Natural Variation and Heritability in Triploid Aspen

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Investigations into the usefulness of triploid aspen[2]) in tree improvement work began with the Swedish discovery of a clone of large European aspen (Populus tremula L.) by NILSSON-EHLE (1936) and the determination by MÜNTZING (1936) that these trees possessed three sets of chromosomes. Subsequent intensive searching by JOHNSSON (1940, 1955) resulted in the location of a number of additional triploid individuals in Sweden.

Since these earliest discoveries, studies involving triploid aspen have been reported by a number of researchers including SARVAS (1958) in Finland, SEKAWIN (1951) reviewing work underway in Russia, and VAN BUIJTENEN, et al. (1957, 1958) in the United States.

The triploid quaking aspen (P. tremuloides MICHX.) clones reported by VAN BUIJTENEN, et al. (1957, 1958), like the European triploid aspen, have been of considerable interest to the pulp and paper industry. This interest stems primarily frcm the growth rate advantage usually observed for the triploid trees. Wood quality and pulping studies have also demonstrated that triploids from the Lake States have slightly higher specific gravity, similar levels of cellulose and lignin, aad fibers 26% longer and 10% wider than neighboring diploid trees.

Since these earlier described Lake States discoveries, additional triploid clones have heen located in Upper Michigan, on Barrie Island[3]) in Lake Huron, in central Wisconsin, and in the Riding Mountain National Park[4]) west of Winnepeg, Manitoba. The most recent triploid discovery shcwn in Figure *1* is located in west central Wisconsin and was brought to the author's attention by Forester RICHARD D. LINDBERG of the Wisconsin Conservation Department. This tree is of particular interest as it is the largest quaking aspen on record in the state of Wisconsin. When measured in 1961 the tree was 96 feet tall, had a d. b. h. of 26.4 inches, and was 68 years old.

The natural variation encountered in wood, pulp, and morphological characteristics results from the combined influence of genetic and environmental factors. Knowledge of the relative influence of these factors is of basic importance. The experimental approach used to study natural variation and to separate the genetic and environmental influences hinges on the use of the variation within the clones as an estimate of environmental influence. Most aspen stands presently under management are of sprout origin. Trees arising as sprouts from the roots of a single tree are identical in genetic make-up and are called a clone. The variation found between trees of the same clone is environmentally caused, whereas differences between clones are due both to heredity and environment. Whithin-clone and between-clone differences can be calculated by using a standard analysis of variance procedure on the measurement data. By comparing the within-clone and the between-clone variation, approximate estimates of gross heritability can be made.

The study described in this article was established to obtain information on natural variation of triploid clones and at the same time obtain estimates of gross heritability of a number of wood, fiber, and morphological characteristics.

Methods and Material

Four triploid clones located in the Bruce Crossing area of Upper Michigan were selected for use in this study. The Sour clones were growing on heavy red clay soils common in that area and were located geographically within approximately 10 miles of each other. Triploid clone no. 2 is a female clone while clones 1, 3, and 4 are male clones.

The first phase of this study consisted of selecting five trees from each clone and characterizing the trees as to growth and morphology. The growth measurements obtained included height, diameter at breast height, form factor, crown size, and age. Morphological properties including straightness of stem, branch angle, natural pruning, and leaf size were also measured.

Four 10-mm. breast-high increment cores were taken from each tree and used in obtaining specific gravity and fiber length information. Fiber length data on the increment cores were obtained by subdividing the four cores into five-year age intervals, compositing the portions of the core of comparable age and measuring 100 fibers in

Figure 1. — Chromosome counts on the largest quaking aspen in Wisconsin confirmed the tree was a triploid.

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[2]) Triploid aspen are trees that have three sets of chromosomes (3n = 57) as contrasted to the normal diploid individuals which have two sets of chromosomes.

[3]) Reported and sampled by A. G. RACEY of Ontario Paper Company Limited. Chromosome numbers verified by The Institute of Paper Chemistry.

[4]) Located by J. S. JAMESON and reported by C. C. THOMSON of the Canadian Department of Northern Affairs and National Resources. Chromosome numbers were verified by The Institute of Paper Chemistry.

each five-year age interval. Fiber length-age curves were plotted for each tree, and data on average fiber length and fiber length at age 30 were computed.

The second phase of this study consisted of obtaining representative wood samples from the described trees by felling and cutting them into 30-inch bolts. Alternate bolts were selected for further study, bolt number one being located at the 24-54 inch level. One-inch disks were taken from the lower end of each of the selected bolts and used to obtain information on specific gravity, decay, and stain.

The selected samples, upon arrival at the Institute, were barked and chipped, and the chips from all bolts from the same tree were combined and thoroughly mixed to form a composite sample. Duplicate kraft cooks were made from the composite sample using a modified 44-liter digester. Equal amounts of pulp from the duplicate cooks were blended and used in performing a TAPPI Standard beater evaluation. Tests made on handsheets included zero-span tensile strength,[5] tensile strength, tear factor bursting strength, formation, and apparent density.

Fiber length was determined on the unbeaten pulp by measuring 300 fibers. The fibers measured were obtained by using a sample of pulp from the composite sample of the two cooks on each tree. The fibers were projected on a fiber-measuring apparatus of Finnish manufacture and measured in millimeters using a ruler. Standard Institute

[5]) Zero-span tensile strength is measured using special clamping jaws in the Instron tester. The test is made using a zero interval between the jaws and is interpreted as being a measure of fiber strength.

Table 1. — Summary of Growth and Form Information on Triploid Aspen.

Clone	Tree No.	Age, yr.[1]	Height, ft., age 50[2]	Volume, cu. ft. age 50[2]	Crown Volume age 50[2]	Branch Angle, degrees	Form Factor[3]	Specific Gravity, g./cc., core	Fiber Length Core, mm. Av.	Fiber Length Core, mm. Age 30
I	1	58	73	12.5	2.08	60	81.7	0.372	1.17	1.26
	2	60	71	12.7	1.28	65	84.8	0.390	1.19	1.33
	3	60	78	14.8	1.57	60	81.5	0.387	1.20	1.25
	4	63	71	9.6	0.94	60	80.9	0.388	1.13	1.30
	5	59	68	7.7	0.53	80	77.5	0.383	1.09	1.25
II	1	45	74	49.0	7.81	60	83.0	0.379	1.16	1.26
	2	45	75	37.5	2.86	80	83.1	0.373	1.09	1.21
	3	47	72	31.5	5.90	70	77.6	0.374	1.10	1.23
	4	44	85	36.2	3.91	80	76.0	0.383	1.14	1.23
	5	47	79	37.5	9.05	70	78.0	0.408	1.10	1.22
III	1	39	74	32.0	3.35	75	82.0	0.382	1.17	1.37
	2	43	73	21.0	0.80	60	78.5	0.376	1.18	1.37
	3	47	80	24.7	1.48	70	81.5	0.388	1.19	1.37
	4	43	70	18.3	0.82	60	78.8	0.381	1.15	1.35
	5	44	73	18.4	1.71	60	73.3	0.396	1.15	1.37
IV	1	51	76	32.5	4.53	70	79.0	0.447	1.12	1.23
	2	53	79	25.0	3.82	75	80.1	0.404	1.05	1.17
	3	59	88	25.2	5.04	70	81.7	0.375	1.09	1.22
	4	57	81	40.0	7.45	65	79.5	0.416	1.10	1.13
	5	56	78	20.7	2.56	70	79.6	0.396	1.10	1.21
Average		51	76	25.3	3.37	68	79.9	0.39	1.13	1.27
Std. dev.		7.2	5.0	11.1	2.5	7.1	2.6	0.02	0.04	0.07

[1]) Total age of trees in 1959.
[2]) Values adjusted to common age 50 years. Crown volume = vol. in cu. ft./1000.
[3]) Diameter outside bark at b. h./diameter inside bark top of first 16-ft. log $\times$ 100.

Table 2. — Summary of Handsheet and Whole-Tree Wood Property Data.

Clone	Tree No.	Unscreened Yield %	Permanganate Number	Average Fiber Length Determin. from Pulp mm.	Unbeaten Apparent Density g./cc.	Average Unbeaten Zero-Span Tensile Strength lb./in.	Average Beaten Zero-Span Tensile Strength lb./in.	Handsheet Properties at 750 cc. Schopper-Riegler Freeness: Apparent Density g./cc.	Bursting Strength pt./100 lb.	Tear Factor	Tensile Strength lb./in.
I	1	51.6	13.1	1.16	11.3	64.0	62.7	14.6	109	1.32	33.2
	2	52.0	13.9	1.13	11.0	58.6	59.2	15.3	107	1.30	32.3
	3	52.0	12.8	1.17	11.2	63.0	61.7	14.5	108	1.27	32.5
	4	51.7	13.8	1.16	11.0	60.4	62.6	14.6	104	1.32	39.2
	5	51.0	13.6	1.08	11.1	59.4	57.6	14.7	102	1.27	32.3
II	1	52.4	11.0	1.11	11.6	52.8	50.6	14.4	81	0.93	29.6
	2	53.7	11.0	1.05	11.7	55.3	52.2	14.8	87	0.96	29.3
	3	53.9	11.8	1.08	11.6	56.1	52.7	14.8	86	0.92	28.2
	4	53.6	12.8	1.16	11.3	56.4	56.3	14.1	98	1.11	30.0
	5	53.7	12.4	1.05	11.0	52.8	54.0	14.2	84	1.07	29.4
III	1	53.6	10.7	1.03	11.0	55.1	53.8	14.5	93	1.12	30.3
	2	53.2	11.2	1.12	11.3	53.9	59.0	14.5	90	1.13	30.8
	3	53.4	11.7	1.16	11.3	61.6	57.2	14.7	97	1.15	30.9
	4	54.0	11.6	1.11	11.6	61.2	60.4	14.8	91	1.20	32.3
	5	53.6	11.8	1.16	11.1	55.1	53.8	14.4	88	1.12	29.8
IV	1	54.4	12.0	1.03	11.1	52.0	47.8	14.9	82	0.93	28.8
	2	55.9	12.2	1.06	11.1	53.4	48.7	14.1	85	1.01	29.3
	3	56.1	12.3	1.12	11.3	56.6	48.8	14.7	89	0.97	31.7
	4	55.5	10.8	1.09	11.0	51.9	47.4	14.3	85	0.92	28.8
	5	54.4	12.6	1.09	11.5	54.2	51.7	14.1	83	0.97	28.5
Average		53.4	12.2	1.10	11.3	56.7	55.0	14.6	92	1.10	30.9
Standard dev.		1.4	1.0	0.05	0.23	3.7	4.9	0.3	9.0	0.14	2.4

methods employed by the Fiber Microscopy Section were used in making up the slides and recording the data. Fibers measured included broken, cut, and undamaged fibers.

Results

A large amount of data was collected on the 20 trees involved in the two phases of this study. Space does not permit publishing a complete account of these data. *Table 1* summarizes a portion of the growth and morphological data obtained and includes specific gravity and fiber length data taken on increment core samples. Age differences between clones and differences in the year that the trees were measured made it necessary to adjust a portion of the basic data to age 50. Absent from *Table 1* is information on leaf size and shape.

Table 2 summarizes the observations made on wood and paper properties obtained by cutting the trees and pulping representative samples of each tree. The handsheet strength properties obtained by making the standard TAPPI evaluations were compared at 750 and 500-cc. SCHOPPER-RIEGLER freeness levels. Close correlations were obtained between paper properties at these two freeness levels, and only the results at the 750-cc. freeness level are presented in *Table 2*. The pulp yield[6]) and permanganate number data presented are the average of duplicate determinations made on each tree. The average zero-span tensile strength values listed are values obtained by averaging the zero-span tensile strength from handsheets for the 5, 10, 30, and 50-minute beating intervals. The unbeaten zero-span tensile strength values given were obtained from handsheets made from unbeaten pulp from the first of the two cooks made on each tree.

Variation and Heritability Estimates For Growth and Morphlogical Characteristics

Knowledge regarding the gains that might be obtained by selection among available triploid clones for such characteristics as specific gravity, fiber length, height, volume growth, form, leaf size, etc., is of basic interest.

The importance of selection depends in part upon the variability that exists in such characteristics and the degree to which these characteristics are inherited. As discussed earlier, an estimate of the gross heritability can be obtained by comparing the variation between clones with the variation that exists between trees within clones. To make this comparison, an analysis of variance of the form shown in *Table 3* was used. The S^2 value as shown in *Table 3* is an estimate of the variation between trees within clones. The variance ratio, which is the ratio of the variance between clones (S_c^2) and the over-all variance ($S^2 + S_c^2$), can be considered as an estimate of gross heritability. It is worthy of mention that the gross heritability estimates have been made on a limited number of clones and that such estimates include nonadditive genetic variation. Heritability figures calculated in this manner can be expected to give heritability predictions higher than narrow sense heritability estimates obtained from parent tree-progeny comparisons.

Table 4 summarizes heritability estimates obtained for the growth and morphological characteristics. Of the characteristics related to growth rate and form, tree volume and crown volume were the ones that had the highest variance ratios and appeared to be under moderate genetic control. Height growth demonstrated less between-clone differences, and genetic improvement by selection appears less promising. Angle of branching and form factor have very low variance ratios. These low ratios resulted, apparently, from uniformly high form factors (76—82) and uniformly satisfactory angle of branching for all clones used in the study.

The variance ratios obtained on the leaf measurements indicate that there are fairly large genetically controlled differences between clones and that such differences could be used to help distinguish differences between clones.

[6])Yield in this report is unscreened yield calculated on a weight basis.

Table 3. — Form Used for Analysis of Variance.

Fiber Length, Age 30				
Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	Estimated by Mean Squares
Total	19	0.0983	0.005	
Clones	3	0.0846	0.028	$\sigma^2 + 5\,\sigma_c^2$
Trees within clones	16	0.0137	0.0009	σ^2
S^2			0.0009	
S_c^2			0.0055	
$S_c^2 / (S^2 + S_c^2)$			0.865	

Table 4. — Heritability Estimates for Wood, Growth and Morphological Characteristics.

Property	Heritability[1])
Height, age 50	0.33
Tree volume, age 50	0.77
Crown volume, age 50	0.62
Branch angle	0.04
Form factor	0.06
Specific gravity, W. T.[2])	0.38
Specific gravity, core[3])	0.26
Fiber length, age 30[3])	0.86
Fiber length, average[3])	0.50
Leaf length	0.56
Leaf width	0.69
Petiole length	0.82
Leaf base angle	0.61
Leaf tip angle	0.87
Number serrations/cm.	0.43

[1]) Gross heritability estimates obtained from variance ratio calculations.
[2]) Measurements based upon whole-tree wood samples.
[3]) Measurements based upon 10-mm. increment core samples.

Variation and Heritability Estimates for Wood Fiber, and Handsheet Properties

One of the primary objectives of this study was to increase our knowledge of the physical properties of pulp produced from triploid aspen. Another objective was to obtain some insight into the variation and gross heritability of wood, fiber, and handsheet properties. Again, as described in the previous section, the analysis of variance technique was used to obtain estimates of the variation between trees within clones (S^2) and the variation between clones (S_c^2). The properties summarized in *Table 2* were used in making this comparison. *Table 5* summarizes the results of the above calculations.

Most interesting to the forest geneticist are the variance ratios obtained for the fundamental wood and fiber properties. Fiber strength, as measured by zero-span tensile strength, had variance ratios of 0.60 and 0.82 and appears to be under fairly strong genetic control. Equally interesting are the high heritability figures obtained for fiber length, unscreened yield, and lignin-free yield. Specific gravity measured both from the increment core and whole tree samples appears to be under less genetic control than the above mentioned properties.

Table 5. — Heritability Estimates for Fiber and Handsheet Strength Properties.

Property	Heritability[1])
Zero-span tensile (beaten)	0.82
Zero-span tensile (unbeaten)	0.60
Yield, unscreened	0.87
Yield, lignin-free basis	0.88
Tear factor, 500-cc. freeness	0.90
Tear factor, 750-cc. freeness	0.88
Bursting strength, 500-cc. freeness	0.83
Bursting strength, 750-cc. freeness	0.76
Tensile strength, 500-cc. freeness	0.57
Tensile strength, 750-cc. freeness	0.54

[1]) Gross heritability estimates obtained from variance ratio calculations.

The basis for calculating the lignin-free pulp yield information presented is worthy of explanation. Equivalent weights of wood were used, and lignin remaining in the pulp after cooking was calculated from the pulp permanganate number. The lignin-free yield figures can, for all practical purposes, be considered as a measure of holocellulose. The variance ratio for yield indicates strong genetic control of this property in the triploid aspen population that was studied.

Bursting strength, tear factor, and tensile strength are handsheet strength properties which are considered to be influenced by fiber dimension, fiber strength, and fiber-to-fiber bonding. Variance ratios were also calculated for the above handsheet properties using the data both at 500 and 750-cc. freeness. The variance ratios obtained were higher than anticipated and indicate fairly strong control over a number of fundamental wood and fiber properties which in turn control handsheet strength properties. Since bursting strength, tear factor, and tensile strength are derived values, subject to measurement error and influenced by processing variables, it is suggested that the ratios obtained for these properties be viewed with a certain amount of reserve.

Whole Tree and Increment Core Wood Property Correlations

Earlier diploid aspen studies by van Buijtenen, *et al.* (1962) indicated that breast-high (b. h.) increment core samples are suitable for estimating certain whole tree wood properties. To check this technique further, specific gravity and fiber length measurements made on 10-mm. increment cores were compared with measurements made on wood and/or pulp samples representative of the whole tree. Simple correlations were calculated as a means of evaluating the usefulness of 10-mm. b. h. increment cores. Whole tree specific gravity, increment core specific gravity, whole tree average fiber length, increment core average fiber length, and increment core fiber length at age 30 were the variables compared. All possible correlations were determined between the variables described, and the results of these calculations are presented in *Table 6.*

The increment core specific gravity and whole tree specific gravity correlation was significant at the 1% level and indicates that specific gravity measurements on b. h. 10-mm. increment cores provide useful estimates of whole tree specific gravity. The increment core average fiber length and whole tree fiber length correlation was significant at the 5% level. This correlation was not as high as expected based on previous experience with diploid aspen. An additional point of interest is the general negative trend

Table 6. — Summary of Whole Tree-Increment Core Wood Property Correlations.

Variables	Correlation Coeff.[1])
Specific gravity, core — Specific gravity, W. T.[2])	+0.728
Specific gravity, core — Fiber length, W. T.	—0.391
Specific gravity, core — Fiber length, core age 30	—0.324
Specific gravity, core — Fiber length, core average	—0.184
Specific gravity, W. T. — Fiber length, W. T.	—0.092
Fiber length, core av. — Fiber length, W T.	+0.450
Fiber length, core av. — Fiber length, core age 30	+0.721
Fiber length, core age 30 — Fiber length, W. T.	+0.342
Fiber length, core av. — Specific gravity, W. T.	—0 058
Fiber length, core age 30 — Specific gravity, W. T.	—0.294

[1]) $r_{.01} = 0.561$; $r_{.05} = 0.444$.
[2]) Measurements on samples representative of whole tree (W. T.)

between fiber length and specific gravity. In no case, however, was the negative trend statistically significant.

Whole Tree Pulp and Increment Core Wood Property Correlations

Another important aspect of this study was the comparison of increment core data with pulp strength data determined by pulping representative samples of whole trees. The increment core measurements used in these comparisons include specific gravity, average fiber length, and fiber length at age 30. The whole tree handsheet strength properties used include tear factor, bursting strength, and tensile strength at 500 and 750-cc. freeness along with average zero-span tensile,[7]) and zero-span tensile on handsheets made from unbeaten pulp. The data on zero-span tensile for handsheets made from unbeaten pulp are of particular interest because this is the type of measurement that can be obtained when 10-mm increment cores are pulped by a small-scale kraft cook.[8]) The measurement data on the 20 triploid trees were used, and simple correlations were run on all possible combinations of the above data. Only those correlations that are significant

Table 7. — Whole-Tree Pulp and Increment-Core Wood Property Correlations.

Variables		Correlation Coefficients[1]) 750 cc.	500 cc.
Zero-span, unbeaten	Burst	+0.852	+0.786
	Tear	+0.801	+0.806
	Tensile	+0.674	+0.640
	Zero-span, average[2])	+0.826	
Fiber length, core average	Burst	+0.463	+0.330
	Tear	+0.537	+0.502
	Zero-span, average[2])	+0.609	
	Zero-span, unbeaten[2])	+0.444	
Fiber length, core age 30	Tear	+0 525	+0.453
	Zero-span, average[2])	+0.560	
Specific gravity, core	Zero-span, average[2])	—0.477	
	Zero-span, unbeaten[2])	—0.487	

[1]) $r_{.01} = 0.561$; $r_{.05} = 0.444$.
[2]) The zero-span measurements used in these calculations were not taken at 750-cc. freeness. The unbeaten values are those measured on handsheets having a zero beating interval, while the zero-span average values were based upon the average values from handsheets made of pulps beaten for 5, 10, 30, and 50-minute beating intervals.

[7]) Zero-span average values were based upon the average values from handsheets made from pulp beaten for 5, 10, 30, and 50-minute beating intervals.

[8]) This small-scale, nondestructive "micropulping" procedure is described in detail in publications by Thode, *et. al.* (1961) and van Buijtenen, *et. al.* (1961).

and/or pertinent to this portion of the study are reported in *Table 7*.

The average fiber length of the cores was found to be significantly correlated with tear at both freeness levels and with burst at 750-cc. freeness. Fiber length at age 30 was also found to be correlated with tear at both freeness levels but was not significantly correlated with burst. Both measures of core fiber length were significantly correlated (1% probability level) with the average zero-span values. The average core fiber measurements were correlated with the unbeaten zero-span measurements.

Also of particular interest are the highly significant correlations between zero-span measurements made on unbeaten pulp handsheets and burst, tear, and tensile data obtained from the whole tree pulping work. A highly significant correlation was also found between the two estimates of zero-span tensile.

Whole Tree Pulp and Whole Tree Wood Property Correlations

An additional group of comparisons that are of basic interest to geneticists and paper technologists alike are those involving wood and handsheet strength data obtained from representative samples of entire trees. The whole tree wood property variables utilized in this comparison include fiber length, specific gravity, and adjusted volume growth. The whole tree pulp handsheet strength data used in these comparisons included bursting strength, tear factor, tensile strength, and apparent density at both 750 and 500-cc. freeness. Included also was yield, average zero-span tensile, and permanganate number measured on whole tree pulp samples.

Simple correlations were calculated between the variables involved and were used as the basis for discussing certain relationships that exist between the above-listed variables. The number of correlation coefficients which resulted was very large and it is again necessary to list only those correlations which are significant and/or pertinent to this portion of the Results section. *Table 8* presents results of these calculations.

Table 8. — Significant Whole-Tree Wood and Whole-Tree Pulp and Handsheet Strength Property Correlations.

Variables		Correlation Coefficients[1]) 750 cc.	500 cc.
Tear factor	Burst	+0.906	+0.914
Tensile strength	Burst	+0.720	+0.641
Zero-span tensile (av.)	Burst	+0.832	+0.773
Yield	Burst	—0.704	—0.648
Permanganate no.	Burst	+0.673	+0.744
Fiber length, W. T.[2])	Burst	+0.620	+0.578
Volume growth	Burst	—0.708	—0.743
Tensile strength	Tear	+0.779	+0.761
Zero-span tensile (av).	Tear	+0.916	+0.900
Yield	Tear	—0.742	—0.755
Permanganate no.	Tear	+0.651	+0.675
Fiber length, W. T.	Tear	+0.566	+0.641
Volume growth	Tear	—0.797	—0.773
Zero-span tensile (av).	Tensile	+0.728	+0.738
Yield	Tensile	—0.561	—0.518
Permanganate no.	Tensile	+0.596	+0.479
Fiber length, W. T.	Tensile	+0.532	+0.529
Volume growth	Tensile	—0.662	—0.717
Yield	Zero-span tensile (av.)	—0.771	
Permanganate no.	Zero-span tensile (av.)	+0.518	
Fiber length, W. T.	Zero-span tensile (av.)	+0.623	
Volume growth	Zero-span tensile (av.)	—0.686	
Yield	Volume growth	+0.468	
Permanganate no.	Volume growth	—0.700	
Fiber length	Volume growth	—0.456	
Yield	Permanganate no.	—0.499	

[1]) Correlation coefficients of the wood and pulp and/or handsheet properties at 750 and 500-cc. SCHOPPER-RIEGLER freeness levels; $r_{.05} = 0.444$; $r_{.01} = 0.561$.

[2]) Whole-tree fiber length measured on representative pulp samples.

Bursting strength, tear factor, and tensile strength were found to be significantly correlated with each other and had comparable correlation patterns. Burst, tear, and tensile strength were positively correlated at both freeness levels with zero-span tensile strength, fiber length, and permanganate number. Similarly, each was negatively correlated with yield and volume growth. Correlation coefficients for burst and tear were higher than those for tensile strength and in all cases were significant at the 1% level of probability.

Zero-span tensile strength was well correlated with tear, burst and tensile strength and, as might be expected, had a similar pattern of correlations. Zero-span tensile was found to be positively correlated with fiber length and permanganate number and negatively correlated with volume growth and yield. Also worthy of mention was the consistent pattern of negative correlation between volume growth and all of the other variables in this comparison with the exception of yield.

Discussion

The reliability of gross heritability estimates depends upon the trees of a clone being truly members of the same clone and on minimizing the environmental differences between clones and within clones. Large environmental differences in either case tend to obscure and make impossible the detection of genetic effects. Some minor between-clone and within-clone differences existed in the sites of this study, but these seem to be relatively unimportant compared to the large crown-size differences that existed between clones.

The variance ratio calculations for crown volume indicated strong genetic control over this factor. Numerous illustrations can be cited which show that crown volume is influenced by both genetic and environmental factors. The difficulty in determining whether the large difference in crown size between clones in this study resulted from the relative genetic vigor of the triploid trees involved or from original differences in stand density must be recognized. The method of calculation used assumes uniform original sprout stand density and takes into account the within-clone variation in crown size that may have arisen due to differences in density of sprouting. Observations made in the clones involved lead the authors to believe that the variance ratios are valid as presented, but to feel that some between-clone differences in original stand density may have existed and that the genetic control of crown volume may be overemphasized. Tree volume was highly correlated ($r = 0.823$) with crown volume, and, similarly, the genetic control of this factor may be less than the variance ratio seems to indicate.

The variance ratios (gross heritability estimates) for growth and morphological characteristics presented are in most instances in good agreement with the results obtained in earlier studies by van Buijtenen, *et al.* (1959 and 1962). Exceptions to the above statements are the variance-ratio differences obtained for branch angle and form factor. The triploid clones gave much lower estimates of heritability, and this may in part be related to the methods for selecting the clones used in each study. Easily recognized clones of uniform age and growing on uniform sites were selected for the diploid clonal study. Triploid clones used were the only ones available and were originally selected because, as triploid suspects, they contained trees of large size and above average form and rate of growth. This bias in selection could be expected to result in smaller differences between clones and might very well influence the variance ratios for such characteristics as form factor and branch angle. The heritability estimates obtained for the leaf measurements indicate that there are large, genetically controlled differences between clones. These results agree quite well with the previous reported diploid study and emphasize the usefulness of leaf measurements in identifying clones.

The analysis of variance and variance-ratio information obtained upon handsheet strength properties was very encouraging from the forest geneticist's point of view. Large differences were obtained between clones in bursting strength, tear factor, tensile strength, and zero-span tensile strength. The variance ratios resulting from these large between-clone differences were in good agreement with earlier diploid aspen studies and are interpreted as indicating fairly strong genetic control over one or more of the several fundamental fiber properties which, in turn, have an important influence on handsheet strength properties.

Zero-span tensile strength measurements, interpreted as a measure of fiber strength, are sensitive to processing and testing variables. Early work with aspen made it clear that special care would be necessary in the various stages of handsheet preparation and testing in order to obtain satisfactory correlations between handsheet strength measurements and zero-span measurements. The improvement in reproducibility of results which has stemmed from recent changes in testing equipment and techniques has been very encouraging. Fiber strength, as measured by the zero-span tensile strength test, appears to be under fairly strong genetic control. Zero-span measurements on both unbeaten and beaten handsheets were found to be significantly correlated with the several handsheet properties examined and suggest that fiber strength may be one of the major factors contributing to the high variance ratios obtained for tear factor, bursting strength, and tensile strength. The highly significant correlations between zero-span values obtained on unbeaten pulp handsheets and other strength properties are particularly interesting because sufficient pulp can be obtained from increment cores to provide this measurement.

The possibility of evaluation of wood quality using small, nondestructive samples is very appealing to the forest geneticist. Correlations between wood properties measured on increment core samples and whole tree pulp quality are helpful in evaluating the usefulness of such data. Increment core measurements in this study were limited to specific gravity and fiber length. Fiber length was found to be significantly correlated with burst, tear, and zero-span tensile strength and appears to provide information useful in estimating the pulping potential of a tree. As mentioned in an earlier paragraph, zero-span measurements on unbeaten fibers were correlated with whole tree tear, burst, and tensile strength values and may be a possibility for improving the accuracy of nondestructive wood quality evaluation procedures.

Also worthy of mention is the consistent negative correlation between volume growth and the major handsheet strength properties. A similar negative volume growth-pulp strength property correlation existed in the earlier diploid pulping study and emphasizes the necessity of independent selection for growth and wood quality objectives.

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Summary

Twenty triploid trees from a total of four clones growing in Upper Michigan were selected as a source of data for an investigation of natural variation of triploid aspen. Detailed growth and morphological data were taken on each tree. Four breast-high, 10-mm. increment cores were obtained and used in determining age, specific gravity, and fiber length. Upon completion of the measurements on standing trees, representative wood samples were obtained by felling the trees, cutting them into 30-inch bolts, and using every other bolt as a source of disk and chip samples. Disks located every 60 inches along the stem were used to obtain whole-tree specific gravity, decay, and stain. The chips sampled from the 30-inch bolts of each tree were composited and duplicate kraft cooks were made using a modified 44-liter digester.

Pulp permanganate number and yield values were obtained on each of the duplicate cooks. Pulp from each of the two cooks for a tree was composited and TAPPI Standard beater evaluations were performed on each of the composite samples. Handsheet data included zero-span tensile strength, tensile strength, tear factor, bursting strength, formation, and apparent density. Analyses of variance and variance ratios were calculated as a means of obtaining estimates of gross heritability. Simple correlations were also run using the data on a number of wood, fiber, and pulp properties as variables. The results of the above comparisons can be summarized as follows:

1. Fiber length, fiber strength, tree volume, and crown volume were characteristics that appear to be under moderate genetic control. Specific gravity appears to be less strongly controlled genetically than the above properties.

2. Leaf size and shape differed greatly between clones and appear to be strongly controlled genetically.

3. Between-clone pulp yield differences were highly significant and the variance ratio obtained suggests that the possibility of genetic improvement of pulp yield is good.

4. Highly significant between-clone differences were obtained in the handsheet properties of bursting strength, tear factor, and tensile strength. The variance ratios indicate fairly strong genetic control over one or more of the several fundamental fiber properties which, in turn, influence handsheet strength properties.

5. Average increment core fiber length measurements were found to be significantly correlated with tear, burst, and zero-span tensile strength of the whole-tree pulps.

6. Fiber strengths, as measured by zero-span tensile strength, were correlated (1% probability level) with tear, burst, and tensile strength and suggest the possible use of zero-span measurements in evaluating pulps and ranking selected trees.

7. Yield and volume growth were negatively correlated with tear factor, bursting, tensile, and zero-span tensile strengths and indicate the necessity for independent selection for these two groups of properties.

Zusammenfassung

Titel der Arbeit: *Natürliche Variation und Heritabilität bei der triploiden Aspe.*

Zwanzig triploide Bäume von insgesamt vier Klonen in Ober-Michigan wurden als Objekt für eine Untersuchung der natürlichen Variation der triploiden Aspe ausgewählt. An jedem Baum wurden eingehende Angaben über Wachstum und Morphologie erhoben. Vier 10 mm starke Bohrspäne wurden in Brusthöhe entnommen und zur Bestimmung des Alters, des spezifischen Gewichts des Holzes und der Faserlänge benutzt. Zur Vervollständigung der Messungen an stehenden Bäumen wurden nach Fällung der Bäume representative Holzproben entnommen, indem die Stämme in Abschnitte von 30 Zoll Länge zerschnitten wurden und jeder zweite Abschnitt Stammscheiben- und Bohrspanproben lieferte. Zur Erfassung des spezifischen Gewichts, des Holzabbaus und der Verfärbung dienten Stammscheiben aus 60 Zoll weiten Abständen entlang des Stamms. Die Bohrspanproben von den 30 Zoll langen Abschnitten eines jeden Baums wurden zusammengetan, und in einem modifizierten Aufbereiter für 44 l wurden doppelte Sulfatkochungen durchgeführt.

Von jeder der Doppelkochungen wurden Werte für Permanganatzahl und Ausbeute erhalten. Der Zellstoff der beiden Kochungen pro Baum wurde gemischt und an jeder der Mischproben TAPPI-Standardprüfverfahren (TAPPI Standard beater evaluations) angewendet. Die Prüfung von Papierprobeblättern umfaßte die Zugfestigkeit von Einzelfasern bei Einspannlänge Null, Zugfestigkeit, Durchreißfaktor, Berstfestigkeit, Entwicklung (formation) und scheinbare Dichte. Varianzanalysen wurden durchgeführt und Varianzquotienten errechnet als Mittel, um Schätzwerte der Heritabilität i. w. S. zu erhalten. Auch einfache Korrelationen wurden errechnet auf der Grundlage der Daten einer Reihe von Holz-, Faser- und Zellstoffeigenschaften als Variable. Die Ergebnisse der obigen Vergleiche können wie folgt zusammengefaßt werden:

1. Faserlänge, Faserfestigkeit, Baumvolumen und Kronenvolumen waren Merkmale, die scheinbar unter mäßiger genetischer Kontrolle stehen. Das spezifische Gewicht erscheint weniger stark genetisch kontrolliert als die obigen Eigenschaften.

2. Größe und Form der Blätter unterschieden sich stark zwischen Klonen und erscheinen genetisch streng kontrolliert.

3. Die Unterschiede in der Zellstoffausbeute zwischen Klonen waren hochsignifikant und der erhaltene Varianzquotient läßt vermuten, daß die Möglichkeit der züchterischen Verbesserung gewiß ist.

4. Hochsignifikante Klonunterschiede wurden erhalten in den Probeblatteigenschaften Berstfestigkeit, Durchreißfaktor und Zugfestigkeit. Die Varianzquotienten zeigen sehr starke genetische Kontrolle einer oder mehrerer der verschiedenen grundlegenden Fasereigenschaften an, welche ihrerseits die Festigkeitseigenschaften der Papierprobeblätter beeinflussen.

5. Die durchschnittlichen Faserlängenmessungen an Bohrspänen waren signifikant mit der Durchreißfestigkeit, der Berstfestigkeit und der Zugfestigkeit bei Einspannlänge Null des Zellstoffs vom ganzen Stamm korreliert.

6. Die Faserfestigkeiten, gemessen als Zugfestigkeit von Einzelfasern bei Einspannlänge Null, waren bei 1% Irrtumswahrscheinlichkeit korreliert mit der Durchreißfestigkeit, Berstfestigkeit und Zugfestigkeit; sie legen nahe, daß Zugfestigkeitsmessungen bei Einspannlänge Null möglicherweise zur Bewertung von Zellstoff und zur Benotung von Auslesebäumen herangezogen werden können.

7. Ausbeute und Volumenwachstum waren mit Durchreißfaktor, Berstfestigkeit, Zugfestigkeit und Zugfestigkeit von Einzelfasern bei Einspannlänge Null negativ korreliert und demonstrieren die Notwendigkeit der unabhängigen Auslese auf diese beiden Gruppen von Eigenschaften.

Résumé

Titre de l'article: *Variabilité naturelle et héritabilité chez le tremble triploïde.*

20 arbres triploïdes appartenant à 4 clones poussant dans le Michigan supérieur ont été choisis pour une étude de la variabilité naturelle du tremble triploïde. Des mesures détaillées de croissance et de forme ont été faites pour chaque arbre. 4 prélèvements à la tarière de 10 mm. ont été faits à hauteur d'homme pour la détermination de l'âge, de la densité et de la longueur des fibres. Après l'achèvement des mesures sur les arbres sur pied, des échantillons de bois ont été prélevés après l'abattage des arbres, coupés en billons de 75 cm; un billon sur deux a servi à constituer des disques et des échantillons de copeaux. Les disques situés tous les 1,50 m le long de la tige ont été utilisés pour obtenir la densité de l'abre entier, les estimations de pourriture et de coloration. Les copeaux obtenus à partir de chaque billon de 75 cm ont été mélangés pour chaque arbre et deux cuissons ont été faites avec un cuiseur de 44 litres modifié.

Les valeurs de l'indice de permanganate et du rendement ont été obtenues à partir de chacune des cuissons. Les estimations normalisées de TAPPI ont été établies pour chacune des deux cuissons de chaque arbre. Les données pour les qualités des feuilles de papier comprenaient la résistance à la tension, le coefficient de déchirure, le coefficient d'éclatement, la valeur de formation et la densité apparente. Les analyses de variance et les rapports des variances ont été calculés pour obtenir des estimations de l'héritabilité au sens large. On a également établi des corrélations simples en prenant comme variables un certain nombre de propriétés du bois, de la fibre et de la pâte. Les résultats des comparaisons établies ci-dessus peuvent être résumés comme suit:

1. Pour la longueur des fibres, la résistance des fibres, le volume d l'arbre, le volume de la couronne, l'influence de l'hérédité paraît relativement faible. Par contre, la den-

sité semble beaucoup plus que les caractères précédents contrôlée par l'hérédité.

2. Les dimensions et la forme des feuilles diffèrent beaucoup d'un clone à l'autre et sont sous une forte dépendance héréditaire.

3. Les différences de rendement en pâte entre les clones sont nettement significatives et les rapports de variance obtenus suggèrent la possibilité d'une amélioration génétique du rendement en pâte.

4. On a relevé des différences nettement significatives entre les clones pour les qualités des feuilles de papier (résistance à l'éclatement, coefficient de déchirure et résistance à la tension). Les rapports de variance suggèrent un contrôle génétique assez fort pour une ou plusieurs des propriétés fondamentales des fibres qui influencent la qualité des feuilles de papier.

5. On a trouvé une corrélation significative entre la longueur des fibres mesurées sur les prélèvements à la tarière et la résistance à la tension, la déchirure et l'éclatement des pâtes faites avec l' arbre entier.

6. La résistance des fibres mesurées par la résistance à la tension «zéro-span» est reliée (au seuil de probabilité de 1%) avec la résistance à la tension, la déchirure et l'éclatement, ce qui permet d'entrevoir la possibilité d'utiliser des mesures «zéro-span» pour l'estimation des pâtes et pour classer les arbres sélectionnés.

7. Il existe une corrélation négative entre la croissance en volume et les résistances à la tension, les coefficients de déchirure et d'éclatement; il est donc nécessaire de sélectionner de manière indépendante ces deux groupes de caractères.

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(Aus dem Institut für Forstgenetik und Forstpflanzenzüchtung in Schmalenbeck der Bundesforschungsanstalt für Forst- und Holzwirtschaft)

Individuelle Reaktion einjähriger Kurztriebnadeln von Pinus silvestris L. auf Befall durch Lophodermium pinastri (Schrad.) und Phoma acicola

Von W. LANGNER

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SCHÜTT (1957) konnte zeigen, daß deutliche Unterschiede im Grad der Anfälligkeit verschiedener Klone von *Pinus silvestris* gegenüber *Lophodermium pinastri* bestehen. Zweijährige Pfropfklone von stark befallenen und nicht bzw. wenig befallenen Auslesekiefern aus 4- bis 6jährigen Kiefernkulturen erwiesen sich nach künstlicher Infektion in ähnlicher Weise anfällig wie die Auslesekiefern.

Nachfolgend wird ein Versuchsergebnis mitgeteilt, das zeigt, wie auch durch das Zusammenwirken von *Lophodermium pinastri* mit *Phoma acicola* Unterschiede im Anfälligkeitsgrad vorgetäuscht werden können. Außerdem bewirkt diese gemeinsame Infektion mit *Phoma acicola* eine bisher noch nicht beobachtete rasche Entwicklung von *Lophodermium* vom Zeitpunkt der Infektion bis zur Fruchtkörperbildung.

Es handelt sich um Sämlinge und Pfropflinge im Quartier, Mittelblock des Schmalenbecker Infektionsgartens (LANGNER 1951, SCHÜTT 1957). Unter sämtlichen Pflanzen dieses Quartiers, insgesamt 49 Klone mit 391 Pflanzen und 6 Sämlingspopulationen mit 212 Pflanzen, waren im Juli/August 1959 apothecienbildende tote Kiefernnadeln gestreut worden, so daß im Frühjahr und Sommer 1961, in großer Gleichmäßigkeit über das Quartier verteilt, genügend Infektionsmaterial in Gestalt abgetöteter Nadeln mit Apothecien vorhanden war. Am 30. 7. 1961 wurde eine Bonitur der Kiefern dieses Quartiers durchgeführt. Dabei wurde festgestellt, daß die in der Vegetationsperiode des gleichen Jahres gebildeten Nadeln sämtlicher 9 Pflanzen des Klones R 64 als Folge einer Infektion mit *Phoma acicola* weißgraue Spitzen aufwiesen. Am 1. 9. 1961 waren dann neben diesen Befallssymptomen auch extreme Schüttesymptome erkennbar *(Abb. 1).* Ebenso stark erkrankt waren auch 5 von insgesamt 47 Pflanzen der Einzelbaumnachkommenschaft 2980, während die übrigen Pflanzen dieser Population und der anderen 5 Nachkommenschaften praktisch gesund geblieben waren. Auch an den 5 erkrankten Sämlingen konnte nachträglich die vorher nicht beachtete weißgraue Verfärbung der Nadelspitzen festgestellt werden. Eine genauere Untersuchung ergab, daß die zahlreichen befallenen, aber noch am Zweige festsitzenden Nadeln bereits dicht mit Pykniden von *Lophodermium pinastri,* aber auch von *Phoma acicola*[1]) besetzt waren, und daß sich in einigen Fällen schon Apothecien von *Lophodermium pinastri* zu bilden begannen. Diese Apothecien wurden zahlreicher und entwickelten sich weiter *(Abb. 2).* Am 5. Okt. konnten an diesen Nadeln sporenwerfende

[1]) Für die Bestimmung des Pilzes danke ich Herrn Prof. Dr. ZYCHA und seinem Mitarbeiter Dr. BUTIN von der Biologischen Bundesanstalt für Land- und Forstwirtschaft, Institut für Forstpflanzenkrankheiten, Hann.-Münden.