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1 **Title**

2

3 Evolution of genetic variation for selected traits in successive breeding
4 populations of maritime pine.

5

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20

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29 **Abstract**

30 Directional selection impacts a trait distribution by shifting its mean
31 and reducing its variance. The change of variance is of major importance as
32 the response to selection in subsequent generations is highly dependent of
33 the genetic variability available in the population. In this contribution,
34 evolution of genetic variation was investigated through the first breeding
35 populations of the French maritime pine (*Pinus pinaster* Ait.) breeding
36 program.

37 We considered three populations: P0 (the forest where plus trees were
38 initially selected), G0 (the plus tree population) and G1 (the population
39 composed of trees selected in the progenies of G0). Analyses focused on the
40 following selected traits: total height (H), girth at 1.30 m (D) and stem
41 deviation to verticality (S). More than 150 000 trees from 25 tests of three
42 distinct populations were studied with an individual genetic model.
43 Accurate genetic parameters were obtained by taking all relationships
44 between trees into account.

45 For H and D, we found a strong decrease of the genetic variation from P0 to
46 G0 corresponding to the initial selection of plus trees, which constitutes the
47 base population of the breeding program. Then, despite the second step of
48 selection applied, no appreciable evolution arose from comparisons between
49 G0 and G1 for these traits. For S, the evolution is less significant as

50 phenotypic variation slightly increased, possibly due to changes of
51 silvicultural practices.

52

53 **Introduction**

54

55 The genetic variation of a population is the key factor in determining
56 its response to natural or artificial selection and thus its evolutionary
57 potential. In the present work, we intended to monitor the changes of the
58 genetic variance as a result of directional selection conducted in breeding
59 populations of maritime pine (*Pinus pinaster* Ait.), a major forest tree
60 species growing in the southwest of France. Monitoring of genetic variation
61 along breeding populations has been undertaken earlier , but on neutral traits
62 in Sitka spruce (Chaisurisri and El-Kassaby, 1994) and in Douglas-fir (El-
63 Kassaby and Ritland, 1996). In contrast to these earlier investigations, our
64 study focuses on traits that underwent selection, hence on genetic variance
65 and not on heterozygosity.

66 Many analytical analyses and simulations predict the evolution of genetic
67 variance of a selected trait (Bulmer, 1971; Van der Werf and Boer, 1990;
68 Verrier et al., 1991; De Rochambeau et al., 2000). Selection is expected to
69 rapidly reduce the genetic variation which then stabilizes except in small
70 populations where the erosion of variation continues due to genetic drift and
71 inbreeding. However many hypotheses underlie these models and few
72 studies have been carried out on real populations under selection (Sorensen
73 and Hill, 1982; Meyer and Hill, 1991; Dupont-Nivet et al., 2001). Dupont-
74 Nivet et al. (2001) observed a strong decrease of genetic variation in the two

75 first generations of a snail population undergoing selection followed by an
76 equilibrium phase. Meyer and Hill (1991) reported a reduction of genetic
77 variation during 23 generations in a population of mice selected for food
78 intake. They concluded that the evolution of allele frequencies played a
79 major role in that trend. Sorensen and Hill (1982) studied populations of
80 *Drosophila* and found various patterns for the evolution of genetic variation
81 according to the initial allele frequencies. The evolution of variability thus
82 appears to depend both on the population considered and on the genetic
83 basis of the trait studied.

84 This paper examines the evolution of genetic variation of the selected traits
85 and their correlations in three successive populations of the French maritime
86 pine breeding program.

87 Maritime pine (*Pinus pinaster* Ait.) represents one million hectares
88 of cultivated forest in Aquitaine (southwestern France). A breeding program
89 has been implemented since the early sixties (Durel, 1992; GIS, 2002) using
90 a recurrent selection scheme which consists of successive cycles of selection
91 of candidate trees and their crossings (Zobel and Talbert, 1984). The dual
92 goals of the program have been to (1) obtain genetic gain in growth and
93 stem straightness and (2) preserve diversity in the breeding populations. The
94 former goal was achieved since an improvement of 15 % for volume and
95 form was observed in the first varieties compared to unimproved material.
96 Today genetic gains amount to 30 % in the most recent varieties

97 (GIS, 2002). The achievement of the latter goal was less studied but it is
98 considered essential because it allows for future gains and for the
99 incorporation of new selection criteria.

100 Genetic variation is estimated for the selected traits based on the
101 “individual model” (Gwaze et al., 2002), also called “animal model” as it
102 was first developed in the context of livestock breeding programs (Kennedy
103 et al., 1988). Its adaptation to trees was implemented since breeding
104 populations are moving into advanced generations (Kerr, 1998). The
105 individual model is adapted from the mixed model (Henderson, 1975). This
106 methodology takes into account all the pedigree information to accurately
107 estimate both the genetic parameters of the base population and the breeding
108 values of all genotypes by restricted maximum likelihood. Advantages of
109 the individual model compared to the more traditional least-squares analysis
110 were outlined by Lynch and Walsch (1998). First, as fixed and random
111 effects are estimated simultaneously, the precision of estimates of
112 environmental and genetic main effects is increased. Second, the individual
113 model is better suited to unbalanced data which are frequent in the case of
114 tree breeding populations, due to unpredictable mortality in long living
115 species. Third, the method takes into account phenotypic values of related
116 individuals over multiple generations and multiple progeny tests, hence
117 increasing the number of phenotypic predictors and diversifying the genetic

118 relatedness among trees. Finally, the individual model accounts for selection
119 provided that all information used in selection is included in the analysis.
120 Durel et al. (1998) were among the first to estimate genetic parameters in a
121 tree population with the individual model. In their study, genetic parameters
122 were computed in an overall analysis across seven generations of apple
123 trees. As for forest trees, the method is now widely used in the radiata pine
124 breeding program to rank genotypes within and across generations
125 (Jayawickrama and Carson, 2000). Others studies have also used the
126 individual tree genetic model on more limited data sets (Gwaze et al., 2001;
127 Gwaze et al., 2002; Dutkowski et al., 2002; Klapste et al., 2007). In the
128 present study we apply the individual model to monitor the changes of
129 genetic variation and correlation over three successive populations for traits
130 that underwent repeated directional selection.

131

132 Materials and methods

133

134 *Breeding populations and progeny tests*

135 For the sake of clarity, the different populations of the maritime pine
136 breeding program are defined as follows (Figure 1):

137 (i) **P0 population** is the Landes population which has proven to be
138 the best adapted maritime pine provenance for Southwestern
139 France (Illy, 1966). Field tests comparing different geographic
140 seed sources, established as early as 1930, clearly showed that
141 the local provenance exhibited the highest survival and growth
142 potentials. Overall the whole Landes forest covers about one
143 million hectares, with no significant population or ecotypic
144 differentiation (Baradat and Marpeau-Bezard, 1988).

145 (ii) **G0 population** is the subset of 635 plus trees i.e. trees
146 phenotypically selected during the sixties within the population
147 P0, of which a sample of 320 were used in this study. During
148 approximately 10 years, adult stands in the Landes forest were
149 visited and outstanding trees in regard to stem volume and
150 straightness were mapped and recorded by using a phenotypic
151 index of selection. Details of the selection procedure are
152 available in Illy (1966).

- 153 **(iii) P1 population** gathers all the progenies obtained in the
154 subsequent improvement steps by crosses between G0 trees. The
155 635 G0 trees were grafted as clonal archives and subsequently
156 crossed using various mating schemes (polycross, factorial or
157 nested designs).
- 158 **(iv) G1 population** is the new breeding population of about 2600
159 trees, individually selected within P1. Index selection combining
160 growth and straightness traits was achieved in the P1 progenies,
161 using family and individual values as phenotypic predictors of
162 the breeding value of selection candidates. About 5 % of the P1
163 trees were selected to build G1 population.
- 164 **(v) P2 population** gathers all progenies obtained by crossing G1
165 trees following the recurrent strategy of the breeding scheme.
166 The 2600 trees of G1 were crossed using different mating
167 designs (mainly polycross and nested mating designs).

Figure 1 168

169 Our analysis focuses on the following three populations: the original
170 population (P0) and the two breeding populations obtained after a selection
171 step (G0 and G1) because their variation can be accurately estimated with
172 the subsequent progeny tests. We compiled data obtained from 25 progeny
173 tests allowing to estimate the genetic variance for the selected traits: 3
174 progeny tests established from unselected seeds collected throughout

175 southwest France forest (to estimate the genetic variance in P0), 7 progeny
176 tests from P1 population and 15 progeny tests from P2 population. They
177 correspond to different mating designs (open pollination, factorial, nested
178 design and polycross) and each progeny test comprises on average 135
179 progenies and 9000 trees (Table 1). From here onwards, “progeny test” will
180 be called “test”. The experimental designs are either complete or incomplete
181 blocks with plot sizes varying between one to 10 trees depending on the test
182 considered. A “block” is a test subdivision comprising several “plots”, each
183 consisting of one progeny and spreads over homogeneous site conditions. A
184 block is complete when it comprises all progenies, it is incomplete when it
185 contains only a subset of progenies.

Table 1 186

187 *Measurements*

188 Two growth traits - total height (H) and girth at breast height (D) - and a
189 trait relative to stem form (S) were measured between 7 and 13 years
190 depending on the test (Table 1). Different assessments were used for S over
191 the years. Thus, we restricted our analysis of S on those tests for which the
192 same assessment was made repeatedly. The assessment consisted of
193 measuring the stem deviation to verticality, as the angle formed by the stem
194 and a virtual vertical axis passing through the base of the stem.

195

196 *Genetic model*

197 The individual model was used to subdivide the phenotypic value of each
198 tree in its genetic and environmental components. As both environmental
199 and genetic effects are computed simultaneously, the best linear unbiased
200 predictor (BLUP) of the genotypes was obtained and the genetic parameters
201 of the base population (i.e. highest ancestors registered) were estimated
202 (Lynch and Walsch, 1998).

203 It is important to note that the genetic variation estimated with an individual
204 model depends on the pedigree considered. When the complete
205 multigenerational relationship matrix is considered, genetic parameters of
206 the base population are estimated. To obtain genetic parameters of an
207 advance population “t”, only the relationship matrix computed from all
208 individuals up to that ancestor population must be kept. The population “t”
209 is thus assumed to be the base population (Sorensen and Kennedy, 1984;
210 Meyer and Hill, 1991).

211

212 The following mixed-model was considered:

213
$$y = X.b + Z_1.a + Z_2.v + e$$

214 where y is the vector of observations

215 b is the vector of fixed effects: “test” and “block (test)”

216 a is the vector of genetic effect: individual additive genetic values

217 v is the vector of plot effect: “block(test)×progeny”

218 e is the vector of residuals

219 X , Z_1 and Z_2 are the incidence matrices linking observations to the
220 effects

221 No “progeny×test” interactions were considered as only few progenies were
222 common to different tests. Furthermore it has been shown that this effect is
223 minor in the Landes area (Bouffier, 2007).

224 The random effects fit a normal distribution whose parameters were:

$$225 \quad E \begin{bmatrix} a \\ v \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \quad \text{and} \quad Var \begin{bmatrix} a \\ v \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 \\ 0 & H & 0 \\ 0 & 0 & R \end{bmatrix}$$

226 The variance-covariance matrices were defined as follows:

$$227 \quad G = A.\sigma_A^2 \qquad H = I.\sigma_v^2 \qquad R = I.\sigma_e^2$$

228 with: A the additive genetic relationship matrix (A was computed
229 from a pedigree file which takes into account all the relationships between
230 individuals)

231 I the identity matrix

232 σ_A^2 the additive genetic variance

233 σ_v^2 the plot variance

234 σ_e^2 the residual variance

235 The estimates of the fixed and random effects were obtained by solving
236 Henderson’s mixed model equations (Henderson, 1975) with the restricted
237 maximum-likelihood (REML) method using the ASReml software (Gilmour
238 et al., 2002).

239 As the variances are assumed to be independent, the phenotypic variance

240 σ_p^2 is expressed as follows:

$$241 \quad \sigma_p^2 = \sigma_A^2 + \sigma_v^2 + \sigma_e^2$$

242

243 *Variation parameters*

244 Univariate analyses were performed for estimating genetic and phenotypic

245 variation. The variation of the selected traits – H, D and S – was first

246 expressed by two widely used standardized assessments: narrow-sense

247 heritability (h^2) and coefficient of additive genetic variation (CV_A). For

248 comparative purposes, Houle (1991) showed that genetic variance is more

249 appropriately standardized by the trait mean (CV_A) than by the phenotypic

250 variance (h^2), and that heritability is rather useful for making predictions

251 about the absolute response to selection, and CV_A for assessing genetic

252 variation. In this study, we used both parameters and we also included the

253 phenotypic coefficient of variation (CV_P). As our study is an overall

254 analysis across many experimental designs established over the past 40

255 years, assessments of CV_P allow us to check for major environmental

256 sources of variation that may have occurred during this period. Heritability

257 and the two coefficients of variation were computed as follows:

$$258 \quad h^2 = \frac{\sigma_A^2}{\sigma_P^2} \quad CV_P = \frac{\sigma_P}{\bar{x}} \quad CV_A = \frac{\sigma_A}{\bar{x}}$$

259 Since ASReml also provides the estimated breeding values for each parent
260 genotype, we also computed a coefficient of variation with the breeding
261 values (CV_{BV}) which can be considered as a third estimate of genetic
262 variation:

$$263 \quad CV_{BV} = \frac{\sigma_{BV}}{\bar{x}}$$

264

265 *Correlation parameters*

266 For correlation estimates, we considered a bivariate analysis but, because of
267 a lack of convergence for the maximum likelihood under the full model, we
268 decided not to include $Z_{2.v}$ in the model. The use of this simplified model
269 implies that, for correlation estimates, σ_A^2 includes both additive and the
270 plot variances. The genetic variance is thus biased upward compared to the
271 full model.

272

273 The estimates of phenotypic (r_P) and additive genetic (r_G) correlations
274 between pairs of traits were obtained with bivariate analyses. Genetic
275 correlations were also estimated with the breeding values (r_{BV}) using
276 Pearson's correlation.

277

278 *Standard errors and statistical tests*

279 The standard errors of h^2 , σ_A^2 , σ_P^2 , r_P and r_G were calculated with ASReml
280 using a standard Taylor series approximation (Gilmour et al., 2002) and
281 those of CV_P , CV_A and r_{BV} were estimated with the approximation
282 proposed by Lynch and Walsh (1998).

283

284 In the following analyses, two estimates x_1 and x_2 associated with standard
285 errors σ_1 and σ_2 were considered significantly different if the statistical

286 test $u = \frac{|x_1 - x_2|}{\sqrt{\sigma_1^2 + \sigma_2^2}}$, which is assumed to be distributed as a standard normal

287 law, was higher than 1.96 (bilateral significance level of 5 %).

288

289 *Methods used to estimate parameters of genetic variation*

290 Three methods were carried out to estimate the variation of the selected
291 traits (Table 2). All of them take advantage of the individual model
292 previously described but are based on different data sets and refer to
293 different populations.

294

295 *Method I:* each test was analysed individually considering the genetic
296 relationship matrix truncated to the parent level. We thereby obtained an
297 estimation of the genetic variation within the parental population. For
298 example, the analysis of a test from the P1 population will provide an
299 estimation of the G0 genetic parameters.

300

301 *Method II:* tests belonging to the same population were analysed all together
302 (and not individually as for Method I) considering also the genetic
303 relationship matrix truncated to the parent level. Thus, estimates of genetic
304 variation within P0 (respectively G0, G1) were obtained from data of tests
305 11 to 13 (respectively 22 to 28, 31 to 47). Similarly, breeding values of P0,
306 G0 and G1 trees and their coefficient of variation (CV_{BV}) can be estimated
307 from their progenies.

308

309 *Method III:* a global analysis was performed with all the tests except tests 11
310 to 13 because no pedigree connection existed between the population P0 and
311 the following ones. The pedigree considered took into account the complete
312 multigeneration genetic relationships. We thus obtained another estimate for
313 the G0 genetic parameters (considered, in this analysis, as the base
314 population) and for CV_{BV} of populations G0 and G1.

315 The same three methods were used to estimate correlations between the
316 selected traits (Table 2).

Table 2 317

318

319 **Results**

320

321 *1. Analyses per test (Method I)*

322 Figure 2 displays the results of each single test analysis for H, D and S.

323 There is a wide range of variation of each parameter (h^2 , CV_A and CV_P)

324 among tests within a population. For example, CV_A of D (Figure 2 b2)

325 varies between 5.1 to 14.1 % (mean standard errors is 0.9 %) among the

326 different tests of population G1. For a given test and trait, CV_{BV} is always

327 lower than CV_A .

328 In most of the tests, H appears to be slightly more heritable and exhibits a

329 lower genetic coefficient of variation than D. The phenotypic coefficient of

330 variation is clearly lower for H (between 8.4 and 18.3 %) than D (between

331 14.5 and 34.7 %). Heritability of S is about of the same magnitude than H or

332 D but the genetic and phenotypic coefficients of variation are much higher

333 (CV_A superior to 20 % and CV_P superior to 50 %).

334 Variation parameters of G0 and G1 are more accurate (ie. lower standard

335 errors) than those of P0 as they are estimated with tests implying more

336 progenies.

Figure 2 337

338 Correlations were estimated for each single test (Figure 3). Note that S is the

339 deviation to verticality, thus a positive correlation between S and a growth

340 trait (H or D) means that straightness is unfavourably correlated with

341 growth. Phenotypic correlations are high between H and D and moderate
342 between S and growth traits. Genetic correlations are higher than the
343 phenotypic ones albeit estimated with a larger standard error. As for the
344 genetic variance, there is a wide range of variation of correlations among the
345 different tests.

Figure 3 346

347 2. *Analyses per population (Method II)*

348 Variation parameters estimated for each entire population with the genetic
349 relationship matrix truncated to the parent level are presented in Figure 2
350 (values linked by a line) and Table 3. For each population, a large set of data
351 was analysed: 6 105 trees were considered for P0, 67 223 trees for G0 and
352 86 582 trees for G1. As a consequence, variation parameters were estimated
353 with low standard errors compared to the estimates from Method I.

354 The evolution of genetic variation over breeding populations is similar for H
355 and D. CV_A decreases between P0 and G0 (from 10.2 % to 5.6 % for H, and
356 from 11.1 % to 7.4 % for D) then remains constant between G0 and G1.

357 Likewise CV_{BV} of these two traits decreases substantially from P0 to G0
358 (from 8.2 % to 5.3 % for H, and from 8.0 % to 5.5 % for D) then slightly
359 from G0 to G1 (from 5.3 % to 4.1 % for H, and from 5.5 % to 4.1 % for D).

360 While CV_P is rather stable from P0 to G0, it tends to decrease between G0
361 and G1. Heritability, which follows the same pattern than CV_A from P0 to
362 G0, slightly increases from G0 to G1.

363 The evolution of genetic parameters for S is similar between P0 and G0 but
364 the trend is weaker and not significant: CV_A decreases from 24.1 % to
365 20.9 % and CV_{BV} from 18.0 % to 17.0 %. Then an increase is observed
366 between G0 and G1 (from 20.9 % to 26.9 % for CV_A and from 17.0 % to
367 20.2 % for CV_{BV}). CV_P slightly increases from P0 to G1.

Table 3 368

369 Method II was also used to estimate the correlations between the three
370 selected traits (Figure 3 and Table 4). No strong pattern can be observed in
371 regard to the standard errors. Nevertheless the genetic correlation between H
372 and D is slightly lower in breeding populations G0 and G1 than in P0. There
373 is no significant change of the correlation between H and S, and between D
374 and S (Table 4).

Table 4 375

376

377 *3. Analysis of the whole data (Method III)*

378 Method III provides an overall estimation of the genetic variation in G0
379 across all populations and tests, by taking into account multigeneration
380 genetic relationships. However this method does not allow the estimation of
381 parameters of P0, as trees from tests 11 to 13 are not genetically related to
382 trees of subsequent populations. Method III is based on a very large sample
383 of trees: for example, 153 805 trees were considered to estimate heritability
384 of H. Stem deviation from verticality (S) exhibits greater genetic variation

385 (both in terms of heritability and genetic variance) than H or D (Table 3).
386 Estimates of variation of G0 are similar between Method III (analysis based
387 on P1 and P2 populations) and Method II (analysis based only on P1
388 population). However, for H and D, the heritability is slightly higher and the
389 phenotypic variation lower when both populations P1 and P2 are
390 considered.

391

392 Method III also facilitates the estimation of CV_{BV} in G0 and G1 with the
393 same data set. No strong evolution from G0 to G1 is highlighted: CV_{BV} of H
394 slightly decreases, no significant change is found for D and CV_{BV} of S
395 slightly increases. Thus these results confirm those obtained by Method II.

396

397 Correlation estimates among traits in G0 population are very similar
398 between Method II and Method III (Table 4). Correlations were also
399 estimated within G0 and G1 trees with the breeding values. Only a slight
400 decrease was observed from G0 to G1 for H–D correlation.

401

402 **Discussion**

403

404 *1. Level of genetic variation for growth traits (H, D) and stem*
405 *deviation to verticality (S)*

406 Our study shows that genetic variation of these traits in natural
407 populations and in the very early breeding populations is moderate
408 (Table 3). Cornelius (1993) compiled genetic parameter (h^2 and CV_A)
409 estimates from 67 published papers, mainly on *Pinus* species. They were
410 based on experimental designs established with progenies of selected trees
411 from natural populations (corresponding thus to our tests with P1 trees) and
412 can therefore be compared to our results. Most of the heritability estimates
413 (respectively CV_A) of H and D varied between 0.05 and 0.40 (respectively
414 between 5 and 15 %). Results from our individual tests are within this range
415 but our study clearly indicates that estimates can be quite variable across
416 tests, suggesting that they are highly dependent on the sampling of genetic
417 entries and the site conditions (Figure 2). Consequently, many authors have
418 tried to compile data from several tests to estimate the genetic parameters of
419 a population more accurately. The heritability of growth traits of the base
420 population of *Pinus elliottii* breeding program (G0 population) varied
421 between 0.12 and 0.16 over a large set of tests (Dieters et al., 1995; Hodge
422 and White, 1992). Jayawickrama (2001) analysed more than 150 000 radiata
423 pines to estimate genetic variation of the plus tree population (G0

424 population): heritability amounted to 0.11 for girth, 0.13 for height and 0.19
425 for straightness. These three analyses based on large data sets reported low
426 to moderate genotype \times environment interactions. Our estimates for
427 population G0 and G1 are of similar magnitude (Table 3 - Method II). As
428 expected, the unselected population P0 displays higher estimates than
429 populations under selection. The high variation across tests (Figure 2)
430 further indicates a need for multiple tests to reliably estimate genetic
431 variation. In this respect, the individual model is a recommended method ,
432 as suggested by the decrease of the standard error of variation parameters as
433 we moved from Method I to Method III (data not shown).

434

435 Regarding the comparison of the level of genetic variation among
436 traits, Cornelius (1993) concluded that H is more heritable than D (0.25 for
437 the median heritability of height vs. 0.19 for diameter), and exhibits higher
438 genetic variance (as shown by the coefficient of genetic variation). While
439 we draw similar conclusions for heritability (h^2 higher for H than for D),
440 there is an opposite trend for the coefficients of variation: both CV_A and
441 CV_P are higher for D than H (Table 3). Lending support to our result,
442 Gwaze et al. (2001) also observed higher heritability and a lower coefficient
443 of variation for height compared to diameter in *Pinus taeda* based on an
444 individual tree model. The coefficients of variation of H and D can be

445 compared in our study without corrections because they have the same
446 dimensionality (Houle, 1991).

447

448 Genetic parameters of S are more difficult to compare across studies
449 because several different phenotypic assessments were used to assess stem
450 straightness. However, as for other studies (Cornelius, 1993;
451 Jayawickrama, 2001), a higher genetic variation is observed compared to
452 the growth traits (Figure 2, Table 3).

453

454 *2. Evolution of the genetic variation of selected traits throughout*
455 *successive populations*

456 Regardless of the method used, phenotypic variation shows no clear
457 evolution for H and D from P0 to G0 but decreases slightly from G0 to G1
458 (Figure 2, Table 3). On the contrary, there is a clear decrease of genetic
459 variation from P0 to G0 and a very minor decrease from G0 to G1. The
460 pattern of genetic variation is consistent among the parameters used (CV_A or
461 CV_{BV}). We will therefore restrict the discussion to CV_{BV} as CV_{BV} was the
462 only parameter that could be used for comparing genetic variation over
463 breeding populations with Method III. CV_{BV} is reduced on average by 35 %
464 for H and by 31 % for D between P0 and G0 (Table 3).

465 There is still a significant decrease of CV_{BV} of growth traits from G0 and
466 G1 according to Method II (by 23 % for H and by 25 % for D, see Table 3).

467 Yet, according to Method III, the most accurate analysis as it gathers both
468 P1 and P2 populations, the decrease is weak for H (12 %) and not
469 significant for D between populations G0 and G1 (Table 3).

470 In conclusion, while mean values of the two growth traits increased
471 as a result of directional selection from G0 to G1, only a very slight
472 reduction of genetic variation was observed. Similarly, King et al. (1998)
473 reported no change of genetic variation between two breeding populations
474 of *Pinus radiata* equivalent to the ones we referred to as G0 and G1.

475 Genetic variance of S follows a similar trend across generations
476 albeit less pronounced: there is a non-significant decrease from P0 to G0
477 followed by a slight increase from G0 to G1 (Table 3). The increase from
478 G0 to G1 is unexpected as stem straightness underwent recurrent directional
479 selection like the two other traits. However, silvicultural practices have
480 changed over time, and may have impacted stem straightness more than the
481 other two growth traits. Intensive treatments such as the use of fertilizers
482 and ploughing that became more frequent in recent times, may have
483 increased the environmental and genetic variation of traits. This is
484 suggested by the larger increase of the phenotypic variance of S from P0 to
485 G1 (Figure 2, Table 3), in contrast to H and D. Under such circumstances,
486 one may suspect that the genetic variance has been impacted as well,
487 blurring the effect of directional artificial selection that we tried to monitor.

488

489 Changes of genetic variance in artificial breeding populations may
490 result from either drift effects due to the reduction of population size, or
491 from directional selection. As the pedigree is known over two generations,
492 the “status number” (N_s) (Lindgren et al., 1996) can be used to provide an
493 estimate of the population effective size. N_s is “the number of unrelated and
494 non-inbred genotypes in an ideal panmictic population, which is expected to
495 produce offspring with the same coefficient of inbreeding as the progeny of
496 the considered population following random mating” (Lindgren et
497 al., 1997). Based on the pedigree data of the tests considered in this study,
498 the status number of G1 amounts to about 90 which can be compared to the
499 320 unrelated plus trees of the G0 population analysed here. The estimated
500 decrease of genetic variance at generation “t” due to the reduction of
501 population size should amount to $\left(1 - \frac{1}{2 N_e}\right)$ of the genetic variance at
502 generation “t-1” where N_e is the effective size (Lynch and Walsh, 1998).
503 Consequently, the reduction of genetic variance due to the reduction of
504 population size remains extremely small, and is therefore most likely to be
505 caused by directional selection.

506 The evolution of genetic variation in populations undergoing selection was
507 first investigated by Bulmer (1971). By considering a quantitative trait
508 controlled by an infinite number of loci, he subdivided genetic variance
509 (V_A) into two components: the “equilibrium genetic variance” also called

510 genic variance (the first term of the following equation) and the
511 “disequilibrium contribution” (the second term):

512
$$V_A = \sum_i Var(g_i) + \sum_{i \neq j} Cov(g_i, g_j)$$

513 with $Var(g_i)$ the variance at the i^{th} locus and $Cov(g_i, g_j)$ the covariance
514 between the i^{th} and the j^{th} loci.

515 Under this model, Bulmer (1971) showed that directional selection induces
516 a negative disequilibrium contribution, and thus the genetic variance
517 decreases over generations. This effect, known as the “Bulmer effect”, is
518 temporary and the disequilibrium contribution progressively approaches
519 zero if selection is relaxed. Bulmer (1971) showed with an analytical model
520 that the decrease of genetic variance under selection is high in the first
521 generations and rapidly stabilised. The equilibrium stage occurs when the
522 effects of selection and recombination counterbalance each other. However,
523 the reduction of the genetic variance can be inflated by the reduction of
524 genic variance. Indeed, the genic variance decreases if the trait under
525 selection is determined by a finite number of genes or if small populations
526 are considered (De Rochambeau et al., 2000).

527 The reduction of genetic variation observed between P0 and G0 is thus
528 mainly explained by the phenotypic selection conducted in the 1960’s to
529 constitute the “plus” trees population, and may be due to the Bulmer effect.

530 A mass selection was performed throughout the Landes forest, using a

531 procedure that permitted the consideration of a genetic component in the
532 phenotypic superiority of selected trees. The method was based on the
533 standardized value of a candidate tree compared to its 30 immediate
534 neighbours (Illy, 1966), thus taking into account environmental effects.
535 Despite the moderate heritability of the selected traits (from 0.20 to 0.50,
536 see Table 3), the extremely high selection rate that was used during the mass
537 selection was sufficient to reduce the genetic variation in the subsequent
538 generation (G0). Illy (1966) reported that one tree out of 70 000 was
539 selected during this selection step (this estimation is based on the number of
540 trees screened for plus trees selection).

541 As a genetic selection step was then achieved to build the G1 population
542 from progenies of G0 trees, we also expected a significant decrease of
543 genetic variation for selected traits. However the decrease was much lower
544 or non significant depending on the method considered. Various hypotheses
545 can be suggested to interpret these results. First, the accuracy of the
546 analyses may not be able to detect a slight decrease of genetic variation.
547 Second, the selection was performed on three criteria (H, D and S);
548 therefore the selection intensity for each of them may be more limited and
549 may have been much lower than the selection intensity used during the first
550 stage (from P0 to G0). Third, the equilibrium phase may be achieved after
551 the selection of the plus trees but this hypothesis is unlikely as only one
552 selection step was performed to obtain the population G0.

553

554 3. *Level and evolution of the correlations between the selected*
555 *traits throughout successive populations*

556 Genetic correlations are highly positive (favourable) between H and D while
557 they are slightly positive (unfavourable) between growth traits and stem
558 deviation to verticality (Figure 3, Table 4). Considering both Method II and
559 Method III, no consistent pattern in the correlation change was found,
560 except for a slight decrease between P0 and G0 for H - D correlation.

561 The evolution of genetic correlation was investigated by simulations
562 according to the relative weights of index selection and to the initial
563 variation of the traits (McMillan et al., 1995). If the initial genetic
564 correlation is positive, simulations suggest a decline towards zero, the rate
565 of change increasing with the heritability of one or both traits. If genetic
566 correlation is negative, there are two contrasting trends: either the
567 correlation increases towards zero if economic weights are unequal or it
568 declines to -1 if they are equal. The slight change of the H - D correlation
569 observed is in agreement with these simulations. As economic weights of
570 growth traits and straightness are similar, we expect an increase of the D - S
571 correlation through the breeding populations. Indeed we found a slight
572 increase for r_{BV} but it appears non significant.

573

574 4. *Conclusion*

575 Our results showed that even if the population effective size has been
576 substantially reduced over successive breeding populations, the genetic
577 variance for the selected traits has not followed the same trend. Indeed, after
578 a decrease when selecting for plus trees, the genetic variation remained
579 fairly constant suggesting the possibility to maintain genetic gains over
580 future generations with this recurrent selection strategy.

581 Lastly we may suppose that genetic variation of unselected traits has been
582 maintained above the level we observed for selected traits. Selection for
583 new criteria could therefore be implemented at the level of G2 without
584 enriching the genetic variation from external genetic resources, provided
585 that genetic correlation between the new criteria and growth or straightness
586 remains low.

587

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589

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596

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693

694 **Figure 1**

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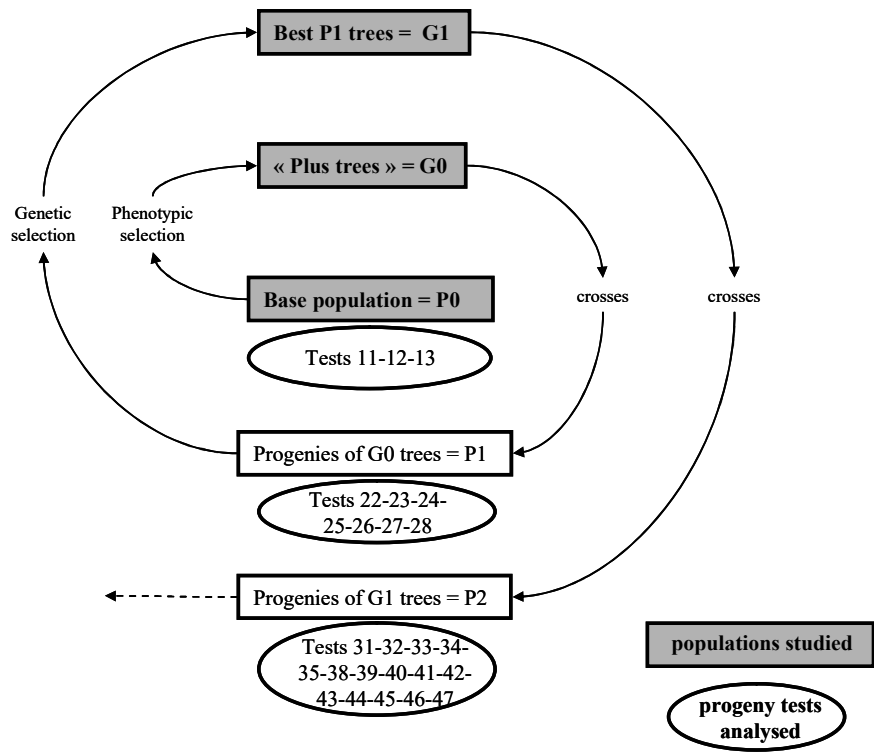
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708 **Figure 2**

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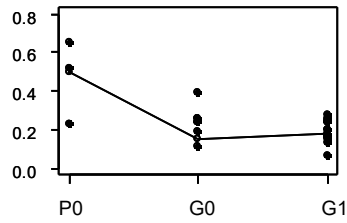
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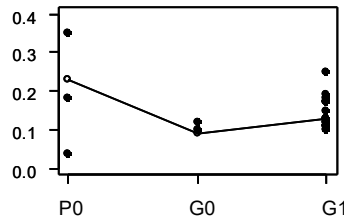
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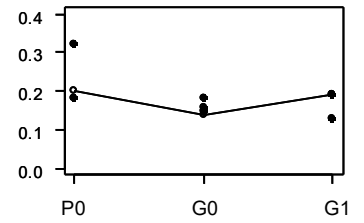
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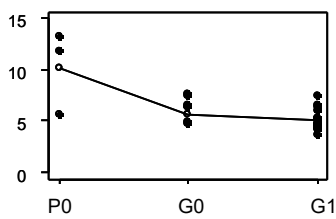
a1) h^2 H



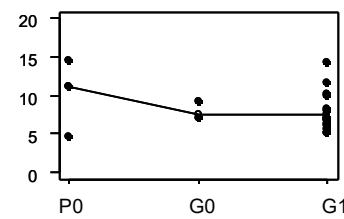
b1) h^2 D



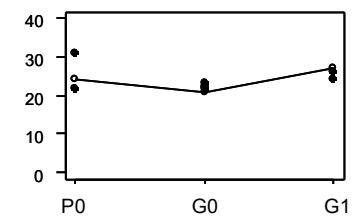
c1) h^2 S



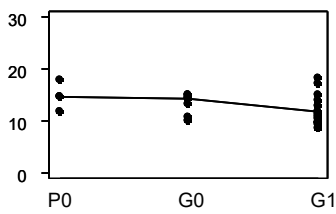
a2) CV_A H



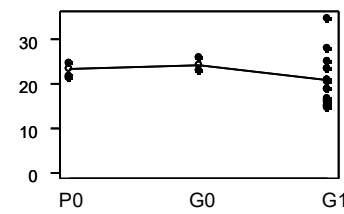
b2) CV_A D



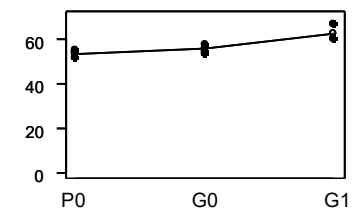
c2) CV_A S



a3) CV_P H



b3) CV_P D



c3) CV_P S

(H = total height ; D = girth at breast height ; S = stem deviation to verticality ; h^2 = heritability ; CV_A = additive coefficient of variation ; CV_P = phenotypic coefficient of variation)

728 **Figure 3**

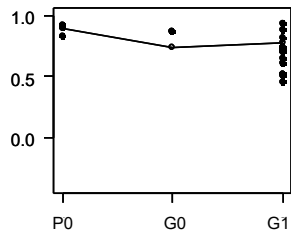
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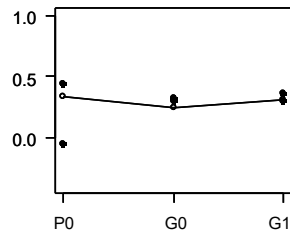
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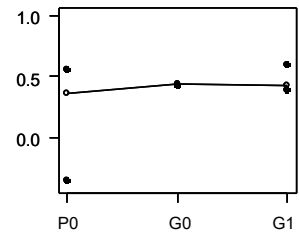
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a1) Genetic correlation H - D



b1) Genetic correlation H - S



c1) Genetic correlation D - S

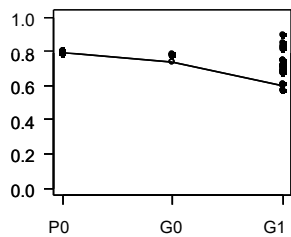
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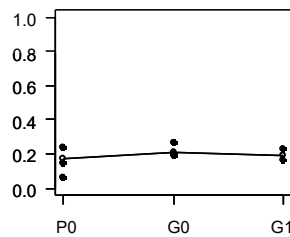
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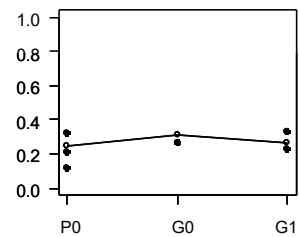
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a2) Phenotypic correlation H - D



b2) Phenotypic correlation H - S



c2) Phenotypic correlation D - S

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(H = total height ; D = girth at breast height ; S = stem deviation to verticality)

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744 **Table 1**

745 Test features.

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| Population | Code | Design | Progenies | Trees | Block | Trees per plot | Plantation year | Measurement age | Height mean | Girth mean | Deviation to verticality mean |
|------------|------|------------------|-----------|-------|-------|----------------|-----------------|-----------------|-------------|------------|-------------------------------|
| P0 | 11 | open pollination | 53 | 1430 | 5 | 3 to 20 | 1972 | 8 | 437.5 | 29.2 | 13.2 |
| | 12 | open pollination | 50 | 1288 | 5 | 8 to 12 | 1973 | 10 | 661.9 | 33.1 | 10.0 |
| | 13 | open pollination | 72 | 3388 | 5 | 3 to 19 | 1974 | 10 | 721.0 | 33.6 | 11.0 |
| G0 | 22 | open pollination | 56 | 15040 | 90 | 10 | 1965 | 7 | 632.5 | - | - |
| | 23 | factorial | 144 | 16420 | 48 | 4 to 12 | 1968 | 7 | 490.1 | - | - |
| | 24 | factorial | 169 | 49769 | 8 | 9 | 1969 | 9 | 678.8 | - | - |
| | 25 | polycross | 261 | 21663 | 50 | 3 to 9 | 1975 | 8 | 583.4 | 31.0 | - |
| | 26 | nested design | 236 | 11745 | 110 | 4 | 1976 | 9 | 654.5 | 30.7 | 7.7 |
| | 27 | nested design | 75 | 3465 | 33 | 4 | 1977 | 10 | 707.0 | - | 8.0 |
| | 28 | nested design | 76 | 4132 | 76 | 8 | 1978 | 10 | 711.0 | - | 9.4 |
| | 31 | nested design | 72 | 5598 | 68 | 1 | 1981 | 8 | 572.0 | 26.1 | 4.3 |
| G1 | 32 | nested design | 28 | 2777 | 97 | 1 | 1982 | 12 | 737.8 | 30.6 | - |
| | 33 | nested design | 157 | 14728 | 50 | 1 | 1985 | 12 | 920.6 | 43.3 | - |
| | 34 | nested design | 66 | 3966 | 72 | 1 | 1986 | 13 | 1023.0 | 47.7 | - |
| | 35 | polycross | 213 | 9188 | 125 | 4 | 1982 | 9 | 764.7 | 33.2 | 6.3 |
| | 38 | polycross | 129 | 6046 | 5 | 10 | 1992 | 11 | 937.4 | 43.9 | - |
| | 39 | polycross | 101 | 3535 | 35 | 1 | 1994 | 8 | 644.0 | 37.1 | - |
| | 40 | polycross | 101 | 3535 | 35 | 1 | 1995 | 8 | 658.3 | 35.6 | - |
| | 41 | polycross | 101 | 3299 | 35 | 1 | 1995 | 8 | 679.5 | 36.3 | - |
| | 42 | polycross | 211 | 7420 | 35 | 1 | 1995 | 8 | 766.8 | 40.1 | - |
| | 43 | polycross | 211 | 7455 | 35 | 1 | 1995 | 8 | 633.0 | 33.2 | - |
| | 44 | polycross | 211 | 7355 | 35 | 1 | 1995 | 8 | 695.7 | 36.4 | - |
| | 45 | polycross | 197 | 6895 | 35 | 1 | 1996 | 8 | 539.8 | 30.5 | - |
| | 46 | polycross | 197 | 5495 | 35 | 1 | 1996 | 8 | 644.7 | 32.9 | - |
| | 47 | polycross | 197 | 6160 | 35 | 1 | 1996 | 8 | 731.5 | 41.3 | - |

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750

751 **Table 2**

752 Methods to estimate variability and correlations in multigenerational
 753 populations using the individual model.

754

| | ANALYSIS | | VARIABILITY | | | CORRELATIONS | | |
|-------------------|----------------------------|---------------------------------------|----------------------------|---------------------|----------|---------------------------|--------------------|----------|
| | Data analysed | Pedigree considered | h^2 and CV_A estimated | CV_{BV} estimated | Results | r_P and r_G estimated | r_{BV} estimated | Results |
| Method I | test 11 | parent level | P0 | P0 | | P0 | P0 | |
| | ... | ... | ... | ... | | ... | ... | |
| | test 22 | parent level | G0 | G0 | Figure 2 | G0 | G0 | Figure 3 |
| | ... | ... | ... | ... | | ... | ... | |
| | test 31 | parent level | G1 | G1 | | G1 | G1 | |
| Method II | ... | ... | ... | ... | | ... | ... | |
| | P0 (tests 11 to 13) | parent level | P0 | P0 | Figure 2 | P0 | P0 | Figure 3 |
| | P1 (tests 22 to 28) | parent level | G0 | G0 | and | G0 | G0 | and |
| | P2 (tests 31 to 47) | parent level | G1 | G1 | Table 3 | G1 | G1 | Table 4 |
| Method III | P1 and P2 (tests 22 to 47) | all relationships between individuals | G0 | G0 and G1 | Table 3 | G0 | G0 and G1 | Table 4 |

755

756

(CV_A = additive coefficient of variation ; CV_{BV} = coefficient of variation of the breeding values ; r_P =

757

phenotypic correlation ; r_G = genetic correlation ; r_{BV} = correlations estimated with breeding values)

758

759

760 **Table 3**

761 Variability estimated per population considering either the pedigree

762 relationships up to the parent level (Method II) or the all pedigree

763 relationships. (standard errors given in brackets).

764 For a given trait and a given parameter, different letters indicate significant

765 difference between estimates.

766

| | Method II | | | | | | Method III | | | |
|----------|-----------|----------------------------|----------------------------|----------------------------|-----------------------------|-----------------------------|------------|--|----|--|
| | P0 | | G0 | | G1 | | G0 | | G1 | |
| H | h^2 | 0.50 (0.08) <i>a</i> | 0.15 (0.01) <i>b</i> | 0.18 (0.01) <i>c</i> | 0.19 (0.01) | - | | | | |
| | CV_A | 10.2 (0.9) <i>a</i> | 5.6 (0.3) <i>b</i> | 5.0 (0.2) <i>b</i> | 5.5 (0.2) | - | | | | |
| | CV_{BV} | 8.2 (0.4) <i>a</i> | 5.3 (0.2) <i>b</i> | 4.1 (0.1) <i>c</i> | 5.0 (0.2) <i>a'</i> | 4.4 (0.1) <i>b'</i> | | | | |
| | CV_P | 14.5 (0.1) <i>a</i> | 14.1 (0.1) <i>b</i> | 11.9 (0.0) <i>c</i> | 12.6 (0.0) | - | | | | |
| D | h^2 | 0.23 (0.05) <i>a</i> | 0.09 (0.01) <i>b</i> | 0.13 (0.01) <i>c</i> | 0.14 (0.01) | - | | | | |
| | CV_A | 11.1 (1.1) <i>a</i> | 7.4 (0.4) <i>b</i> | 7.5 (0.2) <i>b</i> | 8.1 (0.2) | - | | | | |
| | CV_{BV} | 8.0 (0.4) <i>a</i> | 5.5 (0.2) <i>b</i> | 4.1 (0.1) <i>c</i> | 5.8 (0.2) <i>a'</i> | 6.2 (0.1) <i>a'</i> | | | | |
| | CV_P | 23.2 (0.2) <i>a</i> | 24.2 (0.1) <i>b</i> | 20.9 (0.1) <i>c</i> | 21.6 (0.1) | - | | | | |
| S | h^2 | 0.20 (0.04) <i>a</i> | 0.14 (0.02) <i>a</i> | 0.19 (0.02) <i>a</i> | 0.16 (0.01) | - | | | | |
| | CV_A | 24.1 (2.3) <i>a</i> | 20.9 (1.3) <i>a</i> | 26.9 (1.7) <i>b</i> | 23.2 (1.1) | - | | | | |
| | CV_{BV} | 18.0 (1.0) <i>a</i> | 17.0 (0.7) <i>a</i> | 20.2 (0.8) <i>b</i> | 17.2 (0.7) <i>a'</i> | 21.2 (0.8) <i>b'</i> | | | | |
| | CV_P | 53.8 (0.5) <i>a</i> | 55.9 (0.4) <i>b</i> | 62.5 (0.5) <i>c</i> | 58.7 (0.3) | - | | | | |

767

768 (H = total height ; D = girth at breast height ; S = stem deviation to verticality ; h^2 = heritability ; CV_A =

769 additive coefficient of variation ; CV_P = phenotypic coefficient of variation ; CV_{BV} = coefficient of

770 variation of the breeding values)

771

772

773 **Table 4**

774 Correlations between selected traits in the successive populations (standard
775 errors given in brackets).

776 For a given parameter, different letters indicate significant difference

777 between estimates.

778

| | | Method II | | | Method III | |
|---------------------------|----------|----------------------|----------------------|----------------------|-----------------------|-----------------------|
| | | P0 | G0 | G1 | G0 | G1 |
| Correlations H - D | r_P | 0.79 (0.01) <i>a</i> | 0.74 (0.00) <i>b</i> | 0.60 (0.00) <i>c</i> | 0.73 (0.00) | - |
| | r_G | 0.89 (0.01) <i>a</i> | 0.73 (0.03) <i>b</i> | 0.77 (0.03) <i>b</i> | 0.67 (0.02) | - |
| | r_{BV} | 0.91 (0.03) <i>a</i> | 0.81 (0.03) <i>b</i> | 0.85 (0.02) <i>b</i> | 0.78 (0.04) <i>a'</i> | 0.68 (0.02) <i>b'</i> |
| Correlations H - S | r_P | 0.17 (0.01) <i>a</i> | 0.21 (0.01) <i>b</i> | 0.19 (0.01) <i>b</i> | 0.20 (0.01) | - |
| | r_G | 0.33 (0.11) <i>a</i> | 0.24 (0.07) <i>a</i> | 0.31 (0.07) <i>a</i> | 0.27 (0.05) | - |
| | r_{BV} | 0.37 (0.07) <i>a</i> | 0.23 (0.06) <i>a</i> | 0.27 (0.05) <i>a</i> | 0.23 (0.06) <i>a'</i> | 0.32 (0.05) <i>a'</i> |
| Correlations D - S | r_P | 0.25 (0.01) <i>a</i> | 0.31 (0.01) <i>b</i> | 0.26 (0.01) <i>a</i> | 0.29 (0.01) | - |
| | r_G | 0.36 (0.12) <i>a</i> | 0.44 (0.08) <i>a</i> | 0.43 (0.07) <i>a</i> | 0.42 (0.05) | - |
| | r_{BV} | 0.37 (0.07) <i>a</i> | 0.27 (0.05) <i>a</i> | 0.38 (0.05) <i>a</i> | 0.34 (0.05) <i>a'</i> | 0.47 (0.05) <i>a'</i> |

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780 (H = total height ; D = girth at breast height ; S = stem deviation to verticality ; r_P = phenotypic correlation

781 ; r_G = genetic correlation ; r_{BV} = correlations estimated with breeding values)

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