

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

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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.

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

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## 40 1. Introduction

41 Norway spruce (*Picea abies*) is a high-yielding commercial species, with productivity ranging from  
42 6.5 m<sup>3</sup> ha<sup>-1</sup> to 10 m<sup>3</sup> ha<sup>-1</sup> on medium to fertile sites. In Quebec, a province in eastern Canada,  
43 around 300,000 seedlings have been planted annually since 2019, but the species still suffers from  
44 a poor reputation, notably for its susceptibility to the white pine weevil (*Pissodes strobi* Peck  
45 [Coleoptera: Curculionidae]). However, its yields in terms of volume and sawing quality are superior  
46 to those of white spruce, a species widely used in plantations. Even in the presence of weevil  
47 defects, Norway spruce wood traits, such as stiffness, bending strength and wood density, are  
48 superior to those of white spruce in plantation e.g. Mottet et al. (2006). As a matter of fact, the use  
49 of Norway spruce in construction is now possible in both Canada and the United States, since its  
50 inclusion in the lumber classification (NLGA, 2022).

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

62 Despite this, damage in plantations still exists and affects the quality of young plantations and,  
63 above all, interest in Norway spruce. The selection of resistant parents and individuals in base  
64 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 (BVs) as a basis for  
77 ranking candidate trees. In forward selection, BVs 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,

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

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

106 The genetic improvement program for Norway spruce in Quebec originates from a close  
107 collaboration between the Ministère des Ressources naturelles et des Forêts (MRNF) and the  
108 Canadian Forest Service (CFS) since 1969. A first breeding population was created by CFS in  
109 1988 by selecting individuals from Quebec's provenance tests, federal tests in Ontario, and  
110 commercial plantations based on growth and white pine weevil resistance. In parallel, initial  
111 propagation populations (four seed orchards) and open pollinated half-sib progeny tests (series  
112 E390) were established in the 1990s by the MRNF, partially comprising trees selected by CFS. A  
113 second breeding population was partly created by the MRNF in two steps from the E390 series 1)  
114 by selecting and grafting 216 superior trees from 68 progenies that demonstrated higher gains in  
115 height growth and resistance to the white pine weevil and 2) by additional weevil resistance tests  
116 on the grafted trees that led to retain 118 priority trees representing 50 half-sib families. In order to

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

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

## 128 **2. Material and methods**

### 129 **2.1 Study sites and vegetal material**

130 The study is based on a total of 7 full-sib progeny trials from two series, established in 2000 and  
131 2006 respectively (Table 1). The 3 trials in the series 1 (E408-1), comprising 193 families, were  
132 established according to a randomized complete block design, each with five blocks, three-tree  
133 linear plots for each family and a tree spacing of 2 m × 2.5 m. The 193 full-sib families are derived  
134 from a partial diallel mating design among 112 parents from the Norway spruce first breeding  
135 population of Quebec which was established by Canadian Forestry Service in 1988, at the  
136 Valcartier arboretum, near Québec City (see Mottet et al. (2015) for more details). Genetic thinning  
137 in trials took place at Saint-Modeste and Grandes-Piles in different years (Table 1), first by removing  
138 1 tree out of 3 within each family plot of both trials based on growth and deformation due to white  
139 pine weevil, and a second time at Grandes-Piles only by removing trees still based on growth and  
140 deformation due to white pine weevil but without considering the plots. A marking for thinning was  
141 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 Prégent 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.

165

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

## 172 2.3 Models and Genetic parameters

### 173 Models

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

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

180

181 where  $Y_{ijklm}$  : trait value measured on the tree  $m$  of cross  $kl$  in block  $j$  of site  $i$   
 182  $\mu$  : general mean  
 183  $S_i$  : site effect  $i$  ( $i = \text{GPI, REB, STM, ASS, DEQ, LEB, VAL}$ )  
 184  $B(S)_{j(i)}$  : block effect  $j$  of site  $i$  ( $j = 1$  to 5 or 10)  
 185  $GCA_k, GCA_l$  : general combining ability (GCA) effect of female  $k$  and male  $l$ ,  
 186 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  $\varepsilon_{ijklm}$  : 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<sub>6-15 or 20</sub>).

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:

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

213

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

214

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

215 where  $\sigma_A^2$  corresponds to the additive variance defined by  $\sigma_A^2 = 4\sigma_{GCA}^2$ ,  $\sigma_{GCA}^2$  is the parental variance,  
 216  $\sigma_{SCA}^2$  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,  $\sigma_\varepsilon^2$  corresponds to the experimental (inter-  
 218 plot) variance and  $\sigma_w^2$  is the residual (intra-plot) variance. Regarding the qualitative variable CWA<sub>6</sub>.  
 219 <sub>15 or 20</sub>, the estimated residual variance was set to  $\sigma_w^2 = \varphi \ln(\lambda^{-1} + 1)$  where  $\lambda$  corresponds to the  
 220 mean of the phenotypic values and  $\varphi$  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

10

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

### 227 **2.3.2 Type-B correlation**

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

230

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

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

231

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

### 234 **2.3.3 Breeding values**

235 Adjusted breeding values of each parent ( $BV_{adj}$ ) and crossing ( $BV_{cross\ adj}$ , average family breeding  
 236 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,  $\mu$  is the overall mean of  
 240 the trait in the original scale, while  $\mu_{log}$  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.

247 **2.4 Ranking and selection of best individuals**

248 **2.4.1 Ranking with a selection index**

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

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

252 where  $Tot\_vol_{15\ or\ 20} \cdot IBV$  and  $CWA_{6-15\ or\ 20} \cdot IBV$  are the estimated individual breeding values and  
253  $w_i$  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  
254 calculated using standardized values of volume and CWA breeding values, as to make them scale-  
255 independent, but the rankings remained similar with and without standardization. We therefore  
256 decided to stay with the original values to calculate the index, which also allowed us to maintain  
257 consistency with previous in-house analyses (unpublished data). Additionally, the ranks of the  
258 selected trees relative to  $Tot\_vol_{15\ or\ 20} \cdot IBV$  were closer to the index ranks when breeding values  
259 were not standardized, whereas it was the opposite for  $CWA_{6-15\ or\ 20} \cdot IBV$ . However, since  
260  $CWA_{6-15\ or\ 20} \cdot IBV$  is a discrete variable with few different values, there was many ties in the ranks.  
261 A negative sign was assigned to CWA since trees with fewer weevil attacks are the best candidates  
262 for selection.

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

269 **2.4.1 Type A genetic correlation**

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

273

274 
$$r_A = \frac{\sigma_F(Tot\_vol_{15\ or\ 20}, CWA_{6-15\ or\ 20})}{\sqrt{\sigma_F^2(Tot\_vol_{15\ or\ 20}) \cdot \sigma_F^2(CWA_{6-15\ or\ 20})}}$$

275

276 where  $\sigma_F(Tot\_vol_{15\ or\ 20}, CWA_{6-15\ or\ 20})$  corresponds to the genetic covariance between both traits,  
 277 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  
 278 half-sib model was used for this part because the banded Toeplitz covariance structure required to  
 279 obtain variance components of parents did not allow the estimation of covariance between pairs of  
 280 traits, and a model including different effects for male and female resulted in an insufficient memory  
 281 problem.

282 **2.4.2 Tree selection**

283 With the aim of obtaining the best possible gains while respecting a sufficient relatedness threshold  
 284 in our breeding population, the selection of individuals was made using Opsel 2.0 software (Mullin,  
 285 2017). Among other things, it enables us to select a variable number of individuals per family to  
 286 obtain higher gains, unlike a conventional method which sets a maximum number of individuals per  
 287 family to maintain sufficient genetic diversity over many breeding cycles (long term).

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

290 stage selection method was used. A first stage selection was made by identifying 320 superior  
291 trees based on the selection index to target trees with superior growth and weevil resistance but  
292 leaving enough trees for a second selection stage based on shape. For the second stage, these  
293 trees were revisited in the field to apply a mass selection based on their shape (taper, curve at the  
294 base, branching, etc.), to eliminate trees with excessive shape defects. Once these trees had been  
295 removed, a third stage selection exercise was carried out, this time to retain the 70 best trees as  
296 the final selection. For both selection stages using Opsel 2.0 (stages 1 and 3), the maximum  
297 coefficient of group common ancestry (pairing) was set to 0.03, the same value obtained by a  
298 classic sequential selection of 2 individuals per family maximum (threshold calculated, data not  
299 shown) among the 35 best families, and lower than the value of 0.0625 used by Mullin and Belotti  
300 (2016) , but those 70 ST will only contribute to 37% of the whole second breeding population  
301 (70/190).

## 302 **2.5 Sensitivity analyses for various selection scenarios**

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

### 313 **3. Results**

#### 314 **3.1 General performance of Norway spruce**

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

321 Tree growth variations after 15 and 20 years were as expected for those ages and those bioclimatic  
322 domains (Table 2), according to observation in operational plantation plots survey (Prégent et al.,  
323 2016). The De Quen, Reboul and Lebret sites show the lowest growth overall, especially in  
324 diameter and volume, as expected since they are located in the white birch fir forest, i.e. in the  
325 boreal forest, compared to the other sites located in the temperate forest. The most productive sites  
326 are Grandes-Piles and Saint-Modeste (Table 2), located in the sugar maple basswood and balsam  
327 fir yellow birch stands respectively.

#### 328 **3.2 Genetic parameters**

329 It should first be noted that the De Quen and Lebret sites (series 2) were not considered in the  
330 analysis of the weevil trait, given the too low cumulative number of weevil attacks between 6 and  
331 15 years of age on these two sites (Table 2).

332 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  
333 ( $CWA_{6-15 \text{ or } 20}$ ) traits were significantly positive at the 5% threshold, except for the Site $\times$ SCA variance  
334 for DBH and the SCA variance for the volume. The across-parent variance ( $\hat{\sigma}_{GCA}^2$ ) proportion is  
335 higher for tree height and CWA than volume and DBH (Table 3). The ratio between specific  
336 combining ability (SCA) and general combining ability (GCA), which represents the relative



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

341 The estimated individual heritabilities of the various growth traits range from low to moderate (0.05  
342 – 0.16), while the family heritabilities range from moderate to high (0.40 – 0.64) (Table 3). For the  
343 number of cumulative white pine weevil attacks, the individual heritability value is moderate (0.23),  
344 and the family heritability is high (0.80). Type-B genetic correlations for growth traits are low to  
345 moderate (0.29 – 0.53), while for the number of cumulative white pine weevil attacks it is high (0.77)  
346 (Table 3).

347

### 348 **3.3 Selection index, sensitivity analyses and genetic gain**

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

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

356 Moderate negative genetic correlation was obtained between  $Tot\_vol_{15\ or\ 20}$  and  $CWA_{6-15\ or\ 20}$  ( $\hat{r}_A$   
357 =  $-0.32 \pm 0.19$ ), so it's not too high to compromise an effective selection of trees that improves  
358 simultaneously volume and weevil attacks. IBV of these two traits presented at Figure 2 shows that  
359 there are trees (pink dots) that can be good candidates for the selection since they have a superior  
360 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.

## 383 4. Discussion

### 384 4.1 Genetic parameters

385 Significantly positive variance components show that there is a genetic variation for all the traits  
386 measured as shown by Mottet et al. (2015) and confirm that those traits show interesting potential  
387 for selection. The genetic parameter estimates also showed the existence of genetic control for the  
388 quantitative traits measured. The narrow-sense familial and individual heritabilities are in line with  
389 the results of Mottet et al. (2015) and Lenz et al. (2019), who evaluated similar traits at 5, 10 and  
390 15 years old on Norway spruce, and with the results of studies on other conifers (e.g. Perron et al.,  
391 2013, Lenz et al., 2013). Those genetic parameters are required to support Quebec's Norway  
392 spruce breeding and deployment activities, as seed orchards are the only production populations  
393 for this species. Moderate type-B correlations (0.31 - 0.53) for growth traits (height, DBH and total  
394 volume) were under 0.67, a threshold suggested by Ding et al. (2008) for justifying multiple breeding  
395 zones, which suggest the presence of an interaction effect between genetics and environment.  
396 These results differ from Mottet et al. (2015) who estimated higher type-B correlations (TH: 0.66,  
397 DBH: 0.73) at year 10 using 3 of the 7 sites used in the present study. These differences could be  
398 explained by the older age of the trees (10 years older), the smaller number of families (124 in the  
399 present study vs 193 in Mottet et al. (2015)), a slightly different set of parents (96 out of 112 from  
400 Mottet et al. 2015 and 13 new parents in series 2) and a higher environmental variation between  
401 both extreme sites. Even when reanalyzing Mottet et al. (2015) 10-year data with the same subset  
402 of families and trees from the present study (only the trees from the 3 trials of series 1 and the 124  
403 families available at 20 years) the type-B correlation for TH and DBH at year 10 (respectively 0.73  
404 and 0.70) and at year 20 (respectively 0.50 and 0.55) are still different; suggesting the presence of  
405 an age effect for growth traits  $G \times E$ .

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

409 same reaction to weevil attack regardless of the planting site as already observed by Mottet et al.  
410 (2015) for younger trees and a subset of trials and families of the present study. These results are  
411 also consistent with the findings of Mottet et al. (2015) and Lenz et al. (2019), who had found  
412 moderate to high heritabilities and a high type-B correlation for weevil resistance.

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

#### 425 **4.2 Breeding values and selection index**

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

434 weevil damage and based solely on height could lead to the selection of individuals more vulnerable  
435 to the insect. A similar negative relationship has been observed between resistance to the white  
436 pine weevil and DBH and therefore indicates that selection based solely on resistance could  
437 negatively affect DBH and vice versa, as observed in the selection scenario on DBH (Mottet et al.,  
438 2015; Table 4). Despite this, it is possible to find individuals showing gains for weevil resistance  
439 without compromising growth (Alfaro et al., 2008, Lenz et al., 2019). The use of the selection index  
440 for ranking candidate trees seems to be the best way of ensuring gain on both traits.

#### 441 **4.3 Selection and genetic gain**

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

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

459 and weevil resistance, as observed previously (Alfaro et al., 2008, Mottet et al., 2015, King et al.,  
460 1997), using larger databases. In addition, selection based only on height growth after episodes of  
461 white pine weevil attack is probably associated with trees without defects (dead terminal shoots,  
462 bayonets, crook forms and forks) showing higher growth compared with the average despite the  
463 presence of weevil, which could explain the gain in weevil resistance when selecting for height  
464 growth (Table 4). This could also explain, at least in part, the differences observed in the  
465 relationship between white pine weevil resistance and DBH (negative relationship) and white pine  
466 weevil resistance and volume (positive relationship; Figure 2). Indeed, volume is calculated from  
467 DBH and height data, and the latter appear to have different relationships with weevil resistance  
468 (Table 4). Furthermore, it is important to remember that the genetic gains presented for the final  
469 selection follow a mass selection aimed at eliminating the "least beautiful" trees based on their  
470 shape (branch angles and length, stem shape, presence of forks, etc.). It is very likely that these  
471 trees were eliminated based on their poor shape, but that this poor shape was sometimes due to  
472 attacks by the white pine weevil. However, the results in Figure 2 and Table 4 clearly demonstrate  
473 that it is possible to obtain a significant genetic gain on both traits at the same time, while respecting  
474 a threshold on group coancestry. These results are in line with those of Alfaro et al. (2008), who  
475 demonstrated that it is possible to obtain a genetic gain in weevil resistance without considerably  
476 affecting the average growth in Sitka spruce. The removal of trees with undesirable characteristics  
477 means that a gain should indirectly be achieved on form too. Indeed, Norway spruce form traits  
478 appear to be under genetic control (Mioduszewski and Rzońca, 2015) and form quality is being  
479 considered in other breeding programs (Mullin et al., 2011, Rosvall et al., 2011, Ivković et al., 2006,  
480 Raymond, 2011), as it indirectly improves wood quality.

## 481 **5. Conclusion**

482 Growth and weevil resistance traits are under moderate to high genetic control. This study shows  
483 that it is possible to obtain a significant gain on both traits at the same time using a selection index.  
484 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.

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## 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  
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## 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.

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- 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  $SI = 0.10 \times Tot\_vol_{15\ or\ 20} \cdot IBV - 0.90 \times CWA_{6-15\ or\ 20} \cdot IBV$

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

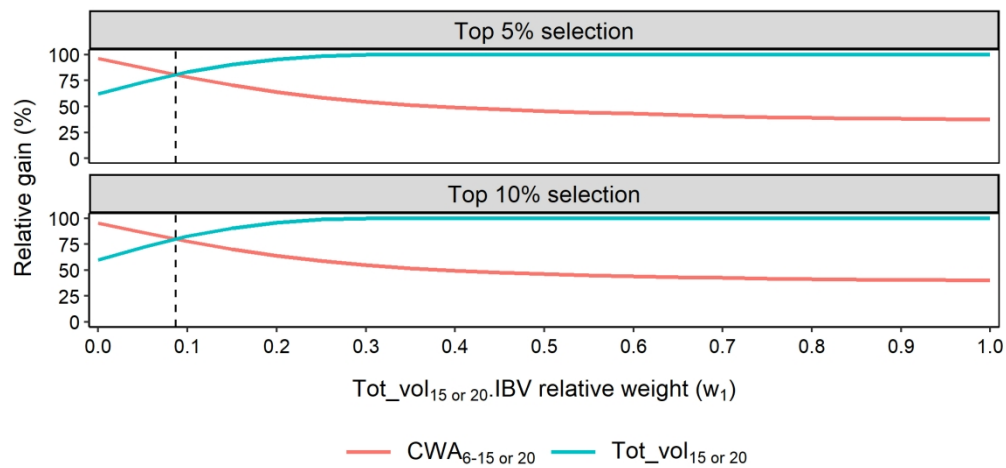


Figure 1 Relative gain as a function of variation in the weight of total volume with bark for a top 5% and 10% selections. The optimal selection index (weights rounded to the nearest 5%) corresponds to  $SI = 0.10 \times \frac{Tot\_vol_{15\ or\ 20}.IBV}{CWA_{6-15\ or\ 20}.IBV}$

181x90mm (300 x 300 DPI)

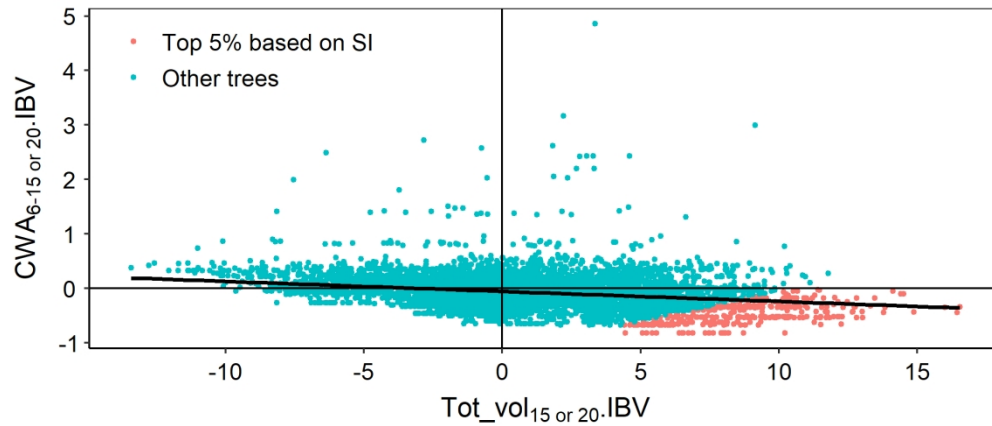


Figure 2 Centered values of IBV for both traits (total volume and cumulative weevil attacks) of the selection index (SI) showing top 5% of trees (pink dots) that could be candidate trees for selection

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 <sub>15 or 20</sub> (%)	80	73	91	56	44	83	77
TH <sub>15 or 20</sub> (cm)	965.3	1032.4	1220.6	514.5	698.5	674.8	802.6
DBH <sub>15 or 20</sub> (mm)	115.5	144.6	183.7	63.5	112.9	81.2	98.0
Tot_vol <sub>15 or 20</sub> (dm <sup>3</sup> )	57.5	91.3	167.1	11.7	41.6	20.6	34.4
CWA <sub>6-15 or 20</sub>	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<sub>15 or 20</sub>, survival rate 15 or 20 years after planting without trees cut during thinning; TH<sub>15 or 20</sub>, tree total height 15 or 20 years after planting; DBH<sub>15 or 20</sub>, tree diameter at breast height 15 or 20 years after planting; Tot\_vol<sub>15 or 20</sub>, tree total volume with bark 15 or 20 year after planting, calculated with taper equation presented in Prégent et al. (2016) and inspired by model 02 of (Kozak, 2004); CWA<sub>6-15 or 20</sub>, 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 (%) <sup>a</sup>	$\frac{SCA}{GCA}$	$\hat{h}_{ind}^2$	$\hat{h}_{fam}^2$	$\hat{h}_w^2$	$\hat{r}_{B\ GCA}$	$\hat{r}_{B\ fs}$
TH <sub>15 or 20</sub>	$\hat{\sigma}_{GCA}^2$	711.18 <sup>b</sup> (218.97)	4.26	0.40	0.16	0.64	0.09	0.48	0.53
	$\hat{\sigma}_{SCA}^2$	284.82 <sup>b</sup> (112.70)	1.71		(0.05)	(0.09)	(0.03)	(0.10)	(0.08)
	$\hat{\sigma}_{S \times GCA}^2$	772.08 <sup>b</sup> (136.07)	4.63						
	$\hat{\sigma}_{S \times SCA}^2$	0 (.)	0.00						
	$\hat{\sigma}_\varepsilon^2$	3671.03 <sup>b</sup> (278.00)	22.00						
	$\hat{\sigma}_w^2$	11250 (279.24)	67.41						
DBH <sub>15 or 20</sub>	$\hat{\sigma}_{GCA}^2$	6.32 <sup>b</sup> (2.48)	1.32	1.11	0.05	0.40	0.03	0.45	0.48
	$\hat{\sigma}_{SCA}^2$	7.03 <sup>b</sup> (3.25)	1.46		(0.02)	(0.11)	(0.01)	(0.14)	(0.10)
	$\hat{\sigma}_{S \times GCA}^2$	7.76 <sup>b</sup> (2.56)	1.62						
	$\hat{\sigma}_{S \times SCA}^2$	5.63 (4.78)	1.17						
	$\hat{\sigma}_\varepsilon^2$	70.01 <sup>b</sup> (8.55)	14.58						
	$\hat{\sigma}_w^2$	383.29 (9.45)	79.85						
Tot_vol <sub>15 or 20</sub>	$\hat{\sigma}_{GCA}^2$	22.53 <sup>b</sup> (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 <sup>b</sup> (10.67)	5.68						
	$\hat{\sigma}_{S \times SCA}^2$	0 (.)	0.00						
	$\hat{\sigma}_\varepsilon^2$	165.78 <sup>b</sup> (15.07)	16.65						
	$\hat{\sigma}_w^2$	744.72 (17.20)	74.80						
CWA <sub>6-15 or 20</sub>	$\hat{\sigma}_{GCA}^2$	0.04 <sup>b</sup> (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 <sup>b</sup> (0.01)	1.45						
	$\hat{\sigma}_{S \times SCA}^2$	0 (.)	0.00						
	$\hat{\sigma}_\varepsilon^2$	0 (.)	0.00						
	$\varphi$	0.70 (0.01)							
	$\lambda$	0.66							
	$\hat{\sigma}_w^2$ <sup>c</sup>	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

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

<sup>b</sup> Variance component significantly positive at the 5 % significance level

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

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	DBH	Tot_vol	CWA	Nbr of ST	Nbr of families	Status number of ST <sup>a</sup>	Proportional gene diversity <sup>b</sup>	Pairwise coancestry
	(cm)	(mm)	(dm <sup>3</sup> )						
<i>Mean ± standard error</i>	778.9 ± 9.4	105.3 ± 1.0	47.4 ± 2.0	0.59 ± 0.04 <sup>c</sup>					
<i>Selection of the same number of ST without constraint on diversity</i>									
TH	10.1%	1.6%	18.1%	29.0% <sup>d</sup>	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 <sub>15 or 20</sub> .IBV	6.6%	4.3%	25.5%	26.5%	70	14	7.2	0.930	0.06
CWA <sub>6-15 or 20</sub> .IBV	4.3%	1.5%	12.9%	51.0%	70	3	3.8	0.869	0.12
Classical <sup>e</sup>	5.9%	3.0%	20.0%	31.1%	70	35	17.8	0.972	0.02
SI <sup>f</sup>	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<sup>g</sup></i>									
Tot_vol <sub>15 or 20</sub> .IBV	6.6%	2.5%	17.0%	28.1%	70	35	17.4	0.971	0.02
CWA <sub>6-15 or 20</sub> .IBV	5.7%	1.4%	13.5%	33.9%	70	35	20.4	0.975	0.02
<b>SI - Final selection</b>	<b>6.2%</b>	<b>2.1%</b>	<b>15.5%</b>	<b>30.3%</b>	<b>70</b>	<b>39</b>	<b>21.2</b>	<b>0.976</b>	<b>0.02</b>

ST, Selected trees; Tot\_vol<sub>15 or 20</sub>.IBV, Individual breeding value of total volume with bark at year 15 or 20; CWA<sub>6-15 or 20</sub>.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,  $SI = (0.1 \times \text{Tot\_vol}_{15 \text{ or } 20}.\text{IBV}) - (0.9 \times \text{CWA}_{6-15 \text{ or } 20}.\text{IBV})$ .

<sup>a</sup> 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.

<sup>b</sup> Proportion of the genetic diversity of the selected group that will be conserved in comparison with the population of candidate trees.

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

<sup>d</sup> 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.

<sup>e</sup> Sequential selection of the best families with a maximum of two ST per family.

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