

Genetically based resistance of black spruce (*Picea mariana*) to the yellowheaded spruce sawfly (*Pikonema alaskensis*)

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Abstract

We evaluated the effect of plant genotype on resistance of black spruce (*Picea mariana* (Mill.) BSP) to the yellowheaded spruce sawfly (*Pikonema alaskensis* (Roh.)) in three half-sib family test sites and in a clonal seed orchard in New Brunswick, Canada. Heritability estimates were positively correlated to the percentage of trees defoliated by the sawfly in the half-sib family tests. At the site where the most damage occurred, the estimated individual heritability of resistance was 0.84, while that based on family means was 0.57. In the clonal seed orchard, the variability among clones explained 39.3% of the variation in defoliation, and individual clone heritability and clone mean heritability estimates were 0.40 and 0.82, respectively. Positive phenotypic and genetic correlations between tree height and damage suggest that selection for resistance may result in slightly slower tree height growth in some cases. These results suggest that there is good potential to select trees resistant to the sawfly that display other commercially desirable traits.

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1. Introduction

Due to increasing pressures on wood supply (Sutton, 1999), there has been a large increase in intensive

silviculture in North American forests (e.g., Quiring, 1990). Although forest management planning has increasingly assumed that intensively managed stands will produce more fiber and timber than unmanaged stands, several formerly secondary insect pests have recently caused substantial damage in precommercially thinned stands of balsam fir, *Abies balsamea* [L.] Mill. (Piene et al., 2001; Parsons et al., 2003) and in plantations of white spruce, *Picea glauca* [Moench.]

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Voss. (Carroll and Quiring, 1993; Carroll et al., 1993) and black spruce (Lavigne, 1997) in eastern Canada, challenging this assumption.

One potentially very useful tactic to limit damage by insect pests in intensively managed stands is planting resistant trees. This tactic can reduce both the economic and environmental cost of insect pest management. Genetically based resistance to major pests of young white spruce (Quiring et al., 1991) and jack pine, *Pinus banksiana* Lamb. (DeGroot and Schnekenburger, 1999) in eastern North America and to interior or sitka spruce, *P. sitchensis* [Bong.] Carr. (Kiss and Yanchuk, 1991; Alfaro et al., 1996) in western North America has been previously reported, suggesting that this tactic could be successfully incorporated into current management systems. Similarly, genetically based variations in phloem phenol content has been associated with resistance of spruces to a bark beetle-associated fungus (Lieutier et al., 2003) and to a galling adelgid (Björkman, 2000), in Europe.

Allocation of tree resources to defense against insects could reduce the amount of resources available for growth, maintenance or reproduction (Stearns, 1976). Thus, selecting for resistance can have a cost. For example, Loehle (1987) reported an inverse relationship between growth rates and tree defense in a comparison among North American conifers. However, King et al. (1997) reported that the fastest growing interior spruce trees were also the most resistant to the white pine weevil (*Pissodes strobi* (Peck)).

The yellowheaded spruce sawfly, *Pikonema alaskensis* (Roh.), is the most important pest of young black spruce plantations in eastern Canada (Martineau, 1985). First-instar larvae, which emerge in June, consume only small parts of the new needles (Katovich et al., 1995). As the larvae develop, they first skeletonize new needles and then consume them entirely, causing serious defoliation and growth reduction (Katovich et al., 1995).

Here we report the results from a study carried out to examine the influence of tree genotype on the susceptibility of black spruce to this sawfly, and to determine whether faster growing trees are more susceptible to defoliation than slower growing ones, as predicted by life history strategy theory (Stearns, 1976).

2. Materials and methods

2.1. Clonal seed orchard

We evaluated the influence of clones on susceptibility of black spruce to the sawfly at a clonal seed orchard located near Fredericton, New Brunswick (45°53'N, 66°48'W) in 2003. Trees from 35 black spruce clones had been planted in 1991 in a randomized complete block design where each tree is surrounded by four different clones at 2 m × 2 m spacing. The site was divided in two replications with 15–22 trees (ramets) (mean = 19) per clone in the first replication and 13–20 trees (mean = 16) per clone in the second replication. The two replications were separated by a windbreak of approximately 8 m, orientated east–west and parallel to the tree-rows.

Sawfly populations were high in 2000, 2002 and 2003 but the site was only sprayed with an insecticide (AmbushTM) in 2000. In August 2003, we examined defoliation of current-year foliage on five southerly facing terminal shoots on each of the fourth, sixth and eighth whorls. Defoliation was visually estimated for each shoot using 10% categories of defoliation, except for 0 and 100% (Lavigne, 1997), and mean percent defoliation was calculated for each tree. We also recorded the height from the base of the tree to the base of the currently growing leader.

The influence of clones and replications on defoliation was evaluated with a two-way analysis of variance (SAS Institute, 1982) using the model:

$$Y_{ijk} = \mu + C_i + R_j + CR_{ij} + e_{ijk},$$

where Y_{ijk} is the percent defoliation on the k th tree of the i th clone in the j th replication; μ the overall mean; C_i the effect of the i th clone; R_j the effect of j th replication; CR_{ij} the interaction effect of i th clone and j th replication; and e_{ijk} the random error component. All terms in the model are considered as random effects, and variance components were estimated using the VARCOMP procedure of SAS (SAS Institute, 1982). Clones were considered random because their selection had not been based on disease or insect resistance characters.

The estimated variance component due to clones (σ_C^2) in the clonal seed orchard was translated into covariance of clones, which represents variation due to all genetic causes, i.e., total genetic variance. Two

types of clone mean heritability (Lush, 1940), the ratio of total genetic to total phenotypic variances, were estimated:

$$H^2 = \sigma_C^2 / (\sigma_C^2 + \sigma_{C \times R}^2 + \sigma_e^2) \quad \text{and}$$

$$H_C^2 = \sigma_C^2 / (\sigma_C^2 + \sigma_{C \times R}^2 / b + \sigma_e^2 / m),$$

where H^2 , σ_C^2 , $\sigma_{C \times R}^2$, σ_e^2 , H_C^2 , r and n are, respectively, individual clone heritability, variance component due to clones, clone \times replication interactions, random error, clone mean heritability, number of replications, and mean number of ramets per clone.

Pearson correlations between height and defoliation were examined with the CORR procedure of SAS (SAS Institute, 1982).

2.2. Half-sib family tests

The susceptibility of black spruce to the sawfly was also assessed at each of three black spruce progeny tests. Seedlings were produced by controlled poly-crosses using unrelated pollen mix and grown in greenhouses during the winter. The three tests were established by: Avenor Maritimes Inc. at Rocky Brook (66°21'N, 47°42'W) in 1994 (NBI 94); Smurfit-Stone Container Corp. near Caribou Depot (66°09'N, 47°35'W) in 1995 (SCI 95); and Stone Container Inc. near Caribou Depot (66°01'N, 47°36'W) in 1996 (SCI 96). NBI 94 was sprayed with OrtheneTM in May 1999 and both NBI 94 and SCI 96 were sprayed in July 1999 with DiazinonTM. The SCI 95 site had never been sprayed with insecticides.

Company personnel assessed each tree as damaged or undamaged by YHSS 5 years after trees had been planted. No other defoliators were observed at these sites. The progeny test at each location was established as a randomized complete block design with 15 replications, each of which contained a two tree plot for each of 31 (NBI 94), 49 (SCI 95) or 44 (SCI 96) different families. However, for this study, replications were reassigned to reduce the number of replications to five by combining three adjacent replications into a new replication. Thus, each new replication contained six trees for each family, and the percentage of trees defoliated by the sawfly was calculated for each family within each reassigned replication.

The influence of tree genotypes on susceptibility of black spruce to the sawfly was calculated with

analyses of variance for each site using the following model:

$$Y_{ij} = \mu + F_i + R_j + e_{ij}$$

where Y_{ij} is the (mean) percentage of trees damaged by the sawfly for the i th family in the j th replication; μ the overall mean; F_i the effect of the i th family; R_j the effect of the j th replication; and e_{ij} the random error.

The effects of test sites could not be compared with one another because different genotypes were planted at different sites. Consequently, analyses were carried out separately for each site. All the terms in the model were considered as random effects, and variance components were estimated using the VARCOMP procedure of SAS (SAS Institute, 1982). The standard deviations of the estimated variance components were calculated as described by Anderson and Bancroft (1952).

The variance component due to family (σ_F^2) was interpreted as the covariance of half-sibs and translated into one-quarter of additive genetic variance. Two types of heritability estimates were calculated following Wright (1976):

$$h_i^2 = 4\sigma_F^2 / (\sigma_F^2 + \sigma_e^2) \quad \text{and} \quad h_F^2 = \sigma_F^2 / (\sigma_F^2 + \sigma_e^2 / r),$$

where h_i^2 and h_F^2 are the individual and family mean heritabilities, respectively; σ_e^2 the variance component due to random error and r the number of replications. The individual heritability (h_i^2) is the appropriate heritability for estimating genetic gains from mass selection, and the heritability of family means (h_F^2) is appropriate for estimating genetic gains from half-sib family selection.

Pearson (phenotypic) correlations between tree defoliation and height were also carried out using the CORR procedure of SAS (SAS Institute, 1982). The correlation was subsequently converted to a type-B genetic correlation using Burdon's (1977) method, where

$$r_{g(x,y)} = \frac{r_{p(xy)}}{\sqrt{h_{gx}^2 \cdot h_{gy}^2}}$$

and $r_{g(xy)}$ the genetic correlation between height (x) and sawfly damage (y); $r_{p(xy)}$ the correlation between family means for x and y ; and h_{gx}^2 , h_{gy}^2 the heritabilities of family means for x and y , respectively.

Type-B genetic correlations are appropriate for correlations between two traits that are measured on the same individuals at different times (Burdon, 1977).

Table 1

Variance components, and percent of total variance in black spruce resistance to the yellowheaded spruce sawfly in a clonal seed orchard in New Brunswick, Canada, that was attributable to replication and block

Source	Estimated variance component (S.D.)	% of total variance
Clone (σ_C^2)	48.7 (48.7)	39.3
Replication (σ_R^2)	2.3 (1.5)	1.8
Replication \times block (σ_{CR}^2)	18.3 (8.1)	14.8
Error (σ_e^2)	54.7 (2.3)	44.1
Total	124	100

3. Results

3.1. Clonal seed orchard

Clones, replications and the interaction between clones and replications explained 39.3, 1.8 and 14.8%, respectively, of the total variation in defoliation by the sawfly (Table 1). The individual clone heritability estimate was 0.4, while that for clone means was 0.82. Height was not correlated to defoliation ($r = 0.02$, $p = 0.46$).

3.2. Half-sib family tests

The percentage of trees defoliated by the sawfly varied from 7.6% at SCI 96 to 67.5% at NBI 94. The heritability estimates were positively correlated to the percentage of trees defoliated at each site. No variation in defoliation at SCI 96, where only 7.6% of trees were defoliated, was attributable to family (Table 2). In contrast, the estimates of individual and family mean heritabilities at NBI 94, where two-thirds of

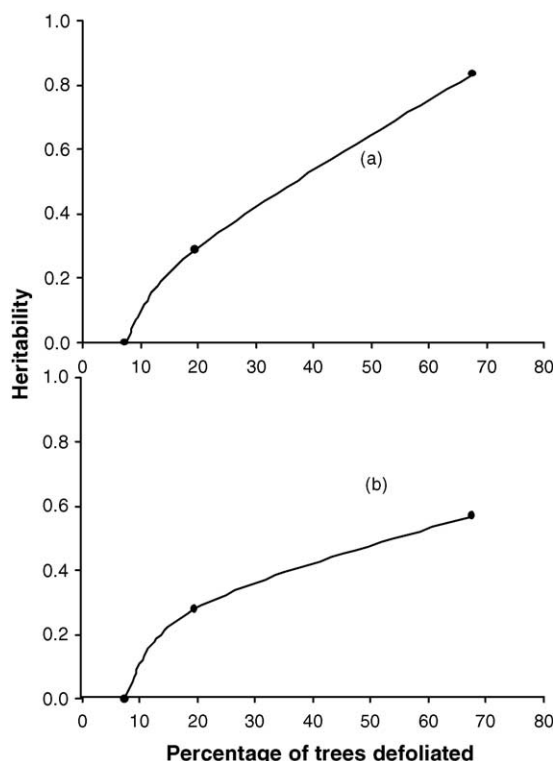


Fig. 1. Relationship between (a) individual and (b) family heritability estimates and percentage of black spruce trees defoliated by the yellowheaded spruce sawfly in the three half-sib family test sites.

trees were defoliated (Fig. 1), were 0.84 and 0.57, respectively.

The percentage of trees defoliated was positively correlated to height at all sites but the relationship was only significant at NBI 94, the site where the highest level of defoliation occurred ($r = 0.37$, $p < 0.001$) (Fig. 2). Using the New Brunswick Tree Improvement Council's data (unpublished) on heritability of height

Table 2

Variance components, and percent of total variance in black spruce resistance to the yellowheaded spruce sawfly in three half-sib family tests in New Brunswick, Canada

Source	NBI 94		SCI 95		SCI 96	
	Variance component (S.D.)	% of total variance	Variance component (S.D.)	% of total variance	Variance component (S.D.)	% of total variance
Family (σ_F^2)	0.0089 (0.0049)	17.8	0.0017 (0.0071)	4.7	0	0
Replication (σ_R^2)	0.0073 (0.0040)	14.5	0.0117 (0.0017)	32.1	0.00048 (0.004)	0.2
Error (σ_e^2)	0.034 (0.0044)	67.7	0.023 (0.0023)	63.2	0.261 (0.029)	99.8
Total	0.0502	100	0.0364	100	0.26148	100

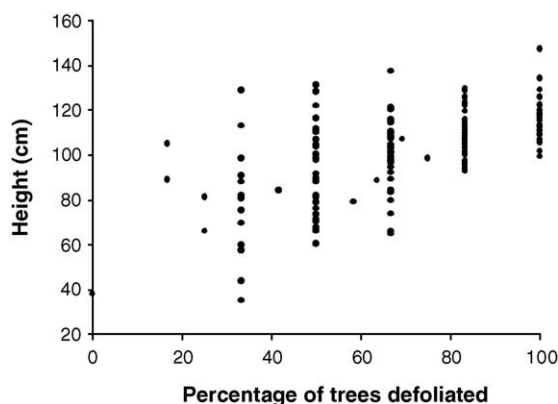


Fig. 2. Relationship between mean family height and percentage of trees defoliated by the yellowheaded spruce sawfly at NBI94.

($h^2 = 0.4$), the approximated genetic correlation was 0.64.

4. Discussion

The variance component due to clones (σ_C^2) was the largest genetic source of variation in the clonal seed orchard. Under the additive-dominance-epistasis genetic model, this variance is composed of $\sigma_A^2 + \sigma_D^2 + \sigma_I^2$, where σ_A^2 , σ_D^2 and σ_I^2 are additive, dominance, and epistatic genetic variances, respectively (Wright, 1976). The individual clone heritability thus represents the relative magnitude of all genetic effects, including additive and interaction effects within and between loci, to total phenotypic variation. The individual clone heritability is used to predict genetic gains from clonal ramet selection. However, since selection is likely to be based on clone means, the appropriate heritability to use is the clone mean heritability. The clone mean heritability estimates are large, indicating that substantial genetic gain may be obtained through clonal selection and deployment.

Results from the half-sib family tests also suggest that there is a strong genetic basis to variation among trees in susceptibility to *P. alaskensis*. Resistance to the sawfly is heritable and thus selection for resistance is possible, and could be incorporated in existing tree improvement programs. The positive relationship between the proportion of trees damaged by the

sawfly and estimates of heritability indicate that the genetic variability in susceptibility is readily expressed when the pest densities are high. Genetically based traits that reduce oviposition or juvenile survival may not be evident, statistically, when insect densities are low or extremely high. Strong et al. (1993) reported a positive relationship between the heritability of resistance of willow and the density of a galling midge in Sweden.

Our assessments of damage in the half-sib tests were based on plot means (i.e., the proportion of damaged trees per six trees in each replication). Although the primary function of the heritability estimates is to predict genetic progress through phenotypic selection, it also provides the relative magnitude of the genetic basis of susceptibility. However, the selection of resistant families will likely be based on the family means, and thus the appropriate heritability to predict the genetic gain is the ratio of the variance component due to families to total phenotypic variance among family means, i.e., family mean heritability. The heritability estimates reported here are substantial, indicating a large degree of additive genetic control, and that selection for sawfly resistance could be effective.

It is unusual to find individual heritability estimates that are higher than the family mean heritability. The higher estimate of individual than family mean heritability reported in this study may have been due, in part, to the low number of replications (5) in the analyses. Prediction of genetic gains involves, along with heritability, selection intensity and phenotypic standard deviation. Furthermore, selection should be practiced on replication-adjusted values, because our heritability estimates did not include the environmental variance component such as variance due to replications (Cotterill, 1987).

Our results are consistent with those of previous studies, which also reported genetically based resistance of interior and sitka spruce to a phloem feeder (Kiss and Yanchuk, 1991; Ying, 1991; Tomlin and Borden, 1997) and of white spruce to a defoliator of current-year foliage (Quiring et al., 1991). Our estimates of heritability are probably conservative, especially for clones, because the most susceptible (i.e., damaged) trees would probably have been excluded during the plus tree selection process.

Selection for resistance of black spruce to the sawfly may have a cost, with respect to height growth. Significant positive phenotypic correlations between defoliation and tree height were only observed in one of the four tests, indicating that the cost of resistance may not be large, or may only be expressed occasionally. However, the moderate genetic correlation between tree height and defoliation indicates that there is at least a small trade-off between growth rate and sawfly resistance.

In general, the current study supports the hypothesis that there is a large genetic basis to resistance of young conifers to herbivorous insects, and thus that tree resistance to insects can be incorporated in tree improvement programs. Selection for growth alone may, however, result in undesired increases in defoliation when the sawfly infestation is high. Therefore, a breeder should be cautioned to consider both growth and resistance traits simultaneously when developing tree improvement programs.

We do not yet know the mechanisms responsible for resistance of black spruce to the sawfly. Previous studies investigating the putative resistance of ponderosa pine, *Pinus ponderosa* Laws., to the pine sawfly, *Neodiprion fulviceps* (Cresson), reported that resistant trees had thicker outer cell layers, more fiber cells, higher toughness and lower soluble nitrogen (Wagner and Zhang, 1993). Resistance of scots pine, *Pinus sylvestris* L., to *N. sertifer* Geoffr. was attributable, in part, to variations in resin acids (Larsson et al., 1986) and their interaction with natural enemies (Björkman and Larsson, 1991). Although preference for both oviposition (Pasquier-Barre et al., 2000) and feeding (Auger et al., 1992) on scots pine by *Diprion pini* L. varied with tree clone, larval performance was not correlated with oviposition preference, making it difficult to infer the relative influences of oviposition preference and juvenile performance on tree resistance.

Due to low insect densities of the yellowhead spruce sawfly at all but one site in each of the three half-sib family tests examined, which prevented us from examining more than one site in each of the three tests, the present study was unable to evaluate genotype \times site interactions. Thus we do not know whether (or not) some genotypes are resistant in a variety of locations. Genotype \times site interactions were significant in other studies examining resistance of spruces (Quiring et al., 1991; Quiring and Butterworth, 1994; Alfaro et al.,

1996) and pines (Wu and Ying, 1998) to insects. Moreover, Alfaro et al. (1996) showed significant relationships between resistance of interior spruce to white pine weevil and elevation, latitude and longitude, as well as between resistance and biogeoclimatic zone. A significant clone \times replication effect on percent defoliation in the present study suggests that site \times genotype interactions may be important, and should be considered before any operational outplanting is carried out.

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