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The above- and belowground carbon pools of two mixed deciduous forest stands located in East-Flanders (Belgium)

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Abstract – Carbon (C) storage was studied in both an oak-beech and an ash stand located in the 80-year-old Aelmoeseneie experimental forest (Gontrode, East-Flanders, Belgium). The total carbon stock amounted to 324.8 tons C ha^{-1} in the oak-beech stand and 321.4 tons C ha^{-1} in the ash stand. In the oak-beech stand 41.5% of the total C was found in the soil organic matter, 11% in the litter layer and 47.5% in the vegetation. In the ash stand, the soil organic matter contained 53.0% of the total C stock, the litter layer only 1.0% and the vegetation 46.0%. Most vegetation carbon was found in the stems of the trees (51.1% in the oak-beech and 58.7% in the ash stand). Although total carbon storage appeared to be very similar, distribution of carbon over the different ecosystem compartments was related to species composition and site characteristics.

carbon pools / mixed deciduous forest / *Fagus sylvatica* L. / *Fraxinus excelsior* L. / *Quercus robur* L.

Résumé – Réservoirs aériens et souterrains de carbone dans deux peuplements forestiers feuillus situés en Flandre Orientale (Belgique). L'immobilisation de carbone (C) a été étudiée dans un peuplement mixte hêtre-chêne et un de frêne, situés dans la forêt expérimentale de Aelmoeseneie âgée de 80 ans. Le stock de carbone est estimé à 324,8 tonnes de C ha^{-1} dans le peuplement de hêtre-chêne et à 321,4 tonnes de C ha^{-1} dans celui de frêne. Dans le peuplement de hêtre-chêne, 41,5 % du C total est localisé dans la matière organique du sol, 11 % dans les couches organiques et 47,5 % dans la végétation. Dans le peuplement de frêne, la matière organique du sol contient 53,0 % du stock de C total, la litière seulement 1,0 % et la végétation 46,0 %. La plus grande partie du carbone de la végétation se situe dans les troncs des arbres (51,1 % dans le peuplement hêtre-chêne contre 58,7 % dans celui de frêne). Bien que les immobilisations de carbone total semblent très semblables, la distribution du carbone dans les différents compartiments de l'écosystème dépend de la composition de l'espèce et des caractéristiques du site.

stock de carbone / forêt mélangée décidue / *Fagus sylvatica* L. / *Fraxinus excelsior* L. / *Quercus robur* L.

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1. INTRODUCTION

Changes in land-use and exploitation of fossil fuels caused an increase of the atmospheric CO_2 concentration from 280 ppm in the middle of the 19th century to 360 ppm at the moment [7, 29]. This increase, together with the rise of the global mean air temperature, will most probably continue in the 21st century. A more complete insight in the global carbon (C) cycle is indispensable to understand the causes and the consequences of the so-called greenhouse effect. The carbon cycle is strongly related to the carbon balance of terrestrial ecosystems. Forest ecosystems are the most important carbon pools on earth. Although only 30% of the land surface is covered with forests [5, 49], these forests contain more than 60% of the carbon stored in the terrestrial biosphere [37]. Moreover, forests store carbon for long time periods [27]. The Ministerial Conference on the Protection of Forests in Europe (16–17 June 1993, Helsinki, Finland) suggested to make an inventory of the biomass stored in the wood and forest stocks, in order to compare carbon stored in, and carbon taken up by, forests with the amount of CO_2 emitted by fossil fuel combustion. At the Conference of Kyoto (1997) most industrial countries agreed on the reduction of the CO_2 exhaust. On the other hand, more and more attention is given to carbon fixation in order to extract CO_2 from the atmosphere [36]. A first step to assess the importance of forests in the global C cycle is to estimate the carbon stocks in these ecosystems.

Within forest ecosystems, the soil seems to be the largest carbon pool: approximately 60 to 70% of the carbon in forests is stored as organic material in the soil [12, 17, 50]. The carbon content of forest soils increases with increasing longitude and altitude [1, 12, 22]. Also climate, topography and texture are important factors related to the soil C content of forests [31, 37]. In general, the accumulation of organic material in the soil increases with decreasing temperature, increasing precipitation, decreasing evapotranspiration/precipitation ratio and increasing clay content [19, 31, 50].

Forests display a litter layer on top of the mineral soil. This litter layer is an important pool of nutrients and organic material [9]. The quantity and quality of the litter determine the decomposition rate. This decomposition defines the availability and mobility of essential elements, and as such, it influences the functional processes in the forest ecosystems [39, 47]. Different types of litter are distinguished [13]: mull, mor and moder. Mull humus is characterised by an intensive microbial activity: degradation of the organic material goes fast and this material is strongly mixed with the underlying mineral soil. Mull humus layers are usually very thin. Mor humus has a low microbial activity, which implements a slow degradation of the organic material and no mixture with the mineral soil. In the mor humus layer, three sublayers can be distinguished: an O^L-layer (litter layer) containing fresh, undegraded litter, an O^F-layer (fermentation layer) existing of fragmented, half degraded litter and an O^H-layer (humification layer) with humidified and compacted organic material. Moder humus has similar characteristics as mor humus, although there is some bioturbation. Both mor and moder humus types reduce the fertility of the ecosystem as many nutrients are immobilised in the accumulated litter [4, 30, 32].

Dead wood is a structural and functional element in a forest ecosystem [8, 11]. Besides its functioning as a microhabitat for fauna and flora, it also influences water, carbon and nutrient cycles [16, 21]. Stand age, location, tree species and management practices determine the amount of dead wood in a forest. In an undisturbed, old forest stand, the rate of die back and the rate of decomposition are in steady state [10, 40]. However, little information is available on the distribution and abundance of dead wood in forest ecosystems.

The carbon stocked in the tree layer varies widely: from 23 to 82% of the total ecosystem carbon pool [6, 27, 41], and this depends highly on the tree species. The tree compartment itself can be split up in an above- and belowground part, and further in leaves, branches and stems and fine and coarse roots respectively. Stand age and site characteristics seem to play an important role in the distribution of the carbon over the different compartments [46]. In forest stands on poor and dry soils, more carbon is allocated to the roots [38]. The ratio fine roots/leaf biomass increases with the age of the stand, while the relative contribution of the leaves and fine roots to the total biomass decreases. The relative importance of the woody tissues on the other hand increases with stand age [46].

The objectives of this paper were to synthesise and compare data about the carbon pools in two mixed deciduous forest types in Belgium: an oak-beech and an ash stand. Both stands have a well-developed shrub layer. The age of the trees and the climate are equal for both stands. Main differences are the dominating tree species and the soil type.

2. MATERIALS AND METHODS

2.1. Site description

This study was conducted in a mixed deciduous forest, called the Aelmoeseneie forest. This forest is property of the Ghent University and it is mainly used for educational and scientific purposes. It is located near the village of Gontrode (50°58' N, 3°48' E), which is situated 15 km south of Ghent (East-Flanders, Belgium). The oldest historical documents which refer to this forest date from the year 864. After 4 years of overfelling during World War I (1914–1918), a replantation was necessary to compensate for the removed wood. Therefore, most of the mature trees are now about 80 years old. The total forested area covers 28 ha. The elevation of the forest soil surface varies between 11 and 21 m a.s.l. The area is gently sloping northwards. The main part of the forest is an individual mixture of mainly broad-leaved species [14, 33].

Since 1993, a zone of 1.83 ha was fenced and closed for the public. The fenced area is used for intensive

Table I. Main stand characteristics of the two experimental areas in the Aelmoeseneie forest (BA: basal area, DBH: diameter at breast height and LAI: leaf area index).

	OAK-BEECH stand	ASH stand
SPECIES COMPOSITION	% of BA	% of BA
Pedunculate oak (*Quercus robur* L.)	48.7	10.6
Common beech (*Fagus sylvatica* L.)	26.6	1.3
Common ash (*Fraxinus excelsior* L.)	4.0	59.5
Japanese larch (*Larix leptolepis* (Sieb. et Zucc.) Endl	12.5	4.5
Common sycamore (*Acer pseudoplatanus* L.)	3.0	15.8
Rowan (*Sorbus aucuparia* L.), hazel (*Corylus avellana* L.), Alder buckthorn *(Frangula alnus* Mill.*)*, regeneration of sycamore (all together)	5.2	9.3
STAND INVENTORY DATA (1)		
Density (trees ha^{-1})	345	403
Mean DBH (cm)	26.1	26.9
BA (m^2)	26.6	30.8
Standing wood volume (m^3 ha^{-1})	301	328
Mean wood volume increment (1990-1997) (m^3 ha^{-1} $year^{-1}$)	5.1	3.8
MAXIMUM LAI (m^2 m^{-2}) (2)		
Tree layer	5.1	2.5
Shrub layer	0.4	2.0
Total	5.5	4.5
HUMUS TYPE	Moder	Mull
SOIL TYPE (FAO classification)	Dystric podzoluvisol	Dystric cambisol
(USDA classification)	Haplic glossudalf	Thapto glossudalfic, aquic, dystric eutrochept

(1) see [44]; (2) leaf fall method, [23].

scientific research. This experimental zone comprises two different forest types: an oak-beech stand (1.06 ha) and an ash stand (0.77 ha). As during the replantation of the forest the difference in soil type [42] was taken into account when choosing the main tree species, the ash stand is situated on the lower part of the forest. Both the species composition and the main stand inventory data are given in *table I*, as well as the maximum LAI of the tree and the shrub layer, the humus and soil type. The differences in chemical soil characteristics of both stands are published by Vandendriessche et al. [42]. Mean annual temperature (measured during the period 1984–1993) is 10.1 °C, with 2.8 °C in the coldest month (January) and 17.4 °C in the warmest month (August). Annual precipitation is 791 mm on average. Mean dates of first and latest frost are 10th November and 13th April respectively, with a mean of 47 frost days per year [33].

In 1994, a measuring tower was constructed in the middle of the scientific zone, at the common border of the two forest stands. This tower, which contains five horizontal working platforms, gives direct access to the crown of the main tree species: oak, beech and ash. Both forest stands are continuously used for integrated scientific research, such as physiological, biogeochemical and soil science studies and modelling activities. Furthermore, two level II observation plots of the European Programme for Intensive Monitoring of Forest Ecosystems are installed in the scientific zone. The results discussed in this paper were obtained during the Belgian research programme BELFOR, which analysed the biogeochemical cycles in a series of Belgian model forests [43].

2.2. Mineral soil

Soil samples were taken in both the oak-beech and the ash stand to determine the carbon content of the mineral soil (up to 1-m depth). In each stand, 10 randomly chosen transects of 25-m length were sampled at six points, each 5 m separated from each other (n = 60). A soil core was used to take samples at different depths: i.e. 0–5 cm, 5–15 cm, 15–50 cm and 50–100 cm. After drying, sieving (mesh of 2 mm) and grinding, the method of Walkley and Black [28] was used to determine the carbon concentration (g C g^{-1} dry soil). It has been reported that this method underestimates the real carbon concentration, and that the results have to be multiplied by 4/3, because only 75% of the organic C in the soil is oxidised by this method [28]. Total carbon content (ton C ha^{-1}) in each soil horizon was calculated from the carbon concentration, the bulk density [42] and the layer thickness. The normal distribution was checked for each soil layer (Kolmogorov-Smirnov test).

2.3. Litter layer

In both stands, the humus layer was collected at different spots of 0.25 m^2, at the same sampling points (n = 60) and at the same moment (May 1996) as used for the mineral soil sampling (see Sect. 2.2.). The O^L-, O^F- and O^H-layers were separated for the oak-beech stand. The material was weighed and dried (80 °C, 48 h). The carbon content of each sample was determined by loss-on-ignition (LOI). The results obtained this way were then used to calculate the mean C content of each layer.

In both stands of the Aelmoeseneie experimental forest, dead wood was collected on 5 randomly chosen plots of 100 m^2 (April 1996) following the methodology described by Janssens et al. [14]. As both stands have already been managed for a long time, only a few dead trees are present. Therefore, all dead wood can be considered as lying on the forest floor. All dead wood with a diameter < 2.5 cm was sampled on one subplot (1 m^2) per plot. This subplot was extended to 25 m^2 for the diameter class 2.5–5 cm. The entire plot (100 m^2) was used for collecting the dead wood with a diameter > 5 cm. The material collected was then weighed and dry weight (80 °C, until constant weight) was determined as well. The carbon concentration of the wood was detected by LOI. Based on the total dry matter and the C concentration, the total C storage in the dead wood could be calculated.

2.4. Carbon pools in the vegetation

For all compartments of the vegetation, a carbon concentration of 50% (on dry matter basis) was assumed [20].

2.4.1. Aboveground carbon pools

The shrub layer is a carbon pool that is neglected in many carbon sequestration studies. However, we wanted to calculate the amount of carbon in this layer too, in order to obtain a more complete insight in the total carbon in the two Aelmoeseneie stands. Ten square plots of 25 m^2 were randomly selected in each stand. In each plot, the complete aboveground shrub layer was removed (January 1996) and dried (80 °C, until constant weight).

Total C storage in the shrub layer was then determined, assuming a carbon concentration of 50% (see above).

In January 1997, all trees (diameter at breast height DBH > 7 cm) were numbered and circumferences at breast height (CBH) and tree heights were measured. Twelve oak trees and six ashes were cut down. For both species, a tree with the mean stem circumference (oak: 96.0 cm, ash: 111.0 cm), the model trees of Hohenadl (mean circumference ± stand. dev.; stand. dev. for oak: 26.2 cm, for ash: 32.4 cm) and some trees with an intermediate circumference were chosen. Stem volumes of these trees were calculated, based on mensuration data of stem discs of one meter length [14]. The following relationships between stem volume (V) and CBH were found:

$$V_{oak} = 0.000039 \times \text{CBH}^{2.200} \qquad (R^2 = 0.97)$$

$$V_{ash} = 0.000200 \times \text{CBH}^{1.853} \qquad (R^2 = 0.96)$$

with volume expressed in m^3 and CBH in cm. Stem volumes of beech, sycamore and larch were calculated based on the tables of Dagnelie et al. [3] with stem circumference and tree height as inputs:

$$V_{beech} = -0.015572 + 0.0009231 \times \text{CBH} - 0.0000071407 \times \text{CBH}^2 - 0.000000077179 \times \text{CBH}^3 - 0.0013528 \times H + 0.0000040364 \times \text{CBH}^2 \times H$$

$$V_{sycamore} = 0.010343 - 0.0014341 \times \text{CBH} + 0.000034521 \times \text{CBH}^2 - 0.00000013053 \times \text{CBH}^3 + 0.00077115 \times H + 0.0000030231 \times \text{CBH}^2 \times H$$

$$V_{larch} = -0.03088 + 0.0014885 \times \text{CBH} - 0.0000049257 \times \text{CBH}^2 - 0.00000012313 \times \text{CBH}^3 - 0.0011638 \times H + 0.0000041134 \times \text{CBH}^2 \times H$$

with V expressed in m^3, CBH in cm and height H in m.

Total stem volume was multiplied by the wood density of the respective species to calculate the total dry weight of the stems of the different tree species. Wood densities on a dry matter basis are 500 kg m^{-3} for oak, 523 kg m^{-3} for ash, 566 kg m^{-3} for young beeches (CBH < 78 cm) and 550 kg m^{-3} for old beeches (CBH > 78 cm) [36]. These values are based on the fresh volume. Wagenführ and Schüber [48] found 590 kg m^{-3} for sycamore and 550 kg m^{-3} for larch.

Regression equations between stem circumference and dry weight of the leaves on the one hand and dry weight of the branches on the other hand were established for oak, beech and ash [14]. These equations were used to calculate the dry weight of the leaves and the branches. As for sycamore and larch (DBH > 7 cm) no regression equations were established, the stem biomass was considered as being 75% of the total biomass, 24% was dedicated to the branches and 1% to the leaves [27]. Multiplying the dry weight by 0.5 (see before) gave the total amount of carbon stored in the leaves and the branches.

2.4.2. Belowground carbon pools

For two of the twelve oak trees (CBH 86 cm and 97 cm) which were used to establish the aboveground carbon pools, the coarse root systems were excavated in order to collect information on the belowground carbon pool. All coarse roots (diameter > 0.5 cm) were collected and weighed. Samples were dried (80 °C , until constant weight) to determine total dry weight of the root system. The coarse root system of the smallest tree studied amounted to 16.3% of the total tree biomass, compared to 17.6% for the larger tree. Duvigneaud [6] found a similar root fraction of 17.0% in a *Querceto-Coryletum* of 80 years. Literature values of root fractions were used to assess the carbon stored in the coarse roots of the other species, e.g. 16.8% for beech, 16.3% for ash and 17.0% for maple and larch [6].

During July and August 1997, soil samples were taken to study the vertical distribution of the fine roots. The used root auger had a total volume of 729 cm^3, and a length of 15 cm. Five depths were studied: 0–15, 15–30, 30–45, 45–60, 60–75 cm. In the oak-beech stand, samples were taken at 7 locations, while in the ash stand 5 locations were sampled. Fine roots (diameter < 0.5 cm) were extracted, dried (60 °C, 48 h) and weighed. A more detailed description of the experimental set-up and the sampling strategy can be found in Vande Walle et al. [45].

3. RESULTS AND DISCUSSION

3.1. Mineral soil

Table II gives the mean carbon content (mg C cm^{-3} soil) of the mineral soil layers in both stands.

In both stands, there was a clear decrease in carbon content with increasing depth in the soil. ANOVA analysis was applied to compare carbon contents in the different layers of both stands. No significant differences between the two stands could be found for the upper two layers (0–5 and 5–15 cm). For the lower layers

Table II. Mean carbon content (mg C cm^{-3} soil) of each mineral soil layer in the oak-beech and the ash stand ($n = 60$) with indication of significant differences between the stands.

Depth (cm)	Carbon content (mg C cm^{-3} soil)		
	Oak-beech stand	Ash stand	
0–5	84.0	71.6	n.s.
5–15	34.7	38.3	n.s.
15–50	11.8	17.2	*
50–100	3.4	7.2	*

n.s.: not significant; * significant at $p < 0.05$.

(15–50 and 50–100 cm), the carbon content was always significantly higher ($p < 0.05$) in the ash stand than in the oak-beech stand. Previous studies have shown that in the ash stand, an extreme diversity of earthworms is present [24]. As those earthworms continuously mix the organic material with the mineral soil, the bioturbation of the soil is more intense in the ash stand, resulting in a more equally distribution of the organic material in this stand than in the oak-beech stand.

It seems that in both stands, large amounts of carbon are stored in the mineral soil (*table III*: oak-beech: 135.0 tons C ha^{-1}, ash: 170.5 tons C ha^{-1}). Dutch investigators found similar, but slightly lower values ranging from 102 to 122 tons C ha^{-1} for comparable forest ecosystems [26] while Janssens et al. [15] found a carbon content of 114.7 tons ha^{-1} over a depth of 1 m in a Belgian Scots pine forest. The forest they examined was, however, situated on a sandy soil. In such soils, carbon is less immobilised by the formation of organo-mineral-complexes than in loamy and clayey soils, as is the case in the Aelmoeseneie forest. Soil texture can partly explain the differences of carbon storage in the mineral soil.

3.2. Litter layer

In the holorganic horizon of the oak-beech stand, an O^L-, O^F- and O^H-layer could be distinguished. Carbon amounts stored in these layers were 0.6, 17.2 and 15.4 tons C ha^{-1} respectively. The O^L-layer in the ash stand only contained 0.1 ton C ha^{-1}, and an O^F- and O^H-layer were lacking.

The litter formed in the ash stand decomposes very rapidly. The above mentioned bioturbation causes the mixing of the organic material with the mineral soil. As

Table III. Carbon content (ton C ha^{-1}) of the soil, the litter and the vegetation compartment of the oak-beech and the ash stand of the Aelmoeseneie forest.

Compartment	Carbon content (ton C ha^{-1})	
	Oak-beech stand	Ash stand
Soil		
Organic material		
0–5 cm depth	*42.0*	*35.8*
5–15 cm depth	*34.7*	*38.3*
15–50 cm depth	*41.3*	*60.1*
50–100 cm depth	*16.8*	*35.8*
Total organic material	134.8	170.0
Dead roots	0.2	0.5
	135.0	**170.5**
Litter		
Holorganic horizon	33.2	0.1
Dead wood		
< 2.5 cm diameter	*1.6*	*1.6*
2.5–5 cm diameter	*0.6*	*0.6*
> 5 cm diameter	*0.3*	*0.8*
Total dead wood	2.5	3.0
	35.7	**3.1**
Vegetation		
Leaves		
Trees	*1.8*	*0.7*
Shrubs	*0.2*	*0.6*
Total leaves	2.0	1.3
Branches trees	42.5	26.9
Stems trees	78.7	86.9
Branches and stems shrubs	2.4	4.3
Coarse roots	25.1	22.8
Fine roots	3.4	5.8
	154.1	148.0
TOTAL	**324.8**	**321.6**

such, almost no litter layer is found in the ash stand. The O^F- and O^H-layer of the oak-beech stand are well developed. Most of the carbon stored in the holorganic horizon is stored in these two layers. Janssens et al. [15] found a storage of 25.5 tons C ha^{-1} in the humus layer of a Belgian Scots pine forest. This is a value close to the 33.2 tons C ha^{-1} which was found for the oak-beech stand. Micro-organisms, which have a C/N ratio of 6 to 16, prefer digestion of litter with a low C/N ratio (< 20) in order to satisfy their nitrogen needs. The C/N ratio of the fresh ash litter in the Aelmoeseneie forest is 24, while the values for oak and beech are 29 and 42 respectively [24]. Due to its lower C/N ratio, the ash litter is faster degraded than the oak and the beech litter. The slow degradation of the dead biomass in the oak-beech stand causes therefore an accumulation of litter, which itself decreases the aeration, and, hence, has a negative effect on the speed of the litter degradation.

The mean C concentration of the dead wood was 48.9% of the dry weight. In *table III*, the C content (ton C ha^{-1}) in the different diameter classes is presented for both stands. In the ash stand (3.0 tons C ha^{-1}), more C was found in the dead wood than in the oak-beech stand (2.5 tons C ha^{-1}). This difference is only due to the dead wood with a diameter > 5 cm. However, the difference was not significant (t-test).

Other investigators [2, 18] found dead wood stocks accounting for 10 to 30% of the total aboveground biomass of forests. Values found here are much lower: 1.3 and 2.0% for the oak-beech and the ash stand respectively. This is caused by the removal of the dead wood in the Aelmoeseneie forest for many decades. As, in view of a new forest management policy, the dead wood is no longer removed since about 10 years, an increase of this dead wood carbon pool can be expected in the future.

3.3. Carbon pools in the vegetation

3.3.1. Aboveground carbon pools

Although the shrub layer showed a high diversity and was well developed in both stands (see *table I*), the total amount of carbon stored in this shrub layer was relatively small, i.e. 2.6 tons C ha^{-1} in the oak-beech stand and 4.9 tons C ha^{-1} in the ash stand. In comparison with the total aboveground carbon pool, only 1.7% was stored in the shrub layer of the oak-beech stand, and 3.3% in the ash stand. These are small fractions, considering the important contribution of the shrub layer to the overall leaf area index (LAI): 7.3% in the oak-beech stand and 44.4% in the ash stand. Although small, this pool should not be neglected. Indeed, the shrub layer in the ash stand contains even more carbon than the litter layer.

The total carbon storage in the leaves, branches and roots of the main tree species are summarised in *table IV*.

The amount of carbon stored in the aboveground tree biomass (leaves, branches and stems) totalled 123.0 tons C ha^{-1} in the oak-beech and 114.5 tons C ha^{-1} in the ash stand. The partitioning over the different compartments was, however, different in the stands. For the oak-beech stand 1.6%, 34.5% and 63.9% of the C is stored in the leaves, branches and stems respectively. This is in contrast with the corresponding values of 1.1%, 23.4% and 75.5% for the ash stand (*table IV*). The larger relative amount of beeches present in the oak-beech stand explains the difference in carbon distribution, as beech trees contain as much carbon in their branches as in the stem wood (*table IV*). An interesting observation is the fact that beech accounted for 37.8% of the carbon stored in the aboveground biomass of the oak-beech stand, while the beech trees only contributed 26.6% of the basal area (*table I*). The main tree species, being oak and beech

Table IV. Contribution of the main tree species in the total carbon storage (ton C ha^{-1}) in the aboveground phytomass pools of the oak-beech and the ash stand.

	Oak-beech			Ash		
	Leaves	Branches	Stems	Leaves	Branches	Stems
Oak	0.95	15.09	41.00	0.21	3.79	10.31
Beech	0.93	22.75	22.75	0.05	1.29	1.29
Ash	0.04	0.95	3.39	0.77	16.58	59.00
Others	0.15	3.71	11.59	0.22	5.21	16.28
Total	1.97	42.50	78.73	1.25	26.87	86.88

in the oak-beech stand and ash in the ash stand, accounted respectively for 84.0% and 66.4% of the total aboveground carbon stock.

Carbon storage in the aboveground biomass of the Aelmoeseneie forest is comparable with the values found in previous studies [6, 15, 27, 34, 41]. Dutch investigators [25] showed that the carbon stock in living biomass is largest for beech forests, a conclusion comparable to results found here.

3.3.2. Belowground carbon pools

The total amount of carbon stored in the coarse roots added up to 25.1 tons C ha^{-1} in the oak-beech stand and 22.8 tons C ha^{-1} in the ash stand, as is listed in *table III*. *Figure 1* illustrates clearly the different vertical distribution of fine roots (diameter < 0.5 cm) in the mineral soil of each stand. In the upper two layers, much more fine roots were found in the ash stand than in the oak-beech stand: almost fourfold in the upper layer (3.0 compared to 0.8 tons C ha^{-1}), and 85% more in the second layer (1.3 compared to 0.7 tons C ha^{-1}). This difference is mainly due to the well-developed shrub layer in the ash stand as these shrub species are mostly rooted in the upper layers of the forest soil. ANOVA-analysis showed that the upper soil layer of the ash stand contained significantly more fine roots than all other layers.

The total carbon storage in the living fine roots amounted to 3.4 tons C ha^{-1} in the oak-beech stand, compared with 5.8 tons C ha^{-1} in the ash stand (*figure 1* and *table III*). Much less dead roots were found, i.e. 0.2 tons C ha^{-1} and 0.5 tons C ha^{-1}, for the oak-beech and the ash stand respectively (*table III*).

The ratio of fine roots to leaves (both expressed in ton C ha^{-1}) was 1.7 in the oak-beech stand, and 4.5 in the ash stand. It was shown that the LAI in the oak-beech stand was 22% higher than in the ash stand (*table I*). When expressed as biomass (ton C ha^{-1} in the leaves), the oak-beech stand contained 54% more carbon in the leaves than was the case for the ash stand (*table III*). This means that the mean specific leaf area (SLA) was higher (0.073 kg DM m^{-2} leaf) in the oak-beech than in the ash stand (0.058 kg DM m^{-2} leaf). This lower SLA in the ash stand increases the relative importance of the carbon storage in the fine roots compared to the leaves. Janssens et al. [15] found for the ratio of fine roots to needles a value of 0.6. In the Scots pine forest they studied there was, however, no shrub layer present, causing a lower amount of fine roots. On the other hand, they found 3.0 tons C ha^{-1} to be stored in the needles, which is far more than the values found here.

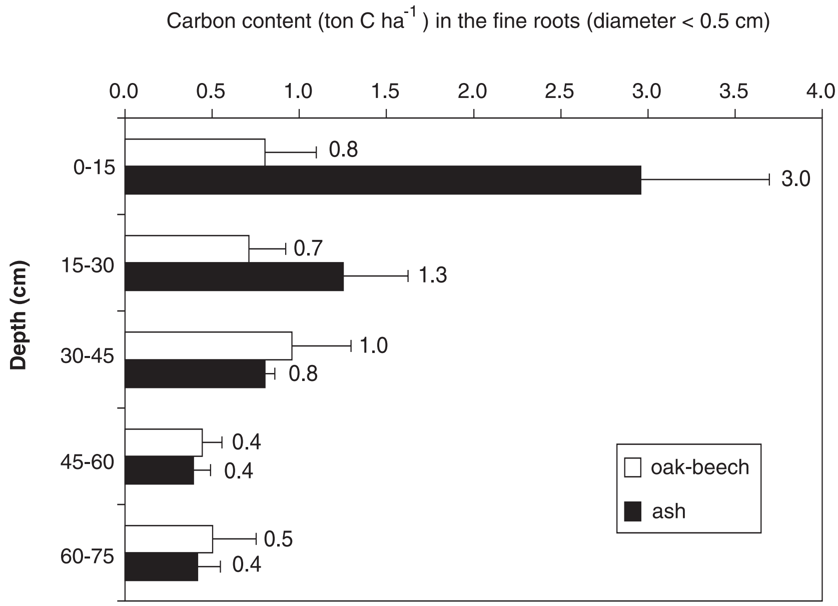

Figure 1. Vertical distribution of the carbon content (ton C ha^{-1}) of the fine roots (diameter < 0.5 cm) in the oak-beech and the ash stand of the Aelmoeseneie forest; error bars indicate one standard error of the mean.

3.4. Overview of the carbon pools

The total carbon pool present in both stands (*table III*) was rather similar, i.e. 324.8 tons C ha^{-1} in the oak-beech stand, and 321.6 tons C ha^{-1} in the ash stand. The distribution of carbon over the different compartments (*figure 2*) was less comparable. The most striking difference was found in the litter layer: while for the oak-beech stand this layer contained 11.0% of the total carbon, it only accounted for 1.0% in the ash stand. On the other hand, the fraction of carbon stored in the mineral soil was much higher in the ash stand (53.0%) than in the oak-beech stand (41.6%). The contribution of the living phytomass was again comparable: 47.4% in the oak-beech and 46.0% in the ash stand. Less than one fifth of all the carbon stored in the vegetation was found in the belowground organs (fine and coarse roots): 18.5% in the oak-beech stand, and 19.3% in the ash stand. Partitioning of the carbon over the living biomass, the litter layer and the mineral soil in the Aelmoeseneie forest is in agreement with the results reported by Nabuurs and Mohren [27].

The contribution of the living (47.4% in the oak-beech and 46.0% in the ash stand) and the non-living compartment (52.6% and 54.0%), are very similar in both stands. As such, one can conclude that although the species composition of the forest stands and the soil characteristics are different, the total amount of carbon stored in the ecosystem is very similar. This is also true for the distribution between living and non-living compartments. It seems that for forest ecosystems of different composition but situated in identical climatic regions, their carbon storage will not change very much. This conclusion is confirmed by the results of Janssens et al. [15], obtained for a Scots pine forest, situated in the same climatic region. Although a different main tree species and another soil type, the pine forest yielded comparable values of 58.0% for the total carbon in the non-living compartment and 42.0% for the living carbon pool.

4. CONCLUSION

The study revealed that both the oak-beech and the ash stand have important carbon stocks. The total amount of carbon stored (resp. 324.8 tons C ha^{-1} and 321.6 tons C ha^{-1}) and the distribution between living and non-

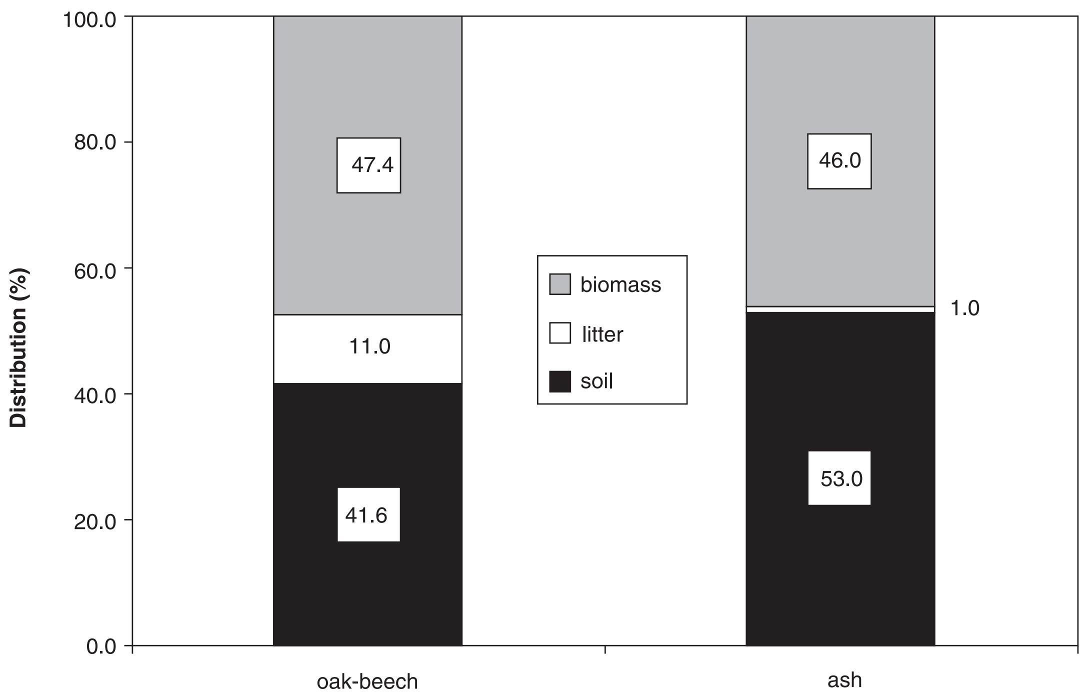

Figure 2. Carbon in the biomass, the litter and the soil compartment of the oak-beech and the ash stand as a percentage of the total amount of C stored in these stands.

living compartments seemed to be very similar. The partitioning of carbon over the different compartments of the ecosystem is highly related to the tree species and the site characteristics. Leaves and branches were proportionally more important in the oak-beech stand than in the ash stand. Due to rapid degradation of fresh litter, the holorganic horizon had a much smaller carbon pool in the ash stand than in the oak-beech stand. On the other hand, more intense bioturbation caused a better mixture of the organic material with the mineral soil, which, therefore, contained more carbon in the ash stand than in the oak-beech stand. The results presented in this paper form the basis for the understanding of the carbon cycle in the experimental forest Aelmoeseneie. Eventually, these data are also valuable for the validation of dynamic vegetation models used to assess the carbon storage in forest ecosystems.

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