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Genecological Variation in *Pinus strobus*: Growth Rate, Date of Fall Needle-Shedding, and Second-Winter Needle Retention¹⁾

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Summary

At a test site in New Jersey, genecological variation in eastern white pine, *Pinus strobus* L., exists not only in growth rate, but also in the time of fall shedding of old needles, and in percent of needles held on trees through a second winter.

We examined a 57-seedlot progeny and provenance test plantation at New Brunswick, NJ after six growing seasons to determine the extent of variation in these characteristics, and their correlation with latitude of origin. Seedlot differences explained 64% of variation in height, 35% of variation in date of fall yellowing of old needles, and 18% of variation in second-winter needle-holding. Variation in all three responses was significantly associated with latitude of origin of female parent.

Key words: genecology, geographic variation, phenology, needle retention, growth, white pine.

Introduction

In contrast to the many reports on comparative height growth of eastern white pine, *Pinus strobus* L. (GARRETT *et al.*, 1973; WRIGHT *et al.*, 1978), very little information has accumulated on variation in its needle-shedding phenology

and holding of needles through a second winter, characteristics of importance to its value as a Christmas tree. In 1922, Sargent stated that needles mostly turn yellow and fall in September of their second season, or persist until the following June. In 1971, Walters noted that most white pines in winter have needles both from the current year and one past year, but some have needles only from the current year's growth. He found no evidence of partial needle drop on trees holding needles through a second winter, or of white pines with needles from more than two growing seasons in the winter. In 1974 COLLINGWOOD and BRUSH stated that needles remain on white pines from three to five years. In 1979, HARLOW *et al.* agreed with SARGENT, stating that they persist until the end of the second season or the following spring. Despite the contradictions, none of these authors made any reference to genecological variation in the amount of needle holdover through the second winter, or in the timing of fall needle-shedding.

Curious about these sparse and conflicting reports, we studied the genecology of needle shedding and winter needle retention at our 6-year-old 57-seed-source test plot in New Brunswick, NJ. Before examining the plantation, we first made some general observations on white pines in our area. Yellowing and shedding of old needles occurred during September and October, with several days' difference in shedding time among trees in the same stand.

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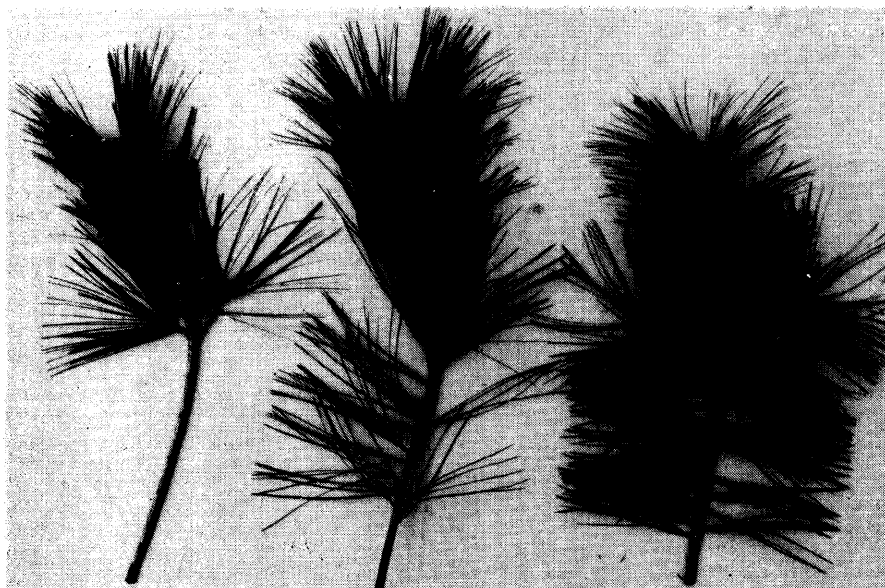


Figure 1. — First-season, partial second-season, and full second-season needle holding (left to right) on eastern white pine. Photo taken in April before elongation of new growth.

Variation in retention was also evident, with some young, vigorous trees up to 3 m high holding only first-season needles through the winter, but a few holding second-season needles. There was a continuum between first-season, partial second-season, and full second-season needle holding (Fig. 1), with gradual increase in holding time taking place as trees mature. Trees c. 5 m high often held only first-season needles near the top but many or all second-season needles on lower branches. Mature trees 10 m to 25 m high all held second-season needles through the winter. Two large trees on our campus that appear to be Himalayan pines (*P. griffithii* McCLELLAND) or white × Himalayan pine hybrids held third-season needles on some branches.

Materials and Methods

In March 1981, we obtained 1,200 2-0 seedlings of 57 different seedlots of white pine from the U.S. Department of Agriculture Forest Service. Of the 57 (Table 1), 47 were half-sib families of open-pollinated seedlings from selected clones grown in seed orchards. Nos. 32 and 54 were both progeny of seed parent clone MD 7, with seed of No. 32 collected in a Pennsylvania seed orchard and No. 54 in a Maryland orchard. Nos. 1 and 20 were mixed seed orchard progeny from New York, No. 43 was grown from bulked seed collected from an Ohio plantation of unknown source, and the remaining 7 were progeny of wild trees in native stands. All seedlings were grown for their first two seasons at Buckingham Forest Tree Nursery, Harmans, Maryland.

Seedlings were planted in 4 randomized blocks on a uniform Nixon loam site at Cook College Horticulture Farm No. 1, New Brunswick, New Jersey. Each seedlot was represented by one 5-tree row plot in each block. No fertilizer was applied in 1981 and 1982; 180 g/tree of 16-8-8 was applied in spring 1983. Simazine³) was used to control weeds in a 0.3 m diameter circle around each seedling in 1981, and a Simazine-Enide mixture in 1982 through 1984. Roundup was used in October 1984.

³) The use of trade or proprietary names is for information purposes only and does not imply endorsement by Silvae Genetica or Rutgers University.

Beginning on 20 August 1986 and continuing weekly until 20 October, one of us (JCE) visually estimated the color of second- or third-season needles as blue-green, turning yellow, bright yellow, or brown (dead). At the end of this period, we determined (by examination or interpolation of data) the date on which each tree's old needles were bright yellow. We used the date of brightest yellow as a phenological marker because it is a brief, well-defined event compared to subsequent browning and shedding, which occur gradually over two weeks.

On 20 October, we visually estimated holdover of second-season needles, rating each tree 0 (all gone), 1 (0% to 25% still on tree), 2 (25% to 50% still on), 3 (50% to 75% still on), 4 (75% to 100% still on). Afterwards, we measured each tree's height to the nearest 0.1 m. We used analysis of variance (SAS, 1982) to determine whether variation in height, date of needle yellowing, and second-winter needle retention were significantly influenced by seedlot, and DUNCAN'S test ($P = 0.05$) to determine significance of differences among seedlots. After significance had been established, we used GLM (SAS, 1982) to regress seedlot mean data for height, date of brightest yellow, and needle retention against latitude of origin of female parent to determine whether latitude was a significant predictor of the three responses.

Results

Plantation mean height was 2.36 m; trees belonging to the tallest seedlot averaged nearly twice as tall as those of the shortest. Mean dates when old needles reached brightest yellow varied from 13 September to 10 October, and mean holdover of second-winter needles ranged from 3% to 86% (Table 1).

Analyses of variance showed that seedlot differences explained 64% of individual tree variation in height, 35% of variation in date of yellowing, and 18% of that in needle-holding ($P < 0.0001$). Regressions of mean height, yellowing date, and needle-holding against latitude of origin were significant ($R^2 = 0.30, 0.26, \text{ and } 0.18$ respectively, $P < 0.0002$) and showed tendencies for height, later needle-

Table 1. — Height (percent of plantation mean), data of fall yellowing, and second-winter needle retention of white pine at New Brunswick, NJ.

No.	Clone	Female Parent		Progeny		
		Origin	Latitude	Height	yellowing(date)	Retention(%)
41	PA 104	Ashton, MD	39° 00'	117	Sep. 30	66
52	MD 3	Harmans, MD	39° 07'	118	Sep. 26	55
62	MD 8	Harmans, MD	39° 07'	131	Oct. 2	86
32	MD 7	Swallow Falls, MD	39° 30'	99	Sep. 28	60
54	MD 7	Swallow Falls, MD	39° 30'	94	Sep. 28	55
60	MD 19	Potomac St. For., MD	39° 30'	88	Sep. 30	57
66	PA 53	Harford County, MD	39° 35'	112	Sep. 27	65
39	PA 111	Montalto, PA	39° 50'	101	Oct. 1	71
3	PA 90	Hagerty's Crossing, PA	40° 45'	110	Oct. 2	58
36	PA 78	Mifflinburg, PA	40° 50'	114	Oct. 10	82
31	PA 19	Stroudsburg, PA	41° 00'	99	Sep. 27	63
45	PA 26	Clearfield County, PA	41° 05'	117	Sep. 22	34
43	mixed	Findley S.P., OH	41° 08'	96	Sep. 24	48
17	PA 18	Pottersdale, PA	41° 10'	91	Sep. 14	12
30	PA 12	Cooksburg, PA	41° 20'	112	Oct. 5	62
33	PA 8	Cooksburg, PA	41° 20'	97	Sep. 30	67
44	PA 9	Cooksburg, PA	41° 20'	108	Sep. 22	49
50	PA 15	Cooksburg, PA	41° 20'	111	Sep. 27	60
46	mixed	Pachaug St. For., CT	41° 37'	108	Sep. 26	70
20	mixed	Sou. NY, nor. PA	42° 00' av.	108	Sep. 28	43
16	PA 77	Oxford, NY	42° 20'	90	Sep. 13	53
34	PA 79	Hobart, NY	42° 21'	104	Oct. 3	75
7	ERL-1	Rindge, NH	42° 44'	110	Sep. 27	43
42	VT 9-1	Brattleboro, VT	42° 52'	110	Sep. 27	45
5	HLY-1	Lyndeboro, NH	42° 54'	113	Sep. 26	55
19	HNBO-3	New Boston, NH	42° 57'	112	Oct. 1	65
49	HNBO-1	New Boston, NH	42° 57'	95	Sep. 25	39
1	mixed	Warren & Saratoga Co's, NY	43° 00' av.	110	Sep. 25	62
9	VT 7-2	Shaftsbury, VT	43° 00'	93	Oct. 8	69
18	VT 6-1	Shaftsbury, VT	43° 00'	108	Sep. 23	39
24	VT 7-1	Shaftsbury, VT	43° 00'	110	Sep. 28	57
27	PA 61	Saratoga Spring, NY	43° 05'	103	Oct. 4	75
22	ME 33	Wells, ME	43° 20'	100	Sep. 26	47
23	ME 32	Wells, ME	43° 20'	105	Sep. 23	45
8	MBO-1	Boscawen, NH	43° 23'	102	Oct. 2	51
25	SCL-1	Claremont, NH	43° 23'	86	Sep. 25	46
65	BSA-1	Sanborton, NH	43° 30'	103	Sep. 24	48
10	VT 3-2	West Rutland, VT	43° 35'	101	Sep. 25	45
51	VT 15-1	W. Rutland St. For., VT	43° 38'	101	Sep. 26	51
11	ME 23	Standish, ME	43° 45'	101	Sep. 26	39
64	ME 10	Durham, ME	43° 55'	107	Sep. 29	70
15	ME 12	Fryeburg, ME	44° 03'	95	Sep. 19	6
21	ME 28	Waldoboro, ME	44° 05'	77	Sep. 23	52
40	VT 2-1	Moretown, VT	44° 15'	91	Sep. 25	11
12	mixed	Adirondacks nr Jay, NY	44° 22'	87	Sep. 18	32
2	--	Searsmont, ME	44° 30'	100	Sep. 27	55
35	ONOR-1	Northumberland, NH	44° 33'	96	Sep. 28	59
48	ME 2	Anson, ME	44° 50'	115	Sep. 25	62
47	--	Ile du Grand Calumet, P.Q.	45° 47'	108	Oct. 6	76
61	WI 133	Chequamegon N.F., WI	45° 55'	72	Sep. 23	6
4	--	Ile aux Allumettes, P.Q.	45° 54'	78	Sep. 16	6
14	--	Deux Rivieres, P.Q.	46° 16'	72	Sep. 21	19
53	ONT 538	Ontario	n.a.	76	Sep. 22	3
55	U 113	Ontonagon County, MI	46° 33'	71	Sep. 14	9
58	Patton 312	Duluth, MN	46° 45'	94	Sep. 26	41
63	MN-27	Beltrami County, MN	47° 38'	63	Sep. 14	26

shedding, and greater needle-holding to increase southward (Fig. 2).

Four Maryland seedlots in our test (nos. 41, 52, 62, and 66) were extreme in all three responses: on average they were taller, shed old needles later in the fall, and held more needles through a second winter. Seedlots from the northwestern edge of white pine's range (nos. 4, 55, 61, and 63) were at the opposite extreme in these responses: they grew slowly here, shed old needles early in the fall, and held few needles through a second winter.

Discussion

Seedlots of white pine collected from native trees in different geographic parts of the species' range have shown

variation in growth rates at test sites in eastern North America (SLUDER, 1963; SLUDER and DORMAN, 1971; GARRETT *et al.*, 1973) and overseas (WRIGHT *et al.*, 1978). Height of trees from the best seed sources has exceeded that of trees from the poorest sources by as much as 100% at age 16 or 17 (FUNK, 1979). Trees of southern Appalachian origin have generally grown faster than local seedlings as far north as lat. 40° N, at about equal rates between 41° and 44° N, and more slowly north of 45° N (GARRETT *et al.*, 1973). Similar correlations between height and latitude of origin have been shown with juvenile growth of improved seed orchard progeny (KUSER and HOBBS, 1984; KUSER *et al.*, 1987).

Other characteristics showing provenance variation related to latitude of origin include number of branches per whorl, needle length, and cone production (GARRETT *et al.*,

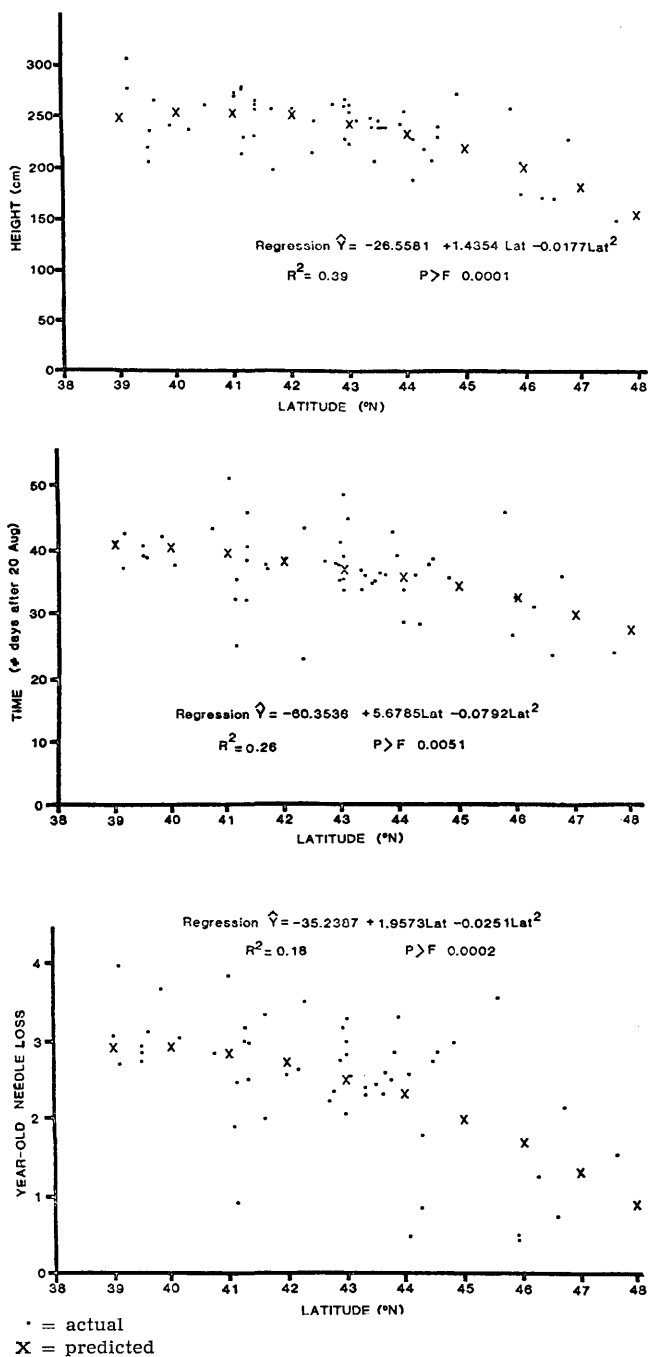


Figure 2. — Height of white pines after six seasons, needle retention, and date of needle-shedding as related to female parent's latitude of origin.

1973); our results add to the list of responses in which there is known geographic variation in this wide-ranging species. It is also our opinion from inspection of our plantation that silver-blue needle color is commoner among trees of southern origin.

Why do white pines shed their second-season (or third-season) needles at a particular time in the fall? Is the phenomenon analogous to the shedding of leaves by deciduous hardwoods at the same time of year? We think so. The pines are presumably preparing for winter. White pine needles can withstand winter temperatures as low as -80°C without injury (SAKAI and WEISER, 1973), but desiccation may be a problem when the ground is frozen and

trees cannot replace moisture loss, even though this is minimized in pines by the needles' waxy coatings. Because of this, it is likely that pines in northern Minnesota, where mean January temperatures average near -15°C and precipitation averages less than 25 mm/month from December to March (USDA, 1949), have undergone selection to minimize winter needle exposure in order to prevent desiccation. On the other hand, pines in central Maryland, where mean January temperatures average 1°C and precipitation is over 75 mm/month during the winter months, are not under the same selection pressure.

We reason that later needle-shedding and greater second-winter needle retention by white pines of southerly origin may be two of the mechanisms enabling them to grow faster. Photosynthesis in conifers can take place at temperatures well below those ambient during the growing season (WARING and FRANKLIN, 1970), and fall photosynthesis has been shown to be related to variation in height growth among jack pine (LOGAN, 1971) and loblolly pine (BOLTZ *et al.*, 1986) provenances. White pines with a larger needle complement would have greater capacity for photosynthesis in the fall, winter, and spring and could increase their carbohydrate reserves before the extension of new shoots. For example, trees of Quebec seedlots nos. 4 and 14 shed old needles early, hold few through the second winter, and grow slowly, whereas those of Quebec seedlot no. 47 keep old needles longer, hold more through the second winter, and grow faster. Seedlot no. 47 comes from an island in a large body of water which ameliorates cold, dry weather and may have allowed selection for rapid growth to outweigh that for resistance to winter desiccation.

Another way in which white pines adapted to warmer parts of the range grow faster is by commencing growth earlier in spring, and continuing shoot extension longer into summer. Pines belonging to Maryland seedlot no. 62 (tallest in our experiment) begin growth earlier and continue later than others (KUSER and HOBBS, 1984).

In planning future breeding work with white pine for Christmas tree use (CARTER *et al.*, 1988), it may become desirable to incorporate data on needle retention and needle-shedding phenology among the characteristics used to identify superior trees.

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Heritability and expected Gain Estimates for Traits of Black Locust in Michigan¹⁾

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Summary

Open-pollinated progeny from 434 families from the natural and naturalized range of black locust were tested at two sites in Michigan. Observations of height, dieback, the number of dominant leaders, length of thorns, borer attack, time of bud-break (opening of wood plates to show green material), and time of leaf initiation (appearance of leaves) were made after one growing season. The analysis of variance showed significant family, block, and site differences for all traits from the combined data. There were no apparent geographic patterns in variation for any of the traits. Single tree heritabilities for length of thorns, time of bud-break, and time of leaf initiation were higher than family heritabilities from the combined data. Estimated genetic gains from combined selection for height, dieback, number of dominant leaders, length of thorns, time of bud-break, and time of leaf initiation were 45%, 46%, 18%, 52%, 32%, and 55%, respectively, when the best 20 individuals from the best 20 families were selected. The data were corrected for block and site effects for genetic gain estimations.

Key words: selection, genetic correlations, genetic variation, half-sib progeny, breeding.

Introduction

Black locust (*Robinia pseudocacia* L.) is used for lumber, poles, beekeeping, fuelwood, land reclamation, forage, and wood fiber. In the United States, it has been widely planted outside its natural range which is limited to the Ozark Plateau and the Appalachian mountains of eastern United States. Very little genetic improvement has been done on the species in the U.S., and literature on the estimated genetic parameters for growth or other traits is lacking.

In Hungary, a black locust breeding program for fast growth, stem straightness, frost resistance, increased nectar yields, and prolonged flowering period was started in 1930 (KERESZTESI, 1983). Selections were made from stands established with materials imported from the United States between 1710 and 1720. The improvement work included induced polyploidy, crossbreeding, and cloning. A half-century's improvement has resulted in the development of many registered cultivars for specific uses.

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In 1978, a species trial consisting of many pines and hardwoods including black locust, was established at various locations in Michigan (MILLER *et al.*, 1987). Even though the survival of black locust was not impressive due to harsh site conditions, it was the fastest growing species in the test. In another species trial its growth was comparable to that of hybrid poplar (MILLER *et al.*, 1987). This observation revealed the potential of black locust as a fast-growing biomass plantation tree.

A provenance test of black locust, done by the University of Georgia (KENNEDY, 1983), showed that the variation in height, diameter, spine length, rachis length, number of pinnae, time of leaf initiation, and time of bud-break of one-year-old seedlings was substantial within the populations tested; there were no apparent geographical trends. KENNEDY suggested the need for progeny tests to select the best families for improvement of the species.

Based on the results, and on the need for high yielding biomass trees in Michigan, a long term breeding plan was initiated by Michigan State University. This paper presents data on the extent of genetic variation present in black locust from half-sib progeny tests of the base population. Heritabilities, genetic gains, genetic correlations, and Spearman correlations are summarized for height, dieback, length of thorns, number of leaders, time of bud-break, and time of leaf initiation.

Materials and Methods

Between 1982 and 1983, open-pollinated seeds were collected from 434 trees, covering the natural and naturalized range of black locust in the Eastern United States and Canada. The seeds were treated with sulfuric acid and sown in the nursery at the Tree Research Center, Michigan State University, East Lansing, Michigan, in the spring of 1984. The seedlings were planted in the spring of 1985 at four sites in Michigan: East Lansing (Ingham County), Kellogg Forest (Kalamazoo County), Tawas (Iosco County), and Brampton (Delta County). The experimental design was a randomized complete block, with four blocks and three tree plots. Blocking was done by soil series at the East Lansing site, but the other three sites were composed of a single soil series. All sites were characterized by good internal soil drainage except for localized pockets.

In March of 1985, all four sites were mowed, and Round-up was applied to reduce weed competition (prior to plant-