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Phenotypic Variation in Cone and Seed Characteristics of Tamarack in Northwestern Ontario

Gwennoth J. O'Reilly and Robert E. Farmer, Jr.

Research associate and professor, Lakehead University School of Forestry, Thunder Bay, Ontario

Variations in cone size and morphology, number of seed per cone, percentage filled seed, percentage insect-damaged seed, and seed dimensions were evaluated in individual tree samples collected in 1984 from nine regions of northwestern Ontario. Nested analyses of variance revealed no major provenance differences in cone or seed morphology, but there was substantial variance among stands within provenances and trees within stands. Percentage of filled seeds was lower in northern (51 to 56°) than in southern (46 to 49°) populations, and samples from Fort Severn on Hudson's Bay, the most northerly source, contained less than 1 % filled seed. Within population variance in characters related to seed productivity (for example, number of seed per cone) was large enough to suggest that selection for these characters may be effective. Tree Planters' Notes *42(3):18-22; 1991.*

One of the often noted barriers to the expanded use of tamarack *(Larix laricina* (Du Roi) K. Koch) in boreal forestry is the species' sporadic cone crops and generally poor seed set under natural conditions (Armson 1983). Because of this, most of the currently limited production of planting stock relies on relatively expensive vegetative propagation. Improvement of seed quality and production under orchard conditions, via either genetic or environmental manipulation, would allow a broader approach to stock production. There are, however, few published data on seed and cone characteristics upon which one might base a strategy for improving production. Therefore, during the course of collecting material for a genetic study of tamarack in northwestern Ontario we formally evaluated phenotypic variation of some seed and cone characteristics in 1984, a year when cone production was relatively high in eastern and central Canada.

Methods

In August and September 1984, before seed dispersal began, cones were collected at nine locations (table 1). The two sampled stands selected in each

Table 1—*Provenance means and range of tree means for cone and seed production characteristics of tamarack in northwestern Ontario*

Provenance	Lat. (deg. N)	Long. (deg. W)	Cone length (mm)	Cone width (mm)	Number scales per cone	Cone scales per mm	Number seed per cone	Percent seed filled	Percent seed insect damaged
01 North Bay	46°	80°	10	7	14	1.36	20	9	20
	60′	52′	(9–12)	(6–9)	(9–17)	(.92–1.70)	(16–24)	(1–26)	(0–82)
02 Sault Ste. Marie	46°	83°	10	6	11	1.18	16	2	50
	80′	70′	(8–11)	(6–7)	(9–14)	(1.01–1.32)	(9–24)	(0–7)	(9–80)
05 Thunder Bay	48°	89°	11	8	14	1.21	27	13	45
	40′	32′	(8–12)	(7–8)	(12–17)	(1.03–1.41)	(21–31)	(3–38)	(1–75)
06 Ft. Frances	48°	94°	12	8	16	1.4	23	25	21
	70′	15′	(9–15)	(6–9)	(9–28)	(.97–1.83)	(11–33)	(12–43)	(0–55)
07 Red Lake	50°	93°	10	7	12	1.29	19	9	35
	80′	30′	(8–12)	(6–8)	(11–14)	(1.01–1.48)	(11–26)	(2–18)	(0–77)
09 Kenogami River	50°	84°	12	7	14	1.13	20	8	66
	60′	45′	(11–14)	(6–8)	(11–16)	(.89–1.25)	(18–26)	(0–22)	(9–97)
10 Moosonee	51°	80°	13	8	16	1.24	27	4	76
	25′	67′	(12–15)	(7–8)	(13–18)	(1.10–1.38)	(23–31)	(2–7)	(61–88)
12 Big Trout Lake	53°	89°	11	7	13	1.17	25	1	27
	83′	87′	(10–12)	(7–8)	(10–16)	(1.02–1.61)	(21–36)	(0–4)	(0–83)
14 Ft. Severn	56°	87°	12	7	16	1.28	29	<1	62
		67′	(10–15)	(6–8)	(13–19)	(1.22–1.40)	(25–33)	(0–2)	(29–83)

location were at least 5 km and usually over 10 km apart. Trees within stands were selected randomly with respect to cone and seed characteristics but were selected because they had at least moderate cone crops. Typically, trees were cut and all current year cones collected. Five of these trees from each of two stands in each provenance were selected for cone analysis, and 10 randomly selected cones from each tree were examined. Before drying, the length and width of these cones were measured with calipers. Each cone was then placed in an individual container and dried at room temperature to extract seed. After dissection to ensure that all seed had been extracted, the number of cone scales, seed, seed filled with a normal embryo and megagametophyte, and seed damaged by insects were recorded for each cone. Number of scales per unit of cone length and percentages of filled and insect damaged seed were computed for each cone. A nested analysis of variance of the form outlined in table 2 was used to evaluate variance in these characters accounted for by provenances, stands within provenances, trees within stands, and cones within trees, all considered as random effects. Tree means were used in computing correlation coefficients for the relationships presented in table 3.

Evaluation of variation in seed size was made using 10 to 20 randomly selected seed from 116 individual tree lots from the collection noted above (table 4). These seed lots were obtained from at least 100 cones per tree. Seed length and wing length were recorded. Total seed length was computed as the sum of these measured characters. A nested analysis of variance based on 10 seed from each of 7 randomly selected trees per provenance (with two exceptions, see table 4) was used to assess variance associated with provenance, trees within provenance, and seed within trees (table 5). Coefficients used in computing variance components were adjusted for unequal sample size by the method of Snedecor and Cochran (1980).

Table 3—*Coefficients of correlation among cone and seed characteristics of tamarack in northwestern Ontario*

	Cone width	Number cone scales	Number seed/cone	Percent filled seed
Cone length	.65**	.73**	.48**	.20
Cone width		.55**	.46**	.28
Number cone scales			.77**	.07
Number seed				.16

**Statistically significant at the .01 level of probability.

Results

Cone length and width and number of cone scales, characters likely to be under relatively strong genetic control (Stoehr and Farmer 1986), varied little from provenance to provenance (tables 1 and 2). Effects of stands and trees within stands were statistically significant for all cone measurements except cone width, which did not vary significantly from stand to

Table 2—*Analyses of variance in tamarack cone and seed characteristics*

Source of variation	Degrees of freedom	Cone length		Cone width		No. scales per cone		Cone scales per mm		No. seed per cone		Arcsin % filled seed		Arcsin % seed insect damaged	
		MS	VC	MS	VC	MS	VC	MS	VC	MS	VC	MS	VC	MS	VC
Provenance	8	157.128	23	18.299*	15	345.261	8	0.796	21	1,797.190*	26	7,082.810**	31	8.499*	39
Stands/ provenance	9	66.573**	28	4.837	5	230.098**	25	0.512*	41	411.583**	9	1,159.430**	9	2.106**	17
Trees/stands	72	10.694**	25	2.979**	29	52.780**	34	0.238**	16	173.436**	29	275.379**	9	0.735**	38
Cones/trees	810	0.931	24	0.441	51	4.460	32	0.029	22	19.730	37	96.732	50	0.105	6

Expected Mean Squares

Provenance	$\sigma^2_C + c\,\sigma^2_T + ct\,\sigma^2_S + cts\,\sigma^2_P$
Stands/ provenance	$\sigma^2_C + c\,\sigma^2_T + ct\,\sigma^2_S$
Trees/stands	$\sigma^2_C + c\,\sigma^2_T$
Cones/trees	$\sigma^2_C + c$

MS = mean square, VC = variance component.
The variance component is expressed as the percentage of total variance.
*Statistically significant at the .05 level of probability.
**Statistically significant at the .01 level of probability.
σ^2_C = variance due to cones within trees
σ^2_T = variance due to trees within stands
σ^2_S = variance due to stands within provenances
σ^2_P = variance due to provenances
C = number of cones per tree
T = number of trees per stand
S = number of stands per provenance
P = number of provenances

Table 4—*Provenance means and range of tree means for seed dimensions of tamarack in northwestern Ontario*

Source	Wing length (mm)	Seed length (mm)	Total length (mm)	Number of trees
02 Sault Ste. Marie	3.6	2.8	6.4	7
	(3.1–4.7)	(2.6–2.8)	(5.8–8.0)	
01 North Bay	3.4	2.5	5.9	8
	(2.9–4.2)	(2.2–2.9)	(5.2–7.0)	
05 Thunder Bay	3.5	2.7	6.2	15
	(2.4–4.2)	(2.1–3.1)	(4.5–7.3)	
06 Ft. Frances	3.4	2.6	6	19
	(2.6–5.4	2.2–3.0)	(4.8–8.0)	
07 Red Lake	3.1	2.4	5.5	16
	(2.6–3.7)	(2.1–2.8)	(4.7–6.4)	
09 Kenogami R.	4.2	2.6	6.8	3
	(4.0–4.5)	(2.5–2.7)	(6.6–7.2)	
10 Moosonee	4.1	2.7	6.8	4
	(3.4–4.8)	(2.6–3.0)	(6.0–7.8)	
12 Big Trout Lake	3.6	2.6	6.2	12
	(2.7–4.5)	(2.2–3.0)	(5.1–7.3)	
14 Ft. Severn	4.5	2.7	7.2	32
	(3.7–5.5)	(2.0–3.2)	(5.8–8.3)	

stand. This low level of stand variation within provenance in cone width resulted in a statistically significant F value for provenances, though provenance variation was low. Together, stands and trees within stands accounted for over 50% of variance in most of the cone size characters. Number of scales per unit of cone length followed the same pattern with wide tree-to-tree differences within provenances. Number of seed per cone was roughly double the number of scales for the three most northern provenances (Moosonee, Big Trout Lake, Ft. Severn) and Thunder Bay. For the remainder of the provenances, 71 to 79% of the seed sites (two per scale) were occupied. Provenance differences were larger for seeds per cone (16 to 29) than for other cone characters, though within-population differences accounted for most (38%) of the variance (table 2).

Percent of seed that were filled with an apparently viable embryo varied among provenances more dramatically than total number of seed, with the most northern provenance (Ft. Severn) having less than one percent filled seed (table 1). There was also a large degree (50%) of variation in this character among cones within trees. Maximum number of filled seed observed in single cones was ten to twelve. As expected, there were modest positive correlations between cone size (length and width) and total seed yield (table 3), but percent filled seed was not related to cone characteristics.

All three sampling levels accounted for significant variance in the degree of insect damage to seed, but the pattern of provenance variation did not follow the same pattern as percent filled seed since cones within trees accounted for very little variance (table 1). While a systematic evaluation of insect-specific damage to individual provenance samples was beyond the scope of this study, a specialist in conifer cone insects (Dr. Y. H. Prévost, School of Forestry, Lakehead University) did generally examine the sample and made the following observations. Most of the seed damage resulted from a furrow through seed produced by free-moving maggots, such as the larvae of *Earomyia aquilonia* McAlpine, which occur in tamarack. Secondly, seed coats were perforated by an exit hole such as those produced by a seed midge of the family Cecidomyiidae.

Provenance differences in total seed length (seed and wing) were not statistically significant, but there was a slight trend towards longer wing length in the three northern provenances within the Hudson Bay lowlands (tables 4 and 5). Most of the variation was related to seed size differences within trees, but significant differences among trees accounted for over 40% of the variance in total seed length.

Discussion

Analyses of cone and seed morphology revealed no major provenance differences or geographic trends and a preponderance of variance among

Table 5—*Analyses of variance in tamarack seed dimensions*

Source of variation	Degrees of freedom	Expected mean squares	Wing length: Mean square	Wing length: Variance component	Seed length: Mean square	Seed length: Variance component	Total length: Mean square	Total length: Variance component
Provenance	8	$\sigma^2_S + s\,\sigma^2_T + st\,\sigma^2_P$	235.31	2	45.3	1	468.36	4
Trees/provenance	52	$\sigma^2_S + s\,\sigma^2_T$	179.54**	41	39.44**	26	322.29**	43
Seed/trees	504	σ^2_S	21.59	56	8.77	73	35.24	53

Variance components are expressed as percentage of total variance.
**Statistically significant at the .01 level of probability.
σ^2_S = variance due to seeds within trees
σ^2_T = variance due to trees within provenances
σ^2_P = variance due to provenances
S = number of seeds per tree
T = number of trees per provenance
P = number of provenances

stands and trees within populations. In a recent related rangewide (New England to Alaska) study of tamarack leaf and cone dimensions, which included provenances in our sample, Parker and Dickinson (1990) noted that canonical variates analysis of nine cone traits resulted in only a weak geographical trend, though some of the northernmost Ontario provenances were separated from the main cluster. Studies of these characters in other north temperate and boreal conifers have shown a variety of patterns, from clear geographic trends (Borghetti et al. 1988, Simak 1967, Lester 1968) to minor unpatterned population differences (Khalil 1984, Bakowsky 1989, Parker and Maze 1984). Although geographic variation in cone morphology may be of little consequence in improving seed production, the preponderance of variance within populations in this study does have important implications in breeding. Genetic data on other boreal conifers, for example *Picea mariana* (Mill) B.S.P. (Stoehr and Farmer 1986), suggests that broad-sense heritability is moderately high for cone morphology. Therefore it appears that selection for large cones and large seed within populations of tamarack will be moderately effective in terms of increasing seed production.

This selection will result in larger numbers of seed per cone, but not necessarily an increase in number of filled seed, since, as our data show, the two characteristics are not related. Percentage filled seed in 1984 was significantly lower in northern provenances (lat. 51 to 56°) than in most of the southern provenances (lat. 46 to 49°), and there were broad tree-to-tree differences.

At least several factors are responsible for variation in percentage of filled seed. First, insect damage, which varies from year to year, was high in cones from some trees. For insect-damaged seed we were not able to distinguish normally filled seed from other seed. Thus the impact of this factor on filled seed cannot be separated from other factors. Second, many unsound tamarack seed have aborted embryos (Farmer and Reinholt 1986), which may be the consequence of inbreeding. Knowles et al. (1987) noted significant levels of self-fertilization in the seed lots used in this study, and Park and Fowler (1982) have shown that selfing reduces filled seed percent. The third factor, which may be particularly responsible for low filled seed percentages in northern provenances, is poor pollination and/or fertilization due to weather conditions. This factor, if it is operative, probably varies in impact from year to year. Brown's observation (1982) of year-to-year variation in percent filled seed in Alaska suggests that weather is an important determinant of seed yield. Payette and Gagnon (1979) and Payette et al. (1982) have shown that tamarack near the tree line in northern Quebec regenerate from seedlings, but their data indicate that percentage of filled seed may be generally low there. In short, while selection for increased number of seeds per cone will probably be effective, improving the quality of these seeds will likely require orchard management techniques such as improved pollination and control of cone insects.

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