

RELATIONSHIPS BETWEEN CELLULOSE, LIGNIN AND NUTRIENTS
IN THE STEMWOOD OF HYBRID ASPEN IN ESTONIAN
PLANTATIONS

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Concentrations of cellulose, lignin and nutrients in the stemwood of four clones of 7-year-old hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.) were studied on 50 permanent experimental plots established for the afforestation of abandoned agricultural lands in Estonia. Quantitative evaluation of hybrid aspen chemical components indicated a relatively high cellulose and low acid-insoluble lignin concentration, and especially a high C/L ratio, compared to other poplar species. Regression analyses showed strong relationships between stemwood N, P, K, cellulose and lignin concentrations, but no dependence on soil chemical composition was established. Height, diameter and annual increment were strongly dependent on stemwood N, K and P. Based on the results obtained, clones of hybrid aspen appear as economically promising for the afforestation of abandoned agricultural lands, in large-scale, short-rotation commercial plantations, for pulpwood and bioenergy production.

Keywords: hybrid aspen, clones, cellulose, acid-insoluble lignin, nutrients, growth

INTRODUCTION

Cellulose, the main polymeric component of the plant cell wall and the most abundant polysaccharide on earth, has a simple chemical composition: the polysaccharide consists of D-glucose residues linked by β -1,4-glycosidic bonds forming linear polymeric chains of over 10000 glucose residues. Although chemically simple, the extensive intermolecular bonding pattern of cellulose generates a crystalline structure which, together with other cell wall components, such as hemicellulose and lignin, result in very complex morphologies.¹ After cellulose, lignins are the second abundant organic C-compounds occurring in the biosphere as a major fraction in wood, usually found in the secondary cell walls. Lignins represent approximately 25% of the terrestrial biomass.

The cell walls of the wood of broad-leaved trees may contain approximately 40-50% cellulose, 17-35% lignins and 15-35% hemicelluloses,^{2,3} as depending on tree species and growth conditions.⁴ The wood of the trees is composed⁵ of cellulose, lignin and hemicelluloses in approximate ratios of 2:1:1. During tree growth, cellulose microfibrils give the cell walls tensile strength, while the lignin from the cellulose fibrils gives them rigidity.

Chemically, lignin is not a strictly defined molecule like cellulose, being characterized by a great deal of variation in its chemical composition and physical properties.⁶ It has taken a long time for scientists to recognize the complexity of lignins. Today, we know that lignin composition varies not only among the different species, but also among

different plant organs and even in different cell layers.^{7,8} For example, it has been noted that lignin concentration recorded in the roots of *Picea abies* L. may be over three times higher than that from the needles of the tree.⁹

As a result of the gradual advance of knowledge, lignins are described as polymeric natural products arising from enzyme-initiated and chemically driven dehydrogenative polymerisation of primary precursors, possessing a *p*-hydroxycinnamyl alcohol structure.¹⁰ Significant progress has been made in recent years towards better understanding lignin biosynthesis. However, the formation and properties of lignins still remain among the “open questions” of tree physiology, requiring the scientists’ extra attention for understanding the processes of heartwood formation and regulation for forestry utilizations.⁶

Genetic improvement of the cell wall polymer synthesis in forest trees is one of the major goals of forest biotechnology, with possible impact on the end-product utilization.¹¹ Several laboratories have produced and are field-testing transgenic trees with significantly reduced lignin and increased cellulose contents, yet with a normal growth and development. Consequently, the recent developments provided opportunities for genetically modifying some important wood properties, so that energy, paper or solid wood products can be now realized.

Since the end of the 1980s, aspen wood has been viewed as an important raw material for the pulp and paper industry. As aspen is low in lignin and high in carbohydrates, its wood is amenable to many kinds of chemical or mechanical pulping.¹²⁻¹⁵ Aspen has thin-walled fibres of narrow diameter, which are ideal for producing a high-density paper sheet with a smooth surface.^{13,16} The white-coloured aspen wood bleaches easily, reducing the use of chemicals and making the production of aspen pulp less harmful to the environment. In boreal and hemi-boreal conditions, aspens are fast-growing, cold resistant trees which may be cultivated in both natural and plantation forest systems for the production of a variety of products, such as pulpwood,

energy wood and aspen logs. Similarly to other *Populus* species, aspens (primarily European aspen (*P. tremula*) in Eurasia and trembling or quaking aspen (*P. tremuloides*) in North America) have been subjected to intensive selection and breeding investigations, for selecting progenies with industrially valuable features, e.g. fast growth, resistance to pests and diseases, improved physico-chemical wood properties, etc. This has been favoured by the high genetic variability of aspens.¹⁷ Both *P. tremula* and *P. tremuloides* have huge natural distributions with several geographical races and natural forms.

In the hemi-boreal and boreal region, a hybrid between *P. tremula* and *P. tremuloides* (known as hybrid aspen) has been found as the most suitable one for growing in short rotations of 20-30 years for the production of pulpwood; even shorter rotation times are recommended for energy wood coppicing systems.¹⁸⁻²³ Hybrid aspen displays superior growth compared to its parent species, as due to heterosis,²⁴ reaching maturity in a twice shorter period than European aspen. The interest in establishing aspen plantations has been driven by several factors. First, there is an increasing demand for aspen pulp in the region. Thus, aspen plantations would help to preserve the old aspen forests. Secondly, the establishment of short-rotation forest plantations is recommended for the abandoned agricultural lands in Estonia and in the neighbouring countries. Forest plantations provide an option to raise the socio-economic value of such agriculturally degraded landscapes.

For Estonian forestry, hybrid aspen is a relatively new tree. About 700 ha of commercial hybrid aspen plantations have been established since 1999 on abandoned agricultural lands.²² All these plantations have been aimed at producing aspen pulpwood in 25-year rotations. The first generation is planted and the combined production of energy and pulpwood is recommended for successive root-sucker generations.²¹ Under Estonian conditions, the early growth of hybrid aspens has been highly variable, as depending on the physico-chemical properties of the previous field soils. Under well-suited conditions, hybrid

aspen has shown^{22,23} fast growth during the first 5-7 years.

Although hybrid aspen has been subjected to intensive selection and monitoring work in experimental plantations in the hemi-boreal region (in several Baltic Sea countries and North America), less studies have focused on its growth and industrial wood properties in large-scale commercial plantations. The current study will provide an overview of cellulose, lignin and nutrient content in hybrid aspen stemwood under various site conditions, at an early age, in relation to tree growth, clonal background and soil properties. For establishing these plantations, selected clones with proven superior growth, compared to the parent species, were used.

The authors assume that a faster growth could also mean lower lignin and higher cellulose contents in wood, compared to pure *P. tremula* and *P. tremuloides*.

MATERIALS AND METHOD

Study area

The study was carried out within the network of permanent experimental plots, on 7-year-old hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.) plantations, established for the afforestation of abandoned agricultural lands in Estonia (Fig. 1). The plantations were established in 1999-2000 with 1-year-old micropropagated plants belonging to 27 different hybrid aspen clones.²²

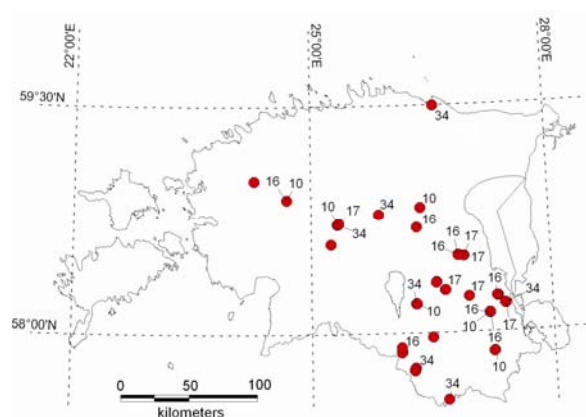


Figure 1: Location of 24 hybrid aspen plantations (marked as circles) where the experimental plots (n = 50) have been established. The numbers indicate the plantations the model trees representing the four most abundant clones (10, 16, 17, 34) were taken from

Plant material analyses

Investigations were carried out on 50 experimental plots, on 24 commercial hybrid aspen plantations over Estonia (Fig. 1). From each experimental plot, one model tree was selected on the basis of the stem diameter at breast height (DBH, cm) from the upper half of the DBH distribution of all trees within the plot. The height (H, m) and annual height increment (AHI, m) of the model trees were also measured. Among 50 model trees, 18 different hybrid aspen clones were present. Four clones were represented by at least 6-8 trees, offering the opportunity to study the variation of wood properties and their relations with soil properties within and among clones. According to the Finnish Plant Production Inspection Centre, these clones are marked as C05-99-10, C05-99-16, C05-99-17 and C05-99-34, although, in the text, only the short versions of clone names (10, 16, 17, 34) will be given. The parameters under study

were analyzed in two data sets: all 50 model trees together (mean of model trees) and separately by four most abundant clones.

For the analysis of wood chemical quality, a stemwood sample disk (length: 5-10 (20) cm) at 1.3 m height was taken from each model tree. These samples were dried at +70 °C to constant weight and milled to 0.5 mm. In all samples, the concentrations of cellulose, acid-insoluble lignin and macronutrients N, P and K were determined.

The concentration of total N (%) in plant samples was determined by the standard Kjeldahl procedure; P (%) was determined spectrophotometrically and K (%) was determined flamephotometrically.

Lignin (L) was determined as acid-insoluble lignin.^{10,25} The air-dried plant material was ground and extracted with acetone (100%) at 5 °C, ethanol (96%), ethanol-benzene solution (1:1, v/v) and water at 60-70 °C, to remove the sugars, proteins, interfering phenolics and other soluble

compounds. The residue was dried at 70 °C for 24 h and used to determine acid detergent fibre (ADF), neutral detergent fibre (NDF) and acid detergent lignin (ADL).

For the determination of fibres, FibertecI&MSystems (Foss AB, Denmark) elaborated by Van Soest²⁵ were used. In the first step, NDF was determined after treatment with a neutral detergent solution (sodium lauryl sulphate and EDTA), the residue consisting of cellulose, hemicellulose and lignin.

The next step was to determine ADF after the treatment of the residues with an acid detergent solution (cetyl trimethylammonium bromide in sulphuric acid solution); the residue consisted of cellulose and lignin.

Finally, ADL was determined after initial treatment for ADF measurement, followed by the removal of the cellulose fraction through extraction with 72% H₂SO₄. A fraction of acid-soluble lignin and cellulose could be lost during this procedure.^{10,25} The acid-resistant residue was recovered by filtration on a glass crucible with asbestos filter, carefully washed and dried at 70 °C for 24 h to constant weight (Precisa 205A SCS, Switzerland). This residue contains only insoluble Klason lignin (hereafter called 'lignin').^{10,26} After weighing, the residue was ashed at 525±25 °C for at least 5 h and lignin was calculated after correcting the mineral elements.²⁵

Simple subtraction rules were used to calculate cellulose (C): ADF – ADL = Cellulose. The results for lignin and cellulose were expressed as dry mass percentage of the plant material (% dw).

The analyses were performed in the Laboratory of Biochemistry of the Estonian University of Life Sciences.

Soil analyses

For a correct assessment of the tree state, the relationships between wood quality and chemical soil properties on the experimental plots were analysed. For the collection of soil samples, steel bore cylinders were used and the soil humus horizon was analysed on four locations from each experimental area. The total N (%) in soil samples was determined by the Kjeldahl procedure. To analyse the available P, K, Ca and Mg amounts (mg·kg⁻¹) in the soil, a Mehlich 3 extractant was used. The soil pH in 1M KCl suspensions was measured in a 10 g to 25 mL ratio. For the characterization of the experimental area, the arithmetic mean values of four analysed subsamples were used. The analyses were performed by the Laboratory of Agrochemistry of the Agricultural Research Centre in Saku (<http://pmk.agri.ee>).

Statistical analyses

Descriptive statistics were calculated and simple regression analysis was performed²⁷ by Statistica 7. The normality of the studied growth, soil and foliar variables was checked by the Kolmogorov-Smirnov test; the soil variables (concentrations of N, P, K, Ca and Mg) were log-transformed, after which the data followed a normal distribution. One-way Anova followed by Tukey's HSD test was used for multiple comparison of the clonal means of the studied variables. The mean values are followed by ± standard error. Pearson correlation coefficients were used to estimate the dependencies between the morphological and chemical parameters in stemwood, as well as between the parameters of stemwood and soil chemical composition. An $\alpha = 0.05$ level of significance was applied in all cases.

RESULTS AND DISCUSSION

To get additional information for interpreting the state of young hybrid aspen trees on the different experimental plots in Estonia, the physical and chemical properties of the soil were investigated. The concentration of N, P, K, Ca and Mg and the level of pH in soil humus horizons from the experimental plots were rather similar, with the exception of the experimental plots for clone 17, which showed some more nutrients, and for clone 16, characterized by relatively lower nutrient concentrations (Table 1). The higher nutrition level was reflected in the growth of clone 17, and the height and annual increment of trees from clone 17 were higher by 21 and 38%, respectively, than the mean, whereas the concentration of cellulose and lignin and the mineral composition in stemwood did not differ statistically from the mean (Table 2).

The present study was expected to evidence essential differences between hybrid aspen clones and to select those suitable for forestry. As known, wood formation in trees is under genetic control and considerable differences appear among species, it even being possible to observe genotypes within species. A comparison of wood chemical components gave evidence of significant differences in cellulose and lignin concentrations among the hybrid aspen clones used in our experiment and other *Populus* species. Stem lignin and cellulose in *P. tremuloides* control trees and transgenic lines altered during lignin biosynthesis,

ranging²⁸ between 10.7-22.2% and 41.4-53.3%, respectively. The concentration of *P. alba* wood cellulose was³ between 46.53-

49.26%, and lignin concentration – between 17.23-25.23%.

Table 1
Chemical composition (mean \pm S.E. and range) of soil humus horizons on different experimental plots

Clone	No plots	pH	P, mg kg ⁻¹	K, mg kg ⁻¹	N, %	Ca, mg kg ⁻¹	Mg, mg kg ⁻¹
10	6	5.9 \pm 0.27 (4.9–6.7)	77 \pm 14.1 (42–141)	118 \pm 20.2 (67–201)	0.15 \pm 0.021 (0.09–0.20)	1817 \pm 285.3 (973–2830)	120 \pm 27.2 (21–186)
16	8	5.8 \pm 0.33 (4.8–7.2)	75 \pm 12.7 (29–132)	101 \pm 19.8 (43–204)	0.14 \pm 0.021 (0.07–0.24)	2164 \pm 667.5 (621–5270)	80 \pm 22.8 (18–209)
17	6	5.3 \pm 0.21 (4.3–5.8)	92 \pm 41.0 (8–291)	128 \pm 34.9 (53–246)	0.33 \pm 0.205 (0.07–1.36)	2627 \pm 1350.2 (832–9340)	189 \pm 100.3 (53–687)
34	7	6.0 \pm 0.35 (4.8–7.39)	60 \pm 16.9 (21–149)	184 \pm 55.0 (63–459)	0.19 \pm 0.035 (0.10–0.32)	2519 \pm 908.1 (1070–7860)	143 \pm 25.9 (80–278)
Mean of plots	50	5.7 \pm 0.11 (4.1–7.3)	79 \pm 7.5 (8–291)	127 \pm 10.7 (43–459)	0.18 \pm 0.027 (0.07–1.36)	2044 \pm 240.8 (621–9340)	138 \pm 18.5 (18–687)

Table 2
Mean characteristics \pm S.E. and ranges of growth and stemwood components of hybrid aspen clones from the experimental plots*

	Mean of model trees	Clone 10	Clone 16	Clone 17	Clone 34
No trees	50	6	8	6	7
H, m	4.2 \pm 0.25 (1.7–8.8)	3.5 \pm 0.34 a* (2.1–4.3)	4.0 \pm 0.44 a (2.6–6.3)	5.1 \pm 0.82 a (1.9–7.4)	3.4 \pm 0.48 a (1.7–5.0)
DBH, cm	3.1 \pm 0.25 (0.9–7.5)	2.9 \pm 0.42 a (1.2–4.1)	3.0 \pm 0.58 a (1.4–6.5)	4.2 \pm 0.81 a (1.0–6.5)	2.3 \pm 0.46 a (0.9–4.3)
AHI, m	0.8 \pm 0.06 (0.2–1.8)	0.6 \pm 0.14 a (0.2–1.1)	0.8 \pm 0.09 ab (0.6–1.3)	1.1 \pm 0.20 b (0.5–1.7)	0.6 \pm 0.10 ab (0.2–1.0)
Cellulose, %	59.6 \pm 0.34 (52.0–65.5)	58.5 \pm 0.72 ab (57.0–60.8)	60.2 \pm 0.96 b (57.5–65.5)	57.0 \pm 0.44 a (55.2–58.1)	60.2 \pm 0.80 ab (56.6–63.3)
Lignin, %	10.9 \pm 0.17 (9.1–13.7)	11.1 \pm 0.52 a (9.8–13.3)	10.9 \pm 0.40 a (9.5–12.4)	11.7 \pm 0.55 a (10.1–13.1)	10.5 \pm 0.58 a (9.3–13.7)
C/L	5.5 \pm 0.10 (4.1–6.8)	5.3 \pm 0.26 a (4.3–5.9)	5.6 \pm 0.23 a (4.6–6.4)	4.9 \pm 0.25 a (4.2–5.6)	5.9 \pm 0.35 ab (4.1–6.8)
N, %	0.25 \pm 0.010 (0.11–0.57)	0.28 \pm 0.028 a (0.20–0.39)	0.23 \pm 0.017 a (0.15–0.28)	0.24 \pm 0.015 a (0.19–0.30)	0.26 \pm 0.020 a (0.19–0.34)
P, %	0.043 \pm 0.0012 (0.028–0.073)	0.048 \pm 0.0039 a (0.037–0.061)	0.045 \pm 0.0027 a (0.035–0.058)	0.044 \pm 0.0021 a (0.035–0.049)	0.041 \pm 0.0024 a (0.035–0.049)
K, %	0.054 \pm 0.0032 (0.030–0.131)	0.054 \pm 0.0039 a (0.047–0.068)	0.050 \pm 0.0023 a (0.043–0.057)	0.056 \pm 0.0024 a (0.049–0.066)	0.066 \pm 0.0023 a (0.044–0.066)

*Letters denote significant differences of means determined by Tukey HSD test after one-way ANOVA

The chemical wood composition of *P. tremula* involved²⁹ 46.3% cellulose and 21.8% lignin. The clones of hybrid aspen in Estonian experiments had much lower lignin (10.5-11.7%) and higher cellulose content (57-60.2%) in stemwood (Table 2), which recommends hybrid aspen as a promising

source for energy, paper or solid wood production. A significant criterion for wood utilisation in the paper industry is the C/L ratio, which was, on the average, 5.5 in the stemwood of aspen clones 10, 16, 17 and 34, indicating that, in hybrid aspen, the cellulose ratio was higher than that of *P. alba*, *Fagus*

silvatica L., *Quercus robur* L., *Salix alba* L. and many other deciduous trees in which this parameter³ is below three.

As known, lignin and cellulose biosynthesis in plants depends on several factors, related both to the plant and to the environment. Regression analysis revealed a linear dependence between the mean concentration of N, P K and cellulose, and a strong relationship between lignin and cellulose in the stemwood of clones (Table 3). The concentration of cellulose was negatively correlated with that of lignin ($p < 0.001$). The negative relationships and the fact that the reduction of the lignin content leads to higher ratios of cellulose in aspen stemwood had been already reported by several authors.^{5,30}

The nitrogen from trees or soil is considered to be an important factor for both lignin and cellulose biosynthesis. For example, a high N fertility increases the concentration of cellulose in long-leaf pine (*Pinus palustris* Mill.) seedlings, resulting,³¹ however, in a lower lignin concentration. Experiments with transgenic aspen (*Populus tremuloides*) lines with low lignin and high cellulose contents in stems, associated with higher N concentrations in leaf tissues, support³² this idea. Also, a significant linear relationships between soil N concentration and the corresponding cellulose in reference plants was observed.³³

Although numerous researches reported relationships between lignin and N in plants and soils,^{2,9,34,35} our results did not reveal any relationships between N in soil or tissues and lignin for the hybrid aspen clones studied (Table 2). However, it is fairly clear that, in the case of N deficiency, high lignin and tannin contents may occur in plants.^{2,9,34} Contrary to previous verified results, Pitre *et al.*³⁵ demonstrated that a high N supply decreases lignin staining in the newly formed secondary xylem, although the Klason lignin content remains unchanged. Consequently, as in our experiments only acid-insoluble Klason lignin was determined, it is impossible to make any final decision on the relationships between N and lignin for hybrid aspen clones. A thorough checking is needed not only for Klason, but also for other forms of lignin.

An increase in pH and Ca and K content in the cell wall compartment favours the oxidation of phenolics, the esterification with cell wall carbohydrate polymers and lignification.³⁶ Moreover, an efficient Ca supply has a significant influence on wood formation in poplar (*Populus tremula* x *Populus tremuloides*) clones.³⁷ We agree with other authors,^{34,38} that K is needed for lignification through a protein and polysaccharide enzymatic process. However, we detected a relationship between K concentration in stemwood and lignification only for hybrid aspen clone 10 (Table 3). Although Dünisch and Bauch³⁹ found a positive influence of K and Mg fertilisation on cellulose in coniferous trees, we did not establish any relationships between cellulose concentrations and K and Mg in soil and in stemwood for hybrid aspen.

It has been often shown that tree growth is correlated with lignin and cellulose concentration in stems. For example, in oak, the cellulose content increases with the radial growth of a tree and decreases with its height.³ On the other hand, intensive lignification may stop the extension of cell walls⁷ and cause growth cessation of plants.² However, our experiment with hybrid aspen clones revealed no statistical relationships between cellulose and lignin concentrations in stemwood and the growth parameters of trees (Fig. 2, Table 3). A comparison of the lignin concentration in the stem with that of other poplar species^{3,28,29} suggests no inhibition in the growth of aspen clones on our experimental plots, as due to a relatively low lignin concentration in their stems. Statistically significant relationships between height growth, diameter and annual increment of clones 17 and 34 and the lignin content in their stems were established (Table 2), but not in the case of mean results (Fig. 2).

Although no relationships were found between lignin and cellulose concentrations in stemwood and growth parameters, strong relationships were established between mean height growth, DBH and all studied macronutrients in stemwood (Table 4).

Table 3
 Linear regressions between average concentrations of cellulose (C), lignin (L) and their ratio (C/L) in stemwood and the morphological and chemical characteristics of the most frequent hybrid aspen clones (10, 16, 17, 34) and the chemical characteristics of soil

Parameter	Mean of 50 model trees			Clone 10			Clone 16			Clone 17			Clone 34		
	C	L	C/L	C	C	L	C/L	L	C/L	C	L	C/L	C	L	C/L
<i>Growth</i>															
H	-0.03	-0.14	0.11	0.59	0.67	-0.60	0.61	0.57	-0.48	-0.05	0.34	-0.28	0.67	-0.60	0.61
DBH	-0.10	-0.09	0.05	0.53	0.58	-0.56	0.56	0.51	-0.43	-0.16	0.39	-0.37	0.58	-0.56	0.56
AHI	-0.14	0.03	-0.07	0.63	0.75	-0.81*	0.80*	0.63	-0.56	-0.69	0.44	-0.61	0.75	-0.81*	0.80*
<i>Wood</i>															
N	-0.47**	0.27	-0.34*	-0.41	-0.68	0.57	-0.56	-0.58	0.45	-0.04	-0.17	0.10	-0.68	0.57	-0.56
P	-0.47**	0.23	-0.34*	-0.43	-0.58	0.48	-0.49	-0.52	0.38	-0.15	-0.19	0.08	-0.58	0.48	-0.49
K	-0.54**	0.26	-0.38*	0.43	0.20	0.06	0.07	0.94*	-0.89*	-0.74	0.05	-0.32	0.20	0.06	0.07
C	1.00	-0.51***	0.70***	1.00	1.00	-0.91**	0.96**	-0.43	0.60	1.00	-0.10	0.45	1.00	-0.91**	0.96**
L	-0.51***	1.00	-0.97***	-0.41	-0.91**	1.00	-0.98***	1.00	-0.98**	-0.10	1.00	-0.93**	-0.91**	1.00	-0.98***
C/L	0.70***	-0.97***	1.00	0.49	0.96**	-0.98***	1.00	-0.98**	1.00	0.45	-0.93**	1.00	0.96**	-0.98***	1.00
<i>Soil</i>															
pH _{KCl}	0.23	-0.09	0.14	0.06	0.06	0.19	-0.04	-0.26	0.27	-0.05	-0.57	0.47	0.06	0.19	-0.04
P	0.07	-0.25	0.22	-0.22	0.44	-0.50	0.51	-0.25	0.36	-0.11	0.03	-0.03	0.44	-0.50	0.51
K	0.06	-0.23	0.22	-0.69	0.22	-0.31	0.29	0.03	-0.04	-0.29	-0.59	0.41	0.22	-0.31	0.29
N	-0.03	-0.10	0.05	0.41	0.10	-0.43	0.36	-0.46	0.39	-0.24	-0.29	0.14	0.10	-0.43	0.36
Ca	0.12	-0.17	0.16	0.41	0.30	-0.37	0.38	-0.19	0.17	0.03	-0.43	0.37	0.30	-0.37	0.38
Mg	0.09	-0.17	0.14	0.45	0.46	-0.49	0.51	-0.54	0.50	-0.05	-0.37	0.27	0.46	-0.49	0.51

Significant correlations are marked as follows: *0.01 < p < 0.05; **0.001 < p < 0.01; *** p < 0.001

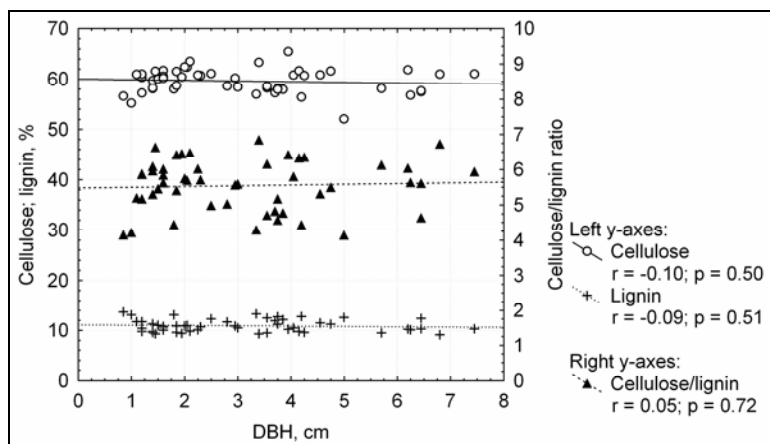


Figure 2: Relations between mean concentrations of cellulose, lignin and their ratio and DBH of trees

Table 4

Linear regressions between average N, P and K concentrations in stemwood, the morphological characteristics of the most frequent hybrid aspen clones (10, 16, 17, 34) and soil chemical characteristics

Stemwood nutrient		Growth parameters				Soil parameters				
		H	DBH	AHI	pH _{KCl}	P	K	N	Ca	Mg
Clone 10	N	-0.90*	-0.91*	-0.53	-0.21	0.16	-0.28	0.16	-0.1	0.18
	P	-0.92**	-0.76	-0.74	0.11	0.2	0.06	0.32	0.2	0.29
	K	0.24	0.6	-0.37	0.88*	-0.17	0.88*	0.34	0.85	0.17
Clone 16	N	-0.94***	-0.92**	-0.3	0.6	-0.26	0.53	0.38	0.54	0.83*
	P	-0.85**	-0.79*	-0.1	0.51	-0.13	0.47	0.28	0.38	0.90**
	K	0.2	0.34	0.54	-0.07	-0.12	-0.02	0.29	-0.15	0.14
Clone 17	N	-0.89*	-0.93**	-0.79	0.44	-0.33	0.24	-0.07	0.18	-0.03
	P	-0.33	-0.38	-0.27	0.08	0.48	0.53	-0.8	-0.6	-0.66
	K	0.75	0.75	0.72	-0.72	0.26	-0.49	-0.45	-0.53	-0.45
Clone 34	N	-0.81*	-0.71	-0.4	0.26	-0.4	-0.2	0.17	-0.08	-0.24
	P	-0.97***	-0.94**	-0.37	0.22	-0.38	0.1	0.01	0.24	0.1
	K	0.14	0.14	-0.22	0.76	0.17	-0.45	-0.44	-0.08	-0.29
Mean of 50 model trees	N	-0.51***	-0.49***	-0.31*	0.09	-0.18	-0.08	-0.03	-0.02	0.04
	P	-0.45**	-0.42**	-0.18	0.09	0	0.01	-0.11	-0.05	0.06
	K	0.41*	0.42*	0.24	-0.52**	-0.34*	-0.2	-0.05	-0.31	-0.09

Significant correlations are marked as follows: * $0.01 < p < 0.05$; ** $0.001 < p < 0.01$; *** $p < 0.001$

CONCLUSIONS

Hybrid aspen stemwood is characterized by a relatively high cellulose and low lignin concentration, which confirms its suitability for biotechnology, pulpwood and energy production or other fields of forest engineering. The clones evidence significant although small differences in wood composition, indicating the importance of considering wood properties, besides growth parameters, in the selection of the most economically promising clones. As hybrid aspen can be grown under a wide variety of

site conditions and – in some situations – requires few inputs, it will undoubtedly be a key species in forestry in the future. Therefore, further basic research on wood formation, especially on lignin and cellulose biosynthesis pathways, is needed.

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