Long-term temporal patterns in ecosystem carbon flux components and overall balance in a heathland ecosystem

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Long-term temporal patterns in ecosystem carbon flux components and overall balance in a heathland ecosystem

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HIGHLIGHTS

- Ecosystem C balance exhibited a sinusoidal-like curvature of C sink/source with age.
- It took seven years for ecosystem cumulative C to recover after cutting.
- C payback from soil to the atmosphere started at the age of 16 years.
- Ecosystem models must consider vegetation age in ecosystem C balance projections.
- Optimizing management cycles could increase ecosystem C sink strength in heathlands.

GRAPHICAL ABSTRACT
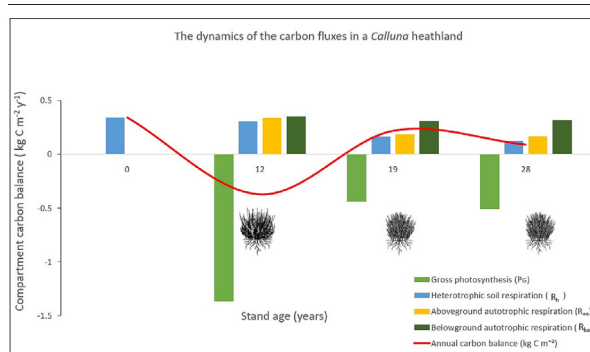
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ABSTRACT

Terrestrial ecosystems have strong feedback to atmospheric CO_2 concentration and climate change. However, the long-term whole life cycle dynamics of ecosystem carbon (C) fluxes and overall balance in some ecosystem types, such as heathland ecosystems, have not been thoroughly explored. We studied the changes in ecosystem CO_2 flux components and overall C balance over a full ecosystem lifecycle in stands of *Calluna vulgaris* (L.) Hull by using a chronosequence of 0, 12, 19 and 28 years after vegetation cutting. Overall, the ecosystem C balance was highly non-linear over time and exhibited a sinusoidal-like curvature of C sink/source change over the three-decade timescale. After cutting, plant-related C flux components of gross photosynthesis (P_G), aboveground autotrophic respiration (R_{aa}) and belowground autotrophic respiration (R_{ba}) were higher at the young age (12 years) than at middle (19 years) and old (28 years) ages. The young ecosystem was a C sink (12 years: -0.374 kg C m^{-2} year^{-1}) while it became a C source with aging (19 years: 0.218 kg C m^{-2} year^{-1}) and when dying (28 years: 0.089 kg C m^{-2} year^{-1}). The post-cutting C compensation point was observed after four years, while the cumulative C loss in the period after cutting had been compensated by an equal amount of C uptake after seven years. Annual ecosystem C payback from the ecosystem to the atmosphere started after 16 years. This information may be used directly for optimizing vegetation management practices for maximal ecosystem C uptake capacity. Our study highlights that whole life cycle observational data of changes in C fluxes and balance in ecosystems are important and the ecosystem model needs to take the successional stage and vegetation age into account when projecting component C fluxes, ecosystem C balance, and overall feedback to climate change.

1. Introduction

Terrestrial ecosystems constitute a major player in the global carbon (C) dynamics and climate feedback (Heimann and Reichstein, 2008). The net C exchange between the terrestrial biosphere and the atmosphere

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determines the magnitude and dynamics of ecosystem C storage and plays a key factor in the future global climate change prediction (Larsen et al., 2007; Koven et al., 2015; Wu et al., 2020). Previous studies suggest that the northern hemisphere terrestrial ecosystems act as a C sink, but these estimations are obtained primarily by indirect methods and with information dominated by forest ecosystems (Valentini et al., 2000). At the global scale, although forest ecosystems play a large role in soil C sequestration, other terrestrial ecosystems, such as shrubland and heathland ecosystems, occupy about 14–18 % of the total land cover (Hansen et al., 2000; Broxton et al., 2014) and often have greater C uptake capacity than e.g. grassland ecosystems (Biederman et al., 2018).

Heathlands as managed landscapes that started developing about 4000 years ago (Gimingham, 1985; Schellenberg and Bergmeier, 2022), play an important role in the traditional European landscape and are widely valued for their natural and cultural significance (Fagúndez, 2013). Meanwhile, some heathland ecosystems could potentially be significant C sinks (Field et al., 2017). Heathlands used to cover a large part of northwest Europe, but human land-use changes have resulted in a large decline in heathland cover in the past 150 years (Ransijn et al., 2015). In recent times, landscape management has been reinstated to protect and conserve heathland ecosystems and their flora and fauna (Fagúndez, 2013), which is generally undertaken by cutting, burning or sod-cutting on a cyclical basis, producing relatively large patches of even-aged vegetation (Diemont and Heil, 1984).

In the time between management-related disturbances, *Calluna vulgaris* (L.) Hull (henceforth referred to as *Calluna*) plants grow and biomass accumulates both in the vegetation and the soil (Diemont and Heil, 1984; Gimingham, 1985). After 6 years of re-growth, *Calluna* plants may have developed a hemispherical shape of up to 50 cm in height with 100 % ground cover (Gimingham, 1985). Plant vitality and biomass production typically start to decline after reaching 15 years and from then on, a net loss of aboveground biomass begins. After 25 years, the central branches die back gradually leading to the establishment of grasses establish in the vegetation gaps (Schellenberg and Bergmeier, 2022). If heathlands are unmanaged with low disturbance levels, grass encroachment or succession to a forest occurs driven by N deposition, climate change, heather beetle attacks, or low grazing pressures (Diemont and Heil, 1984; Fagúndez, 2013; Terry et al., 2004). Clearly, *Calluna*-dominated heathland communities have been shown to have a higher potential for C sequestration than grass dominated communities and even being comparable to that of woodlands (Quin et al., 2015). Therefore, understanding how ecosystem carbon balance changes over time spans of years to decades in heathlands is critical for estimating the maximum ecosystem C accumulation capacity that will potentially change our current heathland ecosystem management strategies and help mitigate the increasing atmospheric CO_2.

In chronosequence studies, clear-cutting at different times is one of the most widely used conventional management practices, which has been widely used in particular in forest ecosystem studies (Aguilos et al., 2014; Law et al., 2003; Uri et al., 2022) but not thoroughly explored in the heathland ecosystems. In the current study, a similar chronosequence has been established within a localized area in a heathland ecosystem allowing for a space-for-time substitution strategy to study changes in the ecosystem over a full lifecycle of the *Calluna*. Previous forest ecosystem studies have shown that significant changes in forest structural and functional traits are related to age, which has a stronger influence on productivity and CO_2 exchange than climate change (Noormets et al., 2012). Clear-cut will influence the ecosystem and soil C cycling and can turn a C accumulating ecosystem into a C emitting system due to the elimination of the canopy photosynthesis (Paul-Limoges et al., 2015; Uri et al., 2022). The ecosystem C compensation point is defined as the number of years after disturbance before the ecosystem act as a C sink again on an annual basis (Aguilos et al., 2014; Kowalski et al., 2004). The time needed for different ecosystem types to reach the C compensation point after clear-cutting varies profoundly. For example, it takes a warm temperate plantation 3 years (Clark et al., 2004; Gholz and Fisher, 1982) and boreal forests 7–20 years (Aguilos et al., 2014; Fredeen et al., 2007) to develop from a C source to

a C sink after clear-cutting. For heathland ecosystems, however, no previous studies have targeted the investigation of the ecosystem C compensation point after clear-cutting. Further, the effect of vegetation age on different flux components of heathland ecosystem C balances is not well known. Therefore, we used the established chronosequence in a managed *Calluna* heathland ecosystem to target these open questions. In particular, we aimed to (a) calculate the annual C balance based on the underlying C flux components of each stand age community, (b) assess the relative importance of different C flux components over time, (c) estimate the cumulative C balance over a 28-year period through a space-for-time approach, and (d) assess the implications of these findings for heathland management.

We hypothesized that (i) immediately after clear-cutting, microbial soil respiration is the dominant process affecting the C balance, and the ecosystem is at its maximum as a C source. (ii) As vegetation grows back, plant gross photosynthesis (P_G) increases, and the overall C balance becomes more dominated by plant processes turning the ecosystem into a C sink. (iii) Compared to a forest ecosystem, the time to reach the C compensation point in the heathland ecosystem is shorter due to its shorter life circle. (iv) As the vegetation continues maturing and eventually starts dying, the ecosystem becomes a C source again.

2. Materials and methods

2.1. Study site

The experimental site is located in a temperate humid heathland ecosystem at Oldebroek, the Netherlands (52°24′N 5°55′E), about 25 m above sea level. This site area is well-drained, nutrient-poor, acidic sandy soil (Haplic Podzol), with an organic layer ranging in thickness between 1.4 and 8 cm (Kopittke et al., 2012; Van Meeteren et al., 2008). Mean annual precipitation is 1018 mm with an annual mean temperature of 10.1 °C. The dominant vascular species at this site are the perennial woody dwarf shrub *Calluna*, and some *Deschampsia flexuosa*, *Molinia caerulea* and *Pinus sylvestris*. *Hypnum cupressiforme* Hedw is the codominant non-vascular species.

2.2. Experimental design – chronosequence trial

The chronosequence experiment was created by separate vegetation clear-cutting management events at different times within a 50 m × 50 m area. The oldest *Calluna* heathland community was located in the northern part of the research site, while middle and young *Calluna* communities were located in the southeastern and southern parts of the site. Different stand ages of the *Calluna* vegetation communities were regarded as a treatment, which was 28 years of age (old), 19 years of age (middle) and 12 years old (young). However, replicates of each treatment were not applicable because of the site inherent nature. Therefore, we chose the quasi-experimental design, in which groups were selected based on the variables that were tested but where randomization and replication processes were not possible (Campbell and Stanley, 2015).

Across each chronosequence age community, eight trail plots (60 cm × 60 cm) were established in April 2011 ($n = 24$) (Fig. 1a). Within each community age, total soil respiration (R_S), net ecosystem exchange (NEE) and ecosystem respiration (R_E) were measured ('Untrenched' plots; $n = 12$), while the other four plots were used to measure the heterotrophic respiration ('Trenched' plots; n = 12). The heterotrophic respiration plots were designed by excavating a narrow trench of 50 cm deep around the area of the plots and used for harvesting aboveground biomass. To prevent the growth of new roots into the plots, a 41 μm nylon mesh was placed inside the trench plots and subsequent plant regrowth was removed on a regular basis. Further trial design details are provided by (Kopittke et al., 2012). Based on the analysis provided by Kopittke et al. (2012), there was no statistical difference of R_H across different community ages. Therefore, we could assume that the Trenched plots represent conditions immediately following clear cutting, i.e. year 0, when $R_H = R_S = R_E = NEE$.
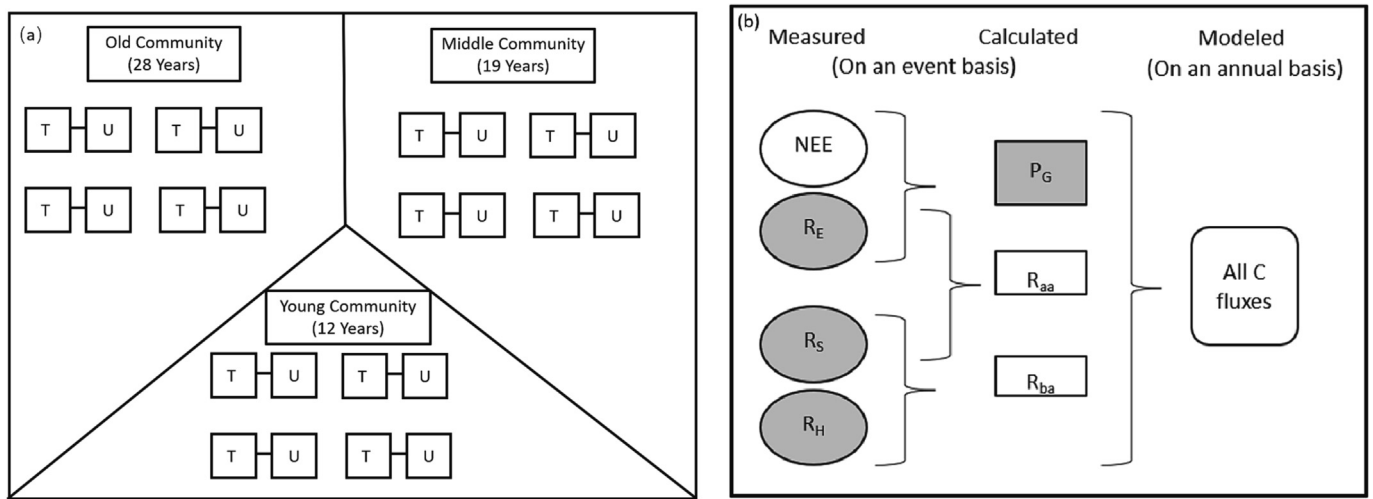
Fig. 1. (a) Layout of the experimental plots. Eight experimental plots (60 cm × 60 cm) were established within each community in April 2011 (*n* = 24). Four of these experimental plots on each community ('Untrenched' plots; *n* = 12) were used to measure total soil respiration (R_S), net ecosystem exchange (NEE) and ecosystem respiration (R_E). The other four plots in each community were used to measure heterotrophic soil respiration (R_H) ('Trenched' plots; n = 12). (b) Flow chart of measurements and modelling of C fluxes. The circles indicate the measured fluxes (like NEE, R_E, R_s, R_H), the squares indicate the fluxes that were calculated based on the measurements (like gross photosynthesis (P_G), aboveground autotrophic respiration (R_{aa}), belowground autotrophic respiration (R_{ba})). The filled circles and squares indicate the fluxes that were modelled (with Eqs. (2) and (1) respectively) to interpolate from the measurements on an event basis to annual values. See Section 2.5 for further explanation.

For NEE and R_E measurements, pre-installed metal-based frames (60 cm × 60 cm) were permanently installed in the vegetated, Untrenched plots. In order to seal the gap between the metal frame and the soil surface, sandbags as well as the metal pins were used. Within each plot, soil collars for Rs measurements (10 cm diameter and 6 cm height) were pre-inserted into the soil about 1 cm with a buffer zone of 20 cm from the plot boundary. Rather than placing the collars randomly, the collars were installed underneath *Calluna* plants in the Untrenched plots. To ensure only Rs was measured, mosses and other vegetation were removed from the inside collars.

2.3. Site meteorological conditions

Hourly-based meteorological data loggers (Decagon Devices Inc.; DC, USA) were used to record the air temperature, relative humidity and Photosynthetically Active Radiation (PAR) from 2 m aboveground level at the center of the site. In order to measure rainfall, a Vaisala tipping bucket rain gauge (Vaisala; Vantaa, Finland) connected to a Decagon datalogger was used. Across each age plot, soil moisture ($m^3 m^{-3}$) and soil temperature (°C) measurements were recorded from 4 to 7 cm below ground surface (5TM Sensor, Decagon Devices Inc., DC, USA).

2.4. Measurements of C fluxes

NEE and R_E were measured with a LI-6400 infrared gas analyzer (LI-COR, Lincoln, NE, USA) attached to a 288 L ultra-violet light transparent Perspex chamber (60 cm × 60 cm × 80 cm) using the method described in Larsen et al. (2007). The time of chamber deployment was about 180 s for NEE and 240 s for R_E. At the start of a measurement a short period (called 'deadband') was removed because the chamber gas concentration change needs to stabilize after chamber deployment and also because it takes some time for plant leaves to stop taking up CO_2 after darkening the chamber. The length of the deadband was identified visually for each measurement during post-processing, leading to deadbands of 10–15 s for NEE measurements and 20–40 s for R_E measurements. After first doing the NEE measurement with the transparent chamber by gently positioning the chamber on the collars, the chamber was lifted and ventilated upwind to

restore the ambient CO_2 concentration inside the chamber. The chamber was then placed on the collar again and this time covered with a fitted blackout-cloth to darken the chamber and stop plant photosynthetic activity. All the fluxes were measured during the daytime between 10:00–17:00. All CO_2 fluxes were calculated based on the development of the CO_2 concentrations inside the chamber after the deadband using the HMR procedure, developed for soil-atmosphere trace-gas flux estimation with static chambers described by Pedersen et al. (2010), implemented in an R-package (Pedersen, 2011). P_G was calculated as NEE minus R_E ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and is here reported with a negative sign. The NEE and R_E measurements and P_G calculations on the young and middle age stands were obtained about once a month from March 2011 to August 2012. At the old age stand, the NEE and R_E fluxes were measured around once a month from November 2010 to August 2012.

Soil respiration measurements were obtained using a Portable Gas Exchange System (LI-6400XT; LICOR Biosciences, Lincoln, NE USA) combined with a soil CO_2 flux chamber (LI-6400-09; LICOR Biosciences) which fitted onto the collars. Soil respiration measurements conducted in May 2011 and continued until August 2012. Further details on soil respiration were provided in Kopittke et al. (2012).

2.5. Modelling of C fluxes and statistical analysis

The observational data of P_G, R_E, Rs, and R_H were used to fit different non-linear models (see below) which were then used to scale fluxes to the entire study period using the hourly plot-level soil temperature and site-level PAR datasets from the different age communities. The modelled hourly flux data were then cumulated to estimate annual flux component C fluxes of each age community. When referenced in the text, model parameters are stated as means with standard errors (SE). To test if fluxes differed between the different ages, the datasets were analyzed using a linear mixed effects model (Pinheiro and Bates, 2000), where the response variables were the CO_2 flux measurements (P_G, R_E, Rs, and R_H), the treatment (age) formed the fixed effects, and the measurement location (plot within treatment) formed the random effects. For all statistical analyses, the R

statistical computing program was used (Version 4.12, R Development Core Team, 2021).

Gross photosynthesis (P_G, μmol CO_2 m^{-2} s^{-1}) was modelled based on the equation proposed by Quin et al. (2015) for a *Calluna* heathland:

$$P_G = \frac{(PAR \times bT)}{PAR + P_K} \tag{1}$$

where *PAR* is the Photosynthetically Active Radiation (μmol photons m^{-2} s^{-1}), *T* is the soil temperature (°C) at 5 cm below the ground surface, P_K is half the saturation constant (value of *PAR* when P_G is at its maximum for the period) and parameter *b* (μmol CO_2 m^{-2} s^{-1} °C^{-1}) describes the temperature sensitivity of P_G.

We used a classic, first-order exponential equation by van't Hoff (1898) to model the different ecosystem component respiratory fluxes (R_E, R_S, R_H) per community:

$$R = R_0 e^{kT} \tag{2}$$

where *R* is respiration (μmol CO_2 m^{-2} s^{-1}), R_0 is basal respiration (μmol CO_2 m^{-2} s^{-1}), *T* is soil temperature (°C) at 5 cm below surface and the parameter *k* is the temperature sensitivity of respiration (°C^{-1}).

2.6. Quantification of annual C fluxes

The aboveground autotrophic respiration (R_{aa}) and belowground autotrophic respiration (R_{ba}) were calculated based on the measured fluxes (R_E, Rs, and R_H) (Fig. 1b). The NEE, R_{aa} and R_{ba} fluxes were calculated on an hourly basis and then all flux components were cumulated to annual estimates. The standard deviation of each C flux component was estimated by a bootstrap procedure with 10,000 iterations of the model fitting and annual upscaling, except for P_G, which was bootstrapped only 100 times due to extensive computer calculation time. The annual C balance estimation was fitted to a Loess curve by the combination of P_G and R_E through time (Fig. 2b). The cumulative C balance in the ecosystem over time was established by a bootstrap procedure with 1000 times iterations of summing the annual C balance estimates.

3. Results

3.1. Compartment C fluxes

Gross photosynthesis C fluxes were significantly affected by the age of the vegetation ($p < 0.001$; Fig. 2a). The highest annual rates of P_G, R_{aa} and R_{ba} were all observed in the young community (Fig. 2a). The greatest difference between the communities was observed during summer months
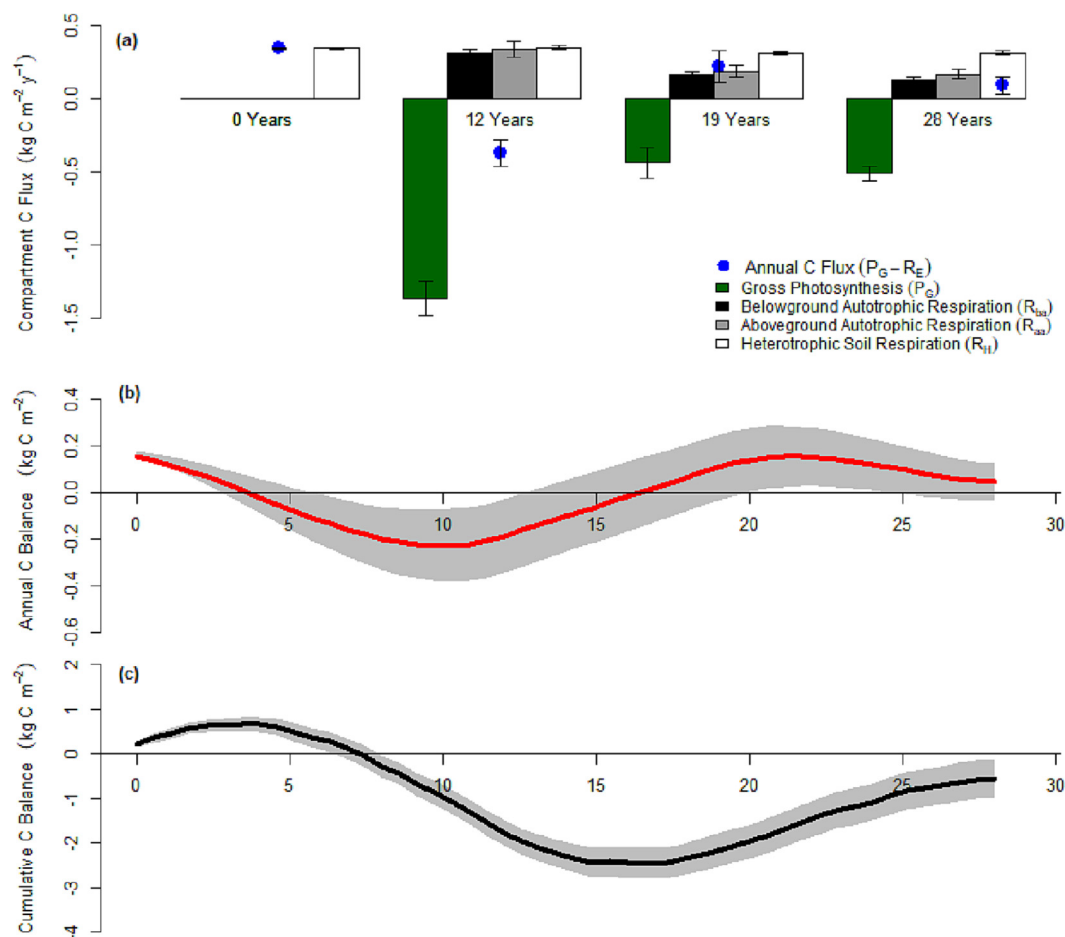

Fig. 2. The *Calluna* heathland C fluxes and balances at different successional stages and development over time. Positive values indicate an ecosystem C source and negative values indicate a C sink. (a) The annual C flux, gross photosynthesis (P_G), belowground autotrophic respiration (R_{ba}), aboveground autotrophic respiration (R_{aa}) and heterotrophic respiration (R_H) in each successional stage community (kg C m^{-2} y^{-1}). The data were modelled based on measurement campaigns and models were subsequently used to predict over the complete study period using continuous soil temperature data from each treatment. The error bars are mean ± standard error (SE) based on the bootstrap iterations. (b) Loess curve of the resulting annual C balance over time fitted based on the P_G and R_E estimates shown in panel a. The grey band indicated the confidence intervals of annual C balance. (c) The cumulative C balance in the ecosystem over time was established by a bootstrap procedure with 1000 times iterations of summing the annual estimates shown in panel b. The grey band indicated the confidence intervals of cumulative C balance.

(Figs. S1 & S2) where CO_2 uptake in the young community was significantly greater than in the old community ($p < 0.001$).

After vegetation cutting, heterotrophic respiration (R_H) from the bare ground was the only contributor to the ecosystem C flux (0 years: 0.342 kg C m^{-2} year^{-1}). We assumed that R_H equals R_E as there was no plant colonization. The age of the vegetation had a significant effect on R_E ($p < 0.001$) and Rs as well ($p < 0.05$), with significantly greater respiration in the young community than in the old community both annually (Fig. 2a) and during every season of the year (Figs. S1–S3). However, no significant effect of community age on R_H ($p = 0.758$) was found across the chronosequence. The ratio of R_H/R_E increased with age of the vegetation from 35 % (young) to 47 % (middle) and 52 % (old), while the ratio between autotrophic respiration ($R_{aa} + R_{ba}$) and R_E decreased with age from 65 % (young) over 53 % (middle) to 48 % (old) (Fig. 3). R_{aa} was always higher than R_{ba} across different community ages, therefore resulting in a higher ratio to R_E across the chronosequence (Fig. 3).

3.2. Modelled C fluxes

The optimal parameter values for the models are shown in Table 1. All model predictions generally followed the seasonal soil temperature pattern, where the lowest C fluxes were observed during winter (Fig. S2). The estimated parameter values of the models (Table 1) showed that the temperature sensitivity of P_G (b) and saturation constant (P_K) decreased with vegetation aging. The maximum basal respiration value (R_0) of R_E was observed at the middle age, while the maximum R_0 of Rs and R_H was found at the young age. Highest temperature sensitivity (k) of R_E was found at the young age, but similar to middle and old age. The k values of Rs and R_H were similar across different age groups.

3.3. The annual and cumulative C balance

The annual C balance calculations (Fig. 2b) indicated that all the investigated ages of heathland were sources of C to the atmosphere, except for the young community. At 0 years, R_H from bare ground was the dominant contributor to C flux (0 year: 0.342 kg C m^{-2} year^{-1}). As plant growth and P_G increased, the ecosystem became a C sink (12 year: −0.374 kg C m^{-2} year^{-1}) but shifted back to a C source as plants aged (19 year: 0.218 kg C m^{-2} year^{-1}) and then started dying (28 year: 0.089 kg C m^{-2} year^{-1}). According to the annual C balance curve, the results showed that the C compensation point, being the time after cutting when annual photosynthesis equals respiration and the ecosystem starts acting as a C sink, was at the age of 4 years, while the C payback occurred at 16 years (Fig. 2b). The estimated cumulative C balance along the chronosequence exhibited a sinusoidal-like recovery curve after cutting (Fig. 2c), with one shift after seven years between the C sink and C source over the 28-year period of the growth cycle. The maximal C strength was found to be after approximately 10 to 12 years, while the peak value of the cumulative C storage was observed after approximately 16 years (−2.671 kg C m^{-2}), after which the ecosystem became a C source.

4. Discussion

Chronosequence studies provide a 'space-for-time substitution' approach, ideal for studying the ecosystem C balance over time as a function of various growth or successional stages after a disturbance. In the current study, historical clear-cutting events had resulted in a mosaic of different aged communities being present within a localized area, which created a chronosequence of *Calluna* heathland successional stages over its entire
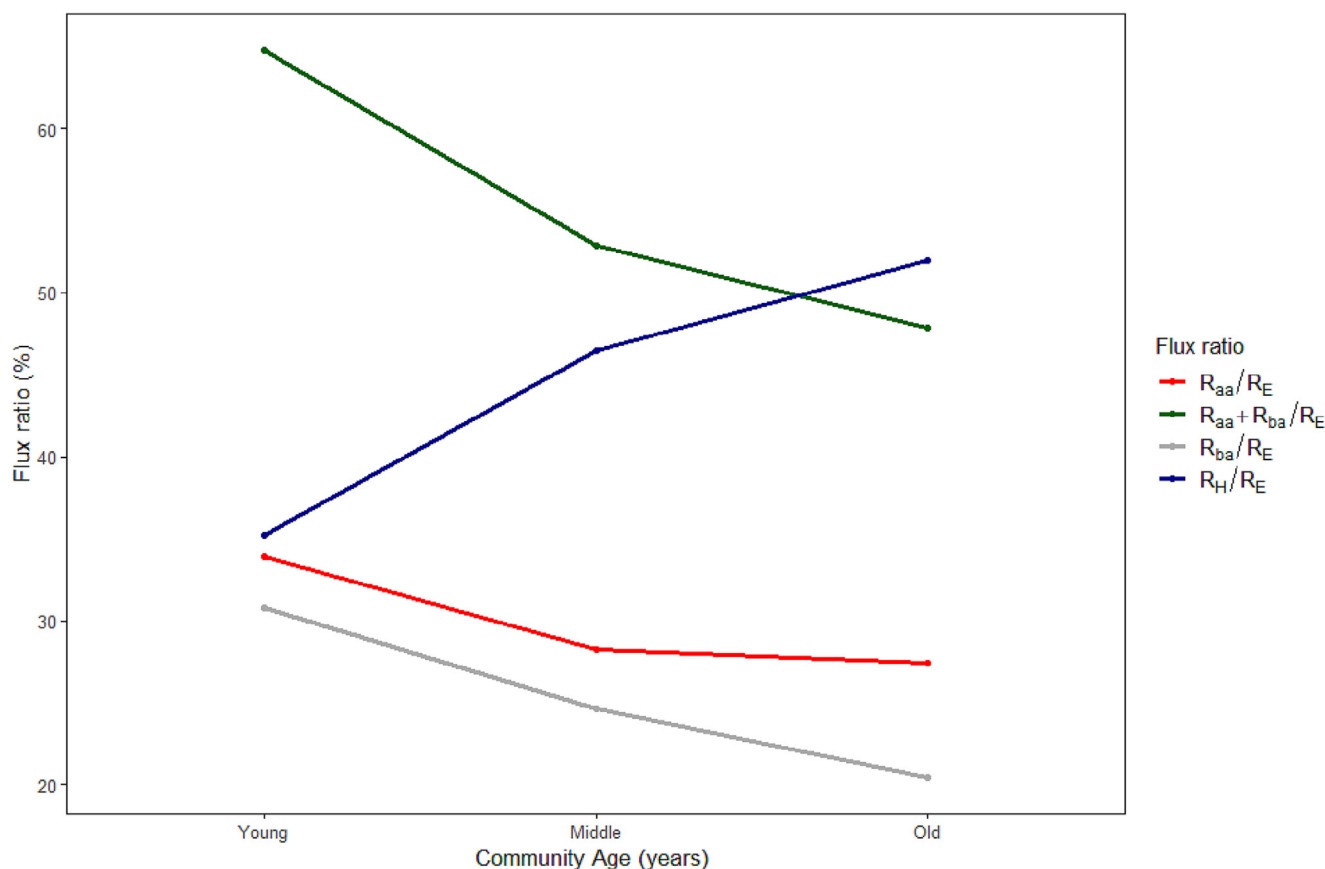

Fig. 3. The flux ratios of aboveground autotrophic respiration (R_{aa}), belowground autotrophic respiration (R_{ba}), heterotrophic respiration (R_H) and the sum autotrophic respiration ($R_{aa} + R_{ba}$) to the ecosystem respiration (R_E) over time.

Table 1

Parameter values ± SE of R_E, P_G, R_S and R_H models for the 12 years, 19 years and 28 years. See text for equations and parameter explanations. further details on the soil respiration related parameters have been published by Kopittke et al. (2012). Results here deviate slightly from those by Kopittke et al. (2012) because of a simplification in the model selection process applied in the current study.

Model	0 Year community	12 Year community	19 Year community	28 Year community
P_G		$b = 1.25 \pm 0.16\ (p < 0.01)$	$b = 0.39 \pm 0.15\ (p = 0.01)$	$b = 0.30 \pm 0.04\ (p < 0.01)$
	–	$P_K = 264.8 \pm 142.9\ (p = 0.07)$	$P_K = 248.5 \pm 438.0\ (p = 0.57)$	$P_K = 41.4 \pm 74.3\ (p = 0.58)$
R_E		$R_0 = 0.17 \pm 0.05\ (p < 0.01)$	$R_0 = 0.40 \pm 0.14\ (p < 0.01)$	$R_0 = 0.31 \pm 0.06\ (p < 0.01)$
	–	$k = 0.22 \pm 0.02\ (p < 0.01)$	$k = 0.13 \pm 0.02\ (p < 0.01)$	$k = 0.14 \pm 0.01\ (p < 0.01)$
Rs		$R_0 = 0.46 \pm 0.06\ (p < 0.01)$	$R_0 = 0.25 \pm 0.04\ (p < 0.01)$	$R_0 = 0.27 \pm 0.04\ (p < 0.01)$
	–	$k = 0.11 \pm 0.01\ (p < 0.01)$	$k = 0.13 \pm 0.01\ (p < 0.01)$	$k = 0.12 \pm 0.01\ (p < 0.01)$
R_H	$R_0 = 0.27 \pm 0.02\ (p < 0.01)$	$R_0 = 0.30 \pm 0.05\ (p < 0.01)$	$R_0 = 0.25 \pm 0.03\ (p < 0.01)$	$R_0 = 0.25 \pm 0.04\ (p < 0.01)$
	$k = 0.10 \pm 0.005\ (p < 0.01)$	$k = 0.10 \pm 0.01\ (p < 0.01)$	$k = 0.10 \pm 0.01\ (p < 0.01)$	$k = 0.10 \pm 0.01\ (p < 0.01)$

life cycle. As all successional stages were found within an area of less than 1 ha, soil conditions across all plots were comparable and important growth conditions like climate (Wilfahrt et al., 2021) and N deposition (Damgaard et al., 2017) were similar. With measurements and modelling of C fluxes within the different stand ages (Fig. 1b), it was possible to explore the variations of C fluxes along the chronosequence trial.

4.1. The dynamics of C uptake and loss along the chronosequence

When vegetation was first cut and the necromass removed, the ecosystem C balance was constituted solely by R_H (0.342 kg C m^{-2} year^{-1}), i.e., NEE = R_E = Rs = R_H (Fig. 2a) at the initial stage (year 0) after the clear cut (Aguilos et al., 2014; Howard et al., 2004). Previous investigations identified that these R_H rates were not significantly influenced by the original age of the vegetation before cutting (Kopittke et al., 2012). Rather, the soil microbial C efflux rates were likely controlled by the quantity and quality of available substrate, soil temperature and other conditions controlling decomposer activity (Kirschbaum, 2006). Given the close proximity of the trial plots in the landscape, these conditions were observed to be similar across the different communities (Kopittke et al., 2012). One to two years after the vegetation had been cut and *Calluna* had not yet re-established, a thin layer of cyanobacteria had established (Sass-Gyarmati et al., 2015). This colonization of cryptogams during early successional stages on sandy soils was similar to that observed in other studies in the Netherlands (Sparrius, 2011). Although the data was not reported in this paper, very low rates of P_G were recorded in these recently cut areas, and it is hypothesized that the low rates of P_G are associated with the cryptogam layer.

Twelve years after vegetation cutting, the C uptake reached a peak value of 1.37 kg C m^{-2} y^{-1}. According to previous grassland and forest ecosystem studies (Gao et al., 2021; Uri et al., 2022), although the actual ages of young and middle age vegetation differ a lot due to different life cycle lengths in different ecosystem types, the highest C productivities are normally observed in young or middle-aged communities, where the high C input could more than compensate for the increase C outputs. From our observations, the young *Calluna* plants were highly productive, the aboveground coverage was significantly greater in the young community (95 % ± 2.5) than on the middle community (82 % ± 3.1) or in the old community (74 % ± 4.8) (Kopittke, 2013). The increasing ratio of aboveground *Calluna* biomass in the transition period from young to middle is much higher than in the period from middle to old as well (Kopittke, 2013). Therefore, high productivity (P_G) therefore is clearly the main driver of the young community annual C balance (Fig. 2). This finding is in contrast to the study of Valentini et al. (2000) in a young forest ecosystem, where ecosystem respiration rather than plant photosynthetic uptake was the main determinant of the C balance.

As described by Gimingham (1985), as *Calluna* grows, the annual production is assigned to the wood frame branches with gradually reduced peripheral growth over time, leading the *Calluna* to get top-heavy at middle and old age. Our observed changes in C fluxes over time correlate well with these growth phases of *Calluna* plants. This change is likely connected to the relatively lower number of leaves and higher concentration of woody stems in the middle and old community compared to the young community

(Gimingham, 1985). In addition, we also observed that individual plants had died and created gaps in the vegetation at these growth phases. Similar trends have been reported for grasslands, where grasses gradually decreased their root to shoot ratio with aging (Gao et al., 2021) as well as for forests where decreased C accumulation efficiency was observed in older stands (Kriiska et al., 2019; Uri et al., 2022). However, overall changes in ecosystem C source/sink activity strongly depends on life cycle length of the dominant plant species in the ecosystem. Heathlands have a life cycle of decades, compared to forests of centuries and grassland within or around ten years (Gao et al., 2021; Uri et al., 2022). This indicates that previous comparative studies of C sequestration in *Calluna*-dominated and grass-dominated communities could be strongly biased because the age of the *Calluna* and grass communities are usually not considered (Quin et al., 2015).

4.2. Underlying C flux components

P_G provides the substrate for both plant and microbial respiration and is always tightly coupled with R_E in terrestrial ecosystems, however, how tightly R_E is coupled directly and indirectly to P_G is still debated (DeLucia et al., 2007). Nonetheless, it is generally agreed that R_E can constitute >50 % of P_G and plays an important role in the terrestrial ecosystem C balance (Baldocchi et al., 2015; Jia et al., 2020). Our results showed that the ratio of R_E to P_G varied from 0.73 (young) to 1.49 (middle) and 1.17 (old), and consequently were highly influenced by the vegetation age. As reported by Valentini et al. (2000), plant respiration exerts a strong control over the retention of C in ecosystems. However, the specific fractions of R_H, R_{aa} and R_{ba} to R_E were rarely investigated and reported in previous studies (Jia et al., 2020; Uri et al., 2022). Through measuring the respiration components, we found that the relation between C balance and age after cutting is mainly dominated by fluxes mediated by plants (Fig. 3), in which the autotrophic respiration decreased ((R_{aa} + R_{ba})/R_E) from 65 % over 53 % to 48 %. According to our result, we can see that $R_{aa} > R_{ba}$ in the young community when P_G is at its maximum (Fig. 2a), which suggests that the younger vegetation age has the highest plant-mediated activity and indicates that the biomass investment into aboveground material might be higher than belowground. As P_G declined in the old community, both R_{aa} and R_{ba} decreased by about 50 % as well from young to the old community. This finding is consistent with Gimingham (1985), who labelled the old communities the 'degenerate' phase, where plant appearance is characterized by central branches of *Calluna* dying out leaving only a peripheral ring of living shoots to maintain a feeble photosynthetic activity.

Over one life cycle, changes in R_H rates were small, which is different from what has been observed for forest ecosystems, where both amount of litterfall and the total organic C stock often increase with stand age (Peltoniemi et al., 2004), leading to higher R_H over time (Wiseman and Seiler, 2004). Compared to forest ecosystems, the *Calluna* litter production as well as the production of root exudates are smaller and the decomposition rate of shrublands is therefore much lower than in forests (Petraglia et al., 2019). But still, an increasing ratio of R_H/R_E was observed as the vegetation aged (Fig. 3), which coincided with decreasing autotrophic respiration. As stated also by Kirschbaum (2006), microbial decomposition is

governed by available substrate, while soil temperature and other climatic conditions exert additional control over the decomposer activity. Across the chronosequence, the soil C stocks in the organic layer at our site are quite stable (Kopittke et al., 2012), supporting the observed stable R_H rates over time (Fig. 2a). However, in the current study, we found that R_S rates changed significantly with community age. Our results therefore align well with Goulden et al. (2011), who reported that changes in R_S rates over time were strongly driven by the variations in R_{ba}. However, in contrast to previous forest ecosystem studies, that showed increasing R_S rates after vegetation cut and at the mature stage but decreased rates in middle age (Uri et al., 2022; Wiseman and Seiler, 2004), our results showed that R_S rates keep decreasing after peaking at the young age stage (Fig. S3).

4.3. Annual and cumulative C balance variations and compensation point

The annual carbon balance loess curve was fitted using the compartment C fluxes (Fig. 2a), which indicated that the curvature of the annual C balance (Fig. 2c) was determined by the measurement time points of young, middle and old communities, respectively (12, 19 and 28 years). Because no data on CO_2 exchange of the ecosystem and the atmosphere was available between years 0 and 12 of the study, based on the data alone, we cannot determine if the time of maximum C uptake capacity for the ecosystem may have taken place before year 12. However, the long-term development of the aboveground biomass of *Calluna* at our site (Kopittke, 2013), was in good accordance with the development phases proposed by Gimingham (1985), who suggested that the *Calluna* pioneer period is around 10 years, followed by a building period from 10 to 15 years and then a maturation period from 15 to 25 years after cutting. During the pioneer period, *Calluna* is characterized by rapid change and high turnover, while the building period is recognized as a time of increased stability and species diversity of the ecosystem. Therefore, it is likely that stable and maximum gross photosynthesis rates would be observed during the building period (10–15 years) rather than during the pioneer period.

The ecosystem C compensation point refers to the time after disturbance that starts to act as a carbon sink (Aguilos et al., 2014; Kowalski et al., 2004). However, the estimated C compensation point varies massively in space and across different ecosystem types due to the omnipresent natural heterogeneity of different landscapes (Aguilos et al., 2014; Clark et al., 2004; Law et al., 2001). In our study, C accumulated in the *Calluna* (leaves, stems and roots) and moss biomass up to twelve years after vegetation cutting. The plants were highly active in C uptake (P_G) and C loss through R_{ba} and R_{aa} (Fig. 2a). As a result, the compensation point was reached in the fourth year after the vegetation cut disturbance (Fig. 2b), which is much shorter than the 7 to 20 years observed for forest ecosystems (Howard et al., 2004; Uri et al., 2022), yet also consistent with the differences of life span between forests and shrubland species.

Nineteen years after vegetation cutting (middle community), the *Calluna* had passed its peak standing biomass, and the rate of both C uptake and C loss decreased (Figs. 2a, S1). There was no significant difference in C uptake and C efflux between the middle and the old *Calluna* community, but the annual C balance in the middle community (0.218 kg C m^{-2} year^{-1}) was higher than in the old community (0.089 kg C m^{-2} year^{-1}; Fig. 2b), which is consistent with previous studies reporting that P_G and C accumulation efficiency decrease in the old community (Goulden et al., 2011; Kriiska et al., 2019). In conclusion, due to the much shorter life span of the *Calluna* heathlands than forests, it takes the heathland about 28 years before the cumulative C balance approaches zero again in the last part of its life cycle.

5. Conclusions

Our current study provides novel insights into the annual and cumulative ecosystem C dynamics and balance over the entire life cycle of the *Calluna* shrubland/heathland, which has been underrepresented in the literature compared to e.g., forest ecosystems. The ecosystem C balance was highly non-linear across a three-decade timescale, exhibiting a sinusoidal-like curvature between C sink/source strength and time after cutting. The C compensation point was observed at the age of four years, while it took seven years before the cumulative C loss in the period after cutting had been compensated by an equal amount of C uptake. C payback from the ecosystem to the atmosphere started from the age of 16 years. This information may be used directly for optimizing vegetation management practices for maximal ecosystem C uptake capacity. Our findings highlight the need to take vegetation age into account in dynamic ecosystem models and particularly when using observations for projecting ecosystem C balance and feedback to climate change. The importance of vegetation age further highlights the need for long-term observations for validating the dynamic ecosystem models and to increase our understanding of the complex nature of C fluxes in these ecosystems that are subject to disturbances and human activities, particularly in the face of global climate change.

CRediT authorship contribution statement

Qiaoyan Li: Conceptualization, final data analysis, investigation and visualization, writing draft and editing.

Klaus Steenberg Larsen: Conceptualization, final data analysis, writing review and editing.

Gillian Kopittke: Field investigation, methodology, initial data analysis, writing review and editing.

Emiel van Loon: Methodology, initial data analysis, writing review and editing.

Albert Tietema: Funding acquisition, field investigation, methodology, initial data analysis, writing review and editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The present work has not been submitted elsewhere for publication, in whole or in part, and all the authors listed have approved the submission of the manuscript.

There is no interest conflict regarding this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162658.

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