect line of known length in a stand of trees and counts 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* = (π 104 *N*) / (2 *l*),

where:

*L* = total length of fallen wood per hectare (m). The conversion factor of 104 converts the data from m m-2 to m ha-1.;

*N* = number of intersections;

*l* = transect length (m).

Using random sampling and a transect length of 25 m, 10 transects were taken in the older growth stands and 20 in the younger 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. The sum of the volumes for each diameter class equals the volume of dead wood (m3) per hectare.

In order to convert the volume of CWD to C stocks a value for wood density was needed, taking the decay process into account in order not to overestimate C stocks in CWD (Merganičová and Merganič 2010). To do this we 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 older growth transects and younger 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 December 2011 dead wood sample and applied to both the previous survey and our survey. The volume of CWD was then converted to C (as described in Merganičová and Merganič 2010). We assumed the same C concentration as in living biomass, because 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.

**Results**

***Tree biomass C***

Since recording began C stocks in the older growth stands have approximately doubled, going from 8.92 kg C m-2 (7.21 to 10.19 kg C m-2) in 1945 to 17.50 kg C m-2 (14.09 to 20.24 kg C m-2) in 2010, and C stocks in the younger growth stands have increased by almost 50%, from 6.30 kg C m-2 (5.39 to 7.23 kg C m-2) in 1977 to 9.21 kg C m-2 (7.72 to 10.65 kg C m-2) in 2002 (Fig. 2). This gives a net accumulation of 8.58 kg C m-2 (6.76 to 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 (2.16 to 3.63 kg C m-2) in the younger growth stands over a 25 year period. The mean estimated C 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 (-1.17 to -0.37 kg C m-2) between 1977 and 1983 in older growth stands. The mean discrete-time 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 (0.986, 0.996). The fastest growth rate of 1.02 (1.017, 1.024) occurred in the older growth stands between 1945 and 1955. The two time periods in the younger growth stands had growth rates of 1.018 (1.025 to 1.021) and 1.011 (1.007 to 1.015) respectively. In other words, the rate of increase in tree biomass C was similar between older and younger growth. [Figure 2 near here]

***Soil Organic 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 SOC storage from individual cores (over the full core depth) ranged from 2.04 kg C m-2 (1.93 to 2.16 kg C m-2) to 35.00 kg C m-2 (34.31 to 35.71 kg C m-2), highlighting the substantial variability within these forest soils. More SOC is stored in the upper layer (0-10 cm) of both the older growth and younger growth stands (Fig. 3) and generally decreases by layer. However, the older growth stands appear to store more SOC below 30 cm depth, compared to younger growth. [Figure 3 near here]

Older growth stands had more SOC per unit area than younger growth stands (older growth mean estimate 11.03 kg C m-2, (10.76 to 11.27 kg C m-2); younger growth mean estimate 7.43 kg C m-2 (7.22 to 7.64 kg C m-2), although this difference was mostly driven by a small number of older growth cores with unusually high SOC. In older growth, 70% of C (68, 71%) was stored in the top 20 cm, whereas in younger growth the top 20 cm stored 81% of C (80, 83%).

***Dead wood C***

The amount of C currently being stored in CWD is 0.63 kg C m-2 (0.27 to 1.20 kg C m-2) in the older growth stands and 0.75 kg C m-2 (0.37 to 1.22 kg C m-2) in the younger growth stands (Table 2). In 1992, the corresponding figures were 0.93 kg C m-2 (0.34 to 1.86 kg C m-2) in older growth and 0.61 kg C m-2 (0.22 to 1.42 kg C m-2) in younger growth. 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 (older growth mean change -0.30 kg C m-2 (-1.09 to 0.34 kg C m-2) compared to the younger growth mean change 0.14 kg C m-2 (-0.52 to 0.63 kg C m-2)). [Table 2 near here]

**Discussion**

***Tree biomass C***

The rapid increase in C stores in living trees during recent decades is clear, both in this study and in other European syntheses (Ciais et al. 2008, Pan et al. 2011, Nabuurs et al. 2003, Pretzsch et al. 2014). Although the older growth and younger growth stands in this study are increasing at similar rates, they are storing vastly different amounts of C. This is likely due to the differing treatments they received in 1943, when the younger growth stands were clear felled (and the timber extracted to aid the war effort), whilst the older growth stands have been mostly untouched since 1870, save for light thinnings in 1902 and probably during the 1920s (Peterken and Jones 1987).

The older growth stands (as of 2010) are currently storing almost twice as much C as the younger growth stands (as of 2002), and as of 2010, had a 66% chance of exceeding the potential maximum carbon stocks for temperate, deciduous forest of 17 kg C m-2 reported by Ciais et al. (2008), suggesting that a rethink of the maximum potential may be necessary. 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 importance of environmental disturbance is evidenced here by the dip after 1976, a major drought year (Rodda and Marsh 2011), which greatly, but temporarily increased CWD to levels recorded in old-growth in North America (Green and Peterken 1997). Similar disturbance impacts have been found in a Swiss mountain forest (Fig. 2), which had similar values to our older growth stands, reaching 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 (Fig. 2) show the amount of C stored in forested areas as being similar to the amount stored in the LPW younger growth stands. European and U.S. forests had very low live C store 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 live C stores in the younger 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 live C store per unit area.

Possible factors behind an increase in live C store 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 carbon storage in the older growth stands (1.42 kg C m-2 (0.88, 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 (Fig. 4). As described in previous forest studies (Westoby 1984, White et al. 2007, Weiner & Freckleton 2010, Pretzsch et al. 2014), 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. 4, 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. 4, 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 (Allen et al. 2016). [Figure 4 near here]

***Soil Organic C***

SOC 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 SOC stores as 10.8 kg m-2 of C for rendzinas and 15.2 kg m-2 of C for brown earths. These amounts are similar to the mean estimate for SOC stores in the older growth stands (11.03 kg m-2 of C) at LPW, however the younger growth stands are storing considerably less (7.43 kg m-2 of C). This difference is mostly driven by a small number of older growth cores with unusually high SOC. Such a wide range of values results from the complexity and number of factors that can affect SOC stores, for example, climate, soil (type, texture, and depth), topography, dominant tree species and management (Lal 2005). Both the older and younger growth stands share the same management history until 1943 when the younger growth stands were clear cut. How clear cutting affects the C content of the soil is still not fully understood. Initially it impacts the forest floor, an important reservoir of stored C. This organic C can be lost to the atmosphere as CO2 through biotic respiration, it can be stabilised to form a humus layer, or it can be transferred to the mineral soils (where most of the C is stored in forest soils) as dissolved organic C (DOC). 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). Yanai et al. (2003) refute Covington’s curve and suggest surface material being mixed into the mineral soil as an alternative explanation for the reduction in forest floor (meaning less C is released to the atmosphere). 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 younger growth stands was largely closed by 1955 (Peterken and Jones 1989), it is possible that the disturbance meant that some SOC was lost or at the very least that SOC accumulation was arrested for a while. Schulp et al. (2008) suggest that organic C stores mainly develop in the upper layer in the first decades after disturbance and that if the stand is undisturbed for longer periods, the C will be transferred to deeper layers. This could explain why the older growth stands store more C below 30 cm depth compared to the younger growth stands. The soils in this study are storing similar percentages of SOC in the top 20 cm (70% in the older growth stands and 81% in the younger growth) to the rendzina soils in the BioSoil survey (Vanguelova et al. 2013), which stored 75% in the top 20 cm. However, the older growth stands store a similar amount of SOC, as well as a similar percentage stored in the top 20 cm, to amounts reported in Vanguelova et al. (2013) whereas the younger growth stands store less SOC overall with a greater percentage being stored in the top 20 cm. This suggests that over time, if undisturbed, more C may be transferred to the deeper layers and therefore the amount of C being stored in the younger growth stands could increase.

***Total ecosystem C (TEC)***

C is apportioned differently in the different aged stands at LPW. Currently, 60% (54%, 64%) of C in the older growth stands is stored in live biomass, 38% (34%, 43%) is stored in soil and 2% (1%, 4%) is stored in CWD. In contrast, storage of C in the younger growth stands is apportioned almost equally between live biomass (53% (48%, 57%)) and soil (43% (39% (57%)) and 5% (2%, 7%) is stored in CWD. The high amount of tree biomass C being stored causes soil C to account for less than two-fifths of TEC in the older 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 most of the older growth LPW soil lies on steep slopes and is shallow, with litter often washed downslope. 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 1970s, after which the tree biomass portion increased rapidly and by the 1990s accounted for 68%.

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 older growth stands, soils in the older growth stands store more C than soils in the younger growth stands, and the soil store accounts for less than 50% TEC in both the older growth and younger growth stands. Increased live C store per unit area in this study is primarily driven by recovery from former forest exploitation, i.e. before 1944 (Allen et al. 2016). 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 live C stores per unit area than LPW. The older growth stands are storing a substantial amount of C and even the younger 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 stores, as forests age and tree biomass C increases faster than soil C. Glatthorn et al. (2017) compared three primeval and three production forests of European beech and found aboveground live biomass stocks were 20% higher in the primeval forests, and that the primeval forests were as productive as the production forests. Therefore, if C stores are to be given as much emphasis as biomass production then due consideration should be given to the role of unmanaged, old growth forests which contain larger trees than are usually found in plantations and managed mixed forests.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **Component** | **Equation** | **a** | **b** | **c** | **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 1. Equations used for main tree species: 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. Components not included in equations: *Acer* – stump, *Betula* – stump, *Fagus* – foliage/stump, *Fraxinus* – stump, *Tilia* – stump.

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| --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |
| **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 (m3/ha): | | 33 | 28 |  | 27 | 41 |
| 0.025- and 0.975-quantiles: | | (24, 43) | (15, 44) |  | (12, 54) | (21, 71) |
|  |  |  |  |  |  |  |
| C stock (kg C m-2): | | 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 | | 7 | 3 |  | 10 | 6 |
| ten transects |  |  |  |  |  |  |

Table 2. Line intercept sampling results for current study (2011) compared to previous study (1992)

**Figure Legends**

Fig. 1 Map of Lady Park Wood showing the distribution of older growth (clear) and younger growth (stippled) stands, the location of cliffs, and the position of the transects studied (Peterken and Jones 1987).

Fig. 2. Change in tree C stock for older growth stands (1945-2010) and younger 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; Hung and Wang 2008) added for comparison of changing C stocks over time.

Fig.3. Variation in C content (natural log kg C m-2) by layer (1: 0-10cm, 2: 10-20 cm, 3: 20-30 cm, 4: >30 cm) for (a) older growth and (b) younger growth stands

Fig. 4. 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: older growth. Open symbols: younger 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 log10(3.2) and log10(100), delimiting the boundaries of possible size-density relationships suggested by White (1985, p. 306).