DIFFERENCES IN CELL-WALL CHEMICAL COMPOSITION AMONG EIGHTEEN THREE-YEAR-OLD *POPULUS* HYBRID CLONES

by

Richard E. Dickson, P. R. Larson, and J. G. Isebrands [1/]

Abstract.--Wood from the third annual ring of 18, nursery-grown, *Populus* clones was analyzed for lignin and wood sugars following extraction. The percentage of chemical constituents ranged widely among the clones; lignin from 18.1 to 25.0 of the weight of ovendry wood; glucose 42.3 to 51.6%; and xylose 16.7 to 21.5%. Analysis of variance indicated significant clonal differences in percentage of lignin, glucose, mannose, xylose, and arabinose, but not in galactose. Orthogonal comparisons indicated certain clones were responsible for much of the variation in some comparisons, whereas parental lines, i.e., *P. nigra, P. euramericana* or *P. deltoides* crosses, were responsible in others. Certain hybrids, (5331) a *P. nigra* hybrid, (5339) a *P. grandidentata x P. alba* hybrid, and (5351) a fast growing clone of unknown parentage, combined rapid growth rates with low lignin, low extractives, and high glucose concentrations. Such combinations would be highly desirable in clonal selection. Considering the wide differences found in the various chemical constituents of *Populus* wood, it would seem feasible that clones could be selected at an early age for a particular wood chemical composition in addition to rapid growth rates.

Additional keywords: Lignin, wood extractives, wood sugars, specific gravity.

INTRODUCTION

As the world-wide demand for wood products obtained from the genus *Populus* has accelerated, research concerning its silviculture, breeding, and utilization has also increased (Maini and Cayford, 1968; Muhle Larsen, 1970; Anon., 1972). Part of this research effort has been directed toward increasing the efficiency of *Populus* cultivation with regard to the production of specific fiber and chemical wood products. Consequently, knowledge of physical and chemical properties of *Populus* wood has become very important. Poplars, in general, are diffuse-porous hardwoods with low specific gravity, low lignin, high cellulose content, and fiber characteristics favorable for many uses. Wood characteristics such as fiber length and specific gravity are known to be influenced by species and clonal differences and by site and growth conditions. The considerable literature relating to variability in these physical characteristics and properties has been recently reviewed by Einspahr, Benson, and Peckham (1968) and Kennedy (1968).

1/ R.E. Dickson, Plant Physiologist; P.R. Larson, Chief Plant Physiologist; J. G. Isebrands, Wood Anatomist; North Central Forest Experiment Station, USDA Forest Service, Rhinelander, Wisconsin 54501.

Lignin content is highly variable in poplar wood. When compared to certain other hardwoods and to softwoods, the lignin content of some poplar species is low (Timell, 1957; Browning, 1963). Among species, poplars of the section Leuce have the lowest and those within the section Aegeiros the highest lignin contents. Lengyel and Hajduczky (1964) recently reported that for six *Populus* "species" the lignin content of ovendry wood ranged from 18.4% for *P. tremula* to 23.7% for P. *serotina.* Einspahr et al. (1968) on the other hand, found little variation in a group of P. *tremuloides* clones in which the lignin content ranged from 17.2 to 19.3%. They concluded that little gain could be expected in this property from tree improvement work.

The carbohydrate content or holocellulose fraction of *Populus* wood is high and may range up to 80% on an oven dry basis (Clermont and Schwartz, 1951). Fractionation of the holocellulose yields a variety of components depending on the extraction procedure. For example, treatment with a strong base yields hemicellulose and alpha-cellulose, whereas complete acid hydrolysis yields the individual wood sugars. The principal wood sugars are glucose, galactose, mannose, xylose, and arabinose, Glucose - 45 to 55% of the total carbohydrates - and xylose - 15 to 20% - are present at the highest concentrations in most hardwoods. The relative proportions of these various carbohydrate fractions have been determined for a wide variety of species (Jayme, 1947; Guillemain-Gouvernel, 1952, 1954; Timell, 1957; Clonaru, Constantinesco, and Ocskay, 1958; Browning, 1963), for various positions within a single tree (Basbous, 1950; Ferrari, 1967), and at various stages of cell-wall development for a single species (Sultze, 1957; Thornber and Northcote, 1961 a and b; Kremers, 1964).

Several studies have shown that neither growth rate (von Wettstein, 1946; Cech, Kennedy, and Smith, 1960) nor site (Wilde and Paul, 1959) had any great effect on chemical composition of *Populus* wood. On the other hand, Lengyel and Hajduczky (1964) found that wood of *Populus* clones with the fastest growth rate contained the lowest cellulose and the highest pentose levels. Considering the importance of wood chemical content and present day emphasis on rapid growth rate and clonal selection, relatively few studies have been directly concerned with the influence of growth and clonal parentage on these factors.

In this study we examined the chemical properties of 18 *Populus* hybrid clones that have potential for intensive culture (Table 1). These hybrids differed widely in their parental backgrounds, and they exhibited highly significant differences in their chemical content.

METHODS

Harvesting

A single, straight, vigorous tree was harvested in the winter after the third growing season from each of 18 clones. The trees were randomly selected from the maximum fiber yield clonal stocks at Rhinelander, Wisconsin. 2/ Three, 1.25 cm thick cross-sections were sawn from each stem 45 to 60 cm above ground line, sealed in plastic bags, and frozen until sub-sampled for specific gravity measurements and wood chemistry determinations.

Laboratory procedures

Two sample blocks of the third annual ring were carefully selected for analysis by examination with a low power microscope. The samples were free of tension wood, included both early and latewood, but excluded transition wood from both sides of the annual ring. Specific gravity was determined on one block by the conventional water-displacement, oven-dry-weight method with an analytical balance. The second block was subdivided into matchstick-size slivers, extracted with benzene:alcohol (Moore and Johnson, 1967), oven dried, and ground to pass a 20-mesh screen in a micro-Wiley mill. The wood hydrolysis, neutralization, and separation of Klason lignin followed the procedures of Saeman, Moore, and Millett (1963) scaled down for 30 mg samples (Larson, 1966). The individual sugars were estimated by gas chromatography after conversion to alditol-acetates (Borchardt and Piper, 1970).

Statistical analysis

Three, replicate, 30 mg samples were hydrolyzed with H_2SO_4 to separate lignin and wood sugars. In addition, each sugar fraction was analyzed twice on the gas chromatograph for a total of 6 observations.

Differences between hybrids were determined by analysis of variance (AOV) for each chemical fraction. Those fractions which were not significantly different required no subsequent analysis. On the other hand, a significant F-test for hybrids required further analysis to identify the source of clonal variation. For this purpose a series of planned orthogonal comparisons partitioned the hybrid sums of squares into its independent components. Using the techniques of Snedecor and Cochran (1967) we designed 17 single degree of freedom comparisons to account for total hybrid sums of squares in the fractions. These independent comparisons often allowed us to identify specific hybrids which were responsible for most of the differences found in the AOV.

2/ Dawson, D. H. North Central Forest Experiment Station, Maximum Fiber Yield Project No. NC-1111.

RESULTS AND DISCUSSION

The clones examined in this study (Table 1) were initially selected by a number of different breeders from different parts of the country for fast growth, disease resistance, drought resistance, or some other selection criteria rather than potential for intensive culture (See Dawson, 1974 for the clone origin). They were derived from parents from several taxonomic sections (Aegeiros, Tacamahaca, Leuce) within the genus *Populus* (Bogdanov, 1968; Muhle Larsen, 1970). This wide genetic base should provide considerable variation in both growth and chemical composition of the wood.

Because glucose concentration is closely correlated with cellulose content and xylose concentration with hemicellulose content of the cell wall, these sugars can be used to estimate alpha-cellulose and hemicellulose, respectively. As a basis for comparing these *Populus* hybrids to other hardwoods and to provide some general background information on wood chemical composition, the cell-wall chemical composition of aspen was compared to that of several hardwoods and white pine- (Table 2). Glucose and xylose combined usually make up 60 to 70% of a summative analysis of the cell wall. Note that in hardwoods glucose and xylose are the major wood sugars while lignin and extractive contents are fairly low. On the other hand, in white pine, glucose and mannose are the major wood sugars whereas lignin and extractive contents are high.

Analysis of variance for lignin and the five wood sugars gave highly significant hybrid differences for all chemical fractions except galactose (Table 3). In order to determine if these differences were associated with specific hybrids or groups of hybrid clones, we partitioned the clonal sums of squares between several arbitrarily selected hybrids and clonal groups (Table 3). Two hybrids, 5351 (designated fast grower in Table 3) and 5260 (Tristis #1) were compared to all remaining hybrid clones. In addition, groups of hybrids or clones with similar parentages, i.e., *P. euramericana*, *P. deltoides*, or *P. nigra* were compared to the remaining hybrids. None of the above comparisons differed significantly for all chemical fractions. This was not surprising because of strong interaction between chemical fractions. For example, a high glucose concentration is often associated with low xylose or lignin content. In addition, the *P. deltoides* hybrids as a group contained uniformly high lignin concentrations while their glucose contents were scattered throughout the hybrid rankings. An examination of the chemical fraction columns, of Table 3 indicates by the magnitude of the sums of squares which hybrid or hybrid group was primarily responsible for the significant AOV test.

Wood Sugars

Glucose and xylose concentration, which are good estimators of cellulose and hemicellulose contents, respectively, could provide valuable information for clonal selections. Among clones, glucose concentration ranged from 42.3 to 51.6%, and xylose concentration from 16.7 to 21.5%

Table 1.--Description of parentages, source numbering code for orthogonal comparisons

Source number	Orthogonal code	Parentages
5351		Unknown - (perhaps some balsam in parentage compare to tristis)
5260		Tristis (P. tristis x P. balsamifera)
4878	1	Populus x P. euramericana (P. deltoides x P. nigra)
5321	2	"
5325	3	"
5326	4	"
5328	5	"
4879	6	"
5265	1	P. deltoides x P. trichocarpa
5334	2	"
5267	3	" x P. cv. Caudina
5271	4	P. cv. Charkowiensis x P. deltoides
5272	1	P. nigra x P. laurifolia
5331	2	P. cv. Betulafolia (nigra clone) x P. trichocarpa
5332	3	" "
5339		Crandon (P. grandidentata x P. alba)
5258		Unknown (retained leaves down stems)
5263		P. cv. Candicans x P. cv. Berolinensis

Table 2.--A comparison of the chemical composition of several North American woods

Species	lignin	extractives	glucose	galactose	mannose	xylose	arabinose
Aspen (P. tremuloides)	16.3	3.8	57.3	0.8	2.3	16.0	0.4
Beech (F. grandifolia)	22.1	2.0	47.5	1.2	2.1	17.5	0.5
Birch (B. papyifera)	18.9	4.5	44.7	0.6	1.5	24.6	0.5
Sugar maple (A. saccharum)	22.7	2.7	51.7	0.1	2.3	14.8	0.8
Elm (U. americana)	23.6	2.2	53.2	0.9	2.4	11.5	0.6
White pine (P. strobus)	29.3	9.8	44.5	2.5	10.6	6.3	1.2

Data compiled from Clermont and Schwartz (1951, 1952); Browning 1963); Timell, 1957).
Values are percentages based on the wt of extractive free wood.

Table 3.--Orthogonal comparisons of the hybrids showing the partitioning of the sum of the squares and the location of the major contributors to the significant differences among the hybrids

Source	df	Lignin ss	Glucose ss	Mannose ss	Xylose ss	Arabinose ss
All hybrids	17	151.39**	550.28**	21.63**	123.64**	2.00**
Fast grower	1[1/]	32.60**	34.82**	0.03	2.70*	0.24**
Tristis	1	29.82**	14.78**	1.39**	6.04**	0.07
Euramericana	1	3.20**	3.95*	2.57**	19.71**	0.04
Deltoides	1	18.69**	1.06	0.38	1.01	0.00
Nigra	1	3.83**	176.44**	1.48**	0.15	0.09
Euramericana						
1 vs 2-6	1	0.84	26.11**	0.04	33.66**	0.01
2 vs 3-6	1	1.60	26.41**	0.74*	1.72	0.07
3 vs 4-6	1	0.08	0.01	1.81**	0.35	0.09
4 vs 5-6	1	0.61	128.33**	0.01	3.12*	0.00
5 vs 6	1	7.94**	0.74	4.63**	19.46**	0.26**
Deltoides						
1 vs 2-4	1	14.69**	0.54	0.05	17.85**	0.00
2 vs 3-4	1	9.10**	11.86**	0.00	2.79*	0.16
3 vs 4	1	3.84**	0.95	1.57**	1.25	0.01
Nigra						
1 vs 2-3	1	1.28	3.18	4.28**	1.13	0.01
2 vs 3	1	7.26**	1.00	0.29	4.04**	0.25**
Crandon vs 5258 & 5263	1	15.87**	90.12**	0.18	6.75**	0.69**
5258 vs 5263	1	0.14	29.89**	2.19**	1.91	0.00
Error	90	0.42	0.98	0.15	0.47	0.03

1/ In single df comparisons the sum of the square = mean squares. Error df for lignin is 36. * = 5% and ** = 1% significance level.

In the first five comparisons a single hybrid (Fast grower, Tristis) or a group of hybrids (Euramericana) are compared to all the remaining hybrids. In the remaining group comparisons each hybrid within the group is compared.

(Table 4). The Crandon hybrid (5339) had the highest glucose concentration, 5351 (the hybrid called fast grower) was above average, the hybrids with *P. nigra* as one parent (5272, 5331, and 5332) had significantly low glucose concentrations, while the glucose concentrations of the *P. euramericana* and *P. deltoides* hybrids were scattered throughout the rankings.

The power of the orthogonal comparisons was clearly shown when group or individual comparisons among the *P. auramericana, P. deltoides,* and *P. nigra* clones were examined for glucose concentration (Table 3). The *P. nigra* group was highly significant when compared to the rest of the hybrids. These hybrids were uniformly low in glucose concentration. A significant within-group difference was shown by *P. euramericana* comparison 4 vs 5 and 6. By referring next to Table 1 for the source number and Table 4 for the glucose concentrations, it is evident that clone 4 (5326) had the lowest and clone 5 (5328) had the highest glucose concentration among *P. euramericana* clones.

The concentrations of the remaining wood sugars also varied considerably among hybrids in this study (Table 4). Comparisons of xylose concentration indicated that *P. tristis* (5260) was significantly low, the *P. euramericana* clones as a group were low (although clone 4878 was the 2nd highest of all hybrids), and the *P. deltoides* and *P. nigra* hybrids were scattered throughout the rankings. Arabinose, galactose, and mannose were present at the lowest concentrations of the 5 wood sugars. The galactose concentration varied little among hybrids and was the only sugar not significant when tested with AOV. Arabinose and mannose exhibited the widest ranges of all the sugars. For example, arabinose ranged from 0.6 to 1.2% of the total carbohydrates, while mannose ranged from 2.7 to 5.4%. In spite of their high variability these sugars would probably have little influence on any selection program.

Lignin and Extractives

Lignin content is of considerable importance to tree breeders because of its inverse relationship to cellulose. A high lignin content reduces yields and increases cost of chlorine required for bleaching pulps. Analysis of variance gave a highly significant difference in lignin contents among the hybrids. When the sum of squares for lignin was partitioned, 5351 (fast grower), *P. tristis,* and the *P. deltoides* group were significantly different when compared to the rest of the clones (Table 3). The reason for these differences can be determined by examining the clonal rankings for lignin in Table 4. Hybrid (5351) and *P. tristis* (5260) had the lowest lignin percentages of all clones, 18.1 and 18.5%, respectively. The *P. deltoides* clones as a group had some of the highest lignin percentages. Within the deltoides group, the lignin percentage of hybrid 1 (5265) was below average while the remaining deltoides hybrids (5334, 5267, and 5271) were all high. For the remaining hybrids, the lignin contents of the nigra clones were high; the Crandon hybrid (5339), a *P. grandidentata x P. alba* cross, was third lowest and the *P. euramericana* clones were scattered throughout the rankings. Interestingly, two of the fast-growing hybrids with balsam poplar parentage had lower lignin contents than the Crandon hybrid.

Table 4.--Wood properties and growth parameters of 18 Populus hybrid clones

Source number	Wood sugars glu-cose	galac-tose	mannose	xylose	arabi-nose	Lig-nin	Extrac-tives	Specific gravity	Ring width 1973 mm	Total height m	Stem diameter cm
4878	49.0	2.2	4.0	21.4	0.9	20.9	3.8	.272	7.8	2.7	2.3
4879	48.2	2.2	4.1	19.3	1.2	19.9	4.6	.297	8.0	4.4	5.6
5258	49.5	1.9	3.5	19.1	1.1	21.6	4.1	.348	2.4	2.7	2.0
5260	46.9	2.2	4.5	17.5	1.1	18.5	3.2	.353	7.7	4.4	3.6
5263	45.6	2.0	4.6	20.2	1.1	21.9	3.0	.317	9.2	5.3	5.1
5265	45.6	2.0	3.9	21.5	1.0	21.0	3.4	.333	8.7	4.4	4.6
5267	47.1	2.4	3.7	19.7	1.1	23.4	2.9	.335	3.4	3.4	2.3
5271	47.4	2.3	4.7	19.3	1.2	25.0	3.5	.333	4.6	3.7	2.5
5272	43.4	2.1	5.4	19.8	1.0	22.3	3.6	.368	8.7	4.0	3.3
5321	44.4	2.5	4.2	17.8	1.1	22.1	4.1	.331	3.7	1.4	1.3
5325	47.1	1.9	4.3	18.1	0.8	21.6	2.8	.353	2.8	2.8	1.8
5326	42.3	2.1	3.5	19.3	0.9	21.6	3.1	.358	6.2	3.1	2.3
5328	50.3	2.2	2.7	16.7	0.8	22.2	3.3	.306	3.6	2.5	1.8
5331	43.9	2.3	3.8	20.7	1.3	20.4	2.2	.363	9.0	5.5	5.8
5332	44.4	2.2	4.3	19.8	0.9	22.6	2.6	.327	11.4	6.0	6.1
5334	48.2	2.6	4.1	20.0	0.8	22.1	3.5	.328	11.4	4.1	4.8
5339	51.6	2.4	3.7	20.6	0.6	18.9	2.8	.349	7.7	5.5	4.6
5351	47.9	1.9	3.8	19.5	1.2	18.1	2.9	.339	6.6	5.0	9.6
Ave.	46.82	2.19	4.05	19.46	1.01	21.34	3.30	.334	6.89	3.96	3.86

The percentage of both lignin and extractives are based on oven dry weight of extractive free wood.

Sugar percentage values were calculated as % total carbohydrates (dry wt of wood - wt lignin).

Height and diameter were measured at the end of the 3rd growing season. Diameter was measured 2.5 cm above ground. Ring width was from the single tree taken for analysis. Height and diameter were the average values for all trees growing in the hybrid source plots.

Even though the extractives constitute a minor percentage of the oven-dry wt of wood, their presence is very important to wood using industries. High levels of extractives not only reduce yield but also cause discoloration and create other problems during pulp production (Levitin, 1970). Although the level of extractives from *Populus* wood is lower than pine or tamarack, it is frequently higher than spruce, hemlock, elm, and maple (Clermont and Schwartz, 1951; 1952).

The extractive percentages were not statistically analyzed in this study because there was only one observation per hybrid. However, these percentages ranged from 2.2 to 4.6% (wt oven-dry wood), or over 100% difference (Table 4). A range of this magnitude approaches that found in a similar number of different hardwood species. Of three hybrids with the lowest extractive contents, two were from the nigra group (Balsam poplar parentage), and one was the Crandon hybrid. The *P. euramericana* clones as a group contained the highest extractive percentages.

Specific gravity and growth rate

High specific gravity is important for maximum dry weight yield. The range in specific gravity of the investigated clones in this study (.096) was almost exactly the same (.095) as reported by Kennedy (1968) for 5 species of *Populus* and (.096) reported by van Buijtenen, Einsphar, and Joranson (1959) for *P. tremuloides.* There appeared to be no relationship between specific gravity and growth rate (Table 4). For example, the *P. nigra* hybrid (5332) and *P. deltoides* hybrid (5334) had the widest ring width and below average specific gravity. On the other hand, the *P. nigra* hybrids (5272 and 5331) had rapid growth rates, (among the top five hybrids as measured by the 1973 ring width) and the highest specific gravity of all hybrids.

The average height and diameter values (Table 4) can be used only as an indication of a particular hybrid's growth potential because these data come from unreplicated plots containing different numbers of individual clones. In addition, height and diameter do not correspond exactly with ring width because they are average values derived from measurements of all plants from a particular hybrid in the source plots, while ring width is from a single tree randomly chosen for analysis. This discrepancy is particularly large for hybrid 5351 which was designated fast-grower in this study. Ring width of the tree chosen for chemical analysis was less than average when compared to the other hybrids; but the average diameter at the end of three years for all the 5351 plants was greater than all of the other clones in this study.

Growth rate alone appeared to have very little influence on the chemical properties of the hybrids. No consistent differences (high or low chemical values) were apparent for the two fastest or slowest growing hybrids. However, the effect of growth could only be tested with a single clone grown at different rates. In this study the clonal or genetic influence was more important than growth rate.

CONCLUSIONS

The hybrid clones in this study varied widely in their chemical properties. Parentage or genetic influence was primarily responsible for differences in chemical properties. For example, certain *P. nigra* hybrids (5331 and 5332) with similar growth rates differed considerably in lignin content. The Crandon hybrid (5339) was low in lignin and high in glucose (cellulose), while the *P. deltoides* clones (5267 and 5271) were the highest in lignin of all the clones. These results confirm information in the literature suggesting that the Leuce poplars have low lignin and high cellulose contents whereas the Aegeiros poplars have high lignin and relatively low cellulose content (Einspahr, et al., 1968; Lengyel and Hajduczky, 1964).

Certain hybrids combined a number of desirable characteristics (Table 5). The *P. nigra* hybrid (5331), which is a cross between the *P. nigra* clone *Betulafolia* and *P. trichocarpa,* had a rapid growth rate, high specific gravity, low lignin, and low extractive content. In addition, it is highly rust resistant (Dawson, 1974). The Crandon hybrid (*P. grandidentata x P. alba)* also combines rapid growth rate and high specific gravity with low lignin and low extractive content. In addition, the glucose (cellulose) content is much higher than the previous *P. nigra* hybrid. The Crandon hybrid is also highly rust resistant. Unfortunately, the Crandon hybrid is difficult to root, is a slow starter when the rooted cuttings are placed in the field, and does not respond as well to added fertilizer and water as some of the other clones.

The *P. deltoides* hybrid (*P. charkowiensis x P. deltoides)* would not be particularly desirable for intensive culture when compared to 5331 and 5339. Growth rate and specific gravity was below average, lignin content was highest of all hybrids tested, and extractive content was well above average. However, this hybrid was high in glucose (cellulose) and highly rust resistant. Thus, it might be a desirable hybrid for a breeding program to introduce these characteristics into rapid growing hybrids for intensive culture.

The clones and hybrids in this study varied widely in their genetic makeup; thus, concentrations of the different chemical constituents were also highly variable. The range in lignin content, for example, was as great as would be expected if different hardwood species from several different genera were tested. These chemical properties are probably under strong genetic control and should be considered in any breeding or selection program. Clones must initially be selected for rapid growth rate and high specific gravity in order to maximize yield. However, if basic chemical and physiological information is available, clones can be further improved by breeding or selecting for desirable chemical characteristics, as well as for rapid growth rate. If given a choice between two rapid growing clones, the one with the best chemical characteristics should be selected.

Table 5.--A comparison of the growth and wood characteristics of three Populus clones which might have potential for intensive culture

	P. nigra hybrid (5331)	Crandon (5339)	P. deltoides hybrid (5271)
Growth			
Height (m)	5.5	5.5	3.7
Diameter (cm)	5.8	4.6	2.5
1973 Ring wdt (mm)	9.0	7.7	4.6
Specific gravity	.363	.349	.333
Lignin (%)	20.4	18.9	25.0
Extractives	2.2	2.8	3.5
Glucose	43.9	51.6	47.4
Xylose	20.7	20.6	19.3

LITERATURE CITED

Anonymous. 1972. Aspen. Proc. Symp. on Aspen, College of Forestry, Univ. of Minn., USDA For. Ser. UCFES, USDA For. Ser. Gen. Tech. Report NC-1.

Basbous, M. 1950. Les hybrides américains de peuplier. Schweiz. Z. Forstw. 101: 418-437.

Bogdanov, P. L. 1968. Poplars and their cultivation. Published by USDA and Nat. Sci. Foundation, Washington, D.C. Israel program for Sci. translation Ltd. TT68-50374.

Borchardt, L. G. and C. V. Piper. 1970. A gas chromatographic method for carbohydrates as alditol-acetates. TAPPI 53: 257-260.

Browning, B. L. 1963. The composition and chemical reactions of wood. In: The Chemistry of Wood (B. L. Browning, Ed.). Interscience pub., John Wiley Sons, New York p. 58-101.

Cech, M. Y., R. W. Kennedy and J. H. G. Smith. 1960. Variation in some wood quality attributes of one-year-old black cottonwood. TAPPI 43: 857-858.

Clermont, L. P. and H. Schwartz. 1951. The chemical composition of Canadian woods I. Pulp and Paper Mag. Canada. 52: 103-105.

_____ and ______ 1952. The chemical composition of Canadian woods II. Pulp and Mag. Canada. 53: 142-143.

Clonaru, A., N. Constantinesco, and S. Ocskay. 1958. La composition chemique du Bois de peuplier en Roumanie et les caracteristiques de la cellulose produite. Int. Union For. Res. Organization 12th Congr. Oxford 1956.

Dawson, D. H. 1974. Rust resistance of *Populus* clones compared in Wisconsin study. Tree Planters' Notes 25 (1): 16-18.

Einspahr, D. E., M. K. Benson, and J. R. Peckham. 1968. Wood property variation in *Populus.* Proc. 8th Lake States Forest Tree Improvement Conf. (1967). U.S. For. Ser. Res. Paper NC-23. p. 24-27.

Ferrari, G. 1967. Within-tree variation of wood chemical composition in *Populus x euramericana.* Proc. 14 IUFRO Congress. Sect. 41 and WG22/41 p. 300-324.

Guillemain-Gouvernel, J. 1952. Étude chimique de différents types de peupliers. Mém. serv. chim. état (Paris), 37: 293-296.

________. 1954. Étude chimique de différents types de peupliers. Mém. serv. chim. état (Paris), 39: 231-233.

Jayme, G. 1947. Uber den Einfluss der Sorte and des Standortes auf die chemische Zusammensetzung and Eignung von Poppelhölzern zur Zellstroff-gewinnung. Das Papier. 1: 182-190.

Kennedy, R. W. 1968. Anatomy and fundamental wood properties of poplar. In: Growth and Utilization of Poplars in Canada. (J.S. Maini and J.H. Cayford, Eds.). Minister of Forestry and Rural Development. Ottawa. p. 149-168.

Kremers, R. E. 1964. Cambial chemistry. A way of looking at a stick of pulpwood. TAPPI 47: 292-296.

Larson, P. R. 1966. Changes in chemical composition of wood cell walls associated with age. Forest Prod. J. 16: 37-45.

Lengyel, P. and G. Hajduczky. 1964. Paper technological investigation of fast growing poplar. Papiripar 8: 125-129.

Levitin, N. 1970. The extractives of birch, aspen, elm, and maple: Review and Discussion. Pulp and Paper Mag. Canad. 71: 81-84.

Maini, J. S. and J. H. Cayford (Eds.) 1968. Growth and utilization of poplars in Canada. Dept. of For. and Rural Development. Forestry Branch. Ottawa. Dept. Pub. 1205.

Moore, W. E. and D. B. Johnson. 1967. Procedures for the chemical analysis of wood products. Tech. manual. Forest Prod. Lab. USDA Forest Serv., Madison, Wis.

Muhle Larsen, C. 1970. Recent advances in poplar breeding. Int. Rev. For. Res. 3: 1-67.

Saeman, J. R., W. E. Moore, and M. A. Millett. 1963. Sugar units present: hydrolysis and quantitative paper chromatography. Methods in Carbohydrate Chem. 8: 54-69.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Iowa State University Press. Ames, Iowa.

Sultze, R. F., Jr. 1957. A study of the developing tissues of aspenwood. TAPPI 40: 985-994.

Thornber, J. P. and D. H. Northcote. 1961(a). Changes in the chemical composition of a cambial cell during its differentiation into xylem and phloem tissue in trees. I. Main components. Biochem. J. 81: 449-455.

Thornber, J. P. and D. H. Northcote. 1961(b). Changes in the chemical composition of a cambial cell during its differentiation into xylem and phloem tissue in trees. 2. Carbohydrate constituents of each main component. Biochem. J. 81: 455-464.

Timell, T. E. 1957. Carbohydrate composition of ten North American species of wood. TAPPI 40: 568-572.

van Buijtenan, J. P., D. W. Einsphar, and P. N. Joranson. 1959. Natural variation in *Populus tremuloides* Michx. TAPPI 42: 819-823.

von Wettstein, W. 1946. Die "Zellulosepoppel" - Ihre Kultur and Züchtung. Züchter. 17/18: 13-19.

Wilde, S. A. and B. H. Paul. 1959. Growth, specific gravity, and chemical composition of quaking aspen on different soil types. USDA For. Serv. FPL Report No. 2144.