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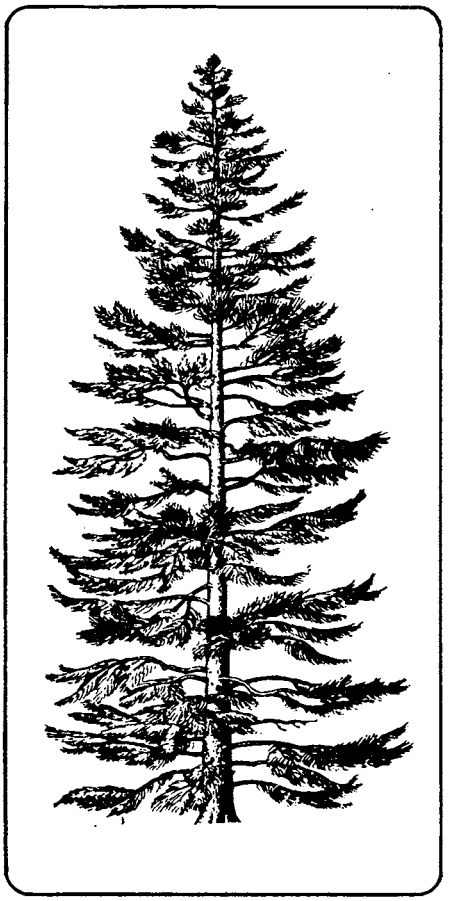

SEPTEMBER 12-13
1967

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Acknowledgements

The Eighth Lake States Forest Tree Improvement Conference, held at Madison, Wisconsin, on September 12-13, 1967, was an opportunity for tree breeders and forest genetics research workers representing Universities and private, State, and Federal organizations to exchange knowledge formally and informally.

The Forest Products Laboratory of the U.S. Forest Service was host. Program arrangements were the joint responsibility of Dean W. Einspahr, Institute of Paper Chemistry, Appleton, (Program Chairman and Vice Chairman of the Lake States Forest Tree Improvement Committee); Donald T. Lester, Department of Forestry, University of Wisconsin; and Harold L. Mitchell, Forest Products Laboratory.

During the first day, papers were formally presented. On the second day a guided tour was made through the Forest Products Laboratory, the University of Wisconsin Department of Forestry greenhouses, and the University outplanting sites in the vicinity of Madison. The meeting also provided the time and facilities for a meeting of the Tree Improvement Committee (NC-51) of the North Central Land Grant Colleges.

The Tree Improvement Committee wishes to thank the North Central Forest Experiment Station of the U.S. Forest Service for publishing these proceedings. The Committee also wishes to thank all individuals who contributed to the Conference, the men responsible for the organization and arrangement of the meeting, and the scientists who presented papers. Our special thanks go to Dr. Earl P. Stephens, Director of Forest Research, U.S. Plywood-Champion Papers, Inc., who presented a stimulating invited paper during the meeting. Dr. Stephens lectured on "Growing Cottonwood . . . Texas Style" without a manuscript. It has, therefore, not been possible to include his comments in the Proceedings.

J. W. Wright, Chairman
Lake States Tree Improvement Committee

Proceedings of the Eighth Lake States Forest Tree Improvement Conference, September 12-13, 1967

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VARIATION IN HEIGHT GROWTH AND GROWTH CESSATION OF 55 YELLOW BIRCH SEED SOURCES

Knud E. Clausen[1]

Yellow birch (*Betula alleghaniensis* Britt.) is an important hardwood species in the Lake States, northeastern United States, and eastern Canada. Since it produces valuable timber, the species is a logical candidate for genetic improvement. An understanding of the variation pattern in a species is, however, basic to any improvement program.

In 1963 the Institute of Forest Genetics, Rhinelander, Wisconsin, initiated a study of natural variation in yellow birch. This paper describes variation in height growth and growth cessation in 2-year-old seedlings grown from the material collected for this study.

Methods

Seed was collected in 1963 and 1964 with the generous assistance of many cooperators in the United States and Canada. Most of the 55 sources used in the study (fig. 1, table 1) include seed of 10 or more trees per stand. Exceptions are sources 3068, 2958, 2996, and 3001 which represent seed of one, four, eight, and eight trees, respectively.

On March 24-26, 1965, three seed lots of each source were sown in flats and covered with moist peat. The flats were kept at 35° F. in a cooler for 4 weeks and then moved to a lathhouse. When germination was complete the seedlings were given supplementary light and grown under long days (18 hours) until transplanted. The seedlings were transplanted into four randomized complete blocks in the Hugo Sauer Nursery at Rhinelander on July 22-28, 1965.

Height growth of 20 seedlings in each plot was measured at the end of the first and second growing season. First-year height is probably confounded with the long-day treatment and the effects of the transplanting; hence only second-year height growth is considered here. To determine when the plants stopped growing during the second year height growth of five seedlings per plot was measured weekly from July 6, 1966, until shoot elongation had ceased.

Results and Discussion

The average hight growth of the 55 seed sources during their second year was 122.3 mm, but the individual sources varied from a low of 86.1 mm to a high of 164.0 mm (table 1). Thus, the West Virginia source (2969) and the Lower Michigan source (2961) grew almost twice as much as Nova Scotia source 3065, which was poorest. All but four sources performed better than the local source (3298). The differences between the sources were highly significant (table 2), but much block variation was also present. The best block, for example, averaged 43 percent more height growth than the poorest one. The differences between the blocks appear to be partially related to their relative proximity to a windbreak, but may also be due to soil differences or other environmental factors.

The seed sources stopped growing an average of 7.2 weeks after July 6, the date of the first measurement, but individual sources varied greatly in time of growth cessation. Source 3243 from eastern Newfoundland ceased growth one week earlier than the average, while the Kentucky source (3294) remained active 1½ weeks later than the average (table 1). Thus, growth cessation of the sources took place over a period of about 2½ weeks or from about August 11 to August 28. The 14 sources which ceased growth at the same time as, or later than, the local source (3298) were all of more southerly origin than the local source. The differences between the sources were highly significant (table 2), and again there was significant variation between the blocks.

Correlation analyses showed that height growth of 2-year-old seedlings is apparently not correlated with latitude, longitude, length of growing season, annual precipitation, and average July temperature of the seed sources; furthermore, height growth appears to vary in a random manner. Although some of the variation between the sources seems to be due to differences in growth rate, these differences do not follow any consistent geographic pattern. Second-year height growth is also uncorrelated with growth cessation, and surprisingly, with first-year height. Whether the pattern of variation in height growth of yellow birch is actually random should become apparent with future measurements.

Growth cessation, on the other hand, is inversely correlated with latitude, directly correlated with average July temperature, weakly correlated with length of growing season and annual precipitation, and independent of longitude (table 3). Generally speaking, northern sources stopped growing earlier than southern sources, indicating photoperiodic control of growth cessation. This result agrees with previous work by Wang and Perry (1958) who reported that photoperiod controlled cessation of shoot elongation in yellow birch and paper birch (*Betula papyrifera* Marsh.).

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Table 1. — Origin, mean second-year height growth, and mean growth cessation of 55 yellow birch seed sources

Source no.	State or province	Degrees of-- Lat.	Degrees of-- Long.	Elevation (ft.)	Growing season (days)	Height growth (mm)	Growth cessation[1/]
3243	Newfoundland	47.2	53.4	50	110	117.9	6.15
3244	"	48.6	58.2	400	110	135.0	6.50
3241	Nova Scotia	46.6	60.5	100	120	146.0	7.10
3065	"	45.4	61.8	450	102	86.1	7.20
3242	"	44.8	65.2	650	130	117.8	7.05
3063	"	44.1	65.8	350	140	101.2	7.65
3068	New Brunswick	46.0	66.4	300	126	146.4	7.30
3066	"	47.4	65.2	300	130	131.4	6.85
3067	"	47.5	67.4	925	70	131.8	6.45
3001	Province of Quebec	49.2	65.1	300	135	95.6	6.25
2998	"	48.2	70.2	1000	107	108.4	6.40
2997	"	47.0	70.3	400	120	100.8	6.80
2999	"	47.4	72.6	1000	107	124.1	6.95
3000	"	47.5	75.0	1500	90	104.0	6.60
3002	Ontario	45.1	76.9	1000	115	136.3	7.20
3003	"	46.1	79.0	1000	115	117.2	6.95
3004	"	46.7	79.6	1000	115	119.8	6.95
3311	"	45.0	81.4	625	145	139.6	7.25
3309	"	47.5	84.8	1000	110	118.4	6.75
2977	Maine	44.8	68.6	250	142	109.8	7.30
2956	"	43.7	70.9	1000	130	96.5	7.25
2985	New Hampshire	44.0	71.4	1900	125	101.6	7.00
2986	"	43.5	71.4	1300	130	145.4	7.60
2982	Vermont	44.7	72.6	1250	115	124.5	7.25
2971	Massachusetts	42.7	73.2	1610	150	116.4	7.35
2980	New York	49.2	74.9	1620	111	130.6	7.40
2996	"	42.5	74.2	2100	135	129.4	7.35
2976	"	42.3	77.3	1300	145	150.6	7.75
2979	Pennsylvania	41.3	76.3	2300	150	132.3	7.35
3312	"	41.6	78.7	1800	120	158.4	7.75
2969	West Virginia	39.0	79.7	2200	145	164.0	8.15
3299	Virginia	37.8	79.1	3000	175	111.7	7.65
2959	North Carolina	35.7	82.3	5160	135	134.1	7.90
2973	Georgia	34.8	83.8	4700	185	111.2	7.35
2953	Tennessee	35.2	85.7	1740	180	115.0	7.90
2954	"	35.7	85.3	1420	185	90.2	7.50
3294	Kentucky	36.9	82.9	3600	180	142.5	8.55
2955	Ohio	39.5	82.5	830	165	131.0	7.65
2958	Indiana	38.3	86.5	700	165	118.7	7.35
2983	Illinois	41.9	89.4	680	164	112.3	7.45
3295	Iowa	42.4	93.1	1050	150	151.1	7.30
2961	Michigan	45.0	85.0	1000	110	163.8	7.55
2960	"	45.9	84.8	625	140	126.6	6.90
2978	"	46.7	87.9	1675	110	130.2	6.60
2987	"	47.0	88.7	1250	140	108.3	6.90
2968	Wisconsin	46.5	92.1	1150	140	123.6	6.80
3298	"	45.7	89.0	1710	110	96.1	7.45
3297	"	44.5	90.4	1100	130	125.1	7.50
2962	"	44.9	87.2	600	145	130.4	7.30
2963	"	43.1	88.4	900	165	114.0	7.00
2964	Minnesota	44.2	94.1	800	150	95.4	6.90
2965	"	47.2	95.2	1480	100	127.6	7.00
2966	"	47.6	92.5	1700	110	122.0	6.75
2967	"	47.8	90.2	1400	130	107.6	6.60
2957	Isle Royale, Michigan	47.9	89.1	750	120	101.2	6.65

1/ In weeks after date of first measurement, July 6, 1966.

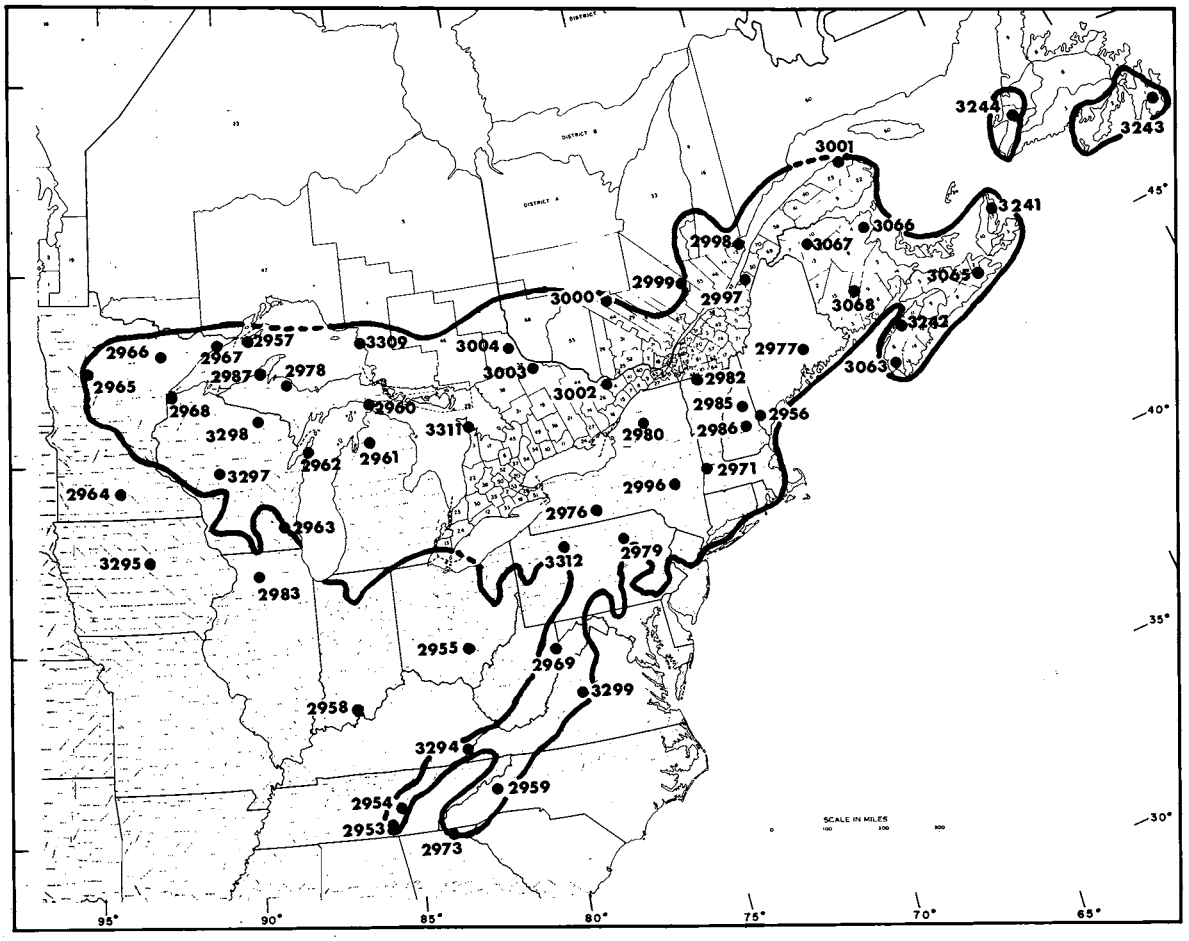

FIGURE 1. — Natural range of yellow birch adapted from maps in Fowells (1965) and Dansereau and Pageau (1966) and location of seed sources.

Table 2. — Analysis of variance of height growth and growth cessation of 55 yellow birch seed sources[1]

Source of variation	Degrees of freedom	Variance ratio (F) Height growth	Growth cessation
Blocks	3	34.39**	29.13**
Sources	54	2.53**	2.21**
Error	162	---	

1/ The analysis is based on plot means.

** Significant at the 1-percent level.

Table 3. — Correlation between height growth and growth cessation of 55 yellow birch seed sources and environmental variables of the seed sources

Environmental variable	Height growth	Growth cessation
Latitude	-.1206	-.7824**
Longitude	.0176	.2157
Length of growing season	-.0523	.5606**
Annual precipitation	.0704	.5168**
Average July temperature	.1031	.6274**

Conclusion

This study provides no evidence of clinal variation in height growth of yellow birch. On the other hand, certain seed sources grew much better or worse than others during the second year in the nursery; it would, however, be premature to consider them ecotypes. Since variation in height growth appears to be random over the natural range of this species, the amount of variation present within more limited geographic areas should be considered. In the Lake States region, for example, the difference between the best and the poorest seed sources was 34 percent for Minnesota, 36 percent for Wisconsin, and 52 percent for Michigan. When the 14 Lake States sources are compared as a group, the southern Minnesota source (2964) is 20 percent shorter and the Lower Michigan source (2961) 37 percent taller than the Lake States average. Thus, much potential growth may be lost if a slow-growing seed source is used for reforestation purposes. More intensive studies of local variation may be necessary in order to determine the pattern of variation associated with environment and to locate the fastest growing seed sources. Yellow birch exhibits much within-stand variation in fruiting characteristics (Clausen, 1967). If a similar pattern is present in growth characteristics, it is probable that certain trees will produce much faster growing progeny than others.

In contrast to the random variation observed in height growth, the study demonstrates that yellow birch exhibits clinal variation in growth cessation. This process is probably controlled to a high degree by photoperiod as it is in many other woody plants.

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SEED SOURCE VARIATION IN TRACHEID LENGTH AND SPECIFIC GRAVITY OF FIVE-YEAR-OLD JACK PINE SEEDLINGS

James P. King[1]

Jack pine (*Pinus banksiana* Lamb.) is widely used in Lake States reforestation because of its ability to make rapid early growth on relatively infertile sites. It is a major pulpwood producing species. Since the quality and yield of pulp are so strongly influenced by tracheid length and specific gravity, information on genetic variation in these characteristics would be useful in planning future jack pine tree improvement programs.

This study was done to: 1) measure tracheid length and specific gravity variation by seed source in the juvenile wood of jack pine; and 2) develop a basis for comparing wood quality variation by seed source in young seedlings with that in mature trees.

Material and Methods

A jack pine seed source test was established in the Hugo Sauer Nursery near Rhinelander, Wisconsin, in spring 1962. This test was initiated by Mr. M. Holst of the Petawawa Forest Experiment Station, Chalk River, Ontario, Canada. He arranged for the collection of seed from 100 natural jack pine stands located over the entire range of the species. The seed collections were distributed among a number of cooperators in Canada and the United States. Ninety-two of the collections are represented in the Rhinelander planting.

The seed was sown in a 5-replicate randomized complete block design. Ten contiguous seed spots of each source are contained in each replication. Each spot was randomly thinned to three seedlings at the beginning of the second growing season and to one seedling at the beginning of the third growing season. Chemical weed control, fertilization, and irrigation promoted vigorous growth.

At the end of the 1966 (fifth) growing season when the test was to be terminated, 34 sources were selected for measurements of tracheid length and specific gravity (fig. 1). For each source, 5 trees of each of the 5 replications were sampled; i.e., 25 trees per seed source or a total of 850 trees.

After considering concepts discussed by Richardson (1961) and Dinwoodie (1961), we decided that, to compare trees, wood samples must be taken at a common internode and common growth ring for all trees. Thus, all samples were taken from the center of the lowest 1964 internode (jack pine is multinodal). A piece of the main stem 3 to 5 centimeters long was cut from each tree and debarked. The entire cross-section (1964, 1965, and 1966 wood) was used for specific gravity determination, but only the outermost portion of the 1966 summerwood for tracheid length determination.

Specific gravity was computed as the ratio of ovendry weight to green volume (in metric units). Green volume was measured by the water-immersion method, and oven-dry weight was measured after drying the samples in a 105°C oven for 48 hours.

Small slivers were then chipped off around the outermost portion of the 1966 summerwood and put into vials containing equal volumes of 10-percent chromic acid and 10-percent nitric acid (Jeffrey's reagent). After about 26 hours, the macerated material was washed by decanting it several times with tap water. The tracheids were then mounted on temporary slides, and 30 to 40 whole tracheids per slide were measured by projecting the slides on a wall-mounted screen with a microprojector. Two of the replications were measured at magnifications of about 350 to 1; the other three at magnifications of 400 to 1. The magnification was recalibrated at least twice a day, and the microprojector was never moved unless an entire replication had been completed.

All the samples in this study were kept separate by nursery replicate. That is, the samples for an entire replicate were collected, weighed, dried, reweighed, macerated, and measured in random order before the next replicate was started. Thus, any variation due to experimental techniques would appear in analysis as between-replicate differences and would not seriously affect seed source comparisons.

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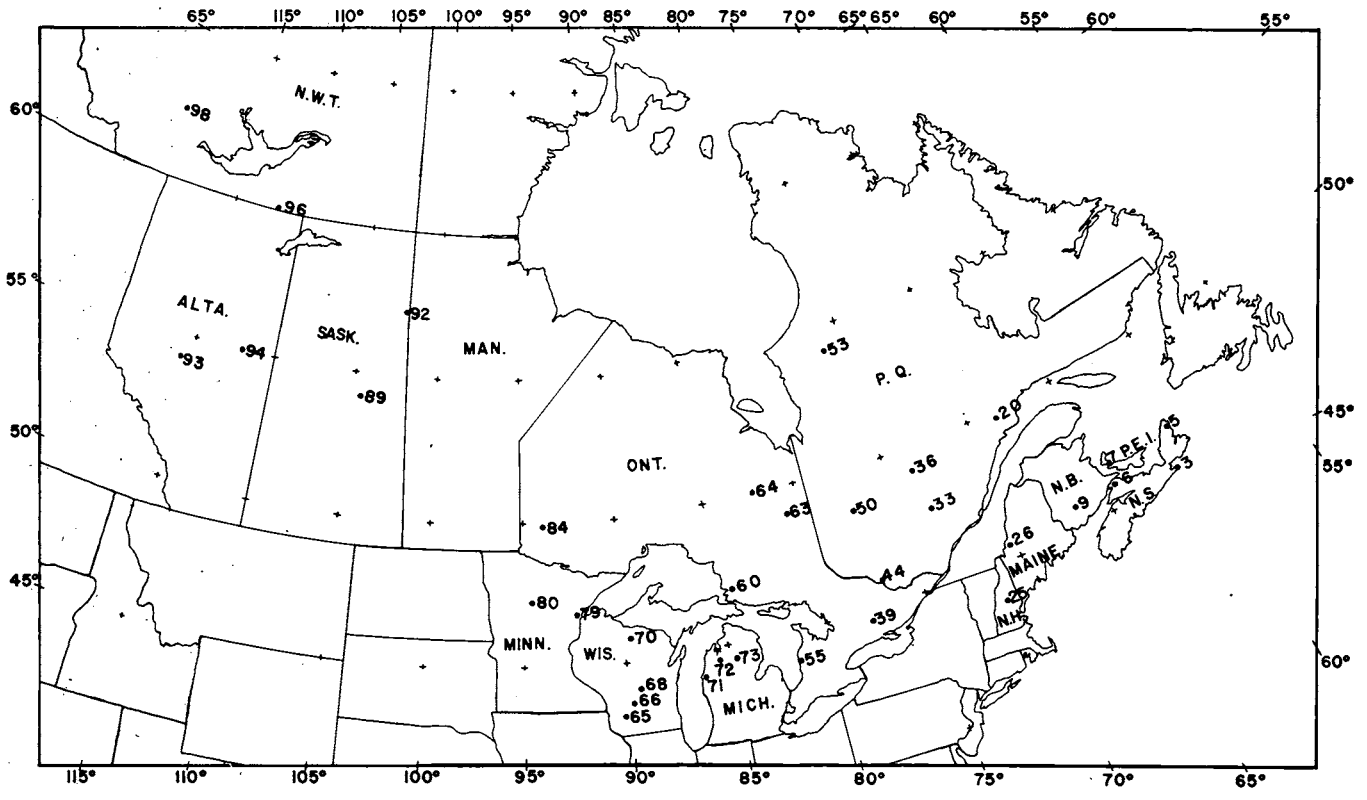

FIGURE 1. — Location of the 34 jack pine seed sources used in the measurement of tracheid length and specific gravity.

Results

There are real differences among seed sources in both tracheid length and specific gravity (tables 1 and 2). The mean tracheid length for all sources was 1.38 mm. The source from Fife Lake, Mich., had the longest tracheids; they averaged 1.62 mm — about 17 percent greater than the mean. The source from Reindeer Lake, Saskatchewan, had the shortest mean tracheid length — 1.12 mm or about 18 percent below the overall mean.

Considering only the nine seed sources from the Lake States, the mean tracheid length was 1.50 mm and ranged from 1.44 to 1.62 mm. The mean tracheid length for the Cloquet, Minnesota, source was 1.45 mm. This agrees well with a study by Kribs (1928) of natural-grown jack pine at Cloquet wherein the tracheid length of 3-year-old wood, one foot above the ground, averaged about 1.42 mm (interpolated from Krib's data).

The variation in specific gravity was less than that of tracheid length. Mean specific gravity for all sources was 0.350. The source at Reindeer Lake, Saskatchewan, had the highest specific gravity — 11 percent above the overall average — and the source at Fort Coulonge, P.Q., had the lowest — 8 percent below average. The average specific gravity of the nine Lake States sources was 0.339, and there were no significant differences between these seed sources.

In this material, strong positive correlations exist between mean seed source tracheid length, 1964 diameter inside bark, and 1964 shoot length (table 3). Strong negative correlations exist between mean seed source specific gravity and tracheid length, diameter inside bark in 1964, and 1964 shoot length.

Covariance analyses (table 4) indicated that seed source differences in tracheid length could not be entirely accounted for by variation in diameter inside bark or 1964 shoot length. Because of the high correlation between 1964 shoot length and the diameter inside bark, the effects of these two variables on tracheid length could not be evaluated independently. Specific gravity differences were also not entirely related to diameter and hence rate of growth.

In general, the more northerly sources had the slowest growth rate and therefore the highest

Table 1. — Mean tracheid length, specific gravity, 1964 shoot length, and 1964 shoot diameter inside bark of 34 jack pine seed sources

Number and location		Tracheid length	Specific gravity	1964 shoot length[1/]	Diameter (inside bark)[2/]
		Mm		Cm	Mm
03	Durell Island, N.S.	1.13	.384	14.4	14.6
05	Neils Harbor, N.S.	1.17	.376	21.2	15.7
06	Thomson Station, N.S.	1.38	.338	31.2	21.6
07	East Bideford, P.E.I.	1.46	.339	29.6	21.5
09	Grand Lake, N.B.	1.35	.351	32.7	22.1
20	Toulnoustook River, P.Q.	1.38	.348	27.8	20.2
25	Welch Mt., N.H.	1.31	.349	31.1	21.7
26	Spencer Lake, Maine	1.41	.337	31.7	22.8
33	Lake Valade, P.Q.	1.39	.338	28.2	23.3
36	Ducharme River, P.Q.	1.38	.351	27.3	22.6
39	Twin Lakes, Ont.	1.46	.347	35.5	24.7
44	Fort Coulonge, P.Q.	1.47	.321	43.1	26.2
50	Lac Villebon, P.Q.	1.39	.345	26.6	22.6
53	Kanaaupscow Lake, P.Q.	1.19	.379	10.4	12.6
55	Clark Point, Ont.	1.46	.350	29.8	23.0
60	Goulais River, Ont.	1.44	.341	31.3	23.3
63	Nellie Lake, Ont.	1.41	.335	28.6	21.9
64	Smoky Falls, Ont.	1.35	.363	20.3	18.4
65	Lone Rock, Wis.	1.45	.337	45.6	27.6
66	Wisconsin Dells, Wis.	1.55	.337	46.9	26.9
68	Waupaca, Wis.	1.51	.334	48.6	27.4
70	Nokomis, Wis.	1.47	.341	42.5	24.8
71	Freesoil, Mich.	1.49	.341	44.7	26.9
72	Fife Lake, Mich.	1.62	.340	46.8	26.2
73	Marl Lake, Mich.	1.51	.337	45.1	25.7
79	Cloquet, Minn.	1.45	.338	42.0	25.4
80	Cass Lake, Minn.	1.47	.343	39.8	25.8
84	Vermillion Bay, Ont.	1.39	.345	32.7	23.1
89	Nipekamew River, Sask.	1.28	.366	19.2	17.4
92	Reindeer Lake, Sask.	1.12	.389	11.0	11.9
93	Whitecourt, Alta.	1.30	.361	19.1	18.5
94	Lac la Biche, Alta.	1.32	.354	21.4	19.3
96	Fort Smith, N.W.T.	1.18	.368	12.5	13.3
98	Fort Simpson, N.W.T.	1.13	.375	11.5	12.9
Mean		1.38	.350	30.3	21.5
$S_{\bar{x}}$		.036	.0052	2.70	1.09

1/ Measured in the nursery to the nearest centimeter.
2/ Measured to the nearest millimeter.

specific gravity and shortest tracheids. There was one notable exception: The two sources from eastern Novia Scotia — relatively low-latitude sources for jack pine — were among the slowest growing. Sources from Wisconsin and Michigan were among the fastest growing and seemed taller as a group than those from southern Ontario, New Brunswick, Quebec, and New England to the east. The data suggest several east-west discontinuities in the jack pine population, but this may be the result of the low number of widely spaced seed sources used in this investigation. Any conclusions regarding population structure of jack pine must await the analysis of the growth data for all 92 sources in the major study.

Table 2. — Summary of analyses of variance of tracheid length, specific gravity, 1964 shoot length, and 1964 shoot diameter inside bark

Item	Source of variation		
	Replication	Seed source	Error
Degrees of freedom	4	33	132
Mean squares for:			
Tracheid length	.0552	.0789 **	.0065
Specific gravity	.00020	.00132 **	.00014
1964 shoot length	248.55	661.50 **	36.45
Diameter inside bark (1964 shoot)	54.42	105.74 **	5.91

** Significantly different at the 1-percent level

Table 3. — Correlation coefficients (r) between mean tracheid length, specific gravity, 1964 shoot length, and 1964 shoot diameter inside bark for 34 seed sources[1]

Characteristic	Tracheid length	1964 shoot length	Diameter i.b. (1964 shoot)	Specific gravity
Tracheid length	1.00	.91	.94	-.89
1964 shoot length		1.00	.96	-.85
Diameter inside bark (1964 shoot)			1.00	-.91
Specific gravity				1.00

1/ All values significant at the 1-percent level with 32 degrees of freedom.

Table 4. — Summary of covariance analyses; all F-values are significant at the 1-percent level

Dependent variable	Independent variable	Seed source F-value
Tracheid length	1964 shoot length	6.33
Tracheid length	Diameter inside bark	5.50
Specific gravity	Diameter inside bark	6.14

Setting the calculated mean squares from our analyses of variance equal to the expected mean square components (of a random effects model) and solving the components, we find that the between-stand genetic component in tracheid length variation is 2.3 times the error component. Since the error component contains the within-stand genetic variation plus measurement errors and within-plot environmental variation, clearly the between-stand genetic variance (for the seed sources represented here) is at least 2.3 times the within-stand genetic variance in tracheid length. Following the same procedure with specific gravity, we find that the between-stand genetic variance is at least 1.7 times the within-stand genetic variance in specific gravity.

Discussion

On the basis of the present study, selection of seed sources for higher specific gravity is apparently not feasible with trees of this age.

There are several reasons for this. First, the overall variation in specific gravity in juvenile wood is too low to allow any meaningful selection. If we eliminate from consideration the slow-growing sources from Nova Scotia and northern Canada and consider only those sources of potential use in a Lake States tree improvement program, we find only one seed source (from Fort Coulonge, P.Q.) that is significantly different from the remaining 22 sources. And this source is significantly lower in specific gravity than the rest. Moreover, the $LSD_{.05}$ is only 4 percent of the overall mean in specific gravity. It seems doubtful that an increased sampling intensity will increase the sensitivity of the test to the point where significantly higher specific gravity sources can be detected among the faster-growing seed sources.

Secondly, although there is a strong negative correlation between specific gravity and growth rate in this juvenile wood, Spurr and Hsuing (1954), after a comprehensive review of the literature, concluded that growth rate had only a minor effect on specific gravity in mature trees. Apparently, as the trees mature, factors other than growth rate assume an increasing importance in determining specific gravity. One such factor is summerwood percent which, in the southern pines (Larson 1957, Schafer 1949, and others), varies independently of growth rate. Attempts to determine the percent of summerwood in the present study were abandoned because of the small amount of summerwood present and because of the presence of false rings in many of the samples. Presumably the specific gravity of wood formed at an age when genetic variation in summerwood percent is evident would be more useful in predicting mature-tree specific gravity than is possible with the specific gravity of 3-year-old material.

The possibility of juvenile selection seems a little brighter for increased tracheid length than for specific gravity. If we consider only the fastest growing sources, we find several that have tracheid lengths significantly different from the others. The literature also suggests that as the trees mature: 1) the average seed source tracheid length will increase; 2) the differences between seed sources will increase; and 3) the source with the highest initial tracheid length may also yield higher tracheid lengths in older trees (Bisset *et al.* 1951, Dadswell and Wardrop 1960, Dinwoodie 1963). However, Dinwoodie's (1963) data on four Sitka spruce (*Picea sitchensis* (Bong.) Carr.) provenances showed that the ranking of the seed sources can shift with age, particularly among sources which did not differ greatly initially.

Thus, while proper seed source selection can result in increased tracheid length, selections based on very young material will probably result in a reduced genetic gain. The magnitude of this loss can only be determined by long-range studies.

Conclusions

1. Jack pine seed sources differ in tracheid length and specific gravity of 3-year-old wood.

2. In material of this age, strong positive correlations exist between mean seed source tracheid length, diameter inside bark, and annual height growth. Strong negative correlations exist between mean seed source specific gravity and tracheid length, diameter inside bark, and annual height growth.

3. With the widely diverse seed sources represented in this study, the between-stand component of genetic variation was much greater than the within-stand variation.

4. Seed sources from northern Canada and eastern Nova Scotia had the slowest growth rate, shortest tracheids, and highest specific gravity. Sources from Minnesota, Wisconsin, and Michigan had the highest growth rate, longest tracheids, and lowest specific gravity.

5. Tracheid length as estimated from 3-year-old wood may give a fair indication of mature-tree tracheid length when a wide range of genetic diversity is under investigation. Specific gravity of 3-year-old material is unlikely to be useful in predicting the density of mature trees.

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VARIATION IN BARK CHARACTERS AND WOOD SPECIFIC GRAVITY OF SUGAR MAPLE[1]

Robert L. Sajdak[2]

The external appearance of the bark of sugar maple (*Acer saccharum* Marsh.) has been described as "deeply furrowed," "fissured with long irregular thick plates or ridges," "somewhat scaly," "sometimes curling," and "highly variable." Adjacent trees in natural stands often have strikingly different external bark characteristics.

Gross variability in bark appearance is unusual within a species. In general, bark appearance is relatively constant, and any variability encountered is often a reflection of vigor. Indeed, some researchers consider external bark characteristics to be helpful in log and tree grading and quite reliable as an indicator of tree vigor (Burkle and Guttenberg 1952, Arbogast 1957). Kennedy and Wilson (1954) in studies of smooth and cork-bark alpine fir (*Abies lasiocarpa* (Hook.) Nutt.) show that a strong relationship exists between age and bark type for four diameter classes. The cork-bark type is consistently older.

The objective of this study was to investigate what relationships may exist between bark type, age, diameter, growth rate, and wood specific gravity in sugar maple.

Materials and Methods

Sixty-one trees were selected from an area of about 30 acres on Copper Range Company lands in Houghton County, Michigan. The stand is predominantly sugar maple and had been selectively logged twice. The site is a fairly uniform loamy sand, deep and well drained with no extreme topography. The stand was selected because it has a good diameter distribution, from 12 to 24 inches d.b.h., and considerable bark variation was noted throughout these classes. Measurements and stereophotographs were taken of the bark. Because of the difficulty in quantifying external bark characteristics, qualitative descriptions were also recorded.

One 8 mm increment core, extending to the pith, was removed from each tree at breast height. The position of extraction was random except for leaning trees; in these, the cores were extracted at right angles to the direction of lean. The cores were placed in water and stored frozen until processed in the laboratory.

The characteristics determined from these cores were: (1) Total age at breast height, (2) growth rate, by averaging the rings per inch for the last 3 inches of radial growth, and (3) wood specific gravity based on green volume and oven-dry weight for each inch of core from the pith outward.

Bark Classes

From many field observations and from a study of the bark photographs, four fairly distinct bark classes were defined:

Bark type 1. — This type is termed "platy" (fig. 1). It could be considered as typical and was most common in the sample. The bark plates are relatively flat and are much broader than the furrows. Occasionally the plates curl and the bark is firm. The furrows are relatively narrow and *V*- or *U*-shaped in cross-section. The furrows have a prominent vertical pattern and are usually ½-inch or less in depth.

Bark type 2. — This type is termed "corrugated" (fig. 2) and usually has a fairly uniform pattern. In large trees the bark resembles that of old-growth red oak (*Quercus rubra* L.). In smaller trees, it resembles white or green ash (*Fraxinus americana* L., *F. pennsylvanica* Marsh.). The bark has ridges and furrows of equal width and is quite firm. The ridge crowns are mostly rounded and the furrow bottoms are rounded or V-shaped in cross-section. The furrows have a prominent vertical pattern and are usually over ½-inch in depth.

Bark type 3. — This type is termed "shell bark" (fig. 3) and resembles somewhat the bark of jack pine (*Pinus banksiana* Lamb.) or black cherry (*Prunus serotina* Ehrh.). It is similar to the platy type, but the plates are of various sizes and often

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FIGURE 1. — Type 1 bark ("platy"). Tree is 22.6 inches d.b.h. at 142 years. Rapid growth rate.

FIGURE 3. — Type 3 bark, ("shell"). Tree is 14.4 inches d.b.h. at 129 years. Medium growth rate.

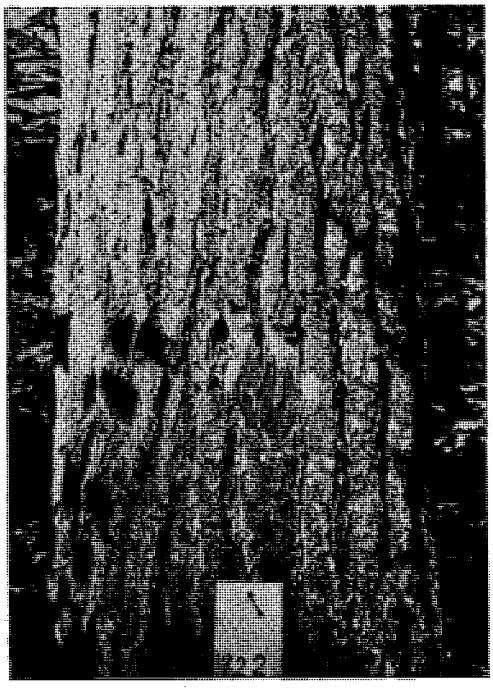

FIGURE 2. — Type 2 bark ("corrugated"). Tree is 20.8 inches d.b.h. at 227 years. Medium growth rate.

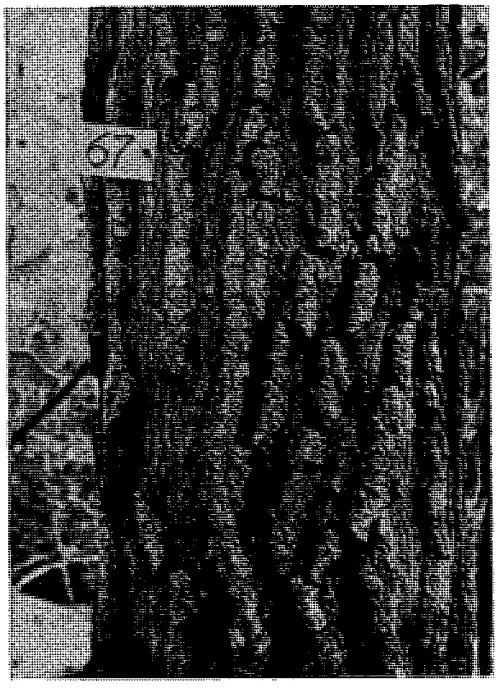

FIGURE 4. — Type 4 bark, ("ropy"). Tree is 11.5 inches d.b.h. at 83 years. Medium growth rate.

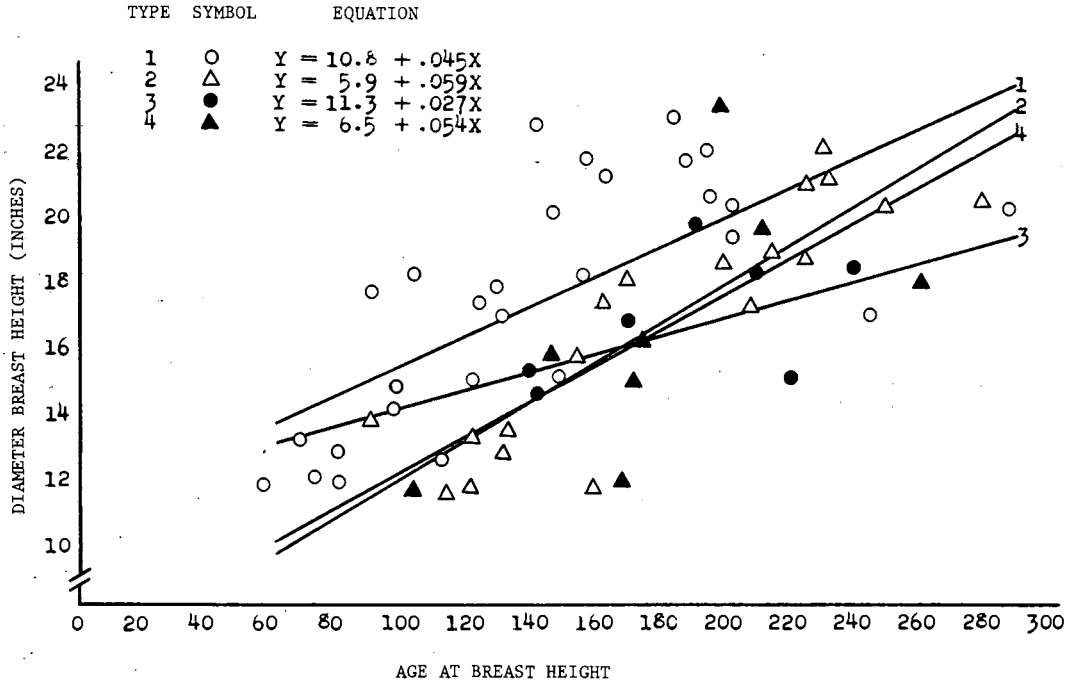

FIGURE 5. — Relationship between diameter breast height and age at breast height for four bark classes.

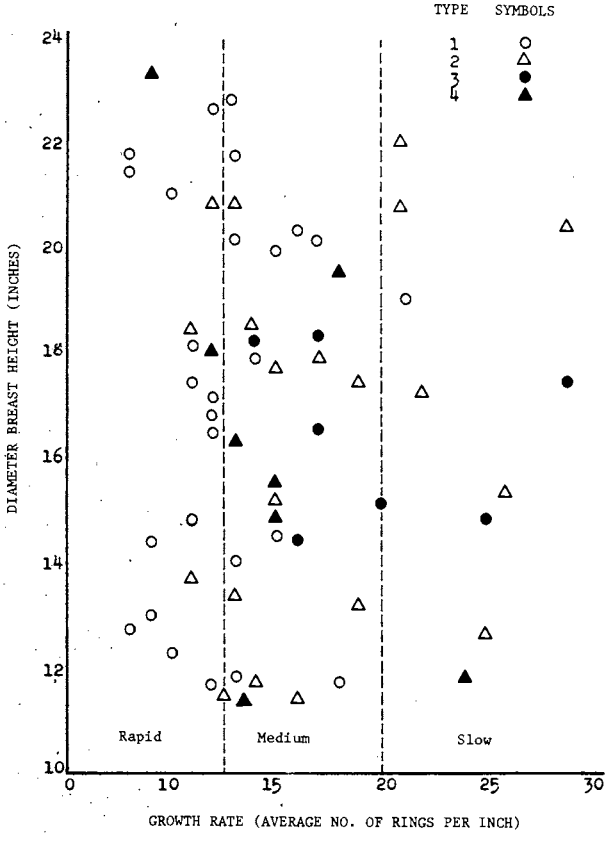

FIGURE 6. — Distribution of sample trees by d.b.h. and growth rate for four bark types. Growth rate is the average number of rings per inch based on the last 3 inches of radial growth.

overlapping. Crossbreaks are common. The furrows are of various depths and have very little vertical pattern.

Bark type 4. — This type is termed "ropy" (fig. 4). It resembles the common hackberry (*Celtis occidentalis* L.). It is similar to the corrugated type except the furrows are very broad and flat in relation to the size of the ridges.

Relationship of Bark Type to Diameter and Age

The relationship of bark type to diameter and age at breast height (fig. 5) indicates that trees with bark type 1 may be the most vigorous. The distribution also indicates that a diameter-limit cut has been practiced in this stand since no trees over 24 inches d.b.h. were found. This practice would tend to remove the more vigorous trees and thus the slope of the regression line for bark type 1 may be lower than in stands with no limit on diameter.

Since nearly one-half of the sample trees are of bark type 1 (N=28), the regression of this type was tested against the combined regression of bark types 2, 3, and 4 (N=34) by covariance analysis. The first step in this analysis is a test of parallelism of the two regression lines. This test was not significant at the 0.05 level. Having found no significant difference in slopes, the next test was to determine whether the regressions differ in level. This test was significant at the 0.01 level.

In figure 6, no relationship is indicated between

bark type and diameter, but a strong relationship is indicated between bark type 1 and the rapid growth rate class. Seventy-five percent of the trees in this class have bark type 1. These data also indicate that some large-diameter trees have a capacity for rapid growth rate.

Specific Gravity

The average specific gravity of the sample trees is .586 compared to .56 as reported in the Wood Handbook (1955) and .585 as reported by Paul (1963) based on samples from 70 trees from 12 stands in 8 states.

Bark type 1 trees tend to have slightly less dense wood (fig. 7); their mean specific gravity is 0.579 while the mean of trees with types 2, 3, and 4 bark is 0.591. Statistical analysis based on the *t* test for group comparisons indicates this difference is significant at the 0.05 level.

Specific gravity in relation to position at breast height (fig. 8) for all trees indicates a high specific gravity near the pith followed by a decrease, then an increase. This conflicts with reports by Lisboa (1961) and Webb (1964) who showed that in some diffuse-porous hardwoods (black willow (*Salix nigra* Marsh), sweetgum (*Liquidambar styracflua* L.) specific gravity is lowest near the pith, and increases and then decreases with age. In this study, however, variation in specific gravity was recorded by position in inches from the pith and not as a function of age. Variation in number of rings per inch was very large, ranging from 10 to 50 rings per inch for the position nearest the pith and from 4 to 65 rings overall.

Correlation coefficients were computed to determine if growth rate was related to specific gravity by position. At no position was a significant correlation obtained. The amount of variation explained by growth rate (rings/inch) at each position was very small, as shown by the coefficient of determination values (r^2) in table 1. This disagrees with Paul (1963) who found growth rate was related to specific gravity after the first or second inch from the pith in sugar maple.

Some of the differences found between this study and other reports may possibly be due to the occurence of mineral stain. Mineral stain in maple is difficult to differentiate from normal

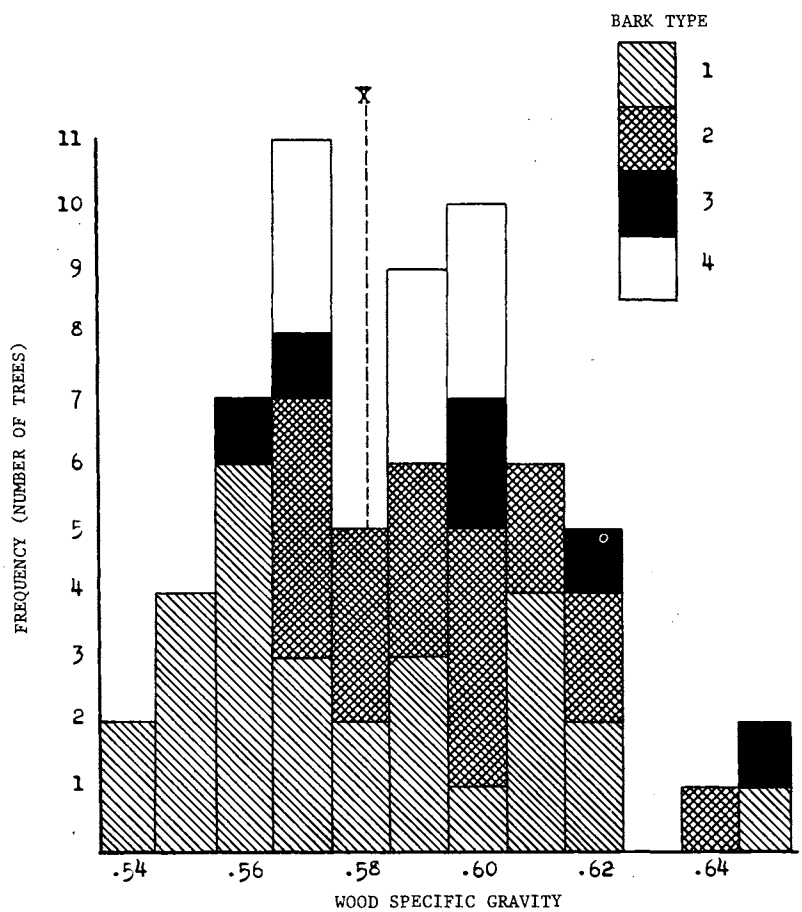

FIGURE 7. — Relationship of bark type and wood specific gravity.

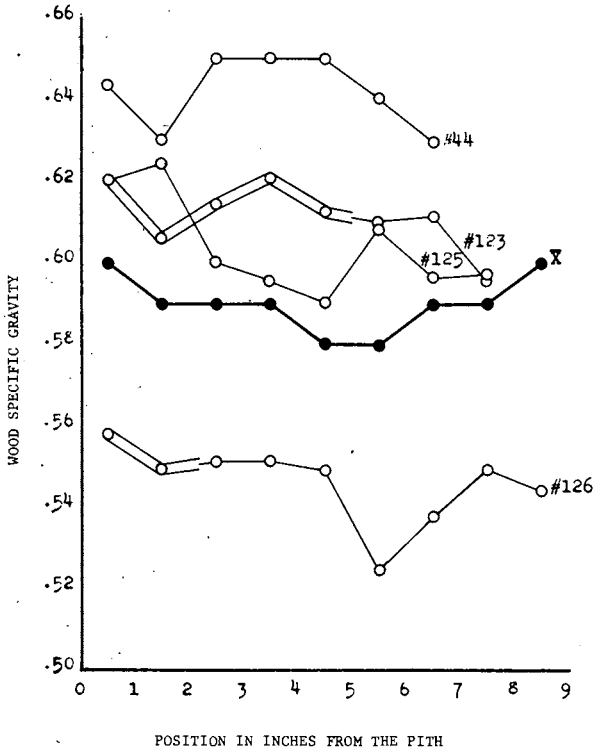

FIGURE 8. — Variation in specific gravity at breast height in relation to position for the average of all trees and for four selected individual trees. The double lines indicate the amount of heartwood.

heartwood. It occurs in the heartwood and in scattered pockets in the sapwood and thus may increase the specific gravity by a significant amount (Good *et al.* 1956, Seidel 1948). Future studies of specific gravity in sugar maple should take mineral stain into consideration, perhaps by ashing the wood and subtracting the weight of ash from the oven-dry weight of the wood.

Summary and Conclusions

The trees in this study were selected because they had a definite bark appearance. It must be stressed, however, that the variation in sugar maple bark is usually continuous; gradations among the four types given here were found on the study area.

The single most consistent indicator of tree vigor as found in bark appearance is the thickness of the outer bark or the depth of furrows. The furrows must be in a prominent vertical pattern and the plates firm.

Bark types are not common to a particular diameter group. Slightly more than one-half the bark type 1 trees are growing at a rate of less than 13 rings per inch as averaged over the last 3 inches of radial growth.

Specific gravity based on the average of 61 trees in a 30-acre stand closely agrees with the average as reported from 12 stands in 8 states. Growth rate and specific gravity are not correlated to a significant degree.

Table 1. — Coefficients of correlation between specific gravity and rings per inch

Position (in. from pith)	n	r	r^2
1	47	.030	.0009
2	58	.108	.0117
3	58	.145	.0210
4	59	.044	.0019
5	55	.023	.0005
6	45	.078	.0061
7	40	.207	.0428
8	23	.000	.0000

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SPECIFIC GRAVITY RELATIONSHIPS IN PLANTATION-GROWN RED PINE

Gregory Baker and James E. Shottafer[1]

Norway or red pine (*Pinus resinosa* Ait.) has been popular in Maine for forest planting because it will rapidly convert grass and weed cover to a forest floor and because it is relatively free from attack by insects and diseases. Since the first commercial thinnings consist of small-sized trees, the most logical market outlet is for pulpwood. Yield of pulp fiber by weight is directly correlated with the specific gravity of the wood. Consequently, several questions arise: What is the average specific gravity of plantation red pine of a given age? Can the tree specific gravity for young, plantation-grown red pine be predicted satisfactorily by the technique used in predicting tree specific gravity of mature, natural-grown red pine? How do some of the variables encountered affect specific gravity of red pine plantations of the same age?

A method of estimating tree specific gravity from increment cores taken at breast height has been reported in numerous publications and for several species of trees. In most cases the method has been applied to mature, natural-grown trees. A McIntyre-Stennis financed pilot study was initiated to test this method on young, plantation-grown red pine, and to study such other variables as could be measured without adding significantly to the cost of the study.

The Plantation

The stand from which the sample trees were selected was planted with 2-1 stock in 1941 and 1942. At the time of cutting, in 1964, the trees were 25 and 26 years old from seed. Five paired blocks 75x100 feet were planted with tree spacings of 2, 4, 6, 8 and 10 feet. In Area No. 1 thinning was to be done as required for good growth. Area No. 2 was left as a check. At the time of sampling, the 2-foot spacing in Area No. 1 had been thinned to 4x4 feet and the 4-foot spacing had been thinned to 8x8 feet.

Sample Tree Selection

Ten trees were selected from each of the 10 blocks. The criteria for selection were that they should have dominant or codominant crowns, single leaders, and no pronounced lean from the vertical — in brief, what might be considered good crop trees to bring to maturity. These trees were randomly selected from the stand, avoiding only the trees on the outer rows.

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Sample Collection

Tree diameter, total height, merchantable height (to a 4-inch top), and length of live crown were measured. Destructive sampling followed standard procedures:

1. Two increment cores at breast height. Random position of first; second at 90° to right.
2. Tree felled, cut into bolts 4.2 feet long.
3. Disks 2 inches thick cut from the top of each bolt and average diameter measured.

Laboratory Determinations

The increment cores were processed to determine specific gravity on a green volume-ovendry basis, and the values averaged for each tree.

The specific gravity of the disks was determined by the method developed by Heinrichs (1954).

Computations

Average weighted tree specific gravity was determined by averaging the specific gravity of the disks at each end of a bolt, multiplying the average by the volume of the bolt in cubic feet, totaling the values, and dividing by the total merchantable volume of the tree.

Average specific gravity of the disks at 4-foot height, 8-foot height, etc., was determined for each 10-tree group and for the entire 100 trees.

Analysis of Data

All data were transferred to IBM cards. A regression analysis was made to establish the equations for predicting average tree specific gravity from the specific gravity of two increment cores at breast height. Wahlgren *et al.* (1966) developed equations for predicting tree specific gravity from increment cores in natural-grown red pine stands. Setting Y equal to average tree specific gravity, and X equal to specific gravity of 2 cores, the equations are:

Plantation-grown: $Y = 0.20564 + 0.35193\ X$
$R^2 = 0.4089$
$F = 27.78$ which is significant to the 1-percent level

Natural-Grown: $Y = 0.20517 + 0.43648\ X$
$R^2 = 0.3780$

Since Wahlgren *et al.* sampled several age classes in the natural-grown red pine, they were able to introduce diameter over age into another equation with significant improvement in the predicting equation; the R^2 was 0.6831. The plantation red pine being of one age, this variable of age could not be used.

Figure 1 shows the two equations on the same graph. While the lines are nearly parallel, indicating a similar relationship between X and Y variables, it is obvious that two distinct populations are involved. The plantation-grown red pine had a mean specific gravity of 0.322 while the natural-grown red pine had an average tree specific gravity of 0.391. The regression line for Wisconsin plantation-grown red pine, reported by Maeglin (1966), assumes a quite different slope, i.e., tree specific gravity increases more rapidly with increase in core specific gravity than in the Maine studies.

Further work is planned to sample successively older plantations in Maine (to about 50 years) to study the effect of age on the regression equation.

Within-Tree Specific Gravity Variation

Within-tree variation in specific gravity has been studied in many species of trees, principally mature, natural-grown trees. In Wahlgren *et al.* (1966) the generalized pattern of specific gravity of the cross-section was a decrease with increased height above the ground for red pine. Maeglin (1966) in his study of red pine plantations in Wisconsin concluded that, except for age differences, the data from plantation-grown red pine of Wisconsin appeared to agree with that of the natural-grown red pine of Maine (fig. 2).

A different pattern of specific gravity distribution vertically in the tree was found in the 25-year-old plantation in Maine. Several groupings of the data were made:

1. Data from all trees (100) were averaged and plotted. This graph (fig. 3) shows a distinct drop in specific gravity from the 4-foot to the 8-foot

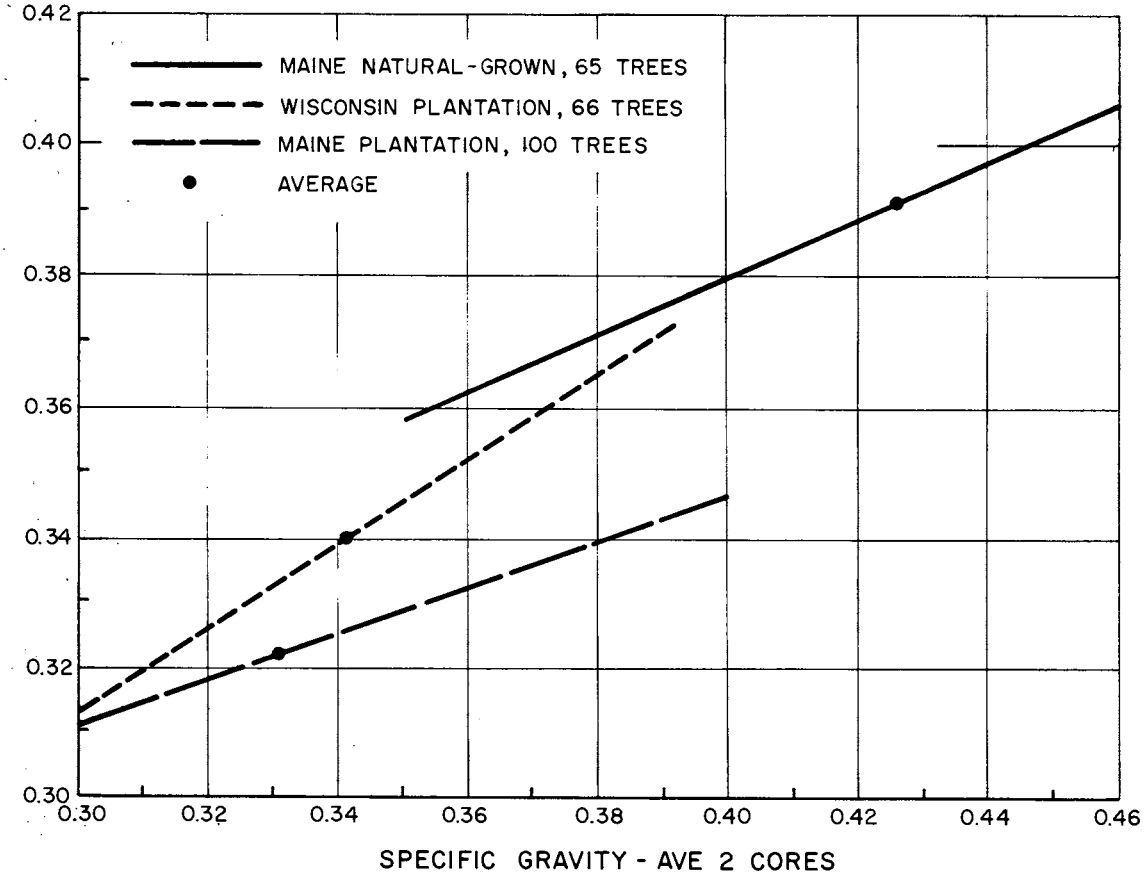

FIGURE 1. — Relationship of core specific gravity to tree specific gravity for red pine. Maine data for natural grown pine from Wahlgren *et al.* (1966); Wisconsin data from Maeglin (1966).

height and then a gradual but consistent increase in specific gravity upward in the tree.

2. Data were grouped by merchantable height classes so that at each level above the ground there were the same number of samples.

a. The data from the shortest merchantable height class (16.8 feet) when plotted show a consistent increase in specific gravity with increase in height.

b. The 21.0-foot and 25.2-foot classes show the same pattern as the all-tree graph.

c. The 29.4-foot class, which was represented by only 3 trees, shows a drop in specific gravity to the 8-foot and 12-foot level, followed by an increase in the 21-foot height and then a leveling off of specific gravity values to the 29.4-foot level.

3. Analysis by tree-spacing blocks of 10 trees each. Here, examination of the data for the two extremes of spacing, 2x2 feet and 10x10 feet, of the check blocks (no. 2 planting) gives the following comparisons:

Average —	*2-foot spacing*	*10-foot spacing*
Diameter (b.h.) inches	4.80	6.90
Total height, feet	34.00	30.00
Merchantable length, feet	20.20	18.50
Volume to 4-inch top, cu. ft.	1.83	2.97
Length of live crown, feet	15.50	22.20

In the 2-foot spacing there is a continuous drop in specific gravity from breast height to a 4-inch merchantable top. This pattern is similar to that found in natural-grown red pine in Maine (Wahl-

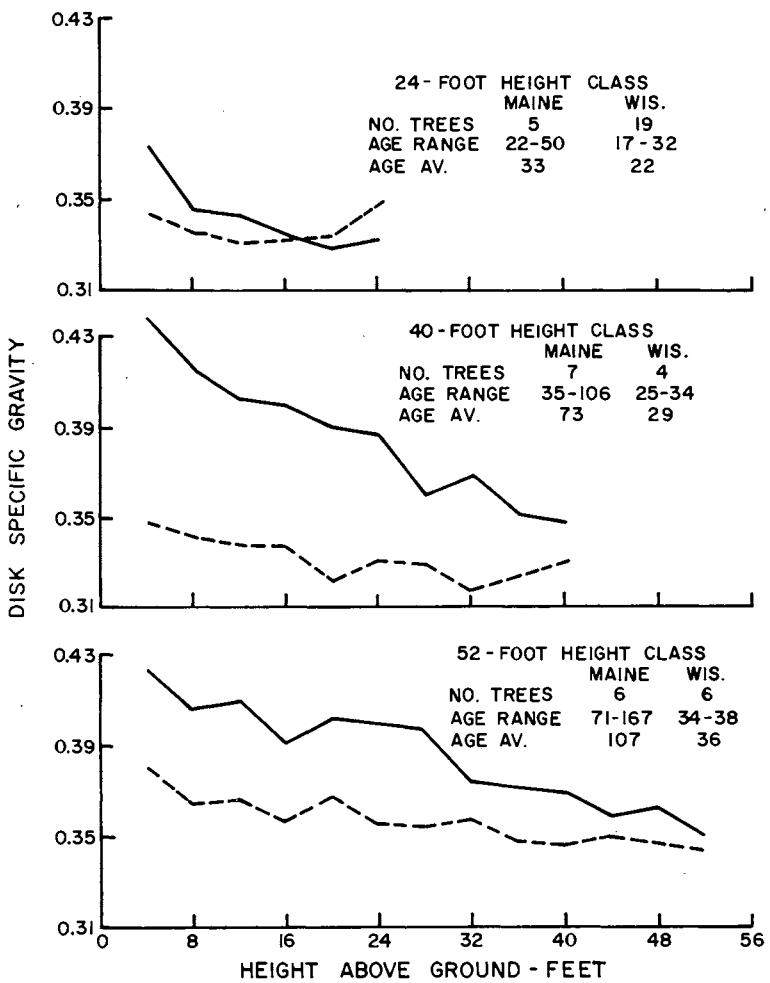

FIGURE 2. — Relationship of three height and age classes to disk specific gravity for red pine. Maine data on natural-grown red pine (solid line) from Wahlgren *et al.* (1966); Wisconsin data on plantation-grown red pine (broken line) from Maeglin (1966).

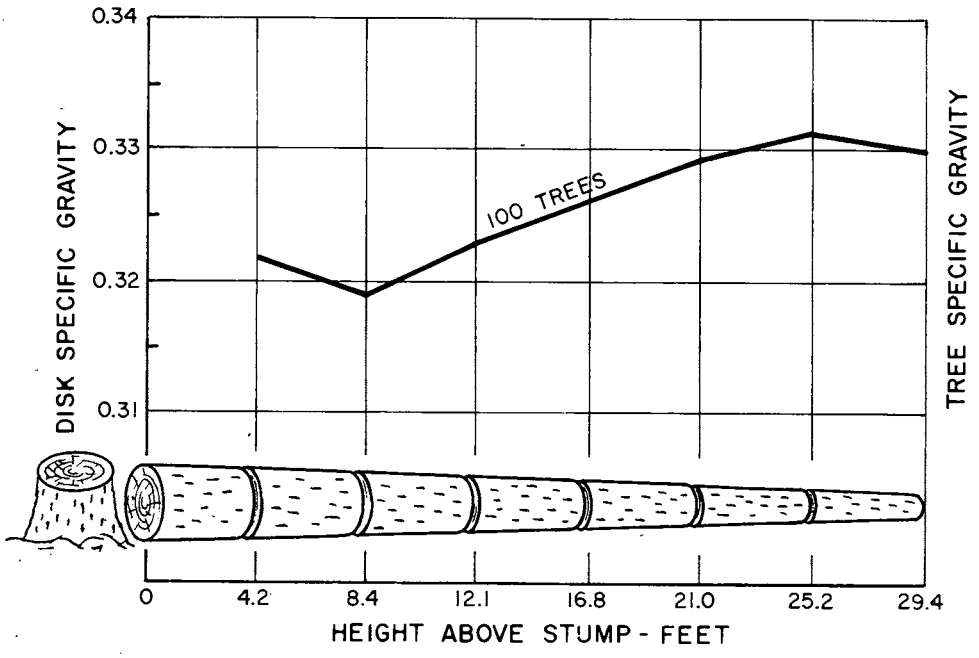

FIGURE 3. — Average specific gravity at various heights above stump for red pine.

gren *et al.*, 1966), although the average values are lower (average tree specific gravity 0.325 vs. 0.391) (fig. 4). In the 10-foot spacing, however, the above pattern was reversed, i.e., specific gravity *increased* from breast height to merchantable top (average tree specific gravity 0.318).

Since the tree age is the same in the two areas, the cause for these differences would appear to be in the growth and form of the trees. The trees in the 2-foot spacing have a smaller average diameter, greater total height with consequently less taper to the trunk, and a live crown average length which is shorter by nearly 7 feet.

This leads us to the tentative conclusion: When comparing plantation-grown trees of the same age, those which have been grown under severe crowding (close spacing) will have the least taper and the smallest diameter. They will average higher

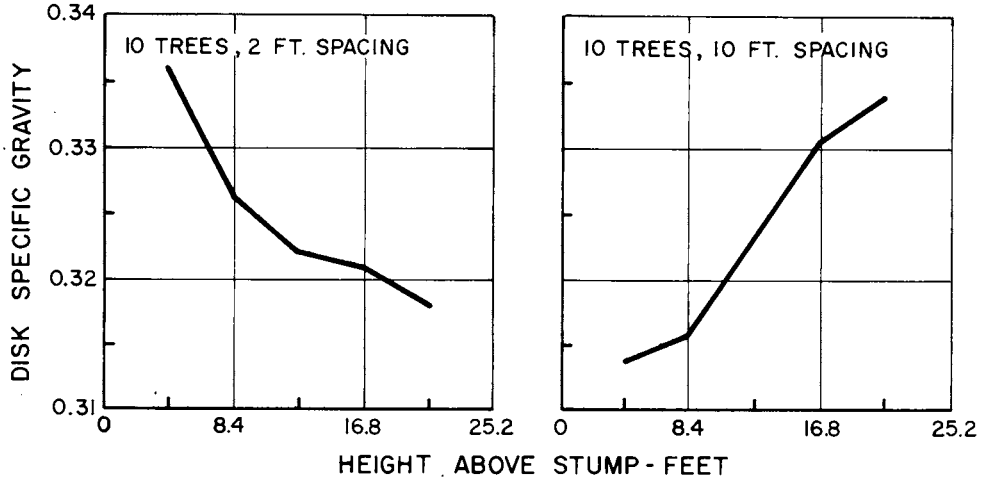

FIGURE 4. — Average disk specific gravity at various heights above stump for red pine.

in specific gravity, and the specific gravity will decrease with height above the ground. Conversely, trees grown at a wide spacing, with larger diameters, more rapid taper, and longer crowns, will average lower in specific gravity, and the specific gravity will increase with height above the ground.

Statistical analysis of the tree specific gravity data (Table 1) has indicated that in no case did a test block, or spacing group, differ significantly from its corresponding control block, unless treatment (thinning) had been involved. A linear trend toward significance was evident, with progressively wider spacings in the central area, until the 95-percent level was reached between the 2x2 and 10x10 blocks. The interaction between areas and blocks was far below any reasonable significance level, however, indicating a uniform response in both test and control areas to spacing changes.

The specific gravity of the trees in the 2x2 spacing that had been thinned to 4x4 was significantly higher than the 4x4 spacing that was thinned to 8x8. As noted above, this difference was not evident in the control blocks, nor was any difference between these blocks and the control blocks with original 4x4 and 8x8 spacing significant. A final comparison of all spacings 8x8 at the time of cutting (8x8 test, 8x8 test-thinned, and 8x8 control) did not indicate any significant differences in tree specific gravity. In all instances, the 95-percent level of significance was applied to the evaluation of the data.

Table 1. — Average tree specific gravity values for various spacings of plantation-grown red pine

Original spacing (ft.)	Area 1 (test)	Area 2 (control)
2x2	1/ 2/ 0.325	0.328
4x4	.321	.328
6x6	.325	.324
8x8	.319	.321
10x10	.318	.318
Area average	.322	.323

1/ Thinned to 4x4 spacing.
2/ Thinned to 8x8 spacing.

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PHOTOSYNTHESIS AND GROWTH OF SELECTED SCOTCH PINE SEED SOURCES[1]

John C. Gordon and Gordon E. Gatherum[2]

A number of problems related to the culture of Scotch pine (*Pinus sylvestris* L.) arose following the increased planting of this species in Iowa. Therefore, a program of controlled-environment experiments to determine the effects of genetic and environmental factors on physiological processes important to the culture of Scotch pine was begun by the Iowa Agricultural Experiment Station. We will report here the results of some of these experiments, done by ourselves and students of the junior author. Some of these results have been published elsewhere, and some have not.

As pointed out by Gatherum (1964), the two principal objectives of the controlled-environment studies are to (1) permit further identification and evaluation of within-species variation of physiological processes in Scotch pine seedlings, and (2) provide a clearer understanding of causes of variation in tree vigor and quality. Because photosynthesis and respiration may be viewed as the basic yield-determining physiological processes in plants, they were selected as dependent factors, measured by the variables CO_2 uptake and CO_2 evolution, respectively. Growth, as measured by the variables fresh and dry weight and stem and needle elongation, was also considered as a dependent factor in the studies to be reported. In making comparisons among treatments and in relating photosynthesis to growth, we defined the two additional dependent factors, photosynthetic capacity and photosynthetic efficiency. Photosynthetic capacity, as we use the term, is measured by the rate of CO_2 uptake of the entire aerial portion of the seedling. Photosynthetic efficiency, on the other hand, is measured by the rate of CO_2 uptake per unit of photosynthesizing foliage. Photosynthetic efficiency is, then, photosynthetic capacity divided by foliar quantity.

The independent factors we studied in relation to photosynthesis and growth were seed source, as indicated by the geographic origin of the seed from which the seedlings were grown, and several factors of the environment important in influencing the physiology of trees: photoperiod, temperature, nitrogen, and light intensity. The specific questions about Scotch pine that these studies were intended to answer were:

1. Does seed source affect photosynthesis and respiration?

2. Do seed source and environmental factors interact in their effect on photosynthesis and respiration?

3. How do the effects of these factors on photosynthesis and respiration relate to their effects on growth?

Materials and Methods

Although the Scotch pine seed sources used (table 1) represent a fairly wide range of latitude, they do not, either randomly or systematically, sample the entire native range of the species. Environmental treatments, when applied before measurement of CO_2 exchange, were carried out in the greenhouse. Environment was controlled during measurement of CO_2 exchange in a chamber described by Broerman *et al.* (1967). Rates of photosynthesis and respiration were measured by monitoring CO_2 uptake and evolution in a closed system with an infra-red CO_2 analyzer.

Results and Discussion

To bring together the results of the several studies, we discuss seed source in conjunction with each environmental factor studied. This is done for convenience, and is not meant to imply that

Table 1. — Scotch pine seed sources used, ISU studies

ISU no. and seed source	Latitude	Longitude	Elevation
	°N	°E	(Meters)
211; Finland	66	26	150
210; Finland	62	24	100
208; Finland	60	23	15
217; USSR	57	25	100
216; Poland	54	20	140
214; Czecho-slovakia	50	16	780
81; Germany	50	9	--
215; Czecho-slovakia	49	21	690
82; Austria	48	16	450
218; Bulgaria	42	25	1,220
113; Turkey	40	33	1,500
115; Turkey	40	31	1,400

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seed source influences CO_2 exchange and growth separately and independently with each of the environmental factors.

Photoperiod

We have not investigated the effect of seed source and photoperiod on photosynthesis directly. However, the effects of seed source and photoperiod on growth and development were studied in first-year seedlings by Jensen and Gatherum (1965). They demonstrated that seed source and photoperiod interact in their effect on height growth and needle elongation. The data indicated that photoperiod could be an environmental factor important in natural selection, since it definitely affected patterns of growth and differentiation in first-year seedlings. The ability of some sources to produce a greater quantity of foliage than others in response to a given photoperiod suggested a relationship between seed source and photosynthetic capacity.

Temperature

Temperature interacted with both photoperiod and seed source in its effect on height growth and needle elongation (Jensen and Gatherum 1965). It did not, however, interact with seed source in its effect on photosynthesis and respiration in second-year seedlings from three sources (208, 216, 214). It is possible that the parent climates of the three sources used in the photosynthesis study are similar enough in growing-season temperatures to preclude differential adaptation of the photosynthetic and respiratory processes to temperature. Additional controlled-environment experiments including more seed sources and more refined physiological measurement are needed before final conclusions about the interacting effects of seed source and temperature on photosynthesis and respiration can be drawn.

Nitrogen

In a study including five seed sources ranging from Bulgaria to Finland (218, 216, 217, 208) and five sand culture nitrogen levels (25 to 500 ppm), nitrogen and seed source had an interacting effect on shoot fresh weight, but not on dry weight, photosynthesis, or respiration (Dykstra and Gatherum 1967). Optimum nitrogen (approximately 400 ppm) increased photosynthetic capacity in all sources, but resulted in a slightly lower photosynthetic efficiency. Probably, part of the reduction in efficiency can be accounted for by mutual shading of needles in the larger-crowned seedlings produced at optimum nitrogen level. However, it is possible that biochemical differences in the distribution of assimilate within the needles also contributed to the reduction.

Light Intensity

Light intensity and seed source interacted in their effect on photosynthetic capacity in an experiment including fourth-year seedlings from four sources (81, 82, 113, 115) (Gatherum *et al.* 1967). Photosynthetic capacity increased with light intensity in the Austrian source up to the highest test intensity, while the German and Turkish sources appeared to reach light saturation (maximum capacity) at lower intensities (fig. 1). No differences in photosynthetic efficiency were observed. This suggests that the differential response to light among the sources was due to differences in quantity and arrangement of foliage, rather than to inherent biochemical differences in the photosynthetic process itself.

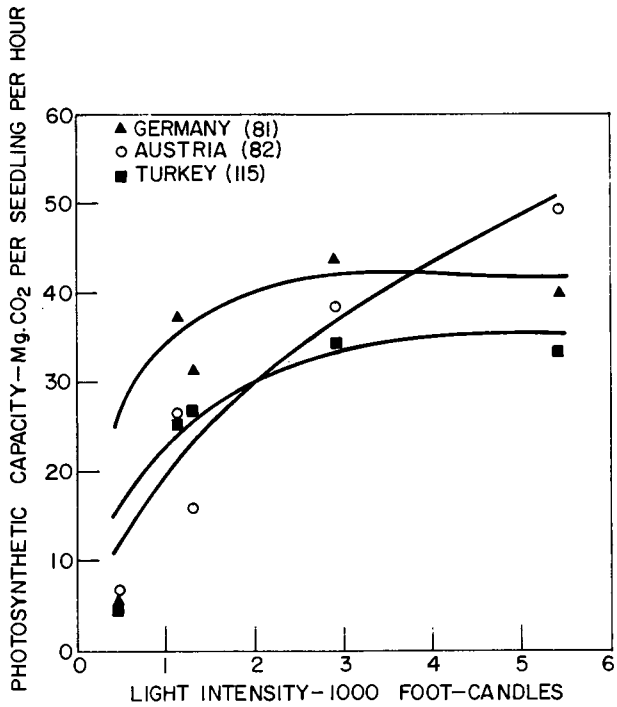

FIGURE 1. — Relationship between photosynthetic capacity and light intensity for fourth-year seedlings of three sources. ISU seed source number is shown in parentheses.

In a subsequent study of first-year seedlings that included eight seed sources (211, 210, 208, 217, 216, 214, 215, 218) and three light intensities (3,000, 6,000 and 9,000 foot-candles), photosynthetic capacity and efficiency both were influenced by the interaction of seed source and light intensity (fig. 2). The interaction appeared to be limited to the two most northerly sources. However, when second-year seedlings of three of the eight sources were tested at the same and at six lower light intensities, no differences in efficiency were

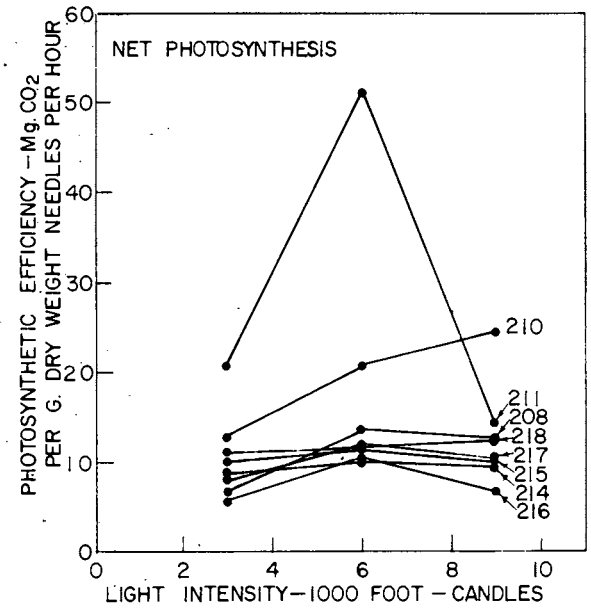

FIGURE 2. — Relationship beteen photosynthetic efficiency and light intensity for first-year seedlings of eight sources. The trend lines are identified at the right by ISU seed source number.

observed. But again, seed source and light intensity interacted in their effect on photosynthetic capacity.

Taken together, these results imply a basic difference in the photosynthetic properties of the crown between first-year and older Scotch pine seedlings. One probable cause of the difference is the presence of a high proportion of functional juvenile needles on first-year seedlings.

Photosynthesis and Growth

Differences among seed sources in photosynthetic efficiency, photosynthetic capacity, growth, and distribution of assimilate (dry weight) were observed in a study including first-year seedlings from eight sources. Photosynethic capacity and seedling height, fresh and dry weight were positively related. Photosynthetic efficiency, however, was inversely related to height, fresh and dry weight, and photosynthetic capacity (table 2). Seedlings that retained the lowest percentage of their total dry weight in their needles had the highest photosynthetic efficiency, and were from the northernmost sources (table 3). This relationship between high photosynthetic efficiency, low photosynthetic capacity and distribution of assimilate may be accounted for by (1) less mutual shading of needles on small-crowned seedlings or

Table 3. — Effect of seed source on percentage distribution of assimilate in first-year seedlings

ISU no. and seed source	Percentage of total dry weight in--		
	Needles	Stem	Roots
211; Finland	41	14	45
210; Finland	46	15	39
208; Finland	55	13	32
217; USSR	56	11	33
216; Poland	54	17	29
214; Czecho-slovakia	60	13	27
215; Czecho-slovakia	58	12	30
218; Bulgaria	58	14	28

Table 2. — Effect of seed source on fresh and dry weight and photosynthetic capacity and efficiency of first-year seedlings

ISU no. and seed source	Total fresh weight	Total dry weight	Photosynthetic capacity	Photosynthetic efficiency
	g.	g.	mg. CO_2/hr./seedling	mg. CO_2/hr./g. dry wt. needles
211; Finland	3.1	1.2	5.0	52.5
210; Finland	10.5	4.6	8.3	21.0
208; Finland	17.0	7.1	13.2	13.1
217; USSR	14.2	5.9	9.0	12.2
216; Poland	16.2	6.6	10.5	10.7
214; Czecho-slovakia	24.5	9.9	14.0	9.6
215; Czecho-slovakia	23.0	9.7	14.9	10.8
218; Bulgaria	18.9	7.7	11.2	12.0

(2) less deposition of storage and structural, non-photosynthetic compounds in the needles, or both. Higher photosynthetic efficiency also may be related to the greater contribution of juvenile needles to total needle weight of the seedlings of the northernmost sources. In any case, the higher photosynethic efficiency of these sources obviously does not represent any sort of "photosynthetic superiority" in the sense of more efficient total dry weight production.

Respiration and Growth

Rates of respiration per seedling and, under some treatments, per gram of needles, varied among seed sources in second-year and older seedlings. No differences in respiration per gram of needles were observed in first-year seedlings, but, as expected, larger seedlings respired more than small ones. The relationship of respiration to growth, in a sense, is more complex than that of photosynthesis. Presumably, any increase in rate of photosynthesis represents a potential increase in dry weight production. It is not true, however, that an increase in respiration necessarily decreases dry weight production. While substrate is oxidized to H_2O and CO_2 during aerobic respiration, and an immediate reduction in dry weight occurs, the chemical bond energy thus generated is necessary for growth processes. Thus, a high respiration rate accompanies the production of new needle tissue. The production of new needle tissue, in turn, can result in greater dry weight production through increased photosynthetic capacity. What should be avoided are seedlings and environmental conditions that result in "excess" respiration. This, however, is extremely difficult to define, let alone identify.

Conclusions

1. Seed source does affect rates of photosynthesis and respiration. However, our work has revealed no differences among sources in photosynthetic efficiency of seedlings older than one year.

2. Seed source and environmental factors can have an interacting effect on photosynthesis and respiration. More controlled-environment experimentation with more seed sources and wider ranges of environmental conditions is needed if the mechanisms of the interactions are to be understood.

3. Photosynthesis, respiration, and growth, as measured in these studies, are not related in a simple manner. A seed source exhibiting rapid growth does not necessarily have a high photosynthetic efficiency, as the term has commonly been used.

4. More physiological and biochemical research is needed if differences among sources in photosynthetic capacity, efficiency, and distribution of assimilate are to be satisfactorily explained. Ideally, such research should precede the use of photosynthesis and respiration characteristics in seed source selection.

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WOOD PROPERTY VARIATION IN POPULUS

Dean W. Einspahr, Miles K. Benson, and John R. Peckham[1]

The use of bigtooth aspen (*Populus grandidentata* Michx.), quaking aspen (*P. tremuloides* Michx.), and cottonwood (*P. deltoides* Bartr.) by the pulp and paper industry has increased greatly during the past decade. This expanded use has stimulated research on the genetic improvement of *Populus*. For the past 12 years an industry-sponsored aspen program has been underway at The Institute of Paper Chemistry (Einspahr and Benson 1964). One of its major goals has been the improvement of wood properties important to pulp and paper quality. During these 12 years a number of selected trees were evaluated and a number of studies have been completed in which wood, fiber, and pulp properties were obtained for individual trees.

This report summarizes wood property measurement data for several species of *Populus* and for both natural and artificially produced aspen hybrids. Although the nature of the data prevents any rigorous statistical treatment, comparable sampling and measurement techniques employed in the several studies permit useful comparisons between native species of *Populus* and the younger aged plantation-grown hybrids.

Materials and Methods

The older trees used in this comparison were growing in natural stands and either were selected for use as parent trees because of form and rate of growth or were randomly located trees that were being evaluated in studies of heritability or natural variation. Ten-millimeter, breast-high increment cores were used as a source of wood from the older trees. At least two cores were used in making the specific gravity and fiber length measurements, and additional cores were taken when micropulping information was determined.

The young trees used had been field planted as 1-0 stock and had grown in the test plantings for 5 to 6 years. These trees were cut, and disks or appropriate-sized wedges from disks were used in the evaluation work. The wood samples were located 16 to 32 inches above the ground and contained only those annual rings that developed after field planting.

Specific gravity determinations were run in duplicate, and the wood samples used for specific gravity were also the source of fibers for the fiber-length measurements. The fiber-length data reported for the 5- and 6-year-old trees were obtained on a ring-by-ring basis for the last three growth rings and were based on approximately 500 fibers from the fifth annual ring. All fibers 0.3 mm and longer including those cut, broken, and intact were measured.

The age-30 fiber-length measurements for the older trees were obtained by dividing the 10-mm increment cores into 5-year intervals, measuring 400 to 500 fibers per 5-year interval, plotting the fiber length-age curve, and taking the age-30 fiber-length value from the curve. For trees that were less than 30 years old, the fiber length for the last 10-year interval was determined and the fiber-length age information was adjusted to age 30, using a previously prepared fiber length-age curve. All fibers 0.3 mm and longer including those cut, broken, and intact were measured.

Information on pulp yield and fiber strength was obtained by micro-pulping small chip samples prepared from increment core or disk samples. Duplicate determinations were made upon the 5- and 6-year-old trees, and single determinations for all other trees. The micropulping procedure used employed a kraft pulping system and a multiunit digester (van Buijtenen *et al.* 1961). The techniques and the cooking conditions employed are reported in detail by Gardner and Einspahr (1964). The data on the percent yield of pulp are based on equivalent weights of wood in each digester. Zero-span tensile strength measurements were conducted on test handsheets, using the procedure described by Wink and Van Eperen (1962), and are interpreted as a measure of individual fiber strength. Alcohol benzene extractives and percent lignin were determined on wood samples using TAPPI standard methods T 6 M-54 and T 13 M-54.

Discussion of Results

Tables 1 and 2 summarize the results of the wood quality evaluation work with aspen and cottonwood carried on over the past 10 years. The greatest amount of evaluation work has been done with specific gravity, and the least number of

[1] *Respectively, Research Associate, Research Fellow, and Supervisor of the Pulping Laboratory, The Institute of Paper Chemistry, Appleton, Wisconsin.* *The authors wish to acknowledge: the financial support of this work by the Lewis W. and Maude Hill Family Foundation of St. Paul, Minnesota, and the ten pulp and paper companies who are members of the Lake States Aspen Genetics and Tree Improvement Group; the valuable assistance of Mrs. Marianne Harder for making many of the fiber-length and specific gravity measurements and helping to tabulate the data; and the help of Mrs. Susan Lebergen and Mr. W. Wink and members of the Paper Evaluation Group in evaluating fiber length and fiber strength.*

Table 1. — Wood and fiber properties of Lake States-grown Populus *and* Populus *hybrids*

Species[1]	Age, yr.	Specific gravity, g./cc.: Average[3]	Range	Fiber length, mm.[2]: Average[3]	Range	Zero-span tensile, lb./in.: Average[3]	Range
P. alba hybrids	18-30	0.392 (2)	0.389-0.394	1.10 (2)	1.00-1.21	--	--
	31+	.358 (4)	.334- .375	.99 (2)	.98-1.00	72.2 (1)	
P. deltoides	18-30	.363 (3)	.357- .372	1.10 (2)	1.05-1.15	--	--
	31+	.352 (10)	.336- .374	.95 (8)	.82-1.05	66.7 (5)	59.0-75.2
P. grandidentata	18-30	.363 (2)	.341- .385	.97 (3)	.94- .99	--	--
	31+	.378 (31)	.325- .433	.97 (40)	.77-1.18	72.9 (5)	67.7-81.8
P. tremuloides (3n)	31+	.391 (34)	.318- .447	1.23 (33)	1.02-1.37	56.9 (23)	48.6-65.9
P. tremuloides	18-30	.390 (123)	.310- .456	.97 (124)	.76-1.20	55.3 (5)	49.3-61.4
	31+	.390 (285)	.331- .476	.93 (283)	.62-1.19	60.5 (66)	49.4-76.7
P. tremuloides	5	.370 (554)	.311- .450	.67 (305)	.46- .94	65.5 (153)	56.2-75.4
P. tremuloides (3n)	5	.362 (72)	.342- .394	.65 (48)	.55- .76	61.8 (24)	56.6-66.5
P. tremuloides x P. tremula (3n)	5	.403 (70)	.347- .481	.75 (48)	.53- .88	61.0 (24)	46.9-77.2
P. tremuloides x P. sieboldii	6	.345 (9)	.318- .366	.72 (4)	.64- .85	61.2 (4)	57.2-64.2
P. tremuloides x P. davidiana	6	.340 (22)	.291- .374	.74 (8)	.70- .84	63.5 (9)	55.2-68.1
P. alba x P. grandidentata	6	.380 (5)	.344- .418	--	--	--	--
P. grandidentata x P. davidiana	6	.345 (12)	.312- .374	.76 (4)	.69- .81	63.7 (3)	60.8-67.2
P. grandidentata x P. alba	6	.373 (9)	.324- .441	.73 (4)	.67- .78	59.0 (4)	55.8-60.4

[1] The P. alba hybrids are naturally occurring hybrids in which the female parent is P. alba and the male parent is believed to be P. grandidentata. 3n indicates trees having three sets of chromosomes (triploids).

[2] Fiber length based on age 30 for mature, natural stand trees, and age 5 for plantation grown trees.

[3] Number in parentheses indicates number of individuals used to obtain the mean and range.

measurements involve lignin and extractive determinations. Comparison of data from wedges from young trees with increment-core data from older trees will tend to reduce slightly the differences between the two types of measurements. The reason is that the core samples weight the center of the tree more than the exterior portion so that the wood samples in this instance are more nearly alike (high in proportion of young wood) than usual.

Specific Gravity

Specific gravity, because of its influence on pulp yield and pulp properties and because it is influenced by cell wall thickness, relative proportion of latewood, proportion of thin-walled vessels, and the presence of reaction wood, is of interest from the tree improvement point of view. The specific gravity data were based on measurements of 1,245 trees. The majority of trees measured were either mature quaking aspen or 5-year-old plantation-grown quaking aspen. Because of the numbers of individuals involved, these data make reliable standards of comparison. Looking first at the mature trees, there appears to be no significant difference between the diploid quaking aspen "age groups" or between diploid and triploid quaking aspen. Bigtooth aspen specific gravity data, although based on fewer trees, seem to indicate that this species may have a slightly lower specific gravity than quaking aspen. It also appears

Table 2. — Pulp and chemical properties of Lake States-grown Populus *and* Populus *hybrids*

Species[1]	Age, yr.	Pulp yield, percent		Lignin, percent		Extractives, percent	
		Average[2]	Range	Average[2]	Range	Average[2]	Range
P. alba hybrids	18-30	--	--	--	--	--	--
	31+	51.5 (1)		20.4 (1)		3.8 (1)	
P. deltoides	18-30	--	--	--	--	--	--
	31+	51.2 (5)	50.5-52.7	22.4 (5)	22.0-22.9	2.1 (5)	2.0-2.2
P. grandidentata	18-30	--	--	--	--	--	--
	31+	51.2 (5)	50.0-52.8	20.3 (5)	20.0-20.6	3.0 (5)	2.7-3.3
P. tremuloides (3n)	31+	55.1 (24)	51.8-59.0	18.3 (24)	16.2-19.9	3.14 (24)	2.38-4.00
P. tremuloides	18-30	51.0 (3)	49.7-52.6	--	--	--	--
	31+	51.8 (61)	47.8-54.4	19.2 (1)		3.5 (1)	
P. tremuloides	5	48.8 (153)	43.6-52.4	18.1 (153)	15.7-20.4	4.64 (153)	2.70-16.7
P. tremuloides (3n)	5	48.2 (24)	46.6-50.2	17.2 (24)	16.6-17.9	6.32 (24)	4.98-7.90
P. tremuloides x *P. tremula* (3n)	5	48.8 (24)	46.8-50.4	17.2 (24)	16.3-18.2	5.38 (24)	4.76-6.37
P. tremuloides x *P. sieboldii*	6	48.0 (4)	47.2-48.9	19.3 (4)	18.4-19.8	4.56 (4)	4.30-4.93
P. tremuloides x *P. davidiana*	6	49.3 (9)	48.0-51.2	18.3 (8)	18.0-18.8	4.64 (8)	4.34-5.18
P. alba x *P. grandidentata*	6	--	--	--	--	--	--
P. grandidentata x *P. davidiana*	6	49.3 (3)	48.4-49.8	17.6 (4)	17.2-18.4	4.90 (4)	4.65-5.40
P. grandidentata x *P. alba*	6	50.1 (4)	49.2-50.7	18.0 (4)	16.9-19.2	4.45 (4)	3.93-4.94

[1] The *P. alba* hybrids are naturally occurring hybrids in which the female parent is *P. alba* and the male parent is believed to be *P. grandidentata*. 3n indicates trees having three sets of chromosomes (triploids).

[2] Number in parentheses indicates number of individuals used to obtain the mean and range.

that the specific gravity of cottonwood and the older *P. alba* hybrids is lower than quaking aspen. Comparison of the younger aged trees (5 and 6 years old) with the mature-tree specific gravity of 0.390 suggests only moderate decreases have resulted despite the relatively young age of the trees involved.

The young triploid hybrids (*P. tremuloides* x *P. tremula* triploid) had the highest average specific gravity of the trees evaluated, and the hybrids between *P. tremuloides* and *P. davidiana* had the lowest specific gravity. The fairly wide range in values reported suggests that the genetic improvement of specific gravity appears to be quite promising.[2]

[2] *Broad sense heritability for specific gravity in aspen has been estimated to be about 0.4 (Einspahr* et al. *1967a, and van Buijtenen* et al. *1962).*

Fiber Length

Fiber length influences a number of pulp strength characteristics and, particularly in the short-fiber hardwoods, longer average fiber length is generally accompanied by higher tear resistance and, to a lesser extent, increases in burst, tensile, and fold (Tappi 1960). Because of the importance of fiber length, parent trees and progeny groups have been evaluated and minimum standards established.

Using the fiber length of diploid quaking aspen (table 1) as a standard of comparison, it appears that bigtooth aspen, quaking aspen, and cottonwood have similar age-30 fiber lengths. Triploid quaking aspen has a fiber length approximately 28 percent longer than the native diploid species

mentioned above. The data for *P. alba* hybrids are too limited to judge adequately the fiber length of this material, but preliminary measurements indicate it is at least as good as that of the native quaking aspen.

The age-5 fiber lengths are, as expected, less than the age-30 fiber measurements. The several aspen hybrids all had average fiber lengths exceeding that of the diploid quaking aspen.

An earlier reported comparison of the age-5 fiber length of the triploid hybrids confirmed its superiority over that of diploid quaking aspen (Einspahr *et al.* 1967b). Despite the restricted number of measurements on the other hybrids, the fifth-year fiber length of several of the materials suggests that these hybrids can be expected to have fiber lengths longer than those of the native aspen. It is also of interest that the fifth-year data reported are approximately equal to the fiber-length averages reported for mature maples. Pulping work with these young aspen and aspen hybrids indicates they will yield pulps satisfactory for the types of papers presently being made from quaking aspen.

Zero-Span Tensile Strength

Zero-span tensile strength is a difficult measurement to make but when properly handled gives an average fiber strength value. Zero-span tensile strength has been shown to be positively related to the more conventional paper tests of burst, tear, and tensile strength and has the advantage that it can be made on a very limited amount of pulp. Because the absolute values obtained are influenced by cooking conditions, sheet formation, and other processing variables, fairly large differences (8 to 10 lb/in.) must exist between the averages in order for the differences to be meaningful.

Based upon earlier experience (Gardner and Einspahr 1964) with this test it seems unlikely that the zero-span tensile strength differences for the 5- and 6-year-old trees are statistically significant. Comparing the fiber strength of the older trees, bigtooth aspen and possibly cottonwood appear to have fiber strength values greater than diploid quaking aspen. A comparison of the young trees with the older trees reveals that the 5- and 6-year-old trees have higher zero-span tensile strength values, although it is doubtful that the differences presented are statistically significant.

Lignin, Extractives, and Pulp Yield

Because of the interrelationships between levels of lignin, extractives, and yield of pulp, these factors are considered together (table 2). Differences between types of materials in the above properties were not large except for the older triploid quaking aspen, which had the highest average pulp yield and relatively low levels of lignin and extractives. The 5- and 6-year-old trees had 2 to 3 percent lower pulp yield than the older bigtooth and quaking aspen. This reduced yield apparently resulted from the higher extractive levels present in the younger aged trees. Lignin levels in the younger trees were 1 to 2 percent less than in the older trees, but despite this lower level of lignin the overall pulp yields were less. The pulp yield and extractive and lignin levels for the younger aged trees are surprisingy uniform considering the differing genetic parentage. The somewhat reduced overall natural variation in the above chemical properties of aspen suggest that only limited gains can be expected if these properties are emphasized in tree improvement work.

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TRACHEID DEVELOPMENT AND WOOD QUALITY IN LARCH SEEDLINGS UNDER CONTROLLED ENVIRONMENT

J. J. Balatinecz and J. L. Farrar[1]

Several environmental factors necessary for tree growth undergo rhythmic and sometimes abrupt changes during the course of a year, and even during a day. Since wood cells are susceptible to outside influenees during their differentiation, certain fluctuations of environmental conditions invariably leave a permanent imprint on xylem anatomy, and hence significantly influence wood quality. Such features as the width of annual increments, cell length, cell diameter, cell wall thickness, and the development of drought and frost rings are affected by environmental factors to some degree. The effects of environment on xylem differentiation may be either direct or indirect, since xylem differentiation is integrated with other physiological processes in the living tree (e.g., photosynthesis, respiration, translocation) which are also subject to environmental influences.

In addition to genetic selection and breeding for desirable wood quality features, the manipulation of environmental factors (e.g., through irrigation, fertilization, and other silvicultural practices) offers man a limited but nevertheless important tool to influence the anatomy of developing wood cells, and hence wood quality. However, this can only be accomplished successfully if the inter-relationships between wood formation and environment are understood.

The effects of photoperiod on wood formation have been investigated extensively in recent years (Larson 1960, 1962, 1964; Phillips and Wareing 1958; Nitsch 1963; Wodzicki 1960, 1961, 1964). The current consensus is that photoperiodic effects on xylem differentiation are indirect, and are mediated by growth regulating substances. Long photoperiods are associated with intense cambial activity and earlywood differentiation, while short photoperiods favour latewood differentiation and eventual cambial quiescence. Under long days, the synthesis of auxins, gibberellins, and auxin synergists, which are generally regarded as growth promoters, is at a high level, while the synthesis of growth inhibitors is at a low level. The effect of short days on the metabolism of the above substances, on the other hand, appears to be opposite.

The effects of precipitation and the resulting soil and internal moisture conditions on wood formation have also been studied (Kennedy 1961; Kramer 1962, 1964; Larson 1963; Zahner 1963; Zahner *et al.* 1964; Edlin 1965; Buckingham 1965). Two hypotheses were developed to explain the influence of internal water stress on wood formation at the cellular level. According to the first view, water deficit has a direct effect on xylem development, in that a decreased turgor pressure may reduce the enlargement of differentiating xylem cells. The number of cambial divisions may also be reduced. According to the second view (Larson 1963), the effect of drought on xylem development is indirect. Water deficits first reduce the growth of terminal meristems and leaves which results in decreased auxin synthesis. The decreased auxin supply brings about the differentiation of latewood cells. Kramer (1964) and Zahner (1963) both emphasized that both the direct and indirect effects of water deficits were important in xylem development. The water balance of differentiating xylem cells influenced not only their enlargement but also their metabolism. Furthermore, water deficits reduced photosynthesis, and thereby the supply of carbohydrates. Kennedy and Farrar (1965) observed that drought caused subnormal lignification in tilted seedlings.

Reports about the influence of temperature on wood formation are relatively few. The available studies nevertheless suggest that temperature plays a very important role in wood formation. Richardson and Dinwoodie (1960) found an inverse relationship between cell wall thickness and night temperatures. Tracheid length and lumen diameter, on the other hand, increased with increasing temperatures, either day or night. They suggested that cell wall thickening was a function of net assimilation rate, which apparently dropped with increasing night temperatures.

Many of the aforementioned results were derived from experiments with seedlings because seedlings are easily obtained and subjected to various treatments. Most conclusions concerning basic physiological processes have general validity; however, many investigators caution against broad generalizations and unreserved interpretation of results for forest-grown trees.

This study examines certain effects of two different photoperiods on the initiation of cambial activity and subsequent xylem development in inactive and actively growing eastern larch (*Larix laricina* (DuRoi) K. Koch) seedlings; explores some influences of mild, intermediate, and severe drought conditions on xylem development; and

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evaluates certain effects of synthetic IAA and TIBA on xylem differentiation under short and long photoperiods, respectively.

Materials and Methods

Two-year-old nursery transplants of 132 eastern larch seedlings 40 to 60 cm tall and 5 to 8 mm in diameter at stem base were studied. The seedlings were transplanted into individual 500 ml containers, using Perlite rooting medium. The rooting medium was subirrigated with complete nutrient solution three times daily. The investigation was carried out in three phases.

Photoperiodic Treatments

First, the effects of two photoperiods (short days and long days) on the initiation of cambial activity and on subsequent xylem differentiation were studied in 96 seedlings. These seedlings were sub-divided into seven groups and exposed to either short days (SD), long days (LD), or both, for 12 weeks:

Group[1]	*No. of weeks exposed to—* SD	LD	*Number of seedlings*
1 (IC)	7	5	12
2 (IC)	0	12	10
3 (AC)	0	12	12
4 (AC)	12	0	24
5 (AC)	3	9	16
6 (AC)	5	7	12
7 (AC)	7	5	10

[1] IC = Inactive cambium at start of treatment; AC = Active cambium.

The short photoperiods were provided in a growth chamber regulated for 10-hour day length, 1,500 ft-c light intensity, and temperatures of 25° C day and 15° C night. Long photoperiods were provided in a greenhouse, where sunlight was supplemented with artificial illumination to obtain a 16-hour day length. Temperatures in the greenhouse ranged from 25° to 29° C during the day, and from 15° to 19° C during the night.

The cambia of seedlings in Groups 1 and 2 were inactive (IC) at the commencement of photoperiodic treatment. These seedlings had their winter chilling requirements met outdoors. However, the seedlings in Groups 3 to 7 had been actively growing (AC) and forming earlywood prior to treatment due to long-day exposures. Thus it was necessary to demarcate the commencement of treatment in these seedlings. All seedlings in Groups 3 to 7 were tilted for 3 days at 60° from the vertical, then put upright for 6 days, and again tilted for 3. This method had been employed by Kennedy and Farrar (1965) to produce two compression-wood marker arcs.

During the 12-week photoperiodic treatment the height growth of seedlings was determined at weekly intervals. At the same time the condition of apices, the appearance of needles, and the setting of resting terminal buds were observed.

The sampling schedule is outlined in table 1. From each seedling three stem pieces, approximately 2 cm long, were excised at 2, 10 and 20 cm from the stem base (lower, middle, and upper stem, respectively), and aspirated in FAA solution. Transverse sections were cut on a sliding microtome and stained by the safranin-fast green technique. All sections were examined microscopically for the pattern of xylem differentiation that accompanied the photoperiodic treatments. The radial and tangential diameters, and tangential double-wall thicknesses of all tracheids (matured after the commencement of treatment) were measured in five typical radial files. These measurements were taken only on sections from the middle stem of the 16 seedlings sampled at the end of 12 weeks. The radial files measured were selected on the basis of maximum tangential diameters to assure that tracheids in the files were cut close to their midlength. The values of tracheid diameters and wall thickness were used to calculate three indices. The cell enlargement index (CEI) was defined as the ratio between the radial (r) and tangential (t) diameters of the cell (r/t). The wall thickness index (WTI) was defined as the ratio between the tangential double-wall thickness (2w) and the tangential diameter (t) of a tracheid (2w/t). The specific gravity index (SGI) was defined as the ratio between the tangential double-wall thickness (2w) and the radial diameter (r) of a tracheid. Since tangential tracheid diameters vary but little from early- to latewood, the r/t and 2w/t ratios directly express the degree of radial enlargement and wall thickening, respectively. A CEI of 0.90 may be used as an arbitrary boundary between early- and latewood rather than Mork's index, which has been criticized by tree physiologists because it confounds wall thickness and radial lumen diameter, two cell features which may vary independently of one another.

Drought Treatments

Twenty actively growing, 2-year-old eastern larch seedlings were divided into four groups, with five seedlings in each group, and exposed to different watering conditions for 3 weeks. All seedlings were tilted prior to treatment, in a manner described previously, to induce two compression-wood marker arcs. One group was exposed to "mild" drought (200 ml water every 5 days), another to "intermediate" drought (100 ml water every 5 days), and another to complete drought (no water). The controls received normal watering by subirrigation. After a 3-week-long drought exposure, normal watering was resumed for all

Table 1. — Sampling schedule for the seedlings

Group	Sampling time (weeks after commencement of treatment)											
	1	2	3	4	5	6	7	8	9	10	11	12
	Number of seedlings sampled											
1	–	–	2	–	2	–	2	–	2	–	–	4
2	–	–	2	–	2	–	2	–	2	–	–	2
3	2	–	2	–	2	–	2	–	2	–	–	2
4	2	2	2	2	2	2	2	2	2	2	2	2
5	–	–	–	2	2	2	2	2	2	2	–	2
6	–	–	–	–	–	2	2	2	2	2	–	2
7	–	–	–	–	–	–	–	2	2	2	2	2

seedlings, and they were grown for an additional 5 weeks. During the entire 8 weeks the seedlings were in a greenhouse under long (16-hour) days. At the end of 8 weeks three stem pieces were excised from each seedling, sectioned, stained, and evaluated microscopically the same way as the samples from the photoperiodic experiments. The external responses of seedlings were also observed.

Treatments With IAA and TIBA

Sixteen actively-growing, 2-year-old eastern larch seedlings were divided into four groups, with four seedlings in each. Two groups (8 seedlings) were exposed to short days (10-hour) for 3 weeks to induce latewood formation, while the other two groups were tilted in the earlier described manner to induce two compression-wood marker arcs. One group (4) of the SD seedlings was treated with IAA, and one group of the LD seedlings was treated with TIBA in the following way. The dead outer bark was removed on a 2-cm portion of the stem of each seedling at a distance 10 cm from the stem base. Three shallow longitudinal blazes were cut into the inner phloem, each at 120° angle from the other, and extending to, but not beyond, the cambium. Immediately after the blazes were cut, the exposed surfaces were sprayed with distilled water. Then a single paper strip (3 sq cm), containing 50 micrograms of IAA or TIBA (50 micro-liters of 1000 ppm solution), was moistened with distilled water and placed over the inner phloem surface. The outer surface and edges were covered with lanolin, which was further covered with a dark masking tape. Controls of both SD and LD groups were also treated but the paper strip did not contain any compound. The SD seedlings remained in the growth chamber, while the LD seedlings were kept in the greenhouse for 3 weeks following treatments. At the end of 3 weeks, three stem pieces 2 cm in length were excised from each seedling, one immediately below the blaze, a second and third at 2 and 4 cm respectively below the blaze. The stem pieces were sectioned, stained, and examined microscopically, as described previously.

Results and Discussion

Photoperiodic Treatments

Growth activity in the buds and cambium of the seedlings in Groups 1 and 2 occurred under both short and long days. The buds of seedlings in Group 1 (initial SD) began swelling around the twelfth day, whereas those in Group 2 (LD) began around the ninth day. The growth of the new needles on the short shoots was nearly completed by the end of the third week in both groups; this coincided with the commencement of long-shoot extension and cell division in the cambial zone. However, by the end of the fifth week the SD seedlings were forming a terminal bud, and their average shoot growth (4.6 cm) was only half that of LD seedlings for the same period. The LD seedlings continued unabated shoot extension growth during the entire 12 weeks.

Swelling of the cambial zone occurred in both Groups 1 and 2 by the third week, indicating that this phase of cambial activity is not a photoperiod-dependent phenomenon, but rather correlated with temperature. Cell division in the cambial zone commenced around the end of the third week, coincidentally with rapid shoot extension, indicating a correlation and dependence of cell division in the cambial zone on endogenous auxins originating in active apical meristems.

The first-matured tracheids had CEI greater than 0.90 (earlywood) in the seedlings of both Groups 1 and 2 (figs. 1 and 2). The average CEI of the first 3-4 cells per radial file was 1.09 in both groups (fig. 7). However, the SD seedlings (Group 1) formed a narrow band of latewood cells (CEI less than 0.90), coincidental to the cessation of shoot extension (figs. 1 and 7). The formation of 3-4 earlywood tracheids per file under short days may seem surprising, but it took place during the short period of shoot extension growth when endogenous auxins were available in sufficient amounts to facilitate earlywood differentiation. The effects of short days only became apparent after the development of the photoreceptive organs (leaves).

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Group	Sampling time (weeks after commencement of treatment)											
	1	2	3	4	5	6	7	8	9	10	11	12
	Number of seedlings sampled											
1	–	–	2	–	2	–	2	–	2	–	–	4
2	–	–	2	–	2	–	2	–	2	–	–	2
3	2	–	2	–	2	–	2	–	2	–	–	2
4	2	2	2	2	2	2	2	2	2	2	2	2
5	–	–	–	2	2	2	2	2	2	2	–	2
6	–	–	–	–	–	2	2	2	2	2	–	2
7	–	–	–	–	–	–	–	2	2	2	2	2

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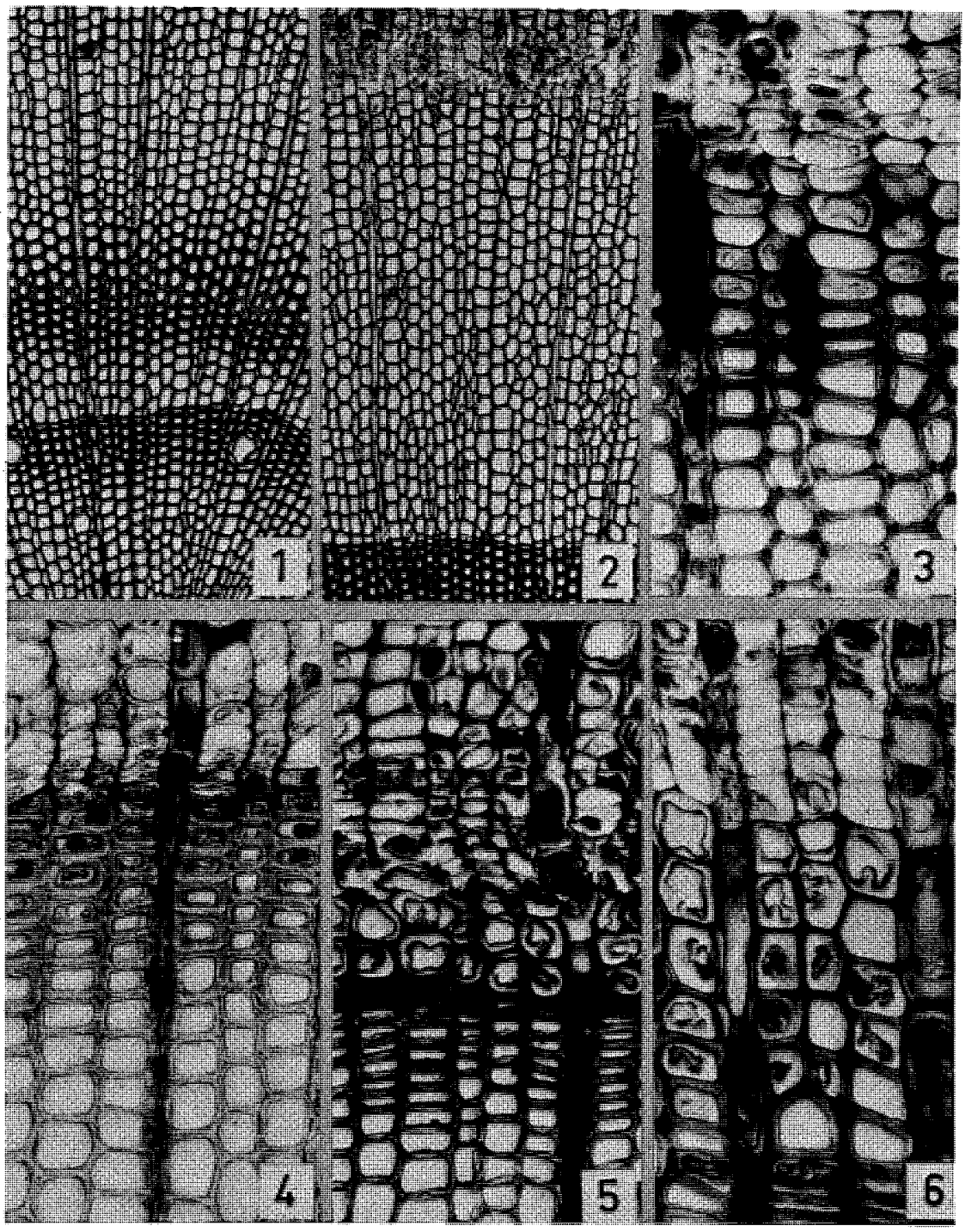


FIGURES 1 to 6. — The pattern of xylem differentiation and tracheid anatomy in larch seedlings under different photoperiods (IC — inactive cambium, AC — active cambium, at commencement of treatment.

(1) Group 1, IC, 7 weeks SD plus 5 weeks LD, lower stem.
(2) Group 2, IC, 9 weeks LD, lower stem.
(3) Group 4, AC, 3 weeks SD, middle stem.
(4) Group 4, AC, 4 weeks SD, lower stem.
(5) Group 5, AC, 3 weeks SD plus 1 week LD, lower stem.
(6) Group 5, AC, 3 weeks SD plus 2 weeks LD, lower stem.

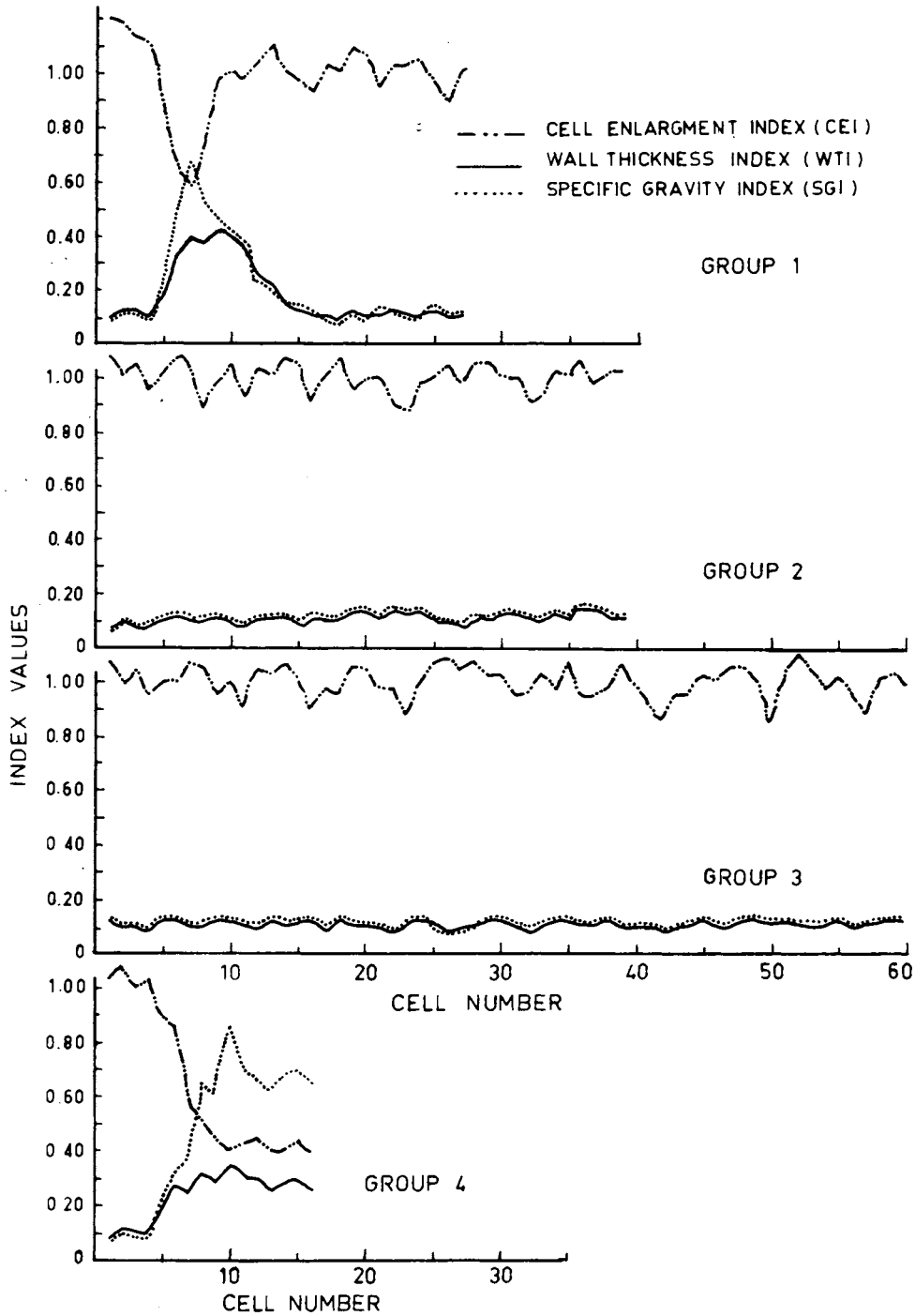


FIGURE 7. — The variation of CEI, WTI, and SGI in the middle stem of seedlings in Groups 1, 2, 3, and 4.

The narrow latewood band (3-4 tracheids per file) in SD seedlings was followed by a band of compression-wood like tracheids (4-5 per file), which apparently formed after the seedlings were transferred to long days at the end of 7 weeks (fig. 1). The formation of this compression wood band was an interesting physiological development. We offer the following explanation. The SD treatment lowered endogenous auxin levels in the seedlings, which was fairly abruptly increased after the seedlings were transferred to long days. Thus the relative increase of auxin facilitated the

development of compression wood. Compression wood development ceased to continue because the cambium and differentiating cells became "accustomed" to the change.

The actively growing seedlings of Groups 3 to 7 also showed some interesting responses to the photoperiodic treatments. The LD control seedlings (Group 3) continued height growth during the entire 12 weeks. The seedlings in the other groups, which were exposed to various periods of SD treatment, showed reduced extension growth after the second week, and were forming resting terminal buds by the end of the third week of short photoperiod.

The seedlings in Groups 5, 6, and 7 were transferred to long days at the end of the third, fifth, and seventh weeks, respectively. The inactive buds in Group 5 began flushing within the first 2 weeks of LD treatment, whereas those in Group 6 began during the third and in Group 7 during the fourth week of LD treatment. The seedlings in Groups 5 and 6 kept their old foliage; however, those in Group 7 lost most of their needles prior to transfer.

The periodic samplings of two seedlings during the treatment, and of two seedlings at the conclusion of treatment (table 1) allowed the assessment of the progress and possible changes in xylem differentiation. In Group 3, earlywood differentiation continued during the entire 12 weeks. There were 73 fully mature tracheids per file in these seedlings, and only minor variations occurred in CEI, WTI, and SGI of tracheids in the radial files (fig. 7). In Group 4 (SD controls), there were only 16 mature tracheids per file at the end of 12 weeks; 10 of these had CEI less than 0.90. Short days caused a reduction in the rate of cell division by the end of the first week, and cell division almost ceased by the third week. The CEI of enlarging tracheids was also reduced between the first and third weeks, while WTI and SGI were increased during the same period (fig. 7). Between the fourth and fifth weeks of SD treatment the cambium became quiescent (fig. 4).

All seedlings in Groups 5, 6, and 7 also formed a band of latewood, since they were all exposed to at least 3 weeks of SD treatment. However, there were differences in the response of these three groups to long days. The seedlings in Group 5, which received only 3 weeks of SD treatment, continued cambial division and xylem differentiation within the first week of LD treatment (fig. 5) and thereafter at a relatively rapid pace (fig. 6). The seedlings in Group 6 recommenced cambial division and xylem differentiation during the second week of LD treatment (fig. 9), while those of Group 7 recommenced during the third week. At the end of 12 weeks, there were 61, 44, and 35 fully mature tracheids per file in Groups 5, 6, and 7, respectively. The variation in CEI, WTI, and SGI of mature tracheids in these latter three groups is shown in figure 8. The CEI of the first 4-5 tracheids per file which matured under long days showed a gradual increase in Groups 5 and 6 (fig. 10), and an abrupt increase in Group 7 (fig. 11). Also, the WTI and SGI showed a gradual decrease in Groups 5 and 6, but an abrupt decrease in Group 7. These differences were probably due to the presence of old needles in Groups 5 and 6, and their absence in Group 7.

The foregoing results confirmed that photoperiod plays a decisive role in the regulation of cambial activity and subsequent xylem differentiation. Short days alone were sufficient to bring about the differentiation of tracheids with low CEI (latewood). Larson (1962, 1964) and Wodzicki (1961, 1964) made similar observations for coniferous seedlings. The effects of photoperiod on xylem differentiation are believed to be mediated by endogenous growth-regulating substances.

Drought Treatments

Wilting of different magnitudes accompanied the various drought treatments. The seedlings under complete drought were affected the most; three out of four died before the completion of treatment. The seedlings under both "mild" and "intermediate" drought wilted in between the 5-day watering intervals, and lost 40 to 70 percent of their foliage by the end of the drought exposure. Three of the five seedlings under "mild" drought and all five under "intermediate" drought formed resting terminal buds by the end of drought treatment. The controls continued height growth throughout the entire period of treatment.

Drought also interfered with cell division in the cambial zone and all phases of xylem differentiation. All three drought treatments were severe enough to "check" several tracheids in the various phases of differentiation (i.e., to cause the death of tracheids prematurely). Thus there were 2-3 tracheids per file with subnormal lignification; as many as 5-6 tracheids were checked in wall thickening; and 4-8 tracheids were checked in the phase of enlargement. This pattern indicates the direct effect of drought on tracheid development. A similar scheme was observed by Kennedy and Farrar (1965) in jack pine (*Pinus banksiana* Lamb.) seedlings.

Drought also interrupted the growth of apical meristems and needles, which in turn reduced endogenous auxin levels and facilitated the differentiation of a relatively wide band of latewood tracheids (fig. 12). This development prevailed for some time after the resumption of watering, and illustrated the indirect effects of drought on xylem development. Larson (1963) proposed that drought directly influenced the growth of the terminal meristems, and only indirectly the tracheid diameter through the intermediate action of auxin. Kramer (1964) and Zahner (1963) emphasized that both the direct and indirect effects of

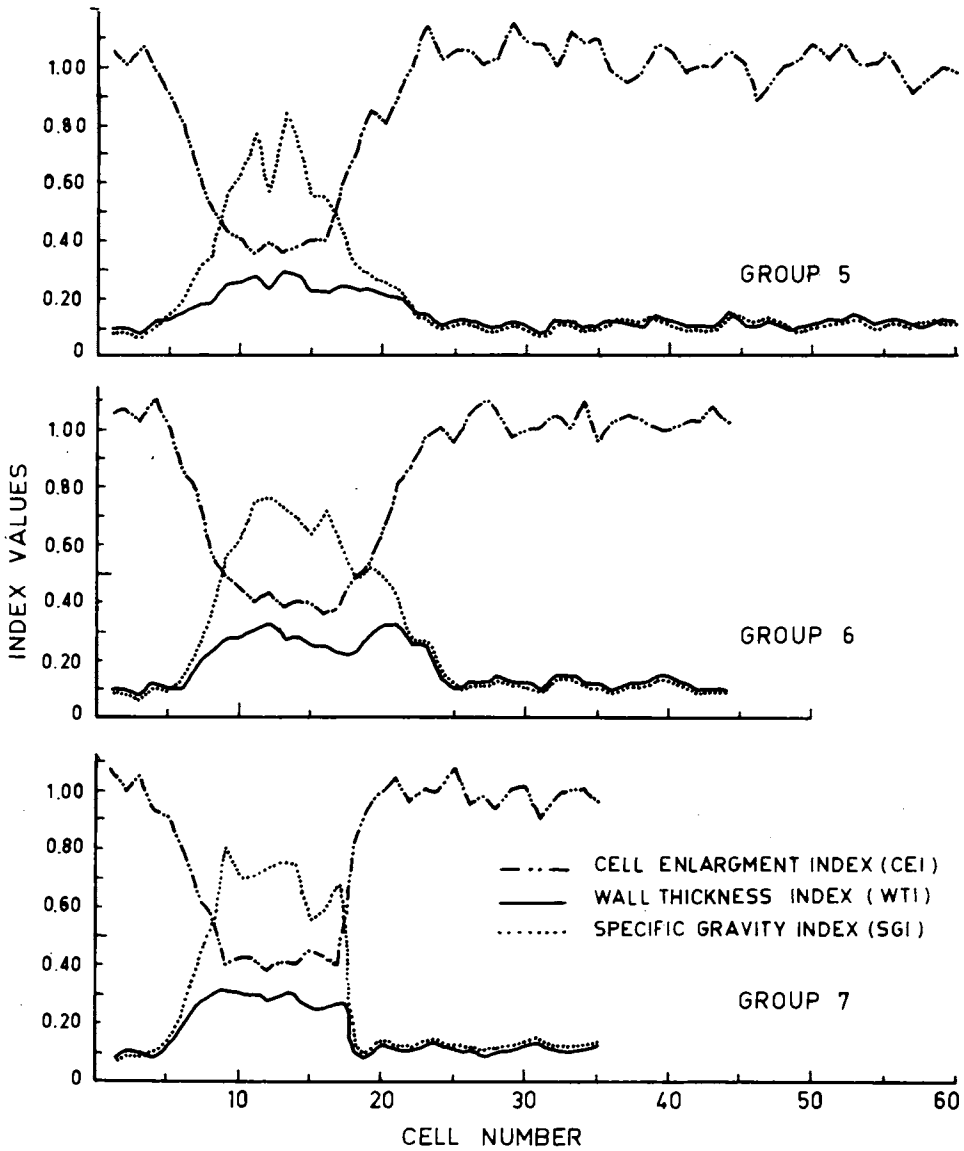


FIGURE 8. — The variation of CEI, WTI, and SGI in the middle stem of seedlings in Groups 5, 6, and 7.

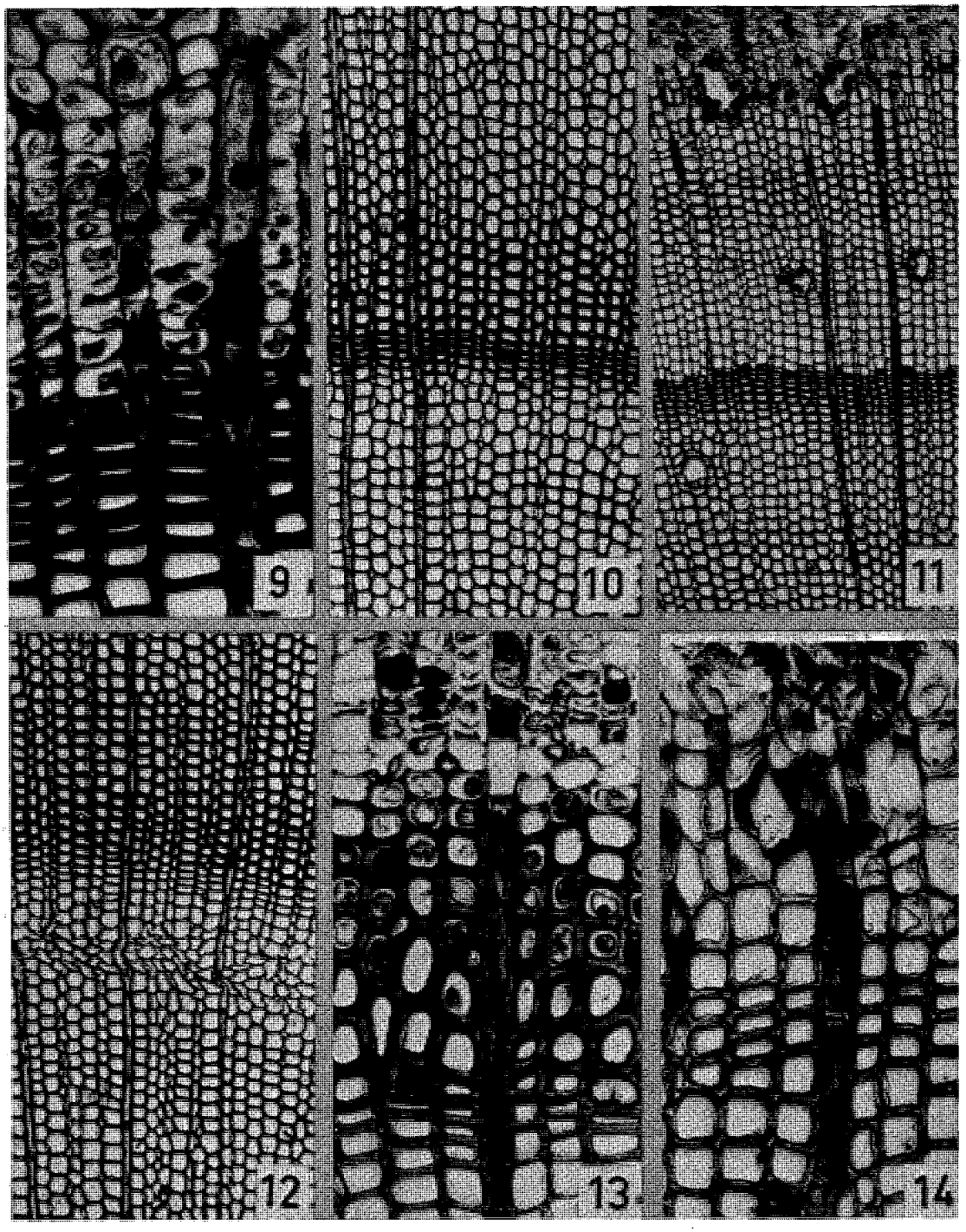
water deficits were important in xylem development.

Treatments With IAA and TIBA

The 3-week exposure to short days, prior to IAA application, facilitated a reduction in CEI and an increase in WTI. In fact, the control seedlings became quiescent by the fourth week. However, the IAA-treated SD seedlings resumed a limited number of cell divisions and continued xylem differentiation (fig. 13). The CEI of newly differentiated tracheids showed considerable increase (greater than 0.90) and their WTI remained fairly high (about 0.25). The newly differentiated tracheids had slightly excessive lignification (characteristic of reaction wood). The growth-stimulating effect of IAA was strongest immediately below the site of application; it was less at 2 cm below, and no apparent effect was present at 4 cm below the blaze.

These results indicated that the SD treatment lowered the level of endogenous auxins sufficiently, first, to cause latewood differentiation and eventually cambial quiescence. However, synthetic IAA could successfully be substituted to reverse this trend temporarily.

The treatment of actively growing LD seedlings with the inhibitor TIBA significantly reduced the enlargement (CEI) of 4-5 tracheids per radial file (fig. 14), while LD controls continued forming



FIGURES 9 to 14. — The pattern of xylem differentiation and tracheid anatomy in larch seedlings under different photoperiods, drought exposure, and treatment with synthetic IAA and TIBA.

(9) Group 6, AC, 5 weeks SD plus 2 weeks LD, lower stem.
(10) Group 6, AC, 5 weeks SD plus 7 weeks LD, lower stem.
(11) Group 7, AC, 7 weeks SD plus 5 weeks LD, lower stem.
(12) The effect of "mild" drought on tracheid anatomy. The "direct" effects of drought are seen in the band of thin-walled, collapsed tracheids, immediately followed by thin-walled tracheids with narrow radial diameters. The "indirect" effects of drought are seen in the following zone of thick-walled tracheids with narrow radial diameters, which formed following drought while the seedling had resting terminal buds.
(13) The effect of IAA treatment on xylem differentiation and tracheid anatomy in an SD larch seedling.
(14) The effect of TIBA treatment on xylem differentiation and tracheid anatomy in an LD larch seedling.

earlywood. It is probable that TIBA, an auxin antagonist, interfered with auxin action during the enlargement phase of tracheid differentiation. Larson (1964) was also able to induce the formation of narrow-diameter tracheids in young red pine growing under long photoperiods.

Summary and Conclusions

Results of this experiment are in agreement with the concept that certain anatomical and hence wood quality characteristics of mature tracheids are determined during differentiation. Photoperiod, water availability, and treatments with synthetic IAA and TIBA all affected the degree of radial enlargement, wall thickness, and hence specific gravity of mature tracheids. Short photoperiods, water deficits, and treatment with TIBA favoured the differentiation of tracheids with low cell enlargement index (i.e., CEI less than 0.90 or latewood), while long photoperiods, adequate water supply, and treatment with IAA favoured the differentiation of tracheids with high cell enlargement index (i.e., CEI greater than 0.90 or earlywood).

The results fitted the theory of limiting factors, i.e., a factor which falls below an optimal threshold will set the pace for physiological events which affect the differentiation of tracheids. Thus, short days alone were sufficient to bring about latewood differentiation, as were water deficits and treatment with TIBA. These observations may have some practical significance. Therefore, in any treatment of forest stands which aims to affect tree growth and wood quality (e.g., irrigation, fertilization, thinning), all environmental conditions should be assessed before treatment is made. The treatment may be wasted or will fail to produce the expected results if one single important environmental factor (e.g., photoperiod) is below a growth-limiting threshold.

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WALNUT WOOD CHARACTERISTICS IN RELATION TO SOIL-SITE CONDITIONS

R. R. Maeglin, N. D. Nelson, and H. E. Wahlgren[1]

It takes little scanning of "Timber Trends in the United States" (U.S. Forest Service 1965) to realize that the hardwood timber of our country needs a great deal of improvement. About 27 percent of the total growing stock of the Nation is hardwoods, 90 percent of the hardwoods are eastern species, and most of them are of poor quality.

But, where does one start to improve the quality? The silviculturist can thin, weed, and prune to improve log quality but what is the effect on intrinsic quality. The geneticist may want to improve the resource, but he must first know the qualities desired, including those of intrinsic wood quality.

For the softwoods, wood quality has long been characterized by wood density. However, the uses of softwoods are generally restricted to engineering and pulp applications, where wood density is important. Hardwoods, on the other hand, have so many diverse applications that wood density loses its importance for most of them.

What then can be used as an indicator of intrinsic wood quality for the hardwoods?

A quick survey of the uses of the various hardwood species certainly gives some indication as to desired qualities. Brown *et al.* (1949) list 49 hardwood species and their uses. Furniture is the largest use, followed by millwork, veneer, and cabinetwork. Other major uses are woodenware, novelties, gunstocks, and flooring.

The first quality consideration for all of these uses is what we would call aesthetics (primarily color). Other quality considerations are texture, shrinkage, machinability, hardness, and strength properties (principally toughness).

With these quality criteria in mind the Forest Products Laboratory, in cooperation with the North Central Forest Experiment Station, initiated a study to evaluate the intrinsic wood quality of black walnut (*Juglans nigra* L.) This work was boosted by the push for increased information on black walnut after the recent symposium on walnut culture (U.S. Forest Service 1966).

This paper is a report on how we are attempting to find a quality criterion for walnut and possibly for other hardwoods. We present no results, just a fresh idea!

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The Black Walnut Problem

The buyers of black walnut have long shown a preference for logs from certain areas. The reasons for this are not definitely known, although several theories have been advanced. Some claim, and with good cause, that defects such as bird peck, shake, and poor tree form are the main reasons for discrimination. These defects may be more prevalent on trees growing near the borders of the geographical range of the species or on poor sites. On the other hand, some think that discrimination by buyers of walnut logs from certain localities is from habit and without valid reason.

To investigate the possible reasons for such discrimination and to evaluate some measures of intrinsic wood quality, the study objectives became, specifically, to determine whether valid differences occur in the wood characteristics and wood properties of trees growing at various locations under different conditions.

The study is to determine whether differences exist in color and extractives, in anatomical features, and in physical and machining properties of wood. Then, if these differences exist, how do they relate to each other and to site?

The study is divided into three sections: Section I to investigate the color, extractive content, and heartwood-to-sapwood ratio of sample material as a measure of aesthetic quality; Section II to evaluate anatomical characteristics as a measure of texture and shrinkage; and Section III to evaluate the physical and machining properties. All three sections will be related to soil properties.

To provide meaningful results, material was selected from fast- and slow-grown trees from good and poor sites. Specifically, material was selected from two general areas, in Indiana and Missouri. The Indiana locations are considered to represent the best growth areas for walnut, while the Missouri locations are generally regarded as inferior.

Sample Material Selection and Handling

Selection of Sample Trees

The selection of suitable trees for analysis was coordinated through the North Central Forest Experiment Station. Station personnel[2] were responsible for obtaining logs through industrial cooperators in Indiana, and National Forests in Missouri.

[2] *Special acknowledgement is due F. B. Clark, Carbondale, Ill.; R. D. Williams, Bedford, Ind.; and N. F. Rogers, Salem, Mo.*

Thirty-two trees were selected to cover the following stand-site combinations:

	Number of trees	
	Missouri	*Indiana*
Good site:		
Slow growth	4	4
Fast growth	4	4
Poor site:		
Slow growth	4	4
Fast growth	4	4
	16	16

Soil Sampling

At the location of each sample tree, soil samples were taken for correlation with wood properties. A composite 6-inch surface sample was taken at random points around each stump to a distance of 20 feet radially. The composite consisted of 8 borings. At two of the eight points, bulk density samples were also taken. These samples are being analyzed for chemical constituents, organic matter, pH, and physical properties.

To classify each soil on which trees were located, a pit was dug. The soils of this pit were classified and subsoil samples were taken for physical analysis.

Sample Bolts

From each of the 32 selected trees, one 5-foot bolt was taken from the 8- to 13-foot portion. These bolts were inspected carefully and all defects and blemishes on the bolt faces and ends were recorded before sawing.

The ends of each bolt were squared and a disk cut for determination of ring count and sapwood width. These disks are being retained intact for future reference.

Eight or more boards were cut from each bolt and numbered systematically, starting with the board whose face was cut first. Numbering of other boards followed the pattern shown in figure 1.

The sawing method for each bolt was marked on the small end, using a template guide. Each board was flat sawn, 1¼ inches thick, 4¼ inches wide, and 4½ feet long, and has heartwood on at least one face. Sawing was done parallel to the outer surface (bark) in an attempt to keep the same growth rings throughout the board.

Selection of Test Samples

Eight boards from each bolt are being used. Random selection was utilized when more than eight boards were sawed from a bolt.

After planing to a uniform 1⅛-inch thickness, each selected board was marked off into four 1-foot samples (fig. 2) starting at the end corresponding to the top of the bolt, and numbered consecutively. One of the four 1-foot samples was selected randomly, and a 6-inch-long piece was added to the bottom end making, in total, an 18-inch piece.

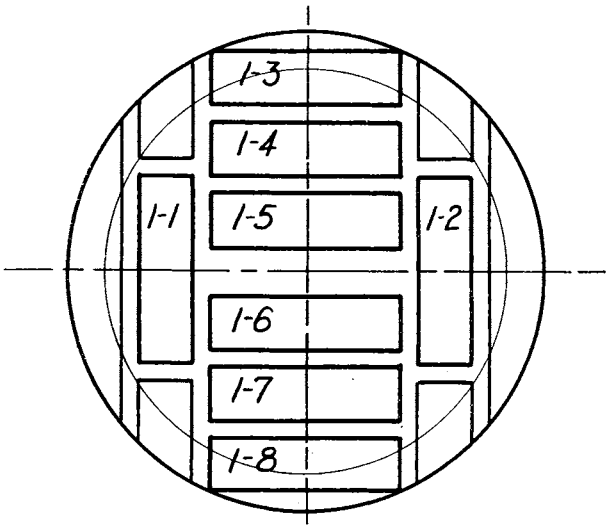

FIGURE 1. — Location of and numbering sequence for boards in the log.

The 18-inch piece was further cut into 6- and 12-inch portions. The 6-inch piece is being used in Sections I and II of the study, while the four 1-foot samples are being used in Section III.

The 6-inch piece was further processed as follows. It was sanded to a uniform 1-inch thickness; each tangential face was then divided into 8 units, ¾ inch long, 1 inch wide, and 3/16 inch thick on the butt end (a total of 16 units per piece) as shown in figure 3. These are being used in the color, extractive, and specific gravity determinations (Section I) and for the anatomical determinations (Section II).

Further sample breakdown was followed by sawing a shrinkage specimen for Section II, 1 inch along the grain, 4 inches wide, and 1 inch in thickness.

Evaluation of Sample Material

As noted earlier, this report is on work that is now underway. All sample material has been collected and prepared. Determinations on the material are now being made to establish whether differences exist, and if so, how they relate to one another.

Section I — Color, Extractives, and Specific Gravity Determinations

Color evaluation. — The evaluation of color is especially important, for aesthetic reasons, in black walnut and some other hardwood species. Basic colors have generally, in the past, been described by qualitative terms such as dark brown, chocolate brown, etc. However, work done by Schwalbe and Ender (1934), Kollman (1939), Sandermann and Luthgens (1953), and many others has given us the opportunity to evaluate color quantitatively. Using the techniques described by Sullivan (1967a, b) the reflectance of each ¾-by 1- by

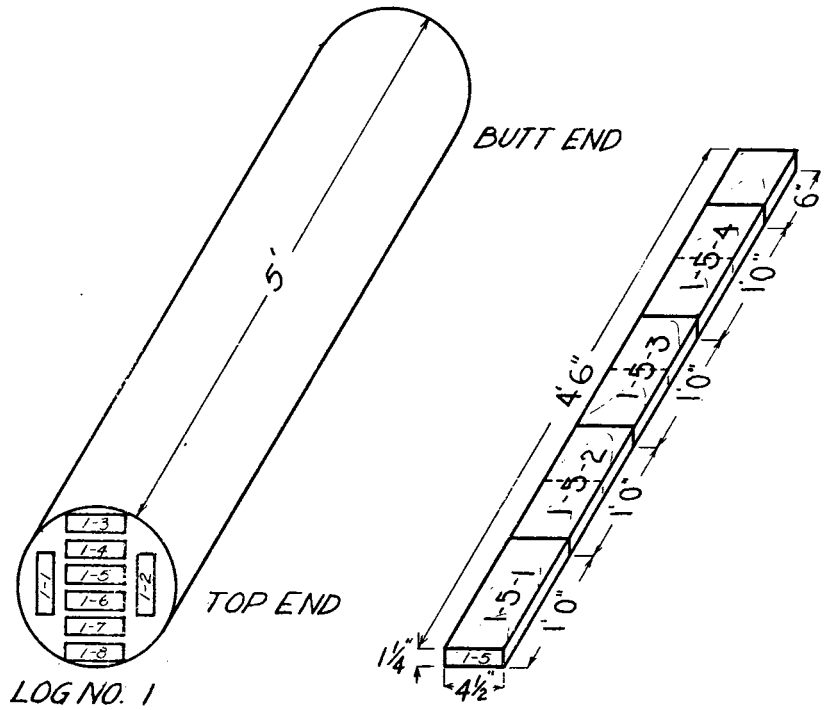

FIGURE 2. — Location of and numbering sequence for 1-foot samples in the boards.

3/16-inch piece (two per board) are being measured with a Beckman Model B spectrophotometer equipped with a reflectance apparatus. Each reflectance value is being measured as a percent of the reflectance of a standard surface, reflectance values being recorded at 10-millimicron intervals from 400 to 700 millimicrons (visible light region of the color spectrum).

These reflectance values are then utilized to derive the color's descriptive variables, i.e., dominant wavelength (millimicrons), saturation (percent of unity), and luminance (percent of unity).

Extractives and specific gravity. — After reflectance values are obtained on each ¾- by 1- by 3/16-inch piece, the material is ovendried and weighed. The samples are than placed in a Lloyd extractor for 3 weeks with alcohol-benzene as the solvent. After extraction, the water-saturated weight is determined and the samples ovendried and reweighed. Specific gravity on an extracted and unextracted basis is being calculated by the maximum moisture method as described by Smith (1955).

Percentage of total extractives is expressed on weight per weight, and on a weight per volume basis.

Section II — Wood Anatomy and Shrinkage Determination

Wood anatomy. — The material for study consists of 512 specimens, each 1 by ¾ by 3/16 inch. These are end matched to the color specimens and are obtained as described in Section I. The specimens are being airdried and then water saturated when measurements are to be made.

A transverse face of each specimen is being surfaced with a sliding microtome and, using a Zeiss integrating eyepiece and a 10X objective, the following are being determined:

1. Number of vessels per unit area.
2. Percent area occupied by vessel lumens.
3. Number of fibers per unit length in both the tangential and radial directions.

Using the formula for a rectangular cell model, the average cell wall thickness is being calculated according to Smith (1965), and from this, the average cell lumen diameter will be calculated.

Shrinkage and specific gravity. — The material for the study of shrinkage consists of 256 specimens, 4 by 1 by 1 inch. These are being obtained as described in Section I and as shown in figure 3.

Volumetric shrinkage and specific gravity are being determined on each specimen at 12-percent moisture content and again in the ovendry condition according to ASTM Standard D143-52. Volumetric shrinkage is being expressed as a percent of the green volume. Specific gravity is being expressed on the green volume-ovendry weight basis.

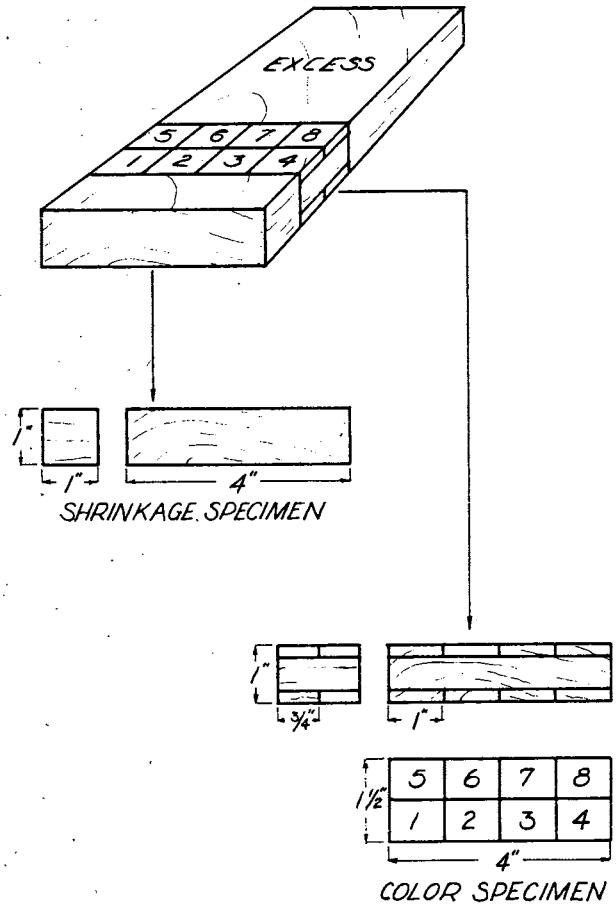

FIGURE 3. — Location of and numbering sequence showing shrinkage and color specimens.

Section III — Machining Characteristics and Mechanical Properties

Planing tests. — All of the 12-inch sample pieces are being dried to an equilibrium moisture content of 12 percent.

The samples are being planed to ⅛ inch on each face at a feed rate of 16 knife cuts per inch, after which all are examined for defects and smoothness.

Hardness and shaping tests. — One 12-inch board sample (adjacent to the 6-inch sample used in Sections I and II) was already selected for the hardness and shaping tests. One of the three remaining board samples is being randomly chosen for these same tests. The remaining two samples are used for the toughness and turning tests.

The hardness tests consist of three indentations of a ball 0.444 inch in diameter on each tangential face of the board; these are performed according to standard procedure (Amer. Soc. for Testing Materials, no date) by measuring the load to embed a 0.444-inch ball to one-half its diameter.

Following the hardness tests, the same pieces are used for the standard shaping tests (Davis 1962).

Toughness and turning tests. — The toughness and turning tests are made on ¾- by ¾- by 11-inch pieces cut from the remaining two 12-inch pieces. Every effort is being made to cut the toughness specimens with a tangential face and with minimum sloping grain. This may necessitate cutting the specimen diagonally from the ¾- by 4- by 12-inch sample. The turning specimens are cut adjacent to the toughness specimens, one from each of the two selected 12-inch pieces, and are ¾ by ¾ by 5 inches in size.

Summary

This is a report, before completion, of a program that the Forest Products Laboratory has embarked on. It is a concentrated program to find, if possible, one or more intrinsic wood quality criteria for black walnut and hopefully for other hardwood species as well. The program attempts to cover all of the main quality attributes desired by hardwood users. Further, it covers the possibility of finding relationships of these quality criteria to soil-site conditions.

The quality attribute most evident in the hardwoods is aesthetics, or color variation; this is being quantitatively evaluated with a spectrophotometer. Wood texture is being evaluated by anatomical characteristics; and shrinkage, specific gravity, machinability, and strength are being evaluated directly.

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STEM ANATOMY VARIATION IN COTTONWOOD GROWING UNDER NUTRIENT-DEFICIENT CONDITIONS

A. N. Foulger and J. Hacskaylo[1]

Investigations of mineral nutrient-tree growth relationships have dealt mainly with associations involving foliage composition, root formation, or volume production of wood. Few studies have been concerned with changes in wood anatomy associated with element deficiency. In 1949 Davis reported that calcium deficiency was accompanied by a reduction of primary tissue and an increase in secondary tissue in loblolly pine (*Pinus taeda* L.) stems. Murphey *et al.* (1962) found that nutrient defiencies affected the percentage of phloem formed and reduced both vessel diameter and the number of rays in sweetgum (*Liquidambar styraciflua* L.) seedlings. There was no apparent change in fibril angle.

The present study was a preliminary investigation into the degree of association between single mineral element deficiencies and anatomic characteristics in the stem of eastern cottonwood (*Populus deltoides* Bartr.) cuttings. All of the observations were made on first-year wood cuttings after 65 days of treatment. These data may, or may not, be applicable to mature plantation-grown trees. The hazards of extrapolating from data concerning rooted cuttings to considerably older stems are self-evident.

Material and Methods

First-year cuttings from a single eastern cottonwood, Wisconsin Clone No. 5, were rooted in quartz sand flats. When they were approximately 10 cm tall, they were planted in polyethylene-lined, 3-gal. crocks filled with HCl-washed silica quartz. Ten nutrient solutions, namely complete (table 1), -boron, -copper, -iron, -magnesium, -manganese, -nitrogen, -phosphrous, -potassium, and -suphur, were supplied to separate, continuously aerated crocks. Nutrient solutions were made from A.C.S. chemicals, with pure iron wire as a source of iron according to a modified Jacobson's method, and deionized water. If a compound supplied two elements to a solution, a sodium or chloride salt of the element not to be omitted was substituted. The pH of the solution was adjusted initially to 5.4 with 0.1 percent NaOH. The water level in the crocks was kept constant throughout the study, while pH was adjusted and nutrient solution changed every 2 weeks. Each treatment was randomly assigned to two trees in separate crocks. The plants were harvested after 65 days' treatment, height and stem diameters recorded on each, and the stems fixed in FAA.

Samples were taken from each stem at one-quarter, one-half, and three-quarters of the distance from the root collar to the stem apex. On a transverse section of the stem at each height, bark width, pith diameter, number and radial diameters of both vessels and fibers were recorded along 12 radii.

Macerations were prepared from stem portions immediately above each transverse section, allowing measurement of 50 fiber lengths and 30 vessel lengths and widths at each height in the stem.

Both the transverse section and maceration data were examined, using analysis of variance. Dunnett's procedure was employed to compare each treatment with the control, using a one-tailed test.

Results

Stem Height

The average stem heights after 65 days' treatment ranged from 138.5 cm for the complete to 38.5 cm for the S-deficient treatment as shown below.

Treatment	*Mean height (cm)*
Complete	138.5
-Boron	43.5*
-Copper	104.6

[1] *Respectively, Assistant Professor and Professor (now deceased) of Forestry at Ohio Agriculture Research and Development Center, Wooster, Ohio. The senior author is now Research Technologist, Forest Products Laboratory, Forest Service, U.S. Department of Agriculture.* *The authors wish to recognize the assistance rendered by Misses G. Kirchhofer and B. March, who made the observations, and by Dr. C. R. Weaver, Statistics Laboratory, The Ohio Agricultural Research and Development Center. The work was supported in large measure by a grant from Champion Papers Incorporated, Knightsbridge, Hamilton, Ohio.*

Table 1. — Compounds in the complete nutrient solution

Compound		Total parts per million of element
$Ca(NO_3)_2 \cdot 4H_2O$	Calcium (Ca)	120.21
	Nitrogen (N)	112.00
KNO_3	Potassium (K)	156.36
KH_2PO_4	Phosphorus (P)	62.05
$MgSO_4 \cdot 7H_2O$	Magnesium (Mg)	48.65
	Sulfur (S)	64.12
Fe - EDTA	Iron (I)	5.00
H_3BO_3	Boron (B)	0.40
$MnCl_2 \cdot 4H_2O$	Manganese (Mn)	0.40
$ZnCl_2$	Zinc (Zn)	0.05
$CuCl_2 \cdot 2H_2O$	Copper (Cu)	0.02
MoO_3	Molybdenum (Mo)	0.03

Treatment	*Mean height (cm)*
-Iron	108.4
-Potassium	98.9
-Magnesium	123.1
-Manganese	124.1
-Nitrogen	49.7*
-Phosphorus	102.9
-Sulfur	38.5*

Deficiencies of B, N, and S resulted in height reductions which were significant at the 5-percent level (indicated by an asterisk in the tabulation).

Fibers

A decrease in fiber length, significant at the 5-percent level, was found at two or more levels in the stem with deficiences of B, K, N, and S (fig. 1). Only in the top specimens did lack of Cu, Fe, Mg, Mn, and P cause significant reductions in fiber length. Both -Cu and -Mn treatments resulted in slight increases in fiber length at the lowest level in the stem.

In addition to a reduction in fiber length, deficiences of K, N, and S were associated with a significant reduction in fiber width at all levels in the stem (fig. 1). Mean fiber width was reduced in the top specimen from the Mg treatment, but no significant decrease or increase in fiber width was associated with a lack of the other elements.

The number of fibers formed was significantly reduced at all three stem levels in the absence of N and S while -B, -K, -Mg, -Mn, and -P were associated with significant reductions at the lower two levels (fig. 2).

Ring width due to fibers, shown in figure 3, has a pattern similar to figure 2. Deficiencies of Mg, N, and S caused a significant reduction at all three levels in the stem, while the absence of B, K, Mn, or P was accompanied by a reduction at the middle and bottom levels. However, a lack of Cu and Fe had no apparent effect on the amount of wood made up of fibers.

Vessels

No significant differences in vessel length were found with any of the treatments (fig. 4). Radial

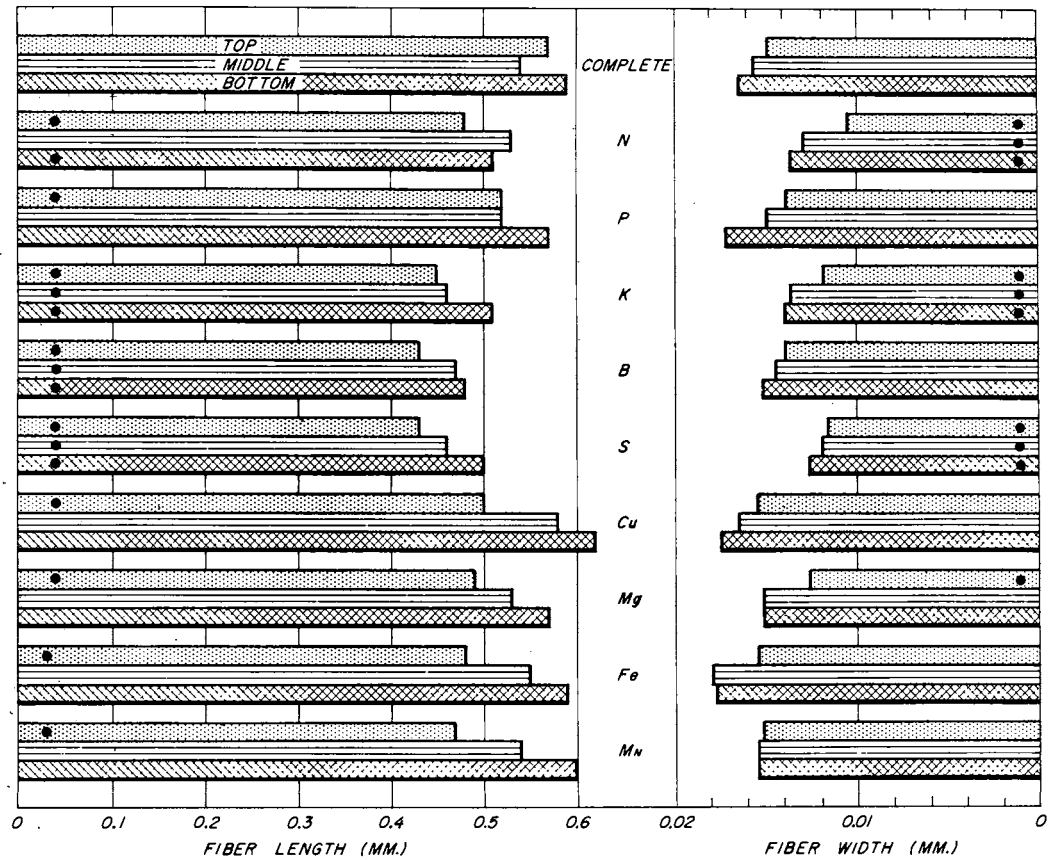

FIGURE 1. — Mean fiber length and width at each level in the stem is shown with the particular element which is absent. In this and following figures a dot indicates a value significantly different (0.05) from the complete treatment value at the corresponding stem position.

vessel width, as measured on the cross sections, showed a significant decrease at all levels in the stem in the absence of N, and S, and in the upper two levels when B was absent. The other treatments showed no effect on vessel width. Vessel widths were slightly larger for the macerated material since the vessel segments had been flattened under the cover slip. These measurements indicated that -B, -N, and -S all were associated with reduced vessel width at all three levels in the stem. A deficiency of K caused a significant decrease in the top and middle of the stems. With the exception of -Mg, where vessel width increased slightly in the top of the stem, -Cu, -Fe, -Mn, and -P reduced vessel segment width significantly in the lower portion of the stem, the latter two also causing a reduction at the middle level.

Only -S was associated with a reduced number of vessels at all three levels in the stem (fig. 2), but all other element deficiencies caused a reduction in the middle and bottom of the stem.

Bark

The bark of young cottonwood has pronounced vertical ridges, which resulted in considerable variation in bark width for the same section. Mean bark thickness was reduced significantly at the top of the stem in the absence of Cu, Fe, K, Mg, Mn, N, and P, and at the bottom with a lack of K, Mg, Mn, N, or S (fig. 5). There was no significant reduction in bark width with the -B treatment.

Pith

Pith diameter was significantly less than the control at all three heights in the stem with B, Cu, K, Mn, N, P, and S deficiences (fig. 5). In the absence of Fe and Mg, pith diameter was reduced in the top and middle of the stem.

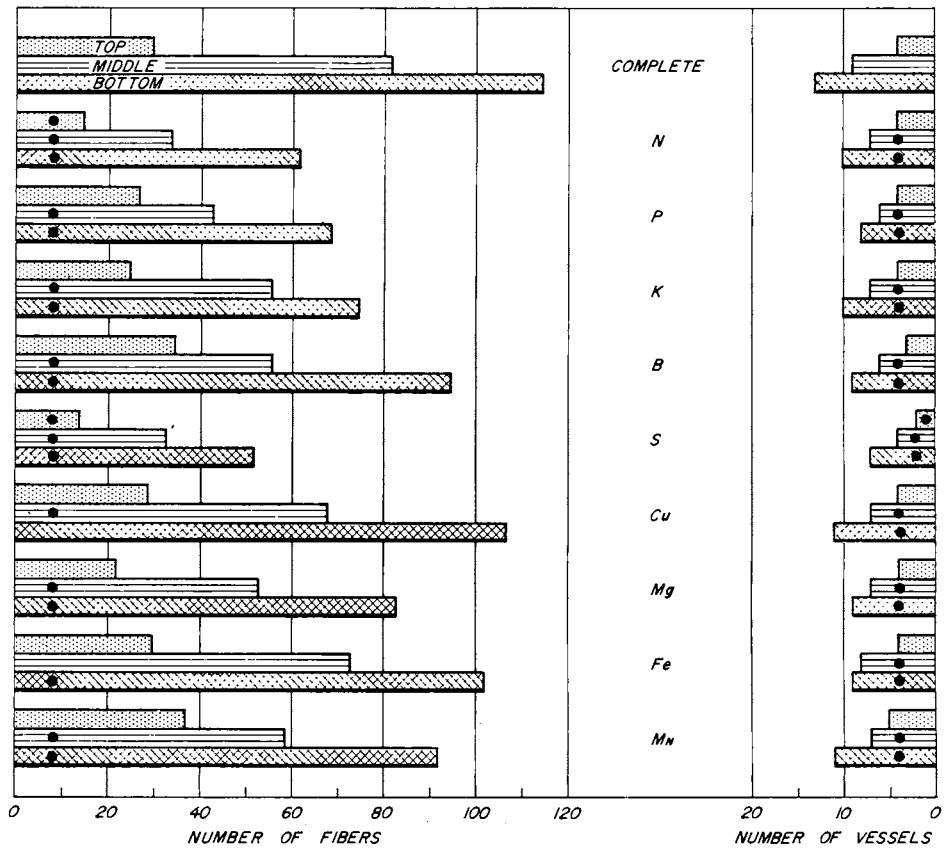

FIGURE 2. — Mean number of fibers and vessels per radius at each level in the stem is shown with the particular element which is absent.

Relationship Between Anatomic Characteristics

Data from all 10 treatments were grouped together by in-stem position (i.e., top, middle, bottom), and analysis of variance was used to determine the amount of correlation between certain of the anatomic characteristics measured. Those pairs of characteristics with a significant correlation are shown in table 2. Both fiber width and vessel width, as measured on the cross sections, showed a significant association with ring width at all three levels in the stem, but the correlation between ring width and macerated vessel width was significant only in the two lower positions. Ring width and fiber length were correlated significantly only at the bottom of the stems, while fiber length varied linearly with change in fiber width in the middle and bottom of the stems. Only vessel segment length at mid-height in the stem showed a significant relationship, at P equals 0.95, with vessel width and with ring width.

Discussion

The sampling method used in the study may be questioned in that comparison is made between points nominally similar in the stem, but which practically may be at quite different distances from the stem apex. From one standpoint, it might have been more desirable to compare points on the stem at a specific distance below the apex. However, the shortest specimen was 34.0 cm tall at the end of the study, and since the specimens were approximately 10 cm tall at the start, sampling would have been limited to the topmost 20 cm of each stem. Because an estimate of overall stem development was desired, it was decided that the sampling system used would give the most meaningful results for this particular study.

Of the various observations, possibly the most noteworthy is the thoroughly debilitating effect of N and S deficiences, which were associated with

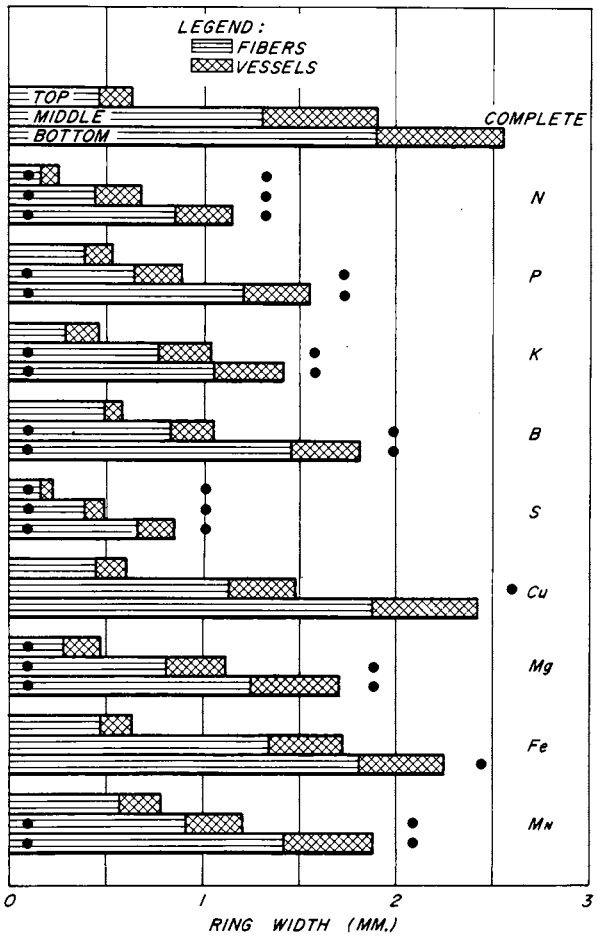

FIGURE 3. — Mean radial ring width due to fibers (lined) and to vessels (hatched). Together the two comprise total ring width at each level in the stem by treatment. Dots on the lined area indicate significant differences in width due to fibers, while dots to the right of the graphs show differences in total ring width.

significant reductions in fiber length and width, vessel width, ring width, bark width, and pith diameter. In addition, the lack of B, K, and, to a lesser extent, P resulted in marked reductions in size and number of fibers and vessels. Not only is there a reduction in the amount of wood formed, but there is a change in fiber and vessel anatomy. On calculating the ratio of vessel-formed wood to fiber-formed wood, the -N treatment showed an increase in the ratio of vessel wood to fiber wood. While these five elements, i.e., N, S, B, K, and P, have an overall effect on stem anatomy, each of the other treatments affected one or more of the facets studied. Significant reductions in both wood and bark width occurred with K, N, P, and S deficiencies while only wood formation was reduced in the absence of B.

Of these five elements, N, S, and probably K are directly involved in protein synthesis. N is essential to all amino acids, and is found in some vitamins. In addition, S is a constituent of the plant hormones biotin and thiamine, while a prolonged lack of K results in a reduction of carbohydrates. The role of B in plants is not known precisely, but this element appears to be necessary in carbohydrate transport, while a deficiency of it reduces the rate of protein synthesis. The nucleic acids contain P, and a lack of P also limits protein production since it plays an important role in energy transfer.

The primary function of the study was to determine which elements were associated with ma-

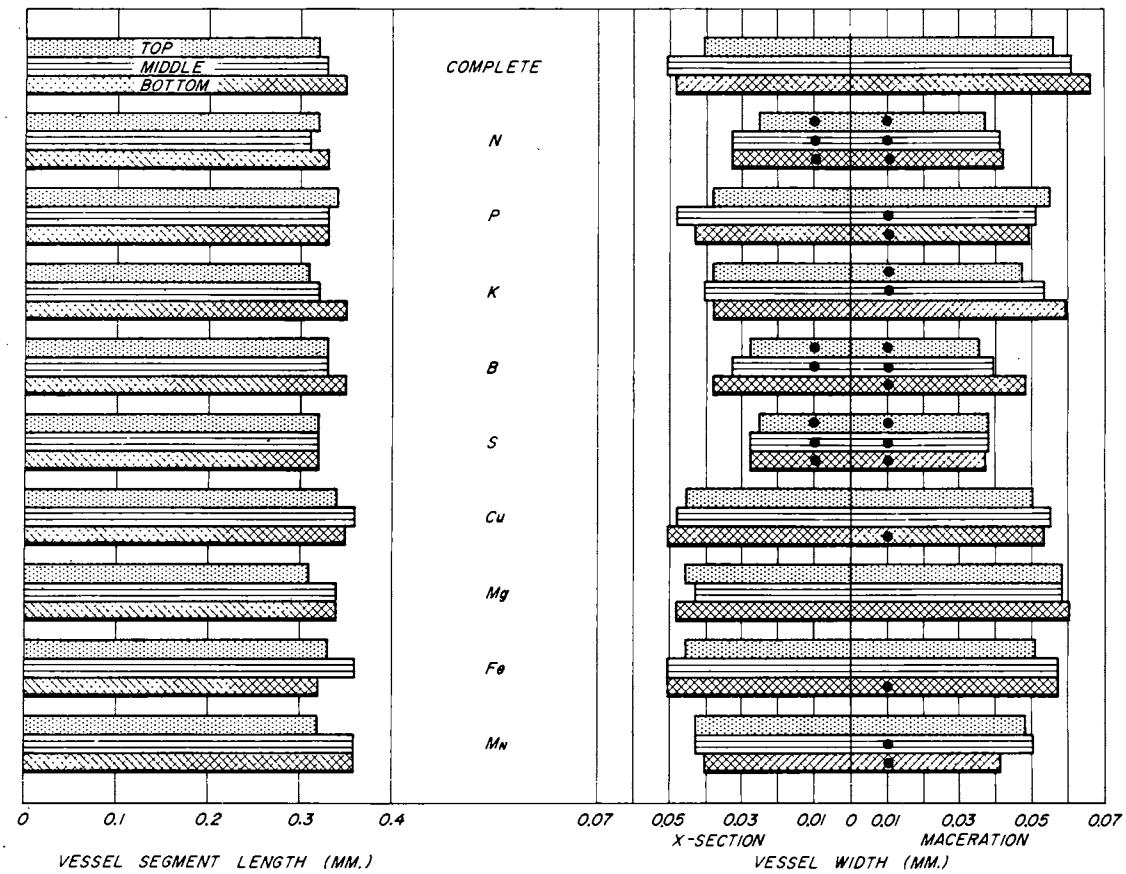

FIGURE 4. — Mean vessel segment length and width at each level in the stem is shown with the particular element which is absent. Two vessel widths are shown; those on the left are cross-section measurements while those on the right are from macerated material.

jor changes in stem anatomy, and with those anatomical aspects of economic importance to the pulp and paper industry. With this in mind, it seems that N, S, B, or K deficiency would cause most embarrassment to the woodland manager in reduced volume production, and, possibly, to the mill production engineer due to altered wood anatomy. Other elements do affect various facets of growth, but absence of the four mentioned above was accompanied by significant departures from "normal" in most of the anatomic characteristics examined.

The effects of the several element deficiencies on foliage appearance and the chemical composition of the roots, stem, and leaves of cottonwood seedlings have been reported elsewhere by Hacskaylo (1966). While the anatomic changes associated with particular element deficiencies were less marked than those of leaf form and color, the variation from "normal" was significant in several instances. It is doubtful if these data can be extrapolated to apply to stands 10 years of age or older. A further complication lies in the fact that nutrient-deficient soils frequently, though not invariably, are lacking in more than one element, and are most unlikely to have one element completely absent.

The data presented herein are applicable to young cottonwood, possibly up to 5 years of age, with some degree of confidence. Additional work is required to determine the effects of varying two or more elements simultaneously, and the effect of nutrient deficiencies on the stem anatomy of older trees.

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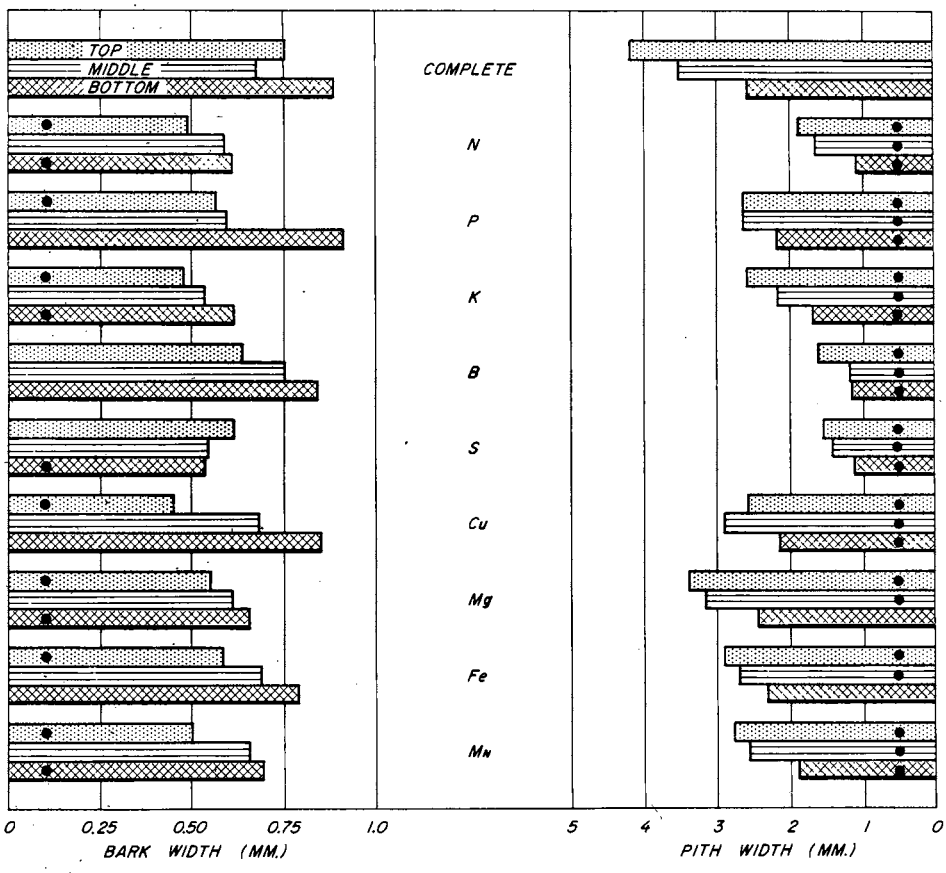

FIGURE 5. — Mean bark width and pith diameter at each level in the stem is shown with the particular element which is absent.

Table 2. — Correlation coefficient, mean and standard error of estimate for pairs of anatomic features by stem position for all specimens taken together

X	Y	Stem position 1/	Correlation coefficient, all positive	Mean Y (mm.)	Standard error of estimate of Y
Fiber length	Fiber width	T	0.511	0.014	0.001
		M	.681*	.015	.001
		B	.716**	.016	.001
Ring width	Fiber width	T	.877**	.014	.001
		M	.894**	.015	.001
		B	.778**	.016	.001
Ring width	Fiber length	T	.364	.487	.039
		M	.562	.519	.032
		B	.738*	.553	.029
Ring width	Vessel width (cross-section)	T	.703*	.038	.006
		M	.854**	.042	.004
		B	.883**	.043	.004
Ring width	Vessel width (maceration)	T	.525	.049	.007
		M	.771**	.051	.005
		B	.668*	.052	.007

1/ T = top; M = middle; B = bottom.
* Significant at the 5-percent level.
** Significant at the 1-percent level.

THE GROWTH AND ANATOMICAL FEATURES OF NUTRIENT-DEFICIENT SEEDLINGS

Fred M. Lamb and Wayne K. Murphey[1]

As the tree improvement and genetic programs supply better planting stock, a more suitable environment must be provided if their full potential is to be realized. This will require much more information than we now have on how nutrient deficiencies affect the growth and anatomy of forest trees. The importance of anatomical studies has been shown by Church (1949) and Harper (1913). They found that one of the first effects of defoliation is a marked reduction in latewood formation. Furthermore, the assumption that anatomical features exert an influence on the physical and mechanical properties of wood through alterations in specific gravity is generally accepted.

This paper reports the effects of various nutrient deficiencies on the growth and anatomical properties of silver maple (*Acer saccharinum* L.) seedlings. The nutrient elements chosen for investigation were calcium (Ca), boron (B), magnesium (Mg), and phosphorus (P). These were selected primarily because of their physiological functions: Calcium and boron are involved in the meristematic activities. Magnesium is a prime constituent of the chlorophyll molecule, and phosphorus is engaged in energy transfer and is a structural component of deoxyribose nucleic acid and ribonucleic acid.

Total height, diameter, and dry weight of the stem were measured to study growth effects. Maximum root length was also measured as an indication of the absorbing capacity of the seedlings. The anatomical features investigated were the vessels representing the conductive cells, the fibers representing the support cells, and the width of secondary xylem.

Methods

To limit genetic variation, seeds of equal size and weight were obtained from a single silver maple tree, and then only those seeds that germinated within a middle 24-hour period were used in the study.

After the seeds had germinated in a tray lined with moist filter paper, the selected materials were transferred to polyethylene-lined pots containing sterilized vermiculite and were supplied for 2 weeks with deionized water only. Then 25 seedlings were placed in a growth chamber, and each group of five seedlings received one of five nutrient solutions. One, a modified Hoagland's solution (Davis 1949, Hoagland 1948, and Went 1957) containing all nutrients, was given to the controls. The other four solutions were prepared in a similar manner except that each had one of the four study elements withheld. In the growth chamber, day length was maintained at 15 hours, temperature was held at 27° C, and the solutions were constantly aerated.

After 12 weeks in the chamber, the seedlings were observed for foliar symptoms denoting the various deficiencies, and growth data were recorded. To study the anatomical features, a 1-inch-long section was cut from each stem directly above the root collar, embedded in celloidin, and sectioned on a sliding microtome. The 10-micron-thick sections were then stained with Safranin Y and Delafield's Haematoxylin and mounted with a synthetic resin. The embedding and stain procedures used are outlined in Sass (1958).

Significance was tested by means of the analysis of variance, using a completely random design. Tukey's HSD (Tukey 1949) was used as a mean separation test to determine which treatments were significantly different .

Foliar Symptoms

Calcium deficiency was characterized by necrotic marginal areas on the older leaves. The young leaves were pale green and distorted, and had curled margins.

The foliage of the magnesium-deficient plants exhibited interveinal necrosis and marginal chlorosis. The plants themselves were characterized by rosetting.

Areas of chlorosis throughout the leaf surface were noted on the boron-deficient plants. The leaves had a silvery appearance and a thickened texture.

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In the early stages of phosphorus deficiency, the older leaves were dark green while the younger leaves were a somewhat lighter shade. As the deficiency progressed, the older leaves became necrotic and the younger ones turned dark green with light green veins.

External Features

The data show that the phosphorus-, magnesium-, and calcium-deficient seedlings were all significantly lower in stem dry weight than the controls (table 1). A significant reduction in maximum stem height occurred in the calcium-deficient seedlings, while both calcium- and boron-deficient series had significantly reduced root lengths. Only the magnesium-deficient series differed significantly from the control in stem diameter.

Anatomical Features

All four nutrient-deficient series had significantly larger fiber diameters than the controls (table 2). All the nutrient-deficient series except magnesium had significantly larger vessel diameters with a corresponding significant reduction in vessel distribution. For the width of secondary xylem, only the magnesium- and calcium-deficient series differed significantly from the controls.

Discussion

The foliar symptoms found in this study serve as evidence that the seedlings were in fact subjected to the various nutrient deficiences. For the most part the symptoms that occurred coincide with the findings of other workers (Childers 1954, Hacskaylo 1960, Hobbs 1944, Mitchell 1939, and Pessin 1937).

Nutrient deficiences primarily cause disruptions of physiological processes which, in turn, may alter growth and anatomical features. Therefore, the results obtained in this study must be considered as secondary effects. We can only speculate as to what the biochemical effects are since little information of this sort is available on forest trees. There is also a question as to how well the effects of nutrient deficiencies on seedlings can be considered as representing those that might occur on larger trees, since juvenile wood is expected to differ from mature wood. Nevertheless, it has been established that early anatomical differences can be used to forecast future trends. With these thoughts in mind, let us consider the effects of each nutrient deficiency in turn.

The minor element, boron, is necessary in only minute quantities, but it is essential for vigorous growth. It affects cell division, nitrogen metabolism, carbohydrate metabolism, active salt absorption, hormone movement and action, and metabolism of pectic substances. It is a constituent of

Table 1. — Seedling means arranged in order of magnitude by nutrient-deficiency treatment[1]

Dry weight of stem		Height		Root length		Stem diameter	
Treatment	Mean	Treatment	Mean	Treatment	Mean	Treatment	Mean
	(Grams)		(Cm)		(Cm)		(Mm)
-B	0.481	-B	27.7	-P	36.0	Control	1.55
Control	.455	Control	27.5	Control	35.8	-B	1.50
-P	.296	-P	21.5	-Mg	34.0	-P	1.40
-Mg	.146	-Mg	20.9	-B	26.4	-Ca	1.29
-Ca	.074	-Ca	14.9	-Ca	10.0	-Mg	1.18

[1] Based on five trees for each treatment. Any two means not scored by the same line are significantly different.

Table 2. — Seedling means of various anatomical features arranged in order of magnitude by nutrient-deficiency treatment[1]

Fiber diameter		Vessel diameter		Vessel distribution[2]		Width of secondary xylem	
Treatment	Mean	Treatment	Mean	Treatment	Mean	Treatment	Mean
	(Microns)		(Microns)		(No.)		(Microns)
-P	16.0	-B	28.8	Control	13	-B	294
-Ca	15.1	-Ca	27.1	-Mg	12	Control	280
-B	14.9	-P	27.1	-P	9	-P	246
-Mg	13.3	-Mg	25.7	-B	9	-Mg	162
Control	10.8	Control	23.8	-Ca	6	-Ca	151

[1] Based on five trees per treatment. Any two means not scored by the same line are significantly different.

[2] Per 25,000 square microns.

membranes, serves to increase the solubility of calcium, and acts in precipitating excess cations. Boron is said to be necessary in the maintenance of conducting tissues. In this study, neither the height, diameter, nor dry weight of stem of the boron-deficient seedlings differed from those of the controls; but the root length did. The roots of the boron-deficient seedlings were more or less stunted. This corresponds to the results of Sommer and Sorokin (1928). The reduction in root growth may seriously affect the development of the seedlings by impairing the uptake of water and the accumulation of salts.

With regard to anatomical features, the boron-deficient seedlings had larger fibers and vessels and consequently fewer vessels per unit area than the controls. These changes may be the result of alterations in physiological processes, such as cell division, caused by the lack of boron. Warington (1926), working on the anatomical effects of boron deficiency, found an abnormal enlargement of the cambial cells.

Calcium is a major element required in large quantities for plant growth. It affects the activities of certain enzymes but is especially important in combining with pectin to form calcium pectate, a constitutent of the intercellular substance. It reduces the toxic effects of magnesium, sodium, and potassium, and neutralizes certain organic acids. At the growing points, calcium has an enzymatic function. The reductions in growth obtained in this study for the calcium-deficient seedlings agree with the results of other workers investigating calcium deficiencies (Hobbs 1944, Mitchell 1939, Pessin 1937, and Wyatt 1961). The growth losses may well result from the lack of calcium (1) to stimulate enzymatic action and possibly (2) to reduce the toxic effect of certain salts and to neutralize certain organic acids.

The calcium-deficient seedlings also differed from the controls in all four anatomical features. These results correspond to those of Davis (1949) who found in calcium-deficient *Pinus taeda* a decrease in cell division accompanied by an increase in cell enlargement and cell differentiation in the secondary xylem. Venning (1953) found a reduction in cambial activity and amount of secondary xylem in calcium-deficient tomato (*Lycoperiscon* spp.) plants. These alterations of the anatomical features may well reflect calcium's enzymatic role in the meristematic regions of the plants.

Magnesium is active in the enzymatic system and is a possible carrier of phosphorus. The reduced stem diameter and dry weight of stem exhibited by the magnesium-deficient seedlings is probably a secondary effect since one of the prime functions of magnesium is as the central component of the chlorophyll molecule. Therefore, a deficiency of this element would greatly reduce the rate of photosynthesis. Pessin (1937) and Wyatt (1961) also showed a reduction in growth due to magnesium deficiency.

As to the anatomical features, the reduction in secondary xylem is understandable as this is in accordance with the general reduction in growth previously noted. However, the enlargement of the fibers occurring without an accompanying

change in the size and distribution of vessels is not so easily understood. Possibly a deficiency of magnesium has a much greater effect on the support cells than on the conductive elements of the secondary xylem.

Phosphorus is necessary for photosynthesis, the synthesis of carbohydrates, and the transfer of energy within the plant. It is a structural component of nucleic acid, which includes RNA and DNA. The reduction in dry weight of the phosphorus-deficient seedlings occurred even though the stems were of approximately the same size as the controls. The phosphorus-deficient seedlings, however, had stems which were composed primarily of young succulent tissue with larger fiber and vessel diameters and correspondingly fewer vessels per unit area than in the controls. These anatomical alterations may well reflect the role of phosphorus in the organization of the cells and in the transfer of hereditary characteristics.

Conclusions

The results of this study indicate that nutrient deficiencies in forest trees may cause disruptions of certain physiological processes which, in turn, may result in reduction of growth and alteration of anatomical features.

Much work remains before the complete effects of nutrient deficiences on growth and anatomy of forest trees are fully understood. The interaction between nutrient elements is highly complex. Therefore, it is difficult to assign one particular anatomical or growth alteration to a deficiency of a single element. This information is vital, however, if the full potential of our tree improvement programs are to be realized outside the laboratory.

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CURRENT WORK IN ONTARIO ON COMPRESSION WOOD IN BLACK SPRUCE IN RELATION TO PULP YIELD AND QUALITY

J. L. Ladell, A. J. Carmichael, and G. H. S. Thomas[1]

In 1959 and 1960, during a series of symposia on wood quality organized jointly by the Ontario Department of Lands and Forests, the Faculty of Forestry of the University of Toronto, and the Ontario Research Foundation (ORF), it became clear that there was a serious lack of information regarding the structure and variability of the wood of the commercially important species of Ontario. Following these symposia a Wood Quality Unit was set up within the Department of Lands and Forests' Research Branch, and at about the same time the Department undertook to sponsor a wood quality research program to be carried out by the Department of Organic Chemistry of the ORF, which for many years had been doing contract research in the fields — among others — of lignin chemistry and the utilization of waste pulping liquor.

As the pulp and paper industry is basic to the economy of Ontario and as black spruce (*Picea mariana* (Mill.) B.S.P.) provides over 50 percent of the raw material used by that industry, it was decided to concentrate on this species. At present the major research effort is directed at attempting to relate specific paper properties to anatomical characters and these latter, in turn, to such factors as growth rate, age, and site. It is hoped that the results will be useful in the management of existing stands as well as furnish information that will assist in the selection of superior trees for breeding purposes.

A multi-unit micro pulp digester, based on a design found to be efficient by the Institute of Paper Chemistry, Appleton, Wis., has been built at the Foundation, while other facilities are currently being used to study problems ranging from the distribution of resins in black spruce in relation to deresination methods in pulp mills to the feasibility of exploiting the foliage of black spruce commercially.

Throughout this work the ORF has cooperated closely with the Wood Quality Unit of the Department of Lands and Forests' Research Branch. This unit has concerned itself with the investigation of field sampling problems and the difficulties of typifying whole tree characteristics from a limited number of increment cores. During these investigations it was observed that a large number of black spruce cores contained compression wood. Compression wood, found typically on the lower side of leaning trees and on the underside of branches, is composed of relatively weak, rounded, thick-walled cells rich in lignin — all factors likely to detract from the quality of pulp and paper. Although much information is available on some aspects of compression wood such as its microstructure and the factors that appear to cause its formation, its distribution within trees and stands and its effect on pulp and paper quality have not been investigated with any thoroughness. The distribution of compression wood in the southern pines has been studied, for example, by Zobel and Haught (1962) and by Einspahr *et al.* (1962), and in *Juniperus procera*, an African species, by Phillips (1940). More recently Low (1964) studied the distribution of compression wood in Scots pine grown in the United Kingdom. The effect of compression wood on the pulp and papermaking properties of loblolly pine (*Pinus taeda* L.) has been investigated by Pillow and his coworkers (1935, 1941), while a study on *Pinus radiata* was reported by Watson and Dadswell (1957).

Moore and Yorston (1945), in an early review of the effect of wood properties on the quality of pulp and paper, give values showing that the inclusion of compression wood in balsam fir (*Abies balsamea* (L.) Mill.) sulfite pulp results in decreased yields and lower burst strength. There are other scattered references to the general effect of compression wood on pulp quality in the northern spruces, as, for example, by Green and Yorston (1939) in a discussion of "acid susceptible" wood. But as far as the writers are aware, compression wood in black spruce has been the subject of only one investigation — and that a minor one — dealing with mechanical pulp (Pillow *et al.* 1959). In view of the frequency, mentioned above, with which compression wood was observed in black spruce increment cores, a detailed study of the distribution of this abnormality in relation to pulp and paper quality appeared to be of basic importance to the research program.

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Amount and Distribution of Compression Wood

In a pilot study, estimates of compression wood were made on discs from the 10- and 75-percent height levels of 20 mature trees on a good site in Parnell Township, Ontario, using an adaptation of the point sampling technique employed, for example, by Ladell (1959), Myint Aung (1962), and Tsoumis (1964) for estimating the ratio of cell wall to lumen, or the frequency of different cell types on microscope sections. A transparent sheet of plastic with a known number of randomly placed dots was placed over discs, smoothed and wetted to accentuate the bands of compression wood, and counts were made of the number of points falling on them. With allowance made for points not falling on the disc (the count field was square), the amount of compression wood relative to the whole could be determined. Trials showed that six counts using approximately 100 points, repeated with the count field randomly placed each time, gave good reproducibility. Indirect evidence of the reliability of the method was subsequently obtained from pulping trials, as will be seen.

The results of this investigation showed that at the 10-percent height level, compression wood content in the 20 trees averaged 5.8 percent, with individual trees ranging from 3.1 to 11.3 percent. Corresponding values at the 75-percent height level were 0.0 to 5.1 percent, with a mean of 2.3 percent. No correlation was found between levels ($r=-0.075$ not significant).

The second and much more detailed investigation involved 11 mature trees from a good lowland site in Challies Township, Ontario. These trees were part of a sample collected earlier in connection with a study of specific gravity distribution. The sampling plan called for random selection with the rejection of trees with perceptible lean or crook, but in fact no such trees fell within the sample although the stand contained such trees. Each tree had been reduced in its entirety to 1-inch discs up to the 90-percent height level. Estimates of compression wood were now made on every 15th disc, using the method described above with the refinement that a series of circular count fields of varying diameters was employed.

Estimates on all discs within each 10-percent height increment were averaged to give nine mean values for each tree centered on the 5-, 15-, 25-percent, etc., up to the 85-percent height level. Generally, five discs contributed to each value, the exact number depending on the height of the individual trees, which varied from 50 to 63 feet.

Table 1 lists the average compression wood contents for each tree. The values in the lefthand column are simple averages; those in the right were obtained by weighting the values for the different levels by wood volume. Simple tree averages ranged from 6.4 to 27.1 percent, with an overall mean of 14.7 percent. The weighted averages ranged from 5.3 to 26.1 percent, with an overall mean of 13.9 percent and a standard deviation of 1.83 percent. As leaning trees were not represented in the sample, the value of 13.9 percent can be considered as an underestimate of the average compression wood content of the stand.

Unweighted compression wood mean values from all trees by tree height tended generally to be high in the crown and at the base of trees (fig. 1). Patterns of variation in individual trees varied widely, however. In four trees — numbers 8, 11, 17, and 20 — the peaks at base and crown were very marked, whereas in another four trees — numbers 7, 14, 15, and 16 — compression wood content tended to increase more or less steadily with height within the tree. In trees numbered 13 and 21, compression wood tended to decrease with height. In spite of the diversity of trends with respect to height displayed by individual trees, compression wood content within trees was remarkably consistent. Except for the 85-percent level, the relationship between compression wood percent at each level and weighted tree means was very close, with correlation coefficients ranging from $+0.788^{**}$ to $+0.961^{***}$ (fig. 2). For the 85-

Table 1. — Average compression wood content in 11 black spruce trees

Tree number	Simple average (percent)	Weighted average (percent)	Tree number	Simple average (percent)	Weighted average (percent)
7	6.4	5.3	16	14.6	12.0
8	10.3	10.8	17	17.3	17.3
11	17.5	16.9	18	13.4	11.2
13	8.3	9.3	20	19.3	18.4
14	27.1	26.1	21	18.2	18.6
15	9.6	7.4	Mean	14.7	13.9

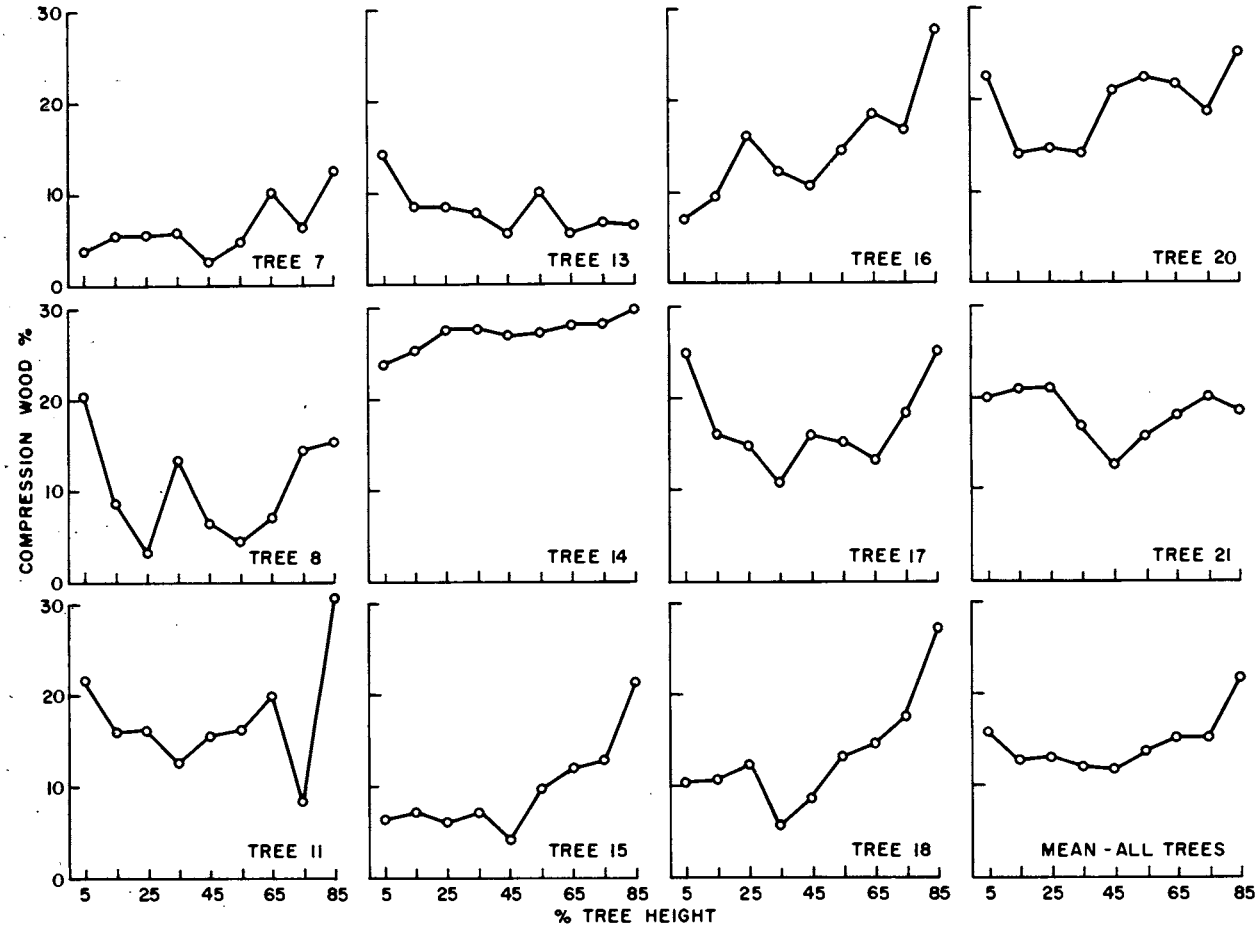

FIGURE 1. — Variation of compression wood content with height in each of 11 black spruce trees and in all trees combined.

percent level r was calculated at 0.597 (not sig.). If the results of the second, more intensive investigation can be confirmed it would appear that, to predict total compression wood from increment cores, the cores should be taken somewhat above breast height, perhaps at the 15-percent level where r was found to be +0.959. Studies of the predictive capability of increment core samples are at present underway, as are other confirmatory investigations.

Pulping Trials

The primary objective of the first pulping trial was to obtain indirect confirmation of the efficiency of the method used to estimate compression wood. As compression wood is abnormally high in lignin, and as high lignin content tends to reduce the yield of pulp, given equivalent pulping conditions, then a negative correlation between pulp yield and compression wood content might be expected — if the latter had been estimated correctly.

Accordingly, from the 11 trees mentioned above, 68 samples of known compression wood content were chipped and cooked for 3 hours using sodium bisulphite. Weight of chemical was 20 percent that of the wood. Liquor to wood ratio was 5 to 1, so that actual concentration of chemical was 4 percent. Percent screened pulp yields were determined for each of the 68 pulps prepared; the relations between percent compression wood and pulp yield were then analyzed statistically, with Kappa number taken to be a covariable;[2] and the coefficient of correlation between yield and compression wood content was calculated. This was —0.745 and significant at over the 0.1-percent level.

[2] *Kappa number, as a measure of residual lignin, indicates the degree to which a pulp has been cooked and is commonly used as a basis for the comparison of pulps.*

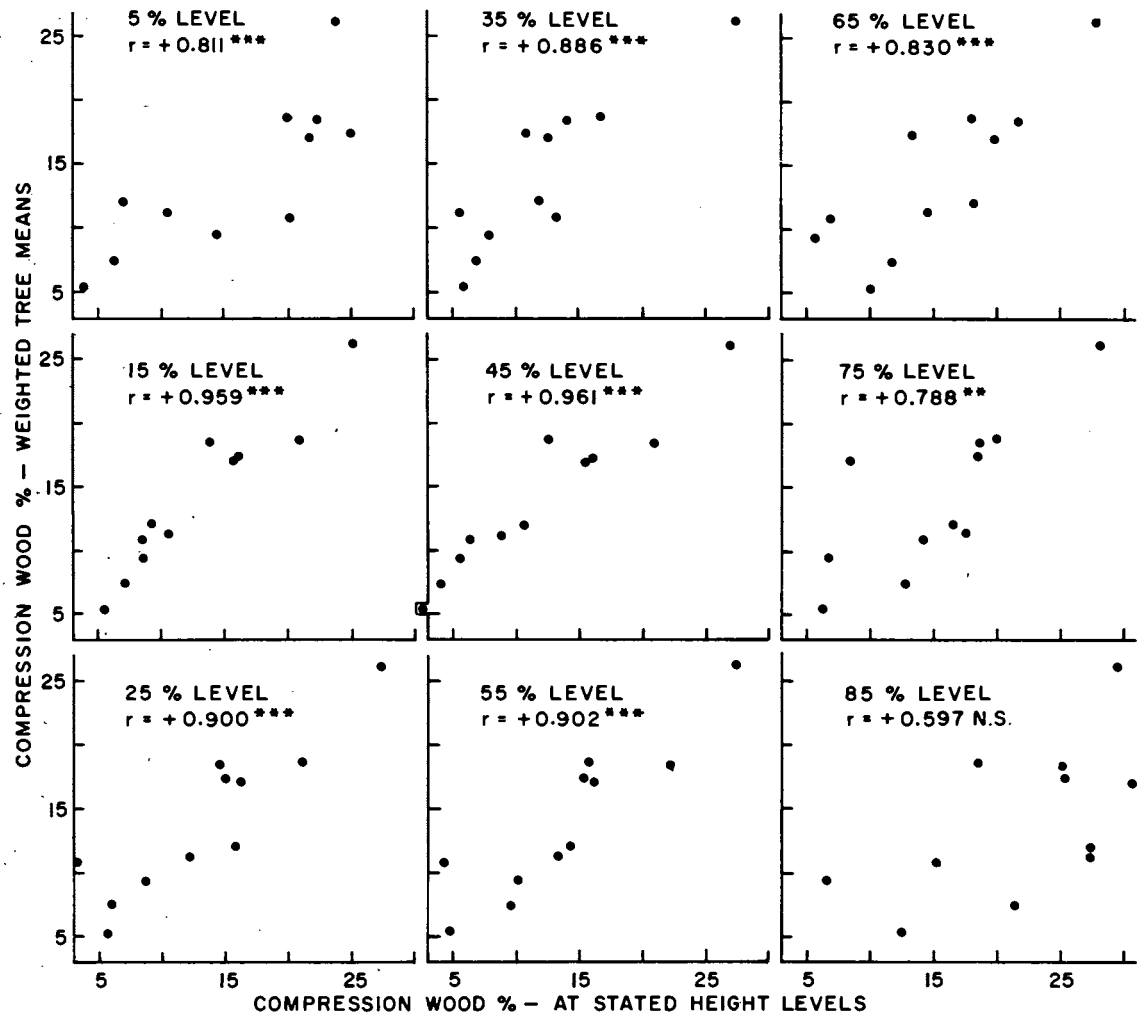

FIGURE 2. — Relation in 11 black spruce trees between the mean compression wood content of entire trees and the compression wood content at nine predetermined height levels.

The regression of yield on compression wood percent was calculated as $Y=53.05-0.2910X$, a linear relation being assumed. The regression was highly significant ($F=82.18^{***}$), with compression wood accounting for 55.5 percent of the variation in yield. An estimate of the effect of compression wood on yield from pulps cooked to known lignin content was obtained by calculating a further regression, with the Kappa number of the pulps as a second independent variable. The regression was $Y=44.99-0.25X_1 + 0.14X_2$ ($F=91.17^{***}$) where X_1 = percent compression wood and X_2 = Kappa number (fig. 3). Each variable was highly significant when the effect of the other was removed. F was 97.23^{***} for compression wood and 45.16^{***} for Kappa number.

It was felt that these results amply proved the accuracy of the point sampling system of estimating compression wood. The results also suggest that compression wood content might prove to be a useful indicator of yield. This possibility is now being examined in the light of specific gravity differences in the same set of samples.

Characteristics of Black Spruce Compression Wood and Effects on Paper Strength

Three mature trees with pronounced lean were selected from a stand in Fournier Township, and a 4-foot bolt centered on the breast height level was removed from each and reduced to ¾-inch discs. As was hoped, compression wood was present in large amounts and in well-defined areas. These areas were delineated, together with zones of opposite and side wood, using the procedure followed by Watson and Dadswell (1957) (fig. 4).

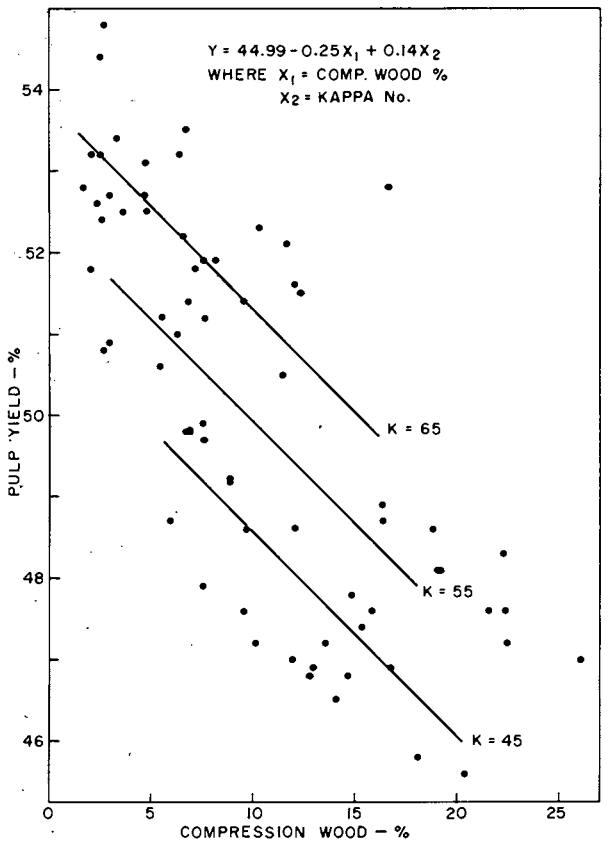

FIGURE 3. — Pulp yield and compression wood for pulps cooked to different lignin contents.

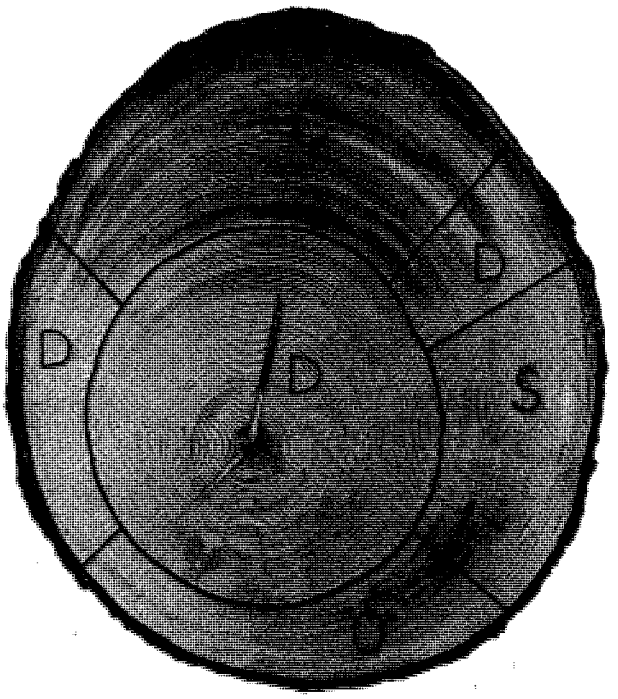

FIGURE 4. — Delineation of discs for pulp and papermaking tests. *C* is taken to be 100-percent compression wood. *S* (sidewood) and *O* (opposite wood) are taken as no compression wood; these were combined to give "normal" or control fraction. *D* is discarded as containing varying amounts of compression wood.

A comparison of chemical and morphological characteristics for the three zones and for control material obtained from the mature wood of a defect-free tree shows that the compression wood zone has a relatively high lignin content, is somewhat lower in pentosans, and displays a markedly higher specific gravity (table 2). These results generally agree with those obtained by other workers. Pillow *et al.* (1935), for example, reported a lignin content of 35.2 percent for the compression wood of loblolly pine (*Pinus taeda* L.) compared to 28.3 percent for normal wood, with pentosans at 12.2 percent compared with 12.4 percent. That compression wood chips, after conditioning and before pulping, tend to equilibrate at a higher moisture content is of some general interest (table 2). The overall mean fiber lengths in the compression and side wood bands were statistically identical, and each was significantly less than the length in the opposite wood zone.

Pulp and papermaking trials were carried out first on pure samples from the three zones. Cooking procedure was essentially the same as that described above. When the trials showed that paper characteristics from the side and opposite wood zones were essentially the same, the chips from the two latter zones from all three trees were combined to form a fraction which was termed "normal" wood. Chips from the compression wood zones from all three trees were similarly pooled. Chips from normal and compression wood were then mixed to give a series of fractions containing different proportions of compression wood on a percentage ovendry weight basis. Percentage dry weight values were later converted to percentage dry volume values by assuming a specific gravity of 0.53 for compression wood and 0.40 for normal wood.

The fractions containing 0-, 5-, 10-, and 100-percent compression wood (by weight) were pulped over a range of cooking times and Kappa numbers. Due to lack of material, only a single cook to give a Kappa number of 80 was made of the 20-, 30-, 40-, and 50-percent compression wood fractions. All pulps were beaten in a PFI mill over a series of predetermined number of revolutions; handsheets were prepared and strength tests carried out according to Tappi Standard T-220 m-60.

Figure 5 shows values for tear, burst, and tensile strength (breaking length) of handsheets from pulps beaten to 350 CSF plotted against percent compression wood by volume. Figure 6 shows strength values expressed as a percentage of those

Table 2.--Miscellaneous characteristics of fractions from black spruce trees with high compression wood content

Sample	Pentosans	Lignins	Conditioned E.M.C.[1/]	Specific gravity	Tracheid length: Mean	Tracheid length: Standard deviation	Tracheid length: Coefficient of variation
	(Percent)		(Percent)		(mm.)	(mm.)	(Percent)
Opposite wood	7.6	25.2	8.8	0.408	3.47	0.29	8.3
Side wood	7.4	25.3	8.6		2.98	.78	26.1
Compression wood	7.2	31.1	9.2	.528	3.08	.13	4.1
Control	7.3	27.0	8.6	.396	3.40	.56	16.3

[1/] Equilibrium moisture content: the moisture content attained by wood under given conditions of temperature and humidity.

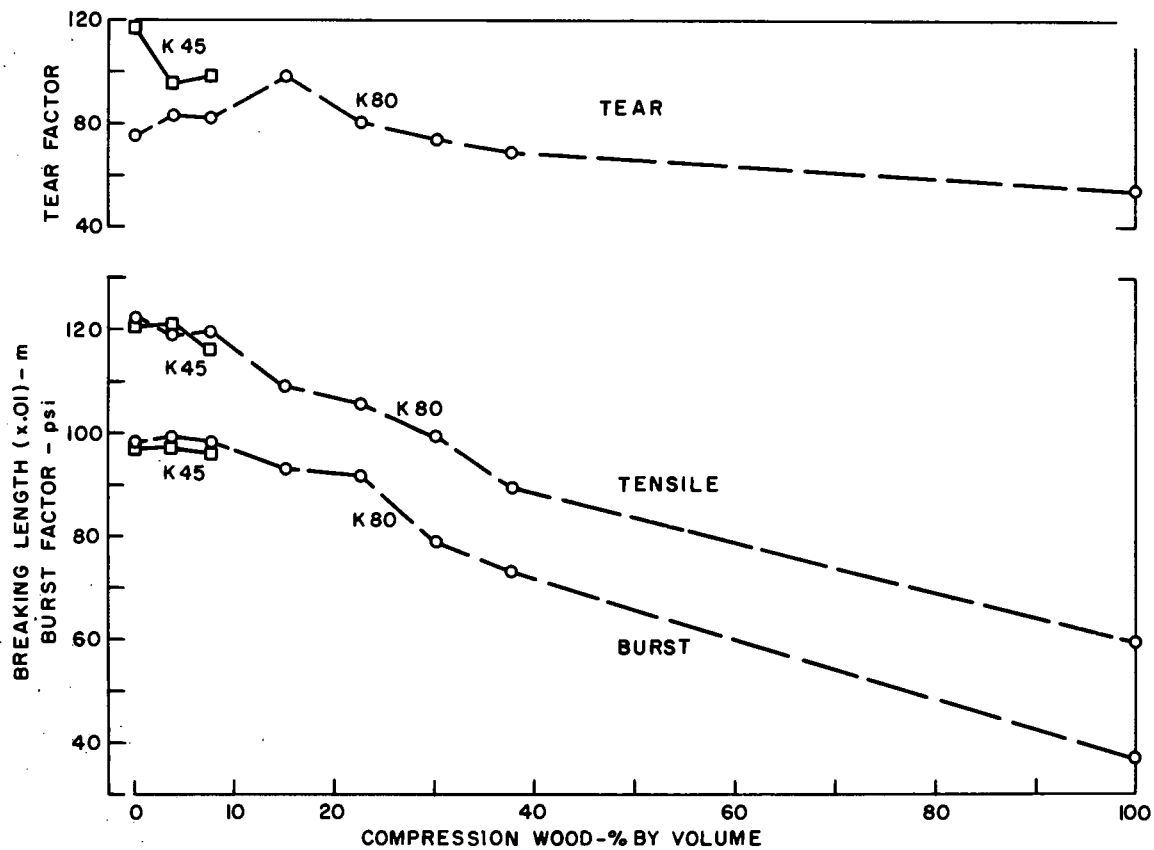

FIGURE 5. — Compression wood content and paper strength.

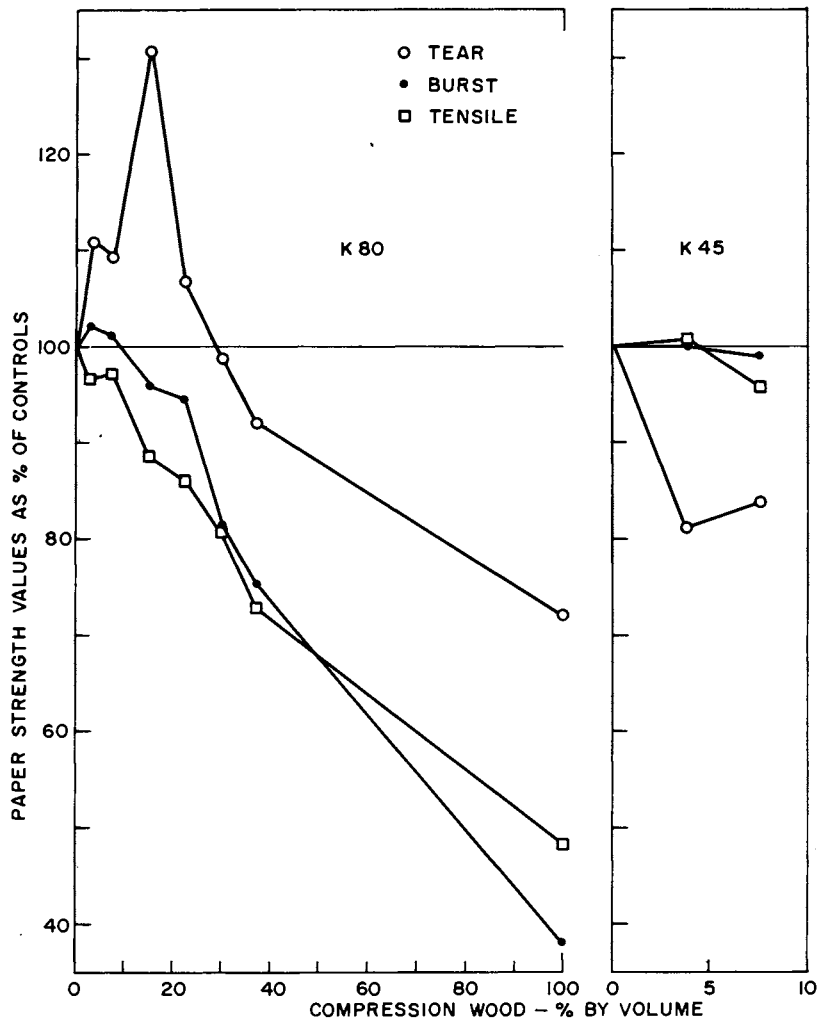

FIGURE 6. — Compression wood and paper strength values expressed as a percentage of the control values.

given by the normal wood fraction. All fractions were cooked to a Kappa number 80, but only three fractions were cooked to the lower Kappa number 45.

Tensile strength of paper made from the pulps cooked to a Kappa number 80 decreased steadily with increasing compression wood content, with pure compression wood having a tensile strength half that of the normal wood used as control. The effect of compression wood when present in the average amount indicated by the investigation discussed earlier — that is, approximately 15 percent by volume — would be to reduce tensile strength by 12 percent. With longer cooking times and Kappa numbers lower than 80, the reduction in tensile strength would be greater than this.

Compression wood in amounts up to about 10 percent appeared to have a beneficial effect on burst strength; the effect, however, disappeared with a longer cook and a lower Kappa number. Compression wood content of 15 percent resulted in a 4-percent decrease in burst strength with the Kappa number 80 pulps. Extrapolation indicated that in the Kappa number 45 pulps the detrimental effect would be even less than this.

The results of the tear tests present some anomalies, with the 15-percent compression wood fractions from the Kappa number 80 pulp giving a tear strength 30 percent greater than the control. It may be that at high Kappa numbers compression wood in small amounts enhances tear strength, but, on the other hand, the results from the Kappa number 45 pulp indicate a 20-percent loss in tear strength. It is felt that this aspect of the results should be treated with reserve.

In summation, these admittedly limited studies indicate that, with the possible exception of tear strength, the strength properties of paper will not

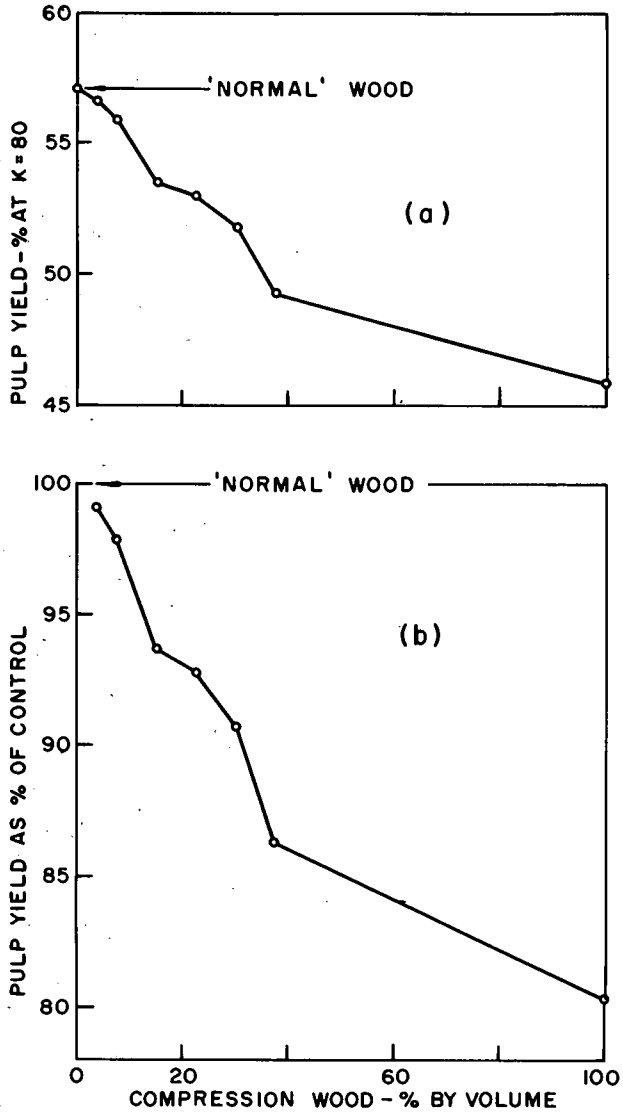

FIGURE 7. — (a) Compression wood content and screened pulp yield; (b) compression wood content and screened pulp yield expressed as a percentage of the yield from "normal" wood.

be affected adversely to an excessive degree by the presence of compression wood in the amounts normally encountered.

The effect on yield, however, could be significant. Screened pulp yields are plotted against compression wood percent in figure 7a, and yield expressed as a percentage of that obtained from the normal compression wood free fraction is plotted in figure 7b. Data presented earlier suggest that 15 percent is not an unrealistic value for the relative amount of compression wood in a stand. This would result in a loss in (chemical) pulp yield of over 6 percent. It would appear then that in a stand of 120-year-old black spruce on a medium site (Site Class 2, Plonski 1956) yielding 2,700 cubic feet or 34 tons of merchantable wood per acre, the loss resulting from the presence of compression wood might be as much as 1 ton per acre, or over 600 tons of usable pulp per square mile.

A more detailed account of this work will appear elsewhere in due course.

Summary

A point sampling system was used to measure the amount of compression wood in over 400 discs from 11 mature black spruce trees grown on a good lowland site in Challies Township, Ontario. Overall mean compression wood content in the 11 trees was found to be 13.9 percent by volume, with mean values in individual trees varying from 5.3 to 26.1 percent. Compression wood content tended to be higher at the base and in the upper crowns of trees. Correlation coefficients were calculated between mean compression wood content for trees and content at each of nine levels within trees. For all except the topmost level sampled, the coefficients were highly significant and ranged between +0.788 and +0.961, indicating strong uniformity of content within trees.

The accuracy of the point sampling method for the determination of compression wood content was confirmed by (sulfite) pulping trials on 68 samples, which showed that compression wood percent and pulp yield were closely correlated ($r=-0.745^{***}$). Other trials indicated that while compression wood present in normal amounts does not result in a serious reduction in paper strength, pulp yields might be reduced by as much as 6 percent. Calculations based on known yields from black spruce stands of the commonest site class showed that reduction in pulp yields of this order would result in a loss of about 1 ton of usable fiber per acre.

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