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Influence of Provenance and Test Location on Wood Formation in Pinus banksiana Lamb. Seedlings

By R. W. KENNEDY[1])

Introduction

The objectives of this study were to determine the degree of variation existing in certain xylem characteristics among 29 widely distributed provenances of jack pine *(Pinus banksiana* LAMB.), and to correlate variations in xylem formation and structure with origin of seed and phenology of leader growth of the seedlings.

The provenances studied were chcsen from the larger number included by HOLST (1963) in his all-range jack pine provenance experiment. The 29 provenances were selected along major transects to give northern, intermediate and southern sources and replicated in test locations at the Petawawa Forest Experiment Station, Chalk River, Ontario, and the Acadia Forest Experiment Station, Fredericton, New Brunswick *(Fig.* 1, *Table 1).* Details of the techniques employed, along with some analysis of the results obtained in the Petawawa experiment have already been published (KENNEDY, 1969). The description of methods used has therefore been abbreviated.

Materials and Methods

Five four-year-old seedlings from each source were randomly selected for study of their growth during their fifth growing season in 1966. In order to mark the progress of annual increment formation, these seedlings were subjected to a minute mechanical injury at the base of the two-year-old (1964) internode three times during the growing season. This permitted calculation of the percentage of the annual increment formed by June 10, July 15 and August 20. Leader growth of the seedlings was measured at approximately weekly intervals until growth was completed.[2])

The xylem characteristics given in *Table* 1 were determined as outlined previously (KENNEDY, 1969). Although the experimental design called for five replications per provenance, a complete set of phenological and xylem data was sometimes unavailable for certain trees. Missing phenological observations were caused by insect and mechanical damage to leaders. Occasional absence of traumatic wound tissue in the xylem was noted, probably owing to the failure of injury-causing pins to penetrate far enough through bark to reach susceptible differentiating xylem.

[1]) Department of the Environment of Canada, Western Forest Products Laboratory, Vancouver, B. C.

[2]) Stem injury and leader measurements were carried out at Petawawa and Acadia Forest Experiment Stations under the direction of M. J. HOLST and H. G. MACGILLIVRAY, respectively.

Results and Discussion

The mean values for various xylem characteristics are presented in *Table* 1 by provenance and test location.

Analysis of variance indicated significant differences in xylem characteristics among provenances, with the single exception of the day of appearance of the first latewood tracheid in the Acadia experiment. Similar analyses between test locations revealed a significantly wider annual increment and earlywood and latewood component in the Acadia material, although height growth achieved during 1966 did not vary significantly between locations. The only other xylem characteristic that varied significantly between locations was the percentage of ring formed by August 20. By this date, the Acadia material had formed 5 percent more of its total increment for the year.

The degree to which the provenances performed similarly at Petawawa and Acadia was measured for each attribute by the correlation existing between paired mean values for each seed source *(Table 2).* The significant coefficients for total ring width and its two component parts show that individual provenances tend to behave similarly between test locations. The lack of a significant relationship with latewood percentage indicates an important genotype-environment interaction. The greatest degree of correlation between xylem characteristics at the two locations was in percentage of ring formed by August 20. This consistency suggests that time of cessation of cambial activity is under strong genotypic control, ending earlier in some provenances than in others regardless of the planting location. Initiation of activity may be under less genotypic control, judging by the lack of correlation between Petawawa and Acadia in percentage of ring formed by June 10.

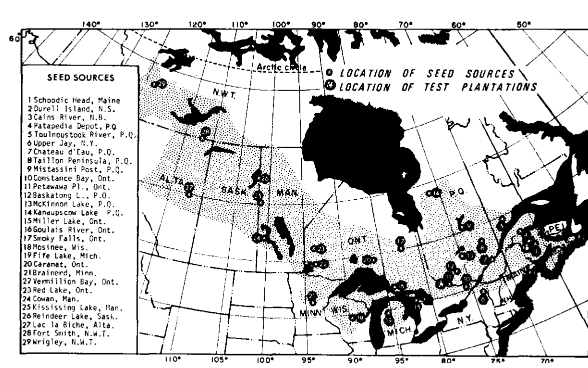

Fig. 1. — Location of provenances and test locations within the natural range of *Pinus banksiana.*

Table 1. — Variation in xylem characteristics by provenance and test location. — Mean values for 1966 increment.

Provenance No.[1]	Transect location (E to W)	Growing-degree days	Ring width (mm)	Earlywood width (mm)	Latewood width (mm)	Latewood percent	Percent of ring by June 10	Percent of ring by July 15	Percent of ring by August 20	Day[2] of Appearance of first latewood	Specific gravity[3]
			PETAWAWA EXPERIMENT								
1	Coastal	2700	1.03	0.67	0.36	33.9	20.5	62.2	77.6	207	0.396
2		2600	1.07	0.68	0.38	36.8	28.4	62.0	78.7	203	0.376
3	N.B. - Que.	2700	2.94	1.60	1.34	42.8	30.8	58.9	76.8	195	0.378
4		2400	2.68	1.58	1.10	40.8	28.0	61.6	84.5	199	0.382
5		1600	1.30	0.80	0.50	39.8	27.2	60.1	81.4	197	0.408
7	Quebec	2900	1.36	0.87	0.51	37.1	33.0	64.2	80.7	194	0.386
8		2300	2.58	1.76	0.81	31.2	35.7	66.5	83.4	202	0.378
9		1400	2.13	1.33	0.80	34.8	31.8	65.2	86.2	192	0.392
6	N.Y. - Ont. - Que.	3600	2.51	1.58	0.94	37.3	37.5	60.1	81.1	200	0.386
10		3200	2.14	1.52	0.62	28.8	34.2	67.0	83.2	205	0.364
12		2500	1.76	1.12	0.64	35.6	27.4	59.8	73.9	208	0.378
13		2100	2.04	1.27	0.77	37.5	22.8	58.0	83.1	203	0.410
14		1000	1.70	1.14	0.56	32.1	35.8	69.4	87.8	195	0.410
15	E. Ontario	2900	3.18	1.70	1.48	45.5	27.8	55.0	77.2	195	0.388
11		2900	3.00	2.01	0.99	33.0	40.6	64.7	79.9	202	0.358
17		2000	2.50	1.37	1.12	44.2	18.6	50.1	74.2	203	0.424
19	Lower Mich. - Mid-Ontario	3300	3.03	1.64	1.38	45.5	32.3	56.4	79.0	195	0.366
16		2400	2.51	1.58	0.93	36.9	30.3	61.9	79.1	198	0.384
20		2000	1.91	1.30	0.62	32.3	33.6	67.4	86.0	197	0.394
18	Wis. - Minn. - W. Ontario	3200	2.45	1.48	0.97	39.1	25.4	63.5	78.6	194	0.364
21		3100	3.07	2.23	0.84	28.3	29.3	64.4	81.0	212	0.352
22		2500	2.76	1.80	0.96	33.6	33.1	64.3	81.8	203	0.406
23		1800	2.05	1.49	0.56	27.4	39.5	66.7	82.8	210	0.376
24	Man. - Sask.	2400	2.40	1.48	0.92	38.8	20.4	61.2	86.4	197	0.414
25		1800	1.36	0.86	0.50	34.1	27.3	63.8	90.6	196	0.394
26		1500	1.13	0.68	0.45	39.5	24.3	64.4	88.8	193	0.408
27	Alta. - N.W.T.	2100	1.94	1.25	0.69	35.7	23.4	63.9	88.4	197	0.398
28		1400	1.64	1.03	0.61	36.2	21.7	66.7	90.4	196	0.418
29		1700	1.17	0.79	0.38	30.1	21.7	65.3	90.0	203	0.400
Average for all provenances			2.11	1.33	0.78	35.1	29.0	62.5	82.5	199	0.389
Variance Ratio			4.92**	5.24**	4.02**	4.07**	1.85*	5.24**	1.85*	1.99*	4.83**
			ACADIA EXPERIMENT								
1	Coastal	2700	3.15	1.90	1.25	39.4	29.8	57.3	82.7	202	0.414
2		2600	2.60	1.57	1.03	39.7	28.5	57.3	83.3	201	0.398
3	N.B. - Que.	2700	2.99	2.05	0.94	32.0	33.3	62.5	86.1	204	0.386
4.		2400	3.75	2.54	1.21	32.9	27.5	57.0	83.3	210	0.394
5		1600	3.18	2.15	1.03	32.5	29.6	68.0	88.4	---	0.382
7	Quebec	2900	3.08	1.94	1.14	36.8	29.2	62.8	87.7	199	0.386
8		2300	2.39	1.55	0.84	34.8	26.2	62.8	87.8	200	0.392
9		1400	3.06	1.86	1.20	39.4	26.3	67.2	90.1	191	0.418
6	N.Y. - Ont. - Que.	3600	2.68	1.84	0.84	32.5	28.6	45.2	82.4	---	0.402
10		3200	3.06	2.04	1.02	34.1	27.6	58.9	84.4	---	0.378
12		2500	3.71	2.30	1.41	37.6	28.0	58.9	84.4	201	0.386
13		2100	3.93	2.44	1.49	38.7	20.4	56.0	84.0	203	0.396
14		1000	1.72	1.07	0.65	38.1	30.7	70.0	93.4	190	0.444
15	E. Ontario	2900	3.42	1.84	1.59	46.6	20.1	46.2	83.4	200	0.400
11		2900	3.98	2.63	1.36	34.1	26.5	54.3	81.8	209	0.394
17		2000	2.17	1.47	0.70	31.2	30.2	64.7	90.3	199	0.398
19	Lower Mich. - Mid-Ontario	3300	4.04	2.42	1.62	40.4	22.7	54.4	82.0	204	0.378
16		2400	2.74	1.76	0.98	36.1	32.2	63.2	88.9	198	0.386
20		2000	2.75	1.78	0.96	34.4	28.9	65.4	88.7	194	0.388
18	Wis. - Minn. - W. Ontario	3200	3.60	2.16	1.44	39.3	28.8	----	83.8	---	0.374
21		3100	4.09	2.51	1.56	38.5	27.0	----	86.0	---	0.356
22		2500	3.11	1.84	1.28	40.9	28.7	56.3	87.6	199	0.388
23		1800	2.74	1.63	1.10	40.6	32.1	65.7	89.1	191	0.394
24	Man. - Sask.	2400	2.38	1.52	0.86	35.5	29.1	68.7	93.5	195	0.406
25		1800	2.58	1.84	0.74	28.6	28.6	----	94.1	208	0.396
26		1500	1.45	0.96	0.50	34.1	25.7	66.9	93.0	199	0.402
27	Alta. - N.W.T.	2100	2.41	1.58	0.83	34.8	30.7	65.0	93.5	196	0.410
28		1400	2.14	1.33	0.81	36.5	25.4	66.3	93.0	191	0.408
29		1700	1.16	0.73	0.43	39.5	22.3	44.9	88.9	208	0.430
Average for all provenances			2.89	1.83	1.06	36.5	26.7	57.9	87.4	199	0.396
Variance Ratio			6.44**	4.72**	4.98**	1.59*	2.13*	5.56**	4.33**	1.30	2.12**

[1] See Fig. 1

[2] Numerical day of year

[3] Extracted, oven-dry weight/green volume

* Significantly different at 5% level
** Significantly different at 1% level

Provenance No. 17 (Smoky Falls, Ontario) provides an outstanding example of a genotype interacting with environment. It was one of only two provenances that displayed a substantially wider ring at Petawawa than at Acadia. It also developed significantly more latewood at Petawawa, resulting in a much larger latewood percentage at this location than at Acadia. The formation of the annual increment was retarded markedly at Petawawa (*Table 1*), resulting in considerable wood formation in the latter part of the growing season under conditions conducive to latewood development.

It was shown previously (KENNEDY, 1969) for the Petawawa experiment that the average date for initiation of the first latewood tracheids corresponded closely in time to the

Table 2. — Correlation coefficients for provenance means between the Petawawa and Acadia locations.

Attribute	r
Ring width, 1966	0.53**
Earlywood width	0.50**
Latewood width	0.44*
Latewood percentage	—0.03
Percentage of ring by June 10	0.18
Percentage of ring by July 15	0.30
Percentage of ring by August 20	0.68**
Date of appearance of first latewood	0.15
Specific gravity (pith-to-bark disk)	0.59**

* Significantly different at 5% level
** Significantly different at 1% level

average date of cessation of leader growth (i. e., leader growth 98 percent completed). The Acadia experiment essentially supports this finding, since the average date of appearance of the first mature latewood tracheid was identical for both experiments (day 199, July 18). This event occurred seven days following achievement of 98 percent of total leader length in the Acadia material, and 17 days after the average date of completion of leader growth in the Petawawa seedlings. Since this time differential can be interpreted as the lag required for tracheid differentiation (KENNEDY and FARRAR, 1965), it appears that latewood initiation occurs coincidentally with cessation of height growth. This result substantiates the observations of LARSON (1964), who concluded that while earlywood production is stimulated during the period of active leader growth, cessation of this activity promotes formation of latewood tracheids. This transition to latewood-type tracheids is apparently mediated by a reduction in indoleacetic acid and possibly other growth hormones as a consequence of reduced vegetative activity (LARSON, 1964; SHEPHERD and ROWAN, 1967; BALATINECZ and KENNEDY, 1968).

Many phenological and xylem attributes showed a significant relationship with provenance, when geographic location was expressed in terms of growing-degree days[3]) at point of origin *(Table 3)*. The total 1965 heights were bigger and the 1966 leaders were longer in those sources originating from areas with the greatest number of growing-degree days. A later completion of leader growth was associated with increasing growing-degree days, since a smaller percentage of total leader length was accomplished by June 10 and a longer time was required to reach 90 and 98 percent of total leader length. Wider rings and greater earlywood and latewood widths were associated with greater growing-degree days, but latewood percentage was not affected. Since a smaller percentage of the 1966 increment was completed by August 20 in those provenances having greater growing-degree days, a delayed cessation of cambial activity is indicated in those provenances originating from milder climates. This is not unexpected, considering the later completion of height growth noted in these provenances.

Specific gravity decreased with greater growing-degree days, but the reduction was not great *(Table 1)*. The degree of association between specific gravity and other xylem and phenology attributes could not be determined, because specific gravity was estimated for the entire internode section encompassing all three rings, while other attributes were limited to only the final growing season.

[3]) Growing-degree days are expressed numerically by the summation of mean daily temperatures exceeding 42° F.

Table 3. — Correlation coefficients relating phenological and xylem attributes to growing-degree days of provenance at point of origin.

Attribute	Petawawa experiment	Acadia experiment
Ring width, 1966	0.51**	0.61**
Earlywood width	0.49**	0.59**
Latewood width	0.47**	0.57**
Latewood percentage	0.18	0.12
Percentage of ring by June 10	0.25	—0.07
Percentage of ring by July 15	—0.30	—0.60**
Percentage of ring by August 20	—0.62**	—0.75**
Date of appearance of first latewood	0.22	0.54**
Specific gravity (pith-to-bark disk)	—0.69**	—0.62**
Total leader length, 1966	0.57**	0.65**
Percentage of leader length by June 10	—0.78**	—0.75**
Date when leader reaches 90 percent of total length	0.78**	0.69**
Date when leader reaches 98 percent of total length	0.61**	0.33
Total seedling height in 1965	0.43*	0.71**

* Significantly different at 5% level
** Significantly different at 1% level

Table 4. — Simple correlation coefficients greater than 0.50 between growth characteristics determined over all trees

	Ring width	Early-wood width	Late-wood width	Late-wood %	% Ring by July 15	Total leader length in 1966	% Leader length reached on June 10	Date when leader reaches 90 % of total length	Day when 1st latewood appears
Total seedling height in 1965	(.39) .66	(.49) .61	(.18) .57			.64 .72			
Ring width		.94 .94	.90 .85			.64 .74	—.60 —.73	.60 .71	
Earlywood width			.69 .61			.71 .65	—.54 —.64	.59 .63	
Latewood width				.62 .57	—.51 (—.32)	(.42) .63	—.56 —.63	(.48) .61	
Latewood %					—.64 (—.24)				—.56 —.66
% Ring by July 15									(—.20) —.54
Total leader length in 1966							—.62 —.71	.67 .73	

Upper figure = r for the Petawawa experiment
Lower figure = r for the Acadia experiment
(Paired values less than 0.50 are in brackets)

Larson (1967) found significant differences in vegetative and wood characteristics among sources in a study of ten *Pinus resinosa* Ait. provenances, but uncovered no consistent relationship with geographic origin or latitude. The larger number of provenances in this present study, along with wider geographic bounds and the choice of growing-degree days to express origin, may have resulted in trends becoming apparent.

Simple correlation coefficients between growth characteristics, determined over all trees regardless of source, are included in *Table 4*. Because of the high degrees of freedom involved (29 provenances $\times$ 5 replicates — 2), many coefficients were statistically significant, but only those greater than 0.50 are presented. Calculation of overall coefficients is not rigorous, owing to the confounding of variation within a provenance with that among provenances. In general, however, a significant correlation among provenances was accompanied by a similarly significant r within a provenance.

As might be expected, total ring width was strongly associated with both earlywood and latewood width. Ring width also was correlated positively with total height growth and with later dates of completion of leader growth. Earlywood and latewood widths were related, and showed the same general association with height growth as total ring width. In the Petawawa material, latewood percentage was correlated with those trees having smaller percentages of their rings completed by July 15. In both experiments, latewood percentage was greater in those trees initiating latewood formation at an earlier date.

Summary

Twenty-nine provenances were examined at two test locations for progress of wood increment formation during the 1966 growing season. Total increments and their earlywood and latewood components were consistently wider for individual provenances at the Acadia location, indicating both environmental and genotypic controls for these attributes. Wider rings, greater widths of early- and latewood, larger seedling heigths and leader lengths were associated with provenances originating from regions of greater growing-degree days. Latewood formation commenced generally at the conclusion of the grand period of leader growth. Latewood percentage was not systematically related to provenance, but showed considerable genotype-environment interaction.

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Natural hybridization between Cuban Caribbean and Slash pines

By M. U. Slee[1])

Introduction

The nursery stock raised from seed collected in a plot of grafted Cuban Caribbean pine *(Pinus caribaea* Mor. var. *caribaea* B. & G.) regularly includes a proportion of seedlings differing from those typical of this species. The grafts are surrounded by Slash pine *(Pinus elliottii* Engelm. var. *elliottii* L. & D.). Observations reported here on two batches of seedlings originating from the grafts suggest that natural hybridization has occurred between the two species.

Material

The grafted plot contains five clones of Cuban Caribbean pine. The ortets of these clones were selected for breeding purposes in 1957 in a 24-year old trial planting of the species at Banyabba Forest in northern New South Wales, Australia (Latitude 29° 30' S.). Immediately after selection the ortets were grafted onto stock plants of Slash pine. Approximately 80 successful grafts resulted and were outplanted in 1958 at Bowenia Forest (Latitude 22° 50' S.) in central Queensland. A plantation of Slash pine, also established in 1958, surrounds the grafted plot.

Flowering of the grafts commenced in 1962 and the first seed was produced in 1964. Seedlings of Cuban Caribbean are characterized by a dark green colour, predominantly three or four secondary needles per fascicle, and the early production of secondary needles (Luckhoff, 1964). The first sowing of the seed from the grafts, made early in 1966, produced some seedlings which were noticeably atypical and a further sowing was made later the same year to examine this variation.

The observations reported were made on the seedlings from the later sowing, which included two batches of seed collected from the Cuban Caribbean grafts in 1965 and 1966 (Batches 65 and 66) and a control batch of Slash pine. Seedfall of Slash pine occurs in March in Queensland and it was therefore impossible to include seed collected from the Slash pine surrounding the Cuban Caribbean grafts. Seed from a routine Queensland collection was used as the Slash pine control. A Cuban Caribbean control could not be incorporated as seed was unavailable.

[1]) Queensland Department of Forestry, Queensland, Australia. Present address: — Department of Forestry, Australian National University, Canberra, A.C.T., Australia.