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Above-ground growth and temporal plant–soil relations in midterm hybrid aspen (Populus tremula L. × P. tremuloides Michx.) plantations on former arable lands in hemiboreal Estonia

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\section*{ABSTRACT}
Short-rotation forestry with hybrid aspen is a novel silvicultural system in northern Europe on former arable lands. However, knowledge about hybrid aspen growth potential in different soil types and the impact of soil physico-chemical properties on tree productivity in the long term is still scanty. We used repeated monitoring of soil properties and tree growth in young (5-year) and midterm (15-year) hybrid aspen plantations in various soil types (corresponding to four forest site types) to determine the temporal changes in tree growth–soil relationships. Growth of midterm hybrid aspen plantations exceeded same-aged native European aspen stands about two-fold. Growth had improved on Aegopodium, remained moderate on moist Dryopteris and was increasingly suppressed on dry Hepatica soils. The pH\textsubscript{KCl}, available Ca, content of clay and layer thickness of the soil A-horizon had a significant effect on tree growth in young plantations, but these effects disappeared in the midterm age. The soil water-holding capacity and available P in the A-horizon had a significant growth-controlling effect on tree growth in both ages. We concluded that former arable soils provide a sufficient supply of major nutrients in midterm hybrid aspen plantations whereas minor changes have occurred in growth–soil relationships between young and midterm age.

\section*{Introduction}
Establishment of intensively managed forest plantations as a practice of short-rotation forestry (SRF) has spread from southern regions to northern Europe during the last few decades (Weih 2004; Tullus et al. 2013). The phenomenon is mainly driven by the rising interest in renewable energy resources (DIRECTIVE/2009/28/EC), pressure to reduce timber harvest from natural forest (Brockerhoff et al. 2008; Paquette & Messier 2010) and the need to sequestrate atmospheric CO\textsubscript{2} (Gustavsson & Sathre 2011; Haas et al. 2014).

Hybrid aspen (Populus tremula L. × Populus tremuloides Michx.) is considered to be one of the most promising tree species for SRF in northern Europe and the Baltic region on previous arable lands (e.g. Ryttner & Stener 2005, 2014; Tullus et al. 2012; Johansson 2013a) aiming at intensive pulp and energy wood production in a 25-year rotation period (Tullus et al. 2012). Hybrid aspen plantations could be an alternative source for aspen pulpwwood and reduce timber harvest from European aspen stands with high biodiversity value (Kouki et al. 2004; Lõhmus 2011). So far, first-generation hybrid aspen plantations’ growth performance has largely been studied in clonal trials (Ryttner & Stener 2005, 2014), or at a young age (<10 years) (Karacic et al. 2003; Tullus et al. 2007, 2010) or the impact of different soil conditions is unclear (Johansson 2013a, 2013b). Hybrid aspen growth performance has not been compared with native European aspen (P. tremula L.) across broad range of sites while comparisons have usually been made on the basis of few stands growing at similar site conditions (e.g. Yu et al. 2001; Heräjärvi & Junkkonen 2006).

A continuous supply of available resources (water, nutrients) from soil and their efficient use by trees is essential for the high productivity of trees in sustainable SRF systems (Binkley et al. 2004; Vance et al. 2014). Improved knowledge about growth-limiting factors in hybrid aspen plantations helps to provide more precise information for us in silvicultural treatments as Populus spp. are considered to be quite demanding in terms of soil quality (Stanturf et al. 2001; Pare et al. 2002; Stark et al. 2015), especially regarding soil water properties (Stanturf et al. 2001; Pinno et al. 2010; Tullus et al. 2010), soil reaction (Hjelm & Ryttner 2016) and the availability of nitrogen (Stanturf et al. 2001; Pinno & Belanger 2009; Fortier et al. 2010) and phosphorus (Tullus et al. 2010; Truax et al. 2012).

Abandoned arable lands, which have a high nutrient content because of fertilization in the past (Hofmann-Schielle et al. 1999; Ritter et al. 2003; Wall & Hytönen 2005), are assumed to be able to meet the nutritional demands of such high-productivity forest plantation systems during the first couple of decades after afforestation (Hofmann-Schielle et al. 2010).
et al. 1999; Lutter et al. 2015). However, knowledge on plant-soil relations in first-generation hybrid aspen commercial plantations on former arable lands in northern Europe covers only early development at a young age (<10 years) (Tullus et al. 2007, 2010), when soil’s physical rather than chemical properties are the decisive growth-limiters (Tullus et al. 2010). Knowledge about plant-soil relations in young hybrid aspen plantations cannot be directly transferred to the latter stages of plantation development as several alterations can be expected in the stand structure and the increasing amounts of above- and belowground litter inputs (Landsberg & Sands 2011). During the early growth stage, in addition to soil nutritional status, other factors might also have a strong impact on tree growth. The time required to overcome planting stress could depend on the quality of the planting material and of the planting, on weather conditions in the initial year(s), on site preparation, on soil type and on weed control (Davis et al. 1999; Kozlowski & Pallardy 2002; Sinnett et al. 2008). On the other hand, competition between trees intensifies in later stages, when increasing tree size also means higher transpiration rates and nutrient demands in order to maintain above-ground productivity (Bréda et al. 1995; Fox et al. 2007). In growth-limiting conditions, trees start to invest assimilated carbon to fine root production, which means that above-ground production will be inhibited (Keyes & Grier 1981; Yuan & Chen 2010). Besides that, fast-growing trees like hybrid aspen can alter soil reaction and nutritional status already during the first five (Rytter 2016) to 15 (Lutter et al. 2016a) years since plantation establishment.

There are only a few studies about the impact of subsoil physico-chemical properties on tree growth in Populus spp. plantations on abandoned arable lands (Pinno et al. 2010; Tullus et al. 2010). However, trees’ nutrient uptake capacity from deeper soil layers is not always proportional to the root system distribution (Göransson et al. 2006, 2008) and trees are able to bring extra nutrients from deeper soil horizons for cycling and therefore support the growth rate (Kahle et al. 2010; Stark et al. 2015).

Several micronutrients that are considered to be essential for higher plants can be in deficit and limit tree growth more in high-productivity SRF systems than in conventional forest stands (Stone 1990; Ericsson et al. 1992; Landsberg & Sands 2011). The impact of soil micronutrients on hybrid aspen growth has not been studied so far in northern European SRF plantations on former arable lands. So far, the impact of micronutrients on Populus spp. growth has been only studied in poplar plantations in temperate (Laureysens et al. 2004) or Canadian boreal conditions (Pinno et al. 2010).

The aims of the current study were: (1) to estimate the above-ground growth characteristics of 15-year-old first-generation hybrid aspen plantations on different former arable soils in Estonia, (2) to clarify the effects of soil physico-chemical properties at different soil depths on tree growth in 15-year-old (midterm) plantations and (3) to evaluate how these effects have changed compared to 5-year-old (young) plantations. Our hypotheses were: (1) height growth of hybrid aspen is exceeding natural European aspen stands on similar forest soils after the first 15 growing seasons and (2) the effect of soil physico-chemical properties on tree growth has become stronger and the growth distinction between the evolving forest site types has increased in midterm plantations compared to young plantations.

Materials and methods

Studied plantations

The study was carried out in commercial hybrid aspen (P. tremula L. × P. tremuloides Michx.) plantations located mainly in central, southern and south-eastern parts of Estonia (Figure 1). The study area lies in the hemiboreal vegetation zone within a transition zone from maritime to continental climate (Ahti et al. 1968). The weather in Estonia is considerably milder than the continental climate characteristic of the same latitude. The mean annual temperature from 2000 to 2014 was 5.8°C and the mean annual
precipitation was 694 mm according to data from the nearest weather stations to the studied plantations (The Estonian Environment Agency).

The studied plantations were established on former mineral lands in 1999 and 2000 with 1-year-old clonal micropropagated plants originating from Finland (Tullus et al. 2007). Trees belonging to 27 hybrid aspen clones were planted randomly in these plantations (Tullus et al. 2007). Site preparation was carried out before planting to reduce weed competition with whole-area or strip ploughing. The average planting density was 1300 trees per hectare (range: 1200–1600) and all the trees were protected with photodegradable plastic tubes against possible damage by rodents and hares (Tullus et al. 2007). None of the studied plantations was fencd to prevent game damage or fertilized after establishment.

### Tree growth measurement

The long-term network of 51 permanent experimental plots, each measuring 0.1 ha, was established in 2003 and 2004 in 24 hybrid aspen plantations to monitor the above-ground growth rate and productivity of the trees (Tullus et al. 2007). As the sizes of hybrid aspen plantations varied from 0.7 to 32 ha and 14 larger plantations consisted of smaller scattered parts with different soil types, the number of experimental plots in one plantation varied from one to five. The tree growth measurement in all plantations was carried out at the age of 5 (Tullus et al. 2007) and 15 years (as part of the current study) at the end of the growing period (Table 2). The stem diameter at breast height over bark (DBH, cm) was recorded for every single tree with the millimetre scale of a standard forest calliper. The height of every tree was measured with Vertex IV (Haglöf Sweden AB) with 0.1 m resolution. The average density at the age of 15 was 963 trees per ha (range: 540–1450).

The total standing volume was calculated by summing the single tree stem volume (dm³) of the studied hybrid aspen plantations at the ages of 5 and 15 years on the studied foresting site types (Löhmus 1974).

### Soil analysis

The first soil monitoring was carried out in 5-year-old hybrid aspen plantations (Tullus et al. 2007) and repeated as part of the current study in 15-year-old plantations with the same methodologies. Results about changes that had occurred in soil characteristics between the two monitorings have been published in a separate article (Lutter et al. 2016a). An one-metre deep soil pit was dug in the centre of each experimental plot, whereby soil type was determined (Lutter et al. 2016a) and soil samples for chemical and physical analyses were collected from the uppermost A-horizon and deeper B-horizon (Table 3).

For soil pH\(_{\text{KCl}}\) determination, 1 M KCl suspension in the ratio of 10 g: 25 ml was used. The total nitrogen (N\(_{\text{total}}\)) was determined in accordance with Kjeldahl (ISO 11261:1995). The available phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu) and manganese (Mn) were determined by the Mehlich method (Mehlich 1984). The available boron (B) was determined by the hot-water extraction procedure (Berger & Truog 1939). The concentration of organic matter was determined by wet oxidation (Tuurin 1935) and converted to soil organic carbon (SOC) by multiplying organic matter content with 0.58 (Kononova & Belchikova 1960). Total nutrient and SOC stocks were calculated by multiplying nutrient concentration with soil bulk density (BD) and given soil layer volume, where the content of gravel was subtracted (Ryter 2012). All the soil chemical analyses were done in the Laboratory of the Agricultural Research Centre in Saku (http://pmk.agri.ee/).

Soil bulk density (BD, g cm\(^{-3}\)) was determined from undisturbed core samples using a steel cylinder (50 cm\(^3\)).

### Table 1. The soil types (IUSS Working Group WRB 2014) and tree densities in 15-year-old hybrid aspen plantations representing different site type groups (n is the number of experimental plots in each group).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hepatica</th>
<th>Oxalis</th>
<th>Aegopodium</th>
<th>Dryopteris</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil type</td>
<td>Cambisols (n = 4)</td>
<td>Retisols (n = 13)</td>
<td>Cambisols (n = 5)</td>
<td>Gleysols (n = 5)</td>
</tr>
<tr>
<td>Leptisols (n = 1)</td>
<td>Umbriisols (n = 6)</td>
<td>Retisols (n = 7)</td>
<td>Histisols (n = 1)</td>
<td></td>
</tr>
<tr>
<td>Luvisols (n = 3)</td>
<td>Umbriisols (n = 6)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Density, trees per ha</th>
<th>690–1180</th>
<th>956</th>
<th>957</th>
<th>1077</th>
</tr>
</thead>
</table>

### Table 2. Mean (AVG) and dominant trees (400) growth characteristics (H = height (m); DBH = diameter at breast height (cm); V = single tree stem volume (dm³); total stem volume per ha (m³)) of the studied hybrid aspen plantations at the ages of 5 and 15 years on the studied foresting site types (Löhmus 1974).

<table>
<thead>
<tr>
<th>Site type</th>
<th>5-year-old</th>
<th>15-year-old</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hepatica</td>
<td>2.3 ± 0.2</td>
<td>2.8 ± 0.3</td>
</tr>
<tr>
<td>Oxalis</td>
<td>3.0 ± 0.2</td>
<td>3.6 ± 0.2</td>
</tr>
<tr>
<td>Aegopodium</td>
<td>3.1 ± 0.2</td>
<td>3.8 ± 0.3</td>
</tr>
<tr>
<td>Dryopteris</td>
<td>2.4 ± 0.2</td>
<td>3.0 ± 1.1</td>
</tr>
<tr>
<td>All</td>
<td>2.9 ± 0.1</td>
<td>3.5 ± 0.2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Total stem volume</th>
<th>DBH(_{\text{AVG}})</th>
<th>DBH(_{\text{400}})</th>
<th>DBH(_{\text{AVG}})</th>
<th>DBH(_{\text{400}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hepatica</td>
<td>1.3 ± 0.2</td>
<td>1.8 ± 0.3</td>
<td>10.7 ± 0.8</td>
<td>13.5 ± 1.0</td>
</tr>
<tr>
<td>Oxalis</td>
<td>2.0 ± 0.2</td>
<td>2.7 ± 0.3</td>
<td>13.3 ± 0.5</td>
<td>16.1 ± 0.5</td>
</tr>
<tr>
<td>Aegopodium</td>
<td>2.0 ± 0.2</td>
<td>2.8 ± 0.3</td>
<td>13.5 ± 0.3</td>
<td>16.7 ± 0.4</td>
</tr>
<tr>
<td>Dryopteris</td>
<td>1.3 ± 0.3</td>
<td>1.9 ± 0.4</td>
<td>11.7 ± 0.4</td>
<td>14.7 ± 0.5</td>
</tr>
<tr>
<td>All</td>
<td>1.8 ± 0.1</td>
<td>2.5 ± 0.2</td>
<td>12.7 ± 0.3</td>
<td>15.7 ± 0.3</td>
</tr>
</tbody>
</table>

### Equation

\[
V = 0.03186 \times \text{DBH}^2 \times H + 0.43 \times H + 0.0551 \times D^2 - 0.4148 \times \text{DBH},
\]

where \(V\) is the single tree stem volume (dm³), \(\text{DBH}\) is the stem diameter at breast height (cm) and \(H\) is the tree height (m).
samples were oven-dried at 105°C to constant weight at the laboratory. The samples of BD in the A-horizon were taken from sub-layers (0–10; 10–20; 20–30 cm) in three replications and calculated as an arithmetical mean. The samples of BD in the deeper soil horizons were taken from the centre of the revealed horizon in three replications and calculated as an arithmetical mean.

Soil-specific surface area (SSA, m² g⁻¹) and soil texture were analysed by one composite sample from the middle of each revealed soil horizon. SSA was determined by adsorption of water vapour on 10 g dry soil surface (Puri & Murari 1964). To estimate soil texture, sand (soil particles with diameter >0.063 mm) was excluded by sieving, and clay (<0.002 mm) and silt (0.002–0.063 mm) fractions were determined by the pipette method (FAO 2006). The relative proportions of these fractions gave the textural class.

Available water content (AWC, mm) in soil is the amount of water which is available for plants, that is, the difference between water content at field capacity and water content at permanent wilting point in the soil (Brouwer et al. 1985). AWC represents the soil’s potential to store water, not the soil’s capacity to retain water. AWC is calculated as

\[ AWC_{\text{A-horizon}} = BD \times (47.7-18.2 \times BD - 0.04 \times SSA - 72/SSA) \times L \times (1-Gr), \]

\[ AWC_{\text{E-horizon}} = BD \times (44.3-18.0 \times BD - 0.08 \times SSA - 41/SSA) \times L \times (1-Gr), \]

\[ AWC_{\text{B(2)-horizon}} = BD \times (46.5-19.1 \times BD - 0.05 \times SSA - 64/SSA) \times L \times (1-Gr), \]

where AWC is the available water content in the soil (mm), BD is the bulk density (g cm⁻³), SSA is the soil-specific surface area (m² g⁻¹), L is the thickness of the layer (mm) and Gr is the proportion of gravel (soil particles with diameter more than 2 mm). In calculations total AWC of the 75 cm soil layer (AWC₀–75) and AWC of three 25 cm sub-layers (AWC₀–25, AWC₂₅–5₀, AWC₅₀–7₅) were used.

In the initial growth–soil analysis of 5-year-old plantations (Tullus et al. 2007) experimental plots were divided into three groups based on soil moisture regime: automorphic soils, semi-hydromorphic soils and hydromorphic soils. In the current analysis the classification of experimental plots was elaborated based on the Estonian classification of forestland site types (Lõhmus 1974). On the bases of soil morphological and stratigraphic characterization, we tentatively divided experimental plots into different forest site type groups (Table 3).

Forest site type is a complex feature of soil moisture, nutrition (soil parent material) and aeration, and is a more dynamic characteristic for describing site properties than soil type alone (Cajander 1949; Lõhmus 1974). The studied hybrid aspen plantations were assigned into the following forest site type groups (Lõhmus 1974): (1) Hepatica site type prevailing on drought-sensitive automorphic soil with calcareous or neutral soil reaction and with lower water-holding capacity (Table 3); (2) Oxalis site type prevailing on nutrient-rich well-drained automorphic soil with clay enrichment in the B-horizon; (3) Aegopodium site type prevailing on nutrient-rich semi-hydromorphic soil with clay enrichment in the B-horizon with limited drainage and temporarily perched water (stagnic properties) and ground water level rising higher than in Oxalis sites (Table 3); (4) Dryopteris site type prevailing on temporarily water-saturated hydromorphic soil with poor drainage and with a higher concentration of Nₜot (Table 3).

### Statistical analyses

We estimated average (arithmetical mean) tree growth characteristics (Hₐvg = height, m; DBHₐvg = diameter at breast height, cm; Vₐvg = stem volume, dm³) in all experimental plots and site type groups. Hₐvg in hybrid aspen plantations was compared to published height growth data about forestland European aspen stands in similar site types (Kivisté 1997). In order to clarify the effect of site type or continuous soil physico-chemical variables on tree growth in young and midterm plantations, we used data from dominant trees, which are less affected by damages and within-stand competition (Calama et al. 2003; Johansson 2013b). We calculated more precisely the arithmetical mean growth characteristics of “future crop trees”, that is, the 400 thickest trees per ha (H₄₀₀; DBH₄₀₀; V₄₀₀), which is considered to be the standard stand density at the time of the final harvest of the first-generation hybrid aspen plantations in the region (Rytter & Stener 2005, 2014).

A linear mixed model for repeated measures was used to study the effect of site type or continuous soil variables
(Supplementary Material, Table S1) on tree growth at the two plantation ages (young and midterm), with R Statistics function `lmer` in package `lme4`. The model considered site or soil variable, plantation age and the interactive effect of soil and age as fixed factors, and experimental plot as a random factor. When the interactive effect was non-significant ($p > .05$) then it was dropped from the final model and only the main effects of time and soil were analysed. In order to meet the assumption of homogeneity of variances, mean annual growth increment of the given growth characteristic (mean annual increment (MAI), growth characteristic = growth characteristic/age) was used as a response variable. Separate models were run for each growth characteristic and soil variable. The size and direction of the effects were evaluated based on standardized model coefficients. If a significant site type effect was observed, then the Tukey least significant difference (LSD) test was performed to compare the group means. Growth characteristics expressing stem volume were log-transformed in order to meet the assumptions of homoscedasticity and normal distribution of residuals.

One-way ANOVA followed by the Tukey LSD test was used to determine significant differences in soil properties between site type groups (Table 3).

In order to analyse how trees growth potential had changed among site type groups, all the studied sample plots were ranked according to their $H_{400}$ at the ages of 5 and 15 years. The change of mean ranking in each group was tested with Student’s $t$-test.

Mean values are presented with standard error. The normality of the variables was tested with the Shapiro–Wilk test. The homogeneity of variances of growth variables at the two plantation ages was checked with Levene’s test. Q–Q plots and residual distributions were used to assess the normality of model residuals. A level of significance of $\alpha = 0.05$ was used to reject the null hypothesis after statistical tests. All statistical analyses were carried out using R Statistics software (R Core Team 2015).

Results

Growth

After 15 years of growth on former arable lands, the average height of all trees was $13.2 \pm 1.1$ m (range: 8.8–17.1 m) in plantations representing *Hepatica* site type, $16.4 \pm 0.6$ m (12.6–20.0 m) in *Oxalis* plantations, $17.3 \pm 0.6$ m (12.8–20.0 m) in *Aegopodium* plantations and $15.1 \pm 0.3$ m (14.6–15.9 m) in *Dryopteris* plantations (Table 2). Average height of the studied hybrid aspen plantations was about double that of native forestland European aspen stands (Kiviste 1997) on similar soils, where mean height varies from 7 to 9 m at the age of 15 (Figure 2).

The significant main effect of site type on tree growth characteristics ($\text{MAI}_{H_{400}}$, $\text{MAI}_{DBH_{400}}$, $\text{MAI}_{V_{400}}$ and MAI of total stem volume) was observed in 5- and 15-year-old plantations, where all studied growth characteristics were significantly lower in *Hepatica* site type than in *Aegopodium* site type. Growth in *Oxalis* and *Dryopteris* site types did not differ from other groups (Table 4). The interactive effect of site type and age was non-significant, thus the site type effect on tree growth was similar at both ages (Table 4). The site type effect was stronger on $\text{MAI}_{H_{400}}$ ($p < .01$) than on other growth characteristics ($p < .05$).

The greatest average stand stem volume (132.2 ± 10.6 m$^3$ ha$^{-1}$) was recorded for *Aegopodium* site type, where $\text{MAI}$ after 15 years was 8.8 m$^3$ ha$^{-1}$ year$^{-1}$ (Table 2), which however did not differ significantly from *Oxalis* and *Dryopteris* site types. The maximum stem volume of studied plantations at the age of 15 was 199.3 m$^3$ ha$^{-1}$, making the MAI 13.3 m$^3$ ha$^{-1}$ year$^{-1}$.

The change of hybrid aspen plantations’ sample plots ranking (based on $H_{400}$) between the ages of 5 and 15 showed that *Aegopodium* site type plantations had significantly ($p = .016$) improved growth ranking compared with other site types in the midterm period (Figure 3). *Hepatica* site type plantations’ ranking position decreased significantly ($p = .020$) in accordance with their overall poor growth potential (Figure 3). Ranking of *Oxalis* and *Dryopteris* site type plantations remained unchanged.

The effect of physico-chemical soil properties on tree growth

Based on repeated-measures analysis of growth–soil relations at the ages of 5 and 15 years, we found that the effect of six soil variables (pH, SOC, Ca, Mg, clay content, A-horizon thickness) on tree growth characteristics ($\text{MAI}_{H_{400}}$ and $\text{MAI}_{DBH_{400}}$) had significantly ($p < .05$) changed with age, while four soil variables ($N_{tot}$, P, Mg and AWC) had a significant main effect on growth with no temporal change (Table 5).

The negative effect of soil A-horizon pH$_{KCl}$ on $\text{MAI}_{H_{400}}$ depended on plantation age ($p = .048$), being significant in 5-year-old plantations but not significant in 15-year-old...
The mean concentration of $N_{\text{tot}}$ in the B-horizon had a significant negative main effect on MAI$_{H400}$ and MAI$_{DBH400}$, and this effect also did not vary with age. Similarly, SOC in A-horizon was negatively related with MAI$_{H400}$ at both ages. The effect of SOC concentration in the B-horizon on MAI$_{H400}$ ($p = .002$) and MAI$_{DBH400}$ ($p = .005$) depended on plantation age, being non-significant at the young age, while a significant negative effect occurred at the midterm age.

A slightly significant negative impact of boron concentration in the B-horizon on MAI$_{H400}$ was revealed ($p = .045$) in 15-year-old plantations while this effect was not observed in 5-year-old plantations. The A-horizon content of clay ($p = .010$ for MAI$_{H400}$ and $p = .002$ for MAI$_{DBH400}$) and the thickness of the A-horizon ($p = .026$ for MAI$_{DBH400}$) were the only soil physical properties whose effect on tree growth had changed with age, both being significant at the young age and non-significant at the midterm age (Table 5). Soil AWC in the studied sublayers of 25–50 cm, 50–75 cm and 0–75 cm showed a significant positive main effect on tree growth in both 5-year-old and 15-year-old plantations (Table 5). AWC in the 0–25 cm layer showed no significant effect on tree growth.

### Discussion

Commercial first-generation hybrid aspen plantations displayed high growth potential by the midterm period on former arable lands in Estonia. This was confirmed by the almost two-fold difference in height growth compared with native European aspen forestland stands at similar site types, confirming our first hypothesis. Apart from the hybrid vigour that caused faster growth of hybrid aspen compared with its parent species (Tullus et al. 2012), previous fertilization of former agricultural lands significantly improved soil nutritional status compared with similar forestland soils (Hofmann-Schielle et al. 1999; Ritter et al. 2003; Wall & Hytönen 2005), and its positive impact on tree growth speed could be long-lasting (Hofmann-Schielle et al. 1999; Falkengren-Gerup et al. 2006; Lutter et al. 2015).
Table 5. The effects (standardized model coefficients and their significance: *p < .05, **p < .01, ***p < .001) of soil variables (soil reaction [pH_{KCl}], nutrient concentrations in A- and B-horizon and stocks in A-horizon and in the top 75 cm soil layer, and AWC) on MAI of tree growth characteristics (MAI_{H400} and MAI_{DBH400}) in the studied hybrid aspen plantations at the ages of 5 and 15 years according to repeated-measures analysis.

<table>
<thead>
<tr>
<th>Soil variable</th>
<th>Soil layer</th>
<th>Growth characteristic</th>
<th>Age</th>
<th>p</th>
<th>p</th>
<th>p</th>
<th>Soil</th>
<th>Soil × age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH_{KCl}</td>
<td>A</td>
<td>MAI_{H400}</td>
<td>&lt;.001</td>
<td>.008</td>
<td>n.e.1*</td>
<td>.048</td>
<td>−0.25 ± 0.08**</td>
<td>−0.13 ± 0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.014</td>
<td>−0.18 ± 0.07*</td>
<td>.074</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>MAI_{H400}</td>
<td>&lt;.001</td>
<td>.049</td>
<td>−0.12 ± 0.06*</td>
<td>.670</td>
<td>n.e.2</td>
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<tr>
<td></td>
<td></td>
<td>MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.004</td>
<td>−0.19 ± 0.06**</td>
<td>.221</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aego_{H400}</td>
<td>.002</td>
<td>.029</td>
<td>−0.15 ± 0.07*</td>
<td>.645</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aego_{DBH400}</td>
<td>.001</td>
<td>.013</td>
<td>−0.14 ± 0.06*</td>
<td>.833</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<tr>
<td></td>
<td></td>
<td>Oxalis_{H400}</td>
<td>.001</td>
<td>.043</td>
<td>n.e.1</td>
<td>.002</td>
<td>−0.01 ± 0.07</td>
<td>−0.23 ± 0.06**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oxalis_{DBH400}</td>
<td>.001</td>
<td>.030</td>
<td>n.e.1</td>
<td>.005</td>
<td>0.06 ± 0.08</td>
<td>−0.19 ± 0.08*</td>
</tr>
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<td></td>
<td></td>
<td>75 cm MAI_{H400}</td>
<td>&lt;.001</td>
<td>.027</td>
<td>−0.15 ± 0.07*</td>
<td>.220</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.003</td>
<td>n.e.1</td>
<td>.011</td>
<td>−0.32 ± 0.09***</td>
<td>−0.08 ± 0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.038</td>
<td>−0.15 ± 0.07*</td>
<td>.587</td>
<td>n.e.2</td>
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<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.017</td>
<td>0.16 ± 0.07*</td>
<td>.518</td>
<td>n.e.2</td>
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<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.001</td>
<td>0.25 ± 0.06***</td>
<td>.643</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<td></td>
<td></td>
<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.003</td>
<td>0.19 ± 0.06***</td>
<td>.340</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<td></td>
<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.001</td>
<td>−0.29 ± 0.07***</td>
<td>.718</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<td></td>
<td></td>
<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.001</td>
<td>−0.25 ± 0.07***</td>
<td>.195</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<tr>
<td></td>
<td></td>
<td>75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.028</td>
<td>−0.13 ± 0.06*</td>
<td>.407</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<td></td>
<td></td>
<td>50-75 cm MAI_{H400}</td>
<td>&lt;.001</td>
<td>.010</td>
<td>−0.17 ± 0.06*</td>
<td>.207</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<tr>
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<td></td>
<td>50-75 cm MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.022</td>
<td>n.e.1</td>
<td>.045</td>
<td>−0.03 ± 0.06</td>
<td>−0.27 ± 0.11*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MAI_{H400}</td>
<td>&lt;.001</td>
<td>.043</td>
<td>n.e.1</td>
<td>.010</td>
<td>−0.25 ± 0.08**</td>
<td>−0.07 ± 0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MAI_{DBH400}</td>
<td>&lt;.001</td>
<td>.092</td>
<td>n.e.1</td>
<td>.002</td>
<td>−0.25 ± 0.08***</td>
<td>0.01 ± 0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AWC 25–50 cm</td>
<td>&lt;.001</td>
<td>.049</td>
<td>0.12 ± 0.06*</td>
<td>.501</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AWC 25–50 cm</td>
<td>&lt;.001</td>
<td>.003</td>
<td>0.18 ± 0.06**</td>
<td>.660</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AWC 50–75 cm</td>
<td>&lt;.001</td>
<td>.020</td>
<td>0.15 ± 0.07*</td>
<td>.524</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AWC 50–75 cm</td>
<td>&lt;.001</td>
<td>.003</td>
<td>0.19 ± 0.06**</td>
<td>.155</td>
<td>n.e.2</td>
<td>n.e.2</td>
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<tr>
<td></td>
<td></td>
<td>AWC 75 cm</td>
<td>&lt;.001</td>
<td>.003</td>
<td>0.19 ± 0.06**</td>
<td>.630</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AWC 75 cm</td>
<td>&lt;.001</td>
<td>.001</td>
<td>0.23 ± 0.06***</td>
<td>.096</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thickness of A-horizon</td>
<td>&lt;.001</td>
<td>.021</td>
<td>0.13 ± 0.06*</td>
<td>.370</td>
<td>n.e.2</td>
<td>n.e.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thickness of A-horizon</td>
<td>&lt;.001</td>
<td>.001</td>
<td>n.e.1</td>
<td>.026</td>
<td>0.28 ± 0.07***</td>
<td>0.10 ± 0.07</td>
</tr>
</tbody>
</table>

Notes: Data are shown only when significant (p-value < .05) soil or “soil variable × age” interactive effect was observed. The standardized model coefficients characterize the size and direction of the soil effect at both ages (β_{p, p}) or mean effect across ages (β_{pooled}) in the case of non-significant interaction.

n.e.1 = not estimated because there was a significant “soil × age” interactive effect.

n.e.2 = not estimated because the “soil × age” interactive effect was non-significant.

* p < .05.

** p < .01.

*** p < .001.

Our second hypothesis about the increased significance of site type effect in midterm hybrid aspen plantations found only weak support. Based on repeated-measures analysis, the site type effect was similar at both ages, while the more robust growth-rank analysis suggested some significant shifts in tree growth potential among site type groups. At both ages (5 and 15 years), greater growth was observed on former arable soils corresponding to Aegopodium forest site types compared to Hepatica site type. Plantations growing on fresh Aegopodium site type soils significantly improved their tree growth ranking in midterm age compared with other site types, and dry Hepatica soils showed significant decrease in tree growth ranking. Such changes can probably be explained by the soil water properties that differed significantly between site types. Fresh Aegopodium site type soils have naturally higher ground water levels according to Löhmus (1974). The importance of soil water properties is more evident during drought periods (Hogg et al. 2008) and soils with higher water-holding capacity in deeper soil horizons can support faster growth of trees during these periods (Martin & Gower 2006; Tullus et al. 2010). When selecting sites for establishing forest plantations it must be borne in mind that the frequency of drought in mid-summer is expected to rise as a consequence of climate change in the Estonian region (Jaagus & Mändla 2014). In contrast to Aegopodium soils, poor growing Hepatica site soil’s water-holding capacity is low because of the high content of stones and limited nutrient uptake in dry conditions (Löhmus 1974), even though the soil nutrient status of Hepatica soils was higher for several nutrients than in Aegopodium or Oxalis. A slower growth rate of trees on Hepatica site type soils was also observed in Estonian midterm silver birch plantations on former arable lands compared with Oxalis soils (Lutter et al. 2015).

Similar results to our study’s best performing Oxalis and Aegopodium site type soils with mean height growth (16–17 m, up to 20 m) have been found for first-generation hybrid aspen in southern Sweden (17–20 m) (Rytter &
The finding that tree growth rate was limited in soils with neutral reaction in the A-horizon on the 5-year-old plantations was no longer evident by the midterm period. This can be explained by a decrease of pH_KCl in the A-horizon during the last 10 years in the studied hybrid aspen plantations (Lutter et al. 2016a). Another explanation is that the uppermost soil layer of previous agricultural lands was intensively limed to cover leaching losses during past land-use (Kõlli & Ritter et al. 2003). The mean MAI in our study was about 9 m³ ha⁻¹ on Oxalis and Aegopodium site types, being 13 m³ ha⁻¹ on the best sample plot on Aegopodium site type at the age of 15. The modest MAI in our study can be explained by lower stand density and colder climate compared to southern Sweden. Moreover, the northern origin planting material used in Estonian hybrid aspen plantations (Tullus et al. 2007) is less productive compared to southern origin genotypes, due to shorter leafy period (Lutter et al. 2016b).

The hypothesized soil factors increasing the effect on tree growth with age was partly supported by the results as both strengthening as well as weakening of the growth–soil associations was observed.

The thickness of the A-horizon was positively related to tree growth in 5-year-old plantations. Soil A-horizon depth has also been found to be an important factor in tree growth in sparse poplar plantations in other studies covering the early growth stage (Pinno et al. 2010). A deeper A-horizon means better conditions for root expansion and larger nutrient pools (Fisher & Binkley 2000) as well as more available water storage (Tullus et al. 2010; Lutter et al. 2015). This finding is also supported by Rosenvald et al. (2014), who found that 99.8% of fine roots were located in the A-horizon in a young hybrid aspen plantation on previous agricultural land. Clay content negatively affected tree growth in 5-year-old plantations. This indicates that root development and nutrient uptake were more enhanced in light-textured soils (Tullus et al. 2010; Nielsen et al. 2014), where root penetration and development are probably easier after the first years of tree planting (Simmet et al. 2008). However, automorphic soils with a higher clay content also have better ability to retain soil moisture (Helling et al. 1964; Martin & Gower 2006; Tullus et al. 2010). The significant positive impact of A-horizon thickness and the negative impact of clay content on tree growth disappeared in the 15-year-old plantations. This tendency is probably due to lowered soil BD in 0–30 cm soil depth as organic material inputs albeit improving soil’s capacity to store water (Hansen 1993; Rawls et al. 2003). More porous soil structure facilitates water transport through the soil, which could be advantageous during water saturation periods (Fisher & Binkley 2000). Another explanation of the vanishing effect of A-horizon thickness could be older trees’ root exploration of deeper soil layers (Kahle et al. 2010; Stark et al. 2015) compared with young trees (Rosenvald et al. 2014).

Soil AWC (estimated for 25–50, 50–75 or 0–75 cm sublayer) was a significant factor to dominant trees’ growth both in 5- and 15-year-old plantations. Soil water properties are related to soil texture (Fisher & Binkley 2000) and poplars prefer well-aerated soil with sufficient moisture content (Stanturf et al. 2001), where the deeper subsoil layer (B-horizon) is fine textured with greater ability for water storage (Martin & Gower 2006; Tullus et al. 2010). Such soils in our study were prevailing mainly in Aegopodium site type. Similarly to hybrid aspen, a significant positive effect of AWC in 0–75 cm soil depth on dominant trees’ height growth was also observed in 15-year-old silver birch SRF plantations (Lutter et al. 2015). However, while hybrid aspen was more significantly affected by AWC in deeper soil layers, the impact of AWC on silver birch was stronger in the uppermost 0–25 cm soil layer (Lutter et al. 2015). The importance of deeper soil AWC to hybrid aspen can be explained by the aspen’s deeper rooting system (Persson 1975; Strong & La Roi 1985). Our findings are in agreement with Canadian studies, where soil texture as a proxy for soil water properties was an important factor describing productivity of poplars (Pinno & Belanger 2009; Pinno et al. 2010) and aspens (Martin & Gower 2006; Pinno & Belanger 2011). Thinnings are recommended to redistribute soil water resources and to improve their availability for the remaining trees (Bréda et al. 1995; Jiménez et al. 2008; Otto et al. 2014).

We found that several studied nutrients showed significant impact on hybrid aspen productivity. However, it should be noted that we studied soil nutrients that are directly available to plants (except N_nit) and total soil nutrient pools are higher as they contain also reserves that are not directly available to plants (Fisher & Binkley 2000). In this study, we analysed plant-soil relations based on the availability and stocks of soil nutrients. At the same time, nutrient uptake by trees depends also on the status of microbial activity in the soil solution near roots (Kreuzwiezer & Gessler 2010). For example, mycorrhizal fungi and nitrogen-fixing bacteria could be responsible for...
80% of nitrogen and up to 75% of phosphorus uptake by plants in temperate and boreal forests (van der Heijden et al. 2008).

High concentrations and stocks of soil base cations (Ca, Mg) showed several negative relations with tree growth at both ages. A lower tree growth rate in soils with higher Ca and Mg is similarly explicable to soil pH_{KCl} – calcareous soils have also higher reserves of soil base cations and soil acidification promotes non-acid base cations replacement with acid (Lutter et al. 2016a). In addition, calcareous soils have high content of stones and gravel that causes soil to have less water-holding capacity as seen for the Hepatica site type. About 60% of Estonian arable soils have a deficiency of plant-available magnesium (Mg < 100 mg kg\(^{-1}\)) (Loide et al. 2010). Soil A-horizon Mg concentration of less than 100 mg kg\(^{-1}\) was observed in about half of the studied sample plots. However, Mg concentration in A-horizon remained at the same level in 15-year-old plantations compared to 5-year-old (Lutter et al. 2016a). Similarly to our study, a negative impact between available Mg in 0–30 cm soil depth and trees productivity was also found in a dense 4-year-old poplar coppice plantation in Belgium (Laureysens et al. 2004). Populus spp. are generally quite Ca demanding (Stanturf et al. 2001; Pare et al. 2002; Meiresonne et al. 2007) and a positive significant impact of soil Ca on sparsely planted hybrid poplars growth rate in abandoned farmlands has been observed (Pinno et al. 2010; Truax et al. 2012). In soil chemistry, Ca and Mg cannot be treated separately as in ion exchange processes Mg behaviour is counterbalanced by the abundance of Ca in the soil solution (Tyler & Olsson 2001). Simultaneously during the study period no unbalanced Ca:Mg ratio was recorded as it stayed within the interval of 10 up to 20:1 (Lutter et al. 2016a), which ensures optimal condition for high crop productivity (Loide 2004). So far, we can conclude that the requirement of soil base cations is met on studied former arable lands after 15 years of afforestation with hybrid aspen; however, it may become problematic for some Oxalis and Aegopodium soils with naturally low base saturation (Löhmus 1974).

Generally, poplars’ growth rate is sensitive to soil nitrogen availability (Stanturf et al. 2001; Pinno & Belanger 2009; Fortier et al. 2010). The negative impact of soil B-horizon N\(_{tot}\) and SOC concentration on tree growth could be because N\(_{tot}\) is the most in moist soils, where anaerobic conditions prevail (Brockett et al. 2012) and N mineralization is limited (Berg 2000; Hobbie et al. 2002). This is confirmed in Dryopteris soils, which had remarkably high N\(_{tot}\) content compared with other site types. N\(_{tot}\) and SOC showed also a slight increment in their concentration from the age of 5 to 15 (Lutter et al. 2016a), which, however, was negatively related to tree growth (Lutter et al. 2016a). A negative relation between tree growth and N\(_{tot}\) in the 0–15 cm soil layer has been found in sparse hybrid poplar plantations in temperate Canadian abandoned farmlands (Truax et al. 2012). Therefore, the results of our study also confirm that higher concentration of N\(_{tot}\) in soil cannot ensure high productivity of trees (O’Connell et al. 2003; Truax et al. 2012) as the amount of N\(_{tot}\) is not directly related with plant-available (mineralized) N (Fortier et al. 2010; Ros et al. 2011).

The impact of available P stock on tree growth was important at both ages. Available P, which is found in higher concentrations in former agricultural lands than forests and mainly depends on previous fertilization (Kölli et al. 2008), is generally sensitive to soil pH and Ca dynamics (Kleinman & Sharpley 2002; Renneson et al. 2015). As soil P concentrations remained unchanged and pH along with Ca decreased (Lutter et al. 2016a), P availability was probably compensated by the release of P that have been previously bounded with Ca (Som-Srivichai et al. 1984). A survey about soil nutrient changes between 5-year-old and 15-year-old hybrid aspen plantations did not reveal any depletion of available P in either the A- or the B-horizon (Lutter et al. 2016a). Available P in the uppermost soil layer was found to be a growth-limiting macronutrient in several studies of sparse Populus spp. plantations on abandoned farmlands (Tullus et al. 2010; Truax et al. 2012) as well as on forest soils (Hjelm & Rytter 2016). We did not notice any significant impact of the B-horizon’s P concentration on tree growth, similarly to Pinno et al. (2010), who reported only a marginal impact of B-horizon P on young hybrid poplars’ productivity. Even though high P concentrations from previous fertilization could be quite long-lasting (Wall & Hyytönen 2005; Lutter et al. 2016a), we can conclude that available P was the only nutrient of which low stocks showed a significant tree growth-regulating effect both in 5- and 15-year-old plantations.

The only micronutrient that showed a significant (negative) relationship with tree growth was available B concentration in the B-horizon in midterm plantations. During the past 10 years in the studied hybrid aspen plantations, available boron had significantly decreased whereas the decrease had been larger in faster-growing plantations (Lutter et al. 2016a). Among the studied site types, the available B concentration in the A-horizon was significantly lower in more productive Oxalis and Aegopodium site types. Boron is in deficit in Nordic conditions (Lehto et al. 2010) and lack of B could start to limit trees’ productivity (Stone 1990; Dell & Huang 1997). We did not detect any limiting impact of soil available micronutrient (Cu, Mn, B) stocks or concentrations on dominant tree growth at the age of 15 and we can conclude that soil Cu, Mn and B reserves are still sufficient for optimal tree growth in midterm plantations on former agricultural lands. However, smaller concentrations of available B in more productive soils suggest that B might become problematic in the second half of the hybrid aspen rotation period.

In conclusion, our study confirms first-generation hybrid aspen plantations’ higher productivity on former agricultural lands during the first 15 years in Estonian conditions compared to native European aspen stands. The highest productivity was observed on soils corresponding to Oxalis and Aegopodium forest site types. Compared to young age with midterm the growth potential had improved on Aegopodium soils, remained moderate on Dryopteris and decreased on Hepatica soils. Therefore, Hepatica site type soils are not recommended for afforestation with hybrid aspen if high productivity is desired. The significant growth factors just in young plantations were: A-horizon pH_{KCl}, available Ca concentration, content of clay and thickness of A-horizon. In the B-horizon, N_{tot}, SOC and available B concentrations had a
significant negative effect on tree growth only in midterm plantations. Soil AWC in deeper soil layers and available P (A-horizon concentration and stock) showed a significant growth-controlling effect on tree productivity in both young and midterm plantations. The results suggest the need for thinning during the second half of the rotation period not only to enlighten the tree crowns but also to redistribute soil resources. As the majority of studied macro- and micronutrients were not proved to restrict tree growth, we can exclude the fertilization need at this point of stand development.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Brockett BFT, Prescott CE, Grayston SJ. 2012. Soil moisture is the major growth-controlling effect on tree productivity in both young and midterm plantations. The results suggest the need for thinning during the second half of the rotation period not only to enlighten the tree crowns but also to redistribute soil resources. As the majority of studied macro- and micronutrients were not proved to restrict tree growth, we can exclude the fertilization need at this point of stand development.

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