

Can. J. For. Res. Downloaded from cdnsiencepub.com by Ministere de l'Energie on 09/12/24
This Just-IN manuscript is the accepted manuscript prior to copy editing and page composition. It may differ from the final official version of record.

1 High genetic gains in growth and resistance to white pine weevil for the next Norway spruce
2 breeding and propagation populations in Quebec, Canada

3

4

5 **Guillaume Otis-Prud’homme¹, Josianne DeBlois¹, Clémentine Pernot¹ and Martin Perron¹**

6

7

8 ORCID: Guillaume Otis-Prud’homme (0000-0001-9113-0115), Josianne DeBlois (0000-0002-
9 9829-4179), Clémentine Pernot (0000-0002-2669-7905), Martin Perron (0009-0002-1449-9992)

10

11

12 ¹Ministère des Ressources naturelles et des Forêts, Direction de la recherche forestière, Québec,
13 QC, Canada

14

15

16 **Corresponding author:** Guillaume Otis Prud’homme, 2700, rue Einstein, Québec, QC G1P 3W8,
17 Canada

18 **Email address:** Guillaume.Otis-PrudHomme@mrnf.gouv.qc.ca

19

20

21

22

23

24 **Abstract**

25 Genetic parameters for growth (height, diameter and volume) and resistance to the white pine
26 weevil were estimated from 209 Norway spruce families aged 15 or 20 years old. Individual
27 heritability values ranged from low to moderate, while family heritability values were moderate to
28 high. This suggests that there is a genetic control for these variables. A selection index was
29 developed to rank individuals on both volume growth and resistance to the white pine weevil. Opsel
30 2.0 software was used for selection to optimize genetic gain while keeping the level of relatedness
31 between selected trees below an acceptable threshold. The selection of the best 70 individuals,
32 i.e., the top 1% of the populations evaluated, resulted in volume gains of 15.5% and weevil
33 resistance gains of 30.3% making it possible to create a new, more productive and weevil-resistant
34 Norway spruce population. These new breeding and propagation populations will be planted in
35 various locations in the province of Quebec and will be used for the operational deployment of this
36 improved material.

37

38 Key words: *Picea abies*, genetic selection, progeny trials, *Pissodes strobi*, selection index

39

1. Introduction

Norway spruce (*Picea abies*) is a high-yielding commercial species, with productivity ranging from 6.5 m³ ha⁻¹ to 10 m³ ha⁻¹ on medium to fertile sites. In Quebec, a province in eastern Canada, around 300,000 seedlings have been planted annually since 2019, but the species still suffers from a poor reputation, notably for its susceptibility to the white pine weevil (*Pissodes strobi* Peck [Coleoptera: Curculionidae]). However, its yields in terms of volume and sawing quality are superior to those of white spruce, a species widely used in plantations. Even in the presence of weevil defects, Norway spruce wood traits, such as stiffness, bending strength and wood density, are superior to those of white spruce in plantation e.g. Mottet et al. (2006). As a matter of fact, the use of Norway spruce in construction is now possible in both Canada and the United States, since its inclusion in the lumber classification (NLGA, 2022).

The white pine weevil is an insect pest that attacks white pine and Norway spruce in Quebec. Among other things, it causes terminal shoot mortality, which results in significant defects in stem quality, such as forking and bending, but does not cause stem mortality. Indeed, damage is mainly observed in young plantations (6-9 m height; Belyea and Sullivan, 1956) of poorly drained and poor-quality sites (Archambault et al., 1993), whereas the weevil's negative effects on growth and quality are negligible for most of the volume harvested, particularly at the end of the rotation (Daoust and Mottet, 2006, Mottet et al., 2006). Furthermore, since thinning must be carried out, the most affected stems will be cut and the quality of the residual stems will be better in the final cut (Daoust and Mottet, 2006). Moreover, it seems that deformed stems show no difference from undeformed stems in terms of sawing quality, contrary to the impact of site selection or silvicultural treatments, for example.

Despite this, damage in plantations still exists and affects the quality of young plantations and, above all, interest in Norway spruce. The selection of resistant parents and individuals in base populations (forward selection) is a strategy with great potential for reducing damage caused by

65 the white pine weevil. Studies have already shown that resistance is under strong genetic control
66 in Norway spruce (Mottet et al., 2015, Lenz et al., 2019) and can be integrated into the development
67 of breeding and propagation populations, for example in Sitka spruce seed orchards (Alfaro et al.,
68 2013). In Quebec, Mottet et al. (2015) showed that the Genetic $\times$ Environment (G $\times$ E) interaction
69 was weak in various evaluation populations, and thus families selected for resistance responded
70 similarly regardless of planting site. However, there was a positive correlation between tree
71 diameter and number of attacks, although it was still possible to find families both superior in
72 diameter growth and demonstrating greater resistance to the white pine weevil.

73 Different multi-trait selection strategies exist and can co-exist in a breeding program, such as
74 independent culling, tandem selection, stage selection or selection index (Hazel and Lush, 1943,
75 Young, 1964), although the selection index will generally give better expected gain (Xie and
76 Yanchuk, 2003). Nowadays these different strategies use breeding values (BV's) as a basis for
77 ranking candidate trees. In forward selection, BV's are individual predictions of genetic gain, taking
78 into account kinship ties (full-sibs or half-sibs) and the performance of individuals from the same
79 family compared with the average of the evaluation population, and are therefore used to estimate
80 the genetic value of individual as a parent (Xie and Yanchuk, 2003).

81 It is important for the breeder to also consider relatedness in these selections. Effectively,
82 inbreeding depression is caused by the crossing of related individuals, resulting in a reduction in
83 the average of a trait such as survival, growth vigour or fertility (Falconer, 1996, Charlesworth and
84 Willis, 2009, Doerksen et al., 2014). The classic method of dealing with this problem was to limit
85 the number of individuals selected per family (Mullin, 1998). Although this method works, it has
86 now been superseded by variable parental contribution methods (Ruotsalainen and Lindgren,
87 2001) and by the arrival of software that optimizes genetic gains by allowing unequal parental
88 contributions, while retaining control over the degree of relatedness in a selected population (e.g.
89 Mullin, 2017, Goda and Isik, 2022). It is also important to take into account the effective size of the
90 population, or the effective number of selected trees (ST) (or status number; Lindgren et al., 1996,

Lindgren et al., 1998), to ensure genetic gains over several generations, while maintaining sufficient diversity. Franklin (1980) first proposed the classic rule of having a minimum effective breeding population of 50. White et al. (2007) argued that a population of 20 to 40 individuals allows selection and genetic gains, but that there is a high risk of inbreeding over several generations. In fact, more authors are now proposing to increase the number of trees in the breeding population to ensure that gains are made over several generations, while maintaining sufficient genetic diversity to support these selections over several generations (White et al., 2007, Frankham et al., 2014, Danusevicius and Lindgren, 2005).

In the context of global change, it is imperative to adjust parent's selection for the reforestation of a given territory to ensure the adaptation and resilience of trees to maintain a high productivity of good wood quality. Effectively, in boreal forest, a plantation rotation of conifer forest trees will take around fifty years and more to develop on the best sites. During this long period, trees will have to cope with numerous abiotic and biotic factors. Therefore, the current breeding objectives of the exotic Norway spruce breeding programs in Quebec are mainly vigour (survival and growth) and white pine weevil resistance, to ensure high productivity and good wood properties in plantations.

The genetic improvement program for Norway spruce in Quebec originates from a close collaboration between the Ministère des Ressources naturelles et des Forêts (MRNF) and the Canadian Forest Service (CFS) since 1969. A first breeding population was created by CFS in 1988 by selecting individuals from Quebec's provenance tests, federal tests in Ontario, and commercial plantations based on growth and white pine weevil resistance. In parallel, initial propagation populations (four seed orchards) and open pollinated half-sib progeny tests (series E390) were established in the 1990s by the MRNF, partially comprising trees selected by CFS. A second breeding population was partly created by the MRNF in two steps from the E390 series 1) by selecting and grafting 216 superior trees from 68 progenies that demonstrated higher gains in height growth and resistance to the white pine weevil and 2) by additional weevil resistance tests on the grafted trees that led to retain 118 priority trees representing 50 half-sib families. In order to

enhance this second breeding population, we expect to select 70 superior individuals from a new progeny tests series. Therefore, between 2000 and 2009 we established a second series of progeny tests (E408 and E411) to evaluate family and candidate trees from the first breeding population of 1988.

The present study focuses on two series of Norway spruce full-sib progeny trials (E408-1 and E408-2), to complete the second breeding population and to add parents in future propagation populations (seed orchards). The objectives are : 1- to evaluate and describe the genetic parameters of these populations for growth traits and the white pine weevil resistance, 2- to select the 70 top-ranking individuals in the two trials series (top 1% of these populations) with a diversity constrain to constitute new breeding and propagation populations that are both productive and resistant to the white pine weevil, and 3- to evaluate the genetic gains of various traits.

2. Material and methods

2.1 Study sites and vegetal material

The study is based on a total of 7 full-sib progeny trials from two series, established in 2000 and 2006 respectively (Table 1). The 3 trials in the series 1 (E408-1), comprising 193 families, were established according to a randomized complete block design, each with five blocks, three-tree linear plots for each family and a tree spacing of 2 m × 2.5 m. The 193 full-sib families are derived from a partial diallel mating design among 112 parents from the Norway spruce first breeding population of Quebec which was established by Canadian Forestry Service in 1988, at the Valcartier arboretum, near Québec City (see Mottet et al. (2015) for more details). Genetic thinning in trials took place at Saint-Modeste and Grandes-Piles in different years (Table 1), first by removing 1 tree out of 3 within each family plot of both trials based on growth and deformation due to white pine weevil, and a second time at Grandes-Piles only by removing trees still based on growth and deformation due to white pine weevil but without considering the plots. A marking for thinning was also carried out at Reboul and Saint-Modeste in 2019 and 2020 respectively, thereby reducing the

142 trees and families available for selection. Thus, the 124 remaining families common to all 3 trials
143 and coming from 96 parents were considered in the present study, representing a total of 3758
144 living trees measured in 2019.

145 The 4 trials in the series 2 (E408-2) include a total of 89 families, not all of which are present at
146 each site. In addition, 9 control provenances were used, 2 of which are found at each site. Coming
147 from the same breeding population as E408-1, the 89 full-sib families originate from a partial diallel
148 mating design comprising 16 different females and 21 different males. However, there are a total
149 of 23 different parents since many (14 parents) are used as both males and females. Fourteen
150 parents were initially common to the series 1, whereas in 2020, 13 remaining parents are common
151 to the first series. Therefore, there are 1 to 15 crosses per female and 1 to 8 crosses per male. In
152 this series, each trial consists of 10 randomized complete blocks with linear two-tree family plots
153 and a tree spacing of 2 m × 2 m. A genetic thinning was conducted for each trial in different years
154 (Table 1) by eliminating 1 tree out of 2 in each family plot based on growth and deformation due to
155 white pine weevil. A total of 3475 living trees measured in 2020 are being evaluated.

156 2.2 Data acquisition

157 The traits of interest measured were height and diameter at breast height (DBH) at 20 years after
158 planting for series 1 (2019) and at 15 years after planting for series 2 (2020). These traits were
159 used to calculate the tree total volume with bark according to the taper equation presented in
160 Prigent et al. (2016) that was inspired by model 02 of (Kozak, 2004). In addition, the cumulative
161 number of weevil attacks between 6 years and 15 or 20 years ($CWA_{6-15 \text{ or } 20}$) was compiled to assess
162 weevil resistance (Mottet et al., 2015). An attack was recorded by the death of the leader shoot and
163 emergence holes for each measurement year and the cumulative number of weevil attacks
164 corresponds to the summation from year 6 to year 15 or 20 inclusively.

All the analyses presented in the next sections were also repeated using the 15-year measurement data from series 1 (2014 measurement) to check the correspondence between selections when all trees were the same age. Since this correspondence was relatively strong, especially for the selection of the best individuals (63% for the 320 best individuals and 70% for the 175 best individuals), it was decided to keep the results of the analyses with the 20-year data for series 1, since they represent the most up-to-date data.

2.3 Models and Genetic parameters

Models

For each trait, the model used for the overall analysis of all trials in both series included two fixed-effect factors, i.e., sites and blocks within site, and two random-effect factors, i.e., parents (males and females) and crosses, as well as the random effect of interactions between the latter and the two fixed-effect factors (sites and blocks). For parents (males and females) and their interaction terms in the following linear model, we used the Xiang and Li (2001) approach with dummy variables:

$$(1) \quad Y_{ijklm} = \mu + S_i + B(S)_{j(i)} + GCA_k + GCA_l + (S \times GCA)_{ik} + (S \times GCA)_{il} + SCA_{kl} + (S \times SCA)_{ikl} + (B(S) \times SCA)_{j(i)kl} + \varepsilon_{ijklm}$$

where Y_{ijklm} : trait value measured on the tree m of cross kl in block j of site i
 μ : general mean
 S_i : site effect i ($i = \text{GPI, REB, STM, ASS, DEQ, LEB, VAL}$)
 $B(S)_{j(i)}$: block effect j of site i ($j = 1$ to 5 or 10)
 GCA_k, GCA_l : general combining ability (GCA) effect of female k and male l , respectively ($k, l = 1$ to 106 (total number of parents), $k < l$),

187 $GCA_k, GCA_l \sim N(0, \sigma_{GCA}^2)$

188 $(S \times GCA)_{ik}, (S \times GCA)_{il}$: GCA by site interaction effect,

189 $(S \times GCA)_{ik}, (S \times GCA)_{il} \sim N(0, \sigma_{S \times GCA}^2)$

190 SCA_{kl} : specific combining ability (SCA) effect of female k and male l

191 $(k \neq l, 209 \text{ crosses}), SCA_{kl} \sim N(0, \sigma_{SCA}^2)$

192 $(S \times SCA)_{ikl}$: SCA by site interaction effect, $(S \times SCA)_{ikl} \sim N(0, \sigma_{S \times SCA}^2)$

193 $(B(S) \times SCA)_{j(i)kl}$: experimental error (plot effect), $(B(S) \times SCA)_{j(i)kl} \sim N(0, \sigma_{\varepsilon}^2)$

194 ε_{ijklm} : residual error (intra-plot effect), $\varepsilon_{ijklm} \sim N(0, \sigma_w^2)$

195

196 Variance estimates were obtained using the SAS MIXED procedure (version 9.4, SAS Institute Inc.,

197 Cary, North Carolina, USA) for the quantitative traits (height, DBH and total volume) and the SAS

198 GLIMMIX procedure (version 9.4, Poisson distribution and log link function) for the qualitative

199 variable CWA_{6-15 or 20}).

200 To determine whether the variance estimates were significantly greater than 0, one-tailed likelihood

201 ratio tests were conducted using the same two SAS procedures (the model with and without the

202 term to be tested for the MIXED procedure and the COVTEST statement for the GLIMMIX

203 procedure). Covariance parameters and their standard errors were estimated using residual

204 (restricted) maximum likelihood (REML) for quantitative traits and residual (restricted) pseudo-

205 likelihood (RSPL) for the qualitative trait. We opted for a reduced mixed model to obtain genetic

206 parameters estimation and parental BLUP prediction to then calculate individual breeding values

207 in line with the work of Mottet et al. (2015), even if a more advanced method, such as an individual-

208 tree mixed model (animal model), could have been used to predict simultaneously parent, family

209 (cross) and individual breeding values (e.g. Isik et al., 2017).

210 2.3.1 Heritabilities

211 Narrow-sense individual, family and within-family heritabilities were calculated for each trait as
 212 follows:

$$(2) \quad h_{ind}^2 = \frac{\sigma_A^2}{(2\sigma_{GCA}^2 + \sigma_{SCA}^2 + 2\sigma_{S \times GCA}^2 + \sigma_{S \times SCA}^2 + \sigma_\varepsilon^2 + \sigma_w^2)}$$

$$(3) \quad h_{fam}^2 = \frac{2\sigma_{GCA}^2}{\left(2\sigma_{GCA}^2 + \sigma_{SCA}^2 + \frac{2\sigma_{S \times GCA}^2}{n_s} + \frac{\sigma_{S \times SCA}^2}{n_s} + \frac{\sigma_\varepsilon^2}{n_s \cdot n_{hbl}} + \frac{\sigma_w^2}{n_s \cdot n_{hbl} \cdot n_{hpe}}\right)}$$

$$(4) \quad h_w^2 = \frac{2\sigma_{GCA}^2}{\left(\frac{(n_s - 1)}{n_s} (2\sigma_{S \times GCA}^2 + \sigma_{S \times SCA}^2) + \frac{(n_s \cdot n_{hbl} - 1)}{n_s \cdot n_{hbl}} \sigma_\varepsilon^2 + \frac{(n_s \cdot n_{hbl} \cdot n_{hpe} - 1)}{n_s \cdot n_{hbl} \cdot n_{hpe}} \sigma_w^2\right)}$$

215 where σ_A^2 corresponds to the additive variance defined by $\sigma_A^2 = 4\sigma_{GCA}^2$, σ_{GCA}^2 is the parental variance,
 216 σ_{SCA}^2 is the variance associated with crosses, $\sigma_{S \times GCA}^2$ corresponds to the site-parent interaction
 217 variance, $\sigma_{S \times SCA}^2$ is the site-cross interaction variance, σ_ε^2 corresponds to the experimental (inter-
 218 plot) variance and σ_w^2 is the residual (intra-plot) variance. Regarding the qualitative variable CWA₆.
 219 15 or 20, the estimated residual variance was set to $\sigma_w^2 = \varphi \ln(\lambda^{-1} + 1)$ where λ corresponds to the
 220 mean of the phenotypic values and φ represents the scaling parameter used to correct the under-
 221 dispersion problem (Nakagawa and Schielzeth, 2010). The terms n_s , n_{hbl} and n_{hpe} represent
 222 respectively the number of sites, the harmonic mean of the number of blocks per site and the

harmonic mean of the number of trees per plot. The standard error of each heritability was calculated using the Delta method (Lynch and Walsh, 1998), based on Taylor series. Broad-sense heritabilities were not estimated, since Quebec's Norway spruce planting strategy did not include full-sib family deployment.

2.3.2 Type-B correlation

Type-B genetic correlations were calculated for the additive effects ($r_{B\ GCA}$) and for full-sib families ($r_{B\ fs}$) across trials (Baltunis et al., 2006) for each trait:

$$(5) \quad r_{B\ GCA} = \frac{\sigma_{GCA}^2}{\sigma_{GCA}^2 + \sigma_{S \times GCA}^2}$$

$$(6) \quad r_{B\ fs} = \frac{2\sigma_{GCA}^2 + \sigma_{SCA}^2}{2\sigma_{GCA}^2 + 2\sigma_{S \times GCA}^2 + \sigma_{SCA}^2 + \sigma_{S \times SCA}^2}$$

The standard errors of these correlations were also calculated using the Delta method, based on Taylor series.

2.3.3 Breeding values

Adjusted breeding values of each parent (BV_{adj}) and crossing ($BV_{crossadj}$, average family breeding values) were calculated using the following equations:

$$(7) \quad BV_{adj} = \begin{cases} 2 GCA + \mu & \text{for quantitative traits} \\ e^{(2 GCA + \mu_{log})} & \text{for CWA}_{6-15 \text{ or } 20} \end{cases}$$

$$(8) \quad BV_{crossadj} = \begin{cases} GCA_{male} + GCA_{female} + \mu & \text{for quantitative traits} \\ e^{(GCA_{male} + GCA_{female} + \mu_{log})} & \text{for CWA}_{6-15 \text{ or } 20} \end{cases}$$

237

238 where GCA , GCA_{male} and GCA_{female} correspond respectively to the general combining ability of the
 239 parent under consideration and the sire and dam of the cross concerned, μ is the overall mean of
 240 the trait in the original scale, while μ_{log} represents the mean in the logarithmic scale.

241 Adjusted individual (tree) breeding values (IBV_{adj}) were obtained indirectly using $BV_{crossadj}$ and
 242 intrafamilial heritability (h_w^2):

243

$$(9) \quad IBV_{adj} = \begin{cases} GCA_{male} + GCA_{female} + h_w^2 \cdot residual + \mu & \text{for quantitative traits} \\ e^{(GCA_{male} + GCA_{female} + h_w^2 \cdot residual + \mu_{log})} & \text{for CWA}_{6-15 \text{ or } 20} \end{cases}$$

244

245 where *residual* corresponds to the difference between the observed and the predicted (by the
 246 model) values of each tree.

2.4 Ranking and selection of best individuals

2.4.1 Ranking with a selection index

To facilitate the ranking and selection of the best trees in a multi-trait selection, a selection index (SI) combining the total volume with bark at 15 or 20 years and the number of cumulative weevil attacks was calculated:

$$(10) \quad SI = w_1 \times Tot_vol_{15 \text{ or } 20} \cdot IBV - w_2 \times CWA_{6-15 \text{ or } 20} \cdot IBV$$

where $Tot_vol_{15 \text{ or } 20} \cdot IBV$ and $CWA_{6-15 \text{ or } 20} \cdot IBV$ are the estimated individual breeding values and w_i are the relative weight given to each trait with $0 \leq w_i \leq 1$ and $w_1 + w_2 = 1$. An initial index was calculated using standardized values of volume and CWA breeding values, as to make them scale-independent, but the rankings remained similar with and without standardization. We therefore decided to stay with the original values to calculate the index, which also allowed us to maintain consistency with previous in-house analyses (unpublished data). Additionally, the ranks of the selected trees relative to $Tot_vol_{15 \text{ or } 20} \cdot IBV$ were closer to the index ranks when breeding values were not standardized, whereas it was the opposite for $CWA_{6-15 \text{ or } 20} \cdot IBV$. However, since $CWA_{6-15 \text{ or } 20} \cdot IBV$ is a discrete variable with few different values, there was many ties in the ranks. A negative sign was assigned to CWA since trees with fewer weevil attacks are the best candidates for selection.

To obtain the weights associated with each of the traits that maximize the overall gain for a given selection (top 5% or 10%), a graph of the relative genetic gain (%), calculated as the ratio of the expected gain to the maximum possible gain from single-trait selection, was generated by varying the weights of the two concerned traits. The intersection of the two curves on the graph (rounded to the nearest 5%) was used to determine the optimal weights for both traits making up the selection index.

2.4.1 Type A genetic correlation

Type A genetic correlation (r_A) between $Tot_vol_{15\ or\ 20}$ and $CWA_{6-15\ or\ 20}$ measured on the same tree was calculated as follows, using a multivariate REML model with the MIXED and IML procedures of SAS (Holland, 2006):

$$r_A = \frac{\sigma_F(Tot_vol_{15\ or\ 20}, CWA_{6-15\ or\ 20})}{\sqrt{\sigma_F^2(Tot_vol_{15\ or\ 20}) \cdot \sigma_F^2(CWA_{6-15\ or\ 20})}}$$

where $\sigma_F(Tot_vol_{15\ or\ 20}, CWA_{6-15\ or\ 20})$ corresponds to the genetic covariance between both traits, while $\sigma_F^2(Tot_vol_{15\ or\ 20})$ and $\sigma_F^2(CWA_{6-15\ or\ 20})$ are the respective family variances of both traits. A half-sib model was used for this part because the banded Toeplitz covariance structure required to obtain variance components of parents did not allow the estimation of covariance between pairs of traits, and a model including different effects for male and female resulted in an insufficient memory problem.

2.4.2 Tree selection

With the aim of obtaining the best possible gains while respecting a sufficient relatedness threshold in our breeding population, the selection of individuals was made using Opsel 2.0 software (Mullin, 2017). Among other things, it enables us to select a variable number of individuals per family to obtain higher gains, unlike a conventional method which sets a maximum number of individuals per family to maintain sufficient genetic diversity over many breeding cycles (long term).

To obtain 70 top-ranking trees (selection of 1%) according to the selection index, i.e. individuals with superior growth and resistance to the white pine weevil, and a low rate of relatedness, a three-

stage selection method was used. A first stage selection was made by identifying 320 superior trees based on the selection index to target trees with superior growth and weevil resistance but leaving enough trees for a second selection stage based on shape. For the second stage, these trees were revisited in the field to apply a mass selection based on their shape (taper, curve at the base, branching, etc.), to eliminate trees with excessive shape defects. Once these trees had been removed, a third stage selection exercise was carried out, this time to retain the 70 best trees as the final selection. For both selection stages using Opsel 2.0 (stages 1 and 3), the maximum coefficient of group common ancestry (pairing) was set to 0.03, the same value obtained by a classic sequential selection of 2 individuals per family maximum (threshold calculated, data not shown) among the 35 best families, and lower than the value of 0.0625 used by Mullin and Belotti (2016) , but those 70 ST will only contribute to 37% of the whole second breeding population (70/190).

2.5 Sensitivity analyses for various selection scenarios

Based on the complete population of candidate trees to selection and after phase of mass selection based on shape quality (see section 2.4.2), a sensitivity analysis was performed to compare the effect of different selection scenarios on genetic gains, on total volume and $CWA_{6-15 \text{ or } 20}$, and diversity. The following three parameters were estimated with Opsel 2.0 for comparison purposes: (1) the effective number of selected trees, or status number, (2) the proportional gene diversity of selected group and (3) the average inbreeding of selected group. The selection scenarios included the classical method of sequential selection of 2 trees per family, as well as the selection on individual traits (total volume and $CWA_{6-15 \text{ or } 20}$) and on the selection index with and without diversity constraint corresponding to a maximum coefficient of group common ancestry of 0.03. For each scenario, the total number of trees selected was set to 70.

3. Results

3.1 General performance of Norway spruce

The 7 plantations used in the present study showed a high success rate. High survival rates at 15 or 20 years (73% to 91%) are observed for 5 of the 7 trials (Table 2). A lower survival rate was observed at De Quen (56%), due to some seedlings uprooting by frost heaving during the first winter and poor drainage problems, and at Asselin (44%), due to heavy snow during the first winter, which caused severe bending at the collar to several seedlings and affected stem tissue, which ultimately caused mortality during the following growing season.

Tree growth variations after 15 and 20 years were as expected for those ages and those bioclimatic domains (Table 2), according to observation in operational plantation plots survey (Prégent et al., 2016). The De Quen, Reboul and Lebret sites show the lowest growth overall, especially in diameter and volume, as expected since they are located in the white birch fir forest, i.e. in the boreal forest, compared to the other sites located in the temperate forest. The most productive sites are Grandes-Piles and Saint-Modeste (Table 2), located in the sugar maple basswood and balsam fir yellow birch stands respectively.

3.2 Genetic parameters

It should first be noted that the De Quen and Lebret sites (series 2) were not considered in the analysis of the weevil trait, given the too low cumulative number of weevil attacks between 6 and 15 years of age on these two sites (Table 2).

All non-zero variances for growth ($TH_{15 \text{ or } 20}$, $DBH_{15 \text{ or } 20}$ and $Tot_vol_{15 \text{ or } 20}$) and weevil resistance ($CWA_{6-15 \text{ or } 20}$) traits were significantly positive at the 5% threshold, except for the Site×SCA variance for DBH and the SCA variance for the volume. The across-parent variance ($\hat{\sigma}_{GCA}^2$) proportion is higher for tree height and CWA than volume and DBH (Table 3). The ratio between specific combining ability (SCA) and general combining ability (GCA), which represents the relative

importance of non-additive genetic effects (Baker, 1978, Yanchuk, 1996), is less than 1 for height and total volume, and greater than 1 for diameter, suggesting a greater non-additive genetic effect for diameter, as observed at younger ages by Mottet et al. (2015). For the weevil resistance trait, the ratio is 0 (Table 3).

The estimated individual heritabilities of the various growth traits range from low to moderate (0.05 – 0.16), while the family heritabilities range from moderate to high (0.40 – 0.64) (Table 3). For the number of cumulative white pine weevil attacks, the individual heritability value is moderate (0.23), and the family heritability is high (0.80). Type-B genetic correlations for growth traits are low to moderate (0.29 – 0.53), while for the number of cumulative white pine weevil attacks it is high (0.77) (Table 3).

3.3 Selection index, sensitivity analyses and genetic gain

For both top 5% and top 10% selection, the selection index optimizing genetics gains of both traits gives a weight (rounded to the nearest 5%) $w_1 = 0.1$ for $Tot_vol_{15\ or\ 20}$ and $w_2 = 0.9$ for $CWA_{6-15\ or\ 20}$ (Figure 1). For example, a selection based solely on volume ($w_1 = 1$), would have led to a lower expected gain for weevil resistance (Table 4).

As the De Quen and Lebret sites (series 2) were not included in the weevil trait analysis, given the too low cumulative number of weevil attacks between 6 and 15 years on these two sites (Table 2), imputation of the family breeding value was used to calculate the selection index for these trees.

Moderate negative genetic correlation was obtained between $Tot_vol_{15\ or\ 20}$ and $CWA_{6-15\ or\ 20}$ ($\hat{r}_A = -0.32 \pm 0.19$), so it's not too high to compromise an effective selection of trees that improves simultaneously volume and weevil attacks. IBV of these two traits presented at Figure 2 shows that there are trees (pink dots) that can be good candidates for the selection since they have a superior volume as well as few weevil attacks. Pearson correlation coefficient of these IBV is $r = -0.28$

361 whereas the Spearman one is $r = -0.30$. Thus, the first selection stage made it possible to isolate
362 trees showing genetic gains on the two main traits, and to continue the selection process by
363 considering a mass selection on shape and the proportional gene diversity on this subsample of
364 performing trees.

365 Sensitivity analyses on all trees without diversity constraints show that selection with the selection
366 index optimizes genetic gains on both traits, compared with selection on a single trait, which
367 maximizes gains on the selected trait, but at the expense of the other trait (Table 4). Selection with
368 Opsel 2.0 on the selection index results in greater gains than conventional sequential selection on
369 the selection index. The proportional gene diversity obtained is high for the classic sequential
370 method, demonstrating its effectiveness in controlling genetic diversity. On the other hand,
371 proportional gene diversity is lower when using Opsel 2.0, especially in the case of selection on a
372 single trait, since the software seeks only to maximize gains and selects largely within a few families
373 (between 3 and 14 families only with Opsel 2.0 and the applied diversity constraint), compared with
374 35 for the classic sequential method.

375 Sensitivity analyses on trees selected following a mass selection on shape and with a constraint
376 on diversity show a slight decrease in gains, especially on volume (Table 4). Selection on a single
377 trait still maximizes the selected trait at the expense of the other trait, but to a lesser extent. Control
378 of genetic diversity is also favorable, although this time the software selects a minimum of 35
379 families, as in the classic sequential method. The final selection was made up of a total of 39
380 different families, each represented by 1 to 4 individuals, for a gain of 15.5% in total volume and
381 30.3% in white pine weevil resistance, while assuming gains on trunk and crown quality as a result
382 of mass selection.

4. Discussion

4.1 Genetic parameters

Significantly positive variance components show that there is a genetic variation for all the traits measured as shown by Mottet et al. (2015) and confirm that those traits show interesting potential for selection. The genetic parameter estimates also showed the existence of genetic control for the quantitative traits measured. The narrow-sense familial and individual heritabilities are in line with the results of Mottet et al. (2015) and Lenz et al. (2019), who evaluated similar traits at 5, 10 and 15 years old on Norway spruce, and with the results of studies on other conifers (e.g. Perron et al., 2013, Lenz et al., 2013). Those genetic parameters are required to support Quebec's Norway spruce breeding and deployment activities, as seed orchards are the only production populations for this species. Moderate type-B correlations (0.31 - 0.53) for growth traits (height, DBH and total volume) were under 0.67, a threshold suggested by Ding et al. (2008) for justifying multiple breeding zones, which suggest the presence of an interaction effect between genetics and environment. These results differ from Mottet et al. (2015) who estimated higher type-B correlations (TH: 0.66, DBH: 0.73) at year 10 using 3 of the 7 sites used in the present study. These differences could be explained by the older age of the trees (10 years older), the smaller number of families (124 in the present study vs 193 in Mottet et al. (2015)), a slightly different set of parents (96 out of 112 from Mottet et al. 2015 and 13 new parents in series 2) and a higher environmental variation between both extreme sites. Even when reanalyzing Mottet et al. (2015) 10-year data with the same subset of families and trees from the present study (only the trees from the 3 trials of series 1 and the 124 families available at 20 years) the type-B correlation for TH and DBH at year 10 (respectively 0.73 and 0.70) and at year 20 (respectively 0.50 and 0.55) are still different; suggesting the presence of an age effect for growth traits $G \times E$.

Weevil resistance, on the other hand, appeared to be under strong genetic control, with moderate individual and high family heritability. In addition, the type-B correlation was high, indicating the absence of interaction between genetics and environment. This suggests that families had the

same reaction to weevil attack regardless of the planting site as already observed by Mottet et al. (2015) for younger trees and a subset of trials and families of the present study. These results are also consistent with the findings of Mottet et al. (2015) and Lenz et al. (2019), who had found moderate to high heritabilities and a high type-B correlation for weevil resistance.

Two strategies are generally proposed for coping with the presence of a strong $G \times E$ interaction, either to select for generalist individuals, who will perform well on several sites, or to take advantage of the interaction and select specialist individuals who will maximize gains on contrasting environments (Li et al., 2017, Raymond, 2011). However, multi-trait selection and the use of selection index complicate these strategies, especially when, as in this study, two selected traits have different patterns of $G \times E$ (Li et al., 2017). In the present study, total volume seemed to respond differently according to planting site, although no climatic trend has been detected to explain this interaction, whereas resistance was observed similarly on all sites. A possible strategy is to select a core breeding population of generalist individuals, i.e., those showing high growth in multiple contrasting environments and showing resistance to white pine weevil, and to select a sub-population of specialist individuals that could be used in future crosses to take advantage of their adaptive traits and maximize gains in a given environment.

4.2 Breeding values and selection index

The presence of genetic control for all traits justified the use of a selection index. The breeding values for families and individuals were calculated for the entire population, for each measured trait (height, DBH, volume and weevil resistance), and were used to establish a selection index maximizing genetic gains on both volume and weevil resistance. This is important since it has already been observed that selection on a single trait can result in a negative gain on another trait (e.g. Bouffier et al., 2009, Cope et al., 2021). The white pine weevil seems to prefer longer, thicker annual shoots on spruce, which often results in delayed height growth caused by insect attack (Alfaro et al., 2008, King et al., 1997). Thus, early selection before the observation of white pine

weevil damage and based solely on height could lead to the selection of individuals more vulnerable to the insect. A similar negative relationship has been observed between resistance to the white pine weevil and DBH and therefore indicates that selection based solely on resistance could negatively affect DBH and vice versa, as observed in the selection scenario on DBH (Mottet et al., 2015; Table 4). Despite this, it is possible to find individuals showing gains for weevil resistance without compromising growth (Alfaro et al., 2008, Lenz et al., 2019). The use of the selection index for ranking candidate trees seems to be the best way of ensuring gain on both traits.

4.3 Selection and genetic gain

Sensitivity analysis of the different selection scenarios demonstrated the benefits of using a selection index and a software to optimize the selection of superior individuals in order to maximize gains while preserving sufficient genetic diversity for long term breeding. The selection scenarios following mass selection were more similar since the population available for selection was greatly reduced but the scenario with the selection index optimized gains on both traits. Although the three-stage selection strategy to consider trunk and crown shape quality might have reduced gains on volume and CWA, overall the selection is improved since it combines gains on growth, resistance to white pine weevil and stem quality.

The final selection of the 70 best individuals, respecting an acceptable genetic diversity threshold, within the two series (7233 individuals in total) represents a selection of the top 1%. This selection of generalist individuals resulted in a volume gain of 15.5% and a weevil resistance gain of 30.3%. These gains are significant considering that they are calculated in relation to the average of the trees evaluated, which are themselves the product of past selections. Although this selection maximizes gains, we still obtain positive gains for our two chosen traits (total volume and CWA), whether we select on a single trait or on the selection index combining the two traits (Table 4). This can be partially explained by the fact that the population evaluated was already improved for growth and weevil resistance, which could explain why there was no negative relationship between growth

and weevil resistance, as observed previously (Alfaro et al., 2008, Mottet et al., 2015, King et al., 1997), using larger databases. In addition, selection based only on height growth after episodes of white pine weevil attack is probably associated with trees without defects (dead terminal shoots, bayonets, crook forms and forks) showing higher growth compared with the average despite the presence of weevil, which could explain the gain in weevil resistance when selecting for height growth (Table 4). This could also explain, at least in part, the differences observed in the relationship between white pine weevil resistance and DBH (negative relationship) and white pine weevil resistance and volume (positive relationship; Figure 2). Indeed, volume is calculated from DBH and height data, and the latter appear to have different relationships with weevil resistance (Table 4). Furthermore, it is important to remember that the genetic gains presented for the final selection follow a mass selection aimed at eliminating the "least beautiful" trees based on their shape (branch angles and length, stem shape, presence of forks, etc.). It is very likely that these trees were eliminated based on their poor shape, but that this poor shape was sometimes due to attacks by the white pine weevil. However, the results in Figure 2 and Table 4 clearly demonstrate that it is possible to obtain a significant genetic gain on both traits at the same time, while respecting a threshold on group coancestry. These results are in line with those of Alfaro et al. (2008), who demonstrated that it is possible to obtain a genetic gain in weevil resistance without considerably affecting the average growth in Sitka spruce. The removal of trees with undesirable characteristics means that a gain should indirectly be achieved on form too. Indeed, Norway spruce form traits appear to be under genetic control (Mioduszeński and Rzońca, 2015) and form quality is being considered in other breeding programs (Mullin et al., 2011, Rosvall et al., 2011, Ivković et al., 2006, Raymond, 2011), as it indirectly improves wood quality.

5. Conclusion

Growth and weevil resistance traits are under moderate to high genetic control. This study shows that it is possible to obtain a significant gain on both traits at the same time using a selection index. These results led to the selection of 70 superior individuals to complete the breeding population of

485 the next breeding cycle of Quebec Norway spruce breeding program and the propagation
 486 population for operational deployment of improved Norway spruce material.

487 **Acknowledgements**

488 We are grateful to all those who made possible the establishment, maintenance and measurements
489 of the Norway spruce trials used in this study. A special thanks to retired Marie-Josée Mottet who
490 leaded the Norway spruce improvement program until 2021 as well as for early discussion of
491 selection process for those candidate tree series and Jean-Sébastien Joannette of MRNF for the
492 trials establishment and maintenance and the data collection.

493 **Competing Interest**

494 The authors declare no conflict of interest.

495 **Author Contributions**

496 GOP: Conceptualization, investigation, formal analysis, validation, methodology, supervision,
497 visualization, writing—original draft; JD: formal analysis, methodology, data curation, software,
498 validation, visualization, writing—review and editing; CP: validation, writing—review and editing
499 MP: Conceptualization, methodology, supervision, investigation, validation, writing—review and
500 editing. All authors have read and agreed to the published version of the manuscript.

501 **Funding**

502 This work is part of project number 112332075 (Genetic improvement of Norway spruce -
503 Amélioration génétique de l'épinette de Norvège) conducted at the Direction de la recherche
504 forestière (ministère des Ressources naturelles et des Forêts, Québec, Canada) and lead by
505 Clémentine Pernot.

506 **Data availability:**

507 Data used in this study belong to the Norway spruce breeding program of the province of Québec
508 and are stored in our institution database. Data are available upon reasonable request to the
509 corresponding author.

510 **References**

- 511 ALFARO, R. I., KING, J. N., BROWN, R. & BUDDINGH, S. M. 2008. Screening of Sitka spruce
512 genotypes for resistance to the white pine weevil using artificial infestations. *Forest Ecology
513 and Management*, 255, 1749-1758.
- 514 ALFARO, R. I., KING, J. N. & VANAKKER, L. 2013. Delivering Sitka spruce with resistance against
515 white pine weevil in British Columbia, Canada. *The Forestry Chronicle*, 89, 235-245.
- 516 ARCHAMBAULT, L., MORISSETTE, J., LAVALLÉE, R. & COMTOIS, B. 1993. Susceptibility of
517 Norway spruce plantations to white pine weevil attacks in southern Quebec. *Canadian
518 Journal of Forest Research*, 23, 2362-2369.
- 519 BAKER, R. 1978. Issues in diallel analysis. *Crop science*, 18, 533-536.
- 520 BALTUNIS, B. S., HUBER, D. A., WHITE, T. L., GOLDFARB, B. & STELZER, H. E. 2006. Genetic
521 analysis of early field growth of loblolly pine clones and seedlings from the same full-sib
522 families. *Canadian Journal of Forest Research*, 37, 195-205.
- 523 BELYEA, R. & SULLIVAN, C. 1956. The white pine weevil: a review of current knowledge. *The
524 Forestry Chronicle*, 32, 58-67.
- 525 BOUFFIER, L., RAFFIN, A., ROZENBERG, P., MEREDIEU, C. & KREMER, A. 2009. What are the
526 consequences of growth selection on wood density in the French maritime pine breeding
527 programme? *Tree Genetics & Genomes*, 5, 11-25.
- 528 CHARLESWORTH, D. & WILLIS, J. H. 2009. The genetics of inbreeding depression. *Nature
529 reviews genetics*, 10, 783-796.
- 530 COPE, O. L., KEEFOVER-RING, K., KRUGER, E. L. & LINDROTH, R. L. 2021. Growth–defense
531 trade-offs shape population genetic composition in an iconic forest tree species.
532 *Proceedings of the National Academy of Sciences*, 118, e2103162118.
- 533 DANUSEVICIUS, D. & LINDGREN, D. 2005. Optimization of breeding population size for long-term
534 breeding. *Scandinavian journal of forest research*, 20, 18-25.
- 535 DAOUST, G. & MOTTET, M.-J. 2006. Impact du charançon du pin blanc (*Pissodes strobi* Peck)
536 dans les plantations d'épinettes de Norvège (*Picea abies* [L.] Karst.) Partie 1: Productivité
537 et qualité des sciages. *The Forestry Chronicle*, 82, 538-549.
- 538 DING, M., GILMOUR, A. & TIER, B. 2008. Increasing the Accuracy of Analyzing GXE Interaction
539 and Integrating the Information to P. Radiata Breeding Program.
- 540 DOERKSEN, T., BOUSQUET, J. & BEAULIEU, J. 2014. Inbreeding depression in intra-provenance
541 crosses driven by founder relatedness in white spruce. *Tree genetics & genomes*, 10, 203-
542 212.
- 543 FALCONER, D. S. 1996. *Introduction to quantitative genetics*, Pearson Education India.
- 544 FRANKHAM, R., BRADSHAW, C. J. & BROOK, B. W. 2014. Genetics in conservation
545 management: revised recommendations for the 50/500 rules, Red List criteria and
546 population viability analyses. *Biological Conservation*, 170, 56-63.
- 547 FRANKLIN, I. R. 1980. Evolutionary change in small populations.
- 548 GODA, K. & ISIK, F. 2022. AgMate: An Optimal Mating Software for Monoecious Species. A
549 LongTerm Breeding Example for *Pinus taeda* L. *agriRxiv*, 20220262199.
- 550 HAZEL, L. & LUSH, J. L. 1943. The efficiency of three methods of selection.
- 551 HOLLAND, J. B. 2006. Estimating genotypic correlations and their standard errors using
552 multivariate restricted maximum likelihood estimation with SAS Proc MIXED. *Crop science*,
553 46, 642-654.
- 554 ISIK, F., HOLLAND, J. & MALTECCA, C. 2017. *Genetic data analysis for plant and animal
555 breeding*, Springer.
- 556 IVKOVIĆ, M., WU, H. X., MCRAE, T. A. & POWELL, M. B. 2006. Developing breeding objectives
557 for radiata pine structural wood production. I. Bioeconomic model and economic weights.
558 *Canadian Journal of Forest Research*, 36, 2920-2931.
- 559 KING, J. N., YANCHUK, A., KISS, G. & ALFARO, R. 1997. Genetic and phenotypic relationships
560 between weevil (*Pissodes strobi*) resistance and height growth in spruce populations of
561 British Columbia. *Canadian Journal of Forest Research*, 27, 732-739.
- 562 KOZAK, A. 2004. My last words on taper equations. *The Forestry Chronicle*, 80, 507-515.

- LENZ, P., AUTY, D., ACHIM, A., BEAULIEU, J. & MACKAY, J. 2013. Genetic improvement of white spruce mechanical wood traits—early screening by means of acoustic velocity. *Forests*, 4, 575-594.
- LENZ, P., NADEAU, S., MOTTET, M. J., PERRON, M., ISABEL, N., BEAULIEU, J. & BOUSQUET, J. 2019. Multi-trait genomic selection for weevil resistance, growth, and wood quality in Norway spruce. *Evolutionary applications*, 13, 76-94.
- LI, Y., SUONTAMA, M., BURDON, R. D. & DUNGEY, H. S. 2017. Genotype by environment interactions in forest tree breeding: review of methodology and perspectives on research and application. *Tree Genetics & Genomes*, 13, 60.
- LINDGREN, D., GEA, L. & JEFFERSON, P. 1996. Loss of genetic diversity monitored by status number. *Silvae genetica*, 45, 52-58.
- LINDGREN, D., GEA, L. & JEFFERSON, P. 1998. Status number for measuring genetic diversity. *International Journal of Forest Genetics*, 4, 69-76.
- LYNCH, M. & WALSH, B. 1998. *Genetics and analysis of quantitative traits*, Sinauer Sunderland, MA.
- MIODUSZEWSKI, S. & RZOŃCA, M. 2015. Variability of morphological features, bud burst and flowering of Norway spruce (*Picea abies* [L.] Karst.) in the seed orchard of the Bielsk Forest District.
- MOTTET, M.-J., DAOUST, G. & ZHANG, S. 2006. Impact du charançon du pin blanc (*Pissodes strobi* Peck) dans les plantations d'épinette de Norvège (*Picea abies* (L.) Karst.). Partie 2: Propriétés du bois des sciages. *The Forestry Chronicle*, 82, 712-722.
- MOTTET, M.-J., DEBLOIS, J. & PERRON, M. 2015. High genetic variation and moderate to high values for genetic parameters of *Picea abies* resistance to *Pissodes strobi*. *Tree Genetics & Genomes*, 11.
- MULLIN, T., ANDERSSON, B., BASTIEN, J.-C., BEAULIEU, J., BURDON, R., DVORAK, W., KING, J., KONDO, T., KRAKOWSKI, J. & LEE, S. 2011. Economic importance, breeding objectives and achievements. *Genetics, genomics and breeding of conifers*, 40-127.
- MULLIN, T. & BELOTTI, P. 2016. Using branch-and-bound algorithms to optimize selection of a fixed-size breeding population under a relatedness constraint. *Tree genetics & genomes*, 12, 4.
- MULLIN, T. J. 1998. *Evaluating the Impact of Management Strategies on Genetic Gain and Diversity in Closed Breeding Populations*, Canadian Forest Service, Atlantic Forestry Centre.
- MULLIN, T. J. 2017. OPSEL 2.0: a computer program for optimal selection in tree breeding. *Arbetsrapport från Skogforsk*.
- NAKAGAWA, S. & SCHIELZETH, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev Camb Philos Soc*, 85, 935-56.
- NLGA 2022. *Standard Grading Rules for Canadian Lumber: Approved by the American Lumber Standards Board of Review and the Canadian Lumber Standards Accreditation Board: Effective December 1, 2022*, National Lumber Grades Authority.
- PERRON, M., DEBLOIS, J. & DESPONTIS, M. 2013. Use of resampling to assess optimal subgroup composition for estimating genetic parameters from progeny trials. *Tree genetics & genomes*, 9, 129-143.
- PRÉGENT, G., PICHER, G. & AUGER, I. 2016. *Tarif de cubage, tables de rendement et modèles de croissance pour les plantations d'épinette de Norvège au Québec*, Direction de la recherche forestière, Forêts, Faune et Parcs Québec.
- RAYMOND, C. A. 2011. Genotype by environment interactions for *Pinus radiata* in New South Wales, Australia. *Tree Genetics & Genomes*, 7, 819-833.
- ROSVALL, O., STÄHL, P., ALMQVIST, C., ANDERSON, B., BERLIN, M., ERICSSON, T., ERIKSSON, M., GREGORSSON, B., HAJEK, J. & HALLANDER, J. 2011. Review of the Swedish tree breeding programme. *Skogforsk, Uppsala, Sweden*.
- RUOTSALAINEN, S. & LINDGREN, D. 2001. Number of founders for a breeding population using variable parental contribution. *Forest Genetics*, 8, 59-68.

616 WHITE, T. L., ADAMS, W. T. & NEALE, D. B. 2007. *Forest genetics*, Cabi.
617 XIANG, B. & LI, B. 2001. A new mixed analytical method for genetic analysis of diallel data.
618 *Canadian journal of forest research*, 31, 2252-2259.
619 XIE, C. & YANCHUK, A. 2003. Breeding values of parental trees, genetic worth of seed orchard
620 seedlots, and yields of improved stocks in British Columbia. *Western Journal of Applied*
621 *Forestry*, 18, 88-100.
622 YANCHUK, A. 1996. General and specific combining ability from disconnected partial diallels of
623 coastal Douglas-fir. *Silvae Genetica*, 45, 37-45.
624 YOUNG, S. 1964. Multi-stage selection for genetic gain. *Heredity*, 19, 131-145.

625

Figure 1 Relative gain as a function of variation in the weight of total volume with bark for a top 5% and 10% selections. The optimal selection index (weights rounded to the nearest 5%) corresponds to $SI = 0.10 \times Tot_vol_{15\ or\ 20.IBV} - 0.90 \times CWA_{6-15\ or\ 20.IBV}$

Figure 2 Centered values of IBV for both traits (total volume and cumulative weevil attacks) of the selection index (SI) showing top 5% of trees (pink dots) that could be candidate trees for selection

Can. J. For. Res. Downloaded from cdnsiencepub.com by Ministere de l'Energie on 09/12/24
This Just-IN manuscript is the accepted manuscript prior to copy editing and page composition. It may differ from the final official version of record.

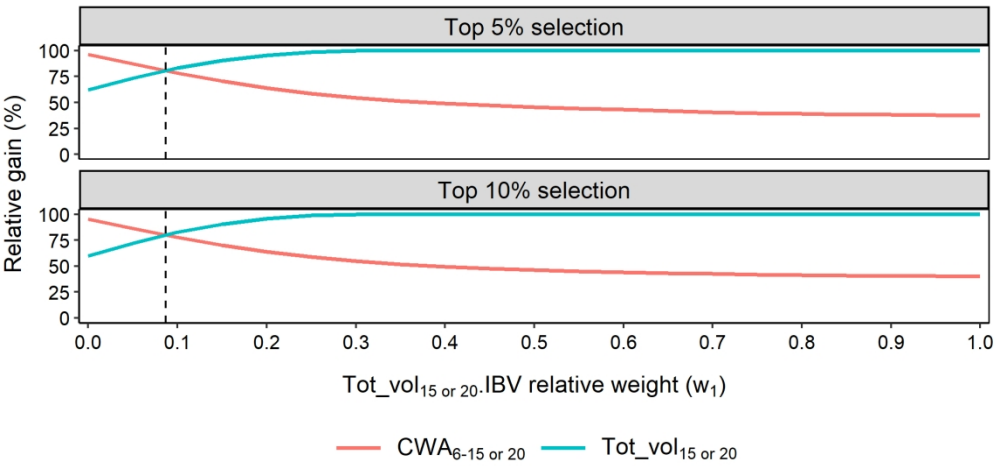


Figure 1 Relative gain as a function of variation in the weight of total volume with bark for a top 5% and 10% selections. The optimal selection index (weights rounded to the nearest 5%) corresponds to SI = 0.10
 $\times \llbracket \text{Tot_vol} \rrbracket_{(15 \text{ or } 20)}.\text{IBV} - 0.90 \times \llbracket \text{CWA} \rrbracket_{(6-15 \text{ or } 20)}.\text{IBV}$

181x90mm (300 x 300 DPI)

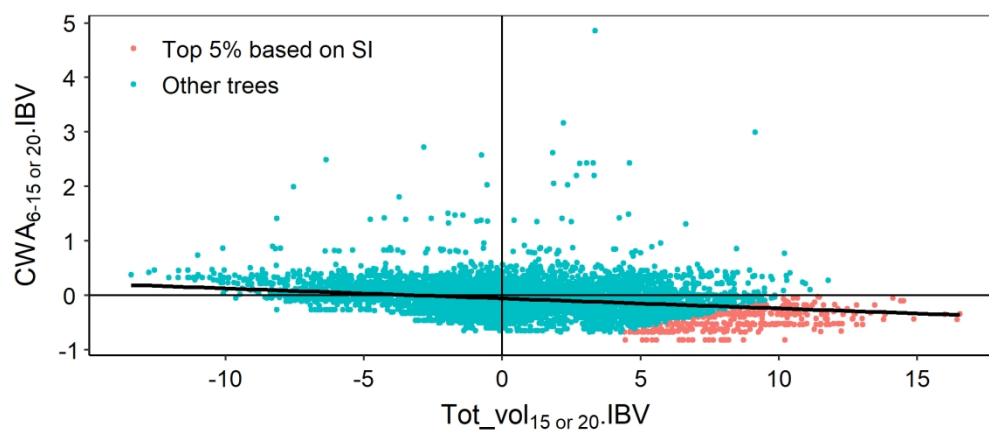


Figure 2 Centered values of IBV for both traits (total volume and cumulative weevil attacks) of the selection index (SI) showing top 5% of trees (pink dots) that could be candidate trees for selection

181x77mm (300 x 300 DPI)

Table 1 Characterization of study trials

	Progeny trials from series E408-1			Progeny trials from series E408-2			
	Reboul	Saint-Modeste	Grandes-Piles	DeQuen	Asselin	Lebret	Valcartier
Bioclimatic domain	5 - Balsam fir white birch	4 - Balsam fir yellow birch	2- sugar maple basswood	5 - Balsam fir white birch	4 - Balsam fir yellow birch	5 - Balsam fir white birch	2 - sugar maple basswood
Lat. (°)	48.43	47.85	46.68	48.19	47.93	48.57	46.98
Long. (°)	-65.46	-69.38	-72.68	-72.17	-68.46	-65.68	-71.48
Elv. (m)	350	130	150	450	270	510	215
Year of establishment	2000	2000	2000	2006	2006	2006	2006
Thinning	-	2013	2010, 2018	2020	2019	2019	2012
Nbr. of families at establishment date	193	192	193	73	87	87	65
Nbr. of families after thinnings	193	192	193, 125	73	87	87	65
Nbr. of families used for analyses	124	124	124	73	87	87	65

Lat. (°), latitude; Long. (°), longitude; Elv., elevation; Nbr. of families, number of families in the trial; Thinning, year of thinnings.

Table 2 Mean value of traits measured on live trees at year 15 or 20 for each trial

Trait*	Progeny trials from series 1			Progeny trials from series 2			
	Reboul	Saint-Modeste	Grandes-Piles	DeQuen	Asselin	Lebret	Valcartier
Survial _{15 or 20} (%)	80	73	91	56	44	83	77
TH _{15 or 20} (cm)	965.3	1032.4	1220.6	514.5	698.5	674.8	802.6
DBH _{15 or 20} (mm)	115.5	144.6	183.7	63.5	112.9	81.2	98.0
Tot_vol _{15 or 20} (dm ³)	57.5	91.3	167.1	11.7	41.6	20.6	34.4
CWA _{6-15 or 20}	0.07	0.69	1.23	0.02	0.95	<0.01	0.75

*20 years for series 1 and 15 years for series 2; Survial_{15 or 20}, survival rate 15 or 20 years after planting without trees cut during thinning; TH_{15 or 20}, tree total height 15 or 20 years after planting; DBH_{15 or 20}, tree diameter at breast height 15 or 20 years after planting; Tot_vol_{15 or 20}, tree total volume with bark 15 or 20 year after planting, calculated with taper equation presented in Prigent et al. (2016) and inspired by model 02 of (Kozak, 2004); CWA_{6-15 or 20}, cumulative weevil attacks between year 6 and year 15 or 20 after planting.

Table 3 Across-trial genetic parameters (standard error in parentheses) for growth traits and a weevil resistance trait

Trait	Variance component	Estimate	Relative magnitude (%) ^a	$\frac{SCA}{GCA}$	$\hat{h}_{ind}^2$	$\hat{h}_{fam}^2$	$\hat{h}_w^2$	$\hat{r}_{B\ GCA}$	$\hat{r}_{B\ fs}$
TH _{15 or 20}	$\hat{\sigma}_{GCA}^2$	711.18 ^b (218.97)	4.26	0.40	0.16	0.64	0.09	0.48	0.53
	$\hat{\sigma}_{SCA}^2$	284.82 ^b (112.70)	1.71		(0.05)	(0.09)	(0.03)	(0.10)	(0.08)
	$\hat{\sigma}_{S \times GCA}^2$	772.08 ^b (136.07)	4.63						
	$\hat{\sigma}_{S \times SCA}^2$	0 (.)	0.00						
	$\hat{\sigma}_\varepsilon^2$	3671.03 ^b (278.00)	22.00						
	$\hat{\sigma}_w^2$	11250 (279.24)	67.41						
DBH _{15 or 20}	$\hat{\sigma}_{GCA}^2$	6.32 ^b (2.48)	1.32	1.11	0.05	0.40	0.03	0.45	0.48
	$\hat{\sigma}_{SCA}^2$	7.03 ^b (3.25)	1.46		(0.02)	(0.11)	(0.01)	(0.14)	(0.10)
	$\hat{\sigma}_{S \times GCA}^2$	7.76 ^b (2.56)	1.62						
	$\hat{\sigma}_{S \times SCA}^2$	5.63 (4.78)	1.17						
	$\hat{\sigma}_\varepsilon^2$	70.01 ^b (8.55)	14.58						
	$\hat{\sigma}_w^2$	383.29 (9.45)	79.85						
Tot_vol _{15 or 20}	$\hat{\sigma}_{GCA}^2$	22.53 ^b (11.06)	2.26	0.27	0.08	0.53	0.05	0.29	0.31
	$\hat{\sigma}_{SCA}^2$	6.03 (6.49)	0.61		(0.04)	(0.15)	(0.02)	(0.12)	(0.11)
	$\hat{\sigma}_{S \times GCA}^2$	56.50 ^b (10.67)	5.68						
	$\hat{\sigma}_{S \times SCA}^2$	0 (.)	0.00						
	$\hat{\sigma}_\varepsilon^2$	165.78 ^b (15.07)	16.65						
	$\hat{\sigma}_w^2$	744.72 (17.20)	74.80						
CWA _{6-15 or 20}	$\hat{\sigma}_{GCA}^2$	0.04 ^b (0.01)	5.80	0	0.23	0.80	0.13	0.77	0.77
	$\hat{\sigma}_{SCA}^2$	0 (.)	0.00		(0.05)	(0.04)	(0.03)	(0.09)	(0.09)
	$\hat{\sigma}_{S \times GCA}^2$	0.01 ^b (0.01)	1.45						
	$\hat{\sigma}_{S \times SCA}^2$	0 (.)	0.00						
	$\hat{\sigma}_\varepsilon^2$	0 (.)	0.00						
	φ	0.70 (0.01)							
	λ	0.66							
	$\hat{\sigma}_w^{2c}$	0.64	92.75						

Abbreviation of traits, see Table 2; Variance components, see section 2.3.1

$\hat{h}_{ind}^2$, narrow-sense individual-tree heritability; $\hat{h}_{fam}^2$, narrow-sense full-sib heritability; $\hat{h}_w^2$, narrow-sense within-family heritability; $\hat{r}_{B\ GCA}^2$, type-B genetic correlation for the additive effects; $\hat{r}_{B\ fs}^2$, type-B genetic correlation for full-sib families

^a Magnitude relative to total (phenotypic) variance ($\hat{\sigma}_p^2 = \hat{\sigma}_{GCA}^2 + \hat{\sigma}_{SCA}^2 + \hat{\sigma}_{S \times GCA}^2 + \hat{\sigma}_{S \times SCA}^2 + \hat{\sigma}_\varepsilon^2 + \hat{\sigma}_w^2$)

^b Variance component significantly positive at the 5 % significance level

^c $\hat{\sigma}_w^{2c} = \varphi \ln(\lambda^{-1} + 1)$

Table 4 Sensitivity analyses without or with constraint on genetic diversity for various selection scenarios illustrating the expected genetic gain in % for traits of interest, as well as various genetic diversity parameters. Results of our final selection with Opsel 2.0, a selection index and after a mass selection on trunk and crown quality, is presented in bold

Selection scenario	Height (cm)	DBH (mm)	Tot_vol (dm ³)	CWA	Nbr of ST	Nbr of families	Status number of ST ^a	Proportional gene diversity ^b	Pairwise coancestry
Mean ± standard error	778.9 ± 9.4	105.3 ± 1.0	47.4 ± 2.0	0.59 ± 0.04 ^c					
<i>Selection of the same number of ST without constraint on diversity</i>									
TH	10.1%	1.6%	18.1%	29.0% ^d	70	9	6.0	0.916	0.08
DBH	3.6%	6.1%	18.0%	-10.7%	70	5	4.2	0.880	0.11
Tot_vol _{15 or 20} .IBV	6.6%	4.3%	25.5%	26.5%	70	14	7.2	0.930	0.06
CWA _{6-15 or 20} .IBV	4.3%	1.5%	12.9%	51.0%	70	3	3.8	0.869	0.12
Classical ^e	5.9%	3.0%	20.0%	31.1%	70	35	17.8	0.972	0.02
SI ^f	6.3%	3.6%	23.6%	41.1%	70	13	6.0	0.917	0.08
<i>Selection of the same number of ST following a mass selection based on trunk and crown quality with constraint on diversity^g</i>									
Tot_vol _{15 or 20} .IBV	6.6%	2.5%	17.0%	28.1%	70	35	17.4	0.971	0.02
CWA _{6-15 or 20} .IBV	5.7%	1.4%	13.5%	33.9%	70	35	20.4	0.975	0.02
SI - Final selection	6.2%	2.1%	15.5%	30.3%	70	39	21.2	0.976	0.02

ST, Selected trees; Tot_vol_{15 or 20}.IBV, Individual breeding value of total volume with bark at year 15 or 20; CWA_{6-15 or 20}.IBV, Individual breeding value of cumulative weevil attacks between year 6 and year 15 or 20; SI, Selection index with optimal weights of both traits, $SI = (0.1 \times \text{Tot_vol}_{15 \text{ or } 20}.\text{IBV}) - (0.9 \times \text{CWA}_{6-15 \text{ or } 20}.\text{IBV})$.

^a Status number from Lindgren et al. (1996). A measure that can be interpreted as the size of a population of non-inbred genotypes. The higher the index, the greater the level of genetic diversity.

^b Proportion of the genetic diversity of the selected group that will be conserved in comparison with the population of candidate trees.

^c Values back transformed in the data scale. Selection on the selection index using Opsel 2.0 freeware (Mullin and Belotti, 2016)

^d For CWA, a positive percentage is associated with a decreasing value of the trait, i.e. a reduction of the cumulative number of weevil attacks.

^e Sequential selection of the best families with a maximum of two ST per family.

^f Selection on the selection index using Opsel 2.0 freeware (Mullin and Belotti, 2016)^g Maximum constraint of 0.03 on the group coancestry