RUST INCIDENCE IN A STUDY OF JACK PINE INTER- AND INTRA-PROVENANCE HYBRIDS[1]

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Abstract. --Two sets of jack pine inter- and intra-provenance hybrids consisting of 48 and 27 full-sib families with parents from six provenances were scored for presence of pine-oak rust galls four years after outplanting in east central Minnesota. Large variation in the percentage of galled trees occurred among provenance crosses (7.5% to 81.7%). Hybrids involving Wisconsin, Saskatchewan, Nova Scotia, and Northwest Territories parents were more resistant than those with Michigan or Ontario parents. The resistance level of inter-provenance crosses was not significantly different from that expected under an additive model. Reciprocals of provenance crosses did not appear to differ.

Jack pine (*Pinus banksiana*) seedlings are highly susceptible to pine-oak gall rust caused by *Cronartium quercuum* f. sp. *banksianae*. Variation in resistance to the disease has been found among Lake States provenances (Hodson, et al., 1982) and among various seed lots collected in Minnesota (Stewart, et al., 1985). The relative resistance of jack pine inter- and intra-provenance crosses and the effects of reciprocal provenance crosses have not been reported. Data related to these questions are presented below.

MATERIALS AND METHODS

Experimental materials were seedlings from two series of jack pine controlled crosses made by the Forestry Sciences Laboratory, Rhinelander, Wisconsin and the Petawawa Forest Experiment Station, Chalk River, Ontario, Canada. Series A consisted of 48 full-sib families representing crosses among and between parents of six provenances: Guysborough, Nova Scotia (NS); Renfrew, Ontario (ONT); Marathon, Wisconsin (WISC); Grand Traverse, Michigan (MICH); Big River, Saskatchewan (SASK); and Fort Smith, Northwest Territories (NWT). Two male parents from each of the first four provenances were crossed with a different female from each of the six provenances resulting in 6 full-sib families within each of 8 male half-sib families. The Ontario, Michigan and Northwest Territories provenances were used in series C. Three males from each provenance were crossed with three different females from each of these provenances.

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Each female was used in one mating giving 27 full-sib families and nine male half-sib families.

Containerized stock was grown by the Forestry Sciences Laboratory in Rhinelander, Wisconsin and the seedlings were planted near Willow River, Minnesota in the spring of 1980. The two series were planted as separate, but adjacent experiments using randomized complete block designs with full-sib families as treatments, 4-tree row plots and five replications. Each tree was measured for total height and scored for the presence or absence of galls in 1983 after four growing seasons.

The proportion of galled trees in a plot was transformed by arcsin square root. Transformed plot proportions were used for analyses, then nontransformed means were substituted into tables.

Analysis of variance was done for both series using the random effects model: proportion of galled trees in a plot = overall mean + replication + provenance cross + rep x cross + family-in-cross + error. Provenance cross means were ranked and tested with Duncan's multiple range test (DMRT) at the .05 level.

Six two-provenance subsets in series A and three in series C consisting of the four possible crosses among two provenances were analyzed separately using the above model to examine the effect of inter- vs. intra-provenance combinations and the effect of reciprocal provenance crossing using orthogonal contrasts.

Average male and female provenance effects were analyzed using a within and between provenance model then ranked and tested with DMRT at the .05 level of significance.

Simple correlations between height and proportion galled were calculated from the transformed data using family means.

RESULTS

Analysis of variance of transformed proportional data showed significant effect of provenance cross and family-in-cross in both series A and C (Table 1). Replication x cross interaction was significant in series C and was used as the error for cross effect. In series A, a pooled error consisting of rep x cross and rep x family-in-cross was used.

Comparison of cross means in Table 2 shows a range of infection from 7.5% to 81.7% in series A and 26.7% to 74.4% in series C. A difference of approximately 30% was needed to separate means at the .05 level of significance. Crosses with Ontario and Michigan parents were found predominantly in the upper range, whereas Nova Scotia, Northwest Territories, and Wisconsin predominate in the lower range.

Table 2 shows percentage infection by provenance cross, including marginal means. Mean provenance effects were significantly different ($p<.05$) for both male and female parents in series A and for female

Table 1. Significance levels from analyses of variance of rust infection of provenance crosses in two jack pine progeny tests in east central Minnesota.

SOURCE	SERIES A	SERIES C
PROVENANCE CROSS	*	*
REP x CROSS	NS	*
FAMILY IN CROSS	*	*

* = p<.05, NS = p>.05

Table 2. Percentage infection of provenance crosses in two jack pine progeny tests in east central Minnesota.

SERIES A

Female Parent Provenances	Male Parent Provenances				
	MICH	ONT	WISC	NS	MEAN
ONT	81.7a	75.8a	58.4abc	45.0bcd	65.2a
MICH	70.8ab	56.6abc	10.0ef	45.0bcd	50.7b
SASK	35.0cde	30.8cdef	31.6cdef	41.7cd	34.6c
WISC	61.7abc	27.5cdef	34.1cdef	7.5f	32.7c
NS	47.2bcd	44.2cd	20.0def	17.6def	32.2c
NWT	43.3cd	20.8def	7.6ef	8.3ef	24.4c
MEAN	56.8a	42.6b	31.7c	27.4c	39.8

SERIES C

Female Parent Provenances	Male Parent Provenances			
	ONT	MICH	NWT	MEAN
MICH	74.4a	45.1bc	70.3ab	62.3a
ONT	58.9ab	65.0ab	46.1bc	56.6a
NWT	27.2c	46.5bc	26.7c	33.4b
MEAN	53.0a	52.3a	44.2a	50.1

* Means within a box followed by the same letter are not significantly different at the .05 level.

parents in series C. Multiple comparison by DMRT (Table 2) showed that families with Ontario and Michigan parentage had the highest infection levels. This was also shown by the ranking of the four intra-provenance crosses in series A, where Michigan and Ontario were in one grouping and Wisconsin and Nova Scotia were in another (Table 2).

A summary of the two-provenance subset data analysis appears in Table 3. Although 50% of the contrasts showed significant differences between inter- and intra-provenance crosses in rust incidence, there was no consistent pattern. In subsets A2 and A6 inter-provenance crosses had significantly less galling than intra-provenance crosses, but in subsets C1 and C3 they had more.

Table 3. Summary of Series A and C analysis of variance for two-provenance subsets from two jack pine progeny tests in east central Minnesota.

Subset[a]	Provenance Cross[b]	Contrast Inter-Intra[c]	Contrast Reciprocal[d]	Contrast Intra-Intra[e]
		SERIES A		
A1 NS, ONT	*	NS	NS	*
A2 NS, WISC	*	*	NS	NS
A3 NS, MICH	*	NS	NS	*
A4 ONT, WISC	*	NS	*	*
A5 ONT, MICH	NS	NS	NS	NS
A6 WISC, MICH	*	*	*	*
		SERIES C		
C1 ONT, MICH	*	*	NS	NS
C2 ONT, NWT	NS	NS	NS	*
C3 MICH, NWT	*	*	*	*

* = p<.05, NS = p>.05

[a] Subset containing all four possible crosses among the two provenances listed.

[b] Indicates level of significance of provenance cross in the subset ANOVA.

[c] Indicates level of significance of 1 df contrast between the two inter-provenance crosses and the two intra-provenance crosses.

[d] Indicates level of significance of 1 df contrast between reciprocal provenance crosses.

e Indicates level of significance of 1 df contrast between the two intra-provenance crosses.

Reciprocal crosses did not show any consistent male or female effect. In the WISC x MICH cross (in subset A6) the WISC males produced progeny with significantly lower infection than the WISC females, but in the WISC x ONT cross (in subset A4) the opposite occurred. In subset C3, the MICH males produced progeny with lower infection than MICH females in contrast to subset A6 where the opposite occurred (Tables 2 and 3).

Level of infection and height were moderately correlated with r = .456 in series A and r — .359 in series C.

DISCUSSION

As would be expected from previous work (Hodson, et al., 1982), variation in rust resistance among jack pine provenance crosses was significant. Percent infection ranged from 7.5% to 81.7% in series A and slightly less in series C. A difference of approximately 30% was necessary for significance using DMRT. Controlled inoculation with more seedlings per cross is needed to obtain finer distinction among levels of infection (Stewart, 1986).

Provenance means did not rank as expected (Hodson et al., 1982). In that study the seed sources farthest from the range of the alternate host, red oak, had the highest level of infection. Hodson et al. (1982) hypothesized that their result was caused by the seed sources in the red oak range being subjected to the greatest selection pressure. In this study, sources from Ontario and Michigan, where pine-oak rust is common had high infection rates, and sources from Nova Scotia, Northwest Territories, and Saskatchewan, where pine-oak rust is absent (Hiratsuka and Powell, 1976) had lower infection rates. Wells and Wakely (1966) and Kinloch (1972) rejected a selection pressure hypothesis for provenance variation in fusiform rust (Cronartium quercuum f. sp. fusiforme) resistance of loblolly pine.

Other possible explanations for these differing results are: (1) variation in inoculum races and differential susceptibility of provenances to the particular races present at different test sites (Snow, 1985), (2) selection for resistance to western gall rust (Endocronartium harknessii) in the Saskatchewan, Nova Scotia, and Northwest Territories provenances, and (3) faster growing trees may offer more succulent tissue for infection by the fungus during the critical few weeks in late spring. Materials from Nova Scotia and the Northwest Territories were significantly shorter than those from Ontario and Michigan as shown by DMRT ($p<.05$) and had lower infection levels. The correlation between height and gall incidence was moderate at .456 and .359 for series A and C, so growth rate does not appear to be the dominant factor. The Wisconsin material ranked at the top of the range for height growth and its low rust incidence is not consistent with the hypothesis of a rapid growth rate-high gall rust association.

Contrasts of two-provenance subsets showed that there was no consistent effect of specific provenance combinations and the data are interpreted as indicating that additive genetic effects are basically responsible for jack pine rust resistance. This is consistent with other observations, such as those of Anderson and Anderson (1962), who found that crosses between jack pine and lodgepole pine produced progeny intermediate in sweetfern rust (Cronartium comptoniae) resistance to the parents. Similarly, Griggs and Walkinshaw (1982) found no effect of specific single parent combinations in fusiform rust resistance of slash pine.

Reciprocal crosses did not show any consistent male or female provenance effect. It is likely that the occasional significant differences between reciprocal crosses were due to the extremely small sample of parents in each provenance leading to particular individuals with high resistance or to the small number of progeny in each cross and the inherent high variability in rust infection in field studies. This lack of reciprocal effects has been reported by Griggs and Walkinshaw (1982) in slash pine resistance to fusiform rust.

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