BioEnergy Research (2020) 13:197–209
https://doi.org/10.1007/s12155-020-10111-0

Effect of Early Thinning Treatments on Above-Ground Growth, Biomass Production, Leaf Area Index and Leaf Growth Efficiency in a Hybrid Aspen Coppice Stand

Heiki Hepner[1] · **Reimo Lutter**[1,2] · **Arvo Tullus**[3] · **Arno Kanal**[4] · **Tea Tullus**[1] · **Hardi Tullus**[1]

Abstract

The bioeconomy strategies in the EU are expected to lead to increased consumption of woody biomass. The empirical knowledge of asexually regenerated hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) coppice stand production and responses to silvicultural treatments is still poor. In hemiboreal Estonia, four different management treatments (corridor thinning with ~67% removal, cross-corridor thinning with ~89% removal, single-tree thinning with ~97% removal and control with no management activity) were applied in a 2-year-old hybrid aspen coppice stand, and effects on tree above-ground biomass and leaf characteristics were investigated during three post-thinning years. Hybrid aspen mean annual increment of above-ground biomass peaked at 6.3 (range: 3.6–8.5) Mg ha^{-1} in year 4, suggesting 4–5 years as an optimal age for bioenergy harvest. The above-ground growth characteristics of dominant trees did not differ from control area. The current annual increment of the height, biomass and leaf growth efficiency (LGE) of dominant trees under single-tree thinning remained even lower compared with the other treatments. Dominant trees were more efficient in resource use, as their LGE values were 21–50% higher compared with the stand average value. Poor growth, high mortality and low LGE in single-tree thinning indicate that the low density of remaining trees created an imbalance between leaf area and parent root system. The hybrid aspen coppice stand showed a high biomass production during early development. We recommend modest early thinning in vegetative hybrid aspen stands to ensure a sufficient balance between leaf area and parent root system.

Keywords Short-rotation forestry · Bioenergy · *Populus* · Aspen regeneration · Root system · Dominant tree

Introduction

In Europe, the demand for woody biomass for bioenergy has increased significantly during the last decade [1]. This is driven by the EU bioeconomy strategy, which aims to increase the renewable share in energy consumption and to develop a resource-efficient and low-emission economy [2]. So far, the main share of woody biomass is coming from logging residues of common forest management and from wood processing industries in Nordic and Baltic countries [3]. Alternative

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✉ Reimo Lutter
reimo.lutter@emu.ee

Heiki Hepner
heiki.hepner@student.emu.ee

Arvo Tullus
arvo.tullus@ut.ee

Arno Kanal
arno.kanal@ut.ee

Tea Tullus
tea.tullus@emu.ee

Hardi Tullus
hardi.tullus@emu.ee

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

[2] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Skogsmarksgränd 17, SE-90183 Umea, Sweden

[3] Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Lai 40, 51003 Tartu, Estonia

[4] Department of Geography, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51003 Tartu, Estonia

sources, including novel silvicultural systems, such as short-rotation forestry (SRF) in marginal land, are highly needed in this region to meet the future demand [4, 5] in order to fulfil the bioeconomy and carbon neutrality goals [2, 6].

In order to be more competitive in the modern bio-based markets in the Nordic countries, SRF aims to produce a wider selection of valuable wood assortments (logs and pulpwood), combined with bioenergy production [7, 8]. Such preconditions are well met by *Populus* spp. [9, 10], such as hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.), making it one of the most promising tree species for SRF in Fennoscandia and the Baltic region [7, 11, 12].

Another economic advantage of hybrid aspen comes from its asexual reproductive strategy: similar to other aspens [13, 14], the new stand will emerge vegetatively from root and stump sprouts [15, 16]. The few studies conducted in the Baltic Sea region and covering the early development period report that hybrid aspen can successfully produce high numbers of new shoots (up to 182,000 trees ha^{-1}) after clearcutting [16–18]. Therefore, the new vegetative stand can be managed by two completely different silvicultural strategies: (i) with very short (< 5 years), coppice-based rotation cycles to produce only woody biomass [15, 18] or (ii) the combined approach with a similar rotation cycle (~25 years) to the first-generation planted stand in order to produce valuable wood assortments such as logs and pulpwood, along with energy wood production [8, 18].

Current knowledge about hybrid aspen root sucker regeneration success, early biomass production and growth potential relies upon only a few studies from southern Sweden [15–17], southern Finland [16] and northern Germany [19]. These studies report very high early biomass production (up to 10–12 Mg ha^{-1}), indicating the optimal rotation cycle of 4 years for bioenergy purpose [15]. The early growth of new sprouts is advanced from the reservoirs of the old root system [13, 20], and therefore, the height growth of the new shoots is significantly faster compared with that of the first-generation planted trees. Therefore, the available growth models developed based on empirical data from the first-generation planted stands [e.g. 21] are obviously not fully eligible for root sucker generation growth predictions and management planning.

The silvicultural purpose of pre-commercial thinning in deciduous stand is to reduce tree level competition for light and nutrients and therefore support the economic goal to enhance the future outcome of higher quality wood assortments [22–25]. Young deciduous trees respond immediately to early thinning by expanding their leaf area for light capture as well as to obtain available site resources [25, 26]. Optimal stand density standards have been proposed for several economically important deciduous species in northern Europe [25–27]. At the same time, knowledge about pre-commercial thinning strategies in vegetatively regenerated European aspen (*P. tremula*) stands is relatively poor in this region because of the low economic value and the high risk of moose damage. More studies about thinning in aspen stands have been conducted in North America with trembling aspen [e.g. 22,28–31]. As the thinning in vegetatively regenerated *P. tremula* forest stands will start in the second half of the rotation cycle (> 15 years), the available stand density regulation standards [25, 27] might not be suitable for hybrid aspen, which grows faster compared with native aspen [12].

The concepts of early management of seed-generated deciduous stands, where the metabolic processes are functioning at an individual tree level (e.g. planted *Populus* spp. stands or seed-based *Betula* spp.), cannot be fully converted to the vegetatively regenerated root-sucker aspen stands, where the neighbouring sprouts are usually interconnected via the parent root system [13, 32, 33]. The current understanding is that clonal aspens are able to share resources (water and carbohydrates) through root connections [34, 35], and therefore, the alterations of clonal sucker above-ground leaf characteristics can have an influence on neighbour tree physiological processes [32, 34]. However, little is still known about the resource sharing for clonal woody species and their responses to management [34].

The first response to the improved light conditions after thinning in young deciduous stands is the expansion of the leaf area. Leaf area and its efficiency to convert photosynthetically active solar radiation to above-ground woody biomass is one of the most important traits to follow in production ecology and eventually in silviculture. Leaf growth efficiency (LGE) can describe tree growth responses to management, competitive status and mortality as well as resistance against pests [36, 37]. For example, LGE is considered to be higher for dominant trees in the stand [36, 38] and depends on several other factors such as stand development stage, management and site quality [36, 37, 39, 40].

In response to knowledge gaps related to the early management of vegetatively regenerated root-sucker aspen stands, we designed the current study to clarify the early responses of above-ground growth characteristics and leaf area to pre-commercial thinning with various intensities.

Against the background, the aims of our study are as follows: (i) to estimate hybrid aspen second-generation sprouting capacity, above-ground growth and biomass production during the first 5 years; (ii) to analyse the early response of the remaining tree above-ground growth characteristics, leaf area index and leaf growth efficiency (LGE) to thinning with various intensities; and (iii) to evaluate the potential of hybrid aspen coppicing for bioenergy production in very short rotations (< 5 years). We tested the following hypotheses: (i) hybrid aspen can successfully regenerate from root suckers and produce high biomass in early development; (ii) early thinning in young hybrid aspen coppice stands advances the remaining leaf area, LGE and above-ground growth; and (iii) LGE of dominant trees is higher than the respective value of competitively less advanced trees.

Materials and Methods

Study Area

The study was carried out in a hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) experimental stand in south-eastern Estonia (58°19′40″N, 26°33′16″E). Estonia is located in the hemiboreal vegetation zone of the transition from maritime to continental climate [41]. During the study period from 2014 to 2018, the mean annual temperature was 6.9 °C, with a mean annual precipitation of 684 mm, according to the nearest (< 10 km) weather station [42]. The variation in weather conditions was low among the study years, except for the prime vegetation period (from April to August) in 2018, where the precipitation was 43% lower and the temperature was 16% higher compared with the mean of 2014 to 2017 [40].

The study area is located in a flat landscape. Prior to afforestation with hybrid aspen in 2000, the area was managed as a crop field. The soil type was uniformly determined as *Retic Umbrisol* [43], based on 1–1.2-m-deep soil pits dug in all the sample plots. *Umbrisols* and *Retisol* are common agricultural soils in the southern Estonia region.

The first rotation hybrid aspen plantation was established with 1-year-old clonal micropropagated plants (14 clones) originating from Finland. As the first-generation plantation was established as a commercial stand, the location and the quantity of the clonal material are unknown. Clear-cutting was performed traditionally with harvester and forwarder machinery in a 14-year-old plantation, covering 2.2 ha area. All the harvested wood (stems and branches) was removed from the site, and clear-cut area was fenced to avoid game browsing in the second-generation stand. The studied second-generation hybrid aspen stand emerged vegetatively in the dormant season of 2013/14.

Corridor thinning treatments were designed in accordance with the study by Rytter [15] and started after the second growing season and performed only once (Fig. 1): (1) systematic corridor thinning, i.e. 2-m-wide corridors were harvested, removing 67% of stems and keeping 1-m wide rows of trees; (2) systematic cross-corridor thinning, i.e. additional 2-m-wide corridors were harvested perpendicularly, removing 89% of stems and keeping 1 × 1-m patches of trees. The additional treatments were (3) single-tree thinning, i.e. single tree selection across the stand, where the stand density after thinning was reduced about 97% and (4) for comparison, control areas with no management activity were included. Thinning was performed with the use of a brush saw, and all harvested trees were left in the stand.

The setup of the trial started in spring 2014, when 12 rectangles (40 × 30 m) were marked in the study area (Fig. 1) and separated by 2-m-wide corridors. After the second growing season, four different thinning treatments were applied in three randomly located replications. Three circular sample plots with a radius of 2 m (12.6 m^2) were established in each replication systematically along the rectangle's diagonal. Thus, each thinning treatment was represented by nine sample plots (Fig. 1). After thinning, the radius of the sample plots was extended to 3 m (28.3 m^2) in corridor and cross-corridor thinning and to 5 m (78.5 m^2) in single-tree thinning.

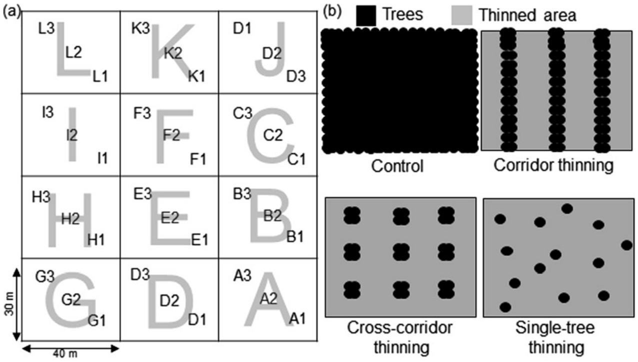

Fig. 1 **a** Setup of the study area (capital letters denote treatment replications as follows: A, F, H – control; B, D, I – corridor thinning; C, E, G – cross-corridor thinning; J, K, L – single-tree thinning). **b** Graphical illustration of the applied thinning treatments

Growth Measurements

Above-ground tree growth data was collected from sample plots during the first five growing seasons since the stand formation (2014–2018), except for the single-tree method, where the measurements started after the third growing season. Total tree height (H), diameter at a height of 30 cm from the ground level (D30) and diameter at breast height (DBH) were measured for all the trees in the plots. Tree height was measured with a telescopic measuring rod (< 800 cm) with 1-cm resolution or with a Vertex IV (Haglöf Sweden AB) measuring tool (> 800 cm) with 10-cm resolution. The D30 and DBH were recorded over the bark with a digital calliper (Mitutoyo Japan) with 0.1-mm resolution. Stem volume index (D30^2 × H, dm^3) was calculated for each individual tree.

Above-ground Biomass Estimations

The above-ground growth characteristics (H and D30) did not vary between the sample plots during the first two growing seasons, i.e. the period before the thinning treatments. Therefore, for year 1 and year 2 above-ground biomass estimations, 10 model trees were selected randomly across the study area in both years in accordance with the D30 distribution. After the 3rd and 4th growing seasons, three model trees per sample plot were selected based on the D30 distribution (a dominant, a medium and a small tree). Altogether, 118 model trees were harvested in year 3 and year 4. Leafless model trees were selected close to the sample plot and harvested. The general growth characteristics of the model trees were measured in the field.

In the laboratory, the trees were partitioned into stem, current-year branches, older living branches and dead branches. All compartments were weighed and subsequently dried to constant weight at 70 °C to estimate the dry matter content of the tree. The whole-tree allometric equations were parameterized for each study year to predict the dry biomass values for all trees in the sample plot according to their D30 (Eq. (1); Table 1). Model trees were not taken after the 5th growing season, and the above-ground biomass for 5-year-old trees was predicted by using the allometric equation of year 4 (Table 1). The predicted individual tree biomass values were summed per sample plot and converted to a hectare basis.

$$AGB = b_0 \times D30^{b}{}_1 \tag{1}$$

where AGB is above-ground leafless dry biomass (g) of a tree, b_0 and b_1 are parameters (Table 1) and $D30$ is the stem diameter over the bark at 30 cm from ground level.

Leaf Area Estimations

Leaf area estimations were carried out during the peak of the leaf area growth in the middle of July during the 3rd and 4th growing seasons. The D30 and DBH of each tree were measured over the bark in all sample plots. Based on the diameter distribution, three model trees (a dominant, a medium and a small tree) were harvested close to each sample plot. Altogether, 118 trees were harvested and analysed in both study years. The general growth characteristics of the model trees were measured in the field. All the leaves were collected from the model trees, and their total fresh weight was determined. After that, 20 sample leaves were selected randomly from homogenized leaf fraction of each model tree. The leaf samples were dried to the constant weight at 70 °C for dry matter estimation. An allometric equation was parameterized for both years to predict the dry leaf mass (DLM, g) for all the trees in the sample plot according to their DBH or D30 (Eq. (2); Table 2). The single leaf blade area was measured for all the sample leaves with WinFolia software (Regent Instruments Canada INC.). Leaf weight per area (LWA, g m^{-2}) was calculated for each leaf, and mean LWA was estimated for each model tree. As the LWA varied among the tree size classes, an allometric Eq. (2) was parameterized for both study years to predict the LWA for all the trees in the sample plot according to their DBH or D30 (Eq. (2); Table 2). Based on the predicted DLM and LWA values, the total leaf area was calculated for each tree and sample plot, which was converted to leaf area index (LAI, m^2 m^{-2}).

$$y = b_0 \times D^{b}{}_1 \tag{2}$$

where y is dry leaf mass (DLM, g) or leaf weight per area (LWA, g m^{-2}), b_0 and b_1 are parameters (Table 2) and D is the stem diameter at breast height (year 3) or the stem diameter over the bark at 30 cm from ground level (year 4).

Leaf growth efficiency (LGE, g wood m^{-2} leaf year^{-1}) was defined as annual growth of above-ground woody biomass per unit of leaf area [37] at the sample plot level, i.e. leaf area was predicted for each individual tree in the sample plot (Eq. (2)), and the current annual biomass production was calculated as the mean difference between the total biomass in year 4 and year 3 of the sample plot. The LGE was calculated separately for all trees and for dominant trees in the fourth growing season.

Statistical Analyses

The normality of the variables was tested with the Shapiro-Wilk test. The homogeneity of the variances of growth characteristics in groups (treatments) was tested by Levene's test. As the variance of the growth variables differed significantly between the study years, the analyses of the thinning effect on growth and leaf characteristics were carried out separately for individual study years (ages of 1 to 5 years).

A linear mixed model with the random effect of replication was used to study the effect of thinning treatments (control, corridor, cross-corridor and single-tree) on average (subscript = avg) and dominant (subscript = 400) tree above-ground growth, biomass and leaf variables of the given individual year. The dominant trees are characterized as the future crop

Table 1 Parameter estimates and goodness of fit of the allometric Eq. (1) for the above-ground dry biomass estimates for each study year, where b_0 and b_1 are parameter estimates, R^2 is the coefficient of determination and the p value shows the significance of the model

Growing season	No. of model trees	Parameter	Estimate	R^2	Model p value
1st	10	b_0	0.1486	0.99	< 0.001
		b_1	2.3791		
2nd	10	b_0	0.1291	0.99	< 0.001
		b_1	2.1117		
3rd	118	b_0	0.1713	0.99	< 0.001
		b_1	2.4027		
4th & 5th[a]	118	b_0	0.1749	0.99	< 0.001
		b_1	2.4337		

[a] 5th growing season dry biomass was predicted according to the year 4 equation

Table 2 Parameter estimates and goodness of fit of the allometric Eq. (2) for calculating dry leaf mass (DLM) and leaf weight per area (LWA) of a tree in the given study year, where b_0 and b_1 are parameter estimates, R^2 is the coefficient of determination and the *p* value shows the significance of the model

Growing season	Parameter	Estimate	R^2	Model *p* value
DLM, g				
3rd DBH	b_0	0.013	0.96	< 0.001
	b_1	2.112		
4th D30	b_0	0.028	0.87	< 0.001
	b_1	2.385		
LWA, g m^{-2}				
3rd DBH	b_0	35.529	0.51	< 0.001
	b_1	0.273		
4th D30	b_0	26.359	0.38	< 0.001
	b_1	0.308		

trees, considering the standard stand density (400 trees ha^{-1}) at the end of the rotation of the first-generation hybrid aspen plantation [11, 12]. This approach minimizes the artificial effect of single-tree thinning on the studied growth characteristics. The mixed model analysis was performed with the R Statistics function lmer in the package lme4. When a significant effect of the thinning treatment was observed, Tukey's HSD test was applied to compare the group means. Mean values are presented with standard error estimates of the LS mean model estimates. The pairwise Student *t* test was used to study the changes of LAI between year 3 and year 4 for each thinning treatment and to compare the LGE values among all trees and dominant trees.

We used Q-Q plots and residual distributions to assess the normality of model residuals. Log-transformation was applied if the normality assumption was not met. The level of significance of $\alpha = 0.05$ was used to reject the null hypothesis after statistical tests. All statistical analyses were carried out using the R Statistics software [44].

Results

Stand Density, Self-Thinning and Mortality

After the first growing season, the new hybrid aspen sprout stand produced on average 94,000 trees ha^{-1} (Fig. 2). Stand density varied among sample plots from 55,000 to 126,000 trees ha^{-1}. The pre-thinning stand density did not differ significantly among the areas where different thinning treatments were applied later. Self-thinning in the control areas reduced the number of living sprouts by 66% to the stand density of 33,000 trees ha^{-1} by the end of the 5th growing season (Fig. 2). After thinning, the stand density in all the treatments differed among each other in all the post-thinning study years ($p < 0.001$). The self-thinning rates of the remaining trees slowed down in the post-thinning period (from year 3 to year 5) for corridor (− 20%) and cross-corridor (− 13%) compared with the control (− 80%). Tree mortality continued in the single-tree treatment, where the stand density decreased by 24% from 2400 to 1800 trees ha^{-1}. In the thinned areas, new sprouts started to emerge after thinning. After the fifth growing season, the density of the newly emerged shoots was 946 trees ha^{-1} in corridor, 7146 trees ha^{-1} in cross-corridor and 3678 trees ha^{-1} in single-tree thinning.

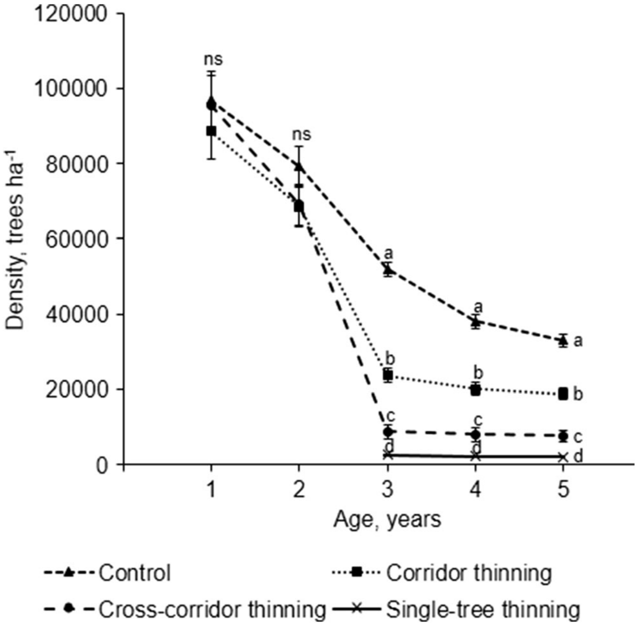

Fig. 2 Effect of thinning treatments on the average density (trees ha^{-1}) of the second-generation hybrid aspen stand. Error bars denote the standard error; letters indicate significant differences ($p < 0.001$) among thinning treatments in each study year

Growth Development

The pre-thinning growth characteristics did not differ significantly among the areas where different thinning treatments were applied later (Fig. 3). After thinning, the $D30_{avg}$ was significantly higher in single-tree thinning compared with the other treatments (Fig. 3a), but the effect on $D30_{400}$ was insignificant during all post-thinning years (Fig. 3d). The response of tree height was opposite to that of diameter growth after the post-thinning years: the effect of thinning was insignificant on H_{avg} (Fig. 3c) but significant on H_{400} (Fig. 3d). The slowest development of H_{400} occurred in the single-tree thinning (Fig. 3d).

The effect of thinning was significant on the current annual increment (CAI) of the height of the dominant trees (Fig. 4b), biomass (Fig. 4c) and stem volume index (Fig. 4d) in the fourth growing season, where single-tree thinning had significantly lower values compared with the other treatments. In the fifth growing season, the significant differences between

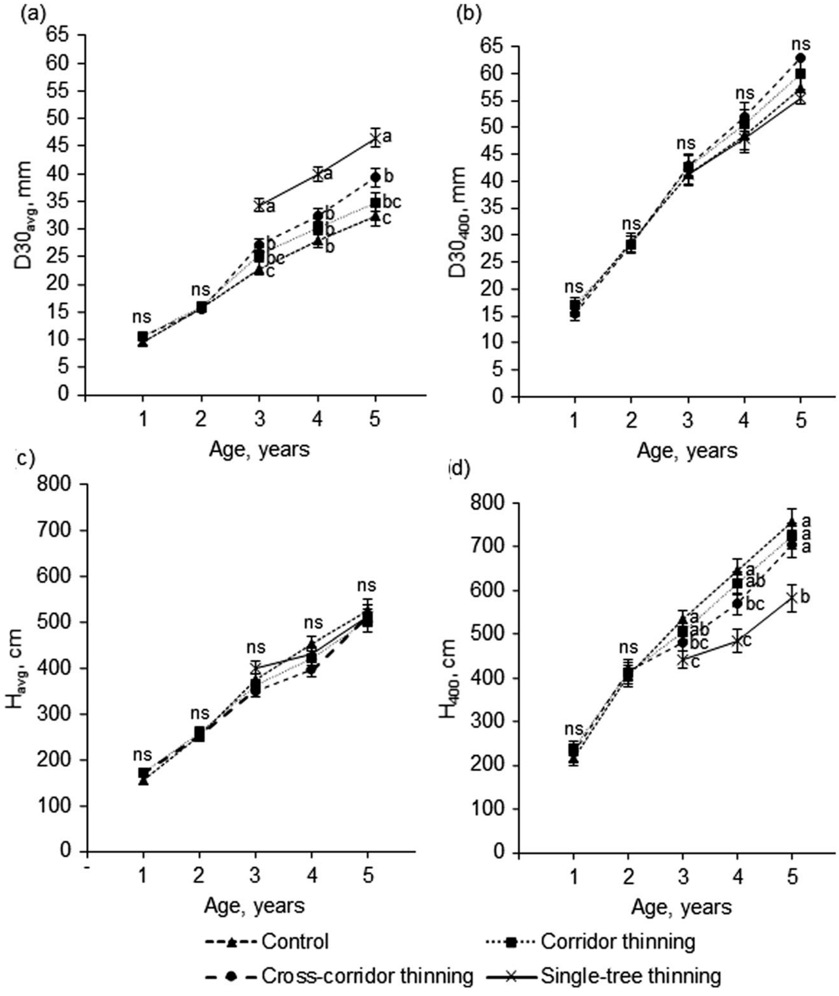

Fig. 3 Effect of thinning treatments on the development of the following growth characteristics in the second-generation hybrid aspen stands: (**a**) average stem diameter at 30 cm from ground ($D30_{avg}$), (**b**) average stem diameter at 30 cm from ground for dominant trees ($D30_{400}$), (**c**) average height and (**d**) average height of dominant trees (H_{400}). Error bars denote the standard error of the LS mean model estimates; letters indicate significant differences ($p < 0.05$) among thinning treatments in each study year

the thinning treatments disappeared for height of the dominant trees (Fig. 4b). However, differences existed for the diameter, biomass and stem volume index, where the dominant trees in the cross-corridor treatment showed significantly higher CAI values for biomass compared with the control and single-tree thinning (Fig. 4c) and significantly higher CAI of diameter and stem volume index compared with the single-tree thinning (Fig. 4a and d). The strongest applied thinning (single-tree) did not improve the above-ground growth of the dominant trees compared with the control (Fig. 4).

Above-ground Biomass Production

The average above-ground biomass of individual hybrid aspens was significantly higher in single-tree thinning stands in all post-thinning years. No significant differences in average above-ground biomass were observed during the first two post-thinning years between the other thinning treatments (Fig. 5a). However, after the fifth year, above-ground biomass in cross-corridor thinning was significantly higher compared with the control areas (Fig. 5a). Thinning had no effect on the total above-ground biomass of the dominant trees (Fig. 5b).

After five growing seasons, the control areas produced an average of 31.4 ± 3.2 Mg ha^{-1} of total woody biomass (Fig. 6), of which dead biomass accounted for 7% (Table 3). This corresponds to a mean annual increment (MAI) of 6.3 (range: 3.6–8.5) Mg ha^{-1} in control areas (Fig. 7). The MAI in control areas peaked in year 4 (6.5 Mg ha^{-1}), and the CAI dropped below the MAI in year 5 (Fig. 7). Generally, the total above-ground woody biomass of the retained trees decreased with increasing thinning intensity (Fig. 6). However, when including the biomass of thinned trees and the newly emerged sprouts, the total produced biomass did not differ between control and corridor thinning, between cross-corridor and corridor thinning and between single-tree and cross-corridor thinning (Table 3). The above-ground biomass of new shoots (0.04 Mg ha^{-1}) was negligible in the cross-corridor thinning while in the cross-corridor and single-tree thinning the new shoots accounted for 0.7 and 0.4 Mg ha^{-1}, respectively (Table 3). For all thinning treatments, the CAI of the above-ground biomass of the remaining trees exceeded the MAI after year 5 (Fig. 7).

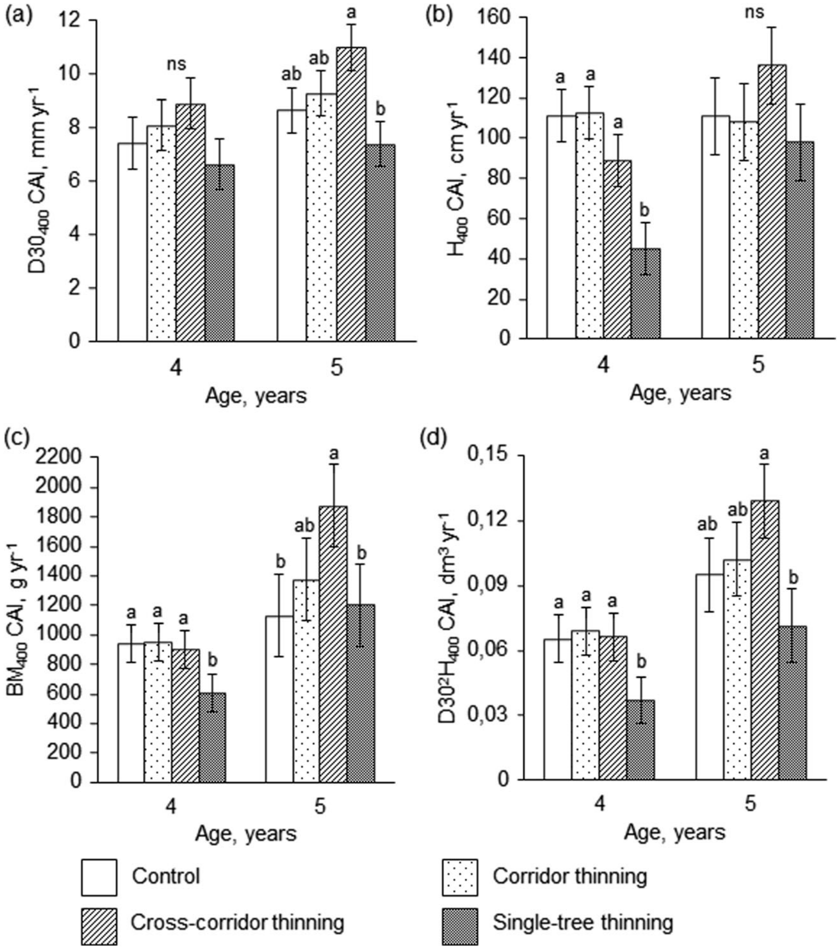

Fig. 4 Effect of thinning treatments on the second-generation hybrid aspen dominant trees current annual increment (CAI) of (**a**) diameter, (**b**) height, (**c**) whole tree biomass and (**d**) stem volume index in the fourth and fifth growing seasons. Error bars denote the standard error of the LS mean model estimates; letters indicate significant differences ($p < 0.05$) among thinning treatments in each study year

Leaf Area Index and Growth Efficiency

The effect of thinning on the LAI was significant in both leaf sampling years, when all the thinning treatments differed among each other, except the cross-corridor and single-tree thinning (Fig. 8). In all treatments, the LAI increased with age after thinning by around 13 to 15% (Fig. 8), except in control areas, where the LAI remained unchanged. The LAI peaked at the age of 3 years in control area, being about 4 m^2 m^{-2} (Fig. 8).

Average leaf growth efficiency (LGE) did not differ significantly among the thinning treatments (Fig. 9). At the same

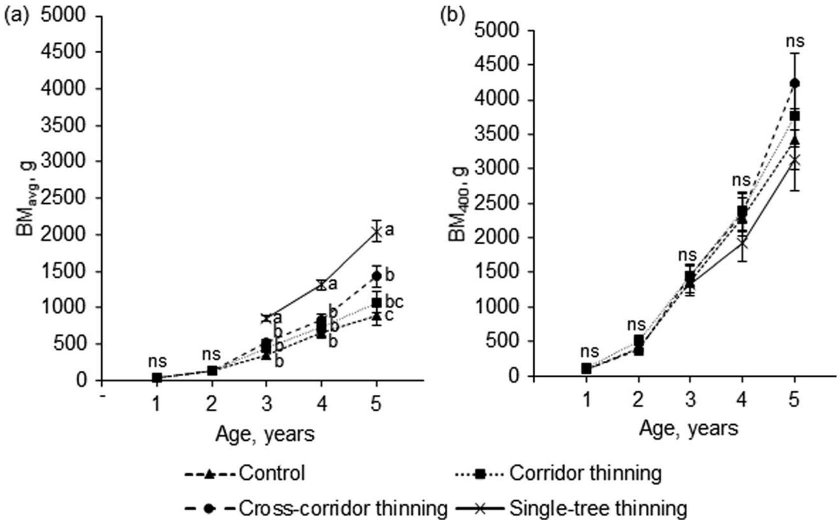

Fig. 5 Effect of thinning treatments on above-ground biomass (stem and branches) development in the second-generation hybrid aspen stands: (**a**) average biomass of all trees (BM$_{avg}$) and (**b**) average biomass of dominant trees (BM$_{400}$). Error bars denote the standard error of the LS mean model estimates; letters indicate significant differences ($p < 0.05$) among thinning treatments in each study year

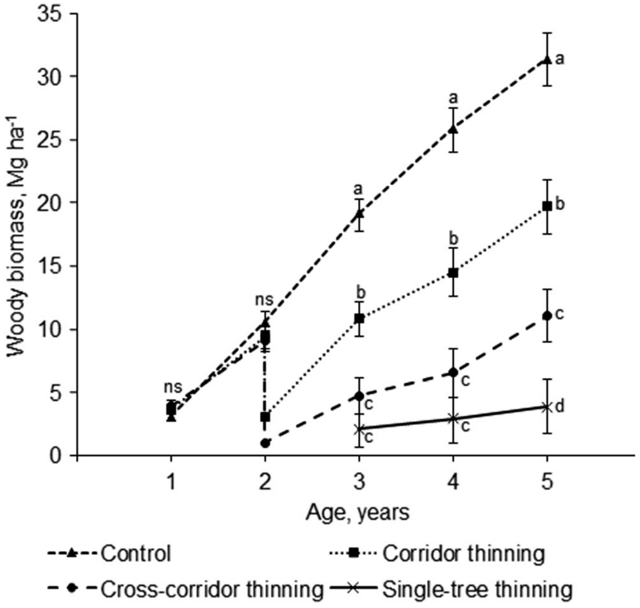

Fig. 6 Effect of thinning treatments on the above-ground biomass development of the residual trees in the second-generation hybrid aspen stand. Error bars denote the standard error of the LS mean model estimates; letters indicate significant differences ($p < 0.05$) among thinning treatments in each study year

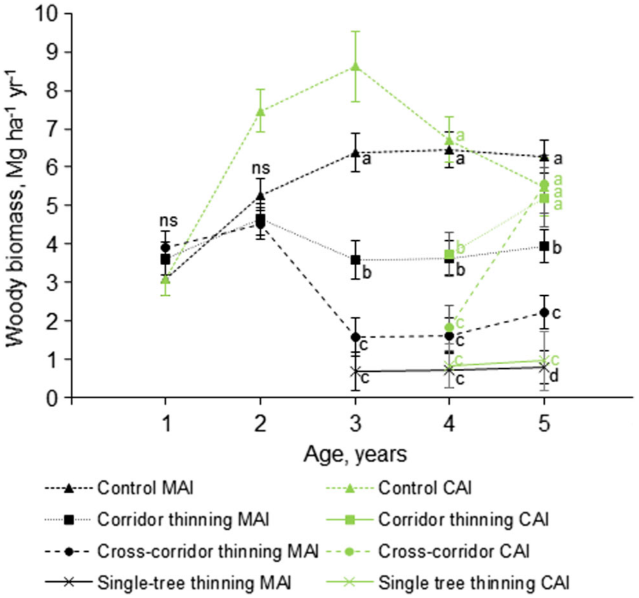

Fig. 7 Effect of thinning treatments on the mean annual increment (MAI) and current annual increment (CAI) of the woody biomass of the residual trees in the second-generation hybrid aspen stands. Error bars denote the standard error of the LS mean model estimates; letters indicate significant differences ($p < 0.05$) among thinning treatments in each study year. CAI was estimated for thinning treatments in year 4 and year 5

time, the effect of thinning was significant on the LGE of dominant trees, where control and corridor thinning exceeded single-tree thinning (Fig. 9). For all thinning treatments, the LGE of dominant trees was 21.4–49.6% higher compared with overall stand average.

Discussion

Growth and Biomass Production Responses to Early Thinning

Our findings confirmed, as hypothesized, that the first-generation planted hybrid aspen stand can be successfully regenerated after clear-cutting of the old stand in the dormant season, after which a dense and vigorous new stand emerges from root and stump sprouts. Similar outcomes have been reported elsewhere in the region [e.g. 15–17]. An average of 94,000 stems ha^{-1} emerged after the first year, which is two-fold lower compared with the 182,000 stems ha^{-1} reported in southern Finland [16]. This can be explained by the different stand cutting age: our stand was 12 years younger than the 26-year-old hybrid aspen stand in Finland [16], and obviously, older trees have a more extensive root system [13]. The sprouting capacity observed in our study is in agreement with the outcomes from studies in southern Sweden [15, 17, 18].

By the end of year five, self-thinning had reduced the initial stand density in the control area by 66%, which is comparable with the self-thinning rate observed in other studies on hybrid aspen [15–17]. Artificial thinning should slow down self-thinning under the improved light and nutritional conditions [27]. Such a response was observed in the corridor and cross-corridor thinning, but surprisingly not in the most intensively managed single-tree method, where density declined further

Table 3 Total produced dry biomass (BM, Mg ha^{-1}) and its distribution into pools (retained alive trees, dead, newly emerged and thinned trees) under different thinning methods at the age of 5 years. Letters denote significant differences among the group means

Treatment	BM_{alive}		BM_{dead}		BM_{new}		*$BM_{thinned}$		Total BM produced
	Mg ha^{-1}	%	Mg ha^{-1}	%	Mg ha^{-1}	%	Mg ha^{-1}	%	Mg ha^{-1}
Control	29.2 ± 3.1a	93.0	2.2 ± 0.5a	7.0	0	0	0	0	31.4 ± 3.2a
Corridor thinning	19.0 ± 1.5b	74.2	0.5 ± 0.1b	1.8	0.04 ± 0.02b	0.2	6.2 ± 0.3c	23.9	25.9 ± 1.6ab
Cross-corridor thinning	10.6 ± 0.9c	53.5	0.5 ± 0.1b	2.3	0.7 ± 0.2a	3.5	8.1 ± 0.6b	40.7	19.8 ± 1.3bc
Single-tree thinning	3.8 ± 0.8d	27.5	0.3 ± 0.1b	2.4	0.4 ± 0.1a	2.6	9.4 ± 0.1a	67.4	13.9 ± 0.6c

*Calculated according to the theoretical thinning intensities from the average total biomass after the second growing season

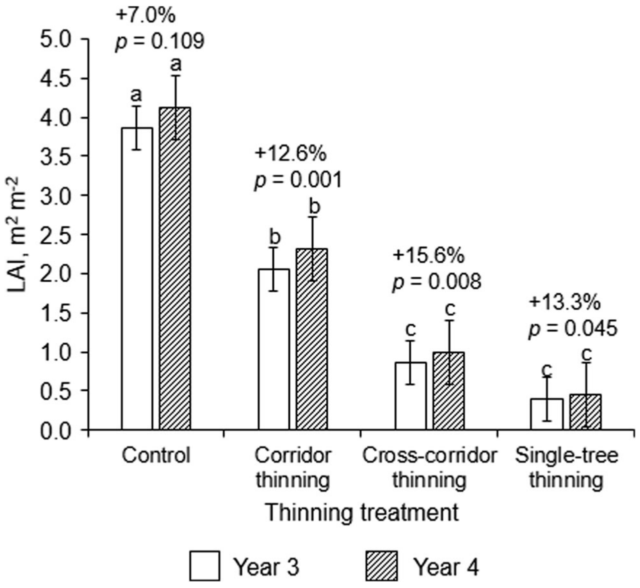

Fig. 8 Effect of thinning treatments on leaf area index (LAI) and its relative change between the third and the fourth growing season (*p* values based on single-sample *t* test) in the studied second-generation hybrid aspen stand. Error bars denote the standard error of the LS mean model estimates; letters indicate significant differences ($p < 0.05$) among thinning treatments in the given study year

by 24% within 3 years after thinning. By the end of year five, the average stand density in the single-tree thinning treatment was around 1800 trees ha^{-1}, which is close to the recommended planting density for a first-generation hybrid aspen stand [7]. Hence, in addition to above-ground growth deceleration in the single-tree thinning method, the mortality of the remaining trees was also relatively high. Although *Populus* spp., with direct root connections, have a better resistance against biotic and abiotic stress [32], intensive thinning may weaken the neighbouring trees complementarity effect through root links among the remaining sparse sprouts.

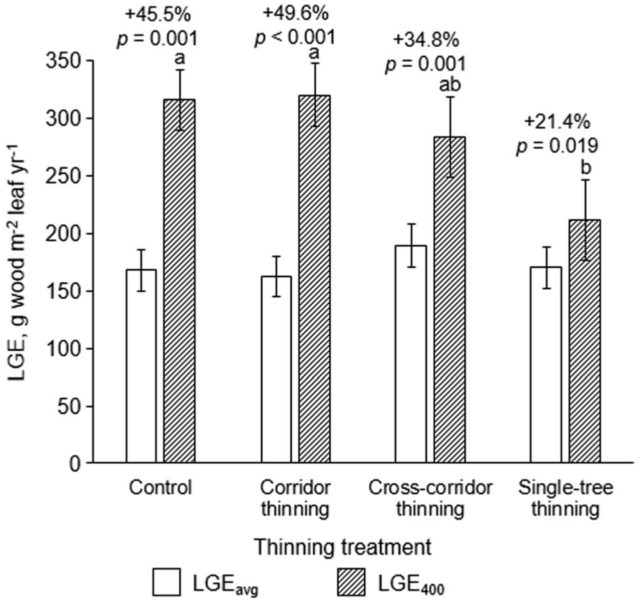

Fig. 9 Effect of thinning treatments on the leaf growth efficiency of average (LGE_{avg}) and dominant (LGE_{400}) trees and their pair-wise comparison. Letters indicate significant differences ($p < 0.05$) among thinning treatments according to Tukey's HSD test

The MAI of the biomass in the control treatment peaked at the age of 4 years at 6.5 Mg ha^{-1} year^{-1} and dropped to 6.3 Mg ha^{-1} year^{-1} in the following year, suggesting an optimal rotation cycle of 4–5 years for bioenergy production. Such early biomass production without fertilization in the early development is high for Estonian pedoclimatic conditions, where a similar production is attainable not before the middle of the 25-year rotation cycle in planted first-generation hybrid aspen plantations [12]. Similar to our outcome, the optimal rotation cycle for bioenergy production was 4 years in a second-generation hybrid aspen stand in southern Sweden [15, 18]. The observed MAI in un-thinned control areas was below the 10–12 Mg ha^{-1} year^{-1} reported for southern Sweden [15, 17, 18] and closer to the 8 Mg ha^{-1} year^{-1}, reported for southern Finland [16]. As expected, the total biomass after 5 years was highest in the control area, but when including the theoretical harvested biomass, no difference was observed. Mc Carthy and Rytter [17] have found that, in similar thinning treatments (excluding single-tree), total biomass production was similar to the control area after 12 growing seasons.

The part of our second hypothesis that early thinning in a young hybrid aspen coppice stand will advance the above-ground growth of the remaining trees was generally not supported by the results. We assumed that the competition release will improve the living crown dimensions in lower crowding [17, 27] and reduce competition for soil resources [45] and light [37]. On the contrary, the CAI values of the height and biomass of dominant trees in the second post-thinning year under the most intensive thinning treatment (single-tree thinning) remained even lower compared with the other treatments. The reason behind the single-tree method's poor response to thinning in terms of both high mortality as well as slower above-ground growth could be the created imbalance between root system and leaf area, i.e. the low number of retained sprouts (with insufficient leaf area) was not able to supply the existing parent root system with carbohydrates [34, 46–48] or increases desiccation and other stress factors [13].

The second-generation hybrid aspens showed a fast height development during the first five growing seasons. The mean height of the dominant trees was 7.3 m, which, in the first-generation planted stands, was reached about 2 to 3 years later (3 to 4 years when also considering seedling pre-growth in the nursery) [12, 21, 49]. Such fast growth can be explained by the boost of carbohydrates from the old root system as well as intensive light competition in a dense crowding [13]. A comparable height development has been reported for second-generation hybrid aspen stands in Sweden and Finland [15–18]. The mean stem diameter after five growing seasons did not exceed the respective value in planted stands of the same age [12, 49]. Thus, trees grown in dense re-sprouting hybrid aspen stands were more slender and therefore could be more susceptible to storm damage after strong release thinning [25]. Obviously, the average diameter in single-tree thinning was higher than in other treatments because the largest trees were selected as residual trees. When excluding single-tree thinning, our results are similar to those of Rytter [15] for southern Sweden, where average diameter, height and dry biomass did not differ among control, corridor and cross-corridor treatments after 4 years. Mc Carthy and Rytter [17] compared the same thinning treatments (corridor and cross-corridor) with no thinning after 12 years and found that the average diameter was lower in denser treatments but no difference was observed on height growth. Long-term thinning experiments with hybrid aspen [17, 25] and trembling aspen [23, 28, 30] indicate that stronger pre-commercial thinning will provide higher individual stem diameter at the stand level in the final felling. However, the effect of thinning is less important on dominant trees [29] and does not always provide higher total yield [23].

Leaf Area and LGE Responses to Thinning

After clear-cutting, aspens have a capacity to recover the leaf area immediately by using carbohydrate reserves from old roots system in order to restore photosynthesis and the C supply to roots [13, 46]. A study by Stener et al. [50] described remarkable rooting area for hybrid aspen where the average distance of hybrid aspen root sucker lateral spread from the old stump was 15 m, but can be up to 49 m. Similarly, a study in young naturally regenerated trembling aspen stands showed that below-ground biomass constituted up to 80% from the total biomass and extensive leaf area was needed to support the respiration costs [46]. Such fast leaf area recovery was also observed for hybrid aspen in our study, where the LAI peaked already at the age of 3 years in the control area, reaching about 4 m^2 m^{-2}. A similar LAI was observed in 7-year-old vegetatively regenerated trembling aspen stand in north-central Alberta, Canada [46]. Such an LAI level is usually not attained in first-generation hybrid aspen stand before the second decade of the development [e.g. 21]. The thinning resulted in an eight times lower LAI in the single-tree thinning compared with the control area.

The second hypothesis was partly supported by the results, as the trees responded positively to thinning by expanding leaf area. Expectedly, the LAI showed a recovery trend after the post-thinning years in all thinning treatments. However, in addition to expanding the LAI of the remaining trees, the recovery of leaf area by the old root system under improved light and soil temperature was also realized by growing new sprouts during the post-thinning years. For example, the density of the newly emerged sprouts (around 3700 trees ha^{-1}) was two-fold higher than that of the retained trees in the single-tree thinning treatment after the 5th year (1800 trees ha^{-1}). Therefore, considering the mutual exchange of resources in root-connected aspens [34, 35], it is possible that the fast above-ground growth recovery of trees in the cross-corridor thinning in the fifth growing season was partly supported by the increased leaf area of the new sprouts (7000 trees ha^{-1}). Potentially, such facilitation effect of the new sprouts could occur later in single-tree thinning, where the retained trees have to withstand a stronger stress.

Our third hypothesis was supported by our results, as the LGE of dominant trees was almost two-fold higher compared with the average value. This indicates that the higher stand density (and leaf area) during the early development period for root-connected aspen means lower maintenance and growth costs per individual tree and better access to soil resources for the dominant, overtopping trees [34, 35]. An exception was single-tree thinning where the difference in LGE was less among all trees and dominant trees, which can be explained by lower crowding in sparse stands, where light conditions are more similar for all individuals and tree size class distribution is less skewed after selective thinning. Our results agree with recent case studies where the leaf area of dominant trees in the stand absorbed light and converted to above-ground biomass more efficiently than the remaining trees [38, 39].

Thinning had an effect on the LGE of dominant trees, where in the single-tree thinning, the remaining trees likely allocated more resources to above-ground pools and therefore showed lower LGE levels for above-ground growth. Therefore, even though thinning should improve the growth efficiency because of better access to light and nutrients [38], strong early thinning in root-connected aspen stands will probably result in a delayed response because the remaining trees must first invest resources to recover the balance between leaf area and root system. Generally, a poor LGE will increase the susceptibility to pathogen and insect attacks [37, 47, 51]. To the best of our knowledge, critical LGE thresholds have not been reported for aspen or any other deciduous species in this region. At the same time, 80 g wood m^{-2} leaf $year^{-1}$ is considered as a critical LGE for Norway spruce, below which the tree becomes vulnerable to bark beetle attacks [37]. In our study, the LGE was more than two times above the value for all the studied thinning treatments.

Management Implications

In agreement with other similar studies in northern Europe [15–17], the high number of new sprouts ensures successful regeneration of hybrid aspen. Therefore, short coppice cycles for bioenergy production could be an alternative system for hybrid aspen [15]. Both corridor thinning treatments enable a combined management method, where the biomass from early corridor thinning can be collected for bioenergy, applying a longer rotation cycle (20–25 years and including later thinnings) for the retained trees for the production of saw logs and pulpwood [8, 15]. The aim of the single-tree thinning method is to select individual future trees already at a young age and to apply a 25-year rotation cycle for the production of saw logs and pulpwood.

Pre-commercial thinning is a common practice in dense deciduous stands to produce more valuable wood assortments [e.g. 25,27]. When the aim in the second-generation hybrid aspen stand is to produce pulp and saw logs in longer rotation, we recommend avoiding a drastic early reduction of stem numbers or even delay with thinning, which may result in decreased above-ground growth and lower LGE levels.

Significant advantages between corridor and cross-corridor treatments were not observed during the first three post-thinning years in the present study. Similarly, Mc Carthy and Rytter [17] found that the only difference between those two systems after 12 years appeared in the diameter growth but not in the total production nor in the height growth. However, dominant trees in cross-corridor thinning accelerated their above-ground growth in year 5 in our study. It can be assumed that cross-corridor thinning stands could be more vulnerable to storm damage, moose browsing and pathogen attacks such as Hypoxylon canker [52]. However, at the same time, such systems can reduce the intensity (cost) of the following thinnings and provide more merchandisable wood assortments. Corridor thinning is less susceptible to abiotic and biotic stresses but probably needs more frequent thinnings before clear-cutting to maintain an optimal crown length.

Conclusions

Hybrid aspen can be successfully regenerated via root suckering after clear-cut at a fertile site under hemiboreal conditions in Estonia. The emerging sucker stand shows high biomass production during the early development and can be managed with 4- to 5-year rotations for bioenergy. During the first three post-thinning years, trees under the most intensive thinning (single-tree method) did not advance in their above-ground growth characteristics and LGE values, indicating an imbalance between leaf area and root system. Apparently, the remaining stand density was not able to provide a similar carbohydrate supply for the old root system when compared with the other, less intensively thinned treatments. Leaf area peaked in un-thinned control areas in year three. In all thinning treatments, leaf area increased significantly in the early post-thinning years. Dominant trees showed 21–50% higher LGE values compared with the stand mean value. We recommend starting the second-generation hybrid aspen management with moderate early thinning to ensure a balance between leaf area and parent root system.

Funding Information This work was supported by institutional research funding IUT (grants IUT21-4, Professor Hardi Tullus, and IUT34-9, Dr. Arvo Tullus), Estonian Research Council grant PSG7 (Dr. Arvo Tullus), and the project P170053MIMK of the Estonian Ministry of Education and Research (Professor Hardi Tullus).

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