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Above-ground biomass production and nutrient accumulation in young stands of silver birch on abandoned agricultural land

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Abstract

During the last decade, more than 400 000 ha of agricultural land was abandoned in Estonia. Such areas are often characterized by rapid natural afforestation with silver birch, which has led to an increase both in the woodland area and in the area of silver birch stands. However, many bioenergetic aspects related to birch stands growing on arable land are still poorly understood. The main aim of the present study was to investigate the above-ground biomass production, nutrient (NPK) accumulation, and foliar characteristics of young silver birch stands on abandoned agricultural land. Five 8-year-old stands of silver birch growing on different soil types were included in the study.

The density of the studied stands varied from 3060 to 36 200 trees per ha and their above-ground biomass varied from 6.0 to 22.9 t DM ha^{-1}. The largest share in the above-ground biomass of the birches (59–80%) was from the stems. The mean stem mass of the birches ranged from 0.29 to 1.79 kg, and the mean total above-ground biomass ranged from 0.36 to 3.03 kg. The leaf area index for the studied stands varied from 1.21 to 4.64 $m^2 m^{-2}$, being the highest for the stand of medium density. Mean single leaf area varied from 9.4 ± 0.2 to 15.4 ± 0.3 cm^2, leaf weight per area varied from 61.1 ± 0.4 to 77.5 ± 0.5 g m^2, and specific leaf area varied from 13.2 ± 0.1 to 16.8 ± 0.1 $m^2 kg^{-1}$. However, no significant differences were found between stand density and the foliar characteristics. There was a strong positive correlation between soil nitrogen concentration and leaf nitrogen concentration ($R = 0.92$); regarding phosphorus concentration, the corresponding correlation was weak ($R = 0.52$) and regarding potassium concentration, no significant correlation was found. The amount of nitrogen accumulated in the above-ground part of the silver birch stands varied between 42.4 and 145.8 kg ha^{-1}, the amount of phosphorus, between 5.9 and 27.9 kg ha^{-1}, and the amount of potassium, between 7.2 and 78.6 kg ha^{-1}. The N:P:K ratios for the foliage were comparable. It is evident that the proportion of nitrogen and phosphorus are close to optimum, while the N:K ratio was lower than optimum value in all cases.

Keywords: Abandoned agricultural land, Silver birch, Betula pendula, Biomass production, Foliar characteristics, Nutrient accumulation

1. Introduction

In Eastern Europe, including Estonia, there is a clear tendency of increase in abandoned agricultural areas, brought about by drastic changes in the political and economic situation [1]. During the last decade, more than 400 000 ha of agricultural land was abandoned in Estonia [2]. One of the alternative land uses is to afforest part of the abandoned agricultural land by establishing deciduous tree plantations. Abandoned agricultural areas in Estonia are often characterized by rapid natural regeneration with fast-growing pioneer deciduous tree species, mainly silver birch (Betula pendula Roth.) and grey alder (Alnus incana L. Moench.), which has led to an increase in the woodland area as well as in the share of deciduous stands growing on abandoned agricultural land. The same tendency is also characteristic of the other countries in the Baltic region [3,4]. In Estonia, the economic importance of deciduous trees started to increase markedly only 10–15 years ago as the priority for Estonian forestry policy before the 1990s was towards coniferous species. Deciduous trees have a number of advantages over conifers on abandoned agricultural land, when young they usually grow faster

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than conifers, they also improve soil conditions, have better wood quality and are less susceptible to Heterobasidion annosum damage.

Silver birch (B. pendula Roth.) and downy birch (B. pubescens Ehrh.) are the most common deciduous tree species in Estonia. The share of birch stands in all stands was 31% in 2003 [5]. The economic importance of birches has also increased during recent decades [6]. Although both species are able to produce stump sprouts, silver birch usually regenerates by seeds in the Estonian conditions [7]. Due to large seed fall [8] and high seed dispersal [9], silver birch regenerates most successfully by seeds in abandoned agricultural areas [10]. Planting of silver birch on abandoned agricultural land has been successful in Estonia [11] as well as in neighbouring countries [12–14]. However, natural regeneration of silver birch on abandoned agricultural land can be more profitable compared with establishment of plantations [15].

Although silver birch is primarily used in saw- and plywood industries, as well as in paper industry, it is a promising short-rotation energy forest species because of its high-productivity potential [16]. Considering the limited reserve of fossil fuels as non-renewable natural resources but also the need to reduce the emission of greenhouse gases, including CO_2, more extensive utilization of biofuels, among them wood, has been discussed. The goal in the European Union is to increase the share of energy generated from renewable sources from 5% to 12% by 2010 [17]. Among the possibilities to reach this goal is to produce energy wood from fast growing deciduous species. Although the main energy sources in Estonia are local oil shale and imported fossil fuels, boilerhouses heated with wood fuel have already started to operate here. However, in the conditions of continuously rising prices of fossil fuels and due to the need to reduce CO_2 emission, use of biofuels and energy forestry will evidently gain more importance in the near future.

The working hypothesis of the present investigation was that young naturally regenerated and planted stands of silver birch on abandoned agricultural land can be an important source of bioenergy for Estonia. At the same time, the productivity potential of silver birch on abandoned agricultural land in the conditions of Estonia has not been studied. Although investigations dealing with establishment and early growth of silver birch stands on abandoned agricultural land have been conducted in Estonia [6,10,11,18], the present study focuses primarily on the biomass production and nutrient accumulation of young silver birch. The main aims of this study were:

(i) to estimate the above-ground biomass production and nutrient (NPK) accumulation in five young stands of silver birch on abandoned agricultural land in relation to stand density and edaphic conditions,
(ii) to analyse the foliar characteristics of silver birch,
(iii) to give silvicultural recommendations for producing biomass for energy.

2. Material and methods

2.1. Study areas

Four naturally regenerated stands of silver birch on abandoned agricultural land and one planted silver birch stand (Kambja) were included in the study (Table 1). Four stands are located in the southeastern part and one is located in northwestern part of Estonia. On the bases of tree measurements and land use related information obtained from landowners, the age of the stands was estimated at 8 years.

2.2. Estimation of biomass and nutrients

Field work was carried out in the studied stands in 2001–2003. One sample plot (130–500 m^2) was established in each stand (Table 1). The stem diameter at breast height (DBH), and the height and the beginning of the live crown of all trees were measured for each sample plot. The above-ground biomass of the stands was determined in August when it was the largest. Dimension analysis [19,20] was used to estimate above-ground biomass. Two of the plots are permanent experimental plots (Haaslava and Kambja) where biomass dynamics has been recorded since 2001 employing the method of model trees. Using a random procedure based on DBH distribution, 10–15 model trees per each sample plot were felled. In all cases the sample trees were felled in the middle of the sample plot to avoid the edge effect. The trees were divided into five classes on the basis of DBH and sample trees were selected according to the frequency of trees for each class. The age of the

Table 1
Main characteristics of the studied stands: location, plot area, number of trees ha^{-1}, mean stem diameter at breast height (DBH), mean height (H), mean height at the beginning of the live crown (C)

Stand	Location	Plot area, m^2	Number of trees ha^{-1}	DBH, cm	H, m	C, m
Haaslava	58°16′N 26°57′E	370	36,200	1.5 ± 0.1^a	3.7 ± 0.1^a	1.2 ± 0.10^c
Väljaküla	57°88′N 26°27′E	130	13,900	2.4 ± 0.1^b	4.4 ± 0.1^b	1.4 ± 0.05^{cd}
Lutsu	58°03′N 27°15′E	230	28,260	1.2 ± 0.1^a	3.2 ± 0.2^a	1.6 ± 0.08^d
Pühatü	58°93′N 24°53′E	320	3060	2.7 ± 0.2^b	4.2 ± 0.1^b	0.3 ± 0.01^a
Kambja	58°14′N 26°43′E	500	4400	3.7 ± 0.1^c	5.3 ± 0.1^c	0.7 ± 0.07^b

Superscript letter indicate a statistically significant difference.

model trees was determined on the basis of the annual rings of the trees using the WINDENDRO software (Regent Instruments Inc.).

The stems of the model trees were divided into five sections. In each section, different compartments including leaves, primary growth of branches, old branches (wood ± bark), stemwood and stembark were separated. From every compartment, a subsample was taken for the determination of dry matter content and for performing chemical analysis. The subsamples were weighed fresh, dried at 70 °C to constant weight and reweighed to 0.01 g. The dry mass of different compartments was calculated for each sample tree by multiplying the respective fresh mass by dry matter content.

To estimate the above-ground biomass of the stand, the following regression equation was used:

$$y = aDBH^b, \quad (1)$$

where y is the above-ground biomass of the model tree, DBH the stem diameter at breast height (cm), a and b the parameter estimates. The parameters of regression Eq. (1) are presented in Table 2.

The masses of different fractions were calculated using the percentage distribution of the fractions obtained on the basis of the model trees. For two stands (Haaslava and Kambja) biomass on the basis of the model trees as well as current annual production (CAP) was determined in three consecutive years. The CAP of the stemwood, bark and branches in the case of the Haaslava and Kambja stands was calculated as the difference between the masses of the respective fractions for the studied year and for the previous year.

The concentrations of nitrogen (N), phosphorus (P) and potassium (K) were determined by tree sections from different fractions of the model trees. As the nutrient concentrations varied dynamically during the vegetation period, NPK accumulation was treated as the concentration of nutrients in the above-ground parts of the trees in the period of maximum leaf mass. The pools of NPK in different fractions of the model trees were calculated as weighted averages considering the share of a particular section in the biomass of the respective fraction of the whole tree as well as the concentration of nutrients in the respective fraction of this tree section. Both the pool of nutrients and the annual demand for nutrients in the above-ground part of the plantation were calculated; the biomass or annual increment of a fraction was multiplied by respective nutrient concentration.

Table 2
Parameters of regression equation (1): a and b—parameter estimates, R^2—coefficient of determination, S.E.—standard error of the estimate, p—probability level

Stand	a	b	R^2	S.E.	p
Haaslava	160.61	2.046	0.993	1.17	<0.001
Väljaküla	152.32	2.246	0.987	1.31	<0.001
Lutsu	160.93	2.046	0.992	1.16	<0.001
Pühatü	180.19	2.079	0.983	1.28	<0.001
Kambja	163.86	2.019	0.992	1.14	<0.001

2.3. Foliar characteristics

The crowns of the model trees were divided into three equal layers. To estimate the foliar parameters (single leaf area, leaf area index (LAI), leaf weight per area (LWA), specific leaf area (SLA), etc.), 20–30 single leaves per each crown layer were collected, and the area and the oven-dry mass of each leaf were measured. The leaves were dried at 70 °C until constant weight and were weighed to 0.001 g. Single leaf area was measured using the WINFOLIA software (Regent Instruments Inc.).

2.4. Soil analysis

In all studied stands, one soil pit (1.0 m deep) was dug. Samples for laboratory analysis were taken from each soil horizon, and the soil type according the FAO-UNESCO classification was determined. The soil types and the topsoil characteristics are presented in Table 3.

2.5. Chemical analysis

The plant samples were analysed for total Kjeldahl nitrogen, phosphorus and potassium concentrations. The block digestion and the steam distillation methods were used for measuring the nitrogen concentration of the plant material (Tecator AN 300). Digestion by flow injection analysis was used to analyse the plant material for Kjeldahl phosphorus concentration (Tecator ASTN 133/94). To analyse the plant material for potassium, the flame

Table 3
Main characteristics of the topsoils under the studied stands

Stand	Soil type	Depth of A horizon, cm	pH_{KCl}	Total N, $g\,kg^{-1}$	Extractable	
					P, $mg\,kg^{-1}$	K, $mg\,kg^{-1}$
Haaslava	Calcic Cambisol	32	5.9	1.19	55	145
Väljaküla	Stagnic Luvisol	30	6.0	0.76	54	164
Lutsu	Stagnic Luvisol	30	5.8	0.64	99	88
Pühatu	Calcic Cambisol	31	6.8	1.60	85	253
Kambja	Cumuli-Gleyic Luvisol	33	5.5	4.62	154	262

photometric method was employed. The soil samples were analysed for pH_{KCl}, total Kjeldahl nitrogen, available (ammonium lactate soluble) phosphorus and potassium by the flame photometric method. All samples were analysed in the Laboratory of Biochemistry, Estonian University of Life Sciences.

2.6. Statistical methods

Normality of DBH and the height of all measured trees were checked by the Lilliefors and Shapiro-Wilkinson tests. For the NPK concentrations of the sample trees, the Kolmogorov–Smirnov test was used. To analyse the effect of the tree section or height class on NPK concentrations in the leaves, stemwood and stembark, one-way analysis of variance (ANOVA) was applied. When the data did not follow the normal distribution, or when there occurred an inhomogeneity of group variance, the nonparametric Kruskal–Wallis analysis of variance was used. Fisher's LSD test and 95% confidence intervals were used to compare the means. Linear and allometric models were employed for estimating the relationships. The measure of the fit of the models was based on the coefficient of determination (R^2), the standard error of the estimate (S.E.), and the level of probability (p). In all cases the level of significance $\alpha = 0.05$ was accepted. Throughout the study, the means are presented with the standard error of the mean (±st. error). To perform statistical analysis, the STATISTICA 7 software was used.

3. Results

3.1. Biomass production

The studied stands were of the same age but with very different densities (Table 1). Mean height and DBH for the stands were in good concordance, i.e. the stands with a larger mean DBH were also higher. The planted stand at Kambja showed a statistically significant ($p<0.05$) larger mean stem diameter and height. Compared with the other areas, the DBH and the height of the trees were significantly smaller for the high-density Haaslava and Lutsu stands. Mean height at the beginning of the live crown was statistically significantly the smallest for the Pühatu stand with the lowest density.

In the present study, the mean dry matter concentration of silver birch was estimated at 43.2±0.4%, being the highest for the stemwood, 62.4±0.7%, and the lowest for the leaves, 26.3±0.8%.

The largest share (59–80%) of the above-ground biomass of the birches was from the stems. The share of the stems was the smallest in the Kambja stand and the largest in the Lutsu stand, 59% and 80%, respectively. Leaf mass accounted for the largest share in above-ground biomass in the Väljaküla experimental plot (18%) and the smallest share in the Lutsu plot (8%). Leaf mass showed good agreement with the concentration of soil nitrogen (R = 0.70) and soil phosphorus (R = 0.68). The share of the branches (26%) was the largest in the Kambja plot with the highest soil fertility and the smallest (12%) in the Lutsu plot with the lowest soil fertility. The largest above-ground biomass, 22.8 t DM ha^{-1}, occurred in Haaslava (36,200 stems ha^{-1}) and the smallest in Rapla, 6.0 t DM ha^{-1} (3060 stems ha^{-1}) (Table 4).

As the studied stands are of the same age, they were compared on the basis of mean stem mass and mean above-ground biomass (Fig. 1). The mean stem mass of the birches ranged from 0.29 to 1.79 kg and the mean total biomass ranged from 0.36 to 3.03 kg. Although accumulated biomass was the largest in Haaslava and Väljaküla, mean stem mass and total above-ground biomass were the largest in the sparser Kambja and Pühatu stands.

For the Kambja and Haaslava stands, current annual production (CAP) for the two last years and bimass dynamics for the age from 6 to 8 years were estimated. In the 7-year-old planted stand of Kambja, the CAP of the stem mass was 2.54 t DM ha^{-1} yr^{-1} and in the naturally grown Haaslava stand of the same age 3.15 t DM ha^{-1} yr^{-1}. However, in the 8-year-old Kambja stand, CAP of stem mass (4.03 t DM ha^{-1} yr^{-1}) exceeded the stem mass production of the natural stand (3.64 t DM ha^{-1} yr^{-1}) (Fig. 2).

Relative increment, which expresses the proportion of current annual production in the total biomass of the stand, was 0.76 and 0.35 for the 7-year-old Kambja and Haaslava stands and 0.66 and 0.37 for the 8-year-old

Table 4
Above-ground biomass (t DM ha^{-1}) in the studied stands

	Haaslava	Väljaküla	Lutsu	Kambja	Pühatu
Stems,	15.65	13.87	8.15	7.88	3.79
Stembark	2.93	2.48	1.47	1.46	0.84
Stemwood	12.72	11.39	6.68	6.42	2.95
Branches,	4.01	4.22	1.26	3.43	1.34
Primary growth	0.92	1.62	0.25	1.19	0.37
Secondary growth	3.09	2.60	1.01	2.24	0.97
Leaves	3.12	3.91	0.81	2.00	0.89
Total	22.78	22.00	10.22	13.31	6.02

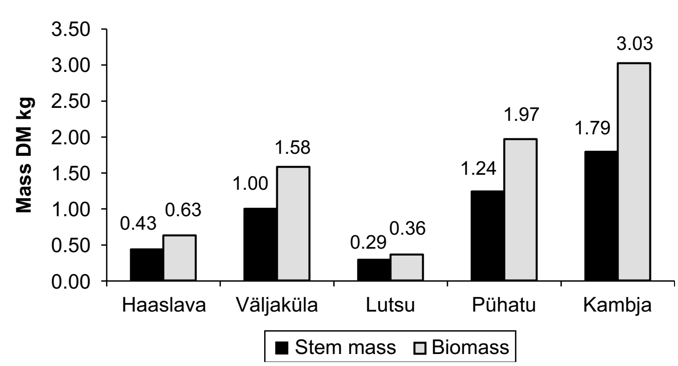

Fig. 1. Mean stem mass and mean total above ground biomass of the birches in the studied stands.

stands, respectively. Foliar assimilation efficiency (current annual production per unit leaf mass) for the 8-year-old Kambja and Haaslava stands was estimated at 4.40 and 2.71 $t\,t^{-1}$ leaf $year^{-1}$, respectively.

To estimate the energy potential of silver birch, current annual energy production was calculated for the Kambja and Haaslava stands. The calculations were based on the calorific value determined in Estonia for the stemwood and bark of silver birch, 19.19 and 23.24 $kJ\,g^{-1}$, respectively [21]. The calorific value for the stemwood is consistent with earlier data from Finland (19.15 $kJ\,g^{-1}$) [22]. The current annual energy production of the stems in the 8-year-old Haaslava and Kambja stands was 72 and 80 $GJ\,ha^{-1}\,yr^{-1}$, respectively. Moreover, taking into account the branches, total annual energy production for the Haaslava and Kambja stands was found to be 108 and 139 $GJ\,ha^{-1}\,yr^{-1}$, respectively.

3.2. Foliar characteristics

According to mean single leaf mass, the stands clearly formed three groups: mean single leaf mass was significantly smaller for the Pühatu and Lutsu experimental plots, while this parameter was the largest for the Kambja plot. Mean single leaf area was also the largest for the Kambja plot. Considering the significantly largest mean leaf mass and mean area of the leaves in Kambja, also mean leaf weight per area (LWA) and specific leaf area (SLA) for this experimental plot were significantly different from the corresponding parameters for the other plots. A strong negative correlation occurred between soil pH and leaf mass ($R = -0.81$). At the same time, Cumuli-Gleyic Luvisol in the Kambja plot was the most acidic and nutrient rich and had the best water regime, while the soil in the Pühatu plot was the most alkaline and drought sensitive. LAI for the studied stands varied from 1.21 to 4.64 $m^2\,m^{-2}$, being the highest for the Väljaküla stand with medium density (Table 5). A strong correlation was observed between soil phosphorus concentration and leaf area ($R = 0.97$) as well as between soil nitrogen concentration and leaf area ($R = 0.82$).

3.3. Nutrient accumulation

For all stands, the highest NPK concentrations were found in the leaves and the lowest in the stemwood (Table 6). The differences in the concentrations between the majority of the fractions were statistically significant; only the difference between the stembark and the branches was not statistically significant. The concentrations in different fractions decreased as follows:

leaves > stembark ⩾ branches (wood + bark) > stemwood.

Nitrogen concentration in the leaves of the naturally regenerated stands was not significantly different, ranging between 24.6 and 28.5 $g\,kg^{-1}$. However, it was significantly higher for the planted stand of Kambja (39.2 $g\,kg^{-1}$) (Table 6). Phosphorus concentration in the leaves was the highest for the Väljaküla stand (4.7 $g\,kg^{-1}$) but it differed

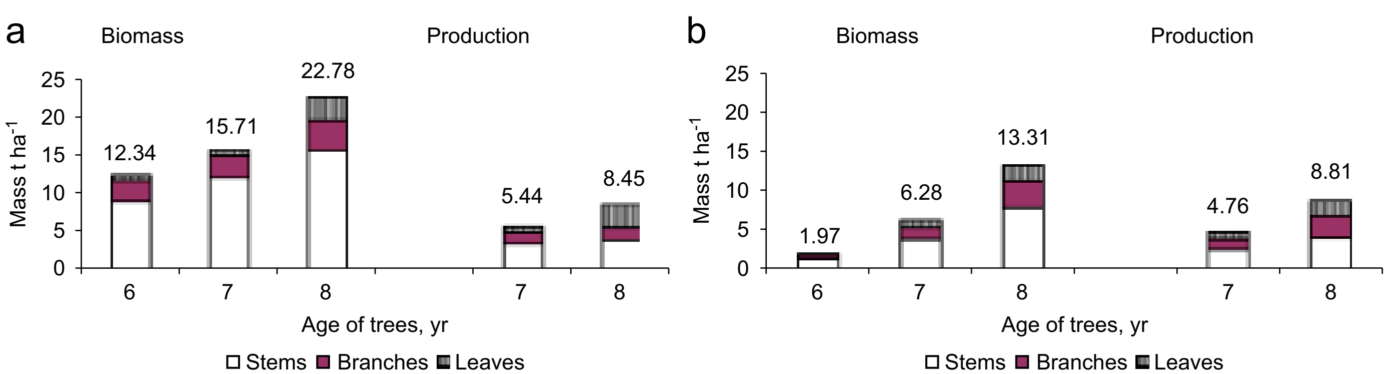

Fig. 2. Above-ground biomass and CAP in the Haaslava (a) and Kambja (b) stands.

Table 5
Mean foliar characteristics for the studied stands: single leaf mass, single leaf area, leaf weight per area (LWA), specific leaf area (SLA) and leaf area index (LAI)

Stand	Leaf mass, mg	Leaf area, cm^2	LWA, $g\,m^{-2}$	SLA, $m^2\,kg^{-1}$	LAI, $m^2\,m^{-2}$
Haaslava	87 ± 2^b	10.9 ± 0.3^b	77.5 ± 0.5^c	13.2 ± 0.1^a	3.63
Pühatu	75 ± 2^a	9.4 ± 0.2^a	76.5 ± 0.4^c	13.4 ± 0.1^a	1.96
Väljaküla	84 ± 2^b	12.7 ± 0.3^c	67.6 ± 0.8^b	15.4 ± 0.1^b	4.64
Lutsu	74 ± 2^a	11.3 ± 0.3^b	66.4 ± 0.5^b	15.4 ± 0.1^b	1.21
Kambja	95 ± 2^c	15.4 ± 0.3^d	61.1 ± 0.4^a	16.8 ± 0.1^c	3.01

significantly only from the corresponding parameter for the Kambja stand.

Correlation analysis showed that nitrogen and phosphorus concentrations in the leaves depended on the concentrations of these nutrients in the soil. For nitrogen concentration, there occurred a strong positive correlation ($R = 0.92$), for phosphorus concentration there occurred a weak negative correlation ($R = -0.52$) and for potassium concentration no correlation was found ($p > 0.01$).

Potassium concentration in the leaves varied in different experimental plots: higher concentrations were found in the Lutsu and Kambja plots and the lowest concentration was found in the Haaslava plot. The analysis of leaf nitrogen concentration in different crown layers of the studied stands did not reveal significant differences between the layers. However, when the sparse stands and the dense stands (Haaslava, Väljaküla, Lutsu) were analysed separately it became evident that nitrogen concentration was significantly higher in the upper crown layer compared with the medium and lower layers. At the same time, there was no significant difference between the medium and the lower layers in any of the cases. Regarding phosphorus and potassium, we failed to establish a similar tendency for different crown layers. NPK concentrations revealed no differences either between different experimental plots or between different crown layers. On the basis of ANOVA, the effect of the height layer on the NPK concentrations of the stembark and wood was significant: NPK concentrations were significantly higher in the upper stem parts than in the lower parts. The effect of the plot on the NPK concentrations of the stembark and wood was not significant.

The amount of nitrogen accumulated in the above-ground part of the silver birch stands varied between 42.4 and 145.8 kg ha^{-1}, the amount of phosphorus between 5.9 and 27.9 kg ha^{-1} and the amount of potassium between 17.2 and 78.6 kg ha^{-1} (Table 7). The NPK demand for producing one tonne of above-ground biomass is presented in Table 7.

The N:P:K ratios, estimated on the basis of the foliage, were similar for the Haaslava, Lutsu and Pühatu stands. For the Kambja stand, the N:P and N:K ratios were found to be lower.

The largest share of all nutrients in the studied stands were accumulated in the leaves: nitrogen, 41–62% (Fig. 3a), phosphorus, 42–68% (Fig. 3b) and potassium, 42–56% (Fig. 3c).

4. Discussion

The significantly larger DBH and height in the Kambja experimental plot was evidently due to the very high soil NPK concentration (Table 3). According to literature data, young birches are sensitive to soil NPK [12] and in the case of fertilization, application of nitrogen and potassium fertilizers yielded the best positive effect [23,24]. The mean height at the beginning of the live crown was significantly the smallest (0.3 m) in Pühatu, which indicates low natural pruning in this sparsest stand (3060 trees ha^{-1}). The stands studied generally displayed evident correlation between stand density and height of the beginning of the live crown, which is consistent with the findings of other authors [6,25].

Table 7
The amounts of nutrients accumulated in the above-ground biomass of silver birch, and the N:P:K ratios for the leaves

Stand	Accumulation, kg ha^{-1}	Demand, kg t^{-1}	N:P:K ratio
Haaslava			
N	145.8	6.3	100
P	20.1	1.0	14
K	61.1	2.6	37
Lutsu			
N	56.2	5.5	100
P	7.8	0.8	14
K	25.8	2.5	47
Väljaküla			
N	168.8	7.7	100
P	27.9	1.3	18
K	78.7	3.6	42
Kambja			
N	138.9	10.4	100
P	14.8	1.1	9
K	50.9	3.8	32
Pühatu			
N	42.5	7.1	100
P	5.9	1.0	15
K	17.2	2.9	42

Table 6
Mean NPK concentrations (g kg^{-1}) of different tree compartments in the studied birch stands

Stand	Leaves			Branches[c]			Stembark			Stemwood		
	N	P	K	N	P	K	N	P	K	N	P	K
Haaslava	25.1 ± 2.7^{a}	3.8 ± 0.2^{a}	9.3 ± 0.2^{a}	4.9 ± 0.2^{a}	0.6 ± 0.1^{a}	2.0 ± 0.1^{a}	6.8 ± 1.2^{a}	0.7 ± 0.1^{a}	2.9 ± 0.5^{a}	2.2 ± 0.3^{a}	0.4 ± 0.1^{a}	1.3 ± 0.2^{a}
Pühatu	25.9 ± 3.0^{a}	3.7 ± 0.2^{a}	10.7 ± 0.8^{ab}	5.5 ± 0.6^{ab}	0.6 ± 0.1^{a}	2.0 ± 0.2^{a}	7.4 ± 1.3^{a}	0.9 ± 0.1^{a}	3.0 ± 0.5^{a}	2.6 ± 0.4^{a}	0.4 ± 0.1^{a}	1.3 ± 0.3^{a}
Väljaküla	28.5 ± 3.1^{a}	4.7 ± 0.3^{b}	11.7 ± 0.9^{b}	5.6 ± 0.6^{ab}	0.7 ± 0.1^{a}	2.6 ± 0.3^{ab}	7.8 ± 2.0^{a}	0.9 ± 0.2^{a}	4.1 ± 1.0^{a}	2.7 ± 0.8^{a}	0.4 ± 0.1^{a}	2.0 ± 0.6^{a}
Lutsu	24.6 ± 3.1^{a}	3.9 ± 0.2^{a}	13.4 ± 0.4^{b}	6.4 ± 0.6^{b}	0.7 ± 0.1^{a}	2.8 ± 0.1^{b}	7.8 ± 0.9^{a}	0.9 ± 0.1^{a}	3.5 ± 0.6^{a}	2.2 ± 0.3^{a}	0.4 ± 0.1^{a}	0.9 ± 0.2^{a}
Kambja	39.2 ± 1.9^{b}	3.7 ± 0.1^{a}	12.7 ± 0.4^{b}	6.5 ± 0.6^{b}	0.7 ± 0.1^{a}	2.5 ± 0.4^{ab}	8.9 ± 1.2^{a}	0.9 ± 0.1^{a}	4.1 ± 0.7^{a}	2.9 ± 0.6^{a}	0.4 ± 0.1^{a}	1.8 ± 0.5^{a}

[c]Current year shoots are excluded.

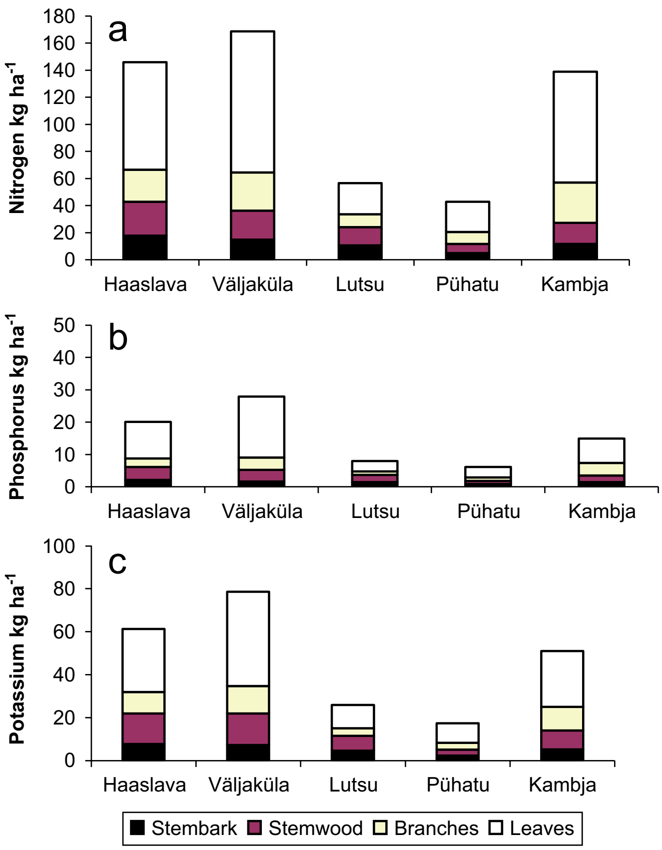

Fig. 3. The amounts of nitrogen (a), phosphorus (b) and potassium (c) accumulated in the total above-ground biomass of silver birch stands.

The only exception was the high density Haaslava plot, where the pruning of the birches was slower compared with the sparser stands.

The mean dry matter concentration of silver birch in this study (43.2±0.4%) is in good accordance with the results of other studies. In Sweden, Telenius [26] calculated the mean dry matter concentration of silver birch as 48.7±0.3%. According to Johansson [27], the mean dry matter concentration (±st. error) of the stems, branches and leaves of silver birch was 58±1%, 53±1% and 40±2%, respectively. The largest proportion of the biomass of the model trees was formed of the stems (59–80% depending on the plot). Similarly, in a study conducted in Sweden, Johansson [27] found that the branches and leaves accounted for a small proportion in the total above-ground biomass of young birches.

Total above-ground biomass in naturally generated young silver birch stands on abandoned agricultural land varies from 6 to 23 t DM ha^{-1}. In the planted stand of Kambja, total above-ground biomass was found to be 13 t DM ha^{-1}. In a study conducted in Sweden, the total production of a 6-year-old birch stand was 14 t DM ha^{-1} (stems + branches) [26]. Johansson [27] calculated the above-ground biomass of 8-year-old silver birch stands (10,000–40,000 stems ha^{-1}) on abandoned agricultural land as 5.7–25.9 t DM ha^{-1}.

Among the studied stands, the biomass of the above-ground part was the largest in the Haaslava stand (36,200 trees ha^{-1}) and Väljaküla stand (13,900 trees ha^{-1}). Although the biomass of the above-ground parts of these stands were similar, their densities differed by almost 2.5 times. In general, the biomass of a stand depends on the number of trees per unit area and on tree size. However, in the present study no significant correlation was found between stand density and biomass of the above-ground part. Obviously, the association between density and biomass is not linear: biomass increases with increasing initial density up to a certain limit beginning from which a further increase in density is not accompanied any more with an increase in biomass. Among the factors ensuring high productivity at lower densities is the foliage. In comparison with the Haaslava plot with exceedingly high density, the Väljaküla plot showed 25% larger leaf mass as well as higher LAI and SLA, which guarantees a larger photosynthesizing area. At the same time, the DBH and the height of the trees in the sparser Väljaküla stand were larger compared with the respective parameters for the Haaslava stand (Table 1). This indicates that cultivation of high-density stands would be justified if the objective is to produce the most biomass. However, when the purpose is to achieve both high production and quality (raw material for plywood and sawmill industries), birch stands with optimal density should be cultivated so that both diameter increment and sufficient pruning are ensured. In a too dense stand competition between the trees is high, which limits growth. Elowson [16] has also pointed out that the production of birch decreases in dense stands. The largest mean stem mass was recorded for the Kambja planted stand where stand density was low and soil conditions were favourable (fertile soil and good water regime). The smallest biomass was recorded for the Rapla plot, which can be explained by very low stand density and unfavourable soil moisture conditions.

Comparison of the obtained current energy productions (72 GJ $ha^{-1} yr^{-1}$ for the Haaslava stand and 80 GJ $ha^{-1} yr^{-1}$ for the Kambja stand) with the energy production of one of the most fast growing tree species, grey alder, revealed that the stem energy production of a grey alder stand of the same age, established on abandoned agricultural land (145 GJ $ha^{-1} yr^{-1}$), exceeded the corresponding value obtained in the present study. However, in older than 25-year-old stands the energy production of birch exceeds that of grey alder [28]. The mean foliar characteristics, single leaf mass (74–95 mg), single leaf area (9.4–15.4 cm^2), LWA (61.1–77.5 g m^{-2}) and SLA (13.4–16.8 $m^2 kg^{-1}$), calculated for silver birch in this study, are in accordance with the results of other studies [27,29]. The highest values of mean LWA were calculated for the Haaslava and Pühatu stands (77.5 and 76.5 g m^{-2}, respectively). It can be concluded that the foliar characteristics measured for young birch stands are affected not only by stand density as the Haaslava stand was the densest (36,200 trees ha^{-1}) and the Pühatu stand was the sparsest

(3060 trees ha^{-1}). The same tendency was also observed for the other experimental plots: although stand density varied to a great degree in the Kambja, Väljaküla and Lutsu plots, their mean LWA values were comparable. LAI reached a maximum value for the Väljaküla stand with medium density. However, there was no association between LAI, stand density and above-ground biomass: LAI was low both for the sparse Pühatu stand and for the dense Lutsu stand. Similar values of LAI were noted for the Kambja and Haaslava stands, although their initial densities were highly different, 4400 and 36,200 trees per ha, respectively. According to Tadaki [30], the normal range of LAI for birches was 2–7 $m^2 m^{-2}$. Johansson [27] reported the LAI values for 7–32-year-old silver birch stands (2280–45,500 trees ha^{-1}) as varying from 0.66 to 4.09 $m^2 m^{-2}$.

Nitrogen concentration in the leaves of silver birch in the studied stands was high (24.6–39.2 g kg^{-1}). In Finland, nitrogen concentration in the leaves of silver birch varied from 26.6 ± 2.7 to 29.7 ± 1.5 g kg^{-1} [31,32]. The highest value in the present study was recorded from Kambja (39.2 ± 1.9 g kg^{-1}) where soil nitrogen content was the highest (4.6 g kg^{-1}). The strong positive correlation between soil nitrogen concentration and leaf nitrogen concentration supports the theory that birches are particularly sensitive to soil nitrogen [23,24]. According to Perala and Alm [33], birches require fertile sites for best growth and are particularly sensitive to available phosphorus. Nitrogen appears another limiting element, while the effects of the other nutrients are not well established. However, it should be borne in mind that the present study involves field soils, which are relatively rich in phosphorus and are also affected by earlier cultivation and fertilization. The results of the study show that at high soil nitrogen concentration, the leaf nitrogen concentration of silver birch can be similar to that of N_2-fixing alders or even exceed it. In Europe, the concentration of nitrogen in alder leaves can vary from 20 to 40 g kg^{-1} [20,31,34–37].

Leaf phosphorus concentration for the Väljaküla stand was significantly higher (4.7 ± 0.3 g kg^{-1}) compared with the other stands (3.7–3.9 g kg^{-1}), which cannot be fully explained by soil properties (Table 3). Soil phosphorus concentration in this area is low and soil pH is comparatively high (6.0), which can reduce the solubility and assimilability of phosphorus. The high leaf phosphorus concentration can be accounted for by the processes taking place in the rhisosphere, which improve the assimilability of this element [38]. The concentration of potassium in the leaves was significantly lower in the Haaslava plot (9.3 ± 0.2 g kg^{-1}) than in the Väljaküla, Lutsu or Kambja plots (Table 6). The occurrence of an association of soil nitrogen and phosphorus concentrations with leaf nitrogen and phosphorus concentrations, and the absence of such an association regarding potassium can be explained by the fact that these elements were analysed from the humus horizon. This is appropriate for nitrogen and phosphorus, which are mainly located in the organic horizons, but not for potassium which is largely released from minerals, in which case potassium concentration in the deeper layers may affect its concentration in plants. Birch has been suggested to have a deeper root system than spruce, being therefore able to take up nutrients from the deeper soil layers [39]. Dultz [40] noted that the Bt horizons of Luvisols derived from till contain more potassium than either the A horizon or the C horizon. As the soil texture in the Lutsu plot is sand, the trees can take up potassium from the deeper, more clayey, soil horizons. And as the mineral feeding of trees is a complex process, also the interrelationships between different nutrients are of importance, and low potassium concentration may be due to the high concentration of Ca and Mg [41].

Potassium concentration was the highest (262 mg kg^{-1}) in the deluvial soil in the Kambja plot and the lowest in the soil of the Lutsu plot (88 mg kg^{-1}), while leaf potassium concentration for these plots did not reveal significant differences, which can be attributed to potassium retranslocation. In the conditions of potassium deficit an essential part of potassium may be retranslocated into the other tree parts before leaf fall, where they are stored until the following vegetation period.

Among the stands studied, the largest share of nutrients were accumulated in the biomass of the above-ground part in the Väljaküla and Haaslava stands where also the biomass of the above-ground part was the largest (Table 4). At the same time, comparison of the Lutsu and Kambja stands, where the biomasses of the above-ground parts were similar, showed that the amounts of NPK bound in biomass were twice as large for all elements in Kambja. As the biomass of the stands studied and hence also the amounts of NPK were different, relative NPK assimilation efficiency, or NPK amount per tonne of biomass, was used for comparison. According to data in the literature, namely nitrogen among all other nutrients has the greatest impact on the productivity of birch [12,23,24]. It is evident from Table 7 that nitrogen assimilation efficiency is the highest, 5.5 kg $tonne^{-1}$ of biomass, in the Lutsu plot and the amount of nitrogen used for producing 1 ton of biomass is the largest in the Kambja plot. The nitrogen feeding of trees depends on net mineralization which in turn depends on the species composition of soil microbes and their activity. This can also explain why nitrogen assimilation in the nutrient poor Lutsu plot was the most efficient. As the stands have different densities, the consequent humidity and temperature differences can affect mineralization of organic nitrogen.

Among the important characteristics describing the feeding conditions of trees is also the N:P:K ratio. According to Ingestad [42], the optimum N:P:K ratio for silver birch is 100:13:65. Regarding phosphorus, the N:P:K ratios for the Haaslava, Pühatu and Lutsu stands were similar and close to the optimum suggested by Ingestad (Table 7). Regarding potassium, the ratio is lower than Ingestad's optimum in all cases. Although potassium concentration is high in the soils of all plots studied, the deficit of this element evidently limits the growth of birch.

Although NPK concentration was highest in the Kambja plot, the share of phosphorus and potassium in the N:P:K ratio was clearly below the optimum. Leaf nitrogen concentration too was higher in the Kambja stand than in the other stands, exceeding even the leaf nitrogen concentration of symbiontly N-fixing alders.

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