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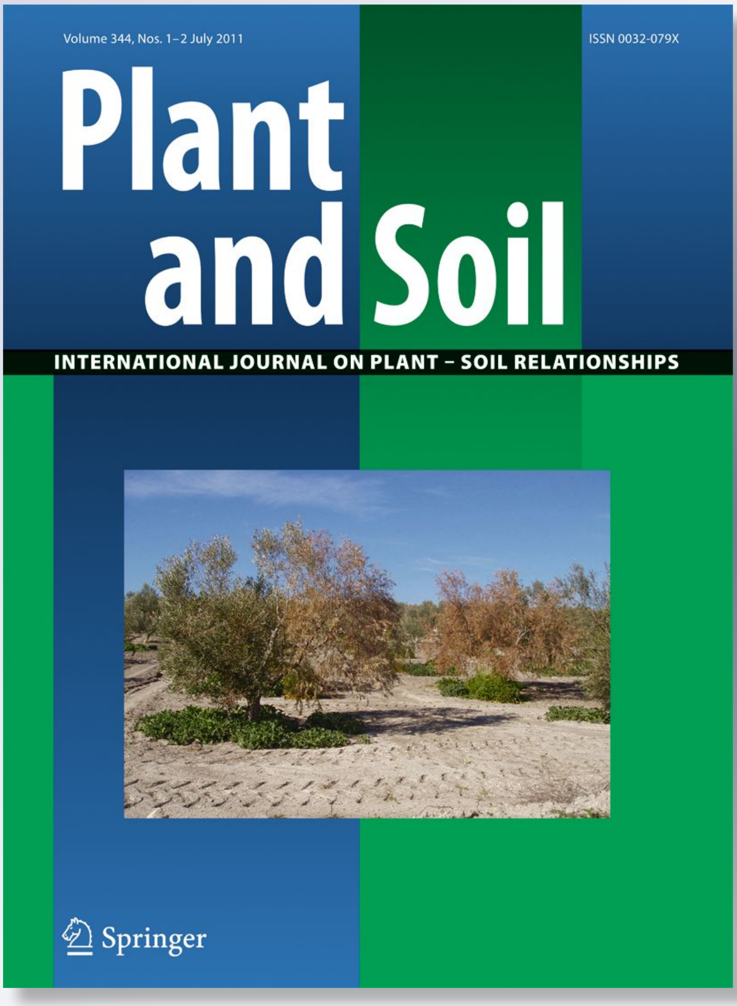

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REGULAR ARTICLE

# Above- and belowground ecosystem biomass, carbon and nitrogen allocation in recently afforested grassland and adjacent intensively managed grassland

**Matthias Peichl · Natalie Anne Leava · Gerard Kiely**

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**Abstract**
*Background and Aims* This study investigated initial land-use change effects on ecosystem biomass, carbon (C) and nitrogen (N) allocation and storage by comparing a recently afforested grassland with an adjacent intensively managed grassland in southern Ireland.
*Methods* Soil C, N and fine root (<2 mm) stocks were determined from soil cores. Above ground biomass, C and N stocks were estimated from biomass clipping, inventory and allometric biomass equations developed for ash (*Fraxinus excelsior* L.) and black alder (*Alnus glutinosa* L.) in the 5-year-old forest plantation.
*Results* Five years after grassland afforestation, the mean fine root stock of 0.31 kg $m^{-2}$ in the forest was about half that of 0.64 kg $m^{-2}$ in the grassland. This decrease was offset by an additional gain of 0.36 kg $m^{-2}$ in tree biomass since afforestation. The above- to below ground biomass ratio shifted from 0.20 in the grassland to 1.59 in the forest. From May to October, mean net N mineralization was significantly lower in the forest compared to the grassland. Soil C and N concentrations in the 0–10 cm soil layer were significantly higher in the forest (62 mg C $g^{-1}$; 5.7 mg N $g^{-1}$) compared to the grassland (45 mg C $g^{-1}$; 3.6 mg N $g^{-1}$). However, the bulk density in the upper forest soil layer was lower than in the grassland. As a result, no differences existed between the respective total (0–30 cm depth) soil C and N stocks. Total ecosystem C and N storage was also similar for the forest (9.5 kg C $m^{-2}$; 0.75 kg N $m^{-2}$) and the grassland (9.3 kg C $m^{-2}$; 0.77 kg N $m^{-2}$).
*Conclusions* A significant change in total ecosystem C and N following afforestation of this intensively managed grassland was not observed. Nevertheless, this study highlights immediate implications from such land-use change activities on biomass, C and N reallocation among the above- and belowground ecosystem pools which may subsequently affect ecosystem biogeochemical cycles.

**Keywords** Allometric equation · Ash (*Fraxinus excelsior* L.) · Black alder (*Alnus glutinosa* L.) · Broadleaf forest · Fine roots · Land-use change · Net nitrogen mineralization · Vegetation and soil carbon and nitrogen

## Introduction

Plant biomass and soil provide important carbon (C) and nitrogen (N) reservoirs and are key components

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of the global C and N cycles (Dixon et al. 1994; Houghton 2005; Lal 2005; Gruber and Galloway 2008; Wang and Houlton 2009). Furthermore, N allocation, availability and turnover are linked to plant growth and thus ecosystem C dynamics (e.g. Booth et al. 2005; Yang et al. 2010). With land-use type being a major factor predetermining ecosystem C and N pools, any land-use change activity (e.g. afforestation of grassland) may lead to significant reallocation of ecosystem biomass, C and N with subsequent implications for above- and belowground biogeochemical processes and ecosystem C and N cycles (Schimel 1986; Post and Kwon 2000; Booth et al. 2005; Mueller and Kogel-Knabner 2009).

Grasslands contain about one third of the global terrestrial C pool with the majority of their C and N stocks located belowground (White et al. 2000). Moreover, managed grasslands are characterized by external inputs and outputs of C and N via fertilizer application, grass harvest and/or grazing activities (Snaydon 1987; Jones and Donnelly 2004). Furthermore, they may experience periodic soil disturbances through ploughing prior to re-seeding or rotational forage crop planting events affecting soil C and N dynamics (Wilkins et al. 2003; Vellinga et al. 2004). In contrast to grasslands, forested lands commonly accumulate biomass in tree biomass components (stem, branches, foliage and roots) and in the organic forest floor layer, and exhibit rather closed C, N and nutrient cycles (Schulze 2000; Vesterdal et al. 2002). Grassland to forest transition (and vice versa) due to land-use change activities is therefore associated with multiple controls affecting the allocation and storage of above- and belowground ecosystem biomass, C and N (Arora and Boer 2010; Wei et al. 2010).

In Ireland, grassland accounts for ~55% of land cover area, while forests occupy only ~10% of the land area (Eaton et al. 2008). However, recent government funding incentives for afforestation efforts have resulted in an increase of forest area during the past decade (Department of Agriculture, Food and Forestry 1996; Teagasc 2007). Moreover, efforts are being undertaken to increase the contribution of broadleaf species (specifically ash (*Fraxinus excelsior* L.)) in Ireland's forests (Teagasc 2007). As a consequence, there is a need to better understand the implications from such changes in land-use type and associated management practices on ecosystem C storage on a regional and national level.

Changes in ecosystem biomass following grassland afforestation are essentially driven by the development of a permanent tree biomass pool. A large body of allometric biomass equations has been gathered over the past decades to estimate tree biomass for various tree species (Ter-Mikaelian and Korzukhin 1997; Zianis et al. 2005), although, the amount of allometric data available for seedling trees, specifically for economically secondary species such as ash and black alder (*Alnus glutinosa* L.), is still limited. The allometric relationship between tree component biomass and tree diameter is however especially sensitive to tree age during the first decade of forest development (Telenius 1999; Peichl and Arain 2007). Therefore, the development and use of appropriate biomass equations is essential for more accurate predictions of biomass pools in newly established forests.

Apart from its effects on plant biomass, changes in land use and management also affect soil organic C (SOC) and N pools through altered litter input, quality and turnover rates (Post and Kwon 2000; Poulton et al. 2003; Booth et al. 2005). Furthermore, site preparation activities (e.g. ploughing, drainage, etc.) prior to plantation establishment may affect soil structure and physical properties, with implications for the soil C and N stocks (e.g. Nordborg et al. 2006). Previous studies investigating the temporal development of SOC stocks following afforestation of agricultural land have reported contrasting results including: increases in SOC stocks (e.g. Post and Kwon 2000; Morris et al. 2007); decreases in SOC stocks (e.g. Scott et al. 1999); initial decrease followed by an increase after a few decades of forest development (e.g. Paul et al. 2002); or no change (e.g. DeGryze et al. 2004). To some extent, these contrasting findings can be attributed to differences in soil characteristics, tree species and previous land-use history (Laganière et al. 2010; Wei et al. 2010).

To date, there are numerous studies on afforestation of abandoned or marginal agricultural land and extensively managed grassland/pastures, whereas less data is available on the development of soil C and N following afforestation of intensively managed grassland. However, after the cessation of management activities (including N fertilizer application, frequent biomass removal and soil compaction/disturbance through cattle and heavy machinery), major effects on ecosystem C and N dynamics may be expected primarily during the initial decade following afforestation of intensively managed ecosystems (Jug et al. 1999; Hamer et al. 2008).

The objective of this study was to investigate the initial changes in ecosystem biomass, C and N allocation and storage following afforestation of intensively managed grassland by comparing a 5-year-old broadleaf afforestation on formerly managed grassland to its surrounding managed grassland in the maritime region of southwest Ireland.

## Materials and methods

### Site description

#### *Grassland*

The study was conducted at the Dripsey grassland research station which is located in southwest Ireland, 25 km north-west of Cork City (Latitude 51°59′N; Longitude 8°45′W; 195 m above sea level). The climate in this region is temperate maritime, with a 30-year-average of annual air temperature and total precipitation of 9.4°C and 1207 mm, respectively (Met Eireann, 1960 to 1990 climate norms at Cork Airport Meteorological Station). The dominant grass species is perennial ryegrass (*Lolium perenne* L.). The underlying soil type is classified as Gleysol (Food and Agriculture Organization (FAO) classification) with a loamy soil texture (420 mg $g^{-1}$ sand, 410 mg $g^{-1}$ silt, 170 mg $g^{-1}$ clay) and consists of a primarily organic rich layer (0 to 10 cm) overlaying a dark brown A horizon (~10 to 20 cm) and a yellowish-brown B horizons (~20 to 30 cm), with the underlying brown, gravelly sand C horizon (parent material) starting at a depth of 30 cm (Scanlon et al. 2004).

The grassland covers approximately 0.75 $km^2$ and consists of many small (0.01 to 0.04 $km^2$) paddock fields which have been managed for cattle grazing and silage for several decades. Based on detailed management information for the individual fields, previous studies determined that about two thirds of the fields are used for cattle grazing from the end of March until late October, and the remaining third is managed for silage/hay harvesting (Jaksic et al. 2006; Peichl et al. 2011). The grassland fields receive approximately 17 to 25 gN $m^{-2}$ $y^{-1}$ in inorganic fertilizer and slurry. The different management practices result in spatial heterogeneity within the grassland, specifically in seasonal biomass dynamics and fertilizer application patterns. However, differences in soil chemistry, physical and nutrient status are generally limited among fields due to the rotational management of the fields over many decades (Khandokar 2003; Lewis 2003; Kiely et al. 2008; unpublished soil nutrient data). Because it was not feasible to extend sampling over a larger number of fields, our objective was therefore to cover the range of typical land-use practices occurring in the grassland (assuming this range to encompass the mean of any variable of interest for the entire grassland) and to mimic the 2:1 ratio between grazed and silage harvest fields. We selected three fields (two primarily grazed fields and one harvested field) that were of similar size (~0.02 to 0.03 $km^2$) and adjacent to the recently afforested area (described in the following section). The first field was topped on a monthly cycle from late March to late August, followed by few days of cattle grazing (stocking density is ~2 livestock units (LU) $ha^{-1}$). The second field was subject to a few days of cattle grazing (~1.5 LU $ha^{-1}$) every one or two weeks from early April to late August, and about monthly throughout autumn. The third field was used for grass harvest (silage). During the study year 2010, only one harvest cut occurred on the 18th of June. In August, cattle grazing occurred for approximately 10 days on that field.

#### *Forest*

In February 2005, a sector of the grassland (0.053 $km^2$ in size) was afforested with broadleaf trees. The afforested area had been previously used for cattle grazing and grass silage for several decades, similar to the adjacent fields. Thus, although pre-afforestation data is limited for the afforested area, its previous soil properties were likely similar to those of the adjacent grassland fields (Khandokar 2003; Lewis 2003).

Prior to tree planting, the area was ploughed and drained through a network of drainage ditches (~30 cm deep). At the time of this study, the forest was 5 years old and composed of ~80% ash (*Fraxinus excelsior* L.) mixed with ~20% black alder (*Alnus glutinosa* L.) and minor appearances (<2%) of pedunculate oak (*Quercus robur* L.). Forest ground vegetation consisted of ryegrass, yorkshire fog (*Holcus lanatus*) and soft rush (*Juncus effusus*), mixed with meadow buttercup (*Ranunculus acris*), greater spearwort (*Ranunculus lingua*), common mouse-ear (*Cerastium fontanum*), and cuckooflower (*Cardamine pratensis*). Initial management treatments include the application of ground rock phosphate (25 $\mathrm{gm}^{-2}$) in April 2005, and manual grass removal once every mid-summer from 2006 to 2008, supported by a one time chemical herbicide spraying in October 2008.

In November 2009, three permanent sample plots (each 400 $\mathrm{m}^2$) were established in the forest. Within each plot, species, base diameter ($\mathrm{D}_{\mathrm{base}}$, 0.1 m), diameter at breast height (DBH; 1.3 m), tree height, and live/dead status were recorded for each tree. Each plot also encompassed three micro-plots (1 $\mathrm{m}^2$) for ground biomass measurements (see section below).

## Plant biomass, C and N pools

### *Tree biomass*

Tree biomass was determined based on species-specific allometric relationships between tree component biomass and tree diameter developed from destructive tree sampling in November 2009. Ten ash and ten black alder trees were selected across the typical $\mathrm{D}_{\mathrm{base}}$ range of each species (1.5 to 5.5 cm for ash, 2.5 to 7 cm for black alder). All trees were harvested as close to the ground as possible, and branches were clipped and separated from the stem. All tree samples were oven dried until they reached a constant weight. Sub-samples were randomly taken along the stem and branches from which the bark was removed to estimate the bark to wood ratio. This ratio was then applied to the whole tree.

Allometric biomass equations were developed separately for ash and black alder species, based on ln-transformed linear relationships between $\mathrm{D}_{\mathrm{base}}$ and the biomass of the individual tree components and the total aboveground biomass (Eq. 1):

$$\ln(B_i) = a_i + b_i \times \ln(D) + \varepsilon_i \qquad (1)$$

where $B$ is the biomass of the tree component $i$ (i.e. wood and bark of stem and branches, total aboveground wood biomass) in kg dry mass, $a$ and $b$ are tree component specific equation parameters, $D$ is $\mathrm{D}_{\mathrm{base}}$ in cm, and $\varepsilon$ is the equation residual. The stand level tree biomass was then calculated using the mean stand $\mathrm{D}_{\mathrm{base}}$ as input variable in the respective component specific allometric biomass equations, multiplied by stem density. The tree coarse root (>2 mm) biomass was assumed to be 14% of the aboveground biomass, as previously suggested for 25 year-old ash trees by Le Goff et al. (2004), although the shoot to root ratio during the first decade of forest development may deviate from that in more mature forests (Peichl and Arain 2007). Bias in the antilog of $B_i$ was corrected with a correction factor (CF) determined as:

$$CF = \exp\left(\frac{SEE^2}{2}\right) \qquad (2)$$

where SEE is the standard error of the estimate (Baskerville 1972; Ter-Mikaelian and Korzukhin 1997). The uncertainty of the stand biomass estimate was computed by propagating the allometric biomass equation error ($\mathrm{E}_{\mathrm{A}}$) and coefficients of variation (CV) of the mean stand tree diameter and stem density among sample plots. The $\mathrm{E}_{\mathrm{A}}$ was computed as:

$$E_A = B \times \sqrt{CF^2 - 1}. \qquad (3)$$

Foliage biomass was estimated from litter-fall data. Litter-fall was collected from early December 2009 to late November 2010 with nine litter traps (0.36 $\mathrm{m}^2$) arranged in a 30 x 30 m grid. Samples were sorted into ash (foliage and twigs of composite leaf) and black alder (foliage only) litter, and oven dried to constant weight. The mean tree foliage was determined by dividing the amount of litter-fall by stem density for each ash and black alder.

### *Ground vegetation*

Forest ground vegetation was measured in each of the nine micro-plots. Ground vegetation was initially clipped in November 2009 and at approximately monthly intervals throughout the growing season in 2010. For each sampling event, the micro-plots were moved by 2 m clockwise to avoid re-sampling of the same area. Samples were oven-dried to determine dry biomass and sorted to estimate the live (green) to dead (brown) ratio.

In each of the three grassland fields, grass was clipped to stubble height in 0.3 x 0.3 m micro-plots initially at four locations along a 60 m transect, and at eight locations from late-August onwards (at which time the fields started to develop considerable patchiness as a result of prolonged selective cattle grazing and dung input). Transects were moved for each sampling date to avoid the re-sampling of previous locations. Clippings were taken approximately every 10 to 14 days during the growing season in 2010, with extensive efforts to sample before and after mowing, harvesting and grazing events. However, in cases when sampling prior to a management event was missed (mowing and grazing occasionally occurred without prior notice as communication with local farmers is limited), standing biomass prior to the event was estimated by linearly extrapolating the growth rate of the previous sampling interval to the day on which the management event had occurred. All clipping samples were oven-dried at 65°C to obtain the dry-weight biomass and separated to determine the live to dead ratio.

### *Fine roots*

Fine root (<2 mm in diameter) biomass and necromass within the upper 30 cm soil layer were determined from sequential soil coring in both the forest and grassland. Soil cores were taken on March 22, June 19 and July 18, 2010, using a soil auger of 5 cm diameter. Three soil core samples were taken to a depth of 30 cm from each of the three forest sample plots and from each of the three grassland fields. Each core was further divided into 10 cm sections.

Fine roots were first separated from soil through water bath extraction and with the help of a fine-meshed sieve. Afterwards, roots were manually picked with tweezers from the remaining soil. Extracted roots were further separated into dead and live roots based on colour and elasticity. Roots with light brown or white colour and high elasticity were defined as live, whereas roots that showed dark brown or black coloration and that were easily torn apart due to low elasticity were considered dead. Once separated, the roots were washed once more and oven-dried to constant weight. Fine root turnover was approximated as the difference between minimum (March) and maximum (June or July) stock divided by the average fine root stock (Vogt and Persson 1991).

### *Biomass C and N stocks*

Sub-samples were taken from the forest and grassland ground vegetation (in June, July, September and November), fine root biomass (bulked June and July samples), litter-fall, as well as from stem wood, branch wood, stem bark and branch bark of the harvested ash and black alder trees. In August 2010, fresh foliage was randomly collected from ash and black alder trees. Litter-fall samples of the composite ash leaf were separated into its foliage and twig component. All sub-samples were sent to a laboratory (Brookside Laboratories, New Knoxville, OH, USA) for chemical analysis of their C and N concentrations using a Carlo Erba NA1500 Series 2 analyzer. Stem wood C and N concentrations were used to determine tree coarse root C and N stocks, although root N in ash seedling trees was previously reported to exceed stem N concentration (Marmann et al. 1997). The C and N stocks of various biomass pools were determined by multiplying biomass with respective C and N concentration. Their associated uncertainties were estimated by propagating the errors of the biomass estimate and C or N concentrations.

## Soil analysis

### *Soil C and N stocks*

Mineral soil samples from each layer (0 to 10 cm, 10 to 20 cm, and 20 to 30 cm) of the soil cores extracted for fine root biomass measurements in March 2010 were air dried and sent to a laboratory (Brookside Laboratories, New Knoxville, OH, USA) for analysis of soil organic C (SOC) and total nitrogen (TN) concentrations. The three sampled layers approximately correspond to the three main layers of the A and B horizons described above. Bulk density of the 0 to 30 cm soil layer was also sampled in 10 cm intervals at three locations within each of the three forest plots, using bulk density rings (8 cm in diameter, 5 cm in depth) inserted horizontally into the soil profile. Oven-dried samples were crushed, sieved through a 2 mm mesh, and bulk density was determined from the dry weight of particles<2 mm over sample ring volume. Bulk density values for grassland were taken from previous data collected in 2007 (Kiely et al. 2008). SOC and TN stocks were calculated separately for each soil layer by multiplying the respective SOC and TN concentration with bulk density. For comparison to the fixed depth method, we also applied the maximum equivalent soil mass correction to compare soil element stocks on the same soil mass per unit area (Lee et al. 2009). Uncertainties of SOC and TN stocks were estimated for each layer by propagating standard errors of the mean concentration and bulk density. At the time of this study, no apparent organic forest floor (LFH) layer had yet developed in the young forest.

### *Net N mineralization*

Net N mineralization rates were determined for forest and grassland from May to October using the soil bag incubation technique (Hart et al. 1994). Four soil samples per forest sample plot and six samples per grass field were collected from 0 to 10 cm depth at the beginning of each month. These samples were mixed and combined into three composite samples for the forest and into six composite samples for the grassland (two per field). Half of each sample was taken back to the lab while the other half was buried in the field within a polyethylene bag and retrieved at the end of the month. All samples were stored frozen until sent to a laboratory (Hill Court Farm Research, Gloucestershire, UK) for analysis of ammonium and nitrate based on fresh soil extraction using a Timberline TL-2800 Total N Ammonia analyzer. Daily net N mineralization rates were calculated for each incubation period from the change in ammonium and nitrate concentrations divided by the number of incubation days.

### Statistical analysis

The log-transformed data was assessed with the independent two-sample Student's *t*-test for significant differences between land-use types (i.e. grassland versus forest) and with a two-way analysis of variance (ANOVA) in combination with the Tukey-Kramer multiple comparison test when 'soil layer depth' was included as a second explaining factor. Significant differences are stated at the level of $P < 0.05$ unless otherwise noted. Statistical analysis was conducted using MATLAB (R2008a, MathWorks, Natick, MA).

## Results

### Biomass allocation

### *Tree biomass*

Five years after afforestation, the mean tree diameter and height of black alder exceeded those of ash by 35% and 25%, respectively (Table 1). Furthermore, while contributing only 20% to total stem density, black alder accounted for about one third of total stem volume and stand basal area.

Adjusted coefficients of determination (adj. $R^2$) suggested strong relationships between tree diameter and aboveground tree biomass for both ash (adj. $R^2$= 0.98) and black alder (adj. $R^2$=0.96), as well as for individual tree components (adj. $R^2$>0.90) (Table 2). At a given diameter, the aboveground tree biomass of black alder was 1.25 greater than ash. The stem to shoot biomass ratio was 0.87 for ash, but only 0.58 for black alder, indicating that almost half of the aboveground tree biomass of young black alder trees is stored within their branches (Fig. 1). For both ash and black alder species, the bark to wood ratios of stem and branches were 0.12 and 0.33, respectively.

### *Ground vegetation*

The mean (± standard error, SE) ground vegetation biomass stock peaked at 364±51 $\mathrm{g\,m^{-2}}$ in August in the forest and at 337±75 $\mathrm{g\,m^{-2}}$ in June in the grassland. The live to dead ratio of ground vegetation however was up to four times higher in the grassland compared to the forest throughout the growing season (Fig. 2).

**Table 1** Forest stand characteristics five years after planting; numbers in parentheses indicate within-stand variability as standard deviation of the means from (*n*=3) sample plots

| Characteristic | Ash | Alder | Total forest |
|---|---|---|---|
| Tree height (m) | 2.4 (0.1) | 3.0 (0.2) | 2.5 (0.1) |
| Tree diameter, DBH (cm) | 1.7 (0.1) | 2.3 (0.3) | 1.8 (0.1) |
| Tree base diameter (cm) | 3.5 (0.4) | 4.8 (0.6) | 3.7 (0.4) |
| Stem density (stems $\mathrm{ha^{-1}}$) | 2592 (189) | 617 (118) | 3242 (296) |
| Stand stem volume ($\mathrm{m^3\,ha^{-1}}$) | 0.032 (0.009) | 0.018 (0.006) | 0.049 (0.015) |
| Basal area ($\mathrm{m^2\,ha^{-1}}$) | 2.6 (0.7) | 1.2 (0.3) | 3.9 (0.9) |

**Table 2** Allometric biomass equations for ash and alder tree components; ln(B) = $a + b\ x$ ln(D), where B = ln-transformed tree component biomass (kg) and D = ln-transformed tree base diameter (cm); standard error (S.E.) of parameter coefficient; standard error of estimate (S.E.E); adjusted coefficient of determination (adj.$R^2$); $n=10$; significance level for all coefficients is $P<0.001$

| Tree component | Parameter | Ash | | | | Alder | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Coefficient | S.E. | S.E.E | Adj.$R^2$ | Coefficient | S.E. | S.E.E | Adj.$R^2$ |
| Stem wood | *a* | −3.687 | 0.164 | 0.117 | 0.98 | −4.164 | 0.282 | 0.135 | 0.95 |
| | *b* | 2.444 | 0.123 | | | 2.318 | 0.180 | | |
| Stem bark | *a* | −5.711 | 0.164 | 0.117 | 0.98 | −6.069 | 0.282 | 0.135 | 0.95 |
| | *b* | 2.444 | 0.123 | | | 2.318 | 0.180 | | |
| Stem total | *a* | −3.563 | 0.164 | 0.117 | 0.98 | −4.025 | 0.282 | 0.135 | 0.95 |
| | *b* | 2.444 | 0.123 | | | 2.318 | 0.180 | | |
| Branch wood | *a* | −6.170 | 0.406 | 0.289 | 0.90 | −5.629 | 0.434 | 0.208 | 0.93 |
| | *b* | 2.695 | 0.305 | | | 2.950 | 0.277 | | |
| Branch bark | *a* | −6.988 | 0.406 | 0.289 | 0.90 | −6.693 | 0.434 | 0.208 | 0.93 |
| | *b* | 2.695 | 0.305 | | | 2.950 | 0.277 | | |
| Branch total | *a* | −5.805 | 0.406 | 0.289 | 0.90 | −5.332 | 0.434 | 0.208 | 0.93 |
| | *b* | 2.695 | 0.305 | | | 2.950 | 0.277 | | |
| Wood total | *a* | −3.604 | 0.170 | 0.121 | 0.98 | −4.036 | 0.282 | 0.135 | 0.96 |
| | *b* | 2.466 | 0.128 | | | 2.549 | 0.180 | | |
| Bark total | *a* | −5.459 | 0.197 | 0.140 | 0.97 | −5.733 | 0.318 | 0.152 | 0.95 |
| | *b* | 2.506 | 0.148 | | | 2.678 | 0.202 | | |
| Tree total | *a* | −3.458 | 0.173 | 0.123 | 0.98 | −3.870 | 0.287 | 0.137 | 0.96 |
| | *b* | 2.472 | 0.130 | | | 2.573 | 0.183 | | |

### *Fine roots*

Total fine roots (sum of live and dead, ± SE) in the 0 to 30 cm soil layer of the forest and grassland increased from 212±29 and 425±26 g$m^{-2}$ in March to a peak of 402±53 and 849±132 g$m^{-2}$ in June, respectively (Fig. 3). Compared to June, total fine root biomass was lower but not significantly different in July for both the forest and the grassland. The

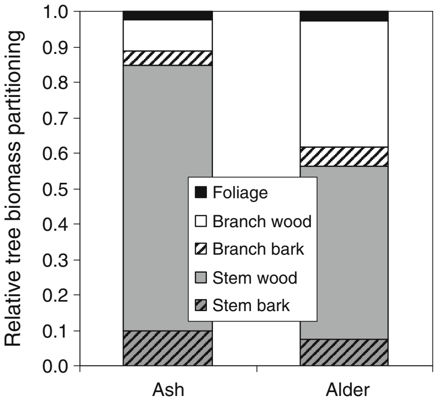

**Fig. 1** Relative partitioning of aboveground tree biomass for ash and black alder 5-years after afforestation

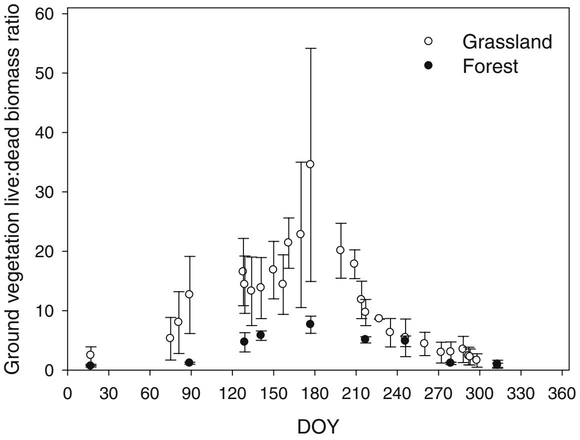

**Fig. 2** Seasonal development of herbaceous ground vegetation live to dead ratio in grassland and forest in 2010; error bars indicate standard error ($n=9$ in the forest; $n=12$ in the grassland); *DOY* day of year

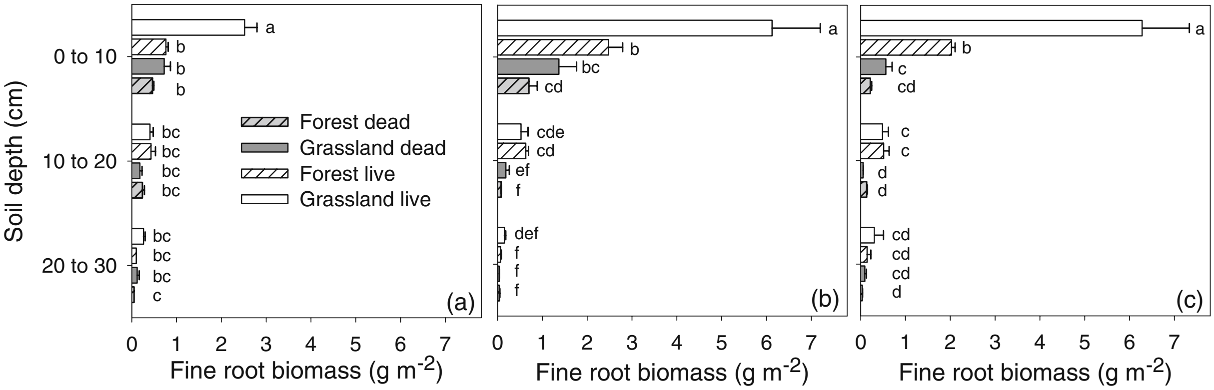

**Fig. 3** Live (*white background bars*) and dead (*shaded background bars*) fine root (<2 mm) mass at depths of 0 to 10, 10 to 20 and 20 to 30 cm in forest (*striped bars*) and grassland (*non-striped bars*) on (**a**) March 22, (**b**) June 19 and (**c**) July 18; error bars indicate standard error ($n$=9); values of bars denoted with different letters are significantly different

live to dead fine root ratio in forest and grassland increased from 1.5 and 3.1 in March to 7.0 and 10.0 in July, respectively. During the summer months, the amount of live fine roots in the upper 10 cm soil layer accounted for 77 and 90% of total live fine roots (0 to 30 cm) at the forest and grassland, respectively, and was about three times greater in grassland compared to the forest. While the difference for fine roots in the uppermost layer was significant, no differences between forest and grassland occurred at depths of 10 to 20 cm and 20 to 30 cm. The mean fine root turnover rate of 0.62 in the forest was similar to the 0.67 in the grassland, although turnover rates in the grassland showed greater variability with individual field values ranging between 0.57 and 0.97.

## Biomass C and N concentrations

Carbon concentrations were similar among ash tree components ranging between 462 and 468 mg g$^{-1}$, but varied within black alder from 470 mg g$^{-1}$ in the stem wood to 523 mg g$^{-1}$ in branch bark (Table 3). The N concentration in wood (6.2 to 7.6 mg g$^{-1}$) was considerably lower than in bark (10.5 to 16.3 mg g$^{-1}$) for both ash and black alder. Furthermore, N concen-

**Table 3** Carbon (C) and nitrogen (N) concentrations and C/N ratio of ash and alder tree biomass components, litter-fall, ground vegetation and fine roots in forest and grassland; values in parentheses indicate standard deviation ($n$=3); n.a. = not applicable

| Tree biomass component | C (mg g$^{-1}$) | N (mg g$^{-1}$) | C/N ratio | C (mg g$^{-1}$) | N (mg g$^{-1}$) | C/N ratio |
|---|---|---|---|---|---|---|
| | | Ash | | | Alder | |
| Foliage | 466 (10) | 23.7 (0.4) | 19.7 (0.3) | 492 (19) | 36.9 (1.7) | 13.3 (0.4) |
| Stem wood | 463 (11) | 6.2 (1.5) | 77.3 (16.8) | 470 (13) | 7.0 (1.6) | 69.3 (14.4) |
| Stem bark | 467 (4) | 10.5 (0.3) | 44.5 (1.2) | 492 (21) | 15.3 (0.7) | 32.2 (2.9) |
| Branch wood | 468 (5) | 7.6 (1.2) | 62.7 (9.4) | 483 (2) | 7.6 (1.9) | 65.7 (10.1) |
| Branch bark | 462 (25) | 13.3 (0.1) | 34.9 (0.4) | 523 (15) | 16.3 (0.7) | 32.1 (0.4) |
| Litterfall - foliage | 515 (2) | 26.6 (0.2) | 19.4 (0.1) | 532 (1) | 41.9 (1.2) | 12.7 (0.3) |
| Litterfall - twig | 484 (3) | 11.3 (0.1) | 42.7 (0.3) | n.a. | n.a. | n.a. |
| | | Forest | | | Grassland | |
| Ground vegetation | 450 (6) | 25.7 (6.4) | 18.6 (4.9) | 445 (15) | 30.3 (7.1) | 15.5 (4.0) |
| Fine roots | 424 (25) | 17.2 (2.1) | 24.9 (3.1) | 389 (23) | 17.1 (1.7) | 22.9 (2.2) |

trations in black alder foliage, stem and branch bark were significantly greater compared to respective ash components. The C/N ratio of the wood (63 to 77) was greater than that of bark (32 to 44) for both ash and black alder. The C and N concentrations of freshly fallen foliage litter in autumn were significantly greater compared to summer foliage for both ash and black alder, while the C/N ratios remained similar.

The mean concentrations of C and N, and the C/N ratios of the ground vegetation and of the fine roots were not significantly different between land-use types (Table 3) or among sample dates (not shown). In both forest and grassland however, N concentration of aboveground biomass (ground vegetation) was significantly greater compared to belowground biomass (fine roots).

## Soil C and N

### *Soil C and N concentrations*

The SOC and TN concentrations decreased with depth in both forest and grassland (Fig. 4a,b). The SOC concentration in the upper 0 to 10 cm soil layer at 62 mg g$^{-1}$ in the forest was significantly greater than the 45 mg g$^{-1}$ in the grassland (Fig. 4a). Soil TN concentration in the upper 0 to 10 cm soil layer at 5.7 mg g$^{-1}$ in the forest was also significantly greater than the 3.9 mg g$^{-1}$ in the grassland (Fig. 4b). We did not observe any differences in the inorganic N concentrations (data not shown), therefore, greater TN concentration in the upper soil layer resulted from a difference in the amount of organic N. SOC and TN concentrations in 10 to 20 cm and 20 to 30 cm soil layers were not different between the two land-use types. The soil C/N ratio in the 0 to 10 cm layer was ~13 in both forest and grassland. Soil pH-levels decreased slightly but significantly from 5.76 in the grassland to 5.26 in the forest.

### *Bulk density*

The bulk density in the upper 0 to 10 cm layer was significantly lower in the forest compared to that measured in the grassland in 2007 (Kiely et al. 2008), but similar at depths of 10 to 20 cm and 20 to 30 cm (Fig. 4c).

### *Soil C and N stocks*

The total (0 to 30 cm depth) SOC and TN stocks of 9.1±0.9 kg C m$^{-2}$ and 0.74±0.06 kg N m$^{-2}$ in the forest were similar to the 9.0±0.6 kg C m$^{-2}$ and 0.76±0.07 kg N m$^{-2}$ in the grassland, respectively (Table 4). In comparison, forest C and N stocks estimates corrected for equivalent soil mass increased to 10.1±1.0 kg C m$^{-2}$ and 0.81±0.07 kg N m$^{-2}$, respectively, although the difference to the grassland mean values remained smaller than the associated uncertainty boundaries.

### *Net N mineralization*

Net N mineralization rates from May to August were consistently lower in the forest compared to the

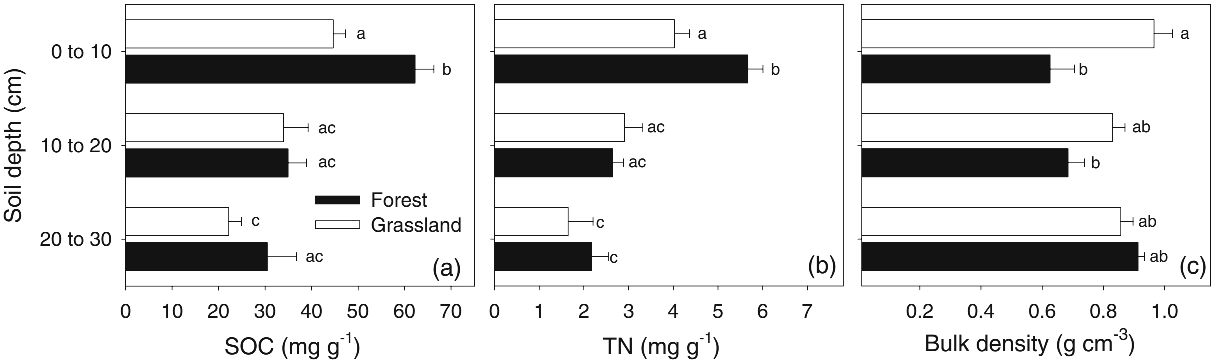

**Fig. 4** Concentrations of (**a**) soil organic carbon (SOC) and (**b**) soil total nitrogen (TN), and (**c**) bulk density [a] at depths of 0 to 10, 10 to 20 and 20 to 30 cm in forest (*black bars*) and grassland (*white bars*); error bars indicate standard error (*n*=9); values of bars denoted with different letters are significantly different. [a] bulk density data for grassland was taken from Kiely et al. (2008)

**Table 4** Ecosystem biomass, carbon (C) and nitrogen (N) pools in forest and grassland; values in parentheses indicate propagated uncertainty from measurement error and sample plot variability as describes in the method section; n.a. = not applicable

| | Forest | | | Grassland | | |
|---|---|---|---|---|---|---|
| Ecosystem pool | Biomass (kg $m^{-2}$) | C pool (kg $Cm^{-2}$) | N pool (kg $Nm^{-2}$) | Biomass (kg $m^{-2}$) | C pool (kg $Cm^{-2}$) | N pool (kg $Nm^{-2}$) |
| Tree biomass | | | | | | |
| Foliage | 0.06 (0.01) | 0.03 (0.01) | 0.002 (0.0002) | n.a. | n.a. | n.a. |
| Stem wood | 0.18 (0.02) | 0.08 (0.01) | 0.001 (0.0002) | n.a. | n.a. | n.a. |
| Stem bark | 0.02 (0.003) | 0.01 (0.001) | 0.0003 (0.00003) | n.a. | n.a. | n.a. |
| Branch wood | 0.04 (0.01) | 0.02 (0.004) | 0.0003 (0.0001) | n.a. | n.a. | n.a. |
| Branch bark | 0.02 (0.003) | 0.01 (0.001) | 0.0002 (0.00004) | n.a. | n.a. | n.a. |
| Total tree aboveground | 0.32 (0.03) | 0.15 (0.01) | 0.004 (0.0003) | n.a. | n.a. | n.a. |
| Tree roots (≥ 2 mm)[a] | 0.04 (0.004) | 0.02 (0.001) | 0.001 (0.00004) | n.a. | n.a. | n.a. |
| Ground vegetation | | | | | | |
| Live | 0.14 (0.02) | 0.06 (0.01) | 0.004 (0.001) | 0.10 (0.02) | 0.05 (0.01) | 0.003 (0.001) |
| Dead | 0.08 (0.02) | 0.04 (0.01) | 0.002 (0.0004) | 0.02 (0.003) | 0.01 (0.001) | 0.001 (0.0001) |
| Fine roots (<2 mm) | | | | | | |
| Live | 0.22 (0.05) | 0.10 (0.02) | 0.004 (0.0001) | 0.50 (0.14) | 0.12 (0.05) | 0.009 (0.0002) |
| Dead | 0.08 (0.02) | 0.04 (0.01) | 0.001 (0.0004) | 0.14 (0.04) | 0.05 (0.01) | 0.002 (0.001) |
| Mineral soil | | | | | | |
| 0 to 30 cm depth | | 9.1 (0.9) | 0.74 (0.06) | | 9.0 (0.6) | 0.76 (0.07) |
| Total aboveground | 0.56 (0.04) | 0.25 (0.02) | 0.009 (0.001) | 0.13 (0.02) | 0.06 (0.01) | 0.004 (0.0001) |
| Total belowground | 0.35 (0.06) | 9.2 (0.9) | 0.74 (0.07) | 0.64 (0.14) | 9.3 (0.7) | 0.77 (0.07) |
| Total ecosystem | 0.91 (0.08) | 9.5 (0.9) | 0.75 (0.07) | 0.76 (0.14) | 9.3 (0.7) | 0.77 (0.07) |

[a] assuming a root to shoot ratio of 0.14 based on Le Goff et al. (2004)

grassland (Fig. 5). In the forest, net N mineralization peaked at 0.68 µ gN $g^{-1}$ day $(d)^{-1}$ in August. In the grassland, maximum net N mineralization reached 1.56 µg N $g^{-1}$ $d^{-1}$ in June. For the period May to October, the daily mean net N mineralization rate of 0.07±0.11 µg N $g^{-1}$ $d^{-1}$ in the forest was significantly ($P<0.01$) lower compared to 0.76±0.17 µg N $g^{-1}$ $d^{-1}$ in the grassland. For the same period, cumulative net N mineralization was 8.9±6.3 and 131±24 µg N $g^{-1}$ in the forest and grassland, respectively.

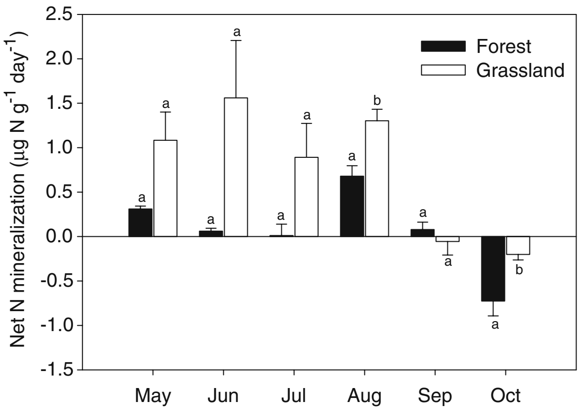

**Fig. 5** Net N mineralization rates in the forest and the grassland during the growing season 2010; *error bars* indicate SE ($n$=3 in forest, $n$=6 in grassland); values of bars denoted with different letters are significantly different for each month

## Ecosystem biomass, C and N pools

The total ecosystem biomass in the forest and grassland was 0.91±0.08 and 0.76±0.14 kg $m^{-2}$, respectively (Table 4). The above- to belowground biomass ratio increased from 0.20 in the grassland to 1.59 in the forest (Fig. 6).

The aboveground C pool in the forest was about five times that of the grassland whereas no difference occurred in the belowground C pool (Table 4). Total ecosystem C storage in the forest and grassland were similar with 9.5±0.9 kg $Cm^{-2}$ and 9.3±0.7 kg $Cm^{-2}$,

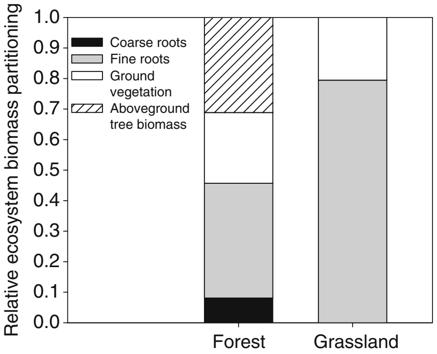

**Fig. 6** Relative partitioning of ecosystem above- and below-ground biomass in the forest and the grassland

respectively. The aboveground N pool in the forest was about twice that of the grassland whereas no difference was observed for the belowground N pool. The total ecosystem N storage was similar with 0.75± 0.07 kg $Nm^{-2}$ in the forest and 0.77±0.07 kg $Nm^{-2}$ in the grassland (Table 4). Belowground C and N storage accounted for >97% of total ecosystem C and N in both land-use types.

## Discussion

### Development of biomass and related C and N stocks following afforestation of managed grassland

### *Tree biomass*

Five years after afforestation, apparent differences in tree biomass development included greater biomass allocation to branches as well as greater height growth and total biomass production by black alder trees compared to ash. Kuznetsova et al. (2011) also reported enhanced branch biomass allocation as well as greater height and diameter growth in 1 to 7 year old black alder plantations compared to silver birch (*Betula pendula* Roth) plantations in Northeast Estonia. Thus, considerable differences in biomass allocation and production among broadleaf tree species may already occur within the first decade following plantation establishment.

Allometric biomass equations published by previous studies for young ash (Bunce 1968; Korsmo 1995; Alberti et al. 2005) and black alder stands (Hughes 1971; Johansson 2000; Kuznetsova et al. 2011) underestimated tree biomass at our forest by 15 to 53% and 7 to 47%, respectively. This indicates greater site productivity and tree height growth at our forest. Enhanced tree biomass production may have resulted from a combination of improved initial soil conditions created through long term fertilizer treatments during previous grassland management and non-limiting soil moisture conditions, a characteristic of the maritime region.

Our observation of greater N concentrations in bark and branches compared to wood and stem, respectively, as well as greater N storage in alder compared to other tree species (i.e. silver birch and Scots pine (Kuznetsova et al. 2011)) a few years after plantation establishment are in agreement with previous studies (Uri et al. 2003; Kuznetsova et al. 2011). It highlights the importance of separating tree species and components for improved estimates of N storage in tree biomass.

### *Ground vegetation and fine roots*

The large and continuously present pool of dead and decomposing herbaceous ground vegetation material in the forest is in strong contrast to the grassland where repeated biomass removal via harvest and grazing resulted in less accumulation of dead herbaceous matter. Furthermore, a lower C/N ratio in ground vegetation compared to fine roots suggests that the shift from fine roots to ground vegetation and leaf litter decomposition as a major source of biomass input into the soil coincides with an increase in the litter quality following grassland afforestation. Such change in litter input dynamics may therefore result in enhanced nutrient and organic matter return to the soil, but also greater onsite respiratory C losses from decomposing ground vegetation, in the forest compared to the grassland.

An initial decrease in fine root biomass, as observed in our study, was also reported for a 16-year-old pine afforestation on former native pasture (Guo et al. 2008). In contrast, Davis et al. (2007) did not observe any change in root biomass of herbaceous species over 10 years following afforestation of an extensive pasture with pine. An initial rapid decline in fine root biomass may be characteristic for afforestation of intensively managed grassland where fine roots may accumulate due to frequent re-growth following mowing and grazing events and thus provide a greater initial fine root biomass pool compared to natural or extensively managed grasslands.

## Development of soil C and N following afforestation of managed grassland

Higher SOC and TN concentrations in the upper 10 cm of the forest soil compared to grassland were likely the result of increased organic matter input from decomposing ground vegetation and tree litter, exceeding possible opposing effects from ploughing, drainage and phosphate addition that commonly stimulate SOM decomposition (Xu et al. 2011). Similar to our study, increased SOC and TN concentrations in the topsoil (0–10 cm) were reported for fallow and recently afforested land compared to land under intensive agricultural management (Jug et al. 1999; Hamer et al. 2008). In contrast, Davis et al. (2007) noted an overall increase in SOC but a decrease in TN concentrations in the upper soil layer within 10 years following afforestation of an extensive pasture with pine. Our results are in agreement with the meta-analysis by Laganière et al. (2010), which suggests that afforestation with broadleaf species in maritime regions show enhanced capacity for accumulation of SOC.

Although not further investigated in this study, land use change may also affect SOC chemical and physical structure, stability and function (Carter et al. 1998; Helfrich et al. 2006; Huang et al. 2011). For instance, Helfrich et al. (2006) found that the SOC stock in grassland was dominated by mineral-associated SOM, whereas particulate organic matter with high contents of litter-derived alkyl-C accounted for 52% of the total SOC content in a spruce forest. In a study by Huang et al. (2011), the soil light fraction was most variable (i.e. initial decrease with subsequent recovery) whereas the soil heavy fraction remained stable within the first 10 years following grassland afforestation. They also observed an increase in the stability of SOM due to greater relative abundance of recalcitrant plant biopolymers 10 years after afforestation. Thus, effects on the SOM fraction will further determine the long-term soil C stock dynamics following grassland afforestation.

Contrary to our initial expectation, the cessation and absence of N fertilization over 5 years did not result in lower soil TN concentrations in the forest compared to the intensively managed grassland. Instead, we observed an increase in shallow soil TN concentration that may have resulted from reduced leaching and reallocation of deep soil N to the surface layer through tree root uptake and subsequent return in organic form via enhanced litter production from trees and herbaceous ground vegetation. Based on our measurements of tree and ground vegetation detritus production and assuming linear growth rates, we estimated a gross input of 0.43 kg C$\,$m$^{-2}$ and 0.024 kg N$\,$m$^{-2}$ from tree and ground vegetation litter to the surface layer over the 5 years following afforestation.

Lower net N mineralization despite higher TN concentrations in the upper forest soil compared to the grassland indicates a weak relationship between soil N stock and transformation processes. Instead, changes in the SOM composition and in the microbial mass and community structure are more likely to explain the shift in the net balance of simultaneous N mineralization and immobilization processes following grassland afforestation. A decrease in net N mineralization was also observed 10 years after abandonment of an intensively managed, subalpine meadow (Zeller et al. 2000) and in a young pine afforestation established on former pasture land (Ross et al. 1999). Zeller et al. (2000) suggested increases in the soil C/N ratio to cause such land-use change related decrease in net N mineralization. However, no change in the soil C/N ratio was observed in our study. Such contrasting findings may result from the fact that SOM is composed of several pools and changes in the whole soil C/N ratio may differ from those of all SOM pools, thereby obscuring changes in the fraction of labile and recalcitrant pools and the relationship to net N mineralization rates (Piñeiro et al. 2006).

It has been suggested to account for bulk density changes by using equivalent soil mass (ESM) estimates when comparing soil element stock development following land-use change (Lee et al. 2009, Don et al. 2011). Don et al. (2011) reported a 28% underestimation of land-use change effects on SOC when using fixed depth versus soil mass corrected data. In our study, the ESM correction increased the mean forest SOC stock by ~10% compared to the fixed depth estimate. The resulting difference to the grassland mean was however still smaller than the associated uncertainty boundaries. Moreover, we did not have pre-afforestation soil data available in which case the use of the ESM method is limited (Lee et al. 2009; Don et al. 2011). The lower bulk density noted in the upper soil layer of the forest may be attributed to loosening up effects from the initial ploughing and/or soil particle erosion during drainage of the site prior to afforestation. Similarly, Nordborg et al. (2006) reported reduced bulk density within the upper 10 cm compared to the lower soil profile in 10-year-old conifer plantations established after soil scarification. In addition, lower bulk density in the upper forest soil layer may have also resulted from tree root establishment and/or the incorporation of low density organic litter material into the soil. The absence of compaction from cattle trampling and machinery may further favour a lower bulk density in forest soil compared to managed grassland (Don et al. 2011). Such effects on bulk density are associated with significant impact on the soil C and N stocks. Considering the controls on bulk density is therefore as important as understanding those on element concentration when evaluating land-use change effects on ecosystem soil C and N storage.

### Ecosystem biomass, C and N allocation and storage following afforestation of managed grassland

The considerable shift in the biomass allocation from below- to aboveground within only 5 years following afforestation of managed grassland was driven by a reduction of fine root biomass combined with the simultaneous accumulation of aboveground tree biomass in the forest. In comparison to the above to belowground ratio of 1.59 observed in our forest, Uri et al. (2009) reported an even higher ratio of 4.5 in a 5-year-old grey alder plantation. A shift from 0.15 in native pasture to 4.1 in 16-year-old pine afforestation was found by Guo et al. (2008). Such alteration of biomass allocation has implications on biogeochemical processes related to input and turnover of C, N, and other nutrients, which altogether may further determine the ecosystem C balance and greenhouse gas exchange.

Despite an apparent shift from below- to aboveground ecosystem C and N storage following afforestation, the ecosystem C and N storage was largely dominated by the soil component and therefore changes in ecosystem C and N allocation were limited. Our estimates of SOC stock in the forest (9.1 kg $\mathrm{C\,m^{-2}}$) and grassland (9.0 kg $\mathrm{C\,m^{-2}}$) are comparable to those reported for a 12-year-old ash afforestation (8.7 kg $\mathrm{C\,m^{-2}}$) and adjacent managed grassland (9.0 kg $\mathrm{C\,m^{-2}}$) in a chronosequence study in Ireland by Wellock et al. (submitted for publication). However, their findings further suggested a decrease of SOC three decades after afforestation. Moreover, a reduction of the belowground N pool was noted 16 years after afforestation of pasture with pine (Guo et al. 2008), and during ash-dominated multi-decadal succession of grassland (Alberti et al. 2008), while, Morris et al. (2007) found an increase of ecosystem N by 0.004 kg $\mathrm{N\,m^{-2}\,y^{-1}}$ over 50 years in a broadleaf afforestation on former agricultural land. Thus, while land-use change is known to affect C and N storage over multiple decades, knowledge is limited on such time frame with respect to afforestation of intensively managed grassland.

### Afforestation of intensively versus extensively managed grassland

The temporal patterns of ecosystem biomass, C and N allocation and storage caused by afforestation of intensively managed (i.e. heavily fertilized and grazed/harvested) grassland, as investigated in this study, may differ from those following afforestation of abandoned arable/extensive pasture land and natural woody encroachment. In support of this argument, Laganière et al. (2010) recently suggested in their meta-analysis that afforestation of extensive pastures and natural grasslands, as well as initial site disturbance resulted in less potential for increasing SOC concentration compared to afforestation of intensively cultivated cropland. Based on the above discussion, distinct features for afforestation of intensively managed grasslands compared to extensive grassland systems are such that: i) the pre-afforestation N input is higher; ii) aboveground biomass remains lower while fine roots accumulate due to frequent grazing/harvesting events; iii) soil nutrient status is often improved (due to controlled fertilizer management); iv) site preparation activities (e.g. ploughing, drainage) are more likely; and v) additional external C and N input and output via management practices occur in intensively managed grasslands. As these controls may exert partly opposite effects, the ultimate response of ecosystem biomass, C and N allocation and storage is essentially determined by their combination and individual contributions. To date most work has focused on the consequences from afforestation of abandoned or extensively cultivated agricultural land, however, more studies assessing those from the conversion of intensively managed grassland to forest are required to better understand the control of pre-afforestation management intensity on subsequent temporal patterns in ecosystem biomass, C and N allocation and storage.

## Conclusions

We compared the ecosystem biomass, C and N allocation and storage in a recently afforested grassland with that in an adjacent intensively managed grassland in the temperate maritime region of southwest Ireland. We observed a considerable shift in biomass allocation from below- to aboveground within 5 years following afforestation. However, ecosystem C and N storage was dominated by the belowground pool in both land-use systems. Compared to the grassland, greater SOC and TN concentrations in the upper forest soil layer were counterbalanced by a decrease in bulk density, resulting in no significant change in total soil C and N stocks. We conclude that significant losses of ecosystem C and N did not occur following afforestation of this intensively managed grassland.

We further suggest that initial patterns in the development of ecosystem biomass, C and N allocation and storage following afforestation of intensively managed grassland may differ from those resulting from afforestation of extensive grassland due to factors such as initially improved site conditions, a greater fine root pool, enhanced external C and N input and output, and soil disturbance during site preparation activities. However, more research on afforestation of intensive managed grassland is needed to further support findings from this study.

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## References

Alberti G, Candido P, Peressotti A, Turco S, Piussi P, Zerbi G (2005) Aboveground biomass relationships for mixed ash (Fraxinus excelsior L. and Ulmus glabra Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Ann For Sci 62:831–836

Alberti G, Peressotti A, Piussi P, Zerbi G (2008) Forest ecosystem carbon accumulation during a secondary succession in the Eastern Prealps of Italy. Forestry 81:1–11

Arora VK, Boer GJ (2010) Uncertainties in the 20th century carbon budget associated with land use change. Glob Chang Biol 26:3327–3348

Baskerville G (1972) Use of logarithmic regression in the estimation of plant biomass. Can J For Res 2:49–53

Booth MS, Stark JM, Rastetter E (2005) Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. Ecol Monogr 75:139–157

Bunce R (1968) Biomass and production of trees in a mixed deciduous woodland. I. Girth and height as parameters for the estimation of tree dry weight. J Ecol 56:759–775

Carter MR, Gregorich EG, Angers DA, Donald RG, Bolinder MA (1998) Organic C and N storage, and organic C fractions, in adjacent cultivated and forested soils of eastern Canada. Soil Tillage Res 47:253–261

Davis M, Nordmeyer A, Henley D, Watt M (2007) Ecosystem carbon accretion 10 years after afforestation of depleted subhumid grassland planted with three densities of Pinus nigra. Global Change Biol 13:1414–1422

DeGryze S, Six J, Paustian K, Morris S, Paul E, Merckx R (2004) Soil organic carbon pool changes following land-use conversions. Glob Chang Biol 10:1120–1132

Department of Agriculture, Food and Forestry (1996) Growing for the future—A strategic plan for the development of the forestry sector in Ireland. Department of Agriculture, Food and Forestry, The Stationery Office, Dublin

Dixon RK, Solomon AM, Brown S, Houghton RA, Trexier MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185–190

Don A, Schumacher J, Freibauer A (2011) Impact of tropical land-use change on soil organic carbon stocks—a meta-analysis. Glob Chang Biol 17:1658–1670

Eaton JM, McGoff NM, Byrne KA, Leahy P, Kiely G (2008) Land cover change and soil organic carbon stocks in the Republic of Ireland 1851–2000. Clim Chang 91:317–334

Gruber N, Galloway JN (2008) An earth-system perspective of the global nitrogen cycle. Nature 451:293–296

Guo LB, Cowie AL, Montagu KD, Gifford RM (2008) Carbon and nitrogen stocks in a native pasture and an adjacent 16-year-old Pinus radiata D. Don. plantation in Australia. Agric Ecosyst Environ 124:205–218

Hamer U, Makeschin F, Stadler J, Klotz S (2008) Soil organic matter and microbial community structure in set-aside and intensively managed arable soils in NE-Saxony, Germany. Appl Soil Ecol 40:465–475

Hart CS, Stark JM, Davidson EA, Firestone MK (1994) Nitrogen mineralization, immobilization, and nitrification. In Weaver AL et al (ed) Methods of soil analysis. Part 2. 2nd ed. SSSA book Series No. 5. SSSA, Madison, WI, USA, p 985–1018

Helfrich M, Ludwig B, Buurman P, Flessa H (2006) Effect of land use on the composition of soil organic matter in density and aggregate fractions as revealed by solid-state 13C NMR spectroscopy. Geoderma 136:331–341

Houghton RA (2005) Aboveground forest biomass and the global carbon balance. Glob Chang Biol 11:945–958

Huang Z, Davis MR, Condron LM, Clinton PW (2011) Soil carbon pools, plant biomarkers and mean carbon residence time after afforestation of grassland with three tree species. Soil Biol Biochem 43:1341–1349

Hughes MK (1971) Tree biocontent, net production and litter fall in a deciduous woodland. Oikos 22:62–73

Jaksic V, Kiely G, Albertson J, Oren R, Katul G, Leahy P, Byrne K (2006) Net ecosystem exchange of grassland in contrasting wet and dry years. Agric For Meteorol 139:323–334

Johansson T (2000) Biomass equations for determining fractions of common and grey alders growing on abandoned farmland and some practical implications. Biomass Bioenerg 18:147–159

Jones MB, Donnelly A (2004) Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated $CO_2$. New Phytol 164:423–439

Jug A, Makeschin F, Rehfuess KE, Hofmann-Schielle C (1999) Short-rotation plantations of balsam poplars, aspen and willows on former arable land in the Federal Republic of Germany. III. Soil ecological effects. For Ecol Manag 121:85–99

Khandokar F (2003) Phosphorus in soils of pasture farms subject to chemical and slurry fertilization. MEngSc Thesis, Dept. of Civil and Environmental Engineering, University College Cork, Ireland

Kiely G, McGoff NM, Eaton JM, Leahy P (2008) SoilC—measurement and modelling of soil carbon stocks and stock changes in Irish soils, STRIVE Report, Environmental Protection Agency, Ireland

Korsmo H (1995) Weight equations for determining biomass fractions of young hardwoods from natural regenerated stands. Scand J For Res 10:333–346

Kuznetsova T, Lukjanova A, Mandre M, Lõhmus K (2011) Aboveground biomass and nutrient accumulation dynamics in young black alder, silver birch and Scots pine plantations on reclaimed oil shale mining areas in Estonia. For Ecol Manag 262:56–64

Laganière J, Angers D, Paré D (2010) Carbon accumulation in agricultural soils after afforestation: a meta-analysis. Glob Chang Biol 16:439–453

Lal R (2005) Forest soils and carbon sequestration. For Ecol Manag 220:242–258

Le Goff N, Granier A, Ottorini J, Peiffer M (2004) Biomass increment and carbon balance of ash (Fraxinus excelsior) trees in an experimental stand in northeastern France. Ann For Sci 61:577–588

Lee J, Hopmans JW, Rolston DE, Baer SG, Six J (2009) Determining soil carbon stock changes: simple bulk density corrections fail. Agric Ecosyst Environ 134:251–256

Lewis C (2003) Phosphorus, nitrogen and suspended sediment loss from soil to water from agricultural grassland. MEngSc Thesis, Dept. of Civil and Environmental Engineering, University College Cork, Ireland

Marmann P, Wendler R, Millard P, Heilmeier H (1997) Nitrogen storage and remobilization in ash (*Fraxinus excelsior*) under field and laboratory conditions. Trees-Struct Funct 11:298–305

Morris SJ, Bohm S, Haile-Mariam S, Paul EA (2007) Evaluation of carbon accrual in afforested agricultural soils. Glob Chang Biol 13:1145–1156

Mueller C, Kogel-Knabner I (2009) Soil organic carbon stocks, distribution, and composition affected by historic land use changes on adjacent sites. Biol Fertil Soil 45:347–359

Nordborg F, Nilsson U, Gemmel P, Örlander G (2006) Carbon and nitrogen stocks in soil, trees and field vegetation in conifer plantations 10 years after deep soil cultivation and patch scarification. Scand J For Res 21:356–363

Paul KI, Polglase PJ, Nyakuengama JG, Khanna PK (2002) Change in soil carbon following afforestation. For Ecol Manag 168:241–257

Peichl M, Arain MA (2007) Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. For Ecol Manag 253:68–80

Peichl M, Leahy P, Kiely G (2011) Six-year stable annual uptake of carbon dioxide in intensively managed humid temperate grassland. Ecosystems 14:112–126

Piñeiro G, Oesterheld M, Batista WB, Paruelo JM (2006) Opposite changes of whole-soil vs. pools C:N ratios: a case of Simpson's paradox with implications on nitrogen cycling. Glob Chang Biol 12:804–809

Post WM, Kwon KC (2000) Soil carbon sequestration and land-use change: processes and potential. Glob Chang Biol 6:317–327

Poulton PR, Pye E, Hargreaves PR, Jenkinson DS (2003) Accumulation of carbon and nitrogen by old arable land reverting to woodland. Glob Chang Biol 9:942–955

Ross DJ, Tate KR, Scott NA, Feltham CW (1999) Land-use change: effects on soil carbon, nitrogen and phosphorus pools and fluxes in three adjacent ecosystems. Soil Biol Biochem 31:803–813

Scanlon TM, Kiely G, Xie Q (2004) A nested catchment approach for defining the hydrological controls on non-point phosphorus transport. J Hydrol 291:218–231

Schimel DS (1986) Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2:345–357

Schulze ED (2000) The carbon and nitrogen cycles of forest ecosystems. In: Ecological Studies 142: Carbon and nitrogen cycling in European forest ecosystems. Heidelberg: Springer

Scott NA, Tate KR, Ford-Robertson J, Giltrap DJ, Smith CT (1999) Soil carbon storage in plantation forests and pastures: land-use change implications. Tellus B 51:326–335

Snaydon R (1987) Managed grasslands—Analytical studies, ecosystem of the world 17B. Elsevier, Amsterdam

Teagasc (2007) A road map for the farm forestry sector to 2015. The Irish Agriculture and Food Development Authority, Forestry Development Unit, Teagasc, Carlow

Telenius BF (1999) Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. Biomass Bioenerg 16:13–23

Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree species. For Ecol Manag 97:1–24

Uri V, Tullus H, Lohmus K (2003) Nutrient allocation, accumulation and above-ground biomass in grey alder and hybrid alder plantations. Silva Fennica 37:301–311

Uri V, Lõhmus K, Kiviste A, Aosaar J (2009) The dynamics of biomass production in relation to foliar and root traits in a grey alder (Alnus incana (L.) Moench) plantation on abandoned agricultural land. Forestry 82:61–74

Vellinga TV, Van den Pol-van Dasselaar A, Kuikman PJ (2004) The impact of grassland ploughing on $CO_2$ and $N_2O$ emissions in the Netherlands. Nutr Cycl Agroecosyst 70:33–45

Vesterdal L, Ritter E, Gundersen P (2002) Change in soil organic carbon following afforestation of former arable land. For Ecol Manag 169:137–147

Vogt K, Persson H (1991) Measuring growth and development of roots. In Lassoie JP, Hinckley TM (eds) Techniques and approaches in forest tree ecophysiology. CRS, Press. pp. 477–501

Wang Y, Houlton BZ (2009) Nitrogen constraints on terrestrial carbon uptake: implications for the global carbon-climate feedback. Geophys Res Lett 36:5

Wei X, Shao M, Fu X, Horton R (2010) Changes in soil organic carbon and total nitrogen after 28 years grassland afforestation: effects of tree species, slope position, and soil order. Plant and Soil 331:165–179

Wellock ML, LaPerle CM, Peichl M, Kiely G. Changes in ecosystem carbon stocks in a grassland-ash (*Fraxinus excelsior* L.) afforestation chronosequence in Ireland (submitted to the European Journal of Forest Research)

White R, Murray S, Rohweder M (2000) Pilot analysis of global ecosystems: grassland ecosystems. World Resources Institute, Washington, DC

Wilkins R, Hopkins A, Hatch DJ (2003) Grassland in Europe. Grassl Sci 49:258–266

Xu X, Wen L, Kiely G (2011) Modeling the change in soil organic carbon of grassland in response to climate change: effects of measured versus modelled carbon pools for initializing the Rothamsted Carbon model. Agric Ecosyst Environ 140:372–381

Yang X, Richardson TK, Jain AK (2010) Contributions of secondary forest and nitrogen dynamics to terrestrial carbon uptake. Biogeosciences 7:3041–3050

Zeller V, Bahn M, Aichner M, Tappeiner U (2000) Impact of land-use change on nitrogen mineralization in subalpine grasslands in the Southern Alps. Biol Fert Soils 31:441–448

Zianis D, Muukkonen P, Mäkipää R, Mencuccini M (2005) Biomass and stem volume equations for tree species in Europe. Silva Fenn Monogr 4:1–63