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Resistance to galling adelgids varies among families of Engelmann spruce (*Picea engelmani* P.)

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RESUME

Cooley gall adelgids, *Adelges cooleyi*, and round gall adelgids, *Adelges abietis*, differentially infested 110 half-sib families of Engelmann spruce, *Picea engelmannii* at 9 study sites in British Columbia. There was a negative genetic correlation (-0.53) between the infestations of the two gall-forming species. Cooley gall abundance exhibited a negative genetic correlation (-0.66) with tree growth, whereas round gall abundance exhibited a positive genetic correlation (0.79) with growth. Heritability (h^2) of resistance against the adelgids averaged about 0.60 for Cooley galls and 0.20 for round galls

INTRODUCTION

World-wide, there are 30 species of spruce (*Picea* spp: Pinaceae) which serve as the primary host for the majority of the 49 or so species of primitive aphids in the family Adelgidae (Carter 1971, Ghosh 1983). Each adelgid species typically causes a uniquely shaped gall to form on the developing shoots of susceptible spruces. Such galls can persist on the affected trees for many years depending on the species of gall-maker and the species and environment of the host spruce, thereby leaving a useful index to a tree's general resistance. For example, in undisturbed plantations in northern Minnesota, we have found galls that were formed as long as 30 years earlier (Mattson et al. 1994).

Usually, the impact of adelgids on tree growth and survival appears inconsequential. But, to be sure, no one has ever measured their long-term impacts on bud demography. Cooley galls, caused by *Adelges cooleyi*, for example, typically kill their subjugated shoots. Round galls caused by A. *abietis* and A. *lariciatus*, on the other hand, do not kill the shoot but allow it to grow in an apparently substandard manner. Ragged spruce galls caused by *Pineus similis* can cause hormonal imbalances in young seedling stems, triggering a cork-screw growth-habit that predisposes them to snow damage. In rare cases, some highly susceptible individual trees have nearly all of their shoots attacked by adelgids and consequently are rendered uncompetitive and eventually die (Mattson, pers. obs). In western North America where there are 15 species of adelgids, it is not uncommon to find galls from as many as 4 species on the same host plant, as is the case for Engelmann spruce, P. *engelmannii*, Sitka spruce, P. *sitchensis*, white spruce, P. *glauca*, and the vast hybrid swarm called interior spruce (mostly P. *engelmannii* x *glauca*) in interior British Columbia.

Numerous field studies in Europe and North America have reported substantive, consistent differences among individual trees in their resistance to the galling adelgids (e.g. see Mattson et al. 1994, Mattson et al. 1998), thereby implying that resistance has an important genetic component to it. For example, Mattson et al. (1998) estimated that broad sense heritability (H^2) of resistance against *Adelges abietis* was about 0.86 (the theoretical maximum being 1.0), using one clonal orchard of *Picea abies* in the southern Paris basin. Of course, such limited studies (i.e. one «population» of trees, one environment, one population of aphids) give but only a glimpse of the possible genetic bases of spruce resistance to adelgids.

This study was undertaken to further basic understanding about the genetics of spruce resistance to insects. Specifically, we investigated the hypothesis that there is substantive family level variation in Engelmann spruce resistance to two common, shoot-galling adelgids: the native, Cooley spruce gall aphid, A. *cooleyi*, and the introduced (from Eurasia), round spruce gall aphid, A. *abietis*, both of which produce very distinctive galls (Rose and Lindquist 1977). We also investigated the heritability (h^2) of such resistance and tested for genetic correlations between plant resistance to the two species of adelgids and between tree growth and resistance. We predicted that (a) tree resistance to one adelgid species would be positively correlated with resistance to the second adelgid owing to trees employing the same or very similar resistance mechanisms against both species, and (b) tree resistance and growth would be positively correlated because the most likely mechanisms of resistance would be rapid inducible defenses, such as strong and swift hypersensitive reactions, that are dependent on vigorous growth (Herms and Mattson 1992, 1997).

METHODS

This study was overlaid on a genetic trial utilizing 110 half-sib Engelmann spruce families originating from the east Kootenay region in S.E. British Columbia. Families were planted in linear, 10 tree plots, replicated in 2-3 blocks at each of 9 different, widely separated geographic sites. Trees were about 15 years of age, and ranged in height from 2-5 m in September 1994 when measurements were made. The first 5 living trees of all families in each replicate were scored for numbers of Cooley and round galls by a pair of forestry technicians. Each tree was examined (one person on each side) for two, 30-second intervals (using a timer) during which Cooley galls were counted, and then round galls counted. Such a brief inspection period was sufficient to provide a reliable difference among differently infested trees. For example, there was a strong linear regression relationship ($p < 0.01$, $r^2 = 50\text{-}75\%$) between such 30 second counts by forestry technicians and one minute counts (virtually 100% censuses) done on the same trees by two highly experienced gall workers (wjm & bab). Usually, the 30 second counts allowed the measurement of nearly all of the galls on lightly infested trees, and at least one-third to one half of them on the heavily infested trees. Tree heights (cm) and tree diameters (mm) were likewise measured at the same time. The round galls were initiated primarily by A. *abietis*, but there may also have been a small fraction of superficially similar round galls caused by A. *laricìatus*, though its distribution in S.E.. British Columbia is not well substantiated. Because over 11,000 trees were to be examined, it was not economically feasible to attempt to definitively segregate these two species of round gall makers, if indeed they occurred together. Therefore, the round gall counts may represent cumulative infestations of two species of adelgids. Due to misunderstandings, the whole tree gall counts were converted to a numerical index, and recorded as infestation classes: 0=0, 1=1-10, 2=11-20, 3=21-30, 4=31-40, 5=41-99 galls.

For statistical analyses and tests, we used the numerical indices directly, but furthermore we converted them back into a semblance of the original data by using a random number generator to pick a gall number within the appropriate numerical range covered by the index assigned to a tree. All such generated numbers (x) were then converted to their $\log_e (x+1)$ equivalent for meeting the assumptions of ANOVA. We used two ANOVA models. One was for analyzing separately each geographic locale or site: $X_{ijn} = \mu + F_i + R_j + F_iR_j + e_{ijn}$, where F is family, R is replicate, and FR are family by replicate interaction effects, e is residual error among individuals. The second was for analyzing the pooled data set across all sites: $X_{ijkn} = \mu + S_k + R_j (S_k) + F_i + F_iS_k + F_i R_j (S_k) + e_{ijkn}$, where S is site. Because of computational overload problems with an unbalanced design arising from missing observations, the pooled data set was manipulated to create a perfectly balanced data set consisting of 82 families and three individual trees per replicate (2) at all study sites. Hence, those statistics for the pooled study refer to this reduced data set, and consist of the class counts for galls. Statistics shown for the individual sites are based on the full set of 110 families, all replicates, and all individual trees, but using the random counts. In every ANOVA, all effects were considered random effects. To estimate the magnitudes of genetic correlations (r_g), and narrow-sense, individual heritabilities (h^2), we computed the variance components for the main effects, and their interactions, and then followed standard estimation protocols (Becker 1984, Falconer 1989, Kiss and Yanchuck 1991, Stonecypher 1992).

RESULTS and DISCUSSION

Variation among sites and families

Cooley galls were common at all 9 sites, but as expected, their abundance differed substantially and significantly among sites (Tables 1,2). For example, they averaged about 7 galls/tree at the least infested site, and 31 galls/tree at the most infested site. Analyses of variance confirmed that there were also substantive, significant ($p<.001$) differences among half-sib families (F) in their resistance to A. cooleyi at all 9 sites. According to a variance components analysis on the overall model testing all of the sites together, family effects accounted for 8.6 % of the total variation (Table 2). At the most heavily infested sites, the majority (>75 percent) of families were in middle to high range infestation classes, i.e. medium to light-heavy infestation classes. Only very few families were in the extremes, i.e. in very light and very heavy infestation categories. This implies that nearly all families are moderately to highly susceptible to A. cooleyi.

Round galls were much less common than Cooley galls at 6 of the 9 sites, but at 3 sites they were equally abundant (Tables 1,2). At the least infested location, round galls averaged about 2/tree, whereas at the most infested location they averaged about 34/tree. Analyses of variance revealed that there were highly significant family effects ($p < .001$) on round gall numbers/tree at all 9 sites. According to a variance components analysis on the overall model, family effects accounted for 2.4% of the total variation (Table 2). At the most heavily infested sites, the majority of spruce half-sib families fell into the medium and heavy infestation classes. As was the case for Cooley gall susceptibility, only few families fell into the very light and very heavy infestation classes. Thus, almost all families are moderately to highly susceptible to the round gall adelgids.

Tree size effects on galling

Because larger trees have larger canopies and offer more potential growing points for adelgid infestations, and families varied significantly in growth rates, we plotted mean galls/tree/family against family diameter (d.b.h.) and height to search for

Table 1. Mean number of galls ($\log_e(x + 1)$) per tree at nine different research sites, and the probability of a larger F value in randomized, complete block design testing the null hypotheses that there are no family, replicate, and family x replicate effects on gall counts per tree. Study sites are ranked in ascending order according to the mean abundance of Cooley galls per tree.

	Cooley galls:				Round galls:			
Study Sites:	mean	Fam	Rep	FxR	mean	Fam	Rep	FxR
E.WhiteRiver	1.768	<.001	0.24	0.07	0.959	<.001	0.06	<.010
Lodge Creek	1.918	<.001	<.001	0.07	1.554	<.001	<.001	<.001
Roche Creek	2.162	<.001	0.07	<.01	2.547	<.001	0.1	<.001
Jumbo Creek	2.513	<.001	<.001	<.001	0.539	<.001	<.010	<.010
Perry Creek	2.733	<.001	<.001	<.001	2.689	<.001	0.02	<.001
Bloom Creek	2.825	<.001	0.09	<.010	3.309	<.001	0.225	<.001
Lussier River	3.137	<.001	0.05	<.010	2.429	<.001	<.001	<.010
Horse Creek	3.173	<.001	0.41	0.12	1.338	<.001	0.47	0.04
WdvrmereCk	3.233	<.001	<.01	<.001	1.755	<.001	0.247	<.001

Table 2. Analysis of variance of data pooled from all sites, using gall class counts, showing degrees of freedom (df), Mean Squares (MS) and components of variance for the main effects for both Cooley and round gall analyses.

		Cooley Galls		Round Galls	
Source of Variation	df	MS	Variance Comp.	MS	Variance Comp.
Sites	8	315.5**	0.62	502.4*	0.99
Reps(sites)	9	91.5*	0.04	13.2*	0.05
Families	81	12.5*	0.20 (8.6%)*	4.5*	0.05 (2.4%)*
FxS	648	1.8*	0.08	1.7*	0.06
FxR(sites)	729	1.3*	0.15	1.3*	0.19
Error	2952	0.9	0.87	0.7	0.74

** significant ($p<0.001$) effects, * percentage of total variance

any such potential relationships. Universally, there was a very poor to negligible relationship between mean Cooley gall counts/tree/family and mean family d.b.h. and height (Table 2.). On the other hand, quite the opposite was true for round galls. Round gall numbers per family clearly increased linearly with mean family height (and diameter) at all study areas, ranging from about 1-3 galls/m of height at the most lightly infested areas, to about 7-12 galls/m of height at the most severely infested areas (table 4.).

To remove the effects of family growth rate which is potentially confounded with the inherent resistance/susceptibility of families, we divided galls/tree by tree height (m) and then transformed the ratio (r) using a $\log_e$ r +.01) transformation before running analyses of variance. We did not employ height as a true covariate in ANOVA because the regression relationship of galls on height was not perfectly collinear among all 110 families.

Converting raw gall counts to galls per unit height did not remove family effects; they were still very highly significant ($p < 0.001$) at all study sites (Table 3.). Although, standardizing galling by height did not eliminate family effects from the model, it did rearrange the individual infestation rankings of families, but largely within their original quartiles. For example, most of those families ranking in the highest and lowest infestation quartiles on the basis of galls/tree still occurred within the highest and lowest infestation quartiles, respectively, after standardization by tree height. However, the internal rankings of almost all these families changed relative to one another. For example, at Bloom Creek, the mean change in round gall family infestation rank (old rank-new rank) was +2.8 for the highest infestation quartile. In other words, the average family increased in mean gall loading by about 3 ranks. For the lowest infestation quartile, the mean change in family rank was -3.5, meaning that rank dropped by more than 3 (i.e. lower average gall loading). Only 5 new families moved into the highest infestation quartile, the other 22 just changed their rank orders. The same was true for the lowest infestation quartile. Therefore, we conclude that there are real and substantive family effects on galling that are confounded to only a small degree with the effects of family growth rates.

Table 3. Statistics for linear regressions of mean Cooley and round gall counts/tree/family versus mean family tree height (cm) at each of 9 study areas. If zero occurs in the slope columns, slopes are not significantly from different from zero. Otherwise, slopes are significantly ($p < .05$) larger than zero. Each regression is based on $\geq$ 216 observations.

Study Sites	Cooley galls:		Round galls:	
	Slope	r^2	Slope	r^2
BloomCrk	-0.0443	0.05	0.0954	0.17
E.WhiteRvr	0.0000	0.00	0.0217	0.29
HorseCrk	0.0378	0.05	0.0204	0.33
JumboCrk	0.0194	0.02	0.0129	0.31
LodgeCrk	0.0138	0.03	0.0483	0.46
LussierRvr	0.0000	0.00	0.1196	0.48
PerryCrk	0.0000	0.00	0.0319	0.12
RocheCrk	0.0220	0.09	0.0722	0.33
WindvCrk	0.0000	0.00	0.0276	0.21

Table 4. Mean number of $\log_e$ (galls/meter of tree height + 0.01) at nine different research sites, and the probability of a larger F value in randomized, complete block design testing the null hypotheses that there are no family, replicate, and family x replicate effects on gall per unit of height per tree. Study sites are ranked in ascending order according to the mean abundance of Cooley galls per tree.

Study	Cooley galls:				Round galls:			
Sites:	mean	Fam	Rep	FxR	mean	Fam	Rep	FxR
E.WhiteRiver	-0.016	<.001	0.09	0.03	-2.002	<.001	0.04	<.001
Lodge Creek	0.199	<.001	<.001	0.016	-0.592	<.001	<.001	<.001
Roche Creek	0.445	<.001	0.10	<.001	1.105	<.001	0.73	<.001
Jumbo Creek	1.003	<.001	<.001	<.010	-3.217	<.001	<.001	<.010
Perry Creek	1.006	<.001	<.001	<.001	0.954	<.001	0.03	<.001
Bloom Creek	1.198	<.001	0.33	<.001	1.789	<.001	0.24	<.001
Lussier River	1.887	<.001	0.06	<.010	0.857	<.001	<.002	<.030
Horse Creek	1.839	<.001	0.31	0.49	-1.132	<.001	0.55	0.010
WdvrmereCk	2.098	<.001	<.01	<.001	-0.057	<.001	0.325	<.001

Genetic correlations between galling and tree growth

To investigate possible genetic relationships between gall infestations and tree growth rates, we calculated the genetic correlations (r_g) between Cooley and round gall infestations and height$_m$ at each of the nine study sites, and on the entire, pooled data set (Table 5). In the case of Cooley galls, all correlations were negative, ranging in value from -0.02 to -.0.79. The pooled data set gave $r_g = -0.21$. The consistent association implies that the tree's traits for fast growth and resistance to Cooley gall aphids are positively linked, as might be the case if resistance depended on rapid inducible

Table 5. Genetic correlations (r_g) between adelgid gall infestations and tree growth (height$_m$), and between Cooley (C) and round (R) galls levels per tree, and estimates of the heritability (h^2) of resistance against adelgids using two measures of infestation, gall no./tree and gall no./m at each of 9 study sites in British Columbia. Each estimate in the table is based upon measurements on approximately 1000-2000 trees, except for the pooled sites.

Study Sites	Genetic correlations:				Heritability (h^2) estimates:			
	C.galls vs height	R.galls vs height	R.galls vs C.galls no./tree	R.galls vs C.galls no./m	C.galls no. Per tree	R.galls no. per tree	C.galls no./m	R.galls no./m
Bloom Creek	-0.79	0.36	-0.51	-0.31	1.0+	0.41	1.0+	0.17
E. White River	-0.49	1.0+	-0.54	-0.71	0.34	0.13	0.44	0.09
Horse Creek	-0.26	1.0+	0.03	-0.59	0.35	0.26	0.44	0.11
Jumbo Creek	-0.42	0.84	-0.49	-0.61	0.32	0.26	0.39	0.21
Lodge Creek	-1.0+	0.62	-1.0+	-1.0+	0.28	0.05	0.32	0.00
Lussier River	-0.37	0.84	-0.48	-0.69	0.95	0.51	1.0+	0.26
Perry Creek	-0.61	1.0+	-0.33	-0.69	0.83	0.12	0.85	0.00
Roche Creek	-0.02	0.84	0.19	0.38	0.78	0.17	0.84	0.09
Wdvrmere Creek	-0.55	0.74	-0.93	-0.85	0.69	0.18	1.0+	0.11
Pooled Sites	-0.66	0.79	-0.53	n.a.[1]	0.61	0.20	n.a.	n.a.

[1] n.a. not available, because analysis was not done for the particular variable of concern.

defenses (such as hypersensitive reactions) which are swiftest and strongest in vigorously growing tissues. On the other hand, for round galls quite the opposite was found. All correlations were positive, ranging from 0.36 to 0.84. The pooled r_g estimate was 0.92. Because round and Cooley gall resistance have different relationships to tree growth, it implies that the resistance mechanisms against them are different.

Correlations Between Cooley and round gall adelgids

To obtain a synoptic view of family resistance to both Cooley and round gall adelgids, we ranked each spruce family according to its percent departure from the grand mean resistance level of all 110 families at each of the 9 study sites. For example, at each locale, every family was rescaled for the two gall types using the following formula: ($_{family}$ gall$_i$ mean-local gall$_i$ grand mean)/local gall$_i$ grand mean x 100, where means are from log$_e$ (x+1) data. These new variables, percent deviations, were then used in a randomized block ANOVA, with study areas treated as blocks, to test again for family differences.

As before, there were highly significant ($p < 0.001$) family effects on the rescaled measures of resistance to galling. To demonstrate the families' resistance relationships to both Cooley and round gall adelgids, we plotted mean round gall rank against mean Cooley gall rank for all 110 families (Figure 1). The result was an obvious left to right sloping scattergram. Such a pattern implies a negative genetic correlation between the resistance traits for these two adelgids. Sixty-eight percent of the families fell into the upper left (27 percent) and lower right (41 percent) quadrants of the graph. Only a meager 11 percent of the families occurred in the lower left quadrant where susceptibility to both species of adelgids is below the grand mean. Therefore, typically, when one resistance trait is high, then the other is low, and vice versa. Contrary to this trend, only one family, f-126, had substantially low levels of both adelgids: its infestations were on average 23 percent below the grand mean for Cooley galls, and 32 percent below the grand mean for round galls. At the other contrary extreme, family f-80, had the highest combined level of both adelgids: its infestations were on average about 20, and 23 percent higher than the respective grand means for Cooley and round galls.

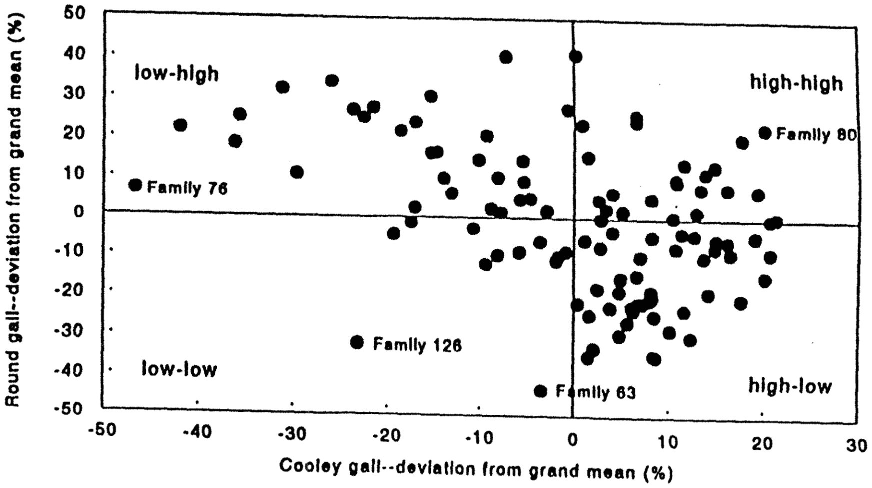

Figure 1. Plot showing the mean round and Cooley gall infestation ranks of each of 110 spruce families, using a family's average percent deviation from the grand mean round and Cooley gall infestation level of all trees, at each of 9 study sites. In other words, each point is the mean of 9 individual deviations measurements for a single family, showing its tendency to be higher, or lower than others with respect to infestations by round and Cooley gall adelgids. For example, Family 126 is identified in the lower left (low-low) quadrant, exhibiting below average levels of both galling adelgids.

Genetic correlations between Cooley and round gall infestations

Using the log$_e$ (x+1) gall counts, we found that there were negative genetic correlations (-0.33 to -0.93) between Cooley and round gall infestations per tree at 7 of 9 sites (Table 5). At 2 sites the correlations were near zero or positive (0.03 and 0.19). Using the entire data (all sites) set in the pooled model gave a substantial, negative genetic correlation of -0.53.

Estimating heritabilities of resistance to adelgids

Heritability estimates depend on the environment in which they are measured, the particular genetic structure of the populations, and a bevy of other factors. Therefore, we computed heritability estimates for each of the 9 study locales, realizing that insect population size and its genetic structure may vary substantially among them.

For Cooley adelgids, h^2 values ranged from 0.28-0.95 with one estimate exceeding 1.0, owing to estimation errors (Table 5). The pooled estimate and its standard error over all sites was 0.61 ± 0.11.

For round gall adelgids, h^2 values ranged from 0.05-0.51 (Table 5). The pooled estimate and its standard error over all sites was 0.20 ± 0.05.

Because each heritability estimate was usually based on about 1000 individual tree measurements, derived from 110 families, the precision of the estimates are reasonably good. For example, the sampling variances of h^2 estimates are approximately 32 x $h^2/1000$ (Falconer 1989), and thus its standard errors are approximately (sqrt (32 x h^2)) / 1000. Although we only calculated standard errors for the overall h^2 estimates (after Becker 1984), it is evident that heritabilities were significantly larger than zero.

CONCLUSIONS

Heritability estimates varied widely across individual sites, but the overall estimates confirmed that h^2 was substantially larger (~0.6) for Cooley galls, than for round galls (~0.2). This may suggest that there is more genetic variation present for Cooley gall resistance, but the lower level of attack by round gall adelgids may have caused the heritability estimates to be less than those for Cooley gall resistance. Not surprisingly, for both gall adelgids there was a tendency for the highest heritability estimates to be linked to the sites with highest insect densities, as has been observed elsewhere by Strong et al. (1993) for a cecidomyiid leaf-galling fly on willow, Salix spp in Sweden.

Nevertheless, these values indicate there are good levels of genetic variation in resistance to both gall-forming insects on interior spruce, and breeding for resistance would be possible. However, relationships between height growth and resistance to both gall forming insects were quite different. Cooley gall abundance was negatively correlated with height growth which suggests faster growing families are more resistant. Whereas, for round gall adelgids, faster growing families are more susceptible. This would make breeding for resistance against both insects more difficult as very few genotypes would be segregating for positive attributes for all three traits (i.e., growth and Cooley and round gall adelgid resistance).

Adjustments to the data to account for differential attack among large and small trees, suggested that tree size per se does not largely change the probability that a tree will be attacked and that family pedigree is more important. Ideally one should know the impact of galling aphids on tree growth which would then permit an assessment of the benefit of developing lines of trees resistant to gall forming adelgids. Unfortunately, nothing is really known about the impact of such gall formers on tree survival and growth.

Understanding of the genetics of tree resistance to phytophagous insects is in its infancy. More research is clearly needed in order to be able to effectively employ natural mechanisms of plant resistance against potential tree pests.

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LES COLLOQUES

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