allozyme results (Timerjanov, 1994). The similarity between patterns of morphological, monoterpene and allozyme differentiation may indicate that they reflect the effect of events related to glaciation. Paleobotanical evidence indicates that refugia probably existed in the Ural mountains. *Larix sukaczewii* may have been restricted to small refugia during Pleistocene glaciation, as *L. occidentalis* (Fins and Seeb, 1986). These small refugia could have acted as "genetic bottlenecks" and resulted in low genetic variation.

The results reported in this paper suggest that historical events have had a marked effect on the pattern of distribution of genetic variation of *Larix sukaczewii* in the Southern Urals. It appears that the genetic characteristics of *Larix sukaczewii* largely reflect the effects of evolutionary factors imposed by relatively recent historical events related to the last glaciation.

References

Altukhov, Yu. P., Krutovski, K. V. and Dukharev, V. A.: Biochemical population genetics of wood forest species. In: Proc. Symp. For. Genet. Breed. and Physiol. of Woody Plants, Voronezh, 1989, Moscow, 16–24 (1989). — Cheliak, W. M., Wang, J. and Pitel, J. A.: Population structure and genic diversity in tamarack, *Larix laricina* (Du Roi) K. Koch. Can. J. For. Res. **18**, 1318–1324 (1988). — Davis, B. J.: Disc electrophoresis. II. Method and application to human serum proteins. Ann. New York Acad. Sci. **121**, 67–75 (1964). — Fins, L. and Seeb, L.W.: Genetic variation in allozymes of western larch. Can. J. For. Res. **16**, 1013–1018 (1986). — Gregorius, H. R.: Genetischer Abstand zwischen Populationen. I. Zur Konzeption der genetischen Abstandsmessung. Silvae Genet. **23**, 22–27 (1974). — Guries, R. P. and Ledig, F. T.: Gene diversity and population structure in pitch pine (*Pinus rigida* Mill.). Evolution **36**, 387–402 (1982). — Krutovski, K. V., Politov, D. V. and Altukhov, Yu. P.: Genetic variability in siberian cedar pine, *Pinus sibirica* Du Tour. IV. Genetic diversity and differentiation between populations. Genetika **25**, 2009–2032 (in Russian) (1989). — Larionova, A. Ya.: Genetic polymorphism and intraspecies variability of *Larix sukaczewii* Dyl. In.: Genet. and Selec. Develop. in For. Manag. Proc. of Sci. Confer. Moscow, 31–33 (in Russian) (1988). — Lewandowski, A. and Mejnartowicz, L.: Levels and patterns of allozyme variation in some European larch (*Larix decudia*) populations. Hereditas **115**, 221–226 (1991). — Liu, Z. and Knowles, P.: Patterns of allozyme variation in tamarack (*Larix laricina*) from northern Ontario. Can. J. Bot. **69**, 2468–2474 (1991) — Maier, J.: Genetic variation in European larch (*Larix decidua* Mill). Ann. Sci. For. **49**, 39–47 (1992). — Milyutin, L. I., Muratova, E. N. and Larionova, A. Ya.: Genetic and taxonomic analysis of *Larix sibirica* and *L. sukaczewii* populations. Lesovedenei **5**, 55–63 (in Russian) (1993). — Nei, M.: Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. USA **70**, 3321–3323 (1973). — Nei, M.: Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583–590 (1978). — Putenikhin, V. P., Andrianov, P. D. and Timerjanov, A. Sh.: The study of population structure and gene resource conservation of *Larix sukaczewii* in the South Urals. In: Proc. Symp. For. Genet. Breed. and Physiol. of Woody Plants, Voronezh, 1989, Moscow, 146–147 (1989). — Semerikov, V. L. and Matweev, A. V.: Genetic diversity of siberian larch populations investigated by means of allozyme loci. Genetika **31,** 602–609 (in Russian) (1995). — Sneath, P. H. and Sokal, R. R.: Numerical Taxonomy. W. H. Freeman, San Francisco (1973). — Timerjanov, A. Sh.: Genetic variation of *Larix sukaczewii* Dyl. in the South Urals. In: Proc. Asia-Pacific Symp. on For. Genet. Improv. Conf. Beijing, China, October 19 to 22, 1994. 12 (1994). — Timerjanov, A. Sh., Shigapov, Z. Ch. and Yanbayev, Yu. A.: Genetic variabiltiy in larch (*Larix sukaczewii* Dyl.) in the Southern Urals. I. Gene control mechanism of isozymes. Genetika **30**, 1243–1247 (in Russian) (1994). — Workman, P. L. and Niswander, J. D.: Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. Amer. J. Hum. Genet. **22**, 24–29 (1970). — Yeh, F. C. and O'Malley, D.: Enzyme variations in natural populations of Douglas fir, *Pseudotsuga menziesic* (Mirb.) Franco, from British Columbia: 1. Genetic variation patterns in coastal populations. Silvae Genet. **29**, 83–92 (1980). — Ying, L. and Morgenstern, E. K.: The population structure of *Larix laricina* in New Brunswick, Canada. Silvae Genet. **40**, 180–184 (1991).

Effect of Age on Selected Wood Quality Traits of Poplar Clones

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Summary

Anatomical properties of 3 Euramerican hybrid poplar (*Populus* x *euramericana* (Dode) Guinier) clones, the Italian 'I-214' and the Hungarian 'Kopecky' and 'Koltay', were investigated. Six trees from each clone were sampled at 2 sites in Hungary. Plantations on the 2 sites were 15 and 10 years old, respectively. Disks were removed at breast height from each tree to study the effect of age on variation of selected wood properties.

Age had significant effect on wood quality traits. Differences in ring widths between clones were significant in the first few years and in the favorable years only.

For anatomical properties, most of the variation was detected within tree. From pith to bark anatomical properties showed a rapid change first, followed by a decreasing rate of change, finally a constant value for each clone on both sites; this has been interpreted as a sign of maturation. The maturation process was affected by site. The better site accelerated maturation but at lower values. The ages of levelling off were not the same for all properties; however, the sequence of maturation was the same on both sites. Fibre length and vessel lumen area were the last to become constant.

For specific gravity, there were significant differences between clonal means. Within-tree specific gravity was generally high near the pith, but each clone exhibited different radial patterns. Regarding strength properties, clonal effect was found non-significant; means were higher near the bark than close to pith. Specific gravity was not the most important

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single factor affecting strength properties. No consistent relationship was found between growth ring width and wood properties when growth rings of the same age were compared.

Regarding the hereditary component in wood quality traits, the genetic differences were confirmed; however, age seems to have a decisive influence on properties measured. This indicates that wood quality in poplars can not be reliably estimated on juvenile wood at an early age.

Key words: poplar clones, juvenile wood, maturation, wood quality, specific gravity, strength properties, early testing.

FDC : 165.441; 165.72; 811; 181.75; 176.1 *Populus* x *euramericana*.

1. Introduction

Specific gravity is the most widely considered wood quality trait because it is believed to have the most significant effect on utilization, and it may be altered by silvicultural and genetic manipulations.

Due to improvements in silviculture and genetics, accelerated growth in intensively managed forest stands may result in trees of harvestable size at younger age and with a higher percentage of juvenile wood than in natural stands (BENDTSEN, 1978). Variation in wood properties within trees along the radius and from the base to the top is associated with the formation of juvenile wood and its relative proportion to mature wood. Its appearance is usually much more evident in conifers than in hardwoods. Juvenile wood has been widely studied and its direct relationship to the age of the cambium is accepted by many investigators (ZOBEL and TALBERT, 1984; ZOBEL and VAN BUIJTENEN, 1989).

In general, wood properties within the juvenile zone are characterized by rapid changes from the pith outward. In the mature zone, nearly all wood properties are relatively constant. For tree breeders, the earliest possible age for reliable determination of mature wood properties is of high importance. From a utilization standpoint, the principal interest is in the effects of age on wood properties, among others on size and distribution of anatomical elements.

1.1. *Anatomical parameters*

Literature regarding the variation in anatomical properties of poplars is extensive and also controversial. SCARAMUZZI (1958) found very little variability in the volume fraction of the different types of longitudinal anatomical elements across the radius of *Populus* x *euramericana* clones with ray volume showing the most variation. However, uniform pattern of ray cells across the radius was observed by CHENG and BENSEND (1979) and by ONILUDE (1982) as well. According to ISEBRANDS (1972), volume percent of vessels increased and percent of fibers decreased with increasing age in eastern cottonwood (*Populus deltoides* BART.). CHENG and BENSEND (1979), ONILUDE (1982) and KROLL et al. (1992) concluded for different poplar species that the vessels produced by the cambium of mature trees were significantly larger and less numerous than those laid down during the juvenile years.

Regarding fibre characteristics, ONILUDE (1982) found a slight trend of increasing fibre lumen area fraction and decreasing fibre wall area fraction and number of fibers per unit area with age. BENDTSEN and SENFT (1986) reported for eastern cottonwood that microfibril angle decreased rapidly from pith to bark until the 15th to 20th annual ring, and then remained relatively constant.

Cell length in poplars was observed as increasing rapidly in the first 10 to 20 years followed by a leveling off (SCARAMUZZI, 1955; BOYCE and KAISER, 1961). Increase of fibre length from pith to bark was reported by several other investigators (INOKUMA et al., 1956; MARTON et al., 1968; HOLT and MURPHEY, 1978; MURPHEY et al., 1979; CHENG and BENSEND, 1979; YANCHUK et al., 1984).

1.2. *Specific gravity, strength properties*

There are different radial patterns of specific gravity observed in hardwoods. It seems that medium to high density diffuse-porous hardwoods generally display an increase in specific gravity from pith to bark. In low density diffuse-porous hardwoods, such as *Populus spp.*, however, density is slightly higher near the pith, i. e. at early age, then decreases substantially a short distance from the pith, to increase again in the mature wood zone after about 15th ring (EINSPAHR et al., 1972; YANCHUK et al., 1983, 1984). Some clones may show no change in wood density along the radius.

By comparison, WHEELER (1987) reported that ring-porous hardwoods tended to have a high density near the pith, which decreased and then increased to some extent outward, caused by changes in fibre wall thickness.

For *Populus*, CURRO (1960), GOHRE (1960), and VALENTINE (1962) found that the major portion of radial variation in specific gravity was related to distance from the pith. Wood close to the cambium was more dense than near the pith but the correlation between juvenile and mature wood was weak, making early prediction of specific gravity unreliable (FARMER and WILCOX, 1966). BLANKENHORN et al. (1988) reported that specific gravity decreased by age.

In a study of 4-year old hybrid poplars, MURPHEY et al. (1979) reported no significant differences in specific gravity among years. Low level of association between specific gravity of juvenile and mature wood was found by ONILUDE (1982) investigating plantation grown cottonwood. Similarly, BENDTSEN and SENFT (1986) observed that the change in specific gravity with age was not very pronounced, accounting for only about a 10% increase from early juvenile to late mature wood in cottonwood. Investigating the relationship between specific gravity and age in quaking aspen, ROSS et al. (1990) reported that specific gravity exhibited only a 15% difference between juvenile and mature wood.

Specific gravity is not an independent property of wood because it is influenced both by anatomical structure and chemical composition. However, it is convenient to treat it as a single property. A relationship between specific gravity and strength properties has been observed to various degrees by many researchers. Specific gravity can be useful in predicting strength properties even though it is not always directly related to the variation of strength within and among trees (KELLOGG and IFJU, 1962; IFJU et al., 1965; BENDTSEN, 1966; KENNEDY, 1968). However, other studies have revealed different results (WILSON and IFJU, 1965; BENDTSEN, 1978; ONILUDE, 1982; BENDTSEN and SENF, 1986; ROSS et al., 1990).

A number of studies have dealt with inter- and intraclonal variation of wood density in poplar species and their hybrids (EINSPAHR et al., 1963; FARMER and WILCOX, 1968; MARTON et al., 1968; FARMER, 1970; PHELPS et al., 1982, 1987; YANCHUK et al., 1983; NEPVEAU et al., 1986; BEAUDOIN et al., 1992). However, little information is available on the variation of strength properties in *Populus* clones.

The objective of this study was to characterize the within-tree variation of selected wood properties in radial direction as a result of age effect in 3 poplar clones grown on 2 different sites. As literature information is sometimes inconclusive or contradicting, the intention of the authors was to clarify the age effects on wood characteristics in order to support selection decisions at an early age.

2. Material and Methods

Fast-growing, genetically improved and vegetatively propagated clones of poplars (*Populus* spp.) and their hybrids have been planted extensively in the north temperate zone. In Hungary, forest tree improvement is focusing on these fast-growing broadleaved species. At present, poplars represent 9 % of the forest area and more than 20% of the annual cut (MOLNÁR et al., 1990).

From among the clones involved in this investigation, 'I-214' represents more than 30% of the poplar plantations in the country. It requires intensive silvicultural treatment, and the wood is considered to be of rather low density compared to other clones. The 'Kopecky' clone can be planted on a variety of sites and does well under both extensive and intensive management regimes. The 'Koltay' clone is considered to be one of the best quality poplar clone with the highest wood density (MÁTYÁS, 1983, 1986).

Three Euramerican hybrid poplar (*Populus* x *euramericana* (DODE) GUINIER) clones were collected from 2 different sites in Hungary. Fifteen year old trees of 3 clones, the Italian 'I-214' and the Hungarian 'Kopecky' and 'Koltay', were investigated in Daka (Site 1). 'Kopecky' and 'I-214' were sampled in Zalavár (Site 2) where the plantation was 10 years old. Site 2 is considered more favorable for poplars because of the soil conditions, more evenly distributed rainfall and reduced temperature extremes.

Six trees were randomly selected for this study from each clone on each site. From each tree, disks about 100 mm thick were cut at breast height. In order to avoid the effect of the prevailing wind, which may cause tension wood, transverse sections with a width of approximately 40 mm were taken in the east-west direction. Sample trees from Site 1 were harvested in the middle of the growing season; therefore, the properties of the 15th growth ring were not analyzed.

For *anatomical* measurements, transverse microtome sections (20 µm) were sliced from each growth ring. After staining with safranine and fast green to distinguish the normal fibers from the gelatinous fibers (SASS, 1958), anatomical characteristics were measured on the mounted slides using an image analyzer. Vessel lumen diameter, vessel lumen area fraction, fibre lumen diameter, fibre lumen area and fibre wall area fractions, ray cell area, and total cell wall area fraction were determined at 100x magnification. An average of 5 measurements on each growth ring were used for further analyses.

Macerated samples were prepared to determine fibre length of the clones. Hydrogen peroxide (30% concentration) and glacial acetic acid mixture with ratio of 1:1 were used to macerate thin, match-stick size wood chips from each growth ring (FRANKLIN, 1945). After washing and staining the fibers, temporary slides were prepared for analysis with the image analysis system. Thirty-five unbroken fibers were measured at 25x magnification from each growth ring, and their mean was used for further analysis.

Specific gravity specimens were obtained from the same segments from which the microtome sections and the macerated material were cut. Radial sample trips of about 5 mm x 5 mm cross section were cut and then divided into specimens by growth rings using a razor blade. The maximum moisture content method (SMITH, 1954) was used to determine

Table 1. – Mean wood properties and coefficients of variations for the three clones on two sites.

			Clone					
		Growth ring	KOPECKY		I-214		KOLTAY	
Property	**Site**	**n**	**mean**	**cv%**	**mean**	**cv%**	**mean**	**cv%**
Growth ring width [mm]	Site 1	14	7.1 AB	56.0	6.7 B	51.7	8.1 A	53.3
		10	8.7 ABa	40.4	8.0 B b	41.4	9.8 A	41.0
	Site 2	10	7.9 B a	49.1	10.0 A a	41.7	-	-
Vessel lumen diameter [µm]	Site 1	14	86.2 A	12.6	81.2 B	15.6	85.8 A	16.6
		10	84.8 A a	14.4	77.7 B a	16.8	82.2 AB	17.9
	Site 2	10	75.5 A b	13.3	77.3 A a	16.4	-	-
Vessel lumen area [%]	Site 1	14	34.3 A	10.3	32.8 B	13.8	34.7 A	14.2
		10	33.7 A a	11.2	31.6 B a	14.0	32.9 AB	13.5
	Site 2	10	28.7 A b	15.2	28.0 A b	17.8	-	-
Fiber lumen diameter [µm]	Site 1	14	16.2 B	11.8	16.4 B	8.9	17.0 A	9.0
		10	15.9 B a	12.9	16.0 B a	9.3	16.6 A	9.3
	Site 2	10	15.2 B a	12.3	15.9 A a	9.8	-	-
Fiber lumen area [%]	Site 1	14	51.2 C	7.2	54.1 B	6.3	56.1 A	5.0
		10	51.2 C b	7.0	53.7 B b	6.1	56.2 A	4.9
	Site 2	10	56.2 A a	10.4	57.0 A a	9.4	-	-
Fiber length [mm]	Site 1	14	1.10 B	16.2	1.12 AB	13.6	1.17 A	15.6
		10	1.03 B a	15.9	1.07 ABa	14.2	1.11 A	16.4
	Site 2	10	1.04 A a	16.6	1.06 A a	15.2	-	-
Cell wall area [%]	Site 1	14	28.4 A	10.5	27.0 B	9.1	25.2 C	9.3
		10	28.6 A a	10.9	27.4 B b	9.0	25.8 C	8.9
	Site 2	10	27.4 A a	13.4	27.4 A a	14.7	-	-
Ray area [%]	Site 1	14	7.4 B	18.4	8.3 A	22.5	7.8 B	15.6
		10	7.8 B b	17.1	9.0 A a	17.8	8.2 B	14.0
	Site 2	10	8.7 A a	23.8	8.3 A b	19.2	-	-
Specific gravity	Site 1	14	0.343 B	7.2	0.304 C	7.2	0.353 A	6.8
		10	0.338 B a	7.3	0.305 C a	7.7	0.356 A	7.3
	Site 2	10	0.348 A b	9.6	0.307 B a	11.2	-	-

Differences between clones within sites for each property are denoted by upper case letters. Differences between sites within clones for each property are denoted by lower case letter. Means with common letters are not significantly different at the 0.05 level as determined by DUNCAN's mean separation procedure.

Table 2. – Mean mechanical properties and specific gravities with the coefficients of variations for the three poplar clones.

	Clone					
	KOPECKY		I-214		KOLTAY	
Property	mean	cv%	mean	cv%	mean	cv%
Specific gravity (bending, compression)	0.3358 B	16.0	0.3042 C	5.2	0.3517 A	5.5
Modulus of rupture [kPa]	30,383 A	14.0	26,062 B	10.1	29,597 AB	10.3
Crushing strength [kPa]	11,709 A	14.7	11,903 A	13.6	12,337 A	11.1
Modulus of elasticity (compression) [MPa]	1,537 A	21.4	1,208 B	16.0	1,488 A	23.7
Specific gravity (tension)	0.3404 A	5.0	0.2932 B	8.1	0.3464 A	6.0
Maximum tensile strength [kPa]	33,170 A	40.8	27,148 A	23.9	30,102 A	42.9
Modulus of elasticity (tension) [MPa]	1,774 A	20.5	1,527 A	18.0	1,746 A	23.9

Differences among clones for each property are denoted by upper case letters. Means with common letters are not significantly different at the 0.05 level as determined by DUNCAN's mean separation procedure.

Table 3. – Analysis of variance for growth ring width, specific gravity, and anatomical properties of clones on each of the two sites.

Source of variations	Df	Property								
		Growth ring width	Specific gravity	Vessel lumen diameter	Vessel lumen area	Fiber lumen diameter	Fiber lumen area	Fiber length	Ray area	Cell wall area
					Site 1 (N=252)					
Clone	2	NS	**	NS	NS	NS	**	NS	*	**
Tree(Clone) (Error I.)	15	**	**	**	**	**	**	**	**	**
Age	13	** (79%)	** (18%)	** (79%)	** (59%)	** (61%)	** (10%)	** (76%)	** (52%)	** (27%)
Clone x Age	26	**	**	**	**	*	NS	NS	*	**
R^2 [%]	-	91.3	79.5	93.3	79.7	84.6	64.8	92.4	72.4	66.2
					Site 2 (N=120)					
Clone	1	*	**	NS	NS	NS	NS	NS	*	NS
Tree(Clone) (Error I.)	10	**	**	NS	**	**	**	**	NS	**
Age	9	** (72%)	** (27%)	** (64%)	** (67%)	** (68%)	** (30%)	** (91%)	** (74%)	** (45%)
Clone x Age	9	**	NS	NS	NS	NS	NS	NS	**	NS
R^2 [%]	-	90.2	80.2	70.1	82.2	84.9	79.8	94.5	82.3	80.9

** – Statistically significant at the 1% level.
* – Statistically significant at the 5% level.
NS – Not significant at the 5% level.
() – Percent of variation explained by the effect of age.

specific gravity of the specimens. Five samples were measured from each growth ring and their averages were used for further analysis.

For *strength* test specimens, a 500 mm long short stem section was also taken from each tree immediately above the breast height disk. Tests were conducted in water-saturated (green) condition on standard (compression, bending) and micro (tension) specimens in 3 age groups along the radius on Site 1 only. Specific gravity of these specimens was also calculated by averaging the specific gravity values of those individual growth rings which were completely or partly included in the samples. A more detailed description of methods is available from the authors.

3. Statistical Analysis

3.1. Clonal and age effects

For wood properties, standard analysis of variance procedures were applied (SAS Institute Inc., 1985) to evaluate clone and age effects separated by sites.

3.2. Model for maturation

Each variable was plotted against age expressed as the growth ring number from pith to bark. Segmented regression analyses were used to describe the relation between the measured properties as dependent variables and age as independent variable. A quadratic model with plateau was fitted to the data for each variable to estimate the perceptible

Table 4. – Analysis of variance for mechanical properties and their specific gravities of three poplar clones on Site 1.

Source of variation	Df N=54	Wood property Specific gravity (bending, compression)	Modulus of rupture	Crushing strength	Modulus of elasticity (compression)	Df N=36	Specific gravity (tension)	Maximum tensile strength	Modulus of elasticity (tension)
Clone	2	**	NS	NS	*	2	**	NS	NS
Tree(Clone) (Error I.)	15	NS	**	*	*	9	NS	NS	NS
Age	2	NS	**	**	**	2	NS	NS	**
Clone x Age	4	**	*	**	*	4	**	NS	NS
R^2 [%]	-	85.6	92.4	78.8	74.4	-	87.0	46.4	84.1

** – Statistically significant at the 1% level.
* – Statistically significant at the 5% level.
NS – Not significant at the 5% level.

point where the association between the 2 variables changed; in other words, to find the approximate point of demarcation between juvenile and mature zones. The segmented regressions were carried out by nonlinear regression techniques using the following theoretical approach:

$$Y = a + bx + cx^2 \qquad \text{if } x < x_0$$
$$Y = p \qquad \text{if } x > x_0$$

Where Y = analyzed property,
x = age (number of growth rings from pith to the bark),
x_0 = age of demarcation,
a, b, c = parameters,
p = plateau.

Procedure of SAS NLIN (SAS Institute Inc., 1985) can fit a segmented model even when the joint point (x_0) is unknown. An example of fitting the model to anatomical data is presented in PESZLEN (1994a).

Each analysis was applied on data sets of the 2 sites separately. Assumptions based on the results of the analyses for one site were validated by results obtained from the other site.

4. Results

Average values of the growth ring width, anatomical parameters, specific gravity, and strength properties together with their coefficients of variation are presented in *table 1* and in *table 2* for the 3 clones by sites.

4.1. Influence of clone and age on anatomical properties

Results of the analysis of variance are compiled in *table 3* and in *table 4*. Regarding trees from Site 1, statistically significant clonal effects were observed on fibre lumen area, ray area, cell wall area, specific gravity, and modulus of elasticity in compression.

Statistically significant tree-to-tree variation was detected for all properties except for vessel lumen diameter and ray area fraction on Site 2 and for tensile strength properties on Site 1. Approximately 10% to 15% of the total variation occurred between trees within clones. This variation is attributed to environmental effects. Age, referred to as ring number or age groups from pith to bark, affected each variable significantly except specific gravity of the strength specimens and maximum tensile strength. It has to be pointed out that for this analysis, samples only of 3 age categories could be analyzed, including more than one growth ring per sample. There were significant clone x age interaction effects on wood properties in many cases.

4.2. Radial trends of property changes

Radial changes of *growth ring widths* are presented in *figure 1*. After the first few years, the clones responded similarly to annual weather fluctuation on Site 1. The width of growth rings increased in the first 3 to 5 years then decreased with age. Differences were significant in the first few years before canopy closure, and in the "favorable" years only. The clonal ranking became stable after the juvenile years (about 10 years). Similar trends were found on Site 2 as well.

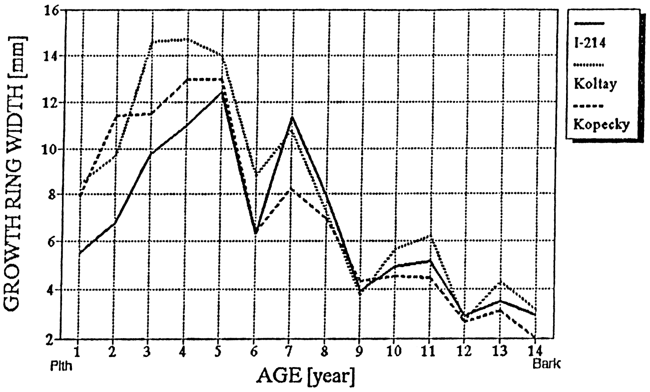


Figure 1. – Radial changes of growth ring widths of six sample trees for each of three clones on Site 1 (15-year old).

The selected *anatomical properties* of the clones showed the following radial trends on both sites. First a rapid increase or decrease that is typical for juvenile wood, followed by a transition zone with decreasing rate of change, and then a relatively constant value for matured wood. In general, the diameter of the cells became larger and the cell wall area decreased with age along the radius.

Results of the segmented regression analysis are presented in *table 5* for Site 1 and Site 2, respectively. The estimated demarcation ages (x_0) between juvenile and mature zones were not identical for each anatomical property, but the sequence of maturation of the characteristics were the same for both sites. This indicates that the maturation order of the different anatomical properties is presumably genetically determined

Table 5. – Results of the non-linear segmented anasis of a quadratic model ($Y = a + bx + cx^2$) with plateau ($Y = p$) for an estimate of the maturation age (x_0) for anatomical properties of clones on each of the two sites.

	Property						
Estimated parameter	**Vessel lumen diameter** [µm]	**Vessel lumen area** [%]	**Fiber lumen diameter** [µm]	**Fiber lumen area** [%]	**Fiber length** [mm]	**Ray area** [%]	**Cell wall area** [%]
				Site 1 (N=252)			
a	49.5299	25.1869	12.4881	48.8808	0.7167	The model was not applicable.*	37.0945
b	9.0010	1.8965	1.0496	2.4324	0.0920		- 1.8236
c	- 0.4689	- 0.0758	- 0.0552	- 0.2801	- 0.0038		0.1050
x_0	9.60	12.51	9.50	4.34	12.01		8.68
p	92.73	37.05	17.47	54.16	1.27		29.17
				Site 2 (N=120)			
a	43.8972	18.3348	9.7310	40.8797	0.6212	12.6923	45.87
b	12.4093	2.7997	2.6430	10.2031	0.1245	- 1.1634	- 7.0911
c	- 0.9938	- 0.1407	- 0.2636	- 1.5436	- 0.0065	0.0578	0.7581
x_0	6.24	9.95	5.01	3.30	9.52	10.07	4.68
p	82.62	32.26	16.36	57.74	1.21	6.84	29.29

* – Not a quadratic model with plateau but a single, slightly decreasing straight line gave better fit to the data points.

and not site-dependent. First the fibre lumen area percent became constant at ages of approximately 4 to 5 years on Site 1 and 3 to 4 years on Site 2; then cell wall area percent, fibre lumen diameter, and vessel lumen diameter became stable around the ages of 8 to 10 years on Site 1 and 4 to 6 years on Site 2. The fibre length and vessel lumen area were the last to reach maturation at the estimated ages of 12 to 13 years and 9 to 10 years for Site 1 and Site 2, respectively.

Not only were the values of the matured anatomical parameters (*p*) lower but also the maturation period of the sample trees started earlier on Site 2 as compared to those on Site 1. The results indicate that site influenced the maturation of these properties. On the better site (Site 2) maturation was accelerated, and the matured values for anatomical properties were lower. The size of a cell produced by division of the cambial initial depends mainly on the size of that cambial initial. If the growth rate is fast, it is possible that the mother cell (produced from the cambial initial) may receive a stimulus for further division before it could grow larger.

Fractional area percentages of cell wall, vessel lumen, fibre lumen, and ray area along the radius from pith outward are illustrated in *figure 2*. As the trees matured, the size of the anatomical elements varied significantly; nevertheless, the cross-sectional distribution of anatomical elements did not change much, it remained relatively constant. Only a slight (8%) decrease in cell wall area percent was detected from pith to bark on both sites. The investigated poplar clones had relatively large pores with thin cell walls. Less than 30% of the total cross sectional area was occupied by cell wall.

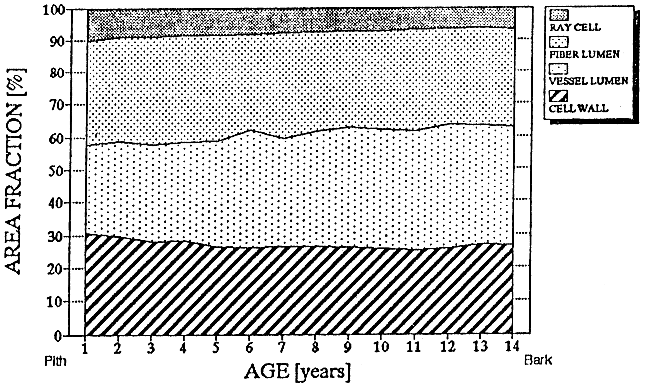


Figure 2. – Radial changes of distribution of anatomical elements based on six sample trees for each of three clones on Site 1 (15-year old).

Analyzing the radial variation in *specific gravity* (*Figure 3*) of trees from Site 1, it is interesting to observe that age-related change for the 3 clones is not identical, the 'Kopecky' clone is not displaying a stabilized value even after 14 growing seasons. Basically, similar trends were detected on Site 2.

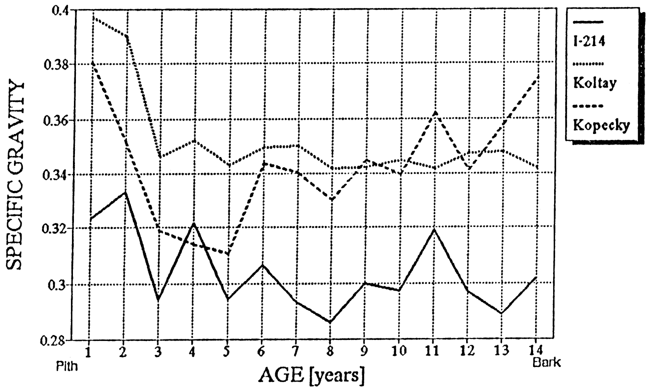


Figure 3. – Radial changes of specific gravities of six sample trees for each of three clones on Site 1 (15-year old).

Average values of *mechanical properties* for 3 different radial positions, by age groups, are presented in *table 6*. Each strength property reached its highest value at age group 1 (closest to the bark) and the lowest at age group 3 (nearest the pith) except maximum tensile strength, which seemed to be independent of sampling position. Comparing the differences of means between age groups, maximum bending strength increased from the pith through the middle position by 15% and from the middle position to the bark by 15%. Compression strength was not significantly different between positions near the pith and middle part, but then increased significantly from the middle position to the bark by 20%. In spite of the similar maximum tensile strengths observed radially, stiffness obtained in tensile test was increasing from pith to middle position, and from middle position to the bark, by 25% and 27%, respectively.

Averages of the mechanical properties of individual clones by age groups are presented in *table 6*. The trend was the same as that for the overall averages described above. In particular, the strength of each clone was higher near the bark than in the middle or close to the pith, except for ultimate tensile strength of each clone, and for crushing strength of 'Koltay'. No significant differences were found between clones for any of the mechanical properties measured in the middle section. However, slight but significant differences occurred between clones close to the bark for bending strength, compression strength, and for stiffness in compression. These results suggest that clonal selections for strength properties may be more efficient beyond the age of about 10 years.

Unlike bending, compression and tensile strength values, specific gravity exhibited significant clonal effect together with non-significant age effect suggesting that differences in specific gravity of clones did not result in differences in mechanical properties. Furthermore, specific gravity did not increase in radial direction with increasing years but strength values increased significantly from pith to bark, as described before *(Table 6)*. Comparing the outcome of the nested models, specific gravity was found to be under strong genetic control as the effect of clones accounted for more than 50% of the total variation. Most of the variation of strength properties occurred within individual trees; in particular, within-tree variation accounted for approximately 80% to 100% of the total (phenotypic) variation.

The generally significant property differences with increasing age, especially between age group 2 and 3 – before and after maturation – indicate that mechanical properties of wood demonstrate the reaching of maturity clearer than specific gravity, which seems to be an improper indicator of mature wood.

5. Discussion

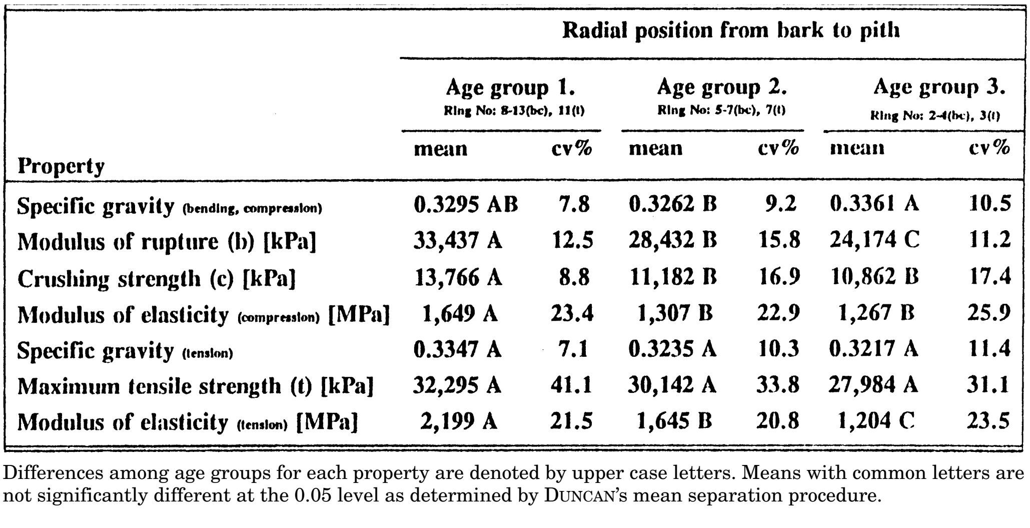
Due to the limitations of the study, only 3 clones could be compared to estimate genetic variation of wood properties. Therefore, results regarding between-clone differences should be interpreted with caution. Genetic differences between clones proved significant for one or few of the anatomical parameters but not for fibre length. Clonal differences in anatomy were small and may be negligible from practical standpoint. Most of the variation occurred within tree. This is probably due to the increase in size of the cambial initials with age that is closely related to the development of the stem and the crown of a tree. The aging process caused larger variation in anatomical properties than the site and the genetical differences. This is especially true for fibre length and has to be considered if selecting for pulp and paper production.

With age, anatomical properties for all the 3 clones on both sites showed first a rapid change, followed by a decreasing rate of change, and finally a stable value. The diameters of the cells became larger and the cell wall area decreased with age. Segmented regression analyses of a quadratic model with plateau were used to estimate the demarcation between juvenile and mature zones. The better site accelerated the maturation but with lower values. A possible explanation is that the size of a cell produced by division of the cambial initial depends mainly on the size of that cambial initial. If the growth rate is fast, it is possible that the mother cell (produced from the cambial initial) may receive a stimulus for further division before it could grow larger.

The demarcation age between juvenile and mature zones were not the same for each anatomical property, but the order of the maturation of the characteristics were the same for both sites. This indicates the physiological control on the maturation process of the anatomical properties which is determined by the development of the stem and the crown during the growth of a tree. Fibre length and vessel lumen area were the last to become constant, and this information could be important to set the rotation of a plantation for specific utilization.

Differences in growth ring widths among the clones were significant in the "good" years only, and the ranking of the clones became stable after about 10 years. Specific gravity values were high in the first 3 growth rings for each clone, then the clones exhibited different trends. In the first few years, the high specific gravity is possibly due to the planting shock and the needs of a thin stem with few leaves, and the high content of gelatinous fibers. However, approximately after the canopy closure, specific gravity exhibited the trend characteristic for the individual clone. 'Koltay' and 'I-214' clones had more or less

Table 6. – Mean mechanical properites and specific gravities with the coefficients of variations for radial positions of the clones.



Property	Radial position from bark to pith					
	Age group 1. Ring No: 8-13(bc), 11(t)		Age group 2. Ring No: 5-7(bc), 7(t)		Age group 3. Ring No: 2-4(bc), 3(t)	
	mean	cv%	mean	cv%	mean	cv%
Specific gravity (bending, compression)	0.3295 AB	7.8	0.3262 B	9.2	0.3361 A	10.5
Modulus of rupture (b) [kPa]	33,437 A	12.5	28,432 B	15.8	24,174 C	11.2
Crushing strength (c) [kPa]	13,766 A	8.8	11,182 B	16.9	10,862 B	17.4
Modulus of elasticity (compression) **[MPa]**	1,649 A	23.4	1,307 B	22.9	1,267 B	25.9
Specific gravity (tension)	0.3347 A	7.1	0.3235 A	10.3	0.3217 A	11.4
Maximum tensile strength (t) [kPa]	32,295 A	41.1	30,142 A	33.8	27,984 A	31.1
Modulus of elasticity (tension) **[MPa]**	2,199 A	21.5	1,645 B	20.8	1,204 C	23.5

Differences among age groups for each property are denoted by upper case letters. Means with common letters are not significantly different at the 0.05 level as determined by DUNCAN's mean separation procedure.

constant values, while specific gravity of the ‘Kopecky’ clone increased with age.

The significant clonal differences for specific gravity are not surprising because among wood properties, specific gravity is considered to be under genetic control. Despite the fact that specific gravity values of the clones were different, mechanical properties were not significantly different, and no significant correlation was found between specific gravity and mechanical properties. This is probably due in part to the narrow range of specific gravity values.

Specific gravity did not prove to be the most important single factor influencing strength properties of Populus clones. It can not be used to reliably predict mechanical behaviour of these hybrids due to the absence of significant relationships and also because the clones in some cases showed different trends. Even though the range of specific gravity for the 3 clones was very narrow (0.275 to 0.350), clonal means were significantly different. No significant clonal effect was detected for strength properties although the ‘I-214’ clone had lower mechanical property. However, the alleged superiority of the ‘Koltay’ clone (Mátyás, 1986) was not seen. This may be due in part to the small sample size although the variances for mechanical properties were similar to those reported elsewhere (Wood Handbook, 1989).

The absence of a consistent relationship between specific gravity and mechanical properties indicated the effect of quality factors rather than that of quantity characteristics of cell wall on the mechanical performance of poplar clones. For example, gelatinous fibers without pattern were found in each sample (Peszlen, 1994b) and may have affected strength properties. Slides made from the specimens were investigated under the microscope and based on visual estimates, gelatinous fibre content did not vary between clones but did vary within tree. It was higher near the pith than near the bark similar to the mechanical properties.

It can be concluded that in case of low specific gravity, the influence of specific gravity on strength properties seems to be less important than that from other factors. At high specific gravity, the differences in the amount of wood substance present and not the differences in its composition affect strength properties. However, at low specific gravity, strength is not determined by the amount of cell wall material, but rather by factors reflecting the quality of cell wall, such as the presence of gelatinous fibers and the microfibril angle.

In summary, results of this study indicated the importance of the age effect on wood quality traits because most of the variation occurred within trees from pith to bark. This has to be considered in decisions on rotation age and on clonal selection. The increase in size of the cambial initials with age that is closely related to the development of the stem and the crown, the formation of heartwood, and the changes of the growing conditions can be the most important influencing parameters. There were significant clone x age interaction effects on wood properties in many cases suggesting that selection of clones based on early testing of wood parameters may not be reliable.

No consistent and significant relationships between growth rate, as defined by either tree size or growth ring width, and wood characteristics were found for the 3 poplar clones on 2 sites. This result suggested that growth rate may be increased without affecting specific gravity and the anatomical properties of poplar clones. It is important to emphasize that there were no consistent relationship between growth rate and wood properties when growth rings of the same age were compared.

6. Conclusions

The following conclusions were reached on the basis of results obtained through the analysis on influence of age and growth rate on selected wood properties of 3 poplar clones from 2 sites in Hungary:

– Age had a significant effect on the development of wood properties. Differences between clones for growth ring width were discernible in the favorable years only. Growth rate and wood properties showed no direct relationship.

– Along the radius, anatomical properties at first showed a rapid change, followed by a decreasing rate of change, finally a stable value. Segmented regression analysis fitting a quadratic model with plateau proved useful to estimate the demarcation between juvenile and mature zones of anatomical characters.

– Maturation process of anatomical properties were affected by site, the better site accelerated the maturation but with lower matured values. The ages of demarcation were not the same for all characters; however, the order of the maturation were the same on both sites indicating a consistent effect of the aging process. Among the measured anatomical properties, fibre length and vessel lumen area were the last to become constant at the estimated ages of 10 to 13 years on Site 1 and 9 to 10 years on Site 2.

– Distribution of cross-sectional area of cell wall, vessel and fibre lumen, and ray area exhibited only slight changes with age. Vessel and fibre lumen area increased approximately 8% from pith to bark.

– Site did not affect specific gravity of the clones. The effect of clones on specific gravity variation within Site 1 accounted for more than 50% of the phenotypic variation indicating strong genetic control on this property. No significant variation was detected between ramets of the same clone, but the age effect manifesting as within-tree variation was significant.

– Regarding modulus of rupture, crushing strength, maximum tensile strength and modulus of elasticity measured in tension, no significant clonal effect was found for the samples on Site 1. Strength values were low for each clone.

– There were significant differences between age group means. The mechanical properties increased with age consistently, except for ultimate tensile strength. Clonal means of strength properties became increasingly different with age, while there were no significant differences in the first years.

– No significant correlations were found between specific gravity and bending and tensile strengths of clones. However, the relationship was clonal specific in compression. Specific gravity did not prove to be the most important single factor influencing strength properties and can not be used to predict mechanical characteristics of *Populus* clones.

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8. References

Beaudoin, M., Hernandez, R. E., Koubaa, A. and Poliquin, J.: Interclonal, intraclonal and within-tree variation in wood density of poplar hybrid clones. Wood and Fiber Science **24**(2): 147 – 153 (1992).— Bendtsen, B. A.: Strength and related properties of a randomly selected sample of second-growth redwood. FPL.53. Forest Service Research Paper Madison, Wisconsin, 14 pp. (cited by Zobel and van Buijtenen, 1989) (1966). — Bendtsen, B. A.: Properties of wood from improved and intensively managed trees. Forest Products Journal **28**(10): 61 – 72

(1978). — Bendtsen, B. A. and Senft, J.: Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. Wood and Fiber Science **18**(1): 23 – 38 (1986). — Blankenhorn, P. R., Bowersox, T. W., Straus, C. H., Stimely, G. L., Stover, L. R. and DiCola, M. L.: Effects of management strategy and site on selected properties of first rotation *Populus* hybrid NE-388. Wood and Fiber Science **20**(1): 74 – 81 (1988). — Boyce, S. G. and Kaiser, M.: Environmental and genetic variability in the length of fibers of eastern cottonwood. TAPPI **44**: 363 – 366 (1961). — Cheng, W. W. and Bensend, D. W.: Anatomical properties of selected *Populus* clones grown under intensive culture. Wood Science **11**(3): 182 – 187 (1979). — Curro, P.: Technological investigation on the wood of some euro-american poplar hybrids – physical and mechanical properties. Agr. For. Expt. Center 3, Italy, 28. (cited by Zobel and van Buijtenen, 1989) (1960). — Einspahr, D.W., Benson, M. K. and Harder, M. L.: Within-tree variation in specific gravity of young quaking aspen. Rept. Inst. Paper Chem. **15**: 8 pp. (cited by Zobel and van Buijtenen, 1989) (1972). — Einspahr, D. W., van Buijtenen, J. P. and Peckham, J. R.: Natural variation and heritability in triploid aspen. Silvae Genetica **12**: 51 – 58 (1963). — Farmer, R. E.: Variation and inheritance of eastern cottonwood growth and wood properties under two moisture regimes. Silvae Genetica **19**(1): 5 – 8 (1970). — Farmer, R. E. and Wilcox, J. R.: Specific gravity in a lower Mississippi Valley cottonwood population. TAPPI **49**: 210 – 211 (1966). — Farmer, R E. and Wilcox, J. R.: Preliminary testing of eastern cottonwood clones. Theoret. and Appl. Genetics **38**: 197 – 201. (cited by Murphey et al., 1979) (1968). — Franklin, G. L.: Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. Nature **155**, 51 (1945). — Gohre, K.: Die Verteilung von Rohwichte im Pappelstamm. Wiss. Abh. Deutsch Akad. Landwiss. Berlin **44**: 51 – 79. (cited by Zobel and van Buijtenen, 1989) (1960). — Holt, D. H. and Murphey, W. K.: Properties of hybrid poplar juvenile wood affected by silvicultural treatments. Wood Science **10**(4): 198 – 203 (1978). — Ifju, G., Wellwood, R. W. and Wilson, J. W.: Improved microtechnique for wood tensile strength and related properties. Forest Products Journal **1**: 13 – 14 (1965). — Inokuma, T., Shimaji, K. and Hamaya, T.: Studies on poplars. (I). Measurement of fiber length and specific gravity of Japanese giant poplar (Populus japano-gigas). Misc. Inf. Tokyo Univ. For. **11**: 77 – 86. (cited by Zobel and van Buijtenen, 1989) (1956). — Isebrands, J. G.: Proportion of wood elements within eastern cottonwood. Wood Science **5**(2): 139 – 146 (1972). — Kellogg, R. M. and Ifju, G.: Influence of specific gravity and certain other factors on the tensile property of wood. Forest Products Journal **12**: 463 – 470 (1962). — Kennedy, R. W.: Wood in transverse compression: Influence of some anatomical variables and density on behavior. Forest Products Journal **18**: 36 – 40 (1968). — Kroll, R. E., Ritter, D. C., Gertjejansen, R. O. and Au, K. C.: Anatomical and physical properties of balsam poplar (*Populus balsamifera* L.) in Minnesota. Wood and Fiber Science **24**(1): 13 – 24 (1992). — Marton, R., Stairs, G. R. and Schreiner, E. J.: Influence of growth rate and clonal effects on wood anatomy and pulping properties of hybrid poplars. TAPPI **51**(5): 230 – 235 (1968). — Matyas, Cs.: An Introduction to Forest Tree Improvement. University of Forestry and Timber Industry, University Multipliers, Sopron, Hungary. 175 pp. (1983). — Matyas, Cs.: Nemesitett Erdeszeti Szaporitoanyag-ellatas. Akademiai Kiado, Budapest, Hungary. 136 pp. (1986). — Molnar, S., Feher, S. and Papai, K.: Latest figures for the variability of wood density of poplar plantations. Faipar XL(7): 208 – 211 (1990). — Murphey, W. K., Bowersox, T. W. and Blankenhorn, P. R. : Selected wood properties of young *Populus* hybrids. Wood Science **11**(4): 182 – 187 (1979). — Nepveu, G., Barneond, C., Polge, H. and Aubert, M.: Clonal variation in growth stresses and some other wood properties in the genus *Populus*. Reliability of the assessment of wood quality using increment cores. Annales de Recherches Sylvicoles, AFOCEL, France, 1985. Paris, France, Association Forêt-Cellulose, p. 337 – 357. (In: Forest Products Abstracts, 1987, **10**(9):255). (1986). — Onilude, M. A.: Quantitative anatomical characteristics of plantation grown loblolly pine (*Pinus taeda* L.) and cottonwood (*Populus deltoides* Bart. ex Marsch.) and their relationship to mechanical properties. Ph. D. Dissertation in Forestry and Forest Products. VPI & SU Blacksburg, Virginia. 175 pp. (1982).— Peszlen, I.: Anatomical properties of poplar clones. IAWA Journal **15**(3): 311 – 321 (1994a). — Peszlen, I.: Gelatinous fibers in *Populus* x *euramericana* clones. Third Pacific Regional Wood Anatomy Conference. November 20 to 24, 1994, Rotorua, New Zealand (1994b). — Phelps, J. E., Isebrands, J. G. and Jowett, D.: Raw material quality of short-rotation, intensively cultured *Populus* clones. I. A comparison of stem and branch properties at three spacings. IAWA Bulletin **3**(3 – 4): 193 – 200 (1982). — Phelps, J. E., Isebrands, J. G. and Teclaw, R. M.: Raw material quality of short-rotation, intensively cultured *Populus* clones. II. Wood and bark from first-rotation stems and stems grown from coppice. IAWA Bulletin **8**(2): 182 – 187 (1987). — Ross, K. D., Shottafer, J. E. and Shepard, R. K. : The relationship between selected mechanical properties and age in quaking aspen. Forest Products Journal **40**(7/8): 54 – 56 (1990). — SAS Institute Inc.: SAS User's Guide: Statistics, Version 5. Edition, SAS Institute Inc., Cary, NC. 923 pp. (1985). — Scaramuzzi, G.: Dimensional data about fibers in *Populus* x *euramericana* (Dode) Guinier cv I-214. Sess. Int. Poplar Comm., Madrid, FAO/CIP/79-C. 20 pp. (cited by Zobel and van Buijtenen, 1989) (1955). — Scaramuzzi, G.: Variation of the volume portions of wood elements within the stem in *Populus* x *euramericana*. Guinier Pap. **4**: 242 – 251. (cited by Zobel and van Buijtenen, 1989) (1958). — Smith, D. M.: Maximum moisture content method for determining specific gravity of small wood samples. USDA For. Serv. For. Prod. Lab., Madison, Wisconsin, No. 2014 (1954). — Valentine, F. A.: Natural variation in specific gravity in *Populus tremuloides* in northern New York. 9. Northeastern For. Tree Impr. Conf., Syracuse, New York. p. 17 – 24. (cited by Zobel and van Buijtenen, 1989) (1962). — Wheeler, E. A.: Anatomical and biological properties of juvenile wood in conifers and hardwoods. 41. Ann. Meet. FPRS Louisville, Kentucky. 2 pp. (cited by Zobel and van Buijtenen, 1989) (1987). — Wilson, J. W. and Ifju, G.: Wood characteristics. VI: Measuring density and strength properties of minute wood specimens. Pulp and Paper Research Institute of Canada, Montreal, Canada. Technical Report, No. 423. (Woodlands Research Index No. 169) (1965). — Wood Handbook: Wood as an engineering material. Agric. Handb. 72. Washington, DC., US Department of Agriculture. Rev. 1987. 466 p. (1987). — Yanchuk, A. D., Dancik, B. P. and Micko, M. M.: Intraclonal variation in wood density of trembling aspen in Alberta. Wood and Fiber Science **15**(4): 387 – 394 (1983). — Yanchuk, A. D., Dancik, B. P. and Micko, M. M.: Variation and heritability of wood density and fibre length of trembling aspen in Alberta, Canada. Silvae Genetica **33**(1): 11 – 16 (1984). — Zobel, B. J. and Talbert, J.: Applied Forest Tree Improvement. John Wiley and Sons, New York, 511 pp. (1984). — Zobel, B. J. and van Buijtenen, J. P.: Wood Variation. Its Causes and Control. Springer-Verlag, Berlin, Heidelberg. 363 pp. (1989).