Variation among Norway spruce provenances, families and clones in susceptibility to the spruce gall adelgid (*Adelges abietis*)

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Abstract

Incidence of the spruce gall adelgid (*Adelges abietis*; "spruce gall aphid" sensu common usage) was assessed as presence/absence in Norway spruce trials in Norway. The trial series comprised a long-term provenance test, a short-term provenance test (36 provenances), three diallel populations (10×10, 10×10, 9×9), a 10×10 factorial cross (100 families), and a clonal test (40 clones). Substantial genetic variation in gall incidence was observed among provenances, among families, and among clones within families. Provenances transferred from low- to mid-elevation Central Europe exhibited higher gall incidence than Nordic and Baltic origins, whereas high-elevation Central European material showed lower incidence. Family-level variation was detected in both natural-population diallels and breeding-population factorial material; a strong agreement was observed between family and derived clone performance (family–clone r ≈ 0.91). Variance-component analyses indicated predominantly additive genetic control, with additional non-additive effects in some crosses. Corresponding narrow-sense heritability estimates were low to moderate (≈ 0.06–0.22). Site effects were evident, with higher expression associated with greater vigor on fertile soils in some trials. Overall, the results indicate that selection for reduced galling is feasible and that provenance choice and site fertility should be considered in deployment and climate-adaptation strategies.

Key words: Norway spruce, spruce gall adelgid, genetic variation, susceptibility, heritability.

Introduction

The spruce gall adelgid, *Adelges abietis* (L.), occurs throughout the native range of Norway spruce (*Picea abies* (L.) Karst.) in Europe (Figure 1) and is also found where spruces have been widely planted beyond this range, including the Mediterranean fringe (with sporadic North-African records) and as an introduced species in North America. It develops characteristics pineapple- or walnut-shaped galls on several spruce species, but most commonly on Norway spruce. This small adelgid (1,5–3 cm in length) typically completes a one-year life cycle with two generations per year, and most individuals stay on the tree on which they are born (Björkman 2000). In the late summer, females lay eggs on needles; these hatch in autumn and new-instar nymphs crawl into a bud to overwinter. In spring, they insert their stylets into the developing shoot and feed on plant solutes, redirecting bud development so that a gall forms if the attack is successful. Examples of galls on Norway spruce branches are shown in Figure 2. The ontogeny of gall development from differentiating bud tissue on Norway spruce trees was described by Plumb (1953).

Adelges abietis is the most encountered adelgid on Norway spruce in the Norwegian conifer forests. Galls typically form at the base of current-year shoot. Tissue distal to the gall often dies, producing short, misshapen internodes and occasional leader forking if the terminal is affected. In Christmas-tree production, heavy galling reduces marketability and frequently results in shoot mortality. While damage is usually aesthetic, repeated severe infestations can cause dieback or stunting, particularly in young stock. Despite its prevalence, effects on individual-tree growth and stand development in Norway remain poorly quantified.

Observations in Norway spruce plantations have shown that individual trees vary widely in their susceptibility to *Adelgis abietis* (Thalenhorst 1972; Rohfrisch 1981). Genetic variation was shown in a progeny test with full-sib families (Eidmannn & Eriksson 1978) and differences in the frequency of galls was demonstrated between families with parents of Swedish and West European origin. In a clonal plantation, Mattson et al. (1998) reported large among-clone differences in adelgid infestation, with high broad-sense heritability (~0.89) but no clear association with region of origin. The genetically level of resistance was also demonstrated in common garden trials with full-sib families reported by Björkman (2000) and Axelsson et al. (2015). Chemical correlates of resistance have also been suggested: earlier work found that phenolic profiles differed between resistant and susceptible Norway spruce, implicating elevated phenols in resistant tissues (Tjia & Houston 1975).

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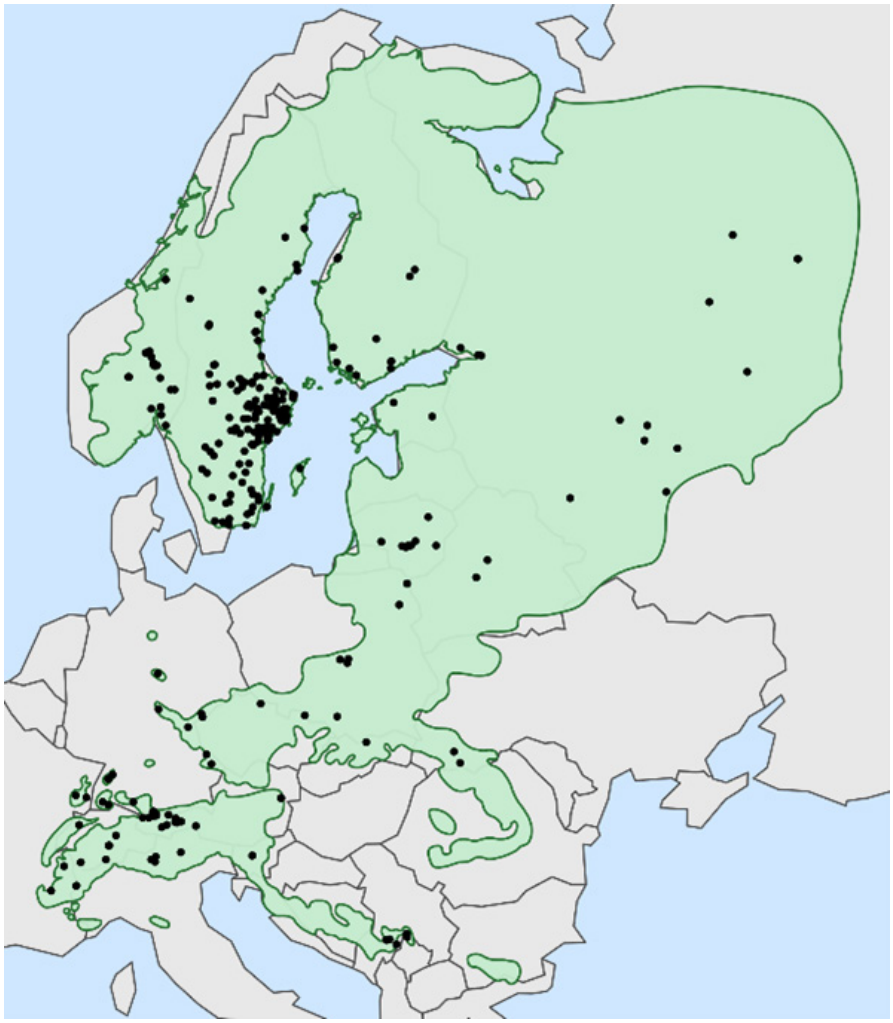

Figure 1
Native distribution of *Picea abies* in Europe (green shading, Caudullo et al. 2024) with georeferenced occurrence records of *Adelges abietis* (black points) obtained from GBIF (2025).

Figure 2
Spruce galls on branches on Norway spruce. Photo: Dan Aamlid, NIBIO.

In this study we analysed data from assessments made of attacks by the spruce gall adelgid in genetic trials covering provenances, families and clones of Norway spruce. Each tree in the trials was scored for presence or absence of galls. We quantified variability at all three genetic levels and estimated genetic parameters for gall incidence, as well as correlations with other traits. To our knowledge, apart from the clonal analysis of Mattson et al. (1998), there are no published studies at this level. Our multi-level analysis provides new estimates to address this gap.

Materials and Methods

Assessments of attack by spruce gall on Norway spruce were made in one long-term provenance trial at a forest site and in four series of short-term trials on agricultural soil that included provenances, families, and clones (Table 1). In each trial, trees were scored individually at the end of the growing season one specific year, and it was recorded whether the tree had no galls or one or more galls on the branches. Thus, the score had a binomial distribution, galls being absent or present. In all trials, height and stem diameter were measured, and stem and branch defects and damage were assessed. In the long-term provenance trial, the timing of bud burst was scored by the Krutzsch scale (Krutzsch 1973). In the other trials, weekly shoot elongation measurements were made during the growing season and the days of shoot initiation and cessation were estimated. Large genetic variation in these traits at all three genetic levels has been reported previously (Fottland & Skrøppa 1989, Skrøppa & Magnussen 1993, Skrøppa et al. 2014, Skrøppa & Steffenrem 2016, Skrøppa et al. 2023).

Table 1
Norway spruce trials in which *Adelges abietis* gall incidence was recorded.

Trial	Number of genetic units	Planted year	Assessment made	Mean percentage of trees with galls
IUFRO 1964/68 provenance trial	200	1968	1977	44
Short-term provenance trial	36	1976	1980	32
Three trials with complete diallels	280	1976	1980	19 14 8
10 x 10 factorial trial	100	1986	1992	37
Clonal trial with clones from 8 families from the 10 x 10 factorial	40	1989	1996	21

Two blocks of the IUFRO 1964/68 provenance experiment

The IUFRO 1964/68 provenance experiment with Norway spruce (Krutzsch 1974) was planted at two sites in Norway. Gall incidence was assessed in autumn 1977 in two blocks at Bjerkøy (59˚12'N, 10˚28'E, 10 m a.s.l.) (Fottland & Skrøppa 1989). In each block, 100 provenances were represented by 25 trees per provenance in a completely randomized design. The provenances in each block were selected to represent the full natural range of the species. Based on geography and climate, 193 of the provenances were grouped in 12 zones (Table 2). Mean tree height in 1977 was 368 and 372 cm in the two blocks, respectively.

Short-term provenance trial

A short-term provenance trial was established at Hogsmark Experimental Farm, Ås (59˚40'N, 10˚43'E, 85 m a.s.l.) in 16 randomized blocks with 4-tree plots planted at 0.6 m spacing (Skrøppa & Magnussen 1993). The trial contained 36 provenances: 20 from Poland, eight from Latvia, three from Slovakia and one each from Romania, Germany, Finland, Sweden and Norway. Twenty-eight of the provenances were grouped into seven more or less homogeneous geographical zones (Table 3). Gall incidence was assessed in autumn 1980, at age seven years from seed, when mean tree height was 138 cm.

Diallel trials

A complete diallel cross was made among standing trees in three natural populations of Norway spruce, with each tree used as both female and male parent. Three trials, each with families from one diallel, was planted at Hogsmark Experimental Farm in 1976 (Skrøppa et al. 2023). Each diallel was planted in a separate trial situated next to the provenance trial described above, and the three diallel trials were located adjacent to one another with border rows of Norway spruce both between the trials and along the outer edges. The diallels were of size 10 x 10 (Diallel 1 and Diallel 2) and 9 x 9 (Diallel 3) and with few missing families. Each trial was established with 48 trees from each family, distributed in 4 tree square family plots at 0.6 m spacing withing 12 completely randomized blocks. In a recent study, it was shown that differences in soil fertility were present among the blocks, a fact that influenced the growth conditions (Skrøppa & Fundova 2025). Gall incidence was assessed in

autumn 1980, at age seven years from seed, when mean tree heights of Diallel 1–300, 121 and 122 cm, respectively. Results from analyses of shoot elongation traits were earlier reported by Skrøppa et al. (2023).

One long-term field trial at a forest site was established with full-sib families from each half-diallel, planted with 4-tree plots in 12 blocks (Solvin et al. 2024). In these trials, tree heights and diameters were measured up to the age of 32 years and assessments of damage, including score of gall incidence, were made.

Factorial 10 x 10 trial

A factorial trial with 100 full-sib families was planted in 1985 at Hogsmark Experimental Farm in 12 completely randomized blocks with 4-tree family plots spaced at 1 m (Skrøppa & Steffenrem 2016). Controlled crosses were conducted in the Stange Norway Spruce Seed Orchard among 10 parental clones of Norwegian (N) origin and 10 clones of East European (E) origin. The Norwegian clones were plus trees selected in natural stands within a limited geographic area of southern Norway. The East European parents were drawn from a set of 30 clones representing five provenances originating from Romania, Belarus, North-east Poland and Latvia, selected for superior performance after 25 years in a provenance trial in northern Sweden. Within each origin group, five parents were used as maternal and five as paternal parents, yielding 100 families that fall into four crossing types by parental origin (maternal × paternal): N×N, E×E, N×E and E×N. Quantitative genetic analyses showed that the families from the East European provenance group (E x E) had the least variation in frost hardiness, tree height and annual shoot growth rhythm, and the lowest heritability values (Skrøppa & Steffenrem 2016). Assessment of gall incidence was made in autumn 1992, at age eight years from seed, when mean tree height was 241 cm.

The 100 full-sib families were planted in seven trials in three Nordic countries, six of these at forest sites (Skrøppa & Steffenrem 2021). In addition to measurements of tree heights, assessments were made of damage, including score of gall incidence,

Clone trial

A clonal trial comprising 40 Norway spruce clones was planted at Hogsmark Experimental Farm in 1989 in a single tree plot design at 1 m spacing, with 24 replicates per clone. The clones were produced as rooted cuttings from five randomly selected trees in each of eight full-sib families from the factorial cross. Of these eight families, three (families 1, 6 and 7) shared no parents and were unrelated to the other families, whereas the remaining five families shared either a maternal or a paternal parent, creating half-sib relationships among pairs of families. Assessment of gall incidence was made in autumn 1996, when mean tree height was 227 cm.

Statistical methods

For each genetic unit (provenance, family or clone), the percentage of trees will galls was calculated. Gall scores of individual trees were transformed to normal scores within blocks using the Blom transformation in SAS (SAS Institute Inc. 2003). This was done to obtain a distribution of the binary trait that meets the assumptions of the linear model needed to make statistical tests and estimate genetic parameters, useful to indicate the importance of genetic variation and possibilities for selection in breeding.

In the provenance trials, analyses of variance of the transformed values were carried out with PROC GLM in SAS, including the effects of zone, provenance(zone) and provenance (zone) × block.

In the diallel trials, transformed gall-incidence scores of the outcrossed families were analyzed using ASReml-R (Butler et al. 2017). The selfed families were not included in the analyses as their performance may be influenced by inbreeding depression which occurs with variation among selfed families (Skrøppa 1996). The statistical model applied for these analyses was:

$$Y_{ijkl} = \mu + GCA_i + GCA_j + RGCA_i - RGCA_j + SCA_{ij} + \beta_{ij} \times RSCA_{ij} + P_{ijk} + E_{ijkl}$$

Here, GCA_i and GCA_j are the general combining abilities of parents i and j, $RGCA_i$ and $RGCA_j$ are the reciprocal parental or maternal effects, SCA_{ij} is the specific combining ability of parents i and j, $RSCA_{ij}$ is the specific reciprocal cross effect and $\beta_{ij} = 1$ for $i<j$, $\beta_{ij} = -1$ for $i>j$. P_{ijk} is the plot effect and E_{ijkl} is the within plot error term. Block effects were not included due to the normal score transformation within each block.

In the ASReml analyses, all effects were treated as random and assumed to be mutually independent and normally distributed with mean 0 and variances σ^2_{GCA}, σ^2_{RGCA}, σ^2_{SCA}, σ^2_{RSCA}, and σ^2_E, respectively, for the general combining ability (GCA), the reciprocal parental (RGCA), the specific combining ability (SCA), the reciprocal cross (RSCA), and the error (E) effects.

The genetic variance of a cross was defined as $\sigma^2_G = 2\sigma^2_{GCA} + 2\sigma^2_{RGCA} + \sigma 2^S_{CA} + \sigma^2_{RSCA}$. The phenotypic variance component, σ^2_{phen}, was obtained as a sum of σ^2_G and all remaining variance components in the fitted model. Narrow sense heritability was then estimated as $h^2 = 4\sigma^2_{GCA}/\sigma^2_{phen}$. Estimates are reported with their standard errors, even when the GCA variance components were not statistically significant. Standard errors were obtained from first order Taylor series approximations as provided by ASReml-R software (Butler et al. 2017). Parent breeding values (BLUPs) were predicted for each diallel, and Pearson correlations among parent BLUPs across traits were calculated to provide proxy estimates of genetic correlations.

Transformed gall-incidence scores in the factorial trial were analysed by PROC GLM and PROC MIXED analyses in SAS for each of the crossing types N x N, Ex E, N x E and E x N based on the model

$$Y_{ijkl} = \mu + F_i + M_j + FM_{ij} + P_{ijk} + E_{ijkl}$$

where F_i is the effect of the maternal parent i, M_j that of the male parent j, FM_{ij} is the interaction between the parents i and j, P_{ijk} is the plot effect and E_{ijkl} is the within plot error term. All effects were assumed to be random and independent and normally distributed with mean 0 and variances σ^2_F, σ^2_M, σ^2_{FM}. σ^2_P, and σ^2_E, respectively. Narrow sense heritabilities were

estimated for the four groups of families by $2(\sigma^2_F + \sigma^2_M)$ divided by $\sigma^2_F + 2_M + \sigma^2_{FM} + \sigma^2_P + \sigma^2_E$.

Results

The IUFRO 1964/68 trial

In the two blocks of the IUFRO trial, the mean percentages of trees with galls were 41 % and 48 %, respectively; provenance means ranged from 0 % to 95 %. When the 193 provenances were grouped into the 12 geographic zones shown in Table 2, zone means ranged from 15 % to 54 %. Zones representing the northern range, higher elevations, and the Baltic countries had the lowest gall incidence, whereas zones from lower and mid-elevation Central Europe had the highest. Analysis of variance of the Blom-transformed incidence indicated highly significant differences among zones ($p<0.0001$).

Table 2
Mean percentage of trees with galls by geographic zone across the two blocks.

Zone	Number of provenances	Percent galls
Germany, Austria, Switzerland	120	54
Sudet-Alps, Beskids	11	44
Tatra Mountains	12	28
Poland lowlands	5	45
Carpathian Mountains	6	15
South-East Europe	5	27
North-East Poland	6	36
Baltic countries	9	20
Denmark, Southern Swedeen	2	39
Norway, Central Sweden	11	26
Finland	2	18
Northern Sweden	4	15

The short-term provenance trial

The mean percentage of trees infested with galls was 32 %, with provenances means ranging from 19 % to 50 %. Block-level incidence ranged from 20 % to 44 % and was unrelated to mean block height ($r = -0.23$). Provenances from the Nordic countries showed the lowest incidence, whereas Central European provenances showed the highest, except from those from high elevations. Analysis of variance of the Blom-transformed scores indicated significant difference among zones ($p < 0.003$), but not among provenances within zones ($p = 0.37$). Provenance mean height was lowest for the Nordic group and was positively correlated with gall incidence ($r = 0.41$). No relationships were detected between gall incidence and the days of shoot growth initiation and cessation ($r < 0.28$).

Table 3
Mean percentage of trees with galls for each geographic zone.

Zone	Altitude (m a.s.l.)	Number of provenances	Percent galls (%)	Height age 7 years (cm)
Nordic countries	15–250	3	20	123
Latvia	45-210	8	27	135
North-East Poland	160-180	4	33	139
East Poland	160-180	2	40	133
South Poland	600-710	5	42	142
South Poland	950-1450	3	31	133
Slovakia	700-810	3	36	147

Diallel trials

Mean gall incidence in the three diallel populations was 19 %, 14 %, and 8 %, respectively. Incidence was considerably lower in selfed families than in outcrossed full-sib families derived from the same parents (selfed means: 7 %, 10 %, and 3 % for Diallels 1–3), and selfed families also exhibited a shorter growing season (Skrøppa 1996). Table 4 lists family means for Diallel 1; for each parent, the averages of its half-sib progenies were similar whether the parent served as the female or the male. Similar relationships were also present in the two other diallels (not shown). The range of half-sib family means was 4–28 % in Diallel 1, 8–21 % in Diallel 2, and 4–12 % in Diallel 3. Block-level incidence varied widely: 1–43 % in Diallel 1, 2 –26 % in Diallel 2, and 2 –12 % in Diallel 3. Mean block height at age seven years was positively associated with gall incidence in Diallel 1 and Diallel 3 (r = 0.89 and r = 0.61, respectively), but not in Diallel 2 (r = 0.05).

Table 4
Percentages of trees with galls for outcrossed and selfed families in Diallel 1; each of the 10 parents was used as both female and male in the controlled crosses. The diagonal entries are the selfed families. Half-sib family means are based on the outcrossed families.

					Father						
Mother	1	2	3	4	5	6	7	8	9	10	Mean
1	0	33	8	2	17	38	42	19	27	4	21
2	46	13	11	10	40	21	35	31	36	6	26
3	22	27	8	5	17	21	38	17	29	6	20
4	6	5	4	2	4	8	9	4	4	2	5
5	17	25	33	0	11	22	25	23	20	13	20
6	10	40	23	0	24	2	40	8	25	10	20
7	47	52	37	2	29	36	.	13	47	10	30
8	17	21	13	0	16	10	10	5	16	10	13
9	27	35	30	2	24	22	27	13	21	17	22
10	17	13	20	2	15	4	10	4	10	2	10
Mean	23	28	20	3	21	20	26	15	24	9	19

Across the three diallels, the GCA variance components for the transformed gall scores had the highest value of the genetic variance components and were highly significant (Table 5), indicating additive genetic inheritance. The SCA and RSCA components were significant only in Diallel 1. In that diallel, parent–parent interactions were indicated: the strongly resistant parent 4 exerted a large effect in crosses with more susceptible parents 2, 7 and 9. No such patterns were observed in Diallels 2 and 3 (not shown). The estimated genetic variances were lowest in Diallel 3, which had the lowest mean gall score. This is also demonstrated by the heritability estimates with values 0.22, 0.11, and 0.06 for Diallels 1–3, respectively.

Table 5
Estimates of variance components and narrow-sense heritability (h^2) for the transformed gall scores in the tree diallels with standard errors of estimates in parentheses.

Source	Diallel 1	Diallel 2	Diallel 3
GCA	0.022 (0.011)	0.01 (0.005)	0.004 (0.002)
RGCA	-	0 (0)	0 (0)
SCA	0.006 (0.003)	0.001 (0.001)	0 (0)
RSCA	0.002 (0.001)	-	0.002 (0.001)
Plot	0.032 (0.006)	0.023 (0.006)	0.008 (0.004)
Error	0.353 (0.009)	0.342 (0.009)	0.253 (0.007)
h^2	0.22 (0.10)	0.11 (0.05)	0.06 (0.03)

Table 6
Estimates of genetic correlations between transformed gall scores and tree height, shoot-growth initiation and cessation.

Diallel	Tree height age 7	Day of shoot initiation	Day of growth cessation
1	-0.04	-0.12	-0.12
2	0.66	-0.43	-0.05
3	-0.23	-0.23	-0.68

The estimated genetic correlations between the transformed gall scores and tree height, shoot-growth initiation and cessation were significant for two trait combinations ($p = 0.04$; Table 6), but no systematic patterns were evident.

In the assessments made in the three field trials at forest sites no galls were observed.

Factorial trial

Mean gall incidence across the100 full-sib families was 37 %, with full-sib family means ranging from 0 % to 84 %. Parents 1–5 and 11–15 were of Norwegian (N) origin, and parents 6–10 and 16–20 were of East European (E) origin (Table 7). The mean incidence for N x N families was 57 %, whereas E x E families averaged 19 %.

At the block level, mean incidence across the 12 bocks varied from 34 % to 42 %, and mean block height at age eight years from 205 to 257 cm. No significant block-level relationship between gall incidence and tree height was detected ($r = 0.40$).

Table 7
Percentages of trees with galls for the full-sib and half-sib families in the 10 x 10 factorial trial. Parents from 1 to 5 and 11 to 15 were of Norwegian (N) origin and those from 6 to 10 and 16 to 20 were of East European (E) origin. The N x N and E x E full-sib families are shown in bold.

Female						Male parent					
Parent	**11**	**12**	**13**	**14**	**15**	16	17	18	19	20	Mean
1	**77**	**60**	**37**	**60**	**68**	51	27	21	27	29	46
2	**33**	**35**	**28**	**28**	**46**	21	8	5	35	0	24
3	**80**	**82**	**46**	**63**	**84**	73	32	37	68	23	59
4	**79**	**26**	**32**	**49**	**80**	30	21	30	57	21	42
5	**80**	**80**	**56**	**61**	**71**	45	33	18	51	19	51
6	38	19	23	36	40	**29**	**14**	**18**	**14**	**5**	24
7	74	41	30	55	70	**36**	**40**	**9**	**55**	**26**	43
8	32	11	22	14	42	**17**	**5**	**8**	**9**	**3**	16
9	58	41	11	42	53	**22**	**26**	**16**	**18**	**11**	30
10	63	58	41	52	71	**33**	**17**	**21**	**24**	**12**	39
Mean	61	45	33	46	62	36	22	18	36	15	37

Within the N x N crosses, the half-sib family means (maternal or paternal) ranged from 34 % to 71 %, whereas within E x E crosses from 8 % to 33 % (Table 7). In the analyses of variance, most female (F) and male (M) variance components were significant ($p < 0.01$), and the interactions among parents (F x M) was strongly significant ($p = 0.005$) in the N x N group (Table 8). All estimated variance components were larger in the N x N than in the E x E crossing group, which also had the lowest heritability estimate. Thus, more exploitable genetic variation was present among the Norwegian than the East European parents. The lower level of variation in the last group was most likely due to the effects of their selection history, which was similarly demonstrated for other traits by Skrøppa & Steffenrem (2016).

Table 8
Mean of percentage of trees with galls and estimates of variance components and heritabilities for transformed gall scores for each crossing type, separately shown in the four columns. Standard errors of estimates are presented in parentheses.

Source	N x N crosses	N x E Crosses	E x N crosses	E x E Crosses
Mean (%)	57	31	42	19
F	0.050 (0.040)	0.028 (0.022)	0.043 (0.003)	0.018 (0.015)
M	0.034 (0.030)	0.039 (0.030)	0.032 (0.025)	0.007(0.007)
F x M	0.017 (0.003)	0.009 (0.007)	0.005 (0.007)	0.009 (0.006)
Plot	0.008 (0.015)	0.004 (0.013)	0.014 (0.015)	0.0
Error	0.559	0.482	0.548	0.357
Heritability	0.20 (0.16)	0.24 (0.18)	0.23 (0.18)	0.12 (0.11)

For half-sib family means, Pearson correlations between the percentage of trees with galls and the days of shoot-growth initiation and cessation were negative and statistically significant when all 20 parents were analysed ($r = -0.78$ and -0.72; see Figure 3). When computed within the N x N and Ex E crossing groups, the correlations were weaker and non significant. Figure 3 clearly shows that the late flushing E x E families had a lower percentage of trees with galls than the N x N families. Within the last group there was no such relationship. Correlation coefficients between tree heights and gall percentages had low values.

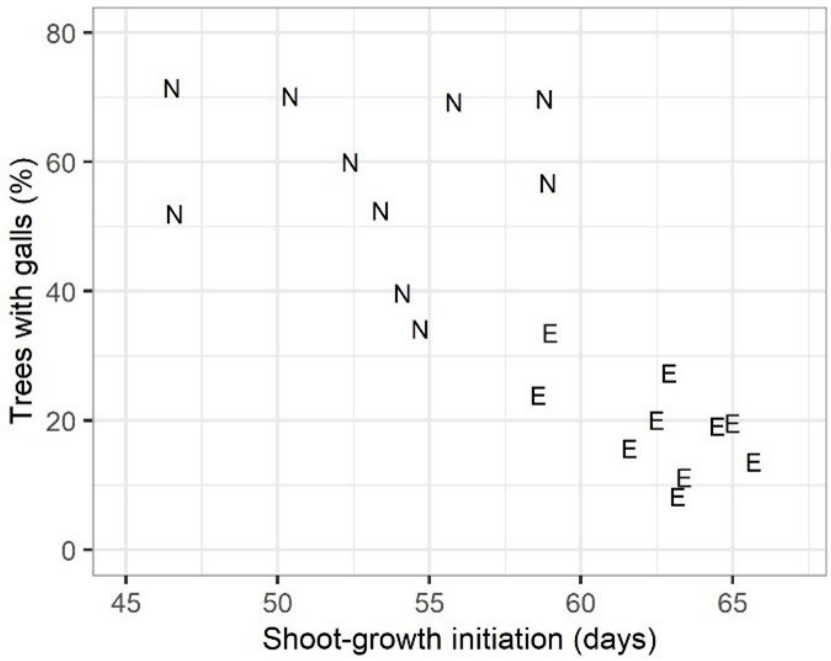

Figure 3
Relationship between the percentage of trees with galls and the day of shoot growth initiation for half-sib family means indicated with N for N x N crosses and E for E x E crosses.

No galls were observed in the assessments made in the field trials in three Nordic countries.

Clone trial

In the clone trial, mean gall incidence was 21 %, with clone means ranging from 0 % to 88 % and family means from 0 % to 41 %. A large variation was also present among clones within families: in seven families at least one clone had no galls, and in one family all clones were free of galls. A strong relationship (r = 0.92) was observed between the family-level gall incidence in the family test (assessed 1992) and in the clonal trial (assessed in 1996), as shown in Figure 4.

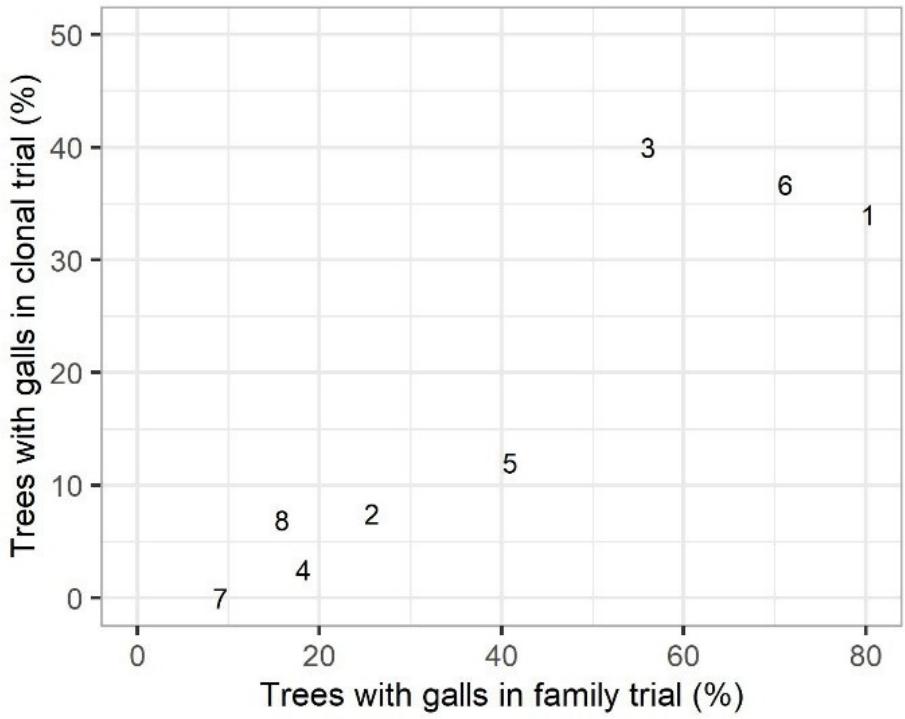

Figure 4
Relationship between the percentage of trees with galls in the family trial (assessed 1992) and in the clonal trial (assessed in 1996). Family means are shown with 1, 2 and 3 for N x N crosses, with 4, 5 and 6 for E x N or N x E crosses and with 7 and 8 for E x E crosses.

Discussion

The main trait observed and analysed was gall incidence, recorded as a binary variable with a Bernoulli distribution (0 = no galls, 1 = at least one gall present). Substantial variation in the number of galls per tree was observed but not captured by this measure. Recording counts of number of galls or using an ordinary severity scale would have generated data for more accurate quantitative genetic analyses; likewise, measuring size of galls would have increased precision. Such information was presented by Pilichowski et al. (2014). These limitations in our study should be considered when interpreting the heritability and correlation estimates.

Genetic variation and inheritance patterns

The results presented demonstrate variation in susceptibility to the spruce gall adelgid at three genetic levels: among provenances, among families, and among clones within families. In both provenance trials, the provenances transferred from low- or mid-elevation Central Europe showed higher gall incidence than Nordic and Baltic provenances. Among half-sib families generated in the diallel crosses, the magnitude of variation was smaller than at the provenance level but still considerable. Population-level differences were also detected but could be due to the low number of parents from the three populations.

A substantial variation among families was also shown in the factorial trial, but with different patterns for the N x N and E x E family groups. These families were generated by crosses among selected trees from a breeding population. In the N x N group, large variation was expressed among progenies from plus trees originating from different natural spruce populations. By contrast, reduced variation was observed for the families from the E x E parents, which had undergone strong

selection after transfer from southern to northern latitudes and after 25 years of growth at the northern site. This pattern mirrors results observed for other traits measured in trials with these materials (Skrøppa & Steffenrem 2016).

Taken together, the diallel and the factorial trials provided information on genetic control and inheritance of susceptibility to the spruce gall adelgid. Strong genetic control was indicated by the agreement between assessments made in different years and tests (families versus derived clones). Additive genetic effects were predominant, with indications of non-additive effects given by the SCA and RSCS components in Diallel 1 and by significant female × male (F x M) component in the N x N crossing group. The estimated narrow-sense heritability values were low to moderate and were lower than the broad-sense clonal heritability (0.86) reported by Mattson et al. (1998) for an unreplicated, wide origin Norway spruce clonal plantation. The heritability estimates presented here correspond to those found by Baines et al. (2009) in the progeny test with interior spruce (*Picea engelmannii* × *glauca*). The lower heritability observed in the E x E family group compared with the N x N families was consistent with similar differences reported for other traits (Skrøppa & Steffenrem 2016).

Comparable evidence from Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in British Columbia, Canada, reinforces these patterns and provides context for trait definition and pest pressure (Mattson et al. 1999). Across 110 half-sib families at nine sites, significant family-level variation in resistance was detected for both Cooley spruce gall adelgid (*Adelges cooleyi*) and round spruce gall adelgid (*A. abietis*). Pooled individual-tree heritability was higher for Cooley galls (≈ 0.60) than for round galls (≈ 0.20), and heritability tended to be greatest at sites with the highest adelgid densities. Family effects persisted after gall counts were standardized by tree height (Mattson et al. 1999).

Trait relationships

The sign of the genetic association between galling and growth differed among diallels. Proxy genetic correlations between gall incidence and height at age 7 were -0.04 (Diallel 1), +0.66 (Diallel 2), and -0.23 (Diallel 3). The positive correlation in Diallel 2, showing more attack of galls for the tall families, agrees with results from Engelmann spruce, where round-gall abundance showed a strong positive genetic correlation with height (pooled $r_g \approx 0.79$) (Mattson et al.1999). Conversely, Cooley gall abundance was negatively correlated with height in the same study (pooled ≈ –0.21), which is similar to the estimates in Diallels 1 and 3.

Within the sets of families in the diallel crosses there was no clear genetic relationship detected between the gall incidence and phenology traits (bud break and shoot growth cessation). The same was observed for the families in the N x N crossing group. This is in agreement with the results of Eidmann & Eriksson (1978) and Björkman (2000) who found that time of bud flush did not influence the frequency of galls. Thus, it is unlikely that differences in phenology is an important factor explaining variation in resistance, as stated by Björkman (2000).

Implications of environment and site conditions

Except for one of the provenance trials, all observations of galls were made in trials on agricultural soil at Hogsmark Experimental Farm. In the short-term provenance trial and the diallel trials, which were placed adjacent to one another, assessments were carried out the same year. These circumstances may have implied some common site and year effects. However, the factorial trial was not located next to these trials and was assessed in a different year. Similarly, the clone trial was planted a distance from the factorial trial and was assessed four years later. Nevertheless, the ranking of families for gall percentages was stable between these two trials. It must be concluded that the trials at this site generate reliable results for testing resistance to the gall-making aphid. However, the environmental conditions at a site on agricultural soil must be favourable for attack by the aphid. The influence of site conditions was further clearly indicated by the absence of galls in the long-term trials at forest sit with the same diallel and factorial families.

Variation in micron-environmental conditions between blocks in a trial may influence the level of attack of the aphid. This was clearly shown in two of the diallel trials where a significant positive relationship was found between mean block height and the percentage of trees with galls was detected. Soil fertility varied considerably among the blocks, and the tallest trees grew under the most fertile conditions (Skrøppa & Fundova 2025). These results suggest that micro-environmental variation in soil conditions contributes to the level of gall induction.

Conclusions

From a general breeding perspective, the predominance of additive genetic effects indicates that selection for reduced gall incidence is feasible. Because heritabilities were low to moderate, accuracy should be increased by recording counts or severity rather than binary incidence and by evaluating under adequate insect pressure across sites that differ in fertility.

From a Nordic perspective, these results are relevant to climate adaptation and provenance transfer. As warming encourages greater use of Central and Eastern European material in Norway, higher gall incidence observed for those provenances should be anticipated and managed. Because resistance appears heritable and environmentally modulated, resistance screening could be incorporated into selection and deployment is needed. For deployment, sites with high fertility should be treated as higher expression environments and resistant stock should be preferred there. In Christmas tree production, resistance should be applied as an explicit culling criterion, and routine monitoring with sanitation of heavily galled shoots can be used as needed. Overall, genetic improvement combined with prudent site matching should allow increasing use of transferred provenances while keeping gall levels manageable.

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