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Ecosystem Carbon and Nutrient Balances in Short-Rotation Hybrid Aspen Coppice Under Different Thinning Methods

Reimo Lutter[1] · **Heiki Hepner**[1] · **Arvo Tullus**[2] · **Hyungwoo Lim**[3] · **Tea Tullus**[1] · **Eele Õunapuu-Pikas**[1,2] · **Reeno Sopp**[1] · **Marju Kaivapalu**[1] · **Kristjan Täll**[1] · **Katri Ots**[1] · **Hardi Tullus**[1]

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Abstract

Coppice plantations have gained a high interest for biofuel production and carbon uptake in short rotation cycles. There is a limited knowledge how such intensive coppice management affects soil fertility and nutrients supply to maintain carbon sink. We studied ecosystem carbon and nutrients balance and allocation during a 5-year period in hybrid aspen coppice under different thinning methods in hemiboreal Estonia. The benchmark value for the changes was defined before the coppice emerged after the clear-cut of the previously planted hybrid aspen plantation. The studied systematical thinning treatments were as follows: corridor thinning with removal of 67% of the trees (CT), cross-corridor thinning with removal of 89% of the trees (CCT), and unthinned (UT) coppice. The UT and CT treatments resulted in a positive carbon balance at the ecosystem level. In all treatments, a decrease of soil acidity, organic C, total N, K, Mg and Mn contents, and an increase of soil Cu and B contents were observed in the 0–20-cm deep layer. The concentrations of leaf N, P, and K were higher in UT than in the two thinning treatments, indicating that the aspens had not entirely recovered from the changed root to shoot ratio 2 years after thinning, whereas the leaf mass fraction of medium- and small-sized trees had already increased. Bioenergy harvest from the UT site in a 5-year rotation would cause 5–18% removal of NPK from the total ecosystem pool. Overall, hybrid aspen coppice showed positive ecosystem carbon balance after the first 5-year period; however, further monitoring of soil properties is needed as we found decrease of soil organic C and nutrients concentrations in short term.

Keywords Bioenergy · Thinning · *Populus* · Soil nutrients · Biomass · Ecosystem C balance

Introduction

The European Union (EU) forest and biodiversity strategies for 2030 include the planting of an additional 3 billion trees on non-forest land to promote sustainable wood-based resources for bioenergy production, prevent the loss of biodiversity, and mitigate climate change [1]. Woody biomass contributes over 60% of the total biomass used for energy production in the EU and is the most important renewable energy source in many member states [2]. Afforestation of former agricultural lands with fast-growing woody plants could provide an additional biomass supply for the production of energy and wood products [3–5]. In the context of global climate change, it is vital to determine whether a particular land-use or management system is a carbon (C) sink or source [6].

Fast-growing coppicing tree species such as willows and poplars are commonly used in bioenergy systems [7, 8]. In particular, the coppice-based bioenergy plantations aim to maximize the production of biomass, which is removed from the ecosystem in short rotation cycles, usually less than 5 years [9–11]. Such intensive management practises raise a question about the sustainability of the bioenergy system regarding the supply of resources [12], i.e., is the existing soil fertility sufficient to maintain the productivity of the

Highlights

- Ecosystem carbon and nutrient balance of coppice systems is poorly known for hybrid aspen.
- We studied hybrid aspen bioenergy coppice under different early thinning methods.
- Hybrid aspen bioenergy coppice was a carbon sink at the ecosystem level.
- Hybrid aspen coppice reduced soil C and some nutrients in short term.
- Bioenergy harvest in a 5-year rotation would cause 5–18% removal of NPK from the ecosystem.

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system [13–15] and contribute to climate mitigation as a C sink at the ecosystem level [16, 17].

Fast growing trees can mitigate flooding and reduce nutrient leaching, but on the other hand, high productivity in bioenergy coppice systems results in a high demand for nutrients and water supply from the soil [18]. The frequent bioenergy harvests with the removal of high amounts of nutrients could reduce the natural nutrient pool [15, 19–21] and cause an additional need for fertilisation [22]. The removal of high amounts of nutrients from the bioenergy system is caused by the whole-tree harvest of small trees where the proportion of nutrient-rich bark and branches is relatively high in comparison to nutrient-low wood [21, 23]. In addition, if harvesting is carried out during the active vegetation period, significant amounts of nutrients contained in the foliage will also be removed from the ecosystem [24].

Maintaining soil fertility in bioenergy systems is the key to climate mitigation as sufficient nutrient supply is one of the main drivers of ecosystem C sequestration capacity [6, 25]. The main C input flux in the bioenergy system occurs during CO_2 fixation into woody biomass and the ecosystem acts as a C sink if the net primary production off-sets the C output fluxes. Existing knowledge of the C balance of coppice systems originates mainly from temperate zone poplar and willow stands, where bioenergy coppice systems are considered to be C sinks rather than sources [9, 26, 27]. Direct extrapolation of the effects of bioenergy systems on ecosystem C balance in the temperate zone to the hemiboreal zone could be inaccurate due to lower soil fertility in Northern Europe [28, 29]. Moreover, previous studies [9, 26, 27] have only focused on C pools and fluxes, whereas ecosystem responses such as soil nutrient supply and their levels in trees should also be evaluated in order to assess the factors driving C sequestration.

In Northern Europe, hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) is considered suitable for the afforestation of former agricultural lands because of its high productivity [30, 31] and ability to improve biodiversity in agricultural landscapes [32, 33]. Hybrid aspen regenerates from the coppice [34] (Tullus et al., 2012), where more than 100,000 stems per hectare can be found in the first year after coppicing [35, 36]. In Northern Europe, hybrid aspen bioenergy coppice can achieve high productivity after 5 years from clearcutting [36–39]. The coppice of hybrid aspen can be managed using very short rotation cycles (approximately five years) for bioenergy production [10, 37] or with 25-year rotation cycles for the combined production of pulp, logs, and bioenergy [10, 36, 37]. Longer rotation cycles aim to grow larger dimension individual trees, and therefore, heavy thinnings have been recommended at the early stages when the stand initiates from coppice [10, 35].

The choice of a sustainable management strategy for hybrid aspen coppice is challenging as the early thinning practise for deciduous tree species in Northern Europe has focused on seed-generated single-tree management [40]. Hybrid aspen regeneration strategy is different as new sprouts from the existing root system of the parent tree will function as one organism [34]. The individual root system of hybrid aspen can produce on average approximately 100 individual trees after coppicing [36, 37]. At the same time, single-tree thinning reduces tree density considerably, which results in growth cessation because of the imbalance between the reduced leaf area and the existing extensive root area [36, 41, 42]. Therefore, it has been recommended to manage hybrid aspen coppice by conducting systematic early thinnings with a lower degree of tree removal by using the corridor method (2-m-wide corridor harvest leaving 1-m-wide tree lines) or with a higher degree of tree removal using the cross-corridor method (by cutting additional 2-m-wide corridors across by leaving 1 × 1 m tree groups) [35, 36] (Fig. 2). The thinned woody biomass can be used for bioenergy production if the trees are removed from the site or for providing a source of nutrients to support the growth of the remaining trees by leaving the cut trees to decompose [35]. However, there is still a lack of information on how those methods affect the nutrient dynamics of the ecosystem, which is necessary to support C sequestration.

To the best of our knowledge, only one previous study from Southern Sweden has investigated soil nutrient cycling in a hybrid aspen coppice [15]. In this study, the authors compared hybrid aspen bioenergy coppice management using corridor and cross-corridor thinning methods over 8 years on former agricultural land and found a significant decrease in soil nitrogen (N) independent from the thinning treatment while the levels of other macronutrients remained unchanged [15]. N and phosphorous (P) are considered the key nutrients required for maintaining the productivity of bioenergy plantations [20, 24]. In addition, the study by Rytter and Rytter [15] covered only the macronutrients in the soil, while the dynamic of micronutrients in hybrid aspen coppice was not investigated. The sustainable supply of microelements in the soil is considered critical not only for maintaining physiological processes [16, 43, 44] but also for avoiding reduced productivity (B) [44].

Bioenergy crop is harvested during the leafless period, which means that the nutrients in the foliage will be released at the harvesting site during decomposition. Leaf nutrient concentrations are important indicators of the nutritional status of the ecosystem, as the sufficient supply of nutrients supports C accumulation both aboveground and in the soil via litter. Nutrient acquisition within the stand depends on their supply from the soil, as well as the competitive status of the trees and the forest management strategy (e.g., thinning)

[45, 46]. Early corridor and cross-corridor thinning can improve the light conditions and soil nutrient availability of individual trees [36, 45] and subsequently improve their productivity. So far, there is limited understanding of how early thinning affects the nutritional status of hybrid aspen trees, soil fertility, and ecosystem C balance, and to what degree are nutrients removed from the ecosystem as a result of bioenergy harvest.

The current study aimed to investigate hybrid aspen coppice ecosystem C balance under different thinning methods during the first 5 years, and to determine the associated trends in the nutrient dynamics of the soil and trees. The specific aims of the present study were as follows: i) assess ecosystem carbon balance during the first 5 years after coppicing, ii) describe early changes in soil fertility and link it with ecosystem characteristics, and iii) estimate nutrient uptake and removal from the ecosystem as a result of bioenergy harvest.

Material and Methods

Study Site

The experimental site was located in southern Estonia (58° 19′ 40″ N, 26° 33′ 16″ E), which belongs to the hemiboreal vegetation zone (Fig. 1). The study area is characterised by a flat landscape and a soil type typical to southern Estonian former agricultural soils—*Retic Umbrisol*. The average temperature and precipitation of the 5-year study period (2014–2018) were 6.9 °C and 684 mm year^{-1}, respectively, according to Estonian Weather Service.

The initial hybrid aspen stand was planted as a commercial plantation using 14 different clones (1-year-old containerized seedlings) and a planting density of 1300 trees ha^{-1}. The clones were planted randomly over the experimental area and there was no information about the location of the specific clones. No forest management activities such as thinning or fertilization were conducted during the 14-year period before the clearcutting.

The coppicing experiment was carried out in a 2-ha area, where the 14-year-old hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) plantation was clear-cut in the winter season of 2013/14. The clearcutting was carried out using the whole-tree harvest method, whereby all trees, including branches and treetops, were removed from the clearcutting area by a forest harvester and forwarder. The clear-cut area regenerated vegetatively with hybrid aspen coppice in the spring of 2014. Hybrid aspen was the dominant tree species in the regeneration and the share of self-seeded accompanying tree species (*Betula* spp. and *Salix* spp.) was negligible. The clear-cut area was fenced to avoid potential damage to the trees by game.

The experimental area was established at the clear-cut site in the spring of 2014 (before the vegetation period), by creating nine 30 × 40 m (0.12 ha) rectangular treatment plots, which were separated from each other by 2-m-wide corridors (Fig. 2). On each rectangle, three mensuration plots were marked. After the first growing season, the mean density of hybrid aspen coppice was 94,000 stems ha^{-1} with an even coverage over the experimental area [36]. After defoliation at the end of the second growing season, the thinning experiment started by implementing the following treatments (three replicate plots per treatment): 1) systematic corridor thinning (CT), where 2-m-wide corridors were cut and 1-m-wide corridors with trees remained (67% removal from the area by reducing the density to 24,000 trees ha^{-1}); 2) systematic cross-corridor thinning (CCT), where in addition to the 2-m-wide corridors, 2-m-wide corridors were cut perpendicularly and 1 × 1 m tree groups remained (89% removal from the area by reducing the density to 9000 trees ha^{-1}); and 3) unthinned area (UT), where no thinning was applied. Both thinning treatments (CT and CCT) were carried out with a brush saw and all cut trees were left on site as deadwood. The thinning treatments were assigned semi-randomly to the treatment plots over the experimental area, ensuring that the same treatment occurred only once per row and per column (Fig. 2). After 5 years, self-thinning had reduced the density of hybrid aspen to 33,000 trees ha^{-1} in UT, to 19,000 trees ha^{-1} in CT, and to 8000 trees ha^{-1} in CCT [36]. Within the 5-year observation period, no additional forest management activities were carried out in the experimental area.

Three mensuration (sample) plots with a radius of 2 m (12.6 m^2) were established on each 0.12 ha rectangular plot after clearcutting in 2014, with a total of nine plots per treatment (Fig. 2). The mensuration plots were distributed diagonally inside the rectangle. After the thinnings at the end of the second growing season in 2015, the radius of the mensuration plots was expanded to 3 m (28.3 m^2) in the CT and CCT treatments (to ensure a critical minimum number of measurable trees) and remained at 2 m for the UT treatment when the measurements continued at the end of 2016.

Growth Measurements and Productivity

In each mensuration plot, the height (*H*, m), diameter at a height of 30 cm from the ground (D30, mm), and diameter at breast height (DBH, mm) of all trees were measured at the end of each growing season. Tree height was recorded with a telescopic measuring rod (< 8 m) and with Vertex IV (Haglöf Sweden AB) (> 8 m). D30 and DBH were measured over bark with a digital calliper (Mitutoyo CD-P15P, Japan).

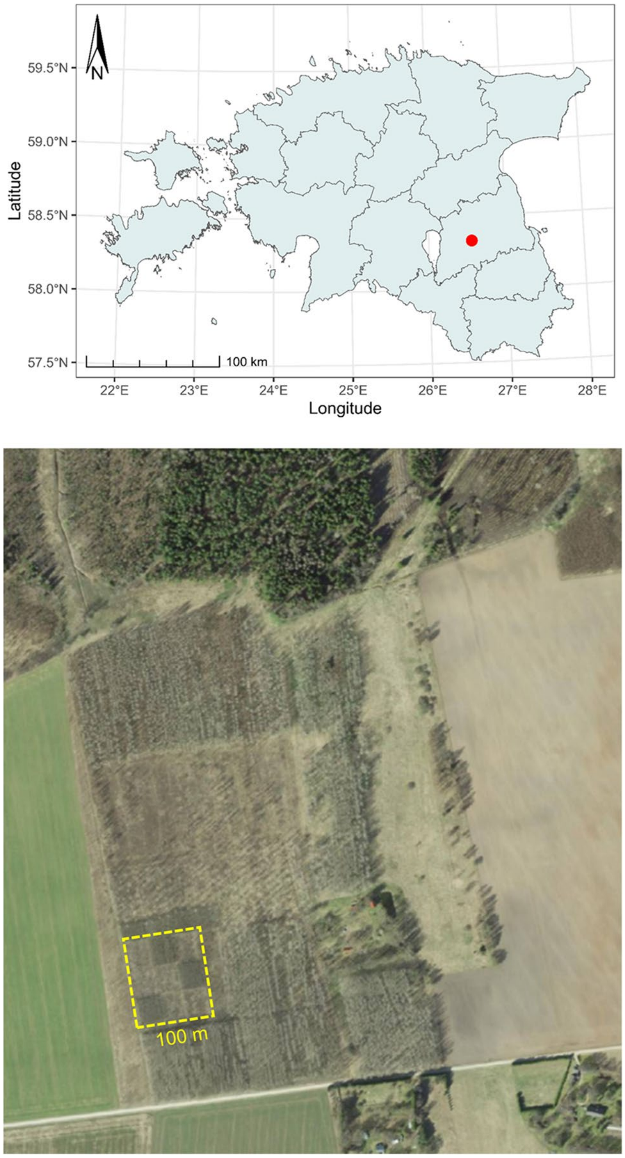

Fig. 1 Location of the studied plantation in Estonia. Orthophoto image obtained from Estonian Geoportal (https://geoportaal.maaamet.ee/eng/)

Nutrients and Carbon in Biomass

Leaf N, P, and K concentrations (%) were studied after the 4th growing season since clear-cutting. Leaf and woody biomass sampling for measuring N, P, K, and C (only for wood) concentrations (%) was carried out after the 4th growing season. Leaf sample trees were harvested in the second half of July, i.e., when the trees had obtained their peak leaf mass of the growing season. Woody biomass sample trees were harvested in the same year after defoliation in November. In both cases, three sample trees per mensuration plot (altogether 81 sample trees per site) were removed based on the height class determined according to the height distribution on each mensuration plot—dominant tree (> 3rd quartile), medium tree (between 1st and 3rd quartiles), and supressed tree (< 1st quartile). Sample trees were harvested outside the mensuration plots to avoid disturbing the plots.

All leaves of the sample trees were removed and their fresh weight was measured (g). Twenty undamaged leaves per sample tree were collected across the crown and taken to the laboratory for measurements and chemical analyses. The fresh weight (g) of the sample leaves was measured and the leaves were then dried at 70 °C to a constant weight for dry matter estimation. The dry mass of the leaves of each individual tree in the stand was predicted using allometric regression equation [36] and summed up to the stand level (kg of leaves per ha):

$$LB = 0.028 \times D30^{2.385}$$

where LB is the dry biomass of the leaves (g), D30 is the stem diameter over the bark at 30 cm from ground level (mm), $R^2 = 0.87$, and $p < 0.001$.

Woody biomass sample trees were taken to the laboratory where they were dried at 70 °C to a constant weight to obtain dry matter concentrations (%). Aboveground woody biomass of the study site (kg of woody biomass per ha) was estimated as part of the present study (Table 1) based on the sample trees and the following allometric regression [36]:

$$AGB = 0.1749 \times D30^{2.4337}$$

where AGB is aboveground leafless dry biomass (g), D30 is the stem diameter over the bark at 30 cm from ground level (mm), $R^2 = 0.99$, and $p < 0.001$.

The sample leaves and biomass sample trees (stem, bark, and branches pooled) were homogenized with a Retsch SM 300 mill (Retsch GmbH Germany) and subjected to macronutrient (N, P, and K) and C content analysis (Table 2). The concentration of leaf nitrogen (N, %) was determined according to the Kjeldahl method, using a Kjeltec Auto 1030 Analyzer (Fross Tecator Sweden AB). After Kjeldahl digestion, the concentrations of leaf and wood phosphorous (P, %) were measured spectrophotometrically with the FIAstar 500 Analyzer (FOSS Tecator Sweden AB), and the concentrations of leaf and wood potassium (K, %) were determined based on the flame-photometrical method, using a Sherwood Model 425 Flame Photometer. The concentrations of N (%) and C (%) in the woody biomass were measured with a varioMAX CNS (Elementar Analysensysteme GmbH Germany). All analyses were done in the Laboratory of Plant Biochemistry and the Laboratory of the Department of Soil Sciences and Agrochemistry at the Estonian University of Life Sciences.

The stand level N, P, K, and C pools and allocation were estimated after the 5th growing season, i.e., at the bioenergy harvest age of the unthinned site in order to estimate the

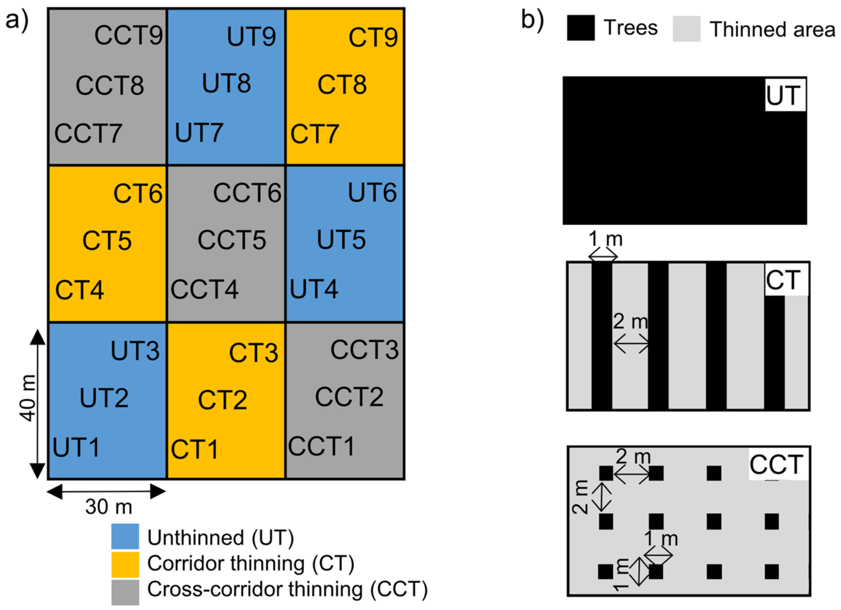

Fig. 2 Study design (**a**) and graphical illustration of thinning treatments (**b**). The numeric notation in the study design scheme (**a**) marks the location of the mensuration plots within each rectangle (i.e., treatment plot). In (**b**), gray represents the thinned area and black represents the area where trees remained

degree of nutrient removal during harvesting. The concentrations of leaf and wood nutrients (N, P, and K) and whole-tree C measured on the 4th growing season were multiplied by the leaf and woody biomass (living trees) of the 5th growing season, assuming no major changes in their nutrient and C concentrations over one year (Table 2). Leaf mass fraction (LMF, %) for the individual model trees was estimated as the ratio of foliage mass (g) to total aboveground tree biomass as measured during the summer leaf model tree sampling after the 4th growing season.

Soil Sampling

Soil sampling of the site was carried out after clearcutting in the spring of 2014 and repeated after the 4th growing season in November 2017 (Table 3). On both sampling occasions, two subsamples were collected next to the sample plots (approximately 50 cm outside of the sample plot border) from the upper 0–20 cm vertical soil layer and pooled into one sample per plot. In order to avoid overlapping of the soil pits, the samples were collected from the north–south direction during the first sampling occasion and from the west–east direction during the second sampling occasion. Forest floor was not sampled as it was absent. Before laboratory analyses, the soil samples were dried at room temperature and sieved to remove stones. Soil bulk density (BD, g cm^{-3}) was estimated in three replicates from soil depths of 0–l0 cm and 10–20 cm with a steel cylinder (43 cm^{3}) horizontally from the vertical profile of soil. Soil BD samples were oven dried at 105 °C to a constant weight, and the mean soil BD over the 0–20 cm soil profile was calculated based on the subsamples.

Soil acidity (pH$_{\mathrm{KCl}}$) was measured according to the ISO 10390 standard. Plant-available phosphorus (P, mg kg^{-1}), potassium (K, mg kg^{-1}), calcium (Ca, mg kg^{-1}), magnesium (Mg, mg kg^{-1}), copper (Cu, mg kg^{-1}), and manganese (Mn, mg kg^{-1}) were measured using the Mehlich III method [47]. Plant-available boron (B, mg kg^{-1}) was measured using the Berger and Truog method [48]. The concentrations of total nitrogen (N$_{\mathrm{tot}}$, %) and soil organic carbon (C$_{\mathrm{org}}$, %) were measured using the varioMAX CNS (Elementar Analysensysteme GmbH Germany). The soil analyses were done in the Laboratory of the Department of Soil Sciences

Table 1 Nutrient and carbon concentrations (mean ± SE, $n = 81$) in leaves and woody biomass after the 4th growing season in the thinning treatments. Woody biomass describes the whole-tree (except leaves) concentrations as stem, bark, and branches were pooled during the grinding

Treatment	Leaves			Woody biomass (stem, bark, and branches)			
	N (%)	P (%)	K (%)	N (%)	P (%)	K (%)	C (%)
UT	2.88 ± 0.067	0.32 ± 0.011	0.80 ± 0.023	0.54 ± 0.007	0.09 ± 0.002	0.32 ± 0.005	47.3 ± 0.07
CT	2.51 ± 0.037	0.29 ± 0.007	0.67 ± 0.037	0.56 ± 0.017	0.09 ± 0.003	0.31 ± 0.005	46.9 ± 0.16
CCT	2.40 ± 0.042	0.25 ± 0.006	0.61 ± 0.009	0.61 ± 0.008	0.09 ± 0.002	0.31 ± 0.006	46.6 ± 0.12

UT unthinned, *CT* corridor thinning, *CCT* cross-corridor thinning and Agrochemistry at the Estonian University of Life Sciences and in the Agricultural Research Centre in Saku. The same methods and laboratories were used for both sampling occasions.

For observations over a long period and across treatments, representation of the soil depth for BD is often biased due to compressions caused by forestry practices (e.g., thinning) or swelling due to litterfall accumulation. To overcome this issue and estimate the changes of soil nutrients and C_{org}, we estimated elemental mass using the equivalent soil mass, normalized by a constant soil mass [49]. Briefly, we first determined the relationship between accumulated element mass and mineral soil mass over the soil depth for each treatment and applied the average mineral soil mass across the treatments from 2014 as a reference mass, to the developed relationship for each plot to predict normalized element mass for each plot.

Ecosystem Carbon Balance

The rotation cycle of hybrid aspen coppice (unthinned treatment in our study) is 5 years [10]. In order to quantify ecosystem carbon balance at the end of the 1st harvest cycle and compare the balance among the thinning methods, we estimated the changes in the carbon stocks of various ecosystem components over a period of 5 years after coppicing. The reference value for ecosystem carbon balance was zero, i.e., the experiment started after the clearcutting of the 14-year-old stand and before the coppice emerged. The benchmark value of zero was chosen as the management model changed to 5-year coppice cycle and it would never recover the old stand C stocks, e.g., aboveground C stock of 15-year-old hybrid aspen first generation stand at the same experimental area was 42.1 Mg C ha^{-1} [50]. The 5-year balance was calculated based on carbon gain (positive accumulated flux) and carbon loss (negative emission flux). As we determined the changes in stable ecosystem carbon stocks after the 5-year period, deadwood contributed to both carbon gain and carbon loss.

The 5-year carbon gain of the ecosystem was determined based on aboveground biomass, coarse roots, and undecomposed deadwood from self-thinning and thinned woody biomass at the 2nd growing season. We did not measure coarse root biomass in the present study although it represents an important carbon stock for *Populus* spp. [51]. As there are no existing allometric equations to estimate coarse root biomass for hybrid aspen coppice, it was estimated to be 20% of the total stand biomass based on previous studies involving *Populus* spp. and other deciduous tree species in boreal and temperate regions where it can range between 10 and 30% [50–53]. Deadwood originating from self-thinning and harvesting was left on the site for decomposition. As the

Table 2 General growth characteristics (mean ± SE) of the hybrid aspen after the 4th (Y4) and 5th (Y5) growing season, and the thinned biomass after the 2nd growing season in the thinning treatments

Treatment	Height (cm)		SLC (%)	BM (Mg ha^{-1})		CAI of BM (Mg ha^{-1})		LBM, Mg ha^{-1}		NSBM, Mg ha^{-1}	TBM, Mg ha^{-1}
	Y4	Y5	Y4	Y4	Y5	Y4	Y5	Y4	Y5	Y5	Y2
UT	4.53 ± 1.2	5.26 ± 1.8	36 ± 2	24.9 ± 2.5	29.2 ± 3.1	6.7 ± 1.0	5.5 ± 1.0	3.1 ± 0.3	3.9 ± 0.4	0	0
CT	4.20 ± 1.2	5.03 ± 1.4	51 ± 2	14.3 ± 0.9	19.2 ± 1.5	3.7 ± 0.3	5.2 ± 0.7	1.8 ± 0.1	2.5 ± 0.2	0.04 ± 0.02	6.2 ± 0.3
CCT	3.96 ± 1.0	5.14 ± 1.5	60 ± 2	6.4 ± 0.6	10.6 ± 0.9	1.8 ± 0.2	4.6 ± 0.5	0.8 ± 0.1	1.4 ± 0.1	0.68 ± 0.19	8.1 ± 0.6

**SLC* share of living crown, *BM* aboveground living biomass, *CAI* current annual increment, *LBM* leaf biomass, *NSBM* aboveground living biomass of new shoots, *TBM* thinned biomass, based on the thinning rate (CT–67% and CCT–89%) from the biomass estimate per treatment plot after the 2nd growing season, *UT* unthinned, *CT* corridor thinning, *CCT* cross-corridor thinning

Table 3 Soil chemical characteristics (mean ± SE) of the 0–20 cm layer after the 4th growing season in the thinning treatments

Treatment	pH_{KCl}	$^{a}C_{org}$ (%)	$^{b}N_{tot}$ (%)	P (mg kg^{-1})	K (mg kg^{-1})	Ca (mg kg^{-1})	Mg (mg kg^{-1})	Mn (mg kg^{-1})	Cu (mg kg^{-1})	B (mg kg^{-1})	^{c}BD (g cm^{-3})
UT	5.29 ± 0.10	1.15 ± 0.07	0.077 ± 0.004	180 ± 7	167 ± 5	883 ± 47	89 ± 7	118 ± 2	1.27 ± 0.05	0.54 ± 0.07	1.29 ± 0.03
CT	5.30 ± 0.11	1.10 ± 0.06	0.080 ± 0.004	170 ± 8	172 ± 13	848 ± 30	87 ± 4	117 ± 3	1.43 ± 0.08	0.55 ± 0.07	1.33 ± 0.05
CCT	5.24 ± 0.07	1.08 ± 0.03	0.082 ± 0.005	180 ± 3	184 ± 9	835 ± 33	80 ± 5	113 ± 3	1.21 ± 0.05	0.39 ± 0.03	1.30 ± 0.02

UT unthinned, *CT* corridor thinning, *CCT* cross-corridor thinning

[a] Soil organic carbon (C_{org})

[b] Soil total nitrogen (N_{tot})

[c] BD–soil bulk density

majority of deadwood was not decomposed, the self-thinned and thinned biomass was multiplied by 0.845 to determine the fraction of weakly decayed deadwood [54] and added to the 5-year carbon gain.

The 5-year carbon loss from the ecosystem was described based on the change of soil C_{org} stocks, as well as self-thinning and thinned woody biomass after the 2nd growing season. The soil C_{org} balance was estimated as a change in the equivalent soil mass pools of the upper 0–20 cm soil layer, i.e., the difference in C_{org} stock between year 0 (after the clearcutting of the 1st generation hybrid aspen stand) and year 4. We assumed C_{org} stock at year 4 to roughly correspond to the coppicing year (year 5). 15.5% of the C in the thinned and self-thinned biomass was assumed lost due to decomposition [54].

For each sample plot, the aboveground remaining living woody biomass was converted to carbon stocks based on the C concentrations of different compartments (Table 1). The woody biomass of coarse roots and new shoots that grew on the thinning treatments were also converted to carbon stock based on the same C concentration (Table 1). The total ecosystem carbon balance after the 5th year was calculated as the difference between the gains and losses of different parts of the ecosystem.

Statistical Analyses

A linear mixed model with the random effect of the replication (rectangle) was applied to test the effect of fixed factors: the sampling year (repeated samplings in year 0 and year 4) and the thinning treatment (unthinned, corridor thinning, and cross-corridor thinning) on the changes (difference between the final and the initial value) in the soil chemical properties, using the R package “*lme4*.” The main effects of the thinning treatment and year and their interaction were tested with Type III Anova using Satterthwaite’s approximation of degrees of freedom. The comparison of the estimated group means was done with the Tukey's test with R package “*emmeans*.”

The effects of the thinning treatments and tree size class on leaf and wood (stem and branches) nutrient concentrations were tested with a linear mixed model (replication = random factor).

The average change in soil chemical characteristics can be close to zero if some plots show an increase and others a decrease. Therefore, we tested the following potential drivers to describe the four-year change in soil chemical characteristics: aboveground living woody biomass, initial soil pH_{KCl}, understorey vegetation cover (based on visual estimation of the cover of vascular plants in 4 m^2 sized plots, located in the center of the mensuration plot, $n = 9$ for each treatment, monitoring in July at study year

4 in 2017) and soil bulk density. After backward stepwise model selection (R package "*MASS*" and command "*stepAIC*"), we applied a general linear model (R command "*lm*") to determine how the changes in the chemical characteristics of the soil were associated with the remaining living biomass at year 5 as well as soil variables. All explanatory variables were standardised to compare the magnitude of their effects (model coefficients). The model variance inflation factors (VIFs) were calculated using the R command "*vif*" to detect potential multicollinearity of the independent variables. The VIF values were below 2, indicating a low level of multicollinearity.

The normality of the studied variables was checked with the Shapiro–Wilk test and the normality of the model residuals with Q-Q plots. If the assumption of normality was not met, log transformation was applied to the given variable. The level of significance of $\alpha = 0.05$ was used to reject the null hypothesis of the statistical tests. All statistical analyses were conducted using the R Statistics software [55].

Results

Ecosystem Carbon Balance After 5 Years

The 5-year balance of ecosystem carbon pools (mean ± 95% CI) was positive for the UT (14.2 ± 7.9 Mg C ha^{-1}) and CT treatment (8.6 ± 7.9 Mg C ha^{-1}) and neutral for the CCT treatment (6.0 ± 7.8 Mg C ha^{-1}) (Table 4). Carbon gain after 5 years was higher in UT than CCT, and CT showed a carbon gain level similar to other treatments, even though the CT aboveground living biomass was almost twice as high in comparison with CCT (Table 2). Soil carbon losses were similar among the studied thinning treatments and encompassed zero (mean ± 95% CI) for all treatments. For the UT site, removal of carbon fixed in the woody biomass for bioenergy production during the dormant season after the 5th growing season was 14.4 Mg C ha^{-1} (includes deadwood).

Changes in Soil Chemical Properties

The effect of the thinning treatment and sampling year interaction was only significant for the soil C:N ratio ($p = 0.005$), where a 10% increase was found in the UT treatment and a 10% decrease in the CCT treatment four years after the clearcutting (Fig. 3c). A significant main effect of time since the clear-cut (year) was found for some soil chemical properties across the thinning treatments (Fig. 3). A significant decrease was found for C_{org} (− 11.8%; $p = 0.002$), N_{tot} (− 11.5%; $p = 0.001$), pH_{KCl} (− 3.4%; $p = 0.002$), plant-available K (− 12.1%; $p < 0.001$), plant-available Mg (− 14.0%; $p < 0.001$), and plant-available Mn (− 13.8%; $p < 0.001$). A significant increase was found for plant-available Cu (+ 8.9%; $p = 0.038$) and plant-available B (+ 40.6%; $p = 0.023$) over all treatments. Changes in plant-available P (Fig. 3e) and Ca (Fig. 3g) were insignificant.

Effect of Stand and Soil Factors on Soil Changes

Soil BD was negatively correlated with ΔN_{tot}, and Δ_{Corg} (Table 5), i.e., their content decreased more when soil BD was higher. Aboveground biomass was positively correlated with the ΔC:N ratio and ΔB. Soil acidity significantly affected ΔB and ΔCa, i.e., plant-available B and Ca improved in plots with a lower soil pH_{KCl} value (Table 4). Vegetation cover was positively correlated with ΔN_{tot} (Table 5).

Effect of Thinning and Tree Size on Leaf Nutrient Concentrations

The concentration of leaf N was significantly higher in the UT site than for other thinning treatments among all size classes of trees (Fig. 4a). For all trees, leaf N concertation was 13% lower for CT and 17% lower for CCT than for the UT site (Fig. 4a). The concentration of leaf P was higher in UT and CT sites for dominant and medium trees, but not for supressed trees where it was lower for CT (− 16%) and CCT (− 25%) methods (Fig. 4b). The concentration of leaf K showed a similar pattern to N and P, being higher in the UT site compared to other thinning methods for medium and supressed trees, but not for dominant trees (Fig. 4c). In the UT site, the concentration of leaf K was higher for the supressed trees than for medium and dominant trees (Fig. 4c).

Woody biomass nutrient concentrations varied less among the thinning methods than those of leaves. Significant differences were only found for wood N concentration, which was lower for the UT site of medium and supressed trees than for other thinning methods (Fig. 4d). Across all tree sizes, the concentration of N was higher for the CCT method than for the UT site (Fig. 4d). In general, the concentration of wood N was higher for dominant trees than for supressed trees, except for the CCT method where the outcome was opposite (Fig. 4d). The concentrations of wood P and K were higher for dominant and medium trees than for supressed trees in the UT site (Fig. 4d, e). The other thinning methods did not reveal differences in the concentrations of wood P and K among the tree size classes (Fig. 4d, e).

Although the stem volume index (DBH^2H) of the model trees did not differ among the thinning treatments

Table 4 Ecosystem carbon balance (change of pools, Mg C ha^{-1}) for different thinning methods 0–5 years after clearcutting of a 14-year-old hybrid aspen stand. Means are presented with 95% confidence intervals and are italicized when the confidence range encompasses zero, *p*-value shows the statistical significance of the thinning treatment effect

	ΔEcosystem (Mg C ha^{-1})	UT	CT	CCT	*p*-value
C gain	ΔAboveground living biomass	+ 13.8 ± 2.4^{a}	+ 9.0 ± 2.4^{b}	+ 4.9 ± 2.4^{b}	0.002
	$^{(1)}$ΔCoarse root biomass	+ 3.5 ± 0.7^{a}	+ 2.3 ± 0.7^{b}	+ 1.2 ± 0.7^{b}	0.002
	ΔNew shoots	*0*	+ 0.04 (0.01–0.3)^{a}	+ 0.3 (0.01–0.3)^{a}	0.133
	$^{(2)}$ΔUndecomposed deadwood from self-thinning	+ 0.6 (0.3–1.5)^{a}	+ 0.2 (0.06–0.4)^{b}	+ 0.1 (0.04–0.2)^{b}	0.002
	$^{(2)}$ΔUndecomposed deadwood from thinning	*0*	+ 2.5 ± 0.5^{b}	+ 3.2 ± 0.5^{a}	0.017
	ΔTotal 5-year C gain	+ 17.9 ± 3.4^{a}	+ 14.0 ± 3.4^{ab}	+ 9.7 ± 3.4^{b}	0.015
C loss	$^{(2)}$ΔDecomposed deadwood from self-thinning	− 0.1 (− 0.3– − 0.05)^{a}	− 0.03 (− 0.07– − 0.01)^{b}	− 0.02 (− 0.04– − 0.01)^{b}	0.002
	$^{(2)}$ΔDecomposed deadwood from thinning	*0*	− 0.5 ± 0.1^{b}	− 0.6 ± 0.1^{a}	0.017
	$^{(3)}$ΔSoil 0–20 cm	*− 3.6 ± 7.1*^{a}	*− 4.9 ± 7.0*^{a}	*− 3.1 ± 7.0*^{a}	0.903
	ΔTotal 5-year C loss	*− 3.7 ± 7.0*^{a}	*− 5.4 ± 7.0*^{a}	*− 3.7 ± 7.0*^{a}	0.899
ΔTotal ecosystem 5-year balance, Mg C ha^{-1}		+ 14.2 ± 7.9^{a}	+ 8.6 ± 7.9^{a}	+ *6.0 ± 7.8*^{a}	0.259

UT unthinned, *CT* corridor thinning, *CCT* cross-corridor thinning

$^{(1)}$Estimated as 20% of the total aboveground biomass

$^{(2)}$Based on aspen deadwood decay rate of 15.5% [54]

$^{(3)}$Soil change was estimated based on samples collected at year 4

The superscript letters (^{a}, ^{b}) show the differences among the thinning methods

in any size class, average foliage mass per tree was significantly higher in CT and CCT than in UT for all size classes (Fig. 5). Leaf mass fraction (LMF) of dominant trees did not differ significantly among the thinning treatments. The LMF of medium trees was significantly higher for the two thinning methods than for UT but did not differ between CT and CCT. The LMF of the suppressed trees differed most notably among all treatments (UT < CT < CCT).

Ecosystem Nutrient Pools 5 Years After Clearcutting

The main pools of nutrients are located in the soil where their share varies between 76.7 and 97.2% of the total ecosystem pool (deadwood excluded), depending on the thinning treatment and the specific nutrient (Fig. 6). Nutrient pools in the wood did not differ between the UT and CT but were lower for the CCT than for the UT site. Leaf N content differed among the thinning methods and was the highest for the UT site. Leaf P and K contents were significantly lower for the CCT method than for the other treatments. Nutrient removal from the UT site at the end of the growing season after year 5 was 169 ± 17 kg N ha^{-1} (7.5% of the total pool), 27 ± 3 kg P ha^{-1} (5.3% from the total pool), and 99 ± 11 kg K ha^{-1} (17.7% of the total pool).

Discussion

Ecosystem Carbon Balance

The main aim of the study was to assess how hybrid aspen coppicing under different thinning methods affects ecosystem C balance during the 5-year cycle of harvesting for bioenergy production. To the best of our knowledge, there have been no previous studies on ecosystem C balance in hybrid aspen coppice systems. We found that the net ecosystem C change 5 years after coppicing was positive and the high productivity of the UT and CT method compensated for the soil C loss. Unthinned hybrid aspen coppice can produce up to 8–10 Mg ha^{-1} yr^{-1} of dry woody biomass during the 5-year rotation cycle [35–37, 39], which is approximately 4–5 Mg C ha^{-1} yr^{-1}. Thinnings can temporarily reduce the carbon sink effect of the forest ecosystem as the stand-level leaf mass is reduced [56, 57]. In this study, we evaluated a 3-year period after thinning, which could be too short for complete leaf mass recovery and for obtaining pre-thinning levels of productivity [36]. In fact, the aboveground living biomass and its current annual increment were nearly two-fold higher in the CT than the CCT treatment at the studied age period [36]. It could be related to the different mechanism of C allocation in the CCT treatment to recover the balance between leaf

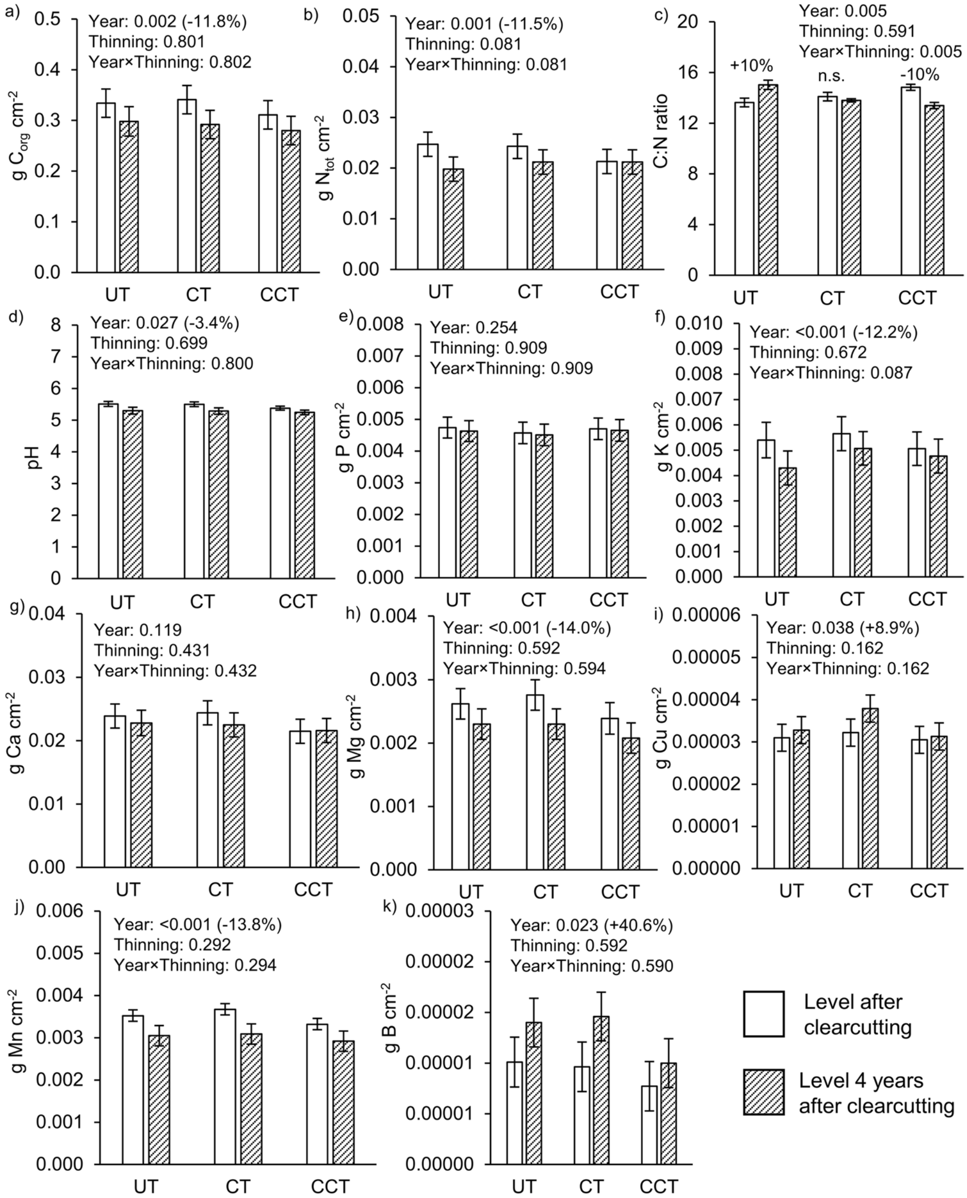

Fig. 3 Four-year changes in soil chemical properties (a-k) of the 0–20 cm profile under different thinning treatments. Soil values (estimated marginal means ± SE) are normalised based on equivalent soil mass according to von Haden et al. (2020) [49]. UT: unthinned; CT: corridor thinning; CCT: cross-corridor thinning. The effects of year, thinning, and year × thinning are characterized by their statistical significance (*p*-value)

and root mass [36, 37]. McCarthy and Rytter [37] studied the same thinning treatments and found the CT and CCT treatments resulted in similar aboveground UT biomass approximately 4–5 years after the start of the thinnings at year 2. Carbon accumulation occurred mainly in the aboveground woody biomass and coarse roots. The deadwood pools represented a minor carbon loss only 3 years after thinning. However, deadwood C differs from that of the living trees, as it can continue to emit carbon as a result of decomposition or accumulate carbon in the soil during the mineralisation process [54, 58]. Similar to our study, previous reports on short-rotation poplar coppice have also found that aboveground woody biomass carbon gain can balance out the loss of soil CO_2 efflux at the ecosystem level [27, 59]. Verlinden et al. [59] found an average annual CO_2 efflux of 589 g m^{-2} yr^{-1} from soil in a poplar coppice plantation in Belgium. Converting our estimate of CO_2 change in soil to the similar scale, the average CO_2 efflux was 333 g m^{-2} yr^{-1}. Verlinden et al. [59] found that the CO_2 efflux was smaller in former croplands (496 g m^{-2} yr^{-1}) than in former pastures (740 g m^{-2} yr^{-1}). As our study site was a former cropland, the converted indirect annual CO_2 efflux rate was lower to that found by Verlinden et al. [59] by direct measurement, considering the geographical differences and the cooler climate of our study site (9.5 °C in Verlinden et al. [59] and 6.9 °C at our site).

The management model for the UT site includes clearcutting after 5 years [10]. By that time, self-thinning will have reduced the initial tree density of aspen coppice by 66% [36].

Table 5 Effect of stand and soil variables on the four-year differences in the soil chemical properties according to the stepwise regression model. The standardised coefficients (β) of the significant predictor variables are indicated in bold. All thinning treatments were included in the regression analysis

Soil variable	Biomass[a]		Initial soil pH		Vegetation cover (%)		Soil bulk density (g cm^{-3})		Model	
	β	p	β	p	β	p	β	p	adj. R^2	p
g C_{org} (cm^{-2})					0.24	0.154	**−0.68**	**<0.001**	0.37	0.001
g N_{tot} (cm^{-2})					**0.35**	**0.041**	**−0.68**	**<0.001**	0.39	0.001
C:N ratio	**0.44**	**0.027**							0.15	0.027
pH_{KCl}	−0.33	0.113			−0.39	0.058			0.10	0.103
g P (cm^{-2})									−0.12	0.878
g K (cm^{-2})									−0.02	0.49
g Ca (cm^{-2})			**−0.55**	**0.003**	−0.28	0.120	−0.30	0.086	0.34	0.005
g Mg (cm^{-2})			−0.36	0.075	−0.32	0.114			0.10	0.111
g Mn (cm^{-2})	−0.27	0.152					−0.36	0.058	0.14	0.061
g Cu (cm^{-2})									−0.10	0.792
g B (cm^{-2})	**0.31**	**0.010**	**−0.56**	**0.005**					0.24	0.014

[a] Log-transformed in the model

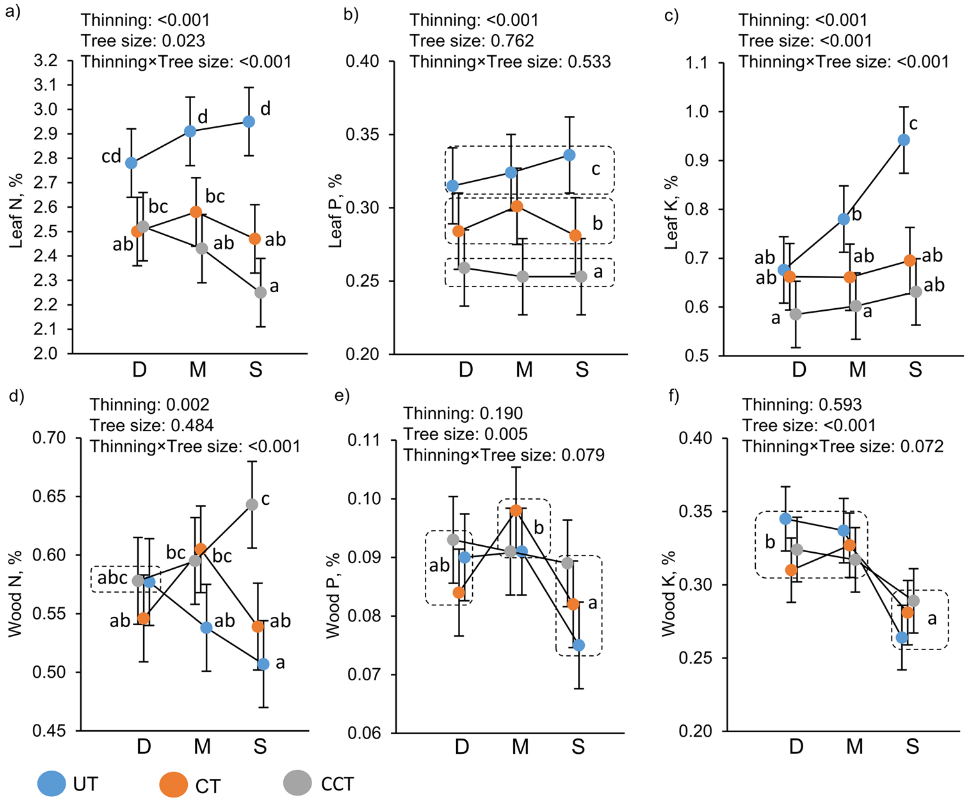

Fig. 4 The effect of the thinning treatment (UT: unthinned; CT: corridor thinning; CCT: cross-corridor thinning) and tree height class (D: dominant; M: medium; S –: supressed) on leaf and wood N (a and **d**), P (**b** and **e**), and K (**c** and **f**) concentrations (estimated marginal mean ± SE). Lowercase letters indicate significant differences in the means among all groups in case of significant interaction effect or among treatment levels in case of significant main effects but non-significant interaction effect

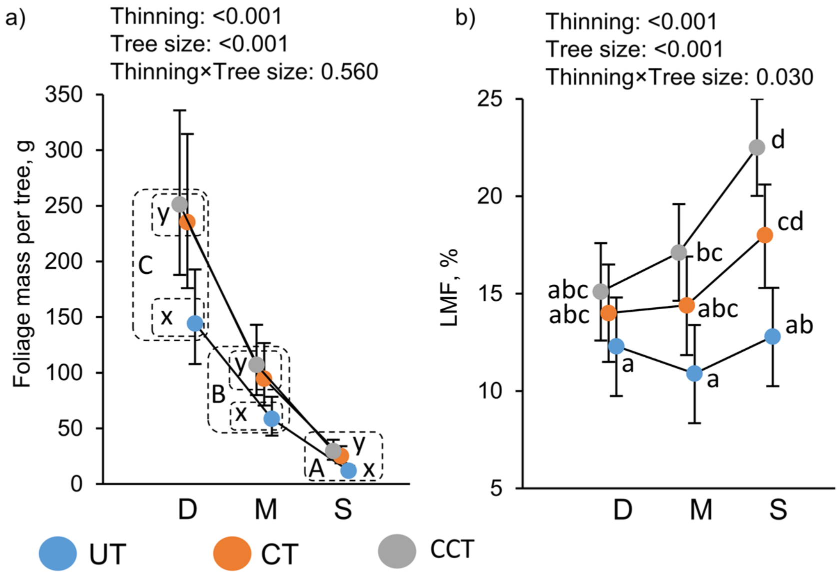

Fig. 5 The effect of thinning treatments (UT: unthinned; CT: corridor thinning; CCT: cross-corridor thinning) and tree height class (D: dominant; M: medium; S: supressed) on estimated marginal means (± SE) of foliage mass and leaf mass fraction (LMF). Letters indicate significant differences in the means among main effect levels in (**a**) and among all groups in (**b**)

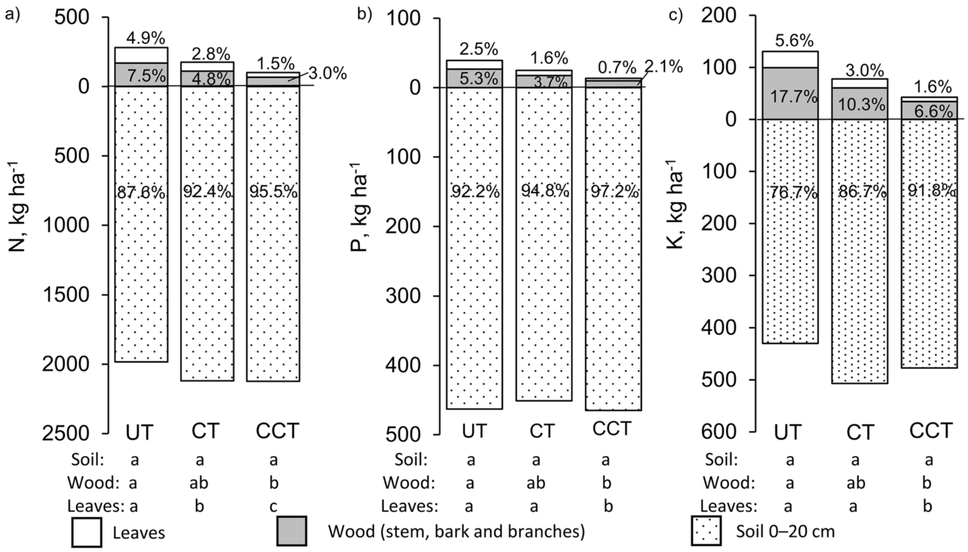

Fig. 6 Allocation of ecosystem nutrient pools aboveground (leaves and woody biomass) and belowground (soil 0–20 cm). Different letters (**a**, **b**, **c**) below the bars indicate significant differences among the thinning methods (Tukey's test, $p < 0.05$) within a given compartment (soil, wood or leaves) for each nutrient. UT: unthinned; CT: corridor thinning; CCT: cross-corridor thinning

However, a notable share of the dead but still standing trees will be harvested together with living trees for bioenergy [4]. We estimated ecosystem carbon balance based on the whole 5-year period, but the time when C input fluxes exceed C output fluxes can also be predicted. At the end of the first growing year the carbon pool of living trees with 20% of roots was + 1.8 Mg C ha^{-1} and that of deadwood from self-thinning − 0.05 Mg C ha^{-1} [36]. Conversion of the total 4-year carbon loss from soil (− 3.8 Mg C ha^{-1}) to an average annual loss (− 0.95 Mg C ha^{-1} yr^{-1}) reveals a positive carbon balance of the unthinned hybrid aspen coppice (+ 0.8 Mg C ha^{-1}) as soon as by the end of the first year after coppicing. The aboveground carbon gain could be lost after the 5-year cycle; however, longer studies are needed to accurately describe the dynamics of soil carbon after multiple rotation cycles.

Changes in Soil Chemical Properties

In relative scale, the greatest change was a 40.6% increase in available boron (B), with the availability of B increasing more significantly in acidic soils. This is in agreement with the general dynamics of B bioavailability, as B becomes more available in acidic soil [44]. The revealed increase in available B is in contrast to the findings of previous studies in older hybrid aspen stands, where B concentration decreased by 20% in the upper 30 cm of the soil layer and the loss was higher in more productive plantations 15 years after the plantation's establishment both on former agricultural lands and grasslands [60]. We would expect the B demand of trees to be low at the early development stage [61].

The contents of C_{org} and N_{tot} showed a similar pattern with an approximately 12% decrease among all studied treatments. Both changes were correlated with bulk soil density, i.e., both C_{org} and N_{tot} decreased more when the bulk density of the soil was higher. This could be associated with soil compaction and disturbance by heavy machinery during the thinnings, which results in the mixing of fresh C material (twigs and branches) with soil [62] and subsequent decomposition after the post-harvest years [63, 64]. Commonly, soil organic carbon pool decreases after clearcutting in conventional forest stands due to increased soil temperature and lower litter input from the new stand generation [63, 64]. Such phenomena held true for the CCT thinning treatment (89% removal of trees) and the CR treatment (67% removal of trees), where the foliage mass was 0.8 Mg and 1.8 Mg of dry matter ha^{-1}, respectively. The dry matter mass of UT foliage was 3.1 Mg of dry matter ha^{-1}, which is similar to hybrid aspen and birch stands > 20 years of age [36, 52], indicating a high nitrogen requirement of the unthinned stand for producing foliage and maintaining high productivity already at the age of 4 years. The difference in litterfall input among the thinning treatments also provides a potential explanation to the observed changes in the C:N ratio. The soil C:N ratio decreased in the CCR treatment, indicating improved decomposition conditions of the organic matter. This also conforms to the positive correlation between the soil C:N ratio and the aboveground biomass as the UT plots with a higher total biomass had higher soil C:N ratios. Rytter and Rytter [15] studied soil C_{org} and N_{tot} changes eight years after similar thinning treatments and at UT sites and did not find any changes in the upper 0–15 cm soil layer for those elements or for the C:N ratio. However, although the total nitrogen remained unchanged, Rytter and Rytter [15] found a decrease in NO_3-N levels independent from the thinning treatment, indicating that mobile N forms are utilised fast to maintain high aboveground productivity as the leaching of NO_3-N is low [65].

Soil pH showed a significant decrease across the studied treatments. Decreases in soil pH are common in former agricultural soils after afforestation with deciduous tree species [60, 66, 67] due to the cessation of liming and inputs of acidic root exudates that are emitted by the trees to adjust nutrients acquisition [68]. The process of soil acidification probably started during the first 14-year-old rotation stand established after agricultural use as a previous study reported decreased pH at this stage [60]. Rytter and Rytter [15] did not find an effect of thinning treatments or year on soil pH in hybrid aspen coppice when investigating unthinned or corridor cleaned stands, which might indicate pH stabilisation or reduced nitrification [69] as they found a decrease in NO_3 concentration.

We found that the contents of plant available K, Mg, and Mn decreased approximately 12–14% over all studied treatments. This is in contrast with the findings of Rytter and Rytter [15], who found increased concentrations of K and Mg in hybrid aspen coppice and explained it with the ability of trees to obtain K and Mg from deeper soil horizons and enrich the upper soil layer with K- and Mg-rich through litterfall. However, as the concentrations of base cations at the present site were higher than the average levels found in abandoned agricultural soils under hybrid aspen plantations [60], it is unlikely that the trees would be able to acquire those elements from deeper layers at the present developmental stage. The reduction of Mn was already an ongoing process during the first rotation stand as it had decreased by 21% since 15 years afforestation [60].

Aboveground Nutrient Pools

Thinnings should reduce competition for light and soil nutrients in the CT and CCT treatments and create better conditions for prolonged rotation cycles aiming to produce larger-dimensioned individual trees. However, we observed higher foliar NPK concentrations in the UT plots compared to the thinned plots. This effect was most significant for leaf N, where the UT treatment resulted in higher N concentrations compared to the CT and CCT treatments among all tree height classes. For P and K, the same trend was revealed for medium and supressed trees. Apparently, a recovery period longer than two years is needed after early thinning of an aspen coppice to recover from the increased root-to-foliage mass ratio [41, 70]. This was also revealed based on aboveground growth in a previous study, where heavy thinnings resulted in a degree of growth retardation in hybrid aspen and a need to recover the leaf area by investing into new shoot growth [36]. Our results indicate that dominant trees are less affected by thinnings as they showed P and K concentrations more similar to the UT site, whereas the effect was stronger on competitively weaker trees. On the other hand, the reduced competition in thinned plots had already enabled the remaining trees to invest into higher foliage mass per individual tree than in the UT treatment. This was observed for the thinned stands, where mean individual tree leaf mass fraction was greater in all tree height classes than in the UT treatment. Hence, lower foliar NPK concentrations were counterbalanced by a greater amount of foliage in UT. Moreover, dormant season woody biomass had higher N concentrations in the thinning treatments, which is in agreement with higher total N uptake to foliage and availability for retranslocation for winter storage.

Together with harvested biomass, nutrients are also removed from the ecosystem. Clearcutting of deciduous hybrid aspen coppice is preferably done during the winter period to ensure higher density and vigour of the coppice, which means that foliar nutrients will be retained on site. Therefore, the degree of nutrient removal as a result of woody biomass harvesting was relatively marginal for the UT treatment regarding both N (169 ± 17 kg N ha^{-1}, which was 7.5% of the total ecosystem pool) and P (27 ± 3 kg P ha^{-1}, which was 5.3% of the total pool), but represented a relatively high 17.7% of the total pool of K (99 ± 11 kg K ha^{-1}). Considering the decrease of K content in the soil, its supply could become critical during the next 5-year harvest cycle from the perspective of maintaining high carbon fixation capacity in the aboveground pool.

Conclusions

We estimated ecosystem carbon balance as well as concurrent soil and tree nutrient dynamics during the first 5 years after different systematic thinning treatments in a hybrid aspen coppice on former agricultural soil. We found that the hybrid aspen bioenergy coppice stand was a carbon sink at the end of the first 5-year rotation. The lighter-intensity early systematic corridor thinning also showed a positive carbon balance after the 5-year period, whereas the stronger cross-corridor thinning did not show significant carbon gain. The content of C_{org}, N_{tot}, K, Mg, and Mn in the soil decreased in short-term in all the studied thinning treatments. Coppice stand soil acidification started during the first-generation stand. The impact of thinning was clearer on tree foliage nutrient concentrations, where the unthinned treatment showed higher NPK concentrations. Lower NPK concentrations in thinned treatments might indicate post-thinning stress and the ongoing recovery period. However, individual tree foliage mass fraction had already increased in response to thinning, especially in medium- and smaller-sized residual trees. The estimated removal of NPK from the unthinned area of the 5-year coppice system was relatively low in comparison to the total ecosystem nutrient pool, with the exception of K, which revealed a reduction of almost 20% of the ecosystem pool. We conclude that the first hybrid aspen coppice cycle can reduce CO_2 emissions at the stand scale, but further studies spanning multiple bioenergy harvesting cycles are needed to accurately assess the long-term stability of soil organic carbon and nutrients and overall climate performance.

Author Contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Reimo Lutter, Heiki Hepner, and Arvo Tullus. The first draft of the manuscript was written by Reimo Lutter and Heiki Hepner, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors declare no competing interests.

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Authors and Affiliations

Reimo Lutter[1] · Heiki Hepner[1] · Arvo Tullus[2] · Hyungwoo Lim[3] · Tea Tullus[1] · Eele Õunapuu-Pikas[1,2] · Reeno Sopp[1] · Marju Kaivapalu[1] · Kristjan Täll[1] · Katri Ots[1] · Hardi Tullus[1]

✉ Reimo Lutter
reimo.lutter@emu.ee

Heiki Hepner
heiki.hepner@emu.ee

Arvo Tullus
arvo.tullus@ut.ee

Hyungwoo Lim
hyungwoo.lim@slu.se

Tea Tullus
tea.tullus@emu.ee

Eele Õunapuu-Pikas
eele.ounapuu-pikas@ut.ee

Reeno Sopp
reeno.sopp@emu.ee

Marju Kaivapalu
marju.kaivapalu@emu.ee

Kristjan Täll
kristjan.tall@emu.ee

Katri Ots
katri.ots@emu.ee

Hardi Tullus
hardi.tullus@emu.ee

[1] Chair of Silviculture and Forest Ecology, Institute of Forestry and Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia

[2] Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Liivi 2, 50409 Tartu, Estonia

[3] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Skogsmarksgränd 17, 901 83 Umeå, Sweden