Carbon cycling and productivity in boreal continuous-cover forestry

- Evaluating different CCF systems against rotation-forestry in boreal Sweden

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Carbon cycling and productivity in boreal continuous-cover forestry- Evaluating different CCF systems against rotation-forestry in boreal Sweden

Kolomsättning och produktivitet i hyggesfritt skogsbruk– en jämförelse mellan olika hyggesfria skogsbrukssystem och trakthyggesbruk i Sveriges boreala skogar

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Abstract

In boreal Sweden, continuous-cover forestry (CCF) is increasingly considered as an alternative method to rotation forestry (RF), but it remains unclear how different CCF systems vary in plant carbon inputs, soil carbon losses and carbon pools. This thesis compared four CCF systems near Vindeln: Åheden and Kulbäcksliden checkerboards, Botsmark gap-felling and Botsmark unmanaged forest (set-aside forests stands). The 2025 carbon flux data of litterfall, vascular understory production, soil microclimate, soil heterotrophic respiration (R_h) and mineral-soil organic carbon (SOC) were analyzed, as well as the tree increment data of different availability. Krycklan Catchment Study from 2016–2018 provided regional RF carbon cycle references, and 2025 Sveaskog RF inventory near Vindeln provided the tree increment reference. Modellings were used when the direct measured data were unavailable, hence the annual carbon balance was not the observed net ecosystem production.

Central values of current tree volume increment ranged from 4.85 to 7.64 $m^3sk\ ha^{-1}\ yr^{-1}$ among the four study systems. Tree litterfall in harvested gaps was 19.9–89.4% lower than that in retained forest, whereas understory vascular plants did not show consistent aboveground net primary production (ANNP) compensation with this reduced C input. Heterotrophic Respiration (R_h) increased non-linearly with soil temperature and was proved strongly associated with litterfall supply in Åheden checkerboard (R^2= 0.824, $p<0.01$). In this checkerboard system, gaps were warmer and wetter, yet temperature-standardized R_h at 10°C was 42% lower than that in the forest cells. The 2025 mineral SOC results did not show any gap or forest cell superior mechanisms among all the CCF systems. NEP estimates ranged from 146.7 to 347.0 g C $m^{-2}\ yr^{-1}$, where Botsmark unmanaged forest (347.0 g C $m^{-2}\ yr^{-1}$) and Åheden checkerboard (315.3 g C $m^{-2}\ yr^{-1}$) had the greatest carbon sequestration among all the systems. Tree volume increment estimates of all the four CCF systems fell within the range of 2025 regional Sveaskog RF P10–P90 (3.26–8.29 $m^3sk\ ha^{-1}\ yr^{-1}$), while the carbon increment contained one of the biggest uncertainties in this thesis due to estimated volume-C conversion rate. Krycklan transferred root production, annualized soil respiration, and missing deadwood pools and fluxes (Krycklan deadwood respiration 4.2 g C $m^{-2}\ yr^{-1}$) all increased the uncertainty in final NEP estimates among all the CCF systems. None of the study system could make the measured carbon fluxes all contributing significantly to their own carbon sink strength while maximizing the tree increment. For these CCF rankings, more comparable results were found in the within-system mechanisms than the cross-systems ones. Hence, I recommend we repeated measuring the complete carbon inputs (e.g. tree inventories), heterotrophic carbon losses, and soil carbon pools in more CCF systems with different time intervals (e.g. observation of SOC changes take decades). I also suggest doing direct measurements (pools and fluxes) of regional roots and deadwood, to make carbon balance and productivity contrast of CCF-RF more reliable in Vindeln or other further studies. Researchers can make more rigorous and practical management implications based on these more detailed experiments.
Keywords: boreal forest, continuous-cover forestry, rotation forestry, forest productivity, carbon balance, heterotrophic respiration,

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Abbreviation

Abbreviation	Description
ANPP	Aboveground net primary production
BNPP	Belowground net primary production
C_B*	Annual carbon balance including modelled components
CAI	Current annual increment
CCF	Continuous-cover forestry
CI	Confidence interval
CO_2	Carbon dioxide
GIS	Geographic information system
ICOS	Integrated Carbon Observation System
IQR	Interquartile range
MAE	Mean absolute error
MAI	Mean annual increment
NEP	Net ecosystem production
NPP	Net primary production
NPP*	Model-completed NPP
PV	Annual percentage volume increment
Q^2	Leave-one-unit-out predictive coefficient
R_h,dw	Heterotrophic respiration from dead wood
R_h,soil	Root-exclusion soil heterotrophic respiration
RMSE	Root mean squared error
SOC	Soil organic carbon

Unit	Meaning
°C	Temperature
K	Lloyd–Taylor activation parameter
cm; cm^3	Sampling depth and soil-core volume
m; m^2	Length and sampled area
$m^3\ m^{-3}$	Volumetric water content
µmol $CO_2\ m^{-2}\ s^{-1}$	Chamber-measured CO_2 concentration
g C $m^{-2}\ yr^{-1}$	Annual carbon input, production, respiration or balance
Mg C ha^{-1}	Mineral-soil SOC stock
$m^2\ ha^{-1}$	Basal area
m^3sk ha^{-1}	Standing stem volume over bark
m^3sk $ha^{-1}\ yr^{-1}$	Current or mean annual volume increment
ha; yr; d; %	Hectare, year, day and percentage

1. Introduction

1.1 Boreal forestry background

Boreal forests account for more than 30% of the global forest carbon stock and contribute substantially to the terrestrial carbon sink. (Yang et al., 2023). Forest management changes the amount of carbon retained in living vegetation. And they also change the pathways plant carbon entering and being decomposed in soils. Evaluating forest carbon cycling therefore requires not only the information of plant biomass, but also carbon input, carbon losses and carbon fluxes (Campioli et al., 2016).

Forestry in boreal Sweden has relied on the rotation system (RF) for more than 100 years. It usually involves clear-cutting followed by multiple measures such as regeneration, stand tending, thinning, and finally harvest (Lundmark et al., 2013). However, drastic changes in canopy cover, stand age structure, and habitat conditions may happen (Kuuluvainen et al., 2012). Alternatively, continuous-cover forestry (CCF) aims to retaining living trees through selective cutting, small-scale clear cuttings, or other spatially structured harvesting methods (Pommerening & Murphy, 2004). However, the effectiveness of CCF depends on multi factors, such as the retained productive stand structure, the gap size and layout, tree species, site productivity, harvesting intervals, and the success rate of tree regeneration (Lundqvist, 2017). For example, the retained tree canopy cover can mitigate environmental fluctuations and maintain structural continuity (Ekholm et al., 2023). Gap-based CCF includes checkerboard (harvested cells alternate with retained forest cells) and gap felling (separate openings are created within the retained forest) systems (Borgstrand, 2014; Goude et al., 2022). Swedish growth models still have low validation in uneven-aged stand structures compared to traditional even-aged stands. Therefore, it remains uncertain whether CCF in boreal Sweden can maintain tree current increment compared with RF, while strengthening other extra advantages (e.g. forest carbon sequestration) (Grzeszkiewicz et al., 2025).

Sveaskog is Sweden's largest single forest owner and more than 90% of their forests are dominated by conifers (Sveaskog, 2026b). Among all the productive forests, the tree species composition in 2025 was approximately 64% Scots pine, 27% Norway spruce, and 9% broadleaved trees (Sveaskog, 2026b). Approximately 27% of forest land is currently assigned for natural succession or conservation management, and excluded from traditional RF management (Sveaskog, 2026b). Additionally, about 16% of their land is not subject to forest management, including open mires, rocky ground, and alpine land (Sveaskog, 2026b). Sustainable tree growth (both ecological and financial) and carbon outcomes are parts of Sveaskog's current four main strategic targets in 2025 (forest growth, climate benefit, biodiversity and ecosystem services, and sustainable financial returns) (Sveaskog, 2026a). For forest owners such as Sveaskog, therefore sometimes it is necessary to maintain acceptable current growth rate, while balancing soil carbon inputs, carbon pools and carbon loss.

And for evaluating the carbon cycle and productivity goals for forest companies, all the variables of carbon fluxes and pools within the CCF and RF systems should be measured and analyzed. Then we can find out which regional data must be monitored before the management decision of tree increment and carbon balance is scaled up in the future.

1.2 Forest carbon-cycle components

The forest carbon balance can be expressed as the difference between annual net primary production (NPP) and heterotrophic respiration (R_h) (Campioli et al., 2016). NPP includes production of trees and understory vegetation above (ANNP) and below ground (BNNP). When microorganisms and other decomposers break down soil organic matter and dead wood, the carbon they released is R_h. Positive net ecosystem production (NEP) indicates that annual biological production exceeds these heterotrophic losses (Peichl et al., 2023). In boreal Sweden, RF remains important carbon sinks. Peichl et al. (2023) found the carbon sink recovered within the first decade in the 50 Krycklan RF stands. The variation in net ecosystem production (NEP) was more explained by tree (net primary production) NPP than heterotrophic respiration (R_h). NEP has a peak in middle-aged stands and then declined with age increases. But the 13 old stands (131–211 years) in the study of Peichl et al. (2023) still had a positive mean NEP of 98 g C m^{-2} yr^{-1}, about 56% of the 13 middle-aged stands (61–78 years, mean 174 g C m^{-2} yr^{-1}). To maintain and enhance forest carbon sequestration, CCF is proposed as an alternative management approach. It maintains continuous tree cover and carbon above and belowground in tree biomass and understory vegetation. CCF is also proved to sustain soil carbon through litterfall, deadwood and fine-root inputs by changing the decomposition process and soil respiration (Sobuj, Peichl & Pommerening, 2026). However, long-term CCF-RF contrast experiments remain limited. They require measuring carbon pools and fluxes together in different CCF and RF systems.

Atmospheric CO_2 can be transferred to forest ecosystem through photosynthesis. And this carbon input goes into aboveground tree growth, understory production and belowground biomass. And part of this production will transfer to aboveground litter (through litterfall) and belowground litter (through root turnover). In boreal Scots pine forests, belowground litter contributed 23–37% of total litter C input, and understory roots accounted for 18–41% of belowground production (Ding et al., 2021). Roth et al. (2023) found a 92.5 g C m^{-2} yr^{-1} of annual litterfall inputs in unmanaged forest, 63.2 in retention forests, 51.2 in gaps and only 9.2 in clear-cuts. And forest harvesting can change all the above and belowground litter input into the soil. Therefore, differences in retained forest structure can not only alter the current tree productivity but also change the amount of carbon returned to the ecosystem through understory, litterfall and roots. Nevertheless, how different CCF structures redistribute these carbon inputs remains poorly quantified in boreal Sweden, also their comparisons to nearby RF systems.

The amount of retained canopy can control the current tree growth, light, litterfall and the physical environment near the soil surface (Zhang, Sjögren & Jönsson, 2024). When we remove the canopy, the soil temperature increases due to more solar radiation (De Frenne et al., 2019). But this could also reduce interception and transpiration of the plants. The gaps may become wetter or drier when drainage, topography and soil condition change (De Frenne et al., 2021). As a main term of carbon-loss in this thesis, soil heterotrophic respiration (R_h) has a nonlinear response to temperature (Lloyd & Taylor, 1994), while moisture and carbon supply can alter this response (Davidson, Belk & Boone, 1998). Krycklan studies show that apparent temperature sensitivity varies among managed boreal stands (Guo et al., 2024). Litter inputs can also alter soil respiration (Chen & Chen, 2018), but the field responses can delay (Bréchet et al., 2018). Soil organic carbon (SOC) is a stock accumulated through past carbon inputs, decomposition and transport, not an annual sequestration rate (Mayer et al., 2020). Short-term gap effects can therefore be weak, depth dependent, and sometimes have opposite results among sites (Tong et al., 2024). Compared with RF, how different CCF structures (checkerboard, gap felling) alter carbon inputs and near-surface microclimate remain unclear, and how these changes result in detectable R_h carbon loss and SOC carbon pools also required regional experiment.

The remaining knowledge gap is how these components vary across different CCF structures near Vindeln. Existing studies only document differences in litter inputs and soil carbon, and substantial variation in respiration across the nearby RF due to management (Roth et al., 2023; Guo et al., 2024). But they did not establish any significant results for the checkerboard and gap-felling systems examined in this thesis. The CCF-RF comparison therefore proceeds from plant carbon production and litter carbon inputs (RQ1), to soil heterotrophic carbon loss and its microclimate context (RQ2), and finally to carbon fluxes and stocks in the RF context (RQ3).

1.3 Aim and research questions

The aim was to determine how four CCF systems near Vindeln vary in their carbon inputs, soil carbon losses, mineral-soil carbon stocks and net ecosystem production (NEP). The C cycle components of these CCF systems were further compared with rotation forests (RF) in the nearby Krycklan catchment and from regional records provided by Sveaskog. The four CCF sites comprised two checkerboard, one gap felling and one set-aside (i.e. unmanaged) forest stands as study systems.
The three research questions are:
RQ1: How do carbon input fluxes vary among different CCFs?

Hypotheses: (1) Tree litterfall would be lower in gaps because of canopy removal. (2) Understory ANPP would be higher in due to increased light. And this increase would compensate for the reduced tree litterfall C input. (3) CCF systems with more retained trees would have higher whole-system increment.

RQ2: How do respiration fluxes vary among different CCFs?

Hypotheses: (1) Gaps soils would be warmer and wetter than the retained forest because reduced canopy would result in more solar radiation, less plant interception and transpiration. (2) R_h would increase non-linearly with soil temperature. (3) At 10 °C, gap R_h would be lower than retained forest because litterfall input reduced (4) Higher tree litterfall C would be related to higher R_h response at standardized temperature at 10 °C, but the strength of this relationship would vary among the CCF systems.

RQ3: How do carbon cycle components (fluxes and stocks) compare between CCF and nearby RF (Krycklan and Sveaskog)?

Hypotheses: (1) Mineral-soil SOC between CCF and Krycklan RF would show fewer observable differences than annual carbon-input fluxes, because of different long-term site history and soil conditions. (2) Åheden checkerboard would have more SOC stock than other CCF systems while it has the biggest harvest gaps (3) Differences in annual carbon balance between CCF and Krycklan RF would not consistently follow differences in NPP, because differences in R_h could offset higher production. (4) Current annual tree-volume increment of the four CCF systems would fall within the regional range of Sveaskog RF stands.

2. Materials and methods

2.1 Study design and datasets description

All continuous-cover forestry (CCF) systems in this study were located near Vindeln (Figure 1a) in Västerbotten County, northern Sweden. They were all boreal forests and dominated by Scots pine (Pinus sylvestris), Norway spruce (Picea abies) and birch (Betula spp.). The Åheden CCF system (in trial 25343) contained a checkerboard harvest system with four retained forest cells (F1-F4) and five harvested cells (G1-G5), each approximately 50 × 50 m. The Kulbäcksliden CCF site (in trial 7201) contained twenty 30 × 45 m checkerboard cells, among which cell K2, K3 and K6 were classified as forest, while cell K1, K4 and K5 were gaps. Both checkerboards were Scots pine dominated, with mixed pine-spruce regeneration in gaps. The Botsmark gap-felling CCF system contained eight circular gaps with a 10 m radius. Four gaps (all trees were harvested and removed) and four gaps with retained dead wood (10%) together consist of approximately 20% of the whole site area. The separate Botsmark unmanaged forest comprised nine forest sampling plots (Figure 1d–g; Table 1).

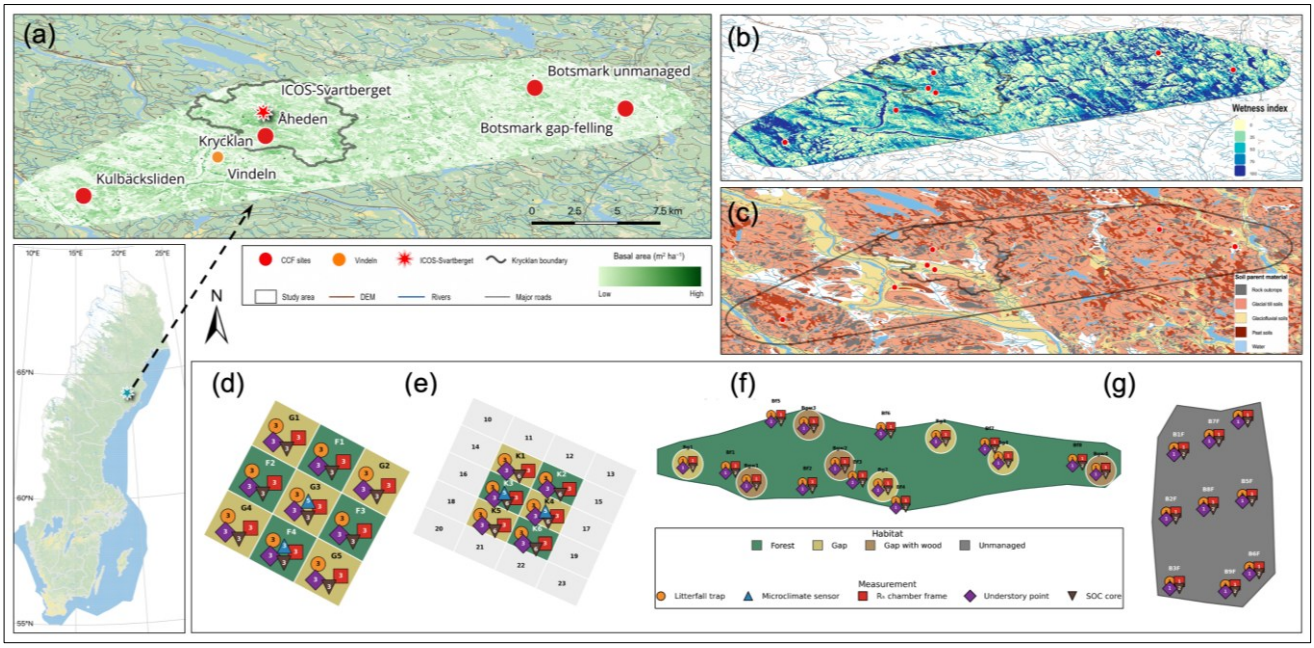


Figure 1. Study area, environmental condition and CCF design of this thesis (a) Location of the study area in Vindeln, Sweden; location of Åheden, Kulbäcksliden, Botsmark gap-felling, Botsmark unmanaged, Vindeln, the ICOS-Svartberget station and the Krycklan catchment. The mapped background shows basal area (m² ha⁻¹; light to dark green; Skogsstyrelsen, 2026), DEM contour, rivers and major roads from Topografi 50 Nedladdning, vektor (Lantmäteriet, 2026). Red circles indicate the four CCF study systems, the orange circle indicates Vindeln, the star indicates ICOS-Svartberget, and the dark outline shows the Krycklan catchment, obtained from DEIMS-SDR (2026). The Sweden inset uses administrative boundaries from Statistics Sweden (SCB, 2026). (b) Spatial variation in the wetness index in the same study-area, expressed on the 0–100 scale (Ågren et al., 2021; https://www.slu.se/mfk) (c) Simplified soil parent material

within the study area, from the Jordarter 1:25 000–1:100 000 grundlager dataset of the Geological Survey of Sweden (SGU, 2026) (d) Åheden checkerboard sampling layout. (e) Kulbäcksliden sampling layout. (f) Botsmark gap-felling sampling layout, including forest, gap and gap-with-wood plots. (g) Botsmark unmanaged forest layout. All the numbers in the CCF systems means different sampling locations in one habitat (forest or gap cells), they are not the times of repeated samplings.

The mapped soil moisture index and soil parent material classes in Figure 1b, c provided environmental context and were not included as explanatory variables in the analyses. Between-system contrasts may therefore indicate pre-existing environmental and management differences.
The CCF systems were compared with two rotation-forestry (RF) references from local and regional scale data. Krycklan provided a comprehensive local reference of carbon-cycle processes, whereas the Sveaskog inventory provided a regional operational reference for standing volume and current tree-volume increment in the area around Vindeln. The study area assumed from the given Sveaskog dataset (with both conservation area and RF productive stands) in the GIS map (Figure 1) was not spatially matched with the real location, because the dataset was anonymized for confidentiality. Its location and range were based on my assumption (to cover all the other locations in this thesis while keeping a good shape) for easier spatial comparison with the CCF systems and Krycklan study, but the magnitude of the area remain similar (approximately 42,000ha).

2.1.1 CCF data availability

The tree-increment data of CCF had different availability. And all the other CCF related data were collected from the 2025 measurements from a current SLU PhD project. The data were from different systems with cells (gap and forest habitats), plots (smaller sample area within different habitats) or clusters (for the same data from repeated measurements or time). Each one had their individual field unit. And for the samplings, there were different categories such as tree growth, CO_2 chamber measurements, soil temperature, soil moisture, litterfall, understory biomass, soil cores, area and date. The repeated measurements were not independent management replicates (Table 1).

Table 1. Data availability for the four CCF systems used in this thesis. The table lists the spatial units and measurement years for tree inventory, litterfall, vascular understory ANPP, microclimate, root-exclusion soil heterotrophic respiration (R_h), and mineral-soil SOC, and identifies unavailable measurements.

System	Data Availability for Thesis
Åheden checkerboard	4 forest cells and 5 gap cells; 1,331 numbered trees in four 0.125-ha forest subplot in 2022; 27 litterfall traps 2025; 27 understory datasets 2025; data from eight microclimate sensors 2025 (3 forest, 5 gap); 27 root-exclusion CO_2 chamber measurements in 2025 (12 forest, 15 gap); 27 complete two-layer SOC (10-30cm) cores 2025

System	Data Availability for Thesis
Kulbäcksliden checkerboard	Six cells (3 forest, 3 gap); repeated forest-ward inventory (2005-2022); 18 litterfall traps 2025 (including reconstructed collections); 36 understory datasets 2025; data from ten microclimate sensors 2025 (5 forest, 5 gap); 18 root-exclusion CO_2 chamber measurements in 2025 (9 forest, 9 gap); 36 complete two-layer SOC (10-30cm) cores 2025
Botsmark gap-felling	16 sampling plots (8 forest, 4 gap, 4 gap with wood); 16 litterfall traps 2025; 32 understory datasets 2025; 16 root-exclusion CO_2 chamber measurements in 2025 (8 forest, 8 gaps); 32 complete two-layer SOC (10-30cm) cores 2025. No repeated tree inventory and no comparable continuous microclimate series were available
Botsmark unmanaged	9 forest plots; 9 litterfall traps in 2025; 18 understory datasets 2025; 9 root-exclusion CO_2 chamber measurements in 2025; 18 complete two-layer SOC (10-30cm) cores 2025. No repeated tree inventory or microclimate data was available

When the data was unavailable or incomplete, the results were estimated from modelling or hybrid methods (measurements and modelling combined).

Soil microclimate

For the data required to analyze the soil microclimate among the CCF sites, Aheden (3 forest, 5 gap) and Kulbacksilden (5 forest, 5 gap) had complete soil temperature and soil moisture with detailed sensor locations (Figure 1d, e; Table 1). Soil microclimate at Åheden and Kulbäcksliden was monitored with TOMST TMS dataloggers (TOMST s.r.o., Czech Republic; Wild et al., 2019). Data for the two CCF systems in Botsmark was not available. Each logger contains three temperature sensors and one soil-moisture sensor. In this study, soil temperature was taken from at 10 cm depth (°C), and soil moisture was expressed as calibrated volumetric water content (VWC) at both sites. Temperature resolution was 0.0625 °C with ±0.5 °C accuracy. Soil moisture was measured from the soil dielectric response and converted to VWC, (VWC= Vwater/Vsoil). Measurements were recorded every 15 min (96 observations d^{-1}). For 2 July–31 October 2025, daily temperature was summarized as the mean and VWC as the median for each logger before forest–gap comparisons.

Soil heterotrophic respiration

CO_2 concentration was measured bi-weekly using chamber measurements from trenched/root-exclusion plots (1× 1m). Then after data processing, the result of this part would be heterotrophic soil respiration (R_h), which could also be regarded as total soil respiration (excluded the plant autotrophic respiration). The chamber measurements comprised 12 field visits from May to October 2025. The sampled CCF layout comprised 27 Åheden plots, 18 Kulbäcksliden plots, 16 Botsmark gap-felling plots and 9 Botsmark unmanaged plots. Before each measurement, the vegetation within the 1× 1m plots were cut again. The opaque flux chamber was placed on a 50×50 cm stainless-steel frame (30-40 cm depth

into soil, with fitted edge to the chamber), then it was connected to a VAISALA CO_2 analyzer (Figure 2b, c) to get the CO_2 concentration values. This frame was used to cut lateral root ingrowth around the subplot. All the living ground vegetation was removed, and the lateral roots was cut and took away from the site 1 year before the measurement to minimize the uncertainty caused by changing soil condition. Some water was poured around the frame-chamber connected surface to make air-insulation of the chamber. The above methods follow the same root-exclusion principle used in the Krycklan carbon flux measurement design (Martínez-García et al. 2022). A 48.5 × 48.5 × 30 cm chamber were used for all the CCF systems.

Each chamber closure lasted for 3 min, with CO_2 concentration recorded every 5 s. The concentration was recorded by VAISALA instrument. And then the CO_2 flux was calculated in MATLAB by fitting a linear regression of concentration-time to obtain dC/dt (ppm s^{-1}). The concentration slope was converted to molar CO_2 accumulation with the ideal gas law (PV = nRT). By using the known chamber volume and the measured air temperature, the µmol CO_2 m^{-2} s^{-1} raw flux data was then obtained. Soil temperature at 10 cm was measured during each chamber measurement.

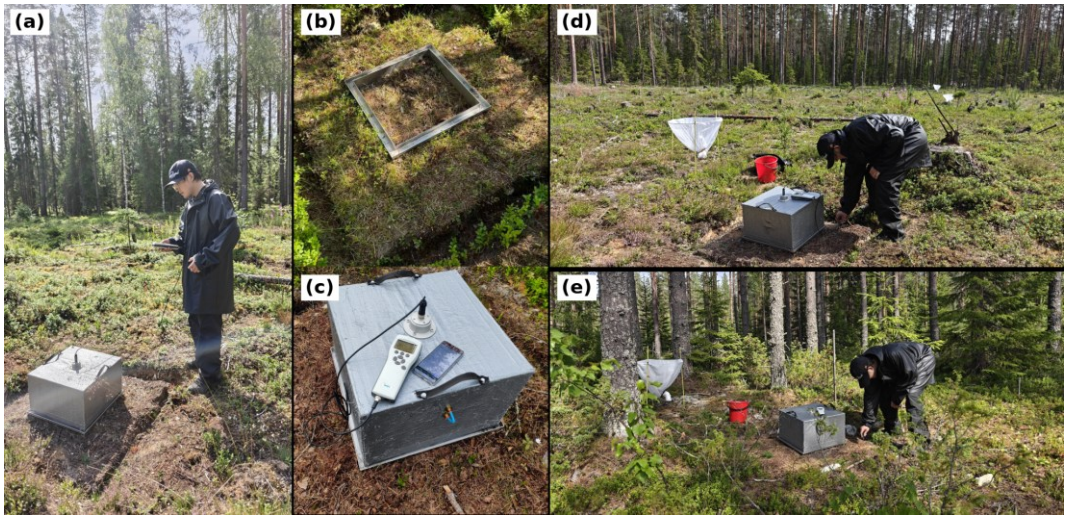


Figure 2. Field sampling and soil-respiration chamber measurements (a) A chamber measurement in Åheden retained forest. (b) A trenching frame before measurement. (c) The opaque chamber and VAISALA measurement equipment. (d) Chamber measurements in Åheden gap. (e) Chamber measurements in Kulbäcksliden gap.

Tree increment

For the tree-growth data sets among the four study systems, they have different data availability. Kulbäcksliden had complete and repeated inventory data for three retained forest wards K2, K3 and K6 from 2005-2022. Åheden had a complete 2021 standing volume and a detailed 2022 numbered-tree inventory until August 2022, but no available remeasurement of the same retained trees afterwards. Botsmark did not have available repeated tree inventory (Table 1). And a current SLU employee will measure it by the end of 2026.

Litterfall

The litterfall was collected using circular net traps in September and November 2025. The traps were placed in the beginning of the 2025, and the sum of the two collection weight was the annual litterfall mass. After collection, all litter samples were dried in the oven at 60 °C for 48 h and then the dry mass was weighed. For each trap, they were separated as needles, leaves, twigs, debris and cones for measuring. Total dry tree-litter mass was the sum of these measured components. The litterfall processing method was the same as Krycklan Catchment Study (Martínez-García et al., 2022). The measured opening diameter of the CCF litter traps was D = 0.318310 m. The corresponding trap area was 0.07958m^2. These values were used to convert annual trap mass to ground-area litterfall. And a carbon fraction $f_C = 0.50$ was used to convert dry litter mass to carbon fluxes (C per m^2 per year). The Kulbäcksliden annual litterfall estimates included a reconstructed of the missing September collections (from the November data). While this did not determine the direction of any potential litterfall mass bias in forest-gap cells, because it eliminated habitat and trap specific variations, as well as the seasonal condition changes of litterfall.

Understory ANPP

Understory vegetation was sampled in 25 × 25 cm quadrats (0.0625 m^2). The green current-year shrubs and older brown, rough and thicker woody parts were separated. The current-year growth was estimated after the weight of the fresh new plants were dried by oven. Samples were dried at 60 °C for 24–48 h, or until fully dry before weighing. The separated fractions (0.50 for shrubs and 0.47 for graminoids) were used in the annual shrub-production calculation below. For graminoids, the whole harvested aboveground mass was the current-year production because the leaves die off over winter every year. Mosses and lichens were not sampled and were excluded from vascular understory ANPP. The same procedure was used across the four study systems. The mass of debris was excluded from living vascular ANPP. The sample values were aggregated to plot or cell clusters before the run of 5,000-iteration bootstrap in R studio.

Soil carbon stock

The 2025 soil carbon Stock (SOC) was sampled with a 5 cm diameter corer. The dataset contained 27, 36, 32 and 18 soil sampling units for Åheden, Kulbäcksliden, Botsmark gap-felling and Botsmark unmanaged, respectively. After removing the organic layer, the soil cores from 10–20 and 20–30 cm depth were kept and analyzed. Samples were dried at 60 °C for 48 h or until the soil was fully dry and then they were sieved through a 2 mm sieve. Stones/coarse fragments and fine roots were separated from the fine-earth fraction. Stone volume was measured from the equal volume of water. Soil C and N concentrations were measured by an elemental analyzer (isotope-ratio mass spectrometer EA-IRMS; Delta V, Thermo Fisher Scientific, Bremen, Germany) in the SLU laboratory. Before the analysis, the samples were dried by oven at 70 °C for at least 18 h. This dried mass was then combusted to CO_2 and N_2 in the elemental analyzer. Then the measured C,N concentration, C/N ratio were simply analyzed in this thesis. The results were corrected for instrumental drift and non-

linearity of the sample size. The measured C concentration was used for the primary SOC calculation. N concentration and C:N were variables found not addressing the research questions in the thesis.

2.1.2 RF reference datasets

Krycklan RF

Data from the 50 permanent RF stands in the Krycklan Catchment Study were used as references for plant carbon production, litterfall, soil heterotrophic respiration and carbon balance (Peichl et al., 2023). Stand means from 2016–2018 were used for the overall carbon comparison. Because of the drought year 2018, the 2016–2017 and 2018 respiration references were displayed separately (Martínez-García et al., 2022). Vascular understory ANPP was taken from the 2017 measurements. The 2017 mineral-soil stock data at the common 10–20 cm depth was used for SOC comparison, available for 44 stands. Data collection and the original carbon-accounting methods were described in those publications. These records were used as simple regional references, not the treatment matched controls.

Sveaskog RF

Sveaskog provides anonymized operational RF records for the Vindeln region in 2025. These data were used only for standing volume and current increment constraints. The original dataset contained 4,297 forest compartments within approximately 42,363 ha area including 7.5% conservation and other non-production areas. After filtering them to production-forest (PG) compartments there were 2,504 compartments remained. For the RF used for regional comparison in this thesis, compartments were further required to contain at least 70% Scots pine plus Norway spruce of all the tree species, leaving 2,249 compartments representing 23,082.2 ha of productive forest. Of these compartments, 1,694 were classified as Scots pine dominated, 190 as Norway spruce dominated and 365 as mixed conifer. A species share of at least 70% defined dominance. This number was from Goude et al. (2022), though they used this for filtering basal area, the writer transferred it to dominant species filtering in this thesis. The full set of 2,249 compartments was used for the regional current-increment comparison with the CCF systems in the results part. But only the pine and spruce dominated compartments were used to fit the species-specific age curve (Figure 3). Carbon-cycle variables such as R_h, litterfall and SOC were not available from Sveaskog. The complete species-by-age summary of the Sveaskog data was retained in Appendix 2 (including pine, spruce, birch and contorta). Lodgepole pine was introduced on a large scale in Sweden during the 1970s and 1980s mainly to increase wood supply (Elfving et al., 2001; Jacobson & Hannerz, 2020).

2.2 Data analysis

2.2.1 Tree carbon increment

Tree volume and carbon increment estimates from the four study systems (Åheden, Kulbäcksliden, Botsmark gap-felling and Botsmark unmanaged) were compared. These estimates were then compared with the regional Sveaskog RF increment distribution.

The latest current volume increments (2022) from Kulbäcksliden forest wards K2, K3 and K6 were averaged, and then scaled by the 0.50 forest fraction:

$$I_{\mathrm{KBL}} = 0.50 \times \frac{I_{K2} + I_{K3} + I_{K6}}{3},$$

where I_{K2}, I_{K3} and I_{K6} are the inventory-derived current volume increments of the three retained forest wards.
To sum up, the tree increment of Kulbäcksliden was based on the 2022 inventory. For Åheden, the primary estimate was modelled with the existing inventory and the individual-tree basal-area-increment model described in Matsala et al. (2026). Åheden's primary model, coefficients and sensitivity scenarios, together with the alternative BEY2 calculation and inputs, were documented in Appendix 1 (Tables A1.1–A1.2). For Botsmark increment (and another abandoned Åheden estimate), means of the 50 Krycklan stand data from 2016–2018 (Peichl et al., 2023) were used to fit a litterfall–aboveground tree-C increment model. The fitted relationship of litterfall–C increment approach was described in Matala et al. (2008). In this thesis, the function was:
$\hat{C}_{tree,site}$ = 36.6645 + 1.06731 L_{tree}, with L_{tree} in g C m^{-2} yr^{-1} (R^2 = 0.310; leave-one-stand-out Q^2 = 0.264).

The predicted forest-habitat tree-C increment was multiplied by 0.80 (gap/system area ratio) for Botsmark gap-felling, 1.00 for Botsmark unmanaged, 4/9 for the abandoned Åheden estimate. For the volume increment (Table 3), these whole-system C estimates were divided by 28.2809. It was a number calculated from 100 × median(AGCtree/Vol) across the same 50 Krycklan stand means. This gave volume-equivalent increments of 6.77 and 6.73 $m^3sk\ ha^{-1}\ yr^{-1}$ in Botsmark gap felling and Botsmark unmanaged forests respectively. Their carbon increment predicted values were 191.4 and 190.4 g C $m^{-2}\ yr^{-1}$. Both exceeded the Krycklan RF litterfall- C increment modelling range. The related uncertainty was estimated using 5,000 joint bootstrap draws of Krycklan stands and target litterfall clusters. For Åheden, Kulbäcksliden and Sveaskog, basic wood density × a carbon fraction of 0.50 was used to calculate volume- stem C increments. The factors were 0.220, 0.175 and 0.240 Mg C m^{-3} for Scots pine, Norway spruce and silver birch, respectively. Thus, 1 $m^3sk\ ha^{-1}\ yr^{-1}$ equals 22.0, 17.5 and 24.0 g C $m^{-2}\ yr^{-1}$ for C increment of different species (Rytter et al., 2016; Thomas & Martin, 2012). The Scots-pine factor was used for Åheden and Kulbäcksliden. Sveaskog factors were weighted by real species composition.
The unit m^3sk includes stem bark and top but excludes branches and foliage. After applying the basic wood density to this volume, the stem-C increment could be estimated. But it did not represent the complete aboveground tree-C increment or tree NPP (Rytter et al., 2016; Thomas & Martin, 2012). Volume–carbon

conversion options and their limitations were summarized in Appendix 2 (Table A2).
Volume increment in the harvested gaps was assumed to be zero. Tree regeneration growth was not included. And vascular understory ANPP was quantified separately. Area fractions based on the forest-gap ratio were used while processing data of tree increment and litterfall: weights of 4/9 for forest and 5/9 for gap in Åheden, 0.5 and 0.5 for Kulbäcksliden, 0.8 forest, 0.1 gap and 0.1 gap with wood for Botsmark gap-felling, and 1.0 for Botsmark unmanaged forest.

Sveaskog age-dependent references

The 2025 standing volume and current increment of the Sveaskog RF was firstly fitted to the Chapman–Richards standing-volume curve for a smooth age-dependent stock curve (Pienaar & Turnbull, 1973).

$V(t) = A\left(1 - exp(-kt)\right)^{m}$ for standing volume and
$I(a) = Amke^{-ka}(1 - e^{-ka})^{m-1}$ for current increment

Where $I(a)$ is fitted current increment ($m^3sk\ ha^{-1}\ yr^{-1}$), a is stand age (yr), and A, k and m are curve parameters estimated independently for pine- and spruce-dominated RF stands.

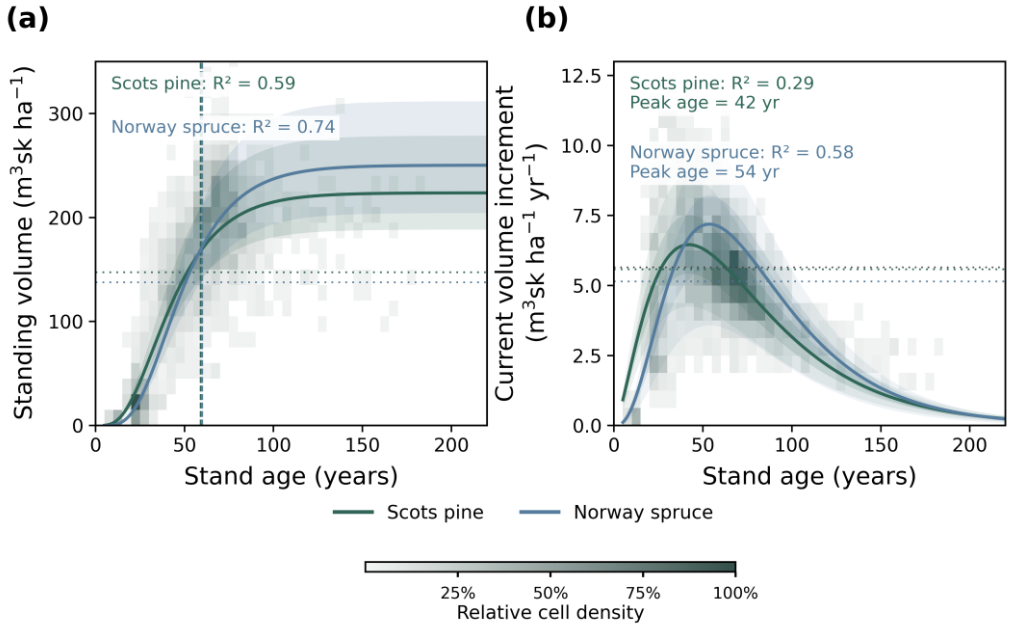


Figure 3. Chapman–Richards curve fitted standing volume and current volume increment in the filtered 2025 Sveaskog RF inventory (a) Standing volume-age curve for Scots pine dominant and Spruce dominant compartment; Ribbons are interquartile range and horizontal lines are mean standing volume (147.4 $m^3sk\ ha^{-1}$ for Scots-pine-dominated and 137.8 $m^3sk\ ha^{-1}$ for Norway-spruce-dominated compartments) (b) current volume increment-age curves. Shading is the number of compartments in each cell divided by the number in the densest cell (relative cell density), not forestry stocking density. Vertical dashed lines show median stand ages (54 years for Scots pine and 58 years for Norway spruce). In (b), darker ribbons are IQR and lighter ribbons are the 10th-90th percentile. Dotted horizontal lines are CAI means for the whole RF (5.65 $m^3sk\ ha^{-1}\ yr^{-1}$), Scots-pine-dominated compartments (5.58), and Norway-spruce-dominated compartments (5.14).

In (Figure 3), Square cells were 5-year age intervals against 15.1 $m^3sk\ ha^{-1}$ for standing volume and 0.62 $m^3sk\ ha^{-1}\ yr^{-1}$ for current increment. All the data was filled into the cells, the densest cell was scaled to 100% relative bin density (age19-24, n = 59 for standing volume and age 62-67, n = 46 for current increment). There were more compartments in the darker cells. The asymptote line in Figure 3 (a) was the modelled maximum standing volume of pine and spruce dominant forest could reach in the lifetime, approximately 224 $m^3sk\ ha^{-1}$ (R2 =0.59) and 250 $m^3sk\ ha^{-1}$(R2=0.74), respectively.

2.2.2 Carbon inputs: tree litterfall and understory ANPP

t = trap. D = 0.318 m

Then for the litterfall carbon per ground area

$$L_C = \frac{m_d}{A_t} f_C$$

m_d = dry litter mass; f_C = 0.50 in the main calculation.

Shrub current-year ANPP was calculated from the separated shrub fractions as:

$$\phi_s = \frac{\Delta l_c}{\Delta l_c + \Delta l_p}$$

$$\mathrm{ANPP}_{s,C} = \frac{m_s \phi_s}{A_q} f_C$$

: s = shrub; c = current-year shoot increment; p = previous-year increment; q = quadrat.

Graminoid ANPP was calculated from total graminoid dry mass as:

$$\mathrm{ANPP}_{g,C} = \frac{0.47 m_g}{0.0625}$$

g = graminoid.

Tree litterfall C and vascular understory ANPP data in each gap or forest habitat were summarized into clusters. The whole system estimate for each CCF were calculated from habitat means and fixed area fractions. And gap-minus-forest differences were also calculated within each site. The CCF results were compared descriptively with the Krycklan RF reference. Uncertainty estimation was described in Section 2.3. The relationship between litterfall C and R_h was analyzed in the soil heterotrophic respiration analysis (Section 2.2.4).
The proportions of litterfall component were shown in (Appendix 2, Figure A1).

2.2.3 Soil microclimate

From the 2 July to 31 October 2025 microclimate data. A logger-day was kept when at least 72 of 96 expected observations were available.

To compare the microclimate difference in forest and gap cells between the two CCF checkerboards (gap effects) in each paired monitoring day d, the value of gap habitat median minus the forest habitat median were presented. The monthly

values in the seasonal figure were calculated from the medians of these daily contrast values. Positive values indicated a warmer or wetter gap. All the dates were categorized by the results of ΔT and ΔVWC. This could define whether gaps were warmer–wetter, warmer–drier, cooler–wetter or cooler–drier than the forest cells. This was a descriptive within-site analysis (the two checkerboards), not a regional test of a universal CCF microclimate effect (Wild et al., 2019).

$\Delta T_d = \tilde{T}_{gap,d} - \tilde{T}_{forest,d}$

$\Delta VWC_d = \tilde{VWC}_{gap,d} - \tilde{VWC}_{forest,d}$

where d was a paired monitoring day; T̃_gap,d and T̃_forest,d were the daily habitat-median soil temperatures (°C); ṼWC_gap,d and ṼWC_forest,d were the daily habitat-median volumetric water contents ($m^3\ m^{-3}$); ΔT_d was the gap-minus-forest temperature contrast (°C); and ΔVWC_d was the corresponding moisture contrast ($m^3\ m^{-3}$).

2.2.4 Carbon loss: soil heterotrophic respiration

Before analysing the data, the data quality was filtered and then the chamber measured soil temperature was transformed to a continuous half-hourly temperature series in 2025 whole year. For the filtering, concentration data of $CO_2 \leq 4$ μmol CO_2 m^{-2} s^{-1} was selected, and then the record would only be accepted when both conditions were met:

$$R^2 \geq 0.80 \quad \text{and} \quad RMSE \leq 0.70.$$

The selected ICOS soil-temperature series was used to calibrate the local chamber at Ts_{10} scale (soil temperature at 10cm depth). The calibration standard was from Peichl et al. (2026) ICOS Svartberget meteorological dataset (The nearest ICOS station to all the study systems in Svartberget).

$$T_{local,g}(t) = a_g + b_g T_{ICOS,g}(t)$$

Where $T_{local,g}(t)$ was reconstructed local soil temperature (°C) for site × habitat group g at half-hour t, $T_{ICOS,g}(t)$ was the selected ICOS temperature, and a_g and b_g were the fitted calibration intercept and slope. All the calculated local values were then used in the Lloyd–Taylor response function (Lloyd & Taylor, 1994). This equation was needed because the chamber measurements provided intermittent R_h values (every 2 weeks measurements in the growing season), but the complete respiration-time data in 2025 was required to calculate the annual carbon loss (Lloyd & Taylor, 1994). The R^2 value of soil temperature- time curves (figures did not shown in this thesis) ranged from 0.717 (Åheden gaps) to 0.928 (Botsmark gap felling forest) in 7 habitats, representing how much the local ICOS soil temperature could adjust the measured ones.

$$R_h(T) = R_{10} \exp\left\{E_0 \left[\frac{1}{10 - T_0} - \frac{1}{T - T_0}\right]\right\}$$

where $R_h(T)$ was root-exclusion soil heterotrophic respiration (μmol CO_2 m^{-2} s^{-1}) at soil temperature T (°C); R_{10} was fitted R_h at 10 °C in the same flux unit; E_0 was the fitted temperature-sensitivity parameter (K); and $T_0 = -46.02$ °C was fixed.

This value was subsequently used for the half-hourly 2025 R_h reconstruction and the annual R_h term later subtracted from NPP^*. Half-hourly CO_2 fluxes were converted to annual carbon mass as

$$R_{H,a} = \sum_{h=1}^{17520} R_H\,(T_h) \times 12.0107 \times 10^{-6} \times 1800$$

a = annual. The constants were the molar mass of C, µmol-to-mol conversion and seconds per half hour.

The factor 12.0107×10^{-6} converted µmol CO_2 to g C and 1800 was the number of seconds in one half-hour, so the annual result was g C m^{-2} yr^{-1}. A 1000-iteration plot-cluster bootstrap was used in R studio to refit the chamber temperature response and annual carbon mass reconstruction for uncertainty check. These daily model values were not independent treatment replicates. Habitat-level annual R_h was converted to different CCF management system means using the fixed design fractions: Åheden = 4/9 forest + 5/9 gap; Kulbäcksliden = 0.50 forest + 0.50 gap; Botsmark gap-felling = 0.80 forest + 0.10 ordinary gap + 0.10 gap-with-wood; Botsmark unmanaged = 1.00 forest.
To examine if litterfall was correlated with R_h, the Lloyd–Taylor model was used to estimate respiration at a standard soil temperature of 10 °C (R_{10}). This standardized the modelled temperature response, but did not remove the soil moisture effects, substrate differences or parameter uncertainty (Lloyd & Taylor, 1994; Hursh et al., 2017).
For each CCF systems, the linear regression model in R studio was used to fit the log-transformed cluster litterfall values (Figure 8, Appendix 3, Table A5), because in each forest or gap, there were more than 1 litterfall traps:
$Log\ (R_{10}) = \beta_0 + \beta_1\ log\ (Litterfall\ C\ mass) + \varepsilon$

Each point represented a matched cluster. The R^2 values labeled in each treatment indicated the proportion of variation in log(R_{10}) for that observation explained by log(litterfall carbon mass). The p-value was used to test whether this result is significant. Regression coefficients, diagnostics and R_{10} changes for 25%, 50% and 100% higher litterfall manipulating were modelled in Appendix 3 (Table A5).

2.2.5 Carbon pools: mineral-soil SOC

Mineral-soil SOC was calculated separately for the 10–20 and 20–30 cm layers. Fine-earth bulk density was calculated from oven-dry sieved soil mass divided by the core volume minus the measured stone volume.

$$\mathrm{SOC}_j = C_j \rho_{b,j} z_j \left(1 - \frac{V_{s,j}}{V_c}\right)$$

For each 10 cm layer, SOC stock was calculated from the measured C mass fraction, fine-earth bulk density, layer thickness and the fine-earth volume fraction, $1 - V_s/Vc$. And the results were converted to Mg C ha^{-1}. Fine roots and coarse fragments were excluded from the reported mineral-soil C stock. The cluster medians were used for habitat summaries and gap: forest ratios.
The SOC comparison with Krycklan was restricted to the common 10–20 cm mineral-soil depth because they have different data availability (0-20cm for

Krycklan and 10-30cm for this thesis). *j = layer; C = carbon mass fraction; ρ_b = bulk density; z = thickness; V_s = stone volume; V_c = core volume.*

2.2.6 Regional reference comparison and annual carbon balance

Regional comparison

The Sveaskog data was used to compare current tree-volume increment of the study systems. And Krycklan provided references for litterfall, understory ANPP, soil heterotrophic respiration, mineral-soil SOC and annual carbon balance.

Annual carbon balance

$NEP = NPP_{\text{tree}} + NPP_{\text{understory}} - R_{\text{H,soil}} - R_{\text{H,dw}}$

The method followed Peichl et.al. (2023) in the Krycklan studies.

NEP > 0 indicated a net carbon sink, and NEP < 0 indicated a net carbon source.

Cwood was the tree carbon increment described in Section 2.2.1. Tree litterfall and understory ANPP were added to calculate the aboveground production, then Krycklan ratios were used to estimate belowground production.

$ANPP_{\text{above}}^{*} = C_{\text{wood}} + L_{\text{tree}} + ANPP_{\text{u}}$

For coarse roots, the median ratio of coarse root production to aboveground tree-C increment across the 50 Krycklan stand were used for 2016–2018 mean was used: 0.2876, with a P10–P90 range of 0.2260–0.3586. For total fine-root production, the median 2018 ratio to aboveground NPP was 0.3859, with a P10–P90 range of 0.1677–1.0154. These were ratios calculated from the reference dataset, not root measurements at the CCF sites (Peichl et al., 2023).

$BNPP_{\text{cr}}^{*} = C_{\text{wood}} \times r_{\text{cr}}$

$BNPP_{\text{fr}}^{*} = ANPP_{\text{above}}^{*} \times r_{\text{fr}}$

$NPP* = C_{\text{wood}} + L_{\text{tree}} + ANPP_{\text{u}} + BNPP_{\text{cr}}^{*} + BNPP_{\text{fr}}^{*}$

$C_B{}^{*} = NPP* - R_{\text{H,soil}}$

The asterisk indicated that the carbon balance including modelled components and should not be described as observed NEP. The estimation used Krycklan transferred root-production ratios and did not include site-specific deadwood respiration or mortality.
Deadwood respiration was included only as a sensitivity analysis, by subtracting the regional Krycklan median of approximately 4.2 g C m^{-2} yr^{-1}. It was not included in the primary CCF values in (Figure 10; Figure 12).

2.3 Uncertainty estimates

According to different data availability, the uncertainty estimate methods used in this thesis varied. When there were subsamples and repeated measurements, they were firstly aggregated to the individual plot, cell or cluster. The measured clusters were repeatedly resampled to examine how much the estimated result

could vary with the available sample., and the 2.5th–97.5th percentiles of these repeated estimates were reported as the 95% bootstrap interval (Efron & Tibshirani, 1993). Arithmetic means were used when habitat values combined into a whole-system estimate. And medians were used to describe habitat and regional distributions because they were less affected by outliers. For microclimate, daily soil temperature was the mean for each logger, whereas VWC was the median. The forest–gap contrasts were calculated from daily habitat medians values (Table 2).

Table 2. Summary of uncertainty and sensitivity methods used in this thesis.

Uncertainty Component	**Sensitivity**
Tree increment	Åheden: the central 80% across 18 model-input scenarios, it was not a confidence interval. Kulbäcksliden: mean of the three retained forest cells. Botsmark: 5,000 joint bootstrap draws of Krycklan stands and target litterfall clusters.
Litterfall and understory ANPP	Cluster values were used in habitats and area-weighted whole-system means. Sampling uncertainty used 5,000 cluster-bootstrap iterations. Forest–Gap differences were adjusted by permutation tests (p-values) for multiple comparisons using the Holm method (Holm, 1979).
Soil microclimate	Monthly forest–gap values were medians of daily contrasts, with IQR (Interquartile range P25-P75) showing daily variability;
Soil heterotrophic respiration	Annual (R_h) uncertainty used 1,000 cluster-bootstrap iterations, repeating temperature calibration, Lloyd–Taylor fitting and annual integration. (R^2), RMSE and extrapolation fractions were reported as model diagnostics.
Mineral-soil SOC	Core values were averaged to management clusters; habitat SOC and Gap:Forest ratios were based on cluster medians. Their 95% intervals were estimated with 7,000 cluster-bootstrap iterations.
Carbon Balance*	Krycklan median root ratios (coarse root = 0.288; fine root = 0.386) were used for the central point of Carbon Balance, and their P10–P90 ranges were used for sensitivity check. Similarly, lower and upper estimates of all the component were combined to show the possible balance range, it was not a 95% CI. A fixed Krycklan median deadwood respiration of about 4.2 g C m^{-2} yr^{-1} was subtracted separately as an additional sensitivity check of the CCF systems.
RF references	Krycklan distributions were summarized mainly by median, IQR and P10–P90. Sveaskog data were calculated by productive forest area means first, and then the median, IQR and P10-P90 were used for regional reference. These were data range, not confident interval

The coefficient of variation (CV = 100 × SD/mean) was used to check spatial variability, because it allowed variables with different units and magnitudes to be compared on the same percentage scale. It was useful to compare the mean and SE between the cells and whole system of the CCF stands. Spatial variability and standard errors were reported for all CCF systems (Appendix 3, Tables A3–A4). Annual R_h values in those tables were sensitivity estimates, not the final Lloyd–Taylor annual flux.

3. Results

3.1 Carbon input fluxes among CCF systems

Among all the CCF systems, the tree litterfall was consistently lower in harvested habitats (gaps), whereas vascular understory ANPP did not show a common compensatory response to this carbon input reduction due to litterfall. Estimate of current tree increment differed among systems, but this was not attributed to CCF design because the estimates came from different evidence classes. And each CCF treatment was represented by only one system.

Table 3. Forest and whole-system carbon-input components and tree increment.

Site	Method	Forest (%)	Litterfall C		Volume increment		Understory ANPP		Note
			Forest	System	Forest	System	Forest	System	
Åheden	Structural				6.39	2.84			Elfving (2010)
Åheden	Litterfall transfer				8.84	3.93			Krycklan
Åheden	Primary (used)	44.4	199.7	100.5	17.19	7.64	108.4	128.1	Matsala et al. (2026)
Kulbäcksliden	Observed	50.0	155.8	117.6	9.70	4.85	176.9	165.4	Repeated inventory
Botsmark gap-felling	Litterfall model	80.0	189.8	175.8	8.46	6.77	122.0	123.6	Krycklan transfer
Botsmark unmanaged	Litterfall model	100.0	144.1	N/A	6.73	N/A	144.2	N/A	Krycklan transfer

Litterfall C and understory ANPP: g C m^{-2} yr^{-1}; volume increment: m^3sk ha^{-1} yr^{-1}. Forest = retained-forest habitat; System = whole-system mean. Only the Åheden primary estimate was used in the CCF comparisons in this thesis. Botsmark increments were modelled estimates, not from inventory measurements.

3.1.1 Tree increment

The 2022 inventory model (Matsala et al., 2026) was selected as the final Åheden tree-increment estimate for the later comparison because it combined the measured data and modelling (Hybrid).

The current stem-volume increment of the four study systems ranged from 4.85 to 7.64 m^3sk ha^{-1} yr^{-1} (Table 3; Figure 11b). Åheden had the highest central value, 7.64 m^3sk ha^{-1} yr^{-1}, calculated from hybrid method, which range was from 5.40 to 10.81 m^3sk ha^{-1} yr^{-1}. It represented 18 different model input scenarios (Appendix 1) and was not a sampling confidence interval. Kulbäcksliden had the lowest central value, 4.85 m^3sk ha^{-1} yr^{-1}, derived from repeated measured inventories. The volume-increment estimates ranged from 4.55 to 5.05 m^3sk ha^{-1} yr^{-1} (Figure 11b).

Botsmark gap-felling and Botsmark unmanaged had modelled volume-equivalent increments of 6.77 and 6.73 m^3sk ha^{-1} yr^{-1} in the whole system. Their 95% joint bootstrap intervals were 5.26–8.51 and 5.30–8.37 m^3sk ha^{-1} yr^{-1} (Figure 11b),

respectively. The tree increment in the harvested gaps were all assumed to be zero (without considering the regeneration), while the litterfall and understory productivity did not.

3.1.2 Litterfall and understory production

Litterfall

Annual tree litterfall C was lower in every harvested habitat than in the corresponding forest habitat (Figure 4c, e). Åheden showed the largest contrast: forest and gap means were 199.7 and 21.1 g C m^{-2} yr^{-1}, with a difference of −178.6 g C m^{-2} yr^{-1}, equivalent to 89.4% of litterfall reduction. Kulbäcksliden forest and gap means were 155.8 and 79.4 g C m^{-2} yr^{-1}, with a difference of −76.4 g C m^{-2} yr^{-1}, or 49.0%.
At Botsmark, forest, normal gap and gap with wood means were 189.8, 152.0 and 86.9 g C m^{-2} yr^{-1} respectively. The normal gap habitat contrast was −37.8 g C m^{-2} yr^{-1} and its 95% interval included zero, whereas the gap with wood habitat contrast was −102.9 g C m^{-2} yr^{-1}, equivalent to a 54.2% litterfall reduction.
After area conversion, the whole-system litterfall C was 100.5 g C m^{-2} yr^{-1} at Åheden, 117.6 at Kulbäcksliden, 175.8 at Botsmark gap-felling and 144.1 in Botsmark unmanaged forest (Table 3; Figure 4d). Their 95% cluster-bootstrap intervals were 83.5–120.0, 84.6–173.1, 150.4–202.4 and 116.3–172.2 g C m^{-2} yr^{-1}, respectively.

Understory ANPP

Vascular understory ANPP did not show a common forest–gap superior value (Figure 4a). The whole-system means were 128.1 g C m^{-2} yr^{-1} at Åheden, 165.4 at Kulbäcksliden, 123.6 at Botsmark gap-felling and 144.2 in Botsmark unmanaged forest (Table 3; Figure 4b). Differences between habitat medians of vascular understory ANPP (gap minus forest) were+27.5 g C m^{-2} yr^{-1} at Åheden, −22.7 at Kulbäcksliden, −1.3 in Botsmark Gap and +16.5 in gap with wood. All their 95% bootstrap interval included zero, and Holm-adjusted permutation p-values ranged from 0.677 to 0.962.

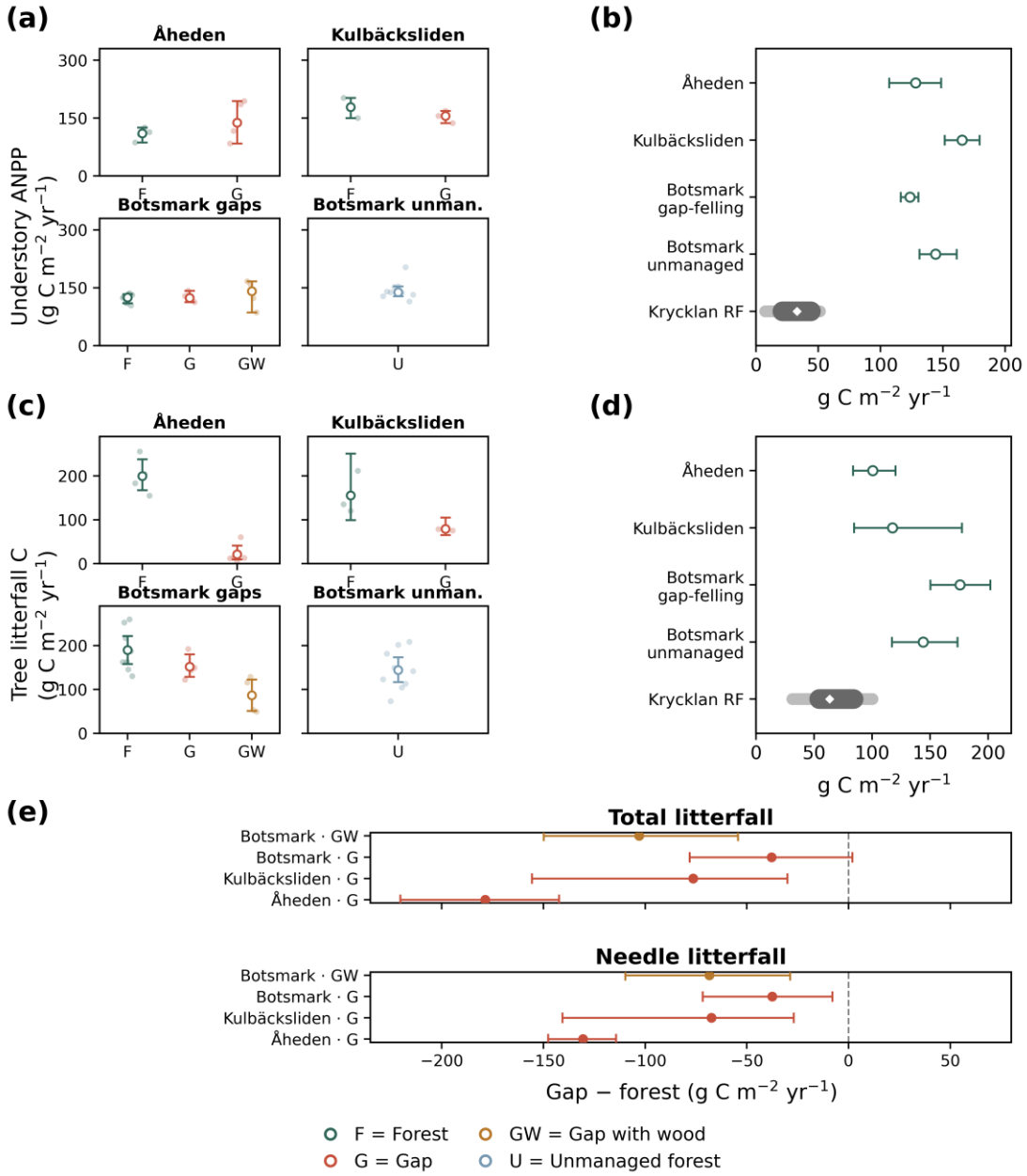


Figure 4. Vascular understory production and annual litterfall in CCF systems and Krycklan RF (a) CCF vascular understory aboveground net primary production (ANPP) by habitat. Translucent points are cluster values; open symbols are habitat medians; vertical bars are 95% cluster-bootstrap intervals for the median. (b) Whole-system understory ANPP. CCF circles are area-weighted arithmetic means of habitat cluster means, with 95% cluster-bootstrap intervals. The Krycklan diamond is the 2017 median across 50 stands; the thick and thin grey bars show the interquartile and 10th–90th percentile ranges. Krycklan understory ANPP is herbs+ grasses+shrubs. (c) CCF annual litterfall C by habitat. Translucent points are cluster means; triangles mark clusters are modelled collection; open circles are habitat means; vertical bars are 95% bootstrap intervals. (d) Whole-system litterfall C, using area-weighted habitat means for CCF and Krycklan. (e) Gap-minus-forest differences in total and needle litterfall C. Dots are differences between habitat means, bars are 95% bootstrap intervals, and the dashed vertical line is zero.

3.2 Soil heterotrophic respiration among CCF systems

The seasonal increase of R_h in the CCF systems was explained by temperature differences, but there was also forest–gap differences. Åheden gaps were warmer and wetter yet had substantially lower R_{10}. And litterfall C was strongly associated with R_{10} within this checkerboard. The microclimate data was unavailable at Botsmark, so that a common moisture–R_h relationship across the study systems could not be evaluated.

3.2.1 Soil microclimate

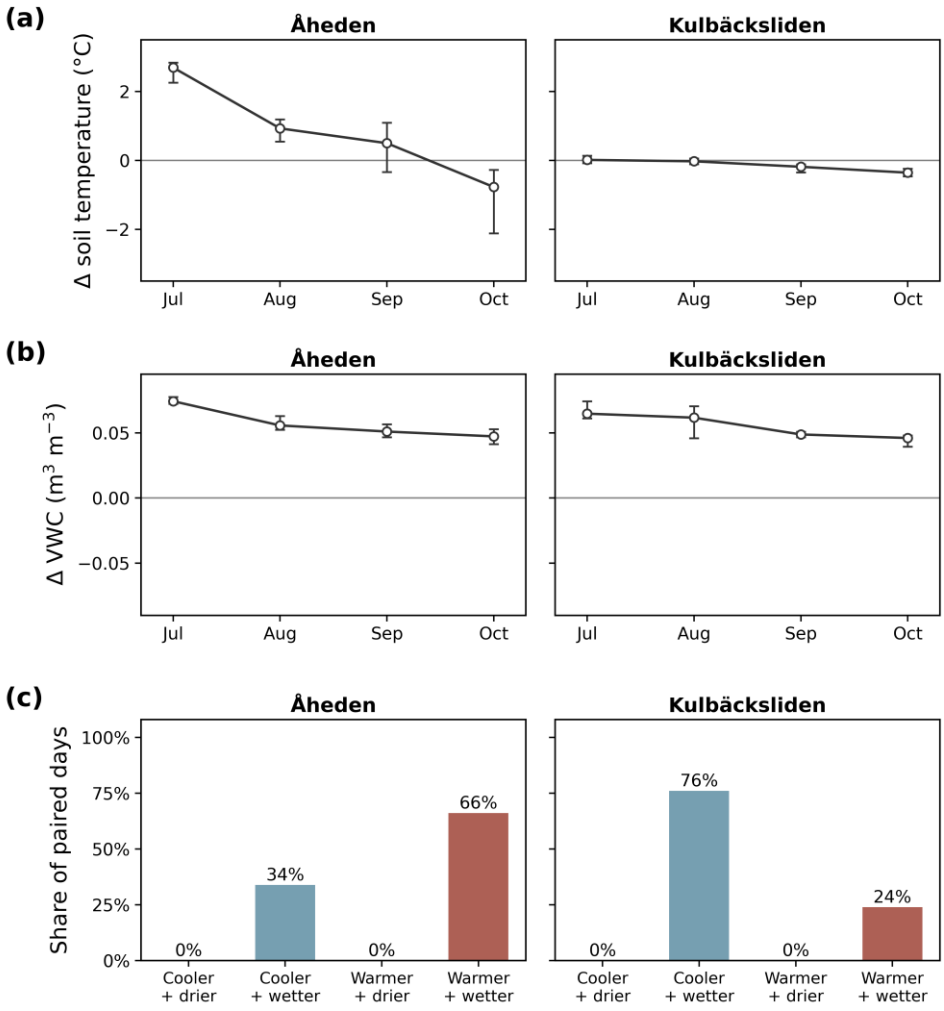


Figure 5. Seasonal soil microclimate contrasts between gaps and retained forest. Monthly gap-minus-forest contrasts are shown for Åheden and Kulbäcksliden from July to October 2025 (a) Soil-temperature contrast at 10 cm depth and (b) volumetric-water-content contrast. Temperature was calculated as daily mean for each logger, water content as a daily median, and habitat values as daily medians. Symbols are monthly medians across paired days, and vertical bars are monthly interquartile ranges; (c) Percentage of the 121 paired days microclimate in the two checkerboards. Positive values indicate warmer or wetter gap soils.

The two monitored checkerboards showed different temperature responses to canopy opening (Figure 5). At Åheden, the monthly median gap-minus-forest temperature contrast was +2.69 °C in July, +0.93 °C in August and +0.50 °C in September, −0.77 °C in October (Figure 5a). At Kulbäcksliden, the corresponding contrasts were +0.01, −0.03, −0.19 and −0.36 °C. Across all 121 paired days in 2025, the median contrast was +0.74 °C at Åheden and −0.12 °C at Kulbäcksliden.

Gap VWC was higher than the forest median on every paired day at both checkerboards. Monthly median gap-minus-forest VWC contrasts declined from +0.074 to +0.047 $m^3\ m^{-3}$ at Åheden and from +0.065 to +0.046 $m^3\ m^{-3}$ at Kulbäcksliden between July and October (Figure 5b). The Åheden gaps had 80 warmer-and-wetter days and 41 cooler-and-wetter days, while the Kulbäcksliden gaps had 29 warmer-and-wetter days and 92 cooler-and-wetter days (Figure 5c).

3.2.2 Carbon loss through soil heterotrophic respiration (R_h)

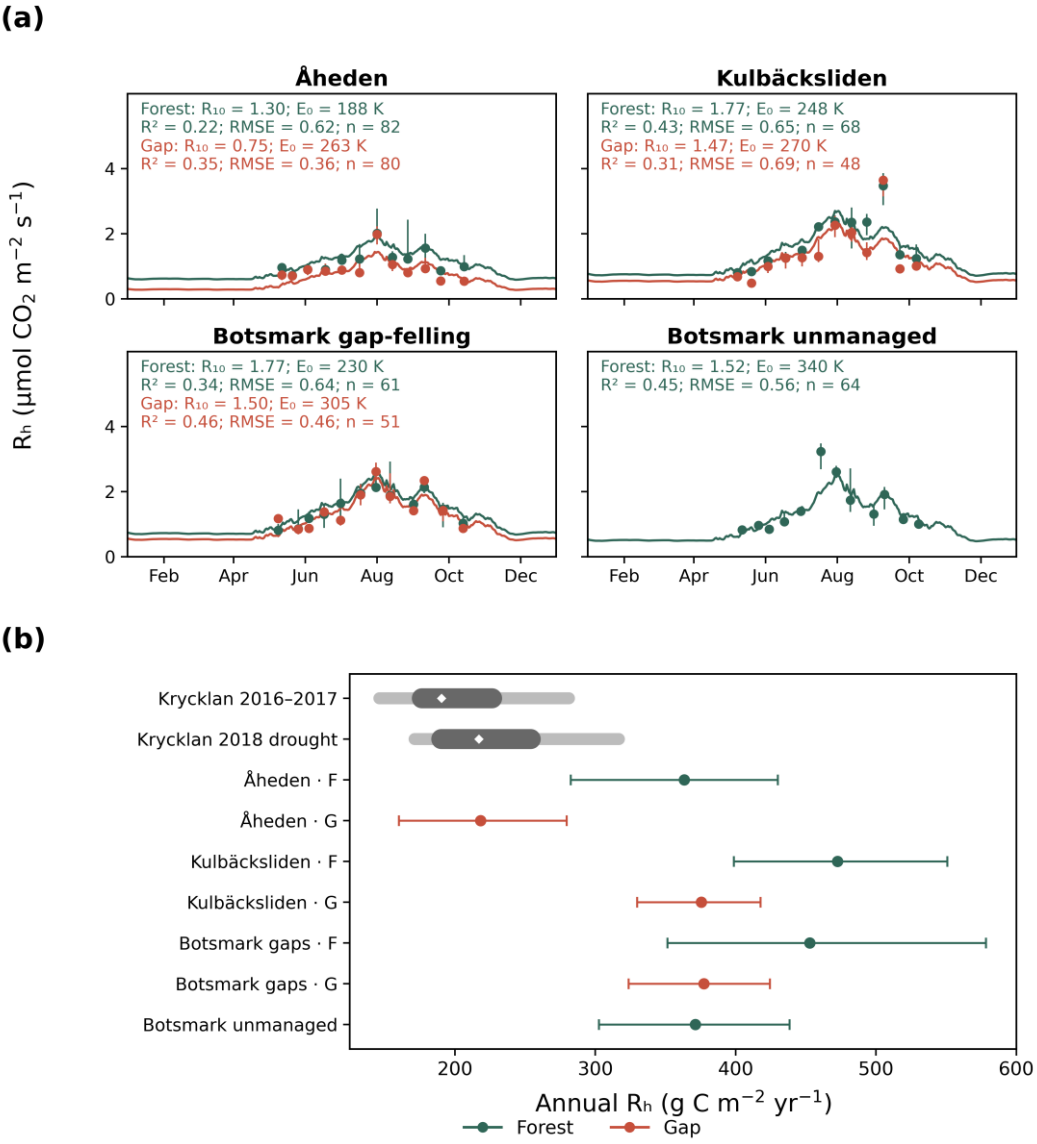


Figure 6. Seasonal reconstruction and annual estimates of soil heterotrophic respiration (R_h) (a) Seasonal R_h patterns for the seven CCF site–habitat groups in 2025. Solid lines show Lloyd–Taylor reconstructions driven by soil temperature measured at 10 cm depth. Open circles represent median chamber measurements for each sampling visit, and vertical bars show the corresponding interquartile ranges. Text within each panel reports R_{10}, defined as the modelled R_h at a reference soil temperature of 10°C, together with the fitted activation parameter E_0, descriptive R^2, RMSE, and the number of chamber observations retained after quality control (n). (b) Annual R_h estimates for the CCF sites and Krycklan rotation-forest reference stands. Filled coloured circles show 2025 Lloyd–Taylor annual estimates obtained by integrating the reconstructed half-hourly fluxes over the year; horizontal black bars show 95% cluster-bootstrap confidence intervals. For Krycklan, diamonds indicate stand-level medians, thick grey bars the interquartile ranges, and thin grey bars the 10th–90th percentile ranges for the 2016–2017 baseline and the 2018 drought year.

Model-assisted annual R_h was 363.3 g C m^{-2} yr^{-1} in Åheden forest and 218.2 in gap; 472.6 and 375.5 at Kulbäcksliden; 452.9 and 377.4 at Botsmark gap-felling; and 371.2 in Botsmark unmanaged forest (Figure 6b). After cell-to-system area conversion, the whole-system annual R_h was 282.7 g C m^{-2} yr^{-1} at Åheden, 424.1 at Kulbäcksliden, 437.8 at Botsmark gap-felling and 371.2 in unmanaged forest (Figure 10a). The highest estimate among all the CCF systems was therefore 54.9% above the lowest. The Krycklan 2016–2017 RF median was 190.4 g C m^{-2} yr^{-1}, with a 10th–90th percentile range of 146.2–281.3. And the 2018 drought-year median was 217.0 (Figure 6b). These RF values were regional references rather than treatment controls.

Across the seven groups, 20.6–34.1% of the Lloyd-Talyor modelled annual R_h was reconstructed at temperatures outside the local chamber range, 31.4–40.6% outside the chamber measurement period, and 11.7–16.1% during winter. The annual values were therefore reported as model-assisted carbon losses, not the direct measurement of 2025 whole year (Section 2.2.4).

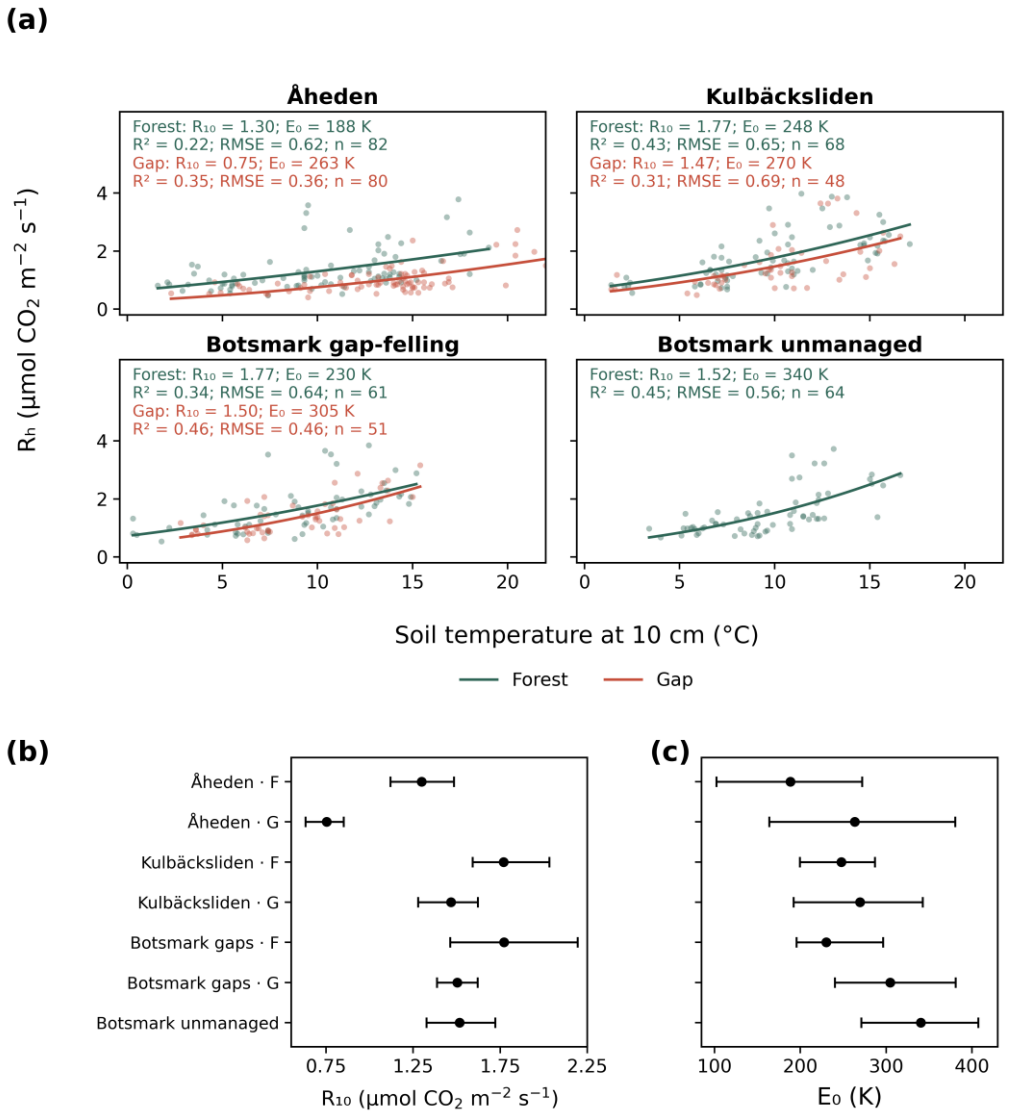


Figure 7. Lloyd-Taylor temperature responses of root-exclusion Rh at 10cm depth of soil in the four CCF systems (a) Chamber measurement and fitted Lloyd–Taylor curves for forest and gap habitats; panel text gives model parameters and diagnostics. (b) Fitted R_{10} and (c) E_0 estimates; points are model estimates and horizontal bars are 95% cluster-bootstrap intervals.

R_h increased non-linearly with local 10-cm soil temperature in all seven site× habitat groups (Figure 7a). R_{10} values of the Lloyd–Taylor fitted curves was 1.300 µmol CO_2 m^{-2} s^{-1} in Åheden forests and 0.754 in gaps; 1.770 and 1.468 in Kulbäcksliden forests and gaps; 1.772 and 1.503 in Botsmark gap-felling forests and all gaps; and 1.517 in Botsmark unmanaged forest. Thus, fitted gap R_{10} was 42.0% lower than forest cells at Åheden, 17.1% lower at Kulbäcksliden and 15.2% lower at Botsmark gap-felling (Figure 7b). Descriptive Lloyd–Taylor R^2 values ranged from 0.218 to 0.458 (Figure 7a).

Litterfall and temperature-standardized R_h

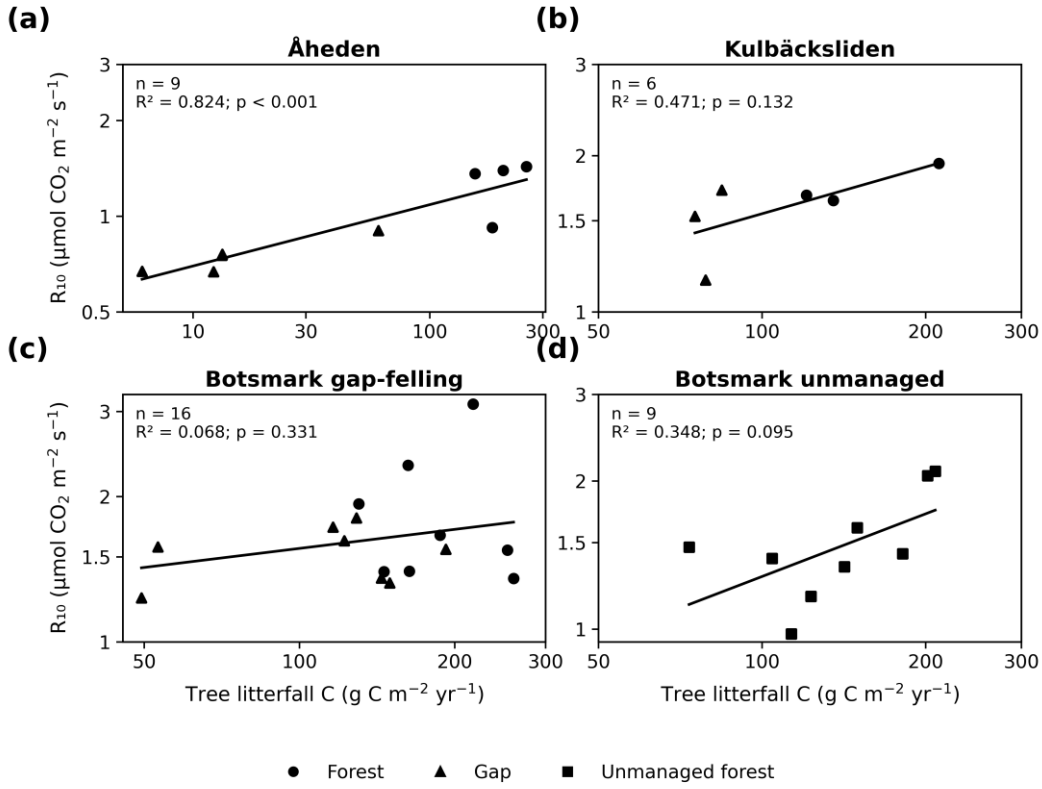


Figure 8. Linear Regression of log (tree litterfall carbon) and log (Rh) at 10℃. Each point is one matched CCF cluster with annual tree litterfall C and heterotrophic-respiration R_{10} estimated from the same sampling unit. Forest, gap, and unmanaged-forest habitats are distinguished by symbol shape. (a) Åheden checkerboard; (b) Kulbäcksliden checkerboard; (c) Botsmark gap-felling; (d) Botsmark unmanaged.

The results in Åheden showed a litterfall–R_h association beyond the normal seasonal temperature response**.** The gaps were typically warmer and wetter than the retained forest cells, but temperature-standardized R_h at 10 °C was much lower. There was a significant correlation between litterfall C and R_{10} ($R^2 = 0.824$, $p < 0.001$; Figure 8a; Table A5).
Kulbäcksliden showed a positive litterfall–R_{10} trend (Figure 8b; Table A5), but the evidence was weaker because the sample had n = 6 and a p-value of 0.132. Botsmark gap-felling had $R^2 = 0.068$ and $p = 0.331$ (Figure 8c; Table A5). These relationships did not establish a common litterfall-R_h effect across all study systems. The results also did not show that microclimate was the dominant driver at Botsmark.

3.3 Carbon-cycle components in comparison with RF

Current mineral-soil SOC stocks did not show any common forest–gap superior in any CCF systems. The modelled annual carbon balance differed among systems, while the central current-increment estimates remained within the broad Sveaskog

RF range. The following comparisons were only descriptive because range of the data, measurement years and evidence classes all differed.

3.3.1 Carbon pools: mineral-soil SOC

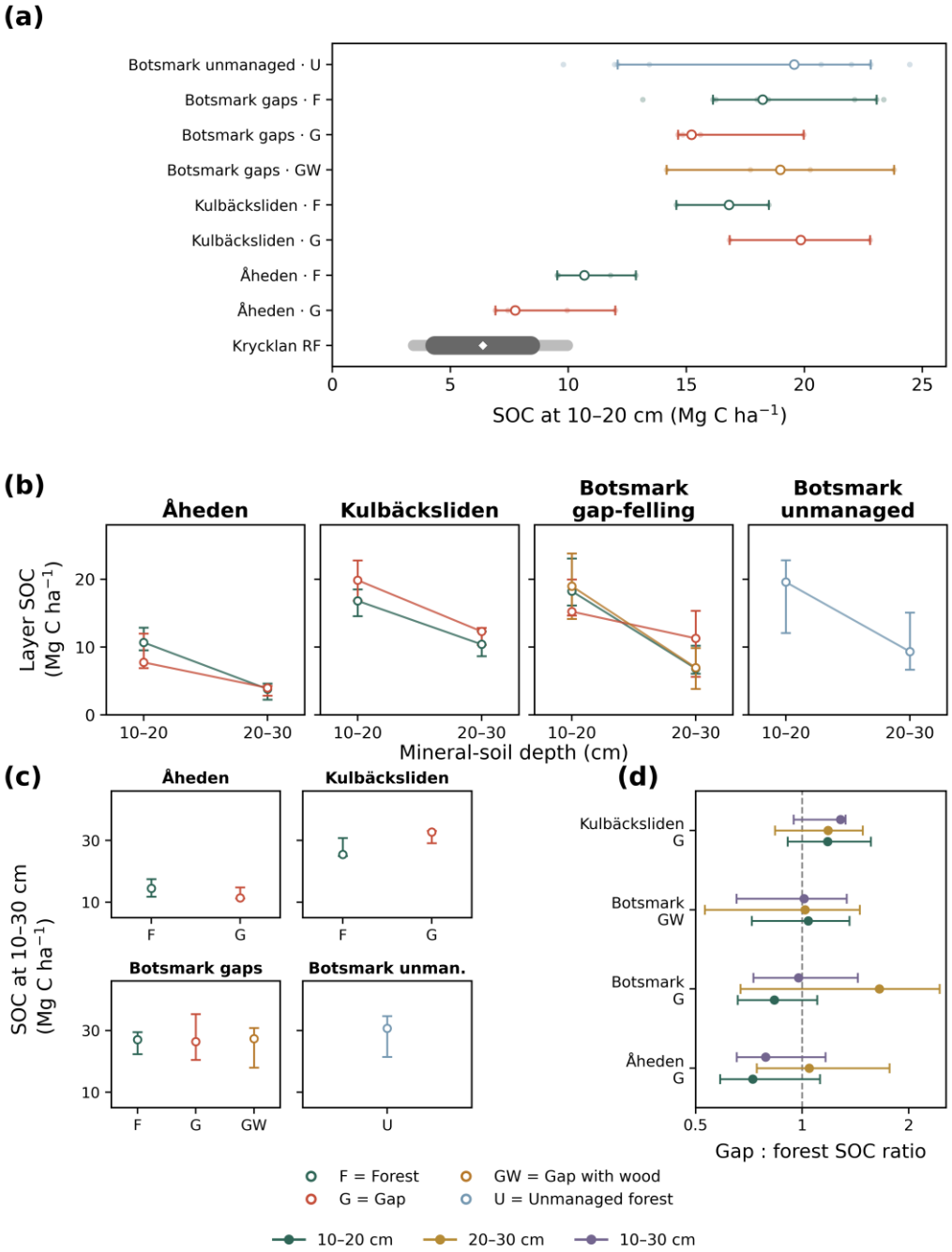


Figure 9. Mineral-soil organic carbon (SOC) in the four CCF systems and Krycklan RF (a) CCF 10–20 cm depth comparison with Krycklan stands. (b) CCF habitat stocks in the sampled 10–20 and 20–30 cm layers.(c) 4 CCF systems stocks in the complete 10-30 cm sampled layers. (d) Gap:Forest ratios for complete 10–30 cm cores; a ratio of 1 indicates equal stocks. Points are cluster medians and bars are 95% cluster-bootstrap intervals.

Mineral-soil SOC did not show a common forest–gap direction (Figure 9). At 10–20 cm depth, median SOC stocks were 10.68 Mg C ha^{-1} in Åheden forest and 7.75 in gap; 16.80 and 19.84 at Kulbäcksliden; 18.23, 15.22 and 18.98 in Botsmark forest, normal gap and gap with wood; and 19.57 in Botsmark unmanaged forest (Figure 9a, b). Complete 10–30 cm SOC medians were 14.49 and 11.43 Mg C ha^{-1} at Åheden, 25.46 and 32.67 at Kulbäcksliden, 27.03, 26.41 and 27.36 in the three Botsmark gap-felling habitats, and 30.66 in unmanaged forest (Figure 9c).

The 10–30 cm gap: forest median ratios were 0.788 at Åheden, 1.283 at Kulbäcksliden, 0.977 in normal Botsmark gap and 1.012 in gap with wood. All 95% cluster-bootstrap interval included 1 (Figure 9d). The Krycklan 2017 10–20 cm reference data had a median of 6.38 Mg C ha^{-1} and a 10th–90th percentile range of 3.44–9.97 across 44 stands (Figure 9a). This was only a regional reference, not a matched treatment control.

3.3.2 Carbon fluxes and annual carbon balance

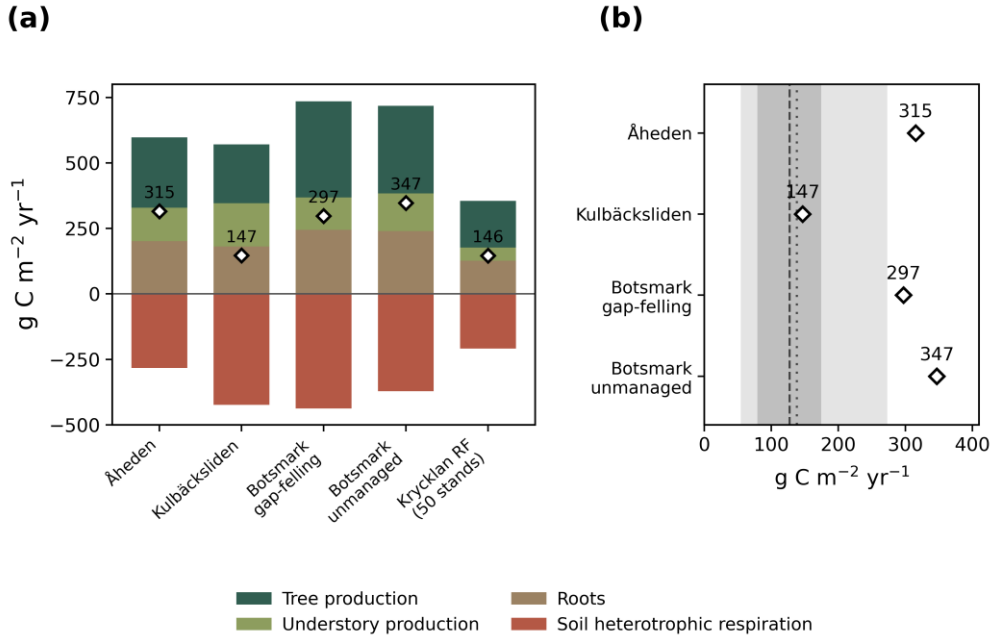


Figure 10. Modelled annual carbon balance for the four CCF systems and Krycklan RF. The four CCF bars are whole-system 2025 estimates, whereas the Krycklan RF bar is the arithmetic mean of the 2016–2018 stand means across 50 permanent stands. (a) Positive bars show tree, understory and model-completed root production; negative bars show soil R_h. Diamonds mark carbon balance=NPP − R_h (not observed NEP); The Krycklan value in panel (a) uses the same component boundary. (b) CCF Balance values placed against the full Krycklan net ecosystem production (NEP) distribution, which also includes deadwood respiration. Shaded bands show the Krycklan interquartile and 10th–90th percentile ranges; dashed and dotted lines mark the median and mean. The CCF points in panel (b) exclude deadwood respiration.*

The Figure 10a calculation combined the carbon input of living-tree C increment, tree litterfall C and vascular understory ANPP, Krycklan-derived coarse and fine

root production, then subtracted the model-assisted annual R_h . Central modelled NPP was 598.0 g C m^{-2} yr^{-1} at Åheden, 570.8 g C m^{-2} yr^{-1} at Kulbäcksliden, 735.2 g C m^{-2} yr^{-1} at Botsmark gap-felling and 718.2 g C m^{-2} yr^{-1} in Botsmark unmanaged forest.

After calculation (Figure 10a, b), the central carbon balance values were +315.3 g C m^{-2} yr^{-1} at Åheden, +146.7 g C m^{-2} yr^{-1} at Kulbäcksliden, +297.4 g C m^{-2} yr^{-1} at Botsmark gap-felling and +347.0 in Botsmark unmanaged forest (Figure 10). The Åheden–Kulbäcksliden NPP difference was only 27.2 g C m^{-2} yr^{-1}, whereas their annual R_h differed by 141.4 g C m^{-2} yr^{-1} and Balance by 168.6 g C m^{-2} yr^{-1}. The two Botsmark systems differed by 17.0 g C m^{-2} yr^{-1} in NPP, but gap-felling annual R_h was 66.6 g C m^{-2} yr^{-1} higher and NEP was 49.6 g C m^{-2} yr^{-1} lower than in unmanaged forest.

The Krycklan 2016–2018 three-year plot-mean NEP reference had a median of 127.5 g C m^{-2} yr^{-1}, a mean of 138.2 g C m^{-2} yr^{-1}, and a 10th–90th percentile range of 54.5–272.9 g C m^{-2} yr^{-1}. Kulbäcksliden NEP fell within this descriptive reference range (P25- P75), whereas the central values for Åheden and both Botsmark systems were above its 90th percentile (Figure 10b). These positions were descriptive because the accounting boundaries and evidence classes differed.

3.3.3 Tree increment in the regional RF context

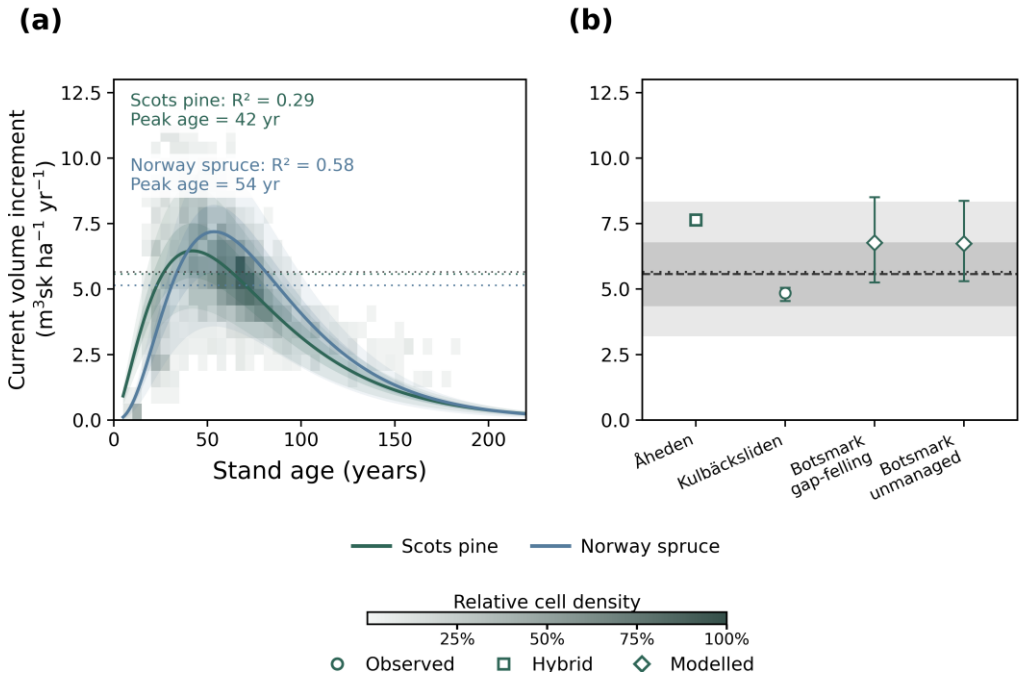


Figure 11. Current tree-volume increment in the regional Sveaskog rotation-forestry (RF) reference and the four CCF systems (a) same in Figure 3 Volume increment-Age curve for 2025 Sveaskog RF (b) Current tree-volume increment estimates for the four CCF systems compared with the Sveaskog production-forest records. The light-grey band is the 10th–90th percentile range and the darker band is the interquartile range; the dashed and dotted horizontal lines indicate the productive-area-weighted median and mean, respectively. These grey reference bands are calculated directly from the observed Sveaskog inventory records and are not simulated from the Chapman–Richards curves in panel (a). Kulbäcksliden is based on observed inventories, Åheden on the primary method hybrid estimate, and the two Botsmark estimates are modelled; the Kulbäcksliden bar shows its measured range, Botsmark bars show 95% joint-bootstrap intervals, and Åheden is shown as a point because its alternative estimation methods do not share a directly comparable uncertainty interval.

The Sveaskog RF reference data showed a clear age-dependent pattern in current volume increment, with fitted peaks at about 42 years for Scots pine and 54 years for Norway spruce (Figures 3b and 11a). The Sveaskog CAI median was 5.58 $m^3sk\ ha^{-1}\ yr^{-1}$, the mean was 5.65, and the P10–P90 range was 3.26–8.29 $m^3sk\ ha^{-1}\ yr^{-1}$.

All central estimates of the four CCF systems fell within the broad RF P10–P90 range: Kulbäcksliden was below the RF median, both Botsmark systems were close to the upper quartile, and Åheden was above the upper quartile but below the 90th percentile (Figure 11b). This Figure 11 could not describe long-term age-related yield comparison.

The CCF systems did not have a certain measured stand age, and their increment estimates came from different methods. The comparison therefore did not demonstrate any long-term yield, age-matched equivalence or a universal CCF advantage.

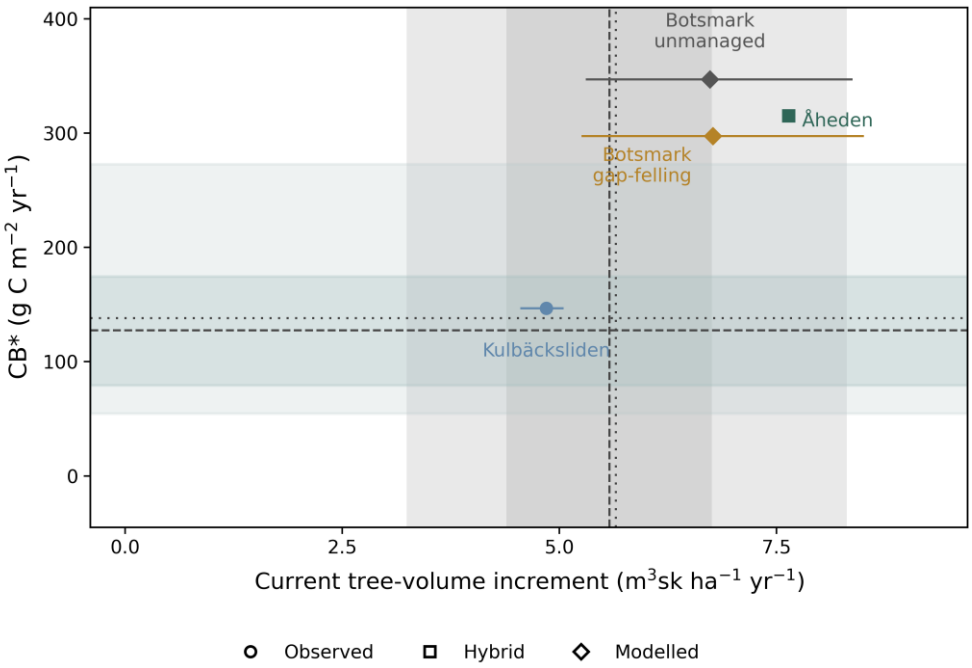


Figure 12. Regional CCF-RF carbon balance and productivity comparison. Each labelled coloured symbol combines whole-system current tree-volume increment on the x-axis with caron balance = NPP − soil heterotrophic respiration (R_h) on the y-axis. Circles indicate observed estimates, squares hybrid estimates, and diamonds modelled estimates. Horizontal bars are defferent uncertainty: the observed ward range is shown for Kulbäcksliden, 95% joint-bootstrap intervals for the two Botsmark systems, and Åheden is the modelled result. The vertical grey bands are derived directly from the 2025 Sveaskog RF operational inventory: the light band is the 10th–90th percentile range and the darker band the interquartile range, while the dashed and dotted vertical lines show the median and mean. The horizontal blue-grey bands show the 2016–2018 Krycklan RF stand-level NEP distribution, with the light and darker bands representing the 10th–90th percentile range and interquartile range, and the dashed and dotted horizontal lines representing the median and mean. The primary coloured CCF points do not include site-specific deadwood heterotrophic respiration.

For the estimated carbon balance analysis in (Figure 12), Åheden combined the highest current increment with a relatively high value of carbon sink compared to the others. Kulbäcksliden had the lowest values for volume increment and carbon balance, but still within the regional reference of both RF. And the two Botsmark systems had almost identical estimated volume increment but different carbon sink strength. These results in Figure 12 were descriptive, not the management trade-off, long-term mechanism, or carbon-productivity rankings or different CCF systems.

4. Discussion

The strength of evidence in this thesis varied, because the 2025 litterfall, understory ANPP, soil heterotrophic respiration (R_h), and soil organic carbon (SOC) data were sampled at the four study systems with different soil parent materials, wetness index, as well as the collection period. While parts of the data were modelled, hybrid or from other studies (Krycklan and Sveaskog data). These differences were important to determine how deep each research question (RQ) could be addressed. Direct 'forest-gap' comparisons help describe patterns within the CCF systems, while cross-system and cross-regional comparisons provide an operational context that help future studies of tree productivity and carbon balance processes in Vindeln.

4.1 Carbon inputs under CCF

Tree increment

Across the four study systems, the central current-increment estimates ranged from 4.85 to 7.64 $m^3sk\ ha^{-1}\ yr^{-1}$. The two checkerboards differed by 2.79 $m^3sk\ ha^{-1}\ yr^{-1}$, whereas the two Botsmark systems differed by only 0.04 $m^3sk\ ha^{-1}\ yr^{-1}$ (0.6%) (Table 3; Figure 11b). The latter comparison was partly a consequence of applying the same litterfall-tree increment model with different forest-area weights (Section 2.2.1). Tree increment is a component of productivity and carbon cycling. But the rankings of different Vindeln CCF systems could not be compared because of the different tree increment estimation methods (Table 3). Two checkerboard experiments found that during the first 6–8 years after cutting, the retained older Scots pine trees near gap edges had approximately 20% higher volume growth than trees further within the retained cells (Borgstrand, 2014; Goude et al., 2022). Compared pine and spruce growth after clear-cuts, their regeneration condition in checkerboard gaps differed due to the edge effect. And pine grew slower in height than spruce (Goude et al., 2022). These results indicated when interpreting checkerboard carbon production, both retained-tree growth and regeneration should be considered. However, the gap regeneration data were not included in the modelled increment at Åheden or Botsmark.
From 21 gap-cut experiments in Finland, the growth of retained trees near gap edges increased, while this growth response almost disappeared 10 m away from the edge into the forest. Basal-area growth would be underestimated by 7% in pine and 11% in spruce stands if this edge effect was not considered (Repola & Valkonen, 2025). The Botsmark gap openings were smaller than those in the Finnish study (0.1–0.6 ha), and their present tree volume estimates did not measure any edge-growth response. However, to investigate this effect, the Botsmark systems could further be compared with the above Finnish study when the inventory is completed.

Litterfall gap–forest comparison

Litterfall is a kind of carbon transfer, and its proportion in net primary productivity (NPP) varies with stand development. Because the ratio of carbon

among leaves, trunks, roots, and understory vegetation changes during the succession of boreal forests (Chen et al., 2017).

Among the gap-forest comparisons within the studied CCF systems, litterfall carbon mass in the gap cells was 89.4% lower in Åheden, 49.0% lower in the Kulbäcksliden, 19.9% lower in Botsmark gap, and 54.2% lower in Botsmark gap with wood (Figure 4c, e). A global meta-analysis with 8,739 paired forest-gap observations (203 paired litterfall observations) across litterfall and decomposition variables found that gaps have an average of 29.5% reduction in annual litterfall compared with forest cells, with a 95% confidence interval of 7.4%–46.3% (X. Zhang et al., 2024). In my thesis, belowground litter carbon inputs and root litter decomposition were not directly measured. Although root litter decomposition may contribute to the measured heterotrophic soil respiration (R_h), the individual contribution from other organic matter decomposition processes could not be distinguished.

Berg and Meentemeyer (2001) synthesized 64 European conifer sites, and showed that litterfall varied with different climate, stand age and tree species. And Albrektson (1988) identified that stand age, site quality and latitude would control needle litterfall of Scots pine in Sweden. Litterfall can vary with retained canopy due to different canopy and tree species composition (Albrektson, 1988; X. Zhang et al., 2024). Equivalent opening diameters were approximately 56.4 m at Åheden, 41.5 m at Kulbäcksliden and 20 m at Botsmark. The perimeter-to-area ratios of them were 0.080, 0.111 and 0.200 m^{-1} respectively. And about 36%, 48% and 75% of their gap opening area were within 5 m of the forest edge (The geometric values above were calculated from the opening dimensions in Section 2.1; Figure 1d–f). This might explain the relatively small litterfall reduction in Botsmark gaps, because it had the smallest gap area. However, this thesis lacks data or sampling methods to eliminate the canopy influence of the forest cells. The litterfall contrast of gap-with-wood and normal gap cannot isolate the deadwood effect from the surrounding living canopy differences.

Understory ANPP gap–forest comparison

Compared with forest cells (115–185 g C m^{-2} yr^{-1}), the CCF gaps (120–160 g C m^{-2} yr^{-1}) did not show noticeable compensatory increase in understory vascular plant ANPP. The lower understory ANNP in CCF gaps is consistent with evidence that boreal understory vegetation is controlled not only by light, but also their composition before treatment, resources availability and stand development (Nilsson & Wardle, 2005; Hart & Chen, 2006). Median vascular understory ANPP of gaps were 24.9% higher in Åheden and 12.7% lower in Kulbäcksliden, compared with the retained forest cells. At Botsmark, the corresponding differences were −1.0% in ordinary gaps and +13.2% in gaps with retained wood (Figure 4a). Similarly, Espinosa del Alba et al. (2021) found no significant change in vascular plant community composition eight years after creating 20-m-diameter gaps (same as Botsmark) in northern Sweden. And Burton et al. (2014) reported more understory productivity in larger gaps (200–380 m^2). In Kulbäcksliden, higher ANPP in retained forest might be result from the site-specific vegetation composition and some forest-adapted dwarf shrubs, which did not necessarily benefit from increased canopy openness (Atlegrim & Sjöberg, 1996).

After canopy removal, the increase in understory ANPP can compensate for the decline in tree productivity for some extent. Sabo et al. (2008) found that in southwestern ponderosa pine stands, ANPP increased with the decline in tree productivity due to significant reduction in canopy density ($R^2 = 0.90$, $P < 0.001$), although the compensation amount was small. This means understory ANPP gained approximately 0.14 kg with every kilo reduction in tree ANPP (only when basal area <5.9 m² ha⁻¹) in their case. This non-boreal example demonstrated a possible ANPP compensation mechanism in Vindeln for further study. But in the four studied CCF systems, the consistent compensatory response was not detected, because all 95% bootstrap intervals for the gap-minus-forest differences in median ANPP included zero (Section 3.1.2).

4.2 Soil microclimate and heterotrophic carbon losses

From the results, seasonal variations in R_h might be due to different temperature. In addition, litterfall supply (maybe substrate) and soil conditions might influence R_h variation at the same temperature (Hursh et al., 2017; Guo et al., 2024).

Microclimate and R_h across CCF systems

Åheden had the lowest R_h with gaps warmer and wetter than forest cells (66% time of the monitored days), whereas Kulbäcksliden had a shorter warmer gap period (24% time of the monitored days) but a 1.5 times higher R_h than Åheden (Figures 5c and 10a). Hence the microclimate patten in the CCF checkerboard system was not unified. Kulbäcksliden had smaller gap–forest contrasts in soil temperature, whereas Åheden had the lowest annual heterotrophic carbon loss. Botsmark gap-felling had almost the same modelled CAI as Botsmark unmanaged forest but had a 17.9% higher R_h of 66.6 g C m^{-2} yr^{-1} (Figures 10a and 11b). Similar modelled tree increment therefore could come with different measured annualized heterotrophic carbon losses. However, there was not always a higher R_h with lower canopy retention. The annual R_h in Uri et al. (2024) was 3.57 ± 0.25 t C ha^{-1} yr^{-1} after shelterwood cutting, and 2.59 ± 0.09 t C ha^{-1} yr^{-1} after clear-cutting.

Gap–forest microclimate comparison

At Åheden, the median gap–forest soil-temperature difference at 10 cm depth was +2.69 °C in July 2025, compared with +0.74 °C across the entire monitoring period (July-October, 121 paired days). At Kulbäcksliden, the corresponding differences were +0.01 °C in July and −0.12 °C during the full monitoring period (Figure 5a). Gaps VWC values were higher than those in the forest cells at both checkerboards (Figure 5b). A meta-analysis of 2,127 paired gap-forest observations across soil variables found that moisture content was increased by 7.6% in mineral soil due to gap openings, and 15.9% in organic layers. The gap temperature was also 5.1% higher in mineral soils (Tong et al., 2024). This structural mechanism can be explained by the heat buffering function of retained forest, because in central Sweden, the maximum air temperature under the forest canopy averaged 28.1 °C in gaps, 22.3 °C in forests, and 17.1 °C in old-growth forests. In summer, the forest was 5.78 °C cooler than the gap. Basal area and canopy coverage differences were the structural determinants influenced

temperature most in their case (Zhang, Sjögren & Jönsson, 2024). These results supported a role of retained canopy in temperature buffering (Zhang, Sjögren & Jönsson, 2024). Although the maximum air temperature in other studies cannot be directly compared to the median temperature at a 10-centimeter soil depth in my thesis, the canopy mechanism remains the similar. In addition, the plant interception and transpiration function would be reduced due to tree canopy removal. And this would potentially increase the soil moisture (De Frenne et al., 2021). Therefore, the warmer and more moist soil conditions in Åheden gaps could be possibly explained. And in Kulbäcksliden gaps, the cooler soil conditions means drainage, evaporation cooling, topography, and edge shading might all influence the temperature difference between gaps and forests (De Frenne et al., 2021; Greiser et al., 2018; Zhang, Sjögren & Jönsson, 2024).

Factors controlling R_h in CCF

Across 50 Krycklan stands, the apparent temperature sensitivity of heterotrophic soil respiration (Q_{10}) averaged 3.3 ± 0.9 (mean ± SD), with a 10th–90th percentile range of 1.6–5.3. This variation was better explained by soil properties than by stand type (Guo et al., 2024). The compensating gradients in forest-floor properties could also influence the annual soil heterotrophic respiration (10th–90th percentile range of 154–290 g C m^{-2} yr^{-1}) in Krycklan stands. (Martínez-García et al., 2022). Temperature-standardization did not directly category the R_h results into substrate supply or moisture dominant (Hursh et al., 2017).
Madsen et al. (2025) compared 12 pairs of Norway spruce stands in southeastern Norway and found 12% higher annual soil respiration and 20% higher tree litterfall in previously clear-cut stands compared with near-natural stands. Their soil-respiration measurements included autotrophic as well as heterotrophic components, so its response could not be transferred directly to trenched soil respiration R_h here in this thesis (Madsen et al., 2025). On a different soil type, Korrensalo et al. (2026) analyzed 8 peatland forests in Finland and measured heterotrophic respiration using root-exclusion chambers measurements 1–8 years after harvesting. The results showed that annual R_h decreased by 14% after harvesting in herb-rich stands; R_h decreased by 26% after clear-cutting in blueberry-type stands; R_h increased by 17% after clear-cutting in the lingonberry-type stands with poor nutrient. These peatland results were used to illustrate site dependence of R_h. But they did not quantify the results in my thesis.

Litterfall and R_h at Åheden

The strong log (litterfall C mass) and log(R_{10}) correlation ($R^2 = 0.824$, $p < 0.001$; Figure 8a; Table A5) indicated that higher tree litterfall C input was associated with higher temperature-normalized soil heterotrophic respiration (R_{10}) among the nine cell clusters in the Åheden checkerboard. The tree litterfall C in Åheden gaps (Figures 4c, e and 7b) was 89.4% lower (21.1 vs. 199.7 g C m^{-2} yr^{-1}), and R_{10} was also 42.0% lower compared with forest cells (0.754 vs. 1.300 μmol CO_2 m^{-2} s^{-1}). These corresponding reductions could be result from a substrate-supply explanation, but the results could not identify how much of the R_{10} contrast was caused by litterfall carbon input in Åheden. Litter-manipulation studies provided some possible evidence for the direction of this mechanism found in my thesis. Chen and Chen (2018) found that litter removal, root removal, and simultaneous

removal of litter and roots reduced soil respiration by 22.8%, 34.1%, and 43.4%, respectively. Xu, Liu and Sayer (2013) also found that litter removal reduced 34% of soil respiration and 39% of mineral-soil microbial biomass C. These results suggested that lower litterfall input might reduce the supply of plant-derived C available to heterotrophic decomposers, which could in turn reduce soil respiration (Chen & Chen, 2018; Xu, Liu & Sayer, 2013).
Substrate is the organic matter provided carbon and energy to heterotrophic decomposers (Zhang et al., 2020). It included fresh aboveground litter, dead-root and root-derived organic matter, forest-floor material and decomposable soil organic matter (Xu, Liu & Sayer, 2013). Tree litterfall C is therefore one measured component of substrate input (Chen & Chen, 2018). Taking other studies into account, substrate inputs in the Åheden gap soils might have decreased due to reduced litterfall. However, canopy structure, root trenching history and soil properties all varied when the forest habitats changed (Hanson et al., 2000; Hursh et al., 2017). And they were not separated by the litterfall linear regression. The carbon-loss mechanism in Åheden checkerboard therefore requires further investigation.

4.3 Carbon-cycle components and balance in the RF context

Soil carbon stock

SOC responses to forest management vary with depth, time since treatment, soil moisture and the carbon concentration calculated, and there were no universal forest-gap superior mechanisms (Mayer et al., 2020; Tong et al., 2024). In short-term comparisons, mineral-soil stock differences can be difficult to detect (Mayer et al., 2020; Lindroos, Mäkipää & Merilä, 2022). After analyzing 52 studies and 2,127 paired observations across soil variables, Tong et al. (2024) found that gaps can reduce SOC and microbial carbon compared to retained forest. However, gaps formed within 3 years after the harvest did not show a significant SOC decline yet. Their meta-analysis detected SOC reductions in some gaps 4–10-year after harvesting, without a universal time response patten (Tong et al., 2024). Larger gaps were also associated with greater SOC reductions in that synthesis (Tong et al., 2024). Larsson et al. (2025) found weak evidence that the organic-layer C decreased 15% after the stands were converted to even-aged management. The result was from 23 pairs of managed and unmanaged forest stands comparison in northern Sweden. And there were no detectable differences observed in mineral soil within 50 cm depth (Larsson et al., 2025). In the directly comparable 10–20 cm soil layer, the SOC in mineral soils at Åheden was closer to that in Krycklan rotational forest. But the SOC values at Kulbäcksliden and Botsmark were higher (Figure 9a). However, these differences could not be interpreted as the higher SOC in CCF than RF, because a survey of 430 plots at Krycklan by Larson et al. (2023) found that SOC had spatial heterogeneity at the landscape scale and was closely related to local soil moisture conditions. They found that 40% of the variation in total SOC, 50% in organic-layer C, and 5% in mineral-soil C could be explained by modelled soil moisture. Therefore, despite the SOC data lacks

chronical replicate, the observed SOC variations among the four study systems and Krycklan RF could not only be attributed to regional management difference. Lindroos, Mäkipää, and Merilä (2022) monitored 10 managed plots in a Finnish boreal forest, and conducted repeated soil surveys in 1995, 2006, and 2016. They found SOC increased by an average of 36 g C m^{-2} yr^{-1} in the organic and 0–40 cm mineral-soil layers during the 21 years of the study period. In contrast, my thesis measured mineral-soil SOC at 10–30 cm only in 2025, providing a comparison of existing carbon stocks between forest and gap habitats, not the SOC changes over time. Therefore, the observed forest–gap differences could not illustrate whether CCF management methods increasing or reducing the SOC. In addition, checkerboard CCF may offer a balance between tree productivity and SOC retention, although its advantage over other CCF systems and RF remains uncertain (Sobuj et al., 2026). Åheden showed the highest estimated tree increment (7.64 m^3sk ha^{-1} yr^{-1}), but no clear SOC advantage over the other systems or Krycklan RF (Figures 9a, c and 11b). It was consistent with the insignificant SOC differences among harvesting treatments reported by Roth et al. (2023).

Carbon fluxes

Mean vascular understory ANPP ranged from 123.6 to 165.4 g C m^{-2} yr^{-1} across the four CCF systems (Figure 4b). The Krycklan RF reference in Figure 4b represents vascular understory ANPP (herbs, grasses and shrubs), whereas the 49–163 g C m^{-2} yr^{-1} range reported by Martínez-García et al. (2022) was understory NPP. It included belowground production, mosses and lichens, and was therefore not directly comparable with my thesis. Within the CCF systems, the reduced litterfall in gaps was not accompanied by a consistent increase in vascular understory ANPP (Figure 4a, c, e).

The annual carbon loss from R_h flux was 282.7 g C m^{-2} yr^{-1} at Åheden. But for the other CCF systems, the R_h ranged from 371.2 to 437.8 g C m^{-2} yr^{-1} (Figure 10a). The latter values were approximately 28–51% higher than the 90th percentile of the published 154–290 g C m^{-2} yr^{-1} Krycklan R_h reference (Martínez-García et al., 2022). These results did not mean CCF increased R_h, because the measurement years, soil conditions, root isolation history, chamber methods, and annualization processes used in different studies could all affect estimated R_h (Hanson et al., 2000; Pumpanen et al., 2004). Cutting the root can alter moisture and substrate conditions, and decomposition of severed roots can bias early measurements (Hanson et al., 2000). In this thesis, the R_h were measured 1 year after the trenching, and the roots were also thrown away from the study area. But it could only eliminate the root decomposition effect. The changing of the soil environment under the frames could not quantify in this thesis.

Carbon balance among the study systems

For the carbon balance components differences among the study systems, the two checkerboards differed by only 27.2 g C m^{-2} yr^{-1} in NPP but by 141.4 C m^{-2} yr^{-1} in R_h. At Botsmark, the higher NPP in gap-felling was offset by its higher R_h. Thus, the differences of the modelled NEP among the above two paired systems

arose mainly from the annualized respiration terms (Figure 10a). And the general CCF–RF differences could not be concluded from the existing datasets.
Carbon balance performance is related with tree increment and soil C. In a 90-year Finnish study of comparing RF and selective cutting forestry, it was found the different post-harvest basal area and harvesting intervals changed annual NEP. And soil C still declined in several uneven-aged management sites compared with RF (Shanin et al., 2016). Another 81-years Norwegian comparison study of management histories found a greater present soil C in the uneven-aged stand (199 versus 178 Mg C ha^{-1} in clear cutting), but 37 Mg C ha^{-1} less cumulated in tree-C (Nilsen & Strand, 2013). These studies showed how carbon input, carbon losses and pools differed in RF and selective cutting comparison, and they do not have a unified patten.
Hence while examining the carbon balance results, the productivity and heterotrophic carbon losses must be interpreted together. Peichl et al. (2023) found that annual NEP in 50 Krycklan RF stands ranged from −56 to +346 g C m^{-2} yr^{-1}. And the NEP spatiotemporal variations were driven more by NPP than heterotrophic respiration. In this thesis, the belowground productivity was calculated using the Krycklan ratio, and deadwood respiration data for each CCF site were missing. These values require future field measurements with more independent replications. Hence, the CCF carbon balance cannot be equated with the observed NEP (Section 2.2.6).

Tree increment in the regional RF context

From the RQ3 study, it indicated the central CAI estimates of these four study systems remain within the broad range of the Sveaskog regional RF. However, forest current annual increment is not long-term site productivity or lifetime yield, because different stand age, retained forest volume, regeneration and rotation time intervals will all affect the long-term increment comparison (Skovsgaard & Vanclay, 2008; Lundqvist, 2017; Ekholm et al., 2023).
The 2025 median current increment for the regional Sveaskog RF was 5.58 m^3sk ha^{-1} yr^{-1}, with a P10–P90 range of 3.26–8.29 m^3sk ha^{-1} yr^{-1}, while the central estimates for the four CCF systems ranged from 4.85 to 7.64 m^3sk ha^{-1} yr^{-1} (Table 3; Figure 11b).
However, this 2025 overlap did not mean equivalent long-term yield of CCF and RF. Ekholm et al. (2023) studied 17 publications comparing growth and yield under selection and rotation harvest systems. Across the simulation studies, the selection-system yield ranged from 67% to 131% of the RF yield, with most of the studies lower than 100% (more yield in RF). And they used two growth-model found the similar value of 80–96%. But they emphasized that CAI of RF changed strongly overtime, whereas it might be more stable under selection management. Hence a short-term CAI comparison can have different comparison results depending on the RF age. The above study concerned selective cutting systems with Norway Spruce dominated, while in this thesis, it was pine-dominated checkerboards and gap-felling systems.
Trubins (2025) simulated the transition of Swedish Scots pine and Norway spruce stands from even-aged management to gap cutting and found that the cumulative tree increment loss was 16–320 m^3 ha^{-1} due to transit period, equivalent to 2.7–32.7 years of average annual growth under rotation forestry. Parkatti et al. (2019)

used two independent growth models to compare CCF with RF and found that the maximum increment yield was achieved through rotation forestry. For CCF productivity, the Norway Spruce dominant sites were preferred over Scots pine ones. The results in Figure 11 showed the overlap between CCF current increment and regional pine RF for further study reference.

4.4 Management implications

For forest companies (Sveaskog for example), the practical value of these results was to consider retained forest structure, tree increment, litter inputs and soil carbon losses together. And, to distribute these observation tasks into different interest groups (landowners, companies, scientists) for implementations.

Harvest intensity and retained stand structure
To maximize tree productivity and carbon sequestration, forest companies like Sveaskog could adapt a system based on retained forest and harvest intensity classifications. It is more scientific than only controls the gap size. 2025 current tree growth in the Åheden area was 7.64 $m^3sk\ ha^{-1}\ yr^{-1}$, but litterfall production in gaps was 89.4% lower than the forest cells (Table 3; Figure 4c, e), suggesting that soil carbon input due to litterfall may have been significantly reduced even tree increment remains high. Experiments in Sweden provided a reference range for harvesting intensity: when approximately 30% of the basal area was harvested, annual volume growth increases to 4.20 $m^3\ ha^{-1}\ yr^{-1}$, compared to 4.52 in the unharvested group (Ekholm et al., 2022). And when the harvesting rate was increased to approximately 45–85%, the range of volume growth expanded to 0.5–6.8 $m^3\ ha^{-1}\ yr^{-1}$. There was significant positive correlation between yield and retained stands within a moderate thinning range (Lundqvist et al., 2007). Regarding carbon processes, a study by Zhang et al. (2018) found: After thinning, when litterfall decreased by an average of 23.7%, the carbon loss due to soil respiration increased by 29.4%. Mayer et al. (2020) further summarized that light thinning (harvest rate ≤ 33%) resulted in a 17% increasing in soil carbon, whereas heavy thinning (harvest rate ≥ 65%) made 8% decreasing in soil carbon. Sobuj, Peichl, and Pommerening (2026) also noted that low to medium intensity CCF harvest was more conducive to the recovery of biomass and carbon stocks, because the management of carbon sink should consider both aboveground and belowground tree biomass. High-intensity harvest interventions might slow the recovery of carbon pools such as understory vegetation, as well as litter/root inputs, and soil carbon processes. Long-term simulations in Sweden further found that when CCF productivity is decrease from 100% to 80%, the long-term climate benefits calculated in their study decrease from 2.06 to 1.83 Mg C $ha^{-1}\ yr^{-1}$. (Lundmark et al., 2016).
The above values of 33% or 65% should not be used directly as operational thresholds for Sveaskog, but they can serve as quantitative reference values for low, medium, and high intensity of harvest. The replicate trials can be further explored in the field before making the management decision. By linking harvesting intensity to indicators such as retained basal area, tree increment, litterfall, and underground carbon process (e.g., roots), it is possible to find a tree

productivity–carbon sink interval. If the harvest continues beyond this threshold, there might be limited yield benefits and declined carbon sequestration. These recommendations require further examination.
Tree NPP includes productivity of foliage, bark, branches and roots as well as stem wood (Peichl et al., 2023), and therefore differs from the stem carbon increment reported here. The merchantable timber yield additionally depends on stem dimensions and quality (del Río et al., 2017) and suitability for specific wood products (Felton et al., 2020).

Gap design and monitor R_h (carbon loss)
RQ2 indicated that gap size and edge effects were directly measurable management variables in forest management. Compared to forest cells, there were more declines of litterfall and R_{10} in Åheden gaps than that in Botsmark (Figures 4e and 7b). And a significant litterfall–R_{10} relationship was observed in Åheden (Figure 8a; Table A5). The magnitude of this decline was also significantly higher than the findings reported by X. Zhang et al. (2024). They found the annual litterfall of 8,739 global gaps reduced by an average of 29.5% (95% CI: 7.4–46.3%). Therefore, the related forest management implication is: Sveaskog could compare harvesting results between a few large gaps and many small gaps with same basal-area removal. Litterfall and R_{10} can be measured at fixed distances from the forest edge to the center of each gap. The aim is to test if the harvest intensity can be maintained to reduce losses in tree-derived C input by altering the gap layout. I do not assume small gap openings would have less carbon loss by R_h.
Secondly, the reference values for monitoring R_h should be set according to different real site conditions. Based on the results related with RQ2, it would be easier for management by selecting small number of representative stands first, with some long-term monitoring variables, such as dominant tree species, site productivity, soil moisture and drainage class. If the R_{10} and litterfall change in the same direction as observed in Åheden, then these sites have soil carbon loss strongly connected to reduced plant-derived C inputs, hence they can keep the current CCF harvesting intensity like Åheden. The litterfall in Botsmark gap felling only explained a small portion of the variability in R_{10} ($R^2 = 0.068$， $p = 0.331$; Figure 8c; Table A5). For sites like it, the management monitoring efforts should hence focus more on soil moisture, soil properties, and belowground carbon input (Hursh et al., 2017) to find the mechanisms before further harvesting decisions are made.

Short and long-term carbon monitoring
For Sveaskog's forest management, annual carbon fluxes and long-term SOC can serve as complementary monitoring indicators. By measuring tree increment, litterfall, understory ANPP, and annual R_h, the rapid annual changes in carbon processes can be monitored. While organic layer and mineral-soil SOC should be remeasured at longer time intervals before the changes can be noticed.

Set benchmark for different CCF
The existing regional RF data (Section 3.3.3) can be used to establish a local 'productivity–retention structure' baseline for nearby CCF management. To make

this comparison more applicable in the real forest management, the CCF stand can be repeatedly compared with the regional RF based on the same dominant species and site-productivity class, while recording retained basal area, mortality, and recruitment. The goal is to determine how much CCF productivity declines compared to the median of the regional RF when retained forest basal area decreases. This approach is directly supported by a study from Sweden: Lundqvist et al. (2007) removed approximately 45%, 65%, and 85% of the original basal area in two uneven-aged Norway spruce experiments, respectively. Then the volume increment ranged from 0.5–6.8 $m^3\ ha^{-1}\ yr^{-1}$ and showed a significant positive correlation with retained standing volume ($p < 0.01$). Therefore, by combining existing RF distributions with repeated inventories of some representative CCF in the nearby region, it is possible to determine how much productive structure can be removed maximum before current productivity begins to fall below the target RF level for the area. This is more sustainable than applying a single, fixed harvesting intensity to all CCFs. Sveaskog is currently using this method to assess CCF productivity. And simple measurements of litterfall, understory production, long-term SOC measurements and R_h could be included in CCF forests. These measurements could help CCF with 'acceptable yield' maintaining long-term carbon storage and sustainable yield.

4.5 Uncertainties and outlook on future research needs

The primary limitation of this study was the scale of dataset. Each managed CCF design was represented by only one system with different soil parent material and wetness index (Figure 1b, c; Table 1). In addition, multiple cells, plots and repeated measurements were subsamples within those sites. At Åheden, Kulbäcksliden, and Botsmark, the repeated plots and measurements could only reflect the forest–gap difference within themself (Hurlbert, 1984).Therefore, the significant decline in litterfall and R_{10} observed in Åheden gaps can only account for the results of this checkerboard system in 2025. This did not mean gap size or spatial layout were the causes. Future research requires to control similar basal-area removal and then compare forest-gap effect (different gap sizes) across same type of CCF systems.

The second limitation was from the tree increment estimates (Table 3; Appendix 1). The results in Kulbäcksliden were from complete inventory, Åheden was from measured individual trees with a growth model, while Botsmark was from Krycklan's litterfall transfer. Grzeszkiewicz et al. (2025) found that the use of growth models in Swedish uneven-aged forests, the results of increment will be underestimated by approximately 2 $m^3\ ha^{-1}\ yr^{-1}$ in average. It was close to the value differences observed among the various CCF estimates in this thesis. Therefore, the current comparison with Sveaskog RF increment could only explain the regional productivity of each CCF in 2025. It cannot provide a long-term CCF-RF yield comparison. In addition, the location and spatial distribution of the 42,000ha anonymized Sveaskog compartments in Vindeln were based on assumption to cover all the CCF and Krycklan stands, hence the regional productivity comparisons did not demonstrate 100% site matching results between

individual CCF and RF stands. Hence, it is important to measure the trees at Åheden and Botsmark over several consecutive years, as well as to record the mortality, regeneration, and retained basal area. Complete litterfall collection is also required for Kulbäcksliden , as most of the September values were reconstructed from the three gap donor traps.

For the carbon balance component, CO_2 concentration was from bi-weekly chamber measurements and then modelled to annual R_h by Lloyd-Taylor model. The significant litterfall–R_{10} relationship at Åheden did not take canopy structure, litter input, root history, and soil conditions into consideration. In addition, the integrated carbon balance could not be considered as observed NEP, as belowground root production was from Krycklan transfer. Deadwood respiration and mortality were also not measured at any CCF site (Peichl et al., 2023). The calculation of tree carbon increment in the CCF was estimated by stem-C biomass. In the results, only 10–30 cm mineral SOC was available, excluded the organic layer (Figure 9; Table 1). The management effects were more noticeable in the organic layer than in mineral soil (Larsson et al., 2025). Mineral SOC should be sampled repeatedly over multiple years in further studies.

Disturbances and biodiversity may influence carbon balance and management decisions of long-term RF–CCF comparisons, but their influences were not measured in this thesis. Windthrow damage was lower in mature managed CCF stands than that with higher opening area (Pukkala et al., 2016). Different tree height, species, root system, and management methods can all alter tree stability under windthrow (Valinger & Fridman, 2011; Wallentin & Nilsson, 2014; Zeng et al., 2004). In addition, climate change may cause wind damage, drought, snow accumulation, and insect infestations, one over another (Seidl et al., 2017; Venäläinen et al., 2020). Data from Krycklan also indicate that mature old-growth forests are more drought-resistant (Martínez-García et al., 2024). In the Vindeln region studies, windthrow was identified as a main disturbance factor required priority study in the future, as wind and snow damage has been observed in long-term managed forest experiments at Svartberget, particularly during the first years after treatment (Valinger et al., 2019).

Retaining live trees and deadwood can benefit many species living in the forest (Fedrowitz et al., 2014; Gustafsson et al., 2020). Management approaches can help to keep different shaded habitats and stand structure. We can find the most balanced management methods between ecology and productivity by observing the species response on retention levels, spatial distribution, and the time elapsed since harvesting (Ekholm et al., 2022). Swedish CCF experiments also indicate that moderate selective cutting has little short-term impact on vascular plant and moss communities (Ekholm et al., 2022). Boreal forests also create habitat for birds, insects, fungi and bryophytes by providing deadwood, old trees and different canopy layers (Berglund & Kuuluvainen, 2021). Food-web interactions involving herbivores, predators, detritivores and soil microorganisms can alter plant production, decomposition and carbon storage. But the specific effects of these interactions were not separately quantified in this thesis (Schmitz & Leroux, 2020).

Boreal forest can also influence northern water balances by regulating evapotranspiration, streamflow, and snow accumulation (Wei et al., 2022). The carbon balance in this thesis also excluded dissolved organic carbon (DOC)

export to streams, leaving an additional pathway of terrestrial carbon loss (e.g. drainage) unquantified (Chi et al., 2020).
This thesis did not assess the fate of harvested wood from the gaps, although carbon removed from forests can remain stored in products. With the changing climate, the forest ecosystem carbon balance should be examined with climate effects together. The latter depends on product use, lifespan and potential substitution of other materials (Biber et al., 2020).
Therefore, future research should make up all the above requirements in the measurements, then the current CCF- RF comparisons (productivity and carbon balance) can be further developed into a more reliable long-term regional result. The main contribution of this thesis is not to identify a CCF system of best carbon sequestration and tree increment performance, but to report all the potential research fields and detailed methods required (also provide some basic findings) before long-term reliable management 'RF-CCF transformation' decisions can be made.

Conclusion

This thesis evaluated how the three CCF systems and one unmanaged forest near Vindeln differed in carbon inputs, soil carbon loss and carbon stocks. These carbon components and current tree increment were placed in the context of Krycklan and Sveaskog RF references for comparisons.

Current tree-volume increment estimates ranged from 4.85 to 7.64 $m^3sk\ ha^{-1}\ yr^{-1}$. Tree litterfall was lower in all harvested gaps than in retained forest cells, but vascular understory ANPP did not show a consistent compensation pattern for the reduced litterfall carbon input. The results therefore indicated the different current tree growth and litterfall inputs within a CCF system.

R_h increased non-linearly with soil temperature in all study systems. In Åheden, litterfall was significantly related with R_{10} ($R^2 = 0.824$, $p < 0.001$), and gap R_{10} was 42% lower than the forest despite warmer and wetter gap conditions (during most of the monitoring period in 2025). Temperature described seasonal R_h variation, while the litterfall carbon input-R_h association suggested that carbon supply worth further research for the R_h mechanism in Åheden checkerboard system. However, these results did not establish fixed causation.

The 2025 mineral-soil SOC stocks did not show a consistent forest–gap variation. NEP (from partial modelled components) among the study systems and the referenced Krycklan RF ranged from 146.7 to 347.0 $g\ C\ m^{-2}\ yr^{-1}$. And the contrasts of the checkerboard systems and the Botsmark systems arisen mainly from differences in annualized R_h. Current-increment estimates of all four study systems fell within the Sveaskog RF P10–P90 range of 3.26–8.29 $m^3sk\ ha^{-1}\ yr^{-1}$. These were only descriptive results, not a long-term regional growth or management ranking.

For further study, retained stand structure, carbon inputs and heterotrophic carbon losses should be considered together. Repeated tree inventories, direct root and deadwood measurements, and long-term SOC monitoring were required to turn the comparison in this thesis into a more complete assessment of CCF-RF carbon cycling.

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Popular science summary

Most productive forests in Sweden are managed with rotation forestry, where a stand is eventually clear-cut and then regenerated. Continuous-cover forestry offers an alternative method by keeping living trees on the site and harvesting smaller groups, gaps or individual trees.

This thesis compared four study systems near Vindeln in northern Sweden. Two were checkerboard systems at Åheden and Kulbäcksliden, where retained forest and harvested squares alternate. A third Botsmark system used small circular gaps, and a nearby unmanaged forest was a reference. The systems were also compared with managed forests in the Krycklan catchment and with a large regional dataset from Sveaskog.

The study examined tree growth, tree leaf litter, understory plant production, soil temperature and moisture, soil respiration and mineral-soil carbon. Some missing components had to be estimated using models, so the annual carbon balances in this thesis should be understood as current estimates rather than complete measurements of the whole ecosystem.

Tree leaf litter was lower in every harvested gap than in the surrounding retained forest. The reduction ranged from about 20% at Botsmark to almost 90% at Åheden. Understory plants did not consistently make up for this tree leaf litter carbon input reduction.

Soil carbon dioxide release increased with temperature, but temperature did not explain all differences. At Åheden, the gaps were warmer and wetter, yet soil respiration at the same reference temperature was 42% lower than in retained forest. The close relationship between tree leaf litter and soil respiration at this site suggested that reduced inputs of needles, leaves and other plant material might help explain lower respiration despite warmer and wetter conditions. Mineral-soil carbon did not show a consistent difference between gaps and retained forest.

Current tree-growth estimates differed among the four study systems, but all were within the broad range of the regional Sveaskog rotation forests. These regional comparisons did not represent any long-term performance. Whole-tree carbon includes bark, branches, leaves and roots, not just the stem.

The main message is that continuous-cover forestry cannot only be evaluated from gap layout or current tree growth. Forest managers should consider retained tree structure, litter inputs, soil carbon losses and long-term carbon stocks together. A more scientific long-term comparisons will require repeated measurements of the same trees, regeneration, mortality, roots, deadwood decomposition and soil carbon.

Appendix 1

Åheden primary tree-increment model

The first and primary method (2022 inventory model) I used to predict Åheden productivity is the Swedish species-specific individual-tree basal-area-increment model of Matsala et al. (2026). This model was developed from 1983–2022 Swedish NFI permanent plots. The 2022 numbered-tree inventory (until August) was used, and it comprised 1,331 numbered tree records from 4 forest subplot (index number 501-504), with 0.125ha area each. Scots pine, Norway spruce and birch with DBH ≥ 4 cm were selected to make the competition population (785 trees). And trees with DBH ≥ 10 cm were selected to make the growth-target population (322 trees).

When there were two perpendicular diameter readings available for one tree, the DBH would be calculated from their geometric mean:

$$DBH_i = \frac{\sqrt{d_{1,i} d_{2,i}}}{10},$$

where $d_{1,i}$ and $d_{2,i}$ were the two readings for tree i in mm and DBH_i was in cm. Then the tree basal area could be calculated:

$$g_i = \frac{\pi DBH_i^2}{40{,}000},$$

with g_i in m² tree⁻¹.

For each target tree i of species s, the published five-year growth model was applied as

$$\eta_{i,s} = \beta_{0,s} + \beta_{1,s}\ln(\mathrm{DBH}_i + 1) + \beta_{2,s}\ln(A + 20) + \beta_{3,s}\frac{\mathrm{SI}}{10} + \beta_{4,s}\frac{D_q}{10}.$$

The remaining stand, competition and climate terms added to $\eta_{i,s}$ were

$$\beta_{5,s}\ln(G + 3) + \beta_{6,s}P_{\mathrm{thin}} + \beta_{7,s}\mathrm{BAL}_i + \beta_{8,s}\frac{T_{\mathrm{sum}}}{1000} + \beta_{9,s}p_{\mathrm{other},i}.$$

The symbols η and β1–β9 were part of our implementation's notation to sum all the 9 long original coefficient in Matsala et al. (2026)

Here A was the age input used by the growth model, SI was site index (m), D_q was quadratic mean DBH (cm), G was subplot basal area (m² ha⁻¹), P_{thin} was the recent-thinning indicator (0 or 1), BAL_i was the basal area of trees larger than tree i in the same cell (m² ha⁻¹), T_{sum} was temperature sum (degree-days) (Odin, Eriksson & Perttu, 1983), and $p_{\mathrm{other},i}$ was the proportion of subplot basal area in species other than the target species. The β coefficients were directly took from Matsala et al. (2026) and did not edit.

Table A1.1 Equation coefficients in the Swedish species-specific individual-tree basal-area-increment model of Matsala et al. (2026).

Coefficient	Scots pine	Norway spruce	Birch
β_0	4.5881	4.8241	3.5790
β_1 (DBH)	1.5668	1.7971	1.8649
β_2 (age)	−0.7671	−0.9398	−0.8549
β_3 (site index)	0.2207	0.2878	0.2435
β_4 (D_q)	−0.0448	−0.0411	−0.1835
β_5 (basal area)	−0.3128	−0.3125	−0.2560
β_6 (recent thinning)	0.1316	0.1240	0.1532
β_7 (BAL)	0.0006	0.0000	−0.0028
β_8 (temperature sum)	0.2044	−0.0740	0.1053
β_9 (other-species basal area)	0.0670	0.1956	0.1242

$T_{\text{sum}} = 4{,}835 - 57.6 \times Lat - 0.9 \times Alt$ (Åheden Latitude=64.2, Altitude=230m)

A = median($\text{Age}_{\text{2021 sample trees}}$) + 1

The central inputs were $A = 110.5$ yr, $SI = 21$ m (pine dominant index), $T_{\text{sum}} = 930.1$ degree-days and $P_{\text{thin}} = 1$. Cell G, D_q, BAL_i and species proportions were calculated from the measured ≥4 cm competition trees.

$$G_p = \frac{1}{a_p} \sum_{j \in C_p} g_j$$

where G_p was subplot basal area (m² ha⁻¹), and g_j was the basal area of competition tree j (m² tree⁻¹).

$$D_{q,p} = \sqrt{\frac{1}{n_p} \sum_{j \in C_p} DBH_j^2}$$

where $D_{q,p}$ was quadratic mean DBH (cm), and n_p was the number of competition trees in subplot p.

$$BAL_i = \frac{1}{a_p} \sum_{\substack{j \in C_p \\ DBH_j > DBH_i}} g_j$$

where BAL_i was the basal area per hectare of competition trees in the same subplot that were larger than target tree i (m² ha⁻¹).

For target tree i of species s, let $C_{p,s}$ be the competition trees of species s in subplot p. Their species-specific basal area was

$$G_{s,p} = \frac{1}{a_p} \sum_{j \in C_{p,s}} g_j$$

and the other-species basal-area proportion was

$$p_{other,i} = 1 - \frac{G_{s,p}}{G_p}$$

$G_{s,p}$ was the basal area of target species s in subplot p (m^2 ha^{-1}). Thus, $p_{other,i}$ was the proportion of cell basal area except for the target species.

Then, the model returned the five-year change in squared diameter:

$$\Delta d_{i,5}^2 = \exp(\eta_{i,s}).$$

This was converted to annual basal area increment for each tree,

$$\Delta g_i = \frac{\pi \Delta d_{i,5}^2}{4 \times 10{,}000 \times 5},$$

and expanded to the subplot scale as

$$I_{G,p} = \frac{\sum_{i \in p} \Delta\, g_i}{a_p},$$

where $a_p = 0.125$ ha. The four subplot values were averaged. Next, I converted the retained forest basal area increment to a volume-increment proxy using the observed 2021 ratio $V/G = 206.1/25.01$ from the Åheden data, and finally multiple by the area ratio 4/9, the whole checkerboard was calculated by:

$$I_{V,\text{Åheden}} = \frac{4}{9}\left(\frac{1}{4}\sum_{p=501}^{504} I_{G,p}\right)\frac{206.1}{25.01}.$$

The estimate was therefore model assisted rather than observed current annual increment. The final primary Åheden Hybrid estimate was: 7.64 m^3sk ha^{-1} yr^{-1}

Then, the sensitivity was evaluated with 18 combinations (3×3×2) of three age inputs (63.5, 110.5 and 153 yr), three temperature-sum multipliers (0.9, 1.0 and 1.1) and two thinning indicators represented for recent checkerboard cutting (0 and 1). The 10th–90th percentiles of these explicit calculations were used as the main method range: 5.4027913–10.8099806 m^3sk ha^{-1} yr^{-1}. The sensitivity age values used were Q25 + 1 = 63.5 yr, Q50 + 1 = 110.5 yr and Q75 + 1 = 153.0 yr. They were not confidence interval for the measured data. These were Matsala et al. (2026) newly developed individual-tree functions, and they were not the individual-tree growth functions implemented in Heureka.

The second method I used was the 2021 regional structural modelling. It combined BEY2 and available Kulbäcksliden forest structural data. I calculated raw predictions for K2, K3, and K6 using the same corrected BEY2 value. Then, each observed CAI value (10.1, 9.1, and 9.9 m^3sk ha^{-1} yr^{-1}) were divided by its respective predicted value to derive 3 calibration factors. Finally, these factors were averaged and then multiplied by the Åheden raw BEY2 value. This

calibration was my own assumption and was not a required step in the published BEY2/Heureka method, only to make the results more regionally based and reliable. Finally, the calibrated retained-forest proxy was multiplied by the fixed 4/9 retained-forest area fraction to express increment for the whole Åheden checkerboard. Table of all the parameters used in the BEY2 model were listed in the appendix. For the detailed formula, see (Elfving, 2010). Because Fahlvik et al. (2014) indicated using the mean-age values for the growth-model input, the pre-set 2021 Åheden stand age of 130 yr was my random guess of this CCF system. The observed 2021 Åheden stock ratio V/G=206.1/25.01=8.2407 was assumed to be applicable for converting predicted basal-area increment to a volume-increment.

BEY2 was a stand-level basal-area-growth function developed for use within the Heureka growth-modelling framework. It was not the complete Heureka decision-support system. The full Heureka simulator linked stand and tree-level growth functions with other parameters such as height growth, mortality and volume development (Elfving, 2010).

Table A1.2 Input values of the BEY2 model

Source	**Values used**
Åheden 2021	Age = 130 yr; G = 25.01 $m^2\ ha^{-1}$; N = 1,345.5 stems ha^{-1}; V = 206.1 $m^3sk\ ha^{-1}$; SI = 21 m; latitude = 64.2°; elevation = 230 m; basal-area shares = 0.7889 pine, 0.1656 spruce, 0.0456 birch.
Åheden 2021	V/G = 206.1/25.01 = 8.2407 $m^3sk\ m^{-2}$.
Åheden forest-gap ratio	Retained-forest fraction = 4/9.
Kulbäcksliden K2/K3/K6	Observed CAI = 10.1, 9.1 and 9.9 $m^3sk\ ha^{-1}\ yr^{-1}$.
Kulbäcksliden K2/K3/K6	All wards age = 71 yr; N = 770/874/785 stems ha^{-1}; G = 34.1/35.9/34.2 $m^2\ ha^{-1}$; V = 333.7/331.0/320.7 $m^3sk\ ha^{-1}$; SI = 25/24/24 m; pine basal-area proportions = 0.997/1.000/0.985.

Appendix 2

Volume–carbon conversion methods

Table A2. Volume–C conversions suggestion for further study.

Method and source	Required data → output	Best use here	Do not use when / main limit
Basic density × fC Rytter et al. (2016), Thomas & Martin (2012)	Annual m³sk increment + species volume shares → stem-wood C increment	When only volume data are available. (Current thesis use for Åheden, Kulbäcksliden and Sveaskog)	Not full tree C or NPP. Direct prediction like Botsmark already expressed in g C
Repeated tree Marklund (1988), Repola (2009), Repola & Ahnlund Ulvcrona (2014)	Matched tree IDs, species, DBH, height, mortality/recruitment → annual component biomass/C	Best for Åheden and Kulbäcksliden. Choose equations matching stand structure	Cannot build annual increment from one inventory; model domain must match tree size and density
Age-dependent BEF Lehtonen et al. (2004)	Species-specific stem volume + meaningful stand age → aboveground tree biomass, then C	Forest like Sveaskog RF stands. Available age and species volume	Poor fit for heterogeneous CCF stands without a stand age. Need two-consecutive-year data
Litterfall-growth transfer Matala et al. (2008) + Krycklan study fit	Measured Ltree + regional calibration + forest-area fraction → modelled annual tree-C term	Current estimate for Botsmark. litterfall exists but repeated tree growth does not	Not observed tree growth. transfer and component boundary must match between sites

Litterfall composition and regional inventory context

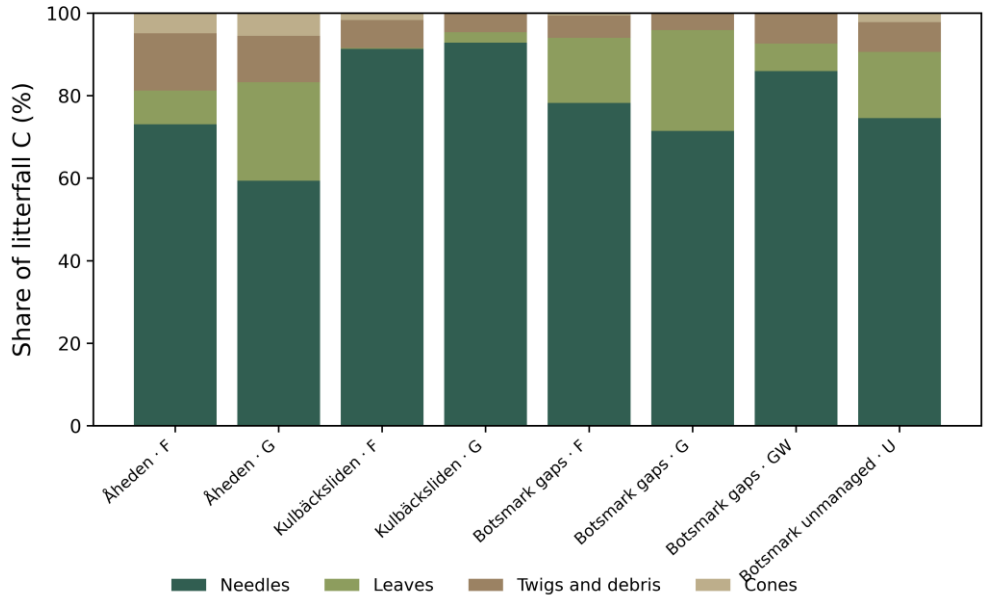


Figure A1. Litterfall component proportions.

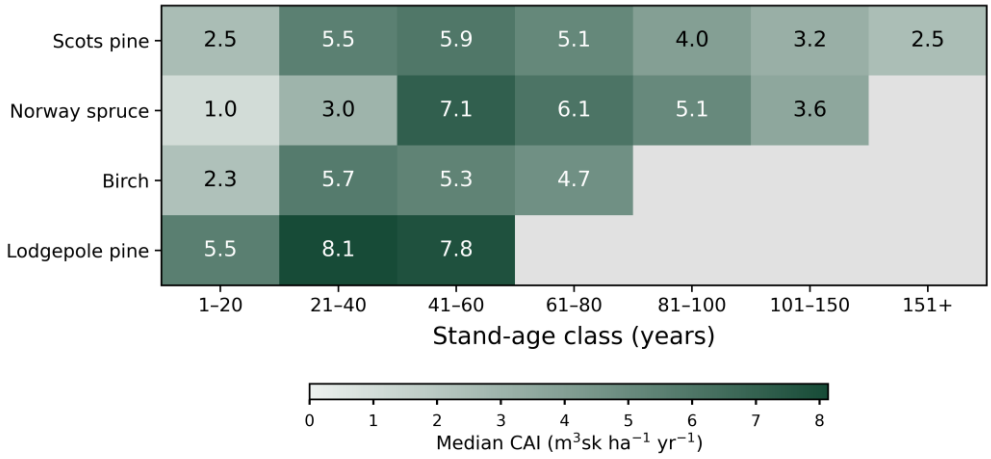


Figure A2. Sveaskog current increment by dominant species group and age class. Values were unweighted compartment medians. Medians for groups with fewer than 10 compartments were not displayed.

Appendix 3

Spatial variability and uncertainty

A sensitivity analysis of the Kulbäcksliden paired plots (one forested plot and one adjacent open area) demonstrated how spatial isolation altered apparent variability without changing the mean values of the 6 equal-area plots (see table). The paired treatment reduced the coefficient of variation (CV) for litterfall from 44.3% to 19.1%. The CV for soil organic carbon (SOC) in the 10–30 cm soil layer was reduced from 12.0% to 1.8%. The CV for temperature-standardized soil heterotrophic respiration (R_{10}) was reduced from 12.5% to 7.0%. The sensitivity of annual soil heterotrophic respiration (sensitivity series) was reduced from 14.9% to 6.8%. Net primary productivity under the canopy (ANPP) was an exception: its standard error (SE) at the paired level increased from 9.44 to 11.02 g C m^{-2} yr^{-1}, because the effect of reducing the number of wards from six to three pairs outweighed the variance eliminated by the clustering. The CV for tree growth across the six subplots was 109.8%, as the yield for all gaps was assumed to be 0. After pairing, the CV for the mean of the blocks was 5.5%. The complete CV table for all the 4 CCF site was in Table A4.

Table A3. Kulbäcksliden uncertainty at two analytical scales. Six-ward statistics treat each equal-area ward as one unit; three-pair statistics use the means of the adjacent gap–forest pairs K1–K2, K4–K3 and K5–K6. CV = 100 × SD/mean.

Variable	Site mean	SE 6wards	CV (%) 6 wards	SE 3 pairs	CV(%) 3 pairs
Current tree-volume increment (m^3sk ha^{-1} yr^{-1})	4.850	2.173	109.762	0.153	5.455
Understory ANPP (g C m^{-2} yr^{-1})	165.388	9.442	13.984	11.024	11.545
Litterfall C (g C m^{-2} yr^{-1})	117.598	21.250	44.262	12.942	19.062
Needle litterfall C (g C m^{-2} yr^{-1})	107.549	18.129	41.289	9.404	15.146
SOC, 10-20 cm (Mg C ha^{-1})	18.220	1.166	15.670	0.298	2.829
SOC, 20-30 cm (Mg C ha^{-1})	11.132	0.658	14.468	0.596	9.268
SOC, 10-30 cm (Mg C ha^{-1})	29.352	1.432	11.953	0.305	1.802
RHsoil at 10 °C, R10 (µmol CO_2 m^{-2} s^{-1})	1.692	0.086	12.465	0.068	6.995
Annual RHsoil, sensitivity (g C m^{-2} yr^{-1})	441.839	26.934	14.932	17.468	6.848

Since all subplots were of equal area, the pairing treatment did not alter the site-level means. They changed the uncertainty presentation by incorporating the checkerboard contrasts within each spatial block and reducing the number of analysis units from six to three. The coefficients of variation (CV) for tree growth in the six wards were extremely high, because the gap cells were assumed to be zero in tree increment. Therefore. these changed values reflect the contrast between habitat states, not a conventional estimate of measurement precision.

Annual soil heterotrophic respiration in the CV tables was the sensitivity calculated from the original measurements, not the final Lloyd–Taylor annual estimate in Section 3.2.2.

Table A4. Coefficient of variation and standard error of the study variables.

System	Variable	Site mean	SE	CV (%)	SE (3 pairs)	CV (3 pairs, %)
Åheden	Current tree-volume increment ($m^3sk\ ha^{-1}\ yr^{-1}$)	7.639	3.042	119.461	—	—
	Understory ANPP (g C $m^{-2}\ yr^{-1}$)	128.061	12.992	30.436	—	—
	Litterfall C (g C $m^{-2}\ yr^{-1}$)	100.483	32.981	98.467	—	—
	Needle litterfall C (g C $m^{-2}\ yr^{-1}$)	68.850	23.308	101.559	—	—
	SOC, 10–20 cm (Mg C ha^{-1})	9.562	0.628	19.693	—	—
	SOC, 20–30 cm (Mg C ha^{-1})	3.503	0.237	20.260	—	—
	SOC, 10–30 cm (Mg C ha^{-1})	13.065	0.781	17.403	—	—
	Soil heterotrophic respiration at 10 °C, R_{10} (µmol $CO_2\ m^{-2}\ s^{-1}$)	1.029	0.120	34.990	—	—
	Annual soil heterotrophic respiration, sensitivity (g C $m^{-2}\ yr^{-1}$)	289.264	32.817	34.035	—	—
Kulbäcksliden	Current tree-volume increment ($m^3sk\ ha^{-1}\ yr^{-1}$)	4.850	2.173	109.762	0.153	5.455
	Understory ANPP (g C $m^{-2}\ yr^{-1}$)	165.388	9.442	13.984	11.024	11.545
	Litterfall C (g C $m^{-2}\ yr^{-1}$)	117.598	21.250	44.262	12.942	19.062
	Needle litterfall C (g C $m^{-2}\ yr^{-1}$)	107.549	18.129	41.289	9.404	15.146
	SOC, 10–20 cm (Mg C ha^{-1})	18.220	1.166	15.670	0.298	2.829
	SOC, 20–30 cm (Mg C ha^{-1})	11.132	0.658	14.468	0.596	9.268
	SOC, 10–30 cm (Mg C ha^{-1})	29.352	1.432	11.953	0.305	1.802
	Soil heterotrophic respiration at 10 °C, R_{10} (µmol $CO_2\ m^{-2}\ s^{-1}$)	1.692	0.086	12.465	0.068	6.995
	Annual soil heterotrophic respiration, sensitivity (g C $m^{-2}\ yr^{-1}$)	441.839	26.934	14.932	17.468	6.848
Botsmark gap-felling	Current tree-volume increment ($m^3sk\ ha^{-1}\ yr^{-1}$)	6.768	1.133	57.407	—	—
	Understory ANPP (g C $m^{-2}\ yr^{-1}$)	123.571	4.601	12.772	—	—
	Litterfall C (g C $m^{-2}\ yr^{-1}$)	175.753	16.288	31.788	—	—
	Needle litterfall C (g C $m^{-2}\ yr^{-1}$)	133.957	11.645	29.817	—	—
	SOC, 10–20 cm (Mg C ha^{-1})	18.578	1.053	19.438	—	—

System	Variable	Site mean	SE	CV (%)	SE (3 pairs)	CV (3 pairs, %)
	SOC, 20–30 cm (Mg C ha^{-1})	7.969	0.857	36.869	—	—
	SOC, 10–30 cm (Mg C ha^{-1})	26.547	1.470	18.992	—	—
	Soil heterotrophic respiration at 10 °C, R_{10} (µmol CO_2 m^{-2} s^{-1})	1.794	0.150	28.753	—	—
	Annual soil heterotrophic respiration, sensitivity (g C m^{-2} yr^{-1})	458.818	38.676	28.913	—	—
Botsmark unmanaged	Current tree-volume increment (m^3sk ha^{-1} yr^{-1})	6.733	0.577	25.718	—	—
	Understory ANPP (g C m^{-2} yr^{-1})	144.214	8.367	17.405	—	—
	Litterfall C (g C m^{-2} yr^{-1})	144.059	15.295	31.851	—	—
	Needle litterfall C (g C m^{-2} yr^{-1})	106.954	14.775	41.444	—	—
	SOC, 10–20 cm (Mg C ha^{-1})	17.422	1.854	31.916	—	—
	SOC, 20–30 cm (Mg C ha^{-1})	11.174	1.751	47.004	—	—
	SOC, 10–30 cm (Mg C ha^{-1})	28.596	2.611	27.388	—	—
	Soil heterotrophic respiration at 10 °C, R_{10} (µmol CO_2 m^{-2} s^{-1})	1.602	0.105	19.586	—	—
	Annual soil heterotrophic respiration, sensitivity (g C m^{-2} yr^{-1})	389.557	25.433	19.586	—	—

Litterfall–R_{10} regression

Table A5. Linear Regression of log(tree litterfall carbon) and log(Rh) at 10℃. And the final columns show the predicted percentage change in R_{10} for 25%, 50%, and 100% increases in litterfall. The amount is modelled, not real data. The purpose is only to test how Rh respond to different litterfall.

Site	n	slope	R^2	p	+25% litterfall	+50%	+100% / twofold
Åheden	9	0.1930	0.824	<0.001 (0.000723)	+4.4%	+8.1%	+14.3%
Kulbäcksliden	6	0.2992	0.471	0.132	+6.9%	+12.9%	+23.0%
Botsmark gap-felling	16	0.1310	0.068	0.331	+3.0%	+5.5%	+9.5%
Botsmark unmanaged	9	0.4233	0.348	0.095	+9.9%	+18.7%	+34.1%

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An interdisciplinary study on natural resource use by the Kawésqar

2026:08 Författare: Sally Thompson
A legacy on the landscape:
The diverging histories of forest roads in Northern Sweden and Southeast Alaska

2026:09 Författare: Alexander Martin
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2026:10 Författare: Xinyao Shang
Effects of Nitrogen Fertilization, Water Treatment, and Environment on Nitrogen Fixation in Boreal Forest Species

2026:11 Författare: Yue Wu
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