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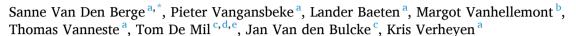
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ORIGINAL ARTICLE

Biomass increment and carbon sequestration in hedgerow-grown trees



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ABSTRACT

The global role of tree-based climate change mitigation is widely recognized; trees sequester large amounts of atmospheric carbon, and woody biomass has an important role in the future biobased economy. In national carbon and biomass budgets, trees growing in hedgerows and tree rows are often allocated the same biomass increment data as forest-grown trees. However, the growing conditions in these linear habitats are different from forests given that the trees receive more solar radiation, potentially benefit from fertilization residuals from adjacent fields and have more physical growing space. Tree biomass increment and carbon storage in linear woody elements should therefore be quantified and correctly accounted for. We examined four different hedgerow systems with combinations of pedunculate oak, black alder and silver birch in northern Belgium. We used X-ray CT scans of pith-to-bark cores of 73 trees to model long-term (tree life span) and short-term (last five years) trends in basal area increment and increment in aboveground stem biomass. The studied hedgerows and tree rows showed high densities (168-985 trees km⁻¹) and basal areas (22.1-44.9 m² km⁻¹). In all four hedgerow systems, we found a strong and persistent increase in stem biomass and thus carbon accumulation with diameter (long-term trend). The current growth performance (short-term trend) also increased with tree diameter and was not related to hedgerow tree density or basal area, which indicates that competition for light does not (yet) limit tree growth in these ecosystems. The total stem volume was 82.0-339.7 m³ km⁻¹ (corresponding to 18.8-100.7 Mg aboveground carbon km⁻¹) and the stem volume increment was 3.1-14.5 m³ km⁻¹ year⁻¹ (aboveground carbon sequestration 0.7-4.3 Mg km⁻¹ year⁻¹). The high tree densities and the persistent increase in growth of trees growing in hedgerow systems resulted in substantial wood production and carbon sequestration rates at the landscape scale. Our findings show that trees growing in hedgerow systems should be included when biomass and carbon budgets are drafted. The biomass production rates of hedgerow trees we provide can help refine the IPCC Guidelines for National Greenhouse Gas Inventories.

1. Introduction

Globally, trees support the biodiversity of ecosystems (Franklin, 1993; Prevedello et al. 2017) and are key components in the water, nutrient and carbon cycle (Dixon et al., 1994; Pan et al., 2011; Sheil, 2018; Thompson et al., 2009). The forest carbon cycle - particularly net primary productivity and carbon storage - is doubtlessly one of the most studied cycles in the biosphere (Clarck et al., 2001; Houghton, 2007). Forest conservation and restoration are important mitigation strategies to reduce the greenhouse effect (FAO, 2010; Grassi et al., 2017; Keenan

and Williams, 2018), and there is increasing awareness of the opportunity and necessity to use forests to increase carbon uptake by woody vegetation (Agrawal et al., 2011; FAO, 2018; Henry et al., 2013).

Trees outside forests are often studied with a different focus, emphasising other relevant services. For instance, in the countryside, trees bordering crop fields function as wind breaks (Rempel et al., 2017) and prevent erosion and run off (Sitzia et al., 2014; Van Vooren et al., 2017). They improve microclimate in adjacent fields (Sánchez et al., 2010) and enrich the soil with organic materials (Cardinael et al., 2016; Follain et al., 2007; Pardon et al., 2017), all potentially contributing to

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higher crop yields and more resilient production systems (Clair and Lynch, 2010; Graves et al., 2007; Rivest et al., 2010). Moreover, trees on agricultural lands also have the potential to make an important contribution to climate change mitigation, as they constitute an additional carbon sink and source of woody biomass for applications in biobased economies (Albrecht and Kandji, 2003; Nair et al., 2010; Nair, 2012; Oldenburger, 2010; Van Noordwijk, 2014; Zhou et al., 2011).

In Europe, agricultural landscapes are often characterized by the presence of hedgerows and tree rows in so called 'bocage' landscapes or in areas where agroforestry is applied (Baudry et al., 2000; Larcher and Baudry, 2013). A hedgerow is a heterogeneous strip of woody vegetation, planted or spontaneously formed, consisting of a clear shrub (≤ 15 m) and tree layer (> 15 m). Tall tree species from the tree layer (e.g. *Quercus robur, Betula pendula.*) usually occur in the shrub layer as well, together with some typical shrub species (e.g. *Prunus sp., Sorbus sp.*). A tree row is a homogeneous linear planting of one particular tree species without a (dense) shrub layer.

However, empirical studies of wood production and carbon storage in hedgerows and tree rows are still limited. The IPCC Good Practice Guidance (IPCC, 2003) and National GHG Inventory Guidelines (IPCC, 2006) provide recommendations on default estimates for assessing carbon stocks and emissions from the Land Use, Land Use Change and Forestry sector. For these estimations they formulate three tiers of detail, ranging from Tier 1 (with average stock change factors for large eco-regions of the world; simplest to use) up to Tier 3 (with high-resolution methods specific for each country and species). The IPCC (2019a) Refinements adapt the Tier 1 coefficients for soil organic and biomass carbon storage in agroforestry systems from Cardinael et al. (2018), who themselves have underpinned the scarcity of relevant data. Tier 2 and Tier 3 coefficients for aboveground woody biomass growth rates in hedgerow-grown species are non-existent (IPCC, 2019a). To date, in most biomass and carbon accounting studies that incorporate hedgerow systems, biomass production and carbon storage are based on estimates of forest-grown trees (Chambers et al., 2015; Schoeneberger et al., 2012; Zhou et al., 2011).

However, differences in growth dynamics and carbon storage of hedgerow-grown trees compared to forest-grown trees can be expected. Trees in hedgerows and tree rows (henceforth referred to as 'hedgerow systems' and 'hedgerow-grown trees', when grouped together) grow in narrow strips where they receive more light than in denser wooded stands (Balandier and Dupraz, 1998; Falloon et al., 2004). They are subjected to more direct wind momentum load resulting in greater branch production (Zhou et al., 2011), wider and deeper rooting (Cardinael et al., 2015; Gilman, 1989) and they benefit from agricultural residual inputs such as fertilizers, pesticides and irrigation (Cardinael et al., 2018). Moreover, the hedgerow microclimate is warmer and dryer during the growing season compared to a forest (Vanneste et al., 2020a; Wehling and Diekmann, 2009), and soils are often less acidic (Van Den Berge et al., 2019). And yet, to our knowledge, there is currently no study available on the trends in aboveground stem biomass increments and carbon storage of trees growing in hedgerow systems.

In this study, we examine growth dynamics, stem biomass increment and stem carbon accumulation in hedgerow-grown pedunculate oak (*Quercus robur* L.), silver birch (*Betula pendula* Roth) and black alder (*Alnus glutinosa* (L.) Gaertn.). We apply tree-ring analysis on wood cores using X-ray CT images (cf. Van den Bulcke et al., 2014), which provide long-term growth data covering the entire lifespan of the trees (*Groenendijk*, 2015). Basal Area Increment (BAI) derived from the tree-ring data provide insights into the species' growth dynamics. Combining these increment measures with wood density measurements with an annual resolution using the absorption-based X-ray images data (De Ridder et al., 2010), gives a long-term view on Increment of the Aboveground stem Biomass (IAB) (Vannoppen et al., 2018).

Our aim was to gain insight into the long-term (tree life span) patterns in growth of trees in different hedgerow systems, i.e. with a different mixture of species and growing under different soil types. We

investigate short-term (last five years) patterns in growth as well to allow us to determine possible differences due to current plot level characteristics. Based on our data, we determine biomass increment and carbon sequestration of these trees, allowing us to formulate Tier 3 estimates for pedunculate oak, silver birch and black alder trees growing in hedgerow systems in Belgium. We estimate the contribution of hedgerow systems to stem biomass production and aboveground carbon storage on a landscape level.

After describing our studied hedgerow systems, we answer the following questions:

- (1) What are the patterns in growth of trees in hedgerow systems throughout their life span? That is, studying the changes in BAI and IAB with tree diameter and tree age for hedgerow-grown trees.
- (2) Which variables relate to the current growth performance of trees in hedgerows and tree rows? That is, investigating the relationship between the mean values for BAI and IAB over the last five years and the neighbourhood competition variables in the plots.
- (3) How much stem biomass is produced and aboveground carbon is stored per running kilometre of hedgerow and tree row? And, as a result, how much carbon is sequestered in the aboveground stem biomass across all the hedgerow systems found in an entire landscape?

2. Material and methods

2.1. Study area and field work

Our study area comprises two municipalities in the province of Antwerp, northern Belgium: Turnhout $(51^{\circ}19'18'N, 4^{\circ}56'15'E; 56 \text{ km}^2)$ and Meerhout $(51^{\circ}7'56'N, 5^{\circ}4'37'E; 36 \text{ km}^2)$ (Fig. 1). Both are typical Flemish municipalities with a low forest cover (16.4% and 12.0%, Informatie Vlaanderen, 2012) and an intensively used countryside with agricultural lands (arable fields and grazing pastures) covering 55.9% and 61.0% of the total land surface (European Environment Agency, 2013). The elevation is 18--35 m above sea level, and the climate is temperate maritime with a total annual rainfall of 755 mm and mean annual temperature of 10.1°C (KMI, 2019).

After a thorough exploration in spring 2017 of the hedgerow systems present in the two landscapes, we focused on four types that were the most characteristic for the study region in terms of structure and species composition: on moist sandy soil of Turnhout (1) tree rows of pedunculate oak (average width \pm standard deviation: 1.2 ± 0.3 m); (2) hedgerows of pedunculate oak mixed with silver birch (width 4.2 ± 1.5 m); and on wet, sandy loam soil in Meerhout (3) tree rows of coppiced black alder (width 2.2 ± 0.4 m); (4) hedgerows dominated by black alder mixed with pedunculate oak (width 3.1 ± 0.9 m). Pedunculate oak (hereafter oak), silver birch (hereafter birch) and black alder (hereafter alder) are described as Central European forest species (Leuschner and Meier, 2018) and are classified as mid-successional, early successional and mid-successional, respectively.

First, we performed a dendrometric inventory in 10 plots in each of the four hedgerow systems during the summer of 2017. All 40 plots covered 50 m², with lengths varying from 8 to 50 m and widths varying from 6 to 1 m, respectively (we adjusted the length of the plot to the measured width of the hedgerow system). In each plot, we performed a full inventory of the standing trees, measuring and identifying all individuals to the species level with stem diameter at breast height larger than 7 cm. For each species, we visually estimated the total canopy cover using a rating scale (5–12%; 12–25%; 25–50%; 50%; 50–75%; 75–100%; 100%) – i.e. percentage crown projection – in the plot. All measured stems (n = 478) were then classified into diameter classes (7–10 cm; 10–15 cm; 15–20 cm; 20–30 cm; 30–50 cm; 50–70 cm; 70–90 cm; 90–120 cm) (Appendix A1).

Second, for the three study species and the four studied hedgerow systems (tree rows vs. hedgerows on moist sandy vs. wet sandy loam soil), we cored two trees per diameter class, thereby covering a wide range of tree developmental stages. Using a 5.15 mm increment borer

Dendrochronologia 70 (2021) 125894

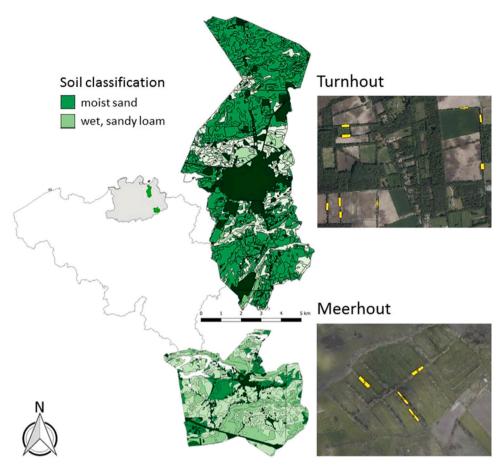


Fig. 1. Study areas Turnhout and Meerhout, municipalities in the province of Antwerp (grey zone), northern Belgium. In Turnhout, we sampled hedgerows and tree rows on moist sand. In Meerhout, we sampled hedgerows and tree rows on wet, sandy loam. Examples of sampled plots in Turnhout and Meerhout are indicated in yellow on the aerial photographs. Soil classification according to the Belgian soil classification system (Tavernier and Maréchal 1972). Map made in QGIS based on the digital soil map of VLM (1998). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Source aerial picture: Geopunt Vlaanderen.

(Haglöfs 0.200" borer, Sweden), we collected two samples per tree at breast height: one parallel to the tree row or hedgerow and the other one perpendicular to it. The cores were stored in paper straws and air-dried. In total, we sampled 73 trees, which resulted in 146 increment cores. We measured the height of each sampled tree with a vertex instrument (Haglöfs Vertex IV, Sweden).

2.2. Tree ring measurements

The cores were inserted in cylindrical holders and conditioned in a climate chamber at 65% humidity, 20 °C \pm 1 °C. The holders were scanned at a resolution of 60 µm with the Nanowood X-ray Computed Tomography (XCT) scanner (NanoWood CT Facility, Ghent University), and the images were reconstructed with the Octopus reconstruction software package (Dierick et al., 2004). We indicated all tree-ring boundaries with the XCT toolchain (software packages available on www.dendro chronomics.ugent.be, De Mil et al. 2016). Ring boundaries of ring-porous oak could be clearly distinguished in the XCT scan images. For the diffuse-porous alder and birch, the ring boundaries were less clear and after scanning, the increment core was removed from the paper straw, the core surfaces were cut with a microtome and sanded, and tree-ring widths were measured with a LINTAB 6 measuring station (Rinntech, Heidelberg, Germany) at a resolution of 10 µm. We then loaded the measured ring width series in the DHXCT package (De Mil et al., 2016) and validated them on the X-ray images. We crossdated all paired cores to ensure correct dating within the tree and crossdated all trees per plot using the CoreComparison package (De Mil et al., 2016). We then calculated the total mean interseries correlation (RBAR) and Expressed Population Signal (EPS) (Wigley et al., 1984) using the dplRlibrary (Bunn, 2008). RBAR/EPS are for oak, alder and birch resp. 0.266/0.874, 0.267/0.8 and 0.328/0.769, and are deemed acceptable for this study. For each core, we extracted the series of annual tree-ring width (TRW, mm) and conditioned wood density (kg m⁻³). We then averaged the two crossdated cores per tree to compose one ring width series and one wood density series for each cored tree. The basic wood density (WD, kg m⁻³) was estimated from the wood density of the conditioned samples by using a conversion factor of 0.821 for oak and 0.828 for alder and birch (Vieilledent et al., 2018). We considered the series' length as the age of the tree, when at least one of the cores of the cored tree contained the pith. When the pith of the tree was missing in each of the two cores of a cored tree, we assessed the age of the tree by estimating the number of rings missing until the pith based on the curvature of the last rings (Vanhellemont et al., 2019).

2.3. Data analysis

For a detailed description of our four studied hedgerow systems, we calculated traditional inventory metrics based on the collected dendrometric data, such as stem density and basal area per running kilometre. Expressing these metrics per unit of length is the default method for linear features such as hedgerows and tree rows in recent studies and the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories (Cardinael et al., 2018; IPCC, 2019a; Jansen and Oosterbaan, 2018). The diameter distributions for each hedgerow system was plotted using a Kernel density estimate via the <code>geom_density</code> function in the <code>ggplot2</code> library. The differences in inventory metrics between the four hedgerow systems were verified by means of the Kruskal-Wallis test (<code>kruskal.test</code> function in the <code>stats</code> package) and grouped using non-parametric multiple comparison (<code>kruskalmc</code> function in the library <code>pgirmess</code>, <code>Giraudoux</code>, 2018).

To study the long-term growth patterns we derived three variables based on tree-ring width (TRW): cambial diameter, Basal Area

Increment (BAI) and Increment of Aboveground Biomass (IAB). The cambial diameter was calculated as the cumulative sum of the TRW for each year, multiplied by two. Cambial diameter is thus the tree diameter as derived from the tree ring analyses and is slightly different (i.e. smaller) than the measured diameter in the field, as the latter includes the tree bark. The Basal Area Increment (BAI, cm²) is defined as the ring area, a two-dimensional variable used as a proxy for overall tree growth as opposed to a one-dimensional variable such as diameter increment or ring width (Vanhellemont et al., 2016; Biondi and Qeadan, 2008). We calculated BAI for each tree ring using the function bai.out in the dplR dendrochronology package (Bunn et al., 2014). The Increment of Aboveground stem Biomass (IAB, g cm⁻¹) was calculated as the product of BAI and WD at a yearly resolution for each cored tree, and thus represents a second proxy of tree growth and carbon sequestration. Since it was demonstrated by Bontemps et al. (2010) that long-term trends in radial growth are similar with trends in height growth, the height dimension of above-ground biomass increment was not considered (conform the study of Vannoppen et al., 2018). For each species we fitted a linear mixed model (using the *lmer* function in the library *lme4*, Bates et al., 2015) to relate BAI and IAB – the two tree growth proxies in our study – and WD to the cambial diameter or cambial age as proxies for developmental stage. A natural log (ln) transformation was applied to the BAI, IAB, WD, cambial age and cambial diameter variables to linearize the relationships. The model included 'Tree ID' and 'Plot' as random effects to account for the repeated measurements within a single tree (time series) and the spatial non-independence of trees within plots. To check for differences in growth response in oak and alder between hedgerows and tree rows, 'hedgerow system' was included in the models as categorical predictor. The model fits for the long-term trends in BAI, IAB and WD were compared among species and among hedgerow systems based on the marginal R^2 and conditional R^2 (Nakagawa and Schielzeth, 2013), which were calculated using the function r.squaredGLMM in the library MuMIn (Barton, 2019).

To study which variables relate to the current growth performance of oak and alder in hedgerows and tree rows (i.e. the second research question), we calculated mean values for BAI and IAB over the last five years (tree rings formed in 2012 - 2016, conform the study of Vanhellemont et al., 2016). We investigated the relationship between these average BAI and IAB values and the competition variables basal area, tree density, and proportion dominant species in the plot. The basal area of the plot is calculated as the average amount of area occupied by all tree stems at DBH in the plot (m^2/m^2) . The tree density of the plot is calculated as the number of trees in the plot $(\#/m^2)$. The proportion dominant species in the plot is calculated as the ratio of the basal area of oak (Turnhout) or alder (Meerhout) in the plot, to the total basal area in the plot (percentage). This ratio gives an indication on 'how' dominant the dominant tree species is. We used linear mixed-effect models with 'tree age' or 'tree diameter' and the competition variables as continuous predictors, together with a group-level (random) effect for 'Plot'.

To upscale to wood production and carbon storage per running kilometre for all four hedgerow systems (i.e. research question 3), we first used the linear relation between diameter and height of the cored trees to estimate the height of all oaks, birches and alder in the dendrometric inventory. We then used the diameter at breast height (DBH) and tree height to estimate trunk volume to an upper girth limit of 22 cm (i.e. 7 cm diameter) of all trees with the equations of Dagnelie et al. (1999) for oak and birch and Claessens (2005) for alder. Important to note is that these equations were developed for trees in a forest context in Belgium (such equations for trees outside forests are non-existent for the time being). Subsequently, we used the relationship between BAI and diameter for the cored trees to predict the 1-year diameter increment of all trees in the dendrometric inventory based on their measured actual diameter. Using the calculated diameter after 1-year of modelled growth, we then calculated the height and volume of the trees after this 1-year of growth. To calculate stem biomass, we first calculated wood density for all trees in the dendrometric inventory based on the diameter

– WD relationship for the cored trees and then multiplied the calculated stem volumes and WD for both the actual trees and the trees after 1-year of modelled growth to calculate biomass increment per tree. We converted stem biomass into carbon to obtain the aboveground stem carbon stock, using a conversion coefficient of 0.48 Mg carbon / Mg dry matter (IPCC, 2006; Lamlom and Savidge, 2003). Finally, to upscale to wood production (stock and yearly increment) and carbon storage and sequestration per region, we used published inventory data: there are about 54 km of hedgerow systems in Turnhout (Vos, 2019) and about 144 km in Meerhout (Province of Antwerp, 2017), with an equal amount of hedgerows and tree rows in both regions (Van Den Berge et al., 2018). We formulated yearly increments and carbon sequestration rates assuming that the diameter distributions in hedgerow systems were in a steady state. We compared the stem wood stocks, carbon stocks, stem volume increments and carbon sequestration rates among the four hedgerow systems by means of the Kruskal-Wallis test and post-hoc test.

Correlations between the studied tree species statistics such as DBH, tree height and age were tested using the Spearman rank correlation test. The tree statistics average TRW, average BAI, average WD and average IAB for oak, alder and birch were compared using the Kruskal-Wallis test. All analyses were done in R version 3.6.1 (R Core Team, 2019) and graphs were made using the *ggplot2* package (R Core Team, 2019; Wickham, 2016).

3. Results

3.1. Inventory metrics and tree statistics in hedgerow systems

Hedgerows of alder and oak had the highest number of trees and coppiced stems (diameter > 7 cm) per unit of length (mean \pm standard deviation: $985.2 \pm 439.6 \text{ km}^{-1}$) followed by tree rows of alder ($881 \pm 692.4 \text{ km}^{-1}$) and hedgerows of oak and birch ($624 \pm 397.9 \text{ km}^{-1}$). These three systems differed significantly (*Kruskal-Wallis Chi square* = 25.3, p < 0.001) from tree rows of oak, which showed the lowest tree density ($168.0 \pm 61.3 \text{ km}^{-1}$). The basal area of hedgerows of oak and birch ($44.9 \pm 17.9 \text{ m}^2 \text{ km}^{-1}$) and hedgerows of alder and oak ($44.0 \pm 12.0 \text{ m}^2 \text{ km}^{-1}$) differed significantly (*Chi square* = 14.9, p = 0.001) from tree rows of oak ($34.2 \pm 12.4 \text{ m}^2 \text{ km}^{-1}$) and tree rows of alder ($22.1 \pm 8.6 \text{ m}^2 \text{ km}^{-1}$). The population structure also differed between hedgerow systems: hedgerows of oak and birch, hedgerows of alder and oak and tree rows of alder showed positively skewed (right-skewed) diameter distributions, whereas tree rows of oak showed a more symmetric hump-shaped diameter distribution (Fig. 2).

The DBH, age and height of the cored trees showed a strong positive correlation (Table 1). Only WD differed significantly between the studied tree species. The wood density of oak was higher than for birch (p < 0.001), which in turn was higher than the density of alder (p < 0.001). The long-term trends in wood density with cambial diameter as predictor differed significantly between the three study species. The estimated intercepts and parameters were strongly significant for birch and oak (p < 0.001), with a positive slope for birch and a negative slope for oak. For alder, wood density was not related to tree diameter (Fig. 3, Appendix B).

3.2. Long-term performance of trees in hedgerows and tree rows

The models relating the growth performances (BAI and IAB) in response to the cambial diameter for all three species provided good fits (alder: $marginal\ R^2=0.54$ and $cnditional\ R^2=0.70$ for BAI, $mR^2=0.54$ and $cR^2=0.70$ for IAB; birch: $mR^2=0.63$ and $cR^2=0.73$ for BAI, $mR^2=0.65$ and $cR^2=0.75$ for IAB; oak: $mR^2=0.76$ and $cR^2=0.88$ for BAI, $mR^2=0.73$ and $cR^2=0.85$ for IAB). The models relating BAI and IAB to cambial age showed trends parallel to the trends in the models using cambial diameter as proxy for developmental stage. Yet, diameter turned out to be a better predictor for growth performance than tree age (better model fit for the diameter models, see Appendix C).

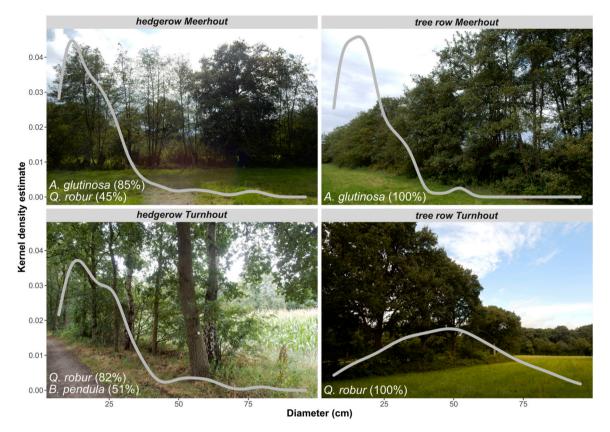


Fig. 2. Presentation of the diameter distributions by means of Kernel density plots for hedgerows and tree rows in Meerhout and Turnhout, each based on tree inventories in ten 50 m² plots in each hedgerow system. Percentages represent crown projection per species in the tree layer.

Table 1Dendrometric and production statistics summarized for the cored alder, birch and oak trees.

	Alder	Birch	Oak
Number of trees	22	11	40
Mean \pm SD DBH (cm)	22.7 ± 12.8	24.0 ± 14.3	36.9 ± 24.4
Mean \pm SD height (m)	[7.6-53.8]	[8.9-55.1]	[7.0-93.3]
Mean \pm SD age (year)	12.6 ± 3.9	14.2 ± 6.1	14.0 ± 6.1
Correlation DBH and age	[4.5–18.4]	[6.0-21.6]	[4.4–27.6]
Correlation height and age	28.1 ± 14.8	34.8 ± 14.5	$\textbf{46.3} \pm \textbf{20.8}$
Correlation DBH and height	[7–59]	[13–56]	[7–98]

DBH: Diameter at breast height. TRW: tree-ring width. BAI: basal area increment. WD: wood density. IAB: increment of the aboveground stem biomass. Mean value and standard deviation (SD) are presented for each variable, with ranges in brackets.

For all three species, the estimated intercept and slope parameters for both response variables BAI and IAB were strongly significant (p < 0.001, Appendix C). Oak showed the strongest positive relation with cambial diameter for both responses (Fig. 4a, b): the effect of ln (cambial diameter) was positive and can be considered as very large and significant for both BAI (beta = 1.05, SE = 0.01, std. beta = 1.05, p <0.001) and IAB (beta = 1.02, SE = 0.01, std. beta = 1.02, p < 0.001). Also birch and alder showed a positive relation with cambial diameter for both responses, however with a less steep slope than oak (Fig. 4a, b): the effect of ln(cambial diameter) was positive and can be considered as large and significant for both BAI and IAB of birch (beta = 0.84, SE =0.03, std. beta = 0.84, p < 0.001) and (beta = 0.88, SE = 0.03, std. beta = 0.88, p < 0.001), respectively and alder (beta = 0.80, SE = 0.03, std. beta= 0.80, p < 0.001) and (beta = 0.80, SE = 0.03, std. beta = 0.80, p < 0.001), respectively. BAI nor IAB differed between hedgerows and tree rows for oak and alder (Fig. 4c, d; Appendix C).

3.3. Relationship between local neighbourhood and current tree performance

For both oak and alder, the current tree performance in terms of BAI and IAB (mean value of the last five years) was best explained by models with tree diameter, plot basal area and proportion of the dominant tree species in the plot as predictors and plot as a random factor (Table 2).

For oak, only the estimated slope for the predictor tree diameter was significant, with positive values in both hedgerows and tree rows (Table 2). For alder, the estimated slopes for tree diameter were significant in the models of BAI in both hedgerows and tree rows. For IAB, however, the estimated slope for diameter was only significant in tree rows (Table 2).

The models for current tree performance including tree age as predictor for developmental stage for both oak and alder showed parallel trends to the models including tree diameter as developmental stage predictor (Appendix D).

3.4. Stem wood productivity and aboveground carbon sequestration in hedgerow systems

Stem wood volume stocks and yearly increments together with the carbon storage and sequestration rates in the aboveground stem biomass in hedgerow-grown trees are presented for all four hedgerow systems in Table 3. Tree rows of oak showed the highest stem wood stocks (Kruskal-Wallis Chi square = 9.4, p < 0.05) and the highest carbon stocks in the stem biomass per running kilometre (Kruskal-Wallis Chi square = 10.0, p < 0.05) compared to the other hedgerow systems (Table 3). Volume increments and carbon sequestration rates in the stem biomass per running kilometre did not differ significantly between hedgerow systems (Table 3).

In total, the hedgerow systems in Turnhout stored 5832.0 (\pm 192.8 standard error) Mg carbon in stem biomass, with an actual carbon

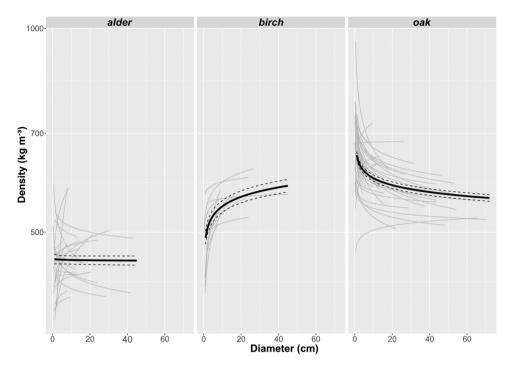


Fig. 3. Wood density vs. cambial diameter along tree ring cores of alder, birch and oak growing in hedgerow systems in northern Belgium. Grey lines represent the wood density series of individual trees; bold black lines show predicted wood density based on linear mixed-effects models; dashed black lines indicate the 95% confidence intervals for the predictions.

sequestration rate in aboveground stem biomass of 213.3 (\pm 53.9 SE) Mg year $^{-1}$. In total, 4096.8 (\pm 197.0 SE) Mg carbon is stored in the stem biomass of hedgerow systems in Meerhout, with a sequestration rate of 136.8 (\pm 50.9 SE) Mg carbon year $^{-1}$.

4. Discussion

4.1. Characteristics of hedgerow systems and hedgerow-grown trees

The diameter distribution in the studied hedgerows of oak and birch was similar to the diameter distribution of an uneven-aged forest stand, in which regeneration causes a high number of individuals in the smaller diameter classes (Fig. 2, Shorohova et al., 2009). The tree rows of oak showed a similar diameter distribution as even-aged forest stands, in which the population structure lacks individuals in the smaller diameter classes (Fig. 2, Shorohova et al., 2009). The diameter distributions of hedgerows and tree rows consisting of coppiced alder followed the pattern of an uneven-aged forest stand with many stems in the smaller diameter classes owing to the management type (i.e. coppicing entails periodically cutting back the tree above the ground level).

The tree density and basal area in the studied hedgerows and tree rows are comparable with the findings of Cardinael et al. (2018) who reported tree densities of 816 (\pm 853 km $^{-1}$ SD) for hedgerows with mainly shrub species and Jansen and Oosterbaan (2018) who found a tree density of 313 km $^{-1}$ and a basal area of 56.1 m 2 km $^{-1}$ for tree rows of Populus cultivars.

Wood density was the highest for oak, followed by birch and alder (Table 1), which is also the case when these species grow in forests (Leuschner and Meier, 2018). The assumption that wood density is constant during a tree's life is not correct and may result in over- or underestimations of carbon sequestration (Vannoppen et al., 2018). The wood density of the studied birch trees clearly increased with increasing diameter (Fig. 3). Our findings are consistent with the wood density trends of birch in forests (Lachowicz et al., 2019). Radial increases in basic wood density are associated with a pioneer habit as an adaptation for structural support (Wiemann and Williamson, 1989; Woodcock and

Shier, 2002). Pioneer species exhibit rapid height and diameter growth by producing wood of low density as juveniles but require greater stability later in development (Nock et al., 2009), possibly due to greater exposure to wind (Wiemann and Williamson, 1988; 1989). In the studied oak trees, wood density clearly decreased with increasing diameter (Fig. 3), probably due to the fact that the older the tree, the higher the ratio earlywood/latewood becomes. Such an increase in earlywood/latewood ratio with diameter is characteristic late-successional species, who allocate their sugars to other organs than latewood (e.g. fruits) as the tree ages (Woodcock and Shier, 2002). As oak is classified as a mid-successional species in forests, the decrease in wood density with diameter in our study was unexpected. Our findings also differ from the results of Vannoppen et al. (2018), who found no long-term trend in wood density of sessile oak (Quercus petraea (Matt.) Liebl.) in forests. In the studied alder trees, density showed no clear trend with diameter, consistent with the findings for forest-grown Alnus rubra Bong. (Parker et al., 1978), A. incana (L.) Moench and A. hybrida A. Br. (Aosaar et al., 2011). However, the regular coppice of alder trees probably affects the relation between diameter and wood density, as the response is quite scattered (Fig. 3).

4.2. The growth of trees in hedgerow systems

Cambial diameter proved to be a better proxy for developmental stage than cambial age, conform the results of Wykoff (1990), Mencuccini et al. (2005) and Bontemps et al. (2009). This is convenient, as tree diameter is easily measurable in the field whereas tree age is not.

Both growth performance proxies BAI and IAB did not show stagnation with increasing diameter of the trees (Fig. 4). Tree growth rates and, hence, rates of carbon gain, for the three species increased continuously with tree diameter, despite the decrease in wood density for oak with increasing diameter (Fig. 3). Also in many tree species in forests, trees with a higher mass show a higher increase in aboveground tree mass (Stephenson et al., 2014). The increase in a tree's total leaf area is sufficient to overcome the decline in growth efficiency with increasing tree size, which causes the whole-tree carbon accumulation

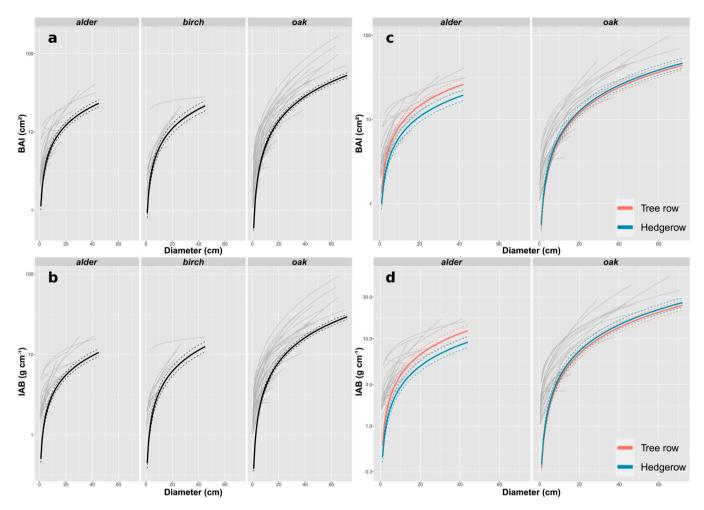


Fig. 4. (a, b) Change in basal area increment (BAI) and increment of aboveground stem biomass (IAB) with cambial diameter throughout the life of the cored alder, birch and oak trees growing in hedgerow systems in northern Belgium. Fig. 4c and d. Change in BAI and IAB for alder and oak with diameter for tree rows vs. hedgerows. Each grey line represents BAI and IAB relationships for an individual tree; black lines show predicted BAI and IAB using linear mixed-effects models (see text). Dashed lines indicate the 95% confidence intervals for the predictions.

Table 2

Effects of tree diameter (measured in the field, in cm) and local neighbourhood variables basal area of the plot (m^2/m^2) and proportion dominant tree (percentage) on current tree performance, i.e. the natural log (ln) of the mean BAI (cm^2) and mean IAB (g/cm) of the last five year (tree rings formed in 2012–2016).

	Oak			Alder				
	Hedgerow		Tree row		Hedgerow		Tree row	
	ln (BAI)	ln (IAB)						
Intercept	6.74**	2.01	5.93***	0.93	5.74***	0.35	5.84***	0.73
Tree diameter	0.07**	0.07***	0.03***	0.04***	0.04**	0.03	0.07**	0.06**
Basal area plot	-3.3	-3.25	-0.5	-0.51	0.25	0.54	-1.65	-1.52
Proportion dominant tree species	-0.85	-1.41	/	/	-0.3	-0.22	/	/
Observations	13	13	11	12				
mR^2 / cR^2	.82 /.88	.79 /.87	.80 /.80	.74 /.74	.59 /.59	.37 /.37	.81 /.90	.67 /.79

Parameter estimates, number of observations, marginal R^2 (m R^2) and conditional R^2 (c R^2) are shown. Significant parameters are indicated in bold, and the superscripts display the p-value levels (*p \leq 0.05; **p \leq 0.01; ***p \leq 0.001).

rate to increase (Stephenson et al. 2014). In hedgerows and tree rows, tree heights and tree crowns are respectively lower and larger than in forests (Van Den Berge et al., 2021a; Vanneste et al., 2020b; Zhou et al., 2011), which probably results in even higher increases in leaf area with increasing tree size, and thus a more enhanced leaf area increase with age.

We found no difference in long-term productivity in relation to diameter for oak growing in hedgerows compared to tree rows. Alder biomass productivity was slightly higher for coppiced trees when mixed with oak compared to monoculture alder tree rows. For both oak and alder, our results indicate that the productivity of tree rows does not exceed that of hedgerows.

4.3. Current growth of trees in hedgerow systems

The current tree growth performance – i.e. BAI and IAB for the five most recent years: 2012–2016 – increased with diameter for all three species in both hedgerows and tree rows. This indicates that the

Table 3 Species-specific estimates for the stem wood volume, carbon stocks, yearly volume increments and carbon sequestration rates (mean \pm standard error) in the aboveground stem biomass per running kilometre of hedgerow and tree row.

Hedgerow system	Stem volume (m ³ km ⁻¹)	Carbon stock (Mg C km ⁻¹)	Volume increment ($m^3 km^{-1} yr^{-1}$)	Tier 3 estimates: carbon sequestration rate (Mg C km $^{\!\! 1}$ yr $^{\!\! -1}$)
Oak-birch hedgerow width (m): 4.2 ± 1.5	328.0 ± 25.2	94.4 ± 6.1	9.4 ± 5.9	2.6 ± 1.7
birch	110.9 ± 14.5	30.1 ± 0.3	3.6 ± 3.4	1.0 ± 0.9
Oak	217.1 ± 20.6	64.3 ± 6.1	5.9 ± 4.8	1.7 ± 1.4
Oak-tree row width 1.2 \pm 0.3 m	339.7 ± 12.4	100.7 ± 3.7	14.5 ± 3.7	4.3 ± 1.1
Alder-oak hedgerow width	143.9 ± 7.3	38.1 ± 2.1	4.5 ± 1.8	1.2 ± 0.5
$3.1\pm0.9~\text{m}$				
Alder	68.1 ± 4.2	15.6 ± 1.0	2.9 ± 1.2	0.7 ± 0.3
Oak	$\textbf{75.8} \pm \textbf{6.0}$	22.5 ± 1.8	1.6 ± 1.3	0.5 ± 0.4
Alder-tree row width 2.2 \pm 0.4 m $$	82.0 ± 7.8	18.8 ± 1.8	3.1 ± 2.1	0.7 ± 0.5

For each hedgerow system the mean width \pm standard deviation is presented. The carbon sequestration rates can be used as Tier 3 estimates (definition *conform* IPCC, 2006) for yearly aboveground carbon sequestration assessments in comparable hedgerow systems: i.e. on similar soil types (Fig. 1) and with similar species composition and diameter distribution (Fig. 2).

conditions in hedgerow systems encourage a persistent tree growth, i.e. growth is not stagnating with the aging of the trees. Nutrient availability is not a limiting factor for tree growth due to possible fertilizer spill-over and high atmospheric deposition inputs of reactive nitrogen from agriculture, traffic and industry in the region (Van Gijseghem et al., 2003). More importantly, even though the studied local neighbourhood variables showed a negative effect on the growth responses, these effects were not significant and were smaller than the positive and strongly significant effect of tree diameter. Hence, it seems that competition for light was not a limiting factor in the current tree performance in the studied hedgerows. After all, the BAI of a healthy mature tree is expected to decline when it experiences stress caused by competition for light, even in good growing conditions (Biondi and Qeadan, 2008). Competition for light will be particularly detrimental for shade-intolerant pioneer species such as birch (Vanhellemont et al., 2016), but also alder and oak are rather intolerant to shade (Leuschner and Meier, 2018). In forests, asymmetric competition for light is widely recognized as the key driver of growth efficiency (Coomes, 2006; Muller-Landau et al., 2006; Price et al., 2010), resulting in the well-known age-related decline in productivity at the scale of forest stands (Binkley, 2004; Stephenson et al., 2014). Indeed, in most forest ecosystems, aboveground biomass and its increment are strongly dominated by the overstory trees, given the low light levels below the overstory canopy (Clarck et al., 2001). In hedgerows and tree rows, all trees are 'overstory' trees and individual competition between trees will not result in a decreasing stand productivity, as light is never scarce.

4.4. Hedgerows and tree rows: productive wood resources and carbon sinks

In the global challenge to understand and tackle climate change, many studies have tried to estimate carbon storage in (agro)ecosystems as an offset for (part of) the anthropogenic CO_2 emissions (Appendix E). However, few studies have reported specific numbers for hedgerows and tree rows as separate ecosystems, independent from the crops they border. In the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories, only the Tier 1 estimates for 'hedgerows' (not species-specific nor soil type-specific) are published, i.e. $0.87 \pm 49\%$ Mg C km⁻¹ yr⁻¹ (IPCC 2019a, adapted from Cardinael et al., 2018). To date, country-, system- and species-specific Tier 3 estimates for hedgerows are not available (Appendix E). As the carbon storage differed greatly between the three species in our study, we communicate species-specific Tier 3 estimates for annual aboveground stem biomass carbon sequestration for oak, birch and alder per running kilometre in our four hedgerow systems (Table 3).

Stem wood volume stocks and increments are impressively high per running kilometre. For forests in Belgium, the IPCC (2019b) reports a carbon sequestration rate in the (total) aboveground biomass of 1.1 Mg

C ha $^{-1}$ yr $^{-1}$. In Turnhout (919.52 ha of forests) and Meerhout (432 ha of forests) this equals a yearly carbon sequestration of 1011.5 and 475.2 Mg C yr $^{-1}$, respectively. The carbon sequestration rate in the hedgerow systems hence equals 21.1% and 28.8% of the sequestration rate in the forests in Turnhout and Meerhout, respectively. Hedgerows and tree rows thus clearly represent a substantial contribution to the biomass and carbon budgets in our study regions.

Sustainable volumes – in forestry traditionally defined as not more than the yearly volume increment itself (den Ouden et al., 2010) – can be harvested in various ways in hedgerow systems. Hedgerows with oak and birch can be managed on the individual tree level, similar to uneven-aged forest stands. Tree rows of oak are more likely to be managed in a clear-cut regime, and the wood may even be valuable as timber when pruning is applied during the trees' lifespan. Coppicing of alder is a traditional method in Belgium with a rotation period varying from 8 to 12 years (Vandekerkhove et al., 2018), but periods up to 60 years are perfectly feasible as well (Nicolescu et al., 2018). However, harvesting from hedgerow systems requires further reflection on the valorisation of hedgerow wood and on the practical and economic feasibility of harvesting itself (Van Den Berge, 2021).

There were some limitations to our work. In our study we did not encounter trees older than 100 years in our dataset; however, life span data until tree death as well as tree mortality and regeneration would be interesting in a further exploration of carbon storage in hedgerow systems. In this work, we did not consider carbon sequestration in the belowground biomass and soil, which can be substantial in hedgerow systems (Cardinael et al., 2017; Van Den Berge et al., 2021b). In this study we have estimated stem wood volumes based on equations suitable for forest-grown trees. However, developing such equations for trees in hedgerow systems would allow for more accurate estimations of stem biomass. Moreover, predicting biomass and carbon values of hedgerow trees for application in markets requires accurate biomass expansion factors (total biomass over stem biomass) to allow estimating total tree biomass (Van Den Berge et al., 2021a). Studying the influence of the orientation of the hedgerow or tree row on the eccentricity of the tree stem would also be an interesting topic to look further into, especially if growing quality wood is a management goal (e.g. in agroforestry systems). It would also be interesting to compare tree growth and carbon sequestration among different management practices applied in hedgerows and tree rows.

5. Conclusion

There is great potential for biomass production in hedgerows and tree rows in arable areas. Hedgerow-grown trees represent substantial biomass stocks per running kilometre despite the small area of land they cover. Individual tree growth did not yet culminate with age for any of the studied trees; trees in hedgerows and tree rows experience low

competition for light and nutrients resulting in high growth performances. Along with their continuous diameter growth, hedgerow-grown trees sequester large amounts of carbon in their aboveground stem biomass and therefore fulfil an important ecosystem service in the context of climate change. The yearly aboveground carbon sequestration in tree stems as quantified in our study can help refine the IPCC Guidelines for National Greenhouse Gas Inventories. To maximize the role of the biosphere in climate change mitigation, we must focus on raising rates of net carbon uptake on land of all trees – including trees in hedgerows and tree rows.

Annexes

Additional Supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX A. Diameter classification of all measured trees.

APPENDIX B. Model outputs for wood density.

APPENDIX C. Model outputs for growth responses BAI and IAB.

APPENDIX D. Model outputs: effect of tree age and local neighbourhood variables on current tree growth.

APPENDIX E. Carbon storage and sequestration rates in agroecosystems: numbers from literature.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2021.125894.

References

- Agrawal, A., Nepstad, D., Chhatre, A., 2011. Reducing emissions from deforestation and forest degradation. Annu. Rev. Environ. Resour. 36, 373–396.
- Albrecht, A., Kandji, S.T., 2003. Carbon sequestration in tropical agroforestry systems. Agric. Ecosyst. Environ. 99, 15–27.
- Aosaar, J., Varik, M., Löhmus, K., Uri, V., 2011. Stemwood density in Young grey alder (Alnus incana (L.) Moench) and hybrid Alder (Alnus hybrida A. Br.) stands growing on abandoned agricultural land. Baltic For. 17 (2), 256–261.
- Balandier, P., Dupraz, C., 1998. Growth of widely spaced trees. A case study from young agroforestry plantations in France. Agrofor. Syst. 43, 151–167.
- Barton, K., 2019. MuMin: Multi-Model Inference. R package version 1.43.6. (https://CR AN.R-project.org/package=MuMin).
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.
- Baudry, J., Bunce, R.G.H., Burel, F., 2000. Hedgerow diversity: an international perspective on their origin, function, and management. J. Environ. Manag. 60, 7–22. Binkley, D., 2004. A hypothesis about the interaction of tree dominance and stand
- production through stand development. For. Ecol. Manag. 190, 265–271.

- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Res. 64, 81–96.
- Bontemps, J.D., Hervé, J.C., Dhôte, J.F., 2009. Long-term changes in forest productivity: a consistent assessment in even-aged stands. For. Sci. 55, 549–564.
- Bontemps, J.D., Hervé, J.C., Dhôte, J.F., 2010. Dominant radial and height growth reveal comparable historical variations for common beech in north-eastern France. For. Ecol. Manag. 259, 1455–1463. https://doi.org/10.1016/j.foreco.2010.01.019.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26 (2), 115–124.
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Mudelsee, M., Qeadan, F., Schulz, M., Zang, C., 2014. dplR: Dendrochronology Program Library in R. R package version 1.6.0. Available from: http://CRAN.R-project.org/package=dplR).
- Cardinael, R., Mao, Z., Prieto, I., Stokes, A., Dupraz, C., Kim, J., Hand Jourdan, C., 2015.
 Competition with winter crops induces deeper rooting of walnut trees in a
 Mediterranean alley cropping agroforestry system. Plant Soil 391, 219–235.
- Cardinael, R., Chevallier, T., Cambou, A., Béral, C., Barthès, B.G., Dupraz, C., Durand, C., Kouakoua, E., Chenu, C., 2016. Increased soil organic carbon stocks under agroforestry: a survey of six different sites in France. Agric. Ecosyst. Environ. 236, 243–255. https://doi.org/10.1016/j.agee.2016.12.011.
- Cardinael, R., Chevallier, T., Cambou, A., Béral, C., Barthès, B.G., Dupraz, C., Durand, C., Kouakoua, E., Chenu, C., 2017. Increased soil organic carbon stocks under agroforestry: a survey of six different sites in France. Agric. Ecosyst. Environ. 236, 243–255.
- Cardinael, R., Umulisa, V., Toudert, A., Olivier, A., Bockel, L., Bernoux, M., 2018. Revisiting IPCC Tier 1 coefficients for soil organic and biomass carbon storage in agroforestry systems. Environ. Res. Lett. 13, 124020 https://doi.org/10.1088/1748-9326/aaeb5f.
- Chambers, M., Crossland, M., Westaway, S., Smith, J., 2015. Hedgerow Harvesting Machinery Trials Report. The Organic Research Centre 2015 [TWECOM].
- Clair, S., Lynch, J.P., 2010. The opening of Pandora's box: climate change impacts on soil fertility and crop nutrition in developing countries. Plant Soil 335, 101–105.
- Claessens, H., 2005. L'aulne glutineux, ses stations et sa sylviculture. Forêt Wallonne asbl, p. 197.
- Clarck, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: concepts and field methods. Ecol. Appl. 11 (2), 356–370.
- Ecol. Appl. 11 (2), 550–570.
 Coomes, D.A., 2006. Challenges to the generality of WBE scaling theory. Trends Ecol. Evol. 21, 593–596.
- , 1999Dagnelie, P., Palm, R., Rondeux, J., Thill, A., 1999 Les Presses Agronomiques de Gembloux.
- den Ouden, J., Muys, B., Mohren, F., Verheyen, K., 2010. Bosecologie en bosbeheer.

 Acco. Leuven, België: Den Haag, Nederland.
- De Mil, T., Vannoppen, J., Van den Bulcke, J., Beeckman, A., Van Acker, H., 2016.
 A field-to-desktop toolchain for X-ray CT densitometry enables tree ring analysis.
 Ann. Bot. 117, 1187–1196.
- De Ridder, M., Van den Bulcke, J., Vansteenkiste, D., Van Loo, D., Dierick, M., Masschaele, B., De Witte, Y., Mannes, D., Lehmann, E., Beeckman, H., Van Hoorebeke, L., 2010. High-resolution proxies for wood density variations in Terminalia superba. Ann. Bot. 107 (2), 293–302.
- Dierick, M., Masschaele, B., Van Hoorebeke, L., 2004. Octopus, a fast and userfriendly tomographic reconstruction package developed in LabView®. Meas. Sci. Technol. 15, 1366–1370.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263 (5144), 185–190. https://doi.org/10.1126/science.263.5144.185.
- European Environment Agency, 2013. Corine Land Cover 2006 raster data, Version 17, Copenhagen K. CRC/TR32 Database (TR32DB), Denmark.
- Falloon, P., Powlson, D., Smith, P., 2004. Managing field margins for biodiversity and carbon sequestration: a Great Britain case study. Soil Use Manag. 20, 240–247.
- FAO, 2010. Managing Forests for Climate Change: Supporting Countries to Manage Fragile Forest Ecosystems. Food and Agriculture Organization.
- FAO. Climate change for forest policy-makers An approach for integrating climate change into national forest policy in support of sustainable forest management – Version 2.0 2018 FAO Forestry Paper no.181, Rome.Licence: CC BY-NC-SA 3.0 IGO.
- Follain, S., Walter, C., Legout, A., Lemercier, B., Dutin, G., 2007. Induced effects of hedgerow networks on soil organic carbon storage within an agricultural landscape. Geoderma 142, 80–95. https://doi.org/10.1016/j.geoderma.2007.08.002.
- Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecol. Appl. 3 (2), 202–205. https://doi.org/10.2307/1941820.
- Gilman, E.F., 1989. Predicting root spread from trunk diameter and branch spread. Arboricult. J. 13 (1), 25–32. https://doi.org/10.1080/03071375.1989.9756398
- Giraudoux, P., 2018. pgirmess: Spatial Analysis and Data Mining for Field Ecologists. R package version 1.6.9. (https://CRAN.R-project.org/package=pgirmess).
- Grassi, G., House, J., Dentener, F., Federici, S., den Elzen, M., Penman, J., 2017. The key role of forests in meeting climate targets requires science for credible mitigation. Nat. Clim. Change 7, 220–226. https://doi.org/10.1038/nclimate3227.
- Graves, A.R., Burgess, P.J., Palma, J.H.N., Herzog, F., Moreno, G., Bertomeu, M., Dupraz, C., Liagre, F., Keesman, K., van der Werf, W., de Nooy, A.K., van den Briel, J. P., 2007. Development and application of bio-economic modelling to compare silvoarable, arable, and forestry systems in three European countries. Ecol. Eng. 29, 434–449. https://doi.org/10.1016/j.ecoleng.2006.09.018.
- Groenendijk, P., 2015. Long-term Trends in Tropical Tree Growth: A Pantropical Study. Ph.D. thesis, Wageningen University, Wageningen.
- Henry, M., Bombelli, A., Trotta, C., Alessandrini, A., Birigazzi, L., Sola, G., Vieilledent, G., Santenoise, P., Longuetaud, F., Valentini, R., Picard, N., Saint-

- André, L., 2013. GlobAllomeTree: international platform for tree allometric equations to support volume, biomass and carbon assessment. iForest Biogeosci. For. 6, 326–330. https://doi.org/10.3832/ifor0901-006.
- Houghton, R.A., 2007. Balancing the global carbon budget. Annu. Rev. Earth Planet Sci. 35, 313–347.
- Informatie Vlaanderen, 2012. Digitale boswijzer Vlaanderen 2012.
- IPCC, 2003. Intergovernmental Panel on Climate Change. Good Practice Guidance For Land Use, Land-Use Change and Forestry. Institute for Global Environmental Strategies (IGES), Hayama. ISBN 4-88788-003-0.
- IPCC, 2006. Intergovernmental Panel on Climate Change 2006. 2006 IPCC Guidelines for National Greenhouse Gas Inventories, Volume 4: Agriculture, Forestry and other land use (AFOLU). Cambridge University Press. https://doi.org/10.1016/j. phrs.2011.03.002.
- IPCC, 2019a. Volume 4: Agriculture, Forestry and Other Land Use (AFOLU). Chapter 5 Cropland. 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories
- IPCC, 2019b. Volume 4: Agriculture, Forestry and Other Land Use (AFOLU). Chapter 4 Forest Land. 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories.
- Jansen, J.J. and Oosterbaan, A. (reds), 2018. Opbrengsttabellen Nederland.
- Keenan, T.F., Williams, C.A., 2018. The terrestrial carbon sink. Annu. Rev. Environ. Resour. 43, 219–243.
- KMI, 2019. Koninklijk Meteorologisch Instituut van België, Klimaatatlas. URL: (https://www.meteo.be/nl/klimaat/klimaatatlas).
- Lachowicz, H., Bieniasz, A., Wojtan, R., 2019. Variability in the basic density of silver birch wood in Poland. article id 9968 Silva Fennica 53 (1). https://doi.org/ 10.14214/sf.9968.
- Lamlom, S.H., Savidge, R.A., 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenergy 25, 381–388.
- Larcher, F., Baudry, J., 2013. Landscape grammar: a method to analyse and design hedgerows and networks. Agrofor. Syst. 87, 181–192. https://doi.org/10.1007/ s10457-012-9534-4.
- Leuschner, C., Meier, I.C., 2018. The ecology of Central European tree species: trait spectra, functional trade-offs, and ecological classification of adult trees perspectives in plant ecology. Evol. Syst. 33, 89–103.
- Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated ageing reduces vigour in trees. Ecol. Lett. 8, 1183–1190. https://doi.org/10.1111/j.1461-0248.2005.00819.x.
- Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A.,
 Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.
 E., Hart, T., Hubbell, S.P., Itoh, A., Kassim, A.R., LaFrankie, J.V., Lee, H.S., Losos, E.,
 Makana, J.R., Ohkubo, T., Sukumar, R., Sun, I.F., Nur Supardi, M.N., Tan, S.,
 Thompson, J., Valencia, R., Muñoz, G.V., Wills, C., Yamakura, T., Chuyong, G.,
 Dattaraja, H.S., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S.,
 Suresh, H.S., Thomas, D., Vallejo, M.I., Ashton, P., 2006. Testing metabolic ecology
 theory for allometric scaling of tree size, growth, and mortality in tropical forests.
 Ecol. Lett. 9. 575–588.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https:// doi.org/10.1111/j.2041-210x.2012.00261.x.
- Nair, P.K.R., Nair, V.D., Mohan Kumar, B., Showalter, J.M., 2010. Carbon sequestration in agroforestry systems. Adv. Agron. 108, 237–307.
- Nair, P.K.R., 2012. Carbon sequestration studies in agroforestry systems: a reality-check. Agrofor. Syst. 86, 243–253.
- Nicolescu, V.N., Carvalho, J., Hochbichler, E., Bruckman, V.J., Piqué, M., Hernea, C., Viana, H., et al., 2018. Silvicultural guidelines for European Coppice forests. In: Unrau, A., Becker, G., Spinelli, R., Lazdina, D., Magagnotti, N., Nicolescu, V.N., Buckley, P., Bartlett, D., Kofman, P.D. (Eds.), Coppice Forests in Europe. Freiburg i. Br. Albert Ludwig University of Freiburg, Germany, pp. 46–63.
- Nock, C.A., Geihofer, D., Grabner, M., Baker, P.J., Bunyavejchewin, S., Hietz, P., 2009. Wood density and its radial variation in six canopy tree species differing in shade-tolerance in western Thailand. Ann. Bot. 104, 297–306.
- Oldenburger, J., 2010 Landscape care wood and other wooded land 2010 EUwood Final report Hamburg/Germany 80 88.June 2010.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333 (6045), 988–993. https:// doi.org/10.1126/science.1201609.
- Pardon, P., Reubens, B., Reheul, D., Mertens, J., De Frenne, P., Coussement, T., Janssens, P., Verheyen, K., 2017. Trees increase soil organic carbon and nutrient availability in temperate agroforestry systems. Agric. Ecosyst. Environ. 247, 98–111.
- Parker, M.L., Smith, J.H.G., Johnson, S., 1978. Annual ring width and density patterns in red alder. Wood Fiber 10 (2), 120–130.
- Prevedello, J.A., Almeida-Gomes, M., Lindenmayer, D.B., 2017. The importance of scattered trees for biodiversity conservation: a global meta- analysis. J. Appl. Ecol. 55 (1), 205–214. https://doi.org/10.1111/1365-2664.12943.
- Price, C.A., Gillooly, J.F., Allen, A.P., Weitz, J.S., Niklas, K.J., 2010. The metabolic theory of ecology: prospects and challenges for plant biology. New Phytol. 188, 696–710
- Province of Antwerp, 2017. Presentation 'Biomassa in Meerhout' whitin the project 'Kempens Energiehout'
- R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rempel, J.C., Kulshreshtha, S.N., Amichev, B.Y., Van Rees, K.C.J., 2017. Costs and benefits of shelterbelts: a review of producers' perceptions and mind map analyses

- for Saskatchewan, Canada. Can. J. Soil Sci. 97 (3), 341–352. https://doi.org/ 10.1139/ciss-2016-0100.
- Rivest, D., Olivier, A., Gordon, A.M., 2010. Hardwood Intercropping Systems. Combining wood and Agricultural Production While Delivering Environmental Services.
- Sánchez, I.A., Lassaletta, L., McCollin, D., Bunce, R.G.H., 2010. The effect of hedgerow loss on microclimate in the Mediterranean region: an investigation in Central Spain. Agrofor. Syst. 78, 13–25. https://doi.org/10.1007/s10457-009-9224-z.
- Schoeneberger, M., Benrup, G., de Gooijer, H., Soolanayakanahally, R., Sauer, T., Brandle, J., Zhou, X., Current, D., 2012. Branching out: agroforestry as a climate change mitigation and adaptation tool for agriculture. J. Soil Water Conserv. 67 (5), 128A–136A. https://doi.org/10.2489/jswc.67.5.128A.
- Sheil, D., 2018. Forests, atmospheric water and an uncertain future: the new biology of the global water cycle. For. Ecosyst. 5, e19 https://doi.org/10.1186/s40663-018-0138-v.
- Shorohova, E., Kuuluvainen, T., Kangur, A., Jõgiste, K., 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. Ann. For. Sci. 66, 201.
- Sitzia, T., Pizzeghello, D., Dainese, M., Ertani, A., Carletti, P., Semenzato, P., Nardi, S., Cattaneo, D., 2014. Topsoil organic matter properties in contrasted hedgerow vegetation types. Plant Soil 383, 337–348.
- Stephenson, N., Das, A., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507 (7490), 90–93.
- Tavernier, R., Maréchal, R., 1972. Carte des Associations des Sols 1/500.000. NGI,
- Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43.
- Van Den Berge, S., 2021. Role of hedgerow systems for biodiversity and ecosystem services in agricultural landscapes. PhD thesis, Ghent University, Ghent, Belgium.
- Van Den Berge, S., Baeten, L., Vanhellemont, M., Ampoorter, E., Proesmans, W., Eeraerts, M., Hermy, M., Smagghe, G., Vermeulen, I., Verheyen, K., 2018. Species diversity, pollinator resource value and edibility potential of woody networks in the countryside in northern Belgium. Agric. Ecosyst. Environ. 259, 119–126. https://doi. org/10.1016/j.agee.2018.03.008.
- Van Den Berge, S., Tessens, S., Baeten, L., Vanderschaeve, C., Verheyen, K., 2019. Contrasting vegetation change (1974–2015) in hedgerows and forests in an intensively used agricultural landscape. Appl. Veg. Sci. 22, 269–281.
- Van Den Berge, S., Vangansbeke, P., Calders, K., Vanneste, T., Baeten, L., Verbeeck, H., Krishna Moorthy, S.P., Verheyen, K., 2021a. Biomass expansion factors for hedgerow-grown trees derived from terrestrial LiDAR. BioEnergy Res. 14 (2), 561–574. https://doi.org/10.1007/s12155-021-10250-y.
- Van Den Berge, S., Vangansbeke, P., Baeten, L., Vanneste, T., Vos, F., Verheyen, K., 2021b. Soil carbon of hedgerows and 'ghost'hedgerows. Agrofor. Syst. 95, 1087–1103. https://doi.org/10.1007/s10457-021-00634-6.
- Van den Bulcke, J., Wernersson, E.L.G., Dierick, M., Van Loo, D., Masschaele, B., Brabant, L., Boone, M.N., Van Hoorebeke, L., Haneca, K., Brun, A., Luengo Hendriks, C.L., Van Acker, J., 2014. 3D tree-ring analysis using helical X-ray tomography. Dendrochronologia 32 (1), 39–46.
- Van Gijseghem, D., Lauwers, L., Sanders, A., et al., 2003. Vermesting. In: Van Steertegem, M. (Ed.), Milieu- en Natuurrapport Vlaanderen: Thema's. MIRA-T 2003. Vlaamse Milieumaatschappij en Lannoo, Leuven.
- Vandekerkhove, K., Vanbeveren, S.P.P., Ceulemans, R., Lecomte, H., Marchal, D., Mills, J., Buckley, P., Unrau, A., Becker, G., Spinelli, R., Lazdina, D., Magagnotti, N., Nicolescu, V.N., Buckley, P., Bartlett, D., Kofman, P.D., 2018. Coppice Forests in Europe. Freiburg i. Br, Albert Ludwig University of Freiburg Germany, 199, 206.
- Vanhellemont, M., Van Acker, J., Verheyen, K., 2016. Exploring life growth patterns in birch (Betula pendula). Scand. J. For. Res. 31 (6), 561–567.
- Vanhellemont, M., Sousa-Silva, R., Maes, S.L., Van den Bulcke, J., Hertzog, L., Verheyen, K., 2019. Distinct growth responses to drought for oak and beech in temperate mixed forests. Sci. Total Environ. 650 (2), 3017–3026.
- van Noordwijk, M., 2014. Climate Change: Agricultural Mitigation in Encyclopedia of Agriculture and Food Systems, Vol. 2 (ed. Van Alfen, N.), 2, pp. 220–231.ISBN: 978-0-08-093139-5.
- Van Vooren, L., Reubens, B., Broekx, S., De Frenne, P., Nelissen, V., Pardon, P., Verheyen, K., 2017. Ecosystem service delivery of agri-environment measures: a synthesis for hedgerows and grass strips on arable land. Agric. Ecosyst. Environ. 244, 32–51. https://doi.org/10.1016/j.agee.2017.04.015.
- Vanneste, T., Govaert, S., Spicher, F., Brunet, J., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Hedwall, P.O., Kapas, R., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K., De Frenne, P., 2020a. Contrasting microclimates among hedgerows and woodlands across temperate Europe. Agric. For. Meteorol. 281, 107818 https://doi.org/10.1016/j. agrformet.2019.107818.
- Vanneste, T., Van Den Berge, S., Riské, E., Brunet, J., Decocq, G., Diekmann, M., Graae, B.J., Hedwall, P.-O., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Wulf, M., Verheyen, K., De Frenne, P., 2020b. Hedging against biodiversity loss: forest herbs' performance in hedgerows across temperate Europe. J. Veg. Sci. 31, 817–829. https://doi.org/10.1111/jvs.12917.
- Vannoppen, A., Boeckx, P., De Mil, T., Kint, V., Ponette, Q., Van den Bulcke, J., Verheyen, K., Muys, B., 2018. Climate driven trends in tree biomass increment show asynchronous dependence on tree-ring width and wood density variation. Dendrochronologia 48, 40–51.

- Vieilledent, G., Fischer, F.J., Chave, J., Guibal, D., Langbour, P., Gérard, J., 2018. New formula and conversion factor to compute basic wood density of tree species using a global wood technology database. Am. J. Bot. 105 (10), 1653–1661.
- Vos, F. 2019. Chasing 'Ghost' Hedgerows and their Soil Organic Matter Legacies in Agricultural Landscapes. A Case Stuy in Turnhout (Belgium). Thesis. Ghent University.
- Wehling, S., Diekmann, M., 2009. Hedgerows as an environment for forest plants: a comparative case study of five species. Plant Ecol. 204, 11–20.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- Wiemann, M.C., Williamson, G.B., 1988. Extreme radial changes in wood specific-gravity in some tropical pioneers. Wood Fiber Sci. 20, 344–349.
- Wiemann, M.C., Williamson, G.B., 1989. Radial gradients in the specific gravity of wood in some tropical and temperate trees. For. Sci. 35, 197–210.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23 (2), 201–213.
- Woodcock, D.W., Shier, A.D., 2002. Wood specific gravity and its radial variations: the many ways to make a tree. Trees 16, 437–443. https://doi.org/10.1007/s00468-002-0173-7.
- $Wykoff, W.R., 1990. \ A basal area increment model for individual conifers in the Northern Rocky Mountains. For. Sci. 36, 1077–1104.$
- Zhou, X.H., Brandle, J.R., Awada, T.N., Schoeneberger, M.M., Martin, D.L., Xin, Y., Tang, Z.H., 2011. The use of forest-derived specific gravity for the conversion of volume to biomass for open-grown trees on agricultural land. Biomass Bioenergy 35, 1721–1731.