Genetic analysis using parent-progeny relationship for wood quality traits in Norway spruce (*Picea abies* (L.) Karst.)

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Abstract

Two-generations pedigree involving 524 plus trees and their open-pollinated (OP) progenies were jointly studied to estimate parent-progeny correlation and heritability. Three wood traits (wood density, MFA, and MOE) were determined by SilviScan in one ramet per plus tree and 12 OP progenies. Three ramets per plus tree and 12 OP were also measured with two indirect methods, Pilodyn and Hitman. The overall correlation between OP-based breeding values and plus tree-based phenotypes was low to moderate for all traits. The correlations between the phenotypic values of the mother trees and the breeding values estimated on their half-sib progenies are low to moderate. Reasons for this may be experimental errors in progeny trials and lack of experimental design in archives, contributing to the parent and progeny correlation. The management practices in the archive may contribute more to such low correlation. Offspring progeny heritability estimates based on SilviScan measurements were higher than parent-offspring regression using one single ramet from the archive. Moreover, when three ramets were measured the parent-offspring regression heritability estimates were higher than those based solely on progeny data for the Pilodyn and Hitman on the standing trees. The standard error of the heritability estimates decreased with increasing progeny size.

Key words

Solid-wood, Norway spruce, parent-offspring regression, heritability, correlation

22 Introduction

23 Norway spruce [*Picea abies* (L.) Karst.] is one of the most important conifer species
 24 in Europe for both economic and ecological aspects [Hannrup et al., 2004]. It is ex-
 25 tensively forested for timber and paper production. Increasing volume production
 26 has traditionally been the main objective of the species breeding program, while
 27 more recently, different aspects related to wood quality have gained increasing at-
 28 tention [Mullin et al., 2011, Rosvall et al., 2011]. For mechanical properties of
 29 wood-based products, wood density, microfibril angle (MFA), and modulus of elas-
 30 ticity (MOE) are considered as the most important traits [Chen et al., 2015, Zobel
 31 and Jett, 1995].

32 The SilviScan technology was developed to measure the radial variation, i.e.
 33 from pith to bark of many trails from the same sample: solid-wood quality traits
 34 including wood density, MFA, MOE [Evans, 1999, Evans, 2006], as well as fiber
 35 traits, such as their cross-sectional dimensions and MFA [Evans, 1994]. Its high
 36 resolution, accuracy and very high efficiency compared to corresponding labora-
 37 tory methods, has contributed substantially to advancements in research and de-
 38 velopment within wood biology, forestry and optimal use of forest resources in
 39 softwoods [Lindström et al., 1998, Lundgren, 2004, Kostianen et al., 2009, McLean
 40 et al., 2010, Piispanen et al., 2013, Fries et al., 2014], on hardwoods [Kostianen
 41 et al., 2013, Lundqvist et al., 2017] and on modelling of trait variations [Wilhelms-
 42 son et al., 2002, Lundqvist S-O, 2005, Franceschini et al., 2012, Auty et al., 2014].
 43 When data from thousands of samples are preferred, which is often the case in oper-
 44 ational tree breeding, SilviScan is however seldom used. Then, rapid indirect meth-
 45 ods may be better suited, if available and good enough. SilviScan is then typically
 46 used to produce benchmark data and for validation of the more rapid procedures.
 47 Examples of such faster and non-destructive methods (NDM) for solid wood traits

are Pilodyn penetration and acoustic velocity [Chen et al., 2015, Kennedy et al., 2013, Vikram et al., 2011]. Pilodyn is an indirect non-destructive, low cost and easy-to-use instrument for measuring wood density. In Norway spruce and other conifer species, strong genetic correlations were observed between Pilodyn penetration and wood density measured with SilviScan [Chen et al., 2015, Cown, 1978, Despons et al., 2017, Fukatsu et al., 2011, King, 1988, Sprague et al., 1983, Yanchuk and Kiss, 1993]. Further, acoustic velocity measured by Hitman ST300 (Christchurch, New Zealand) apparatus has shown an efficient indirect method for the estimation of MFA and it has already been used on many species, such as Scots Pine (*Pinus sylvestris* L.) [Hong et al., 2015], white spruce (*Picea glauca* [Moench.] Voss) [Lenz et al., 2013], and Norway spruce [Chen et al., 2015]. Models for estimation of wood stiffness from density and MFA have been developed for many species and were also implemented in early versions of SilviScan [Evans and Elic, 2001]. An analogous model using the proxy measurements of acoustic velocity and Pilodyn penetration on standing trees was shown to be efficient for the selection for wood stiffness in Norway spruce [Chen et al., 2015]. However, Pilodyn measures wood density only in the outermost annual rings, therefore, it has also been suggested that it may not be reliable for ranking of the whole tree in case where the correlation is low between the outermost rings and inner rings [Wessels et al., 2011] or if the diameter of tree is wide.

As part of the Norway spruce breeding program in Sweden, large numbers of superior genotypes (plus trees) are maintained in ex-situ grafted clonal archives. These serve as base breeding populations where crossings of selected parental genotypes are conducted with the purpose of generating cross-pollinated progenies for the next generation in the breeding cycle. There is an interest to estimate heritability using these clonal archive, particularly using the relationship between archived parent and their progenies, and clonal heritability (repeatability) for wood quality

75 traits. Clonal archives are usually established using grafted scions from selected
76 trees, without implementation of experimental design, and subject to management
77 activities, such as pruning, topping and thinning at late ages. These operations may
78 affect growth greatly but may have less impact on the genetic property of wood
79 quality traits. This is because wood quality traits have higher heritability and little
80 G by E [Chen et al., 2016, Hayatgheibi et al., 2017, Hong et al., 2014, Lenz et al.,
81 2010, Wu et al., 2008]. Therefore, the parent-offspring relationship may still be
82 used to estimate heritability for wood quality traits. The purpose of this study was
83 to examine effectiveness of using parent-offspring to estimate heritability using the
84 archived parent and progeny in field tests by:

- 85 1. Investigating the correlation and regression between the phenotypic values
86 measured in clonal archives and the breeding values (BV) estimated in their half-
87 sib progenies.
- 88 2. Comparing heritability estimates based on progeny only and based on parents-
89 offspring regression and clonal repeatability for solid-wood quality traits.
- 90 3. Finally, we also investigated the effect of progeny and ramet number on
91 heritability estimate.

92 **Materials and methods**

93 **Plant material**

94 The study was based on two generations of pedigree involving: (1) 524 mother
95 plus-tree clones/genotypes from two different clonal archives in Ekebo and Mal-
96 tesholm in southern Sweden. (2) Their corresponding 524 open-pollinated (half-
97 sib) families consisting of at most six individuals for each of the two progeny trials.
98 For the 524 mother trees, originally there were ca. 10 ramets grafted for each
99 clone at the time of establishment, however, at the time of sampling the major-

ity of the genotypes had only three ramets remaining. The trees were grafted on seedling rootstocks 28-30 years prior to sampling. As part of their maintenance, the clone archives had been thinned, and the trees topped. The two progeny trials were, S21F9021146 aka F1146 (Hreda, Eksj, Sweden) and S21F9021147 aka F1147 (Erikstorp, Tollarp, Sweden) were established in 1990. Increment cores had been sampled in 2010 and analysed with SilviScan at age 21-years old [Chen et al., 2014], whilst Pilodyn penetration depth and velocity were measured at ages 22 and 24, respectively [Chen et al., 2015].

Measurements and data

The radial variations in wood density, MFA and MOE have been assessed in previous studies with SilviScan from increment cores of up to 12 progenies per half-sib family, followed by the calculation of area-weighted averages, representing the trait averages of all wood formed in the stem cross-sections at each cambial age. In this study, the corresponding data was generated also for the ramets from the archives. Below, widths of annual rings are used to identify outliers and DBH to compensate for differences in between tree competition on pre-treatments of data. For all other calculations, such as estimation of heritability and the comparison of methods, averages for stem cross-sections at different cambial ages (ring numbers) were used.

Data was also assessed through the use of the indirect proxies Pilodyn, Velocity and MOE(ind). The first two of these were measured on the standing trees with Pilodyn 6J Forest and Hitman ST300 instruments. MOE was estimated from these indirect measurements using the formula:

$$MOE(ind) = (1/Pilo) * 10,000 * AV^2$$

126 where Pilo is the Pilodyn penetration depth (mm) and AV is the velocity of
127 the wave through the material (km/s), which has a high inverse correlation with
128 MFA [Chen et al., 2014]. These data were previously presented in [Chen et al.,
129 2014, Chen et al., 2015]. In this study, such data was generated on up to three
130 ramets of each mother clone/genotype in the clonal archive. When more than one
131 ramet was available, the average of each measurement was used for further Pearson
132 correlation analysis. The evaluations were based on data for up to ring 16 to avoid
133 problems of representability, as fewer trees were represented at the highest cambial
134 ages.

135 **Data adjustments**

136 The SilviScan data produced from the increment cores of the progeny trials when
137 taken together and compared to those from the mothers, should be more informa-
138 tive about the family. They include data on up to 12 trees per family, whereas only
139 one single ramet per each of the 524 mother tree genotypes was sampled for phe-
140 notyping with SilviScan at the clone archive level. Therefore, to identify outliers,
141 we calculated for each family the 99% confidence intervals for the widths of rings
142 with the same cambial age (ring number). The mother trees with more than seven
143 rings of widths outside the 99% confidence interval of their progeny were consid-
144 ered outliers. When investigating the effect of removing outliers, these mother trees
145 and their progenies were removed from the analysis.

146 For an overall comparison on how trees grown in the trials versus those in the
147 archive had developed with age, averages for rings of the same number were calcu-
148 lated from SilviScan data across all progeny trees in the two trials and all mothers in
149 the archive, respectively. These averages were plotted versus ring number (Figure
150 1), showing different characters of the developments of ring width and wood den-
151 sity between trials and archive. We assumed that this was caused by differences in

152 between tree competition. To adjust the data for this, we constructed a competition
153 index for the mother trees (Competition).

154 The original competition index is defined as follows [Hegy, 1974]:

155

$$156 \quad CI_i = \sum_{j=i}^n \left[\frac{DBH_j / DBH_i}{R_{ij}^2} \right]$$

157

158 where DBH_j is the diameter at breast height at 1.3 m of j th neighbour tree,
159 DBH_i is the diameter at breast height at 1.3 m of subject tree i , R_{ij} is the linear
160 distance between i th subject tree and the j th neighbour tree. Since in this study, we
161 only had the information of whether the DBH of the tree standing beside is larger
162 or smaller than the subject tree, we set the ratio of DBH (nominator of this fraction)
163 to be 0.5 if DBH of neighbour tree was smaller than subject tree; 1.5 if DBH of
164 neighbour tree larger than subject tree and 1 if they had same DBH. Once the index
165 was produced, it was used as a fixed effect for adjusting density, MFA and MOE.

166 Correlation and heritability estimates from un-adjusted and adjusted datasets
167 are presented in Figure 2 and Figure 3, respectively. Data adjustment contributed
168 little to the improvement of MOE estimates. For density, outlier removal resulted
169 in the highest improvement, followed by adjustment for competition. For MFA,
170 use of un-adjusted data provided the highest correlation and heritability, and outlier
171 removal the lowest. Further heritability estimates were based only on data adjusted
172 for competition.

173 **Breeding value (BV) of mothers based on progeny tests** A linear mixed model
174 used for the estimation of parental BV and variance components can be expressed
175 in matrix form as:

176

$$177 \quad y = Xb + Zu + e$$

178

179 where y is a vector of measured data, b is a vector of fixed effects with its design
180 matrix X , u is a vector of random effects with its design matrix Z , e is a vector
181 of residuals. Fixed and random effect solutions are obtained by solving the mixed
182 model equation [White and Hodeg, 1989]:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + I\alpha \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

183 where b is the fixed effects including site, block within site and provenance, u is the
184 random effect which is the family. I is the identity matrix with dimensions equal
185 to the number of mothers, α is a ratio of residual variance and genetic variance
186 explained by the random family effect.

187 **Pearson correlation**

188 For the Silviscan data, Pearson correlation was calculated between the mother tree
189 BVs estimated from progeny trials and the mother tree phenotypic data from the
190 archive. For Pilodyn and Velocity, Pearson correlation was calculated between
191 mother tree BVs estimated from progeny trials and the mean phenotypic value of
192 mother trees. For indirect measurements the mean phenotypic value of mother trees
193 based on data from one and three ramets, and the Silviscan data based on only one
194 ramet sampled.

195 **Population heritability**

196 As stated above, two methods for calculating heritability were compared. The first
197 one is based on parental-offspring regression. We use linear regression to model the
198 mother-offspring pairs for each trait value:

199

$$Y = \beta_0 + \beta_1 X$$

201

202 where Y is the phenotype value for the offspring and X is the phenotype value
203 for a mother. Since genetic covariance between parents and offspring is equal to
204 $\frac{1}{2}\sigma_A^2$ [Falconer and Mackay, 1996], we can get

205

$$\beta_1 = \frac{Cov(X,Y)}{VarX} = \frac{\frac{1}{2}\sigma_A^2}{\sigma_P^2}$$

207

208 The individual tree narrow-sense heritability is

209

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

211

212 So from the slope of the regression, the estimation of the h^2 can be obtained
213 from

214

$$\hat{h}^2 = 2\hat{\beta}_1$$

216

217 This way, the parent-offspring based heritability was computed for SilviScan
218 data and standing tree data for Pilodyn, Hitman velocity and estimated MOE.

219 The second method is one based on half-sib family progeny analysis where
220 $h^2=4*\text{variance between families/variance of phenotype}$. In our study, the heritabil-
221 ities were calculated for each cambial age (ring number) from the area-weighted
222 averages representing stem cross-sections.

223 **Progeny size effect on heritability**

224 In order to investigate how many progenies are needed when using parent-offspring
 225 regression for heritability estimation with multiple (one to three) ramets of the
 226 mother trees, we used a subset of progeny trees where each family had exactly six
 227 progenies in each of the two trails. Thus, in total, 180 families and 2160 progeny
 228 trees were included in the analysis. From this subset, one to six progenies were ran-
 229 domly selected per family, with site and heritability being estimated using parent-
 230 offspring regression. The process was bootstrapped 500 times, the means and stan-
 231 dard errors of the heritability were then estimated for comparison.

232

233 **Results**

234 **Phenotypic-breeding value (BV) correlation**

235 The averages of SilviScan data across rings of same number of trees and families for
 236 the clonal archive and progeny tests, respectively, were plotted versus ring number
 237 in Figure 1 for comparison. In the progeny trials, the ring widths increased in the
 238 rings closest to the pith, reaching 5 (mm) in ring 3. Then it decreased to stabilize
 239 at 2 mm (ring 10), when wood density started to increase from a previously rather
 240 stable level. Such patterns are expected as reactions to increasing competition. Ad-
 241 versely, in the archive, the ring width increased and wood density decreased steadily
 242 across the first 10 rings, after which they turned to show changes in opposite direc-
 243 tions, patterns which are expected as reactions to successively reduced competition.
 244 For MFA and MOE, the curves representing archives and trials show similar char-
 245 acters, respectively.

246 The correlations between BVs estimated from progeny and phenotypic values

per ring for mother tree are presented in Figure 2. For density and MOE, correlations increased with annual rings (i.e., higher correlations at the outer most rings) for the un-adjusted, as well as, for the competition adjusted and outlier removal data. However, the last two or three annual rings experienced a decrease in correlation values. Competition adjustment and outlier removal resulted in increased correlations for density and MOE for the majority of rings. When using un-adjusted density data, the correlations increased steadily with ring number from 0.03 to 0.40, after competition adjustment the maximum correlation reached 0.43, and after outlier removal it reached 0.47. In the case of MOE, correlations using un-adjusted data increased from 0.06 to 0.25 at ring 6. It continued to increase marginally to 0.26 at ring 14, after which it decreased in the outermost rings. Competition adjustment and outlier removal followed similar patterns and reached maximum correlations of 0.27 and 0.28, respectively. In the case of MFA, correlations decrease after annual ring 6. Both adjustment and outlier removal caused correlation decrease for all rings. Correlations for the un-adjusted MFA data ranged from 0.18 reached at ring 6 to 0.05 in the outermost ring. After competition adjustment and outlier removal the highest correlation reached were 0.17 and 0.16, respectively. While the lowest correlation dropped to minimum values of 0.02 and 0.05, .

The estimated correlations between BV of progeny and phenotypic value of mother tree were 0.29, 0.13 and 0.23 for Pilodyn, Velocity and MOE(ind), respectively. When using three ramets of the mother trees, the correlation increased to 0.32, 0.15 and 0.28, respectively.

Heritability

Heritability estimations for stem cross-sections at each age (ring number) are presented in Figure 3 on SilviScan data and one single ramet from the archive. For density, they increase steadily from low level up to 0.32 at age 15 years. Whilst

when using un-adjusted data, it increased to 0.36 and 0.37 with the competition adjusted and outlier removed data, respectively. For MOE all types of data provide similar graphs, increase from low level to roughly ring 6, then marginal increases to 0.21 for un-adjusted data and 0.23 for the two adjusted types at ring 15. For MFA, heritabilities using all types of data ranged across all rings between 0.07 and 0.13 with maximum values of 0.13 at ring 6 for all alternatives. This was followed by a slow decline towards the same minimum value at ring 15, during which the outlier removed graph showed a somewhat lower path. Thus, the data adjustments had clear positive effects on heritability only for wood density, with 13% for competition adjustment and 16% for outlier removal from a level of 0.32. For MOE they gave slight improvements from the level of about 0.20, while no benefits were obtained from these types of data adjustments for MFA.

Heritability estimations of the whole stem cross-sections based on progeny data and parent-offspring regression are presented in Table 1. Heritability estimates based on parent-offspring regression were higher for density (0.35), MFA (0.15) and MOE (0.28) measured with Silviscan compared to use of the indirect methods and phenotyping of only one ramet from the archive: Pilodyn (0.27), Velocity (0.13) and MOE(ind) (0.13), although not significantly if considering the standard errors. However, when indirect measurement data from three ramets of the parent were analysed they gave higher estimates for all three wood quality traits (0.41, 0.19 and 0.30) than use of SilviScan data and only one ramet. Heritability estimates based on half-sib progeny correlation were higher for all three wood properties (0.43, 0.29, 0.38) than parent-offspring heritability based on a single ramet data using Silviscan, and also higher than indirect measurement methods (0.31, 0.20, 0.28) in half-sib progeny. However, heritability estimates based on half-sib progeny correlation were similar to the heritability estimates based on the parent-offspring regression of indirect method using three ramets of the parent for all three wood properties.

300 The repeatabilities of Pilodyn, Velocity and MOE(ind) of mother trees were 0.52,
301 0.30 and 0.45, respectively, which were higher than progeny-offspring and half-sib
302 progeny heritability estimates based on both Silviscan traits and indirect traits

303 **Effect of progeny size on parent-offspring heritability estimate** 304 **and standard error**

305 The most prominent consequence of increasing the progeny size is the decrease in
306 the standard errors (i.e., more precise estimation of heritability) (Figure 4). When a
307 progeny size four was selected, heritability stabilizes for MOE, whereas it decreases
308 for Velocity and reaches a maximum value at progeny size 6 for the Pilodyn trait.
309 The mean heritabilities of Velocity, Pilodyn and MOE(ind) are in the range of 0.26
310 to 0.28, 0.56 to 0.59 and 0.32 to 0.34 respectively.

311 **Discussion**

312 **Low to moderate correlation between clonal archives and progeny** 313 **tests**

314 In operational breeding, selection of clones for crossings to the next generation
315 (backward selection) is usually conducted through evaluation of their half-sib or
316 full-sib progenies grown in common-garden experiments, so called progeny trials.
317 This is a method that involves multiple actions such as crossing (in case of full-sib
318 progenies), seedling production, seedling establishment (often in multiple sites),
319 and assessment and evaluation of multiple tree properties. The high demand in
320 time and costs of such a process motivated the first question of this study: could
321 the mothers be ranked based on tree properties assessment directly on the trees of
322 the mother clone/genotype from the clonal archives? To answer this question, we

323 estimated solid wood properties, known to be highly heritable and little G x E, in
324 524 mother clones in a clonal archive and in their half-sib progenies established in
325 two test sites.

326 Our study reveals a low to moderate correlation between the phenotypic values
327 assessed directly in the mother trees and the breeding values (BV) estimated on
328 their half-sib progenies. This result is similar with use of both the Silviscan and
329 the indirect measurements. Among the three solid wood properties, wood density
330 had a moderate correlation between parent and progeny except at young ages, and
331 unstable at the highest cambial age. The correlation reached above 0.4, on use of un-
332 adjusted data at cambial age 13, for competition adjusted data at ring 11, and when
333 outliers were removed at ring 7. MFA/Acoustic Velocity had the lowest correla-
334 tion, with no age reaching higher than 0.19. MOE showed intermediate correlation,
335 reaching above 0.2 after age 4, and for this trait, adjustment by outlier removal or
336 competition index brought little improvement to the estimates. Despite the high
337 heritability of these solid wood properties [Hannrup et al., 2004, Steffenrem et al.,
338 2009], it cannot be ruled out that the management activities, such as grafting, top-
339 ping and thinning, may have affected the correlation between mother parent and
340 progenies. However, the low and moderate correlation between parent and proge-
341 nies did not affect greatly the estimates of heritabilities compared to estimates from
342 progenies only.

343 The heritability estimates for density, MFA and MOE obtained in our study, us-
344 ing the tested approach based on SilviScan data from only one single ramet from the
345 archive was lower than previous reported for wood density and MFA in white spruce
346 (0.65, 0.36 and 0.29; [Lamara et al., 2016], Scots pine (0.40, 0.39 and 0.30; [Hong
347 et al., 2015] and lodgepole pine (0.48, 0.31, 0.21; [Hayatgheibi et al., 2017]. If the
348 SilviScan data was replaced with data from the indirect methods, the heritabilities
349 decreased. However, if use of the indirect methods was combined with an increase

of up to three ramets from the archive, the heritabilities of pilodyn was higher and comparable with such reported for Scots pine, but lower than the values observed for white spruce and lodgepole pine. Under these conditions, the heritability for MOE(ind), was close to that for white spruce and Scots pine, but higher than the values for lodgepole pine. For velocity, the heritability was lower than in all those previous studies. Thus, it is reasonable to believe that the heritability had been higher and become comparable with other species if we had SilvScan data for more ramets. We also estimated relatively high clonal repeatability for Pilodyn (0.52) and MOE(ind) (0.45), which are higher than the narrow sense heritability. Both non-additive genetic variation and imperfect experimental design in the archive may have contributed to such higher clonal heritability.

Heritability estimates improve with number of ramets and progeny size

In conifers, narrow-sense heritability is often based on half-sib progeny correlations. As an alternative, narrow-sense heritability can be computed from parent-offspring regression [Falconer and Mackay, 1996]. This approach has been commonly used in crops [Casler, 1982, Fernandez and J. C. Miller, 1985, Vogel et al., 1980]. More recently, it has also been applied for wood quality traits (wood density and spiral grain) in Norway spruce [Steffenrem et al., 2016]. The author reported similar heritabilities and standard errors for both methods of narrow-sense heritability computing, parent-offspring regression and progeny data. This is in line with results mentioned in simulation studies on wild populations of both binary and continuous traits [de Villemereuil et al., 2013], and on real data using eight morphological traits of a natural population of the great reed warbler (*Acrocephalus arundinaceus*) [kesson et al., 2008]. In our study, Silvscan-based narrow-sense her-

375 itabilities based on progeny were higher, but comparable to results based on parent-
 376 progeny regression using the indirect method, where data for all three ramets of the
 377 mother trees was available. Thus, we can conclude that the highest values of narrow-
 378 sense heritability estimates were obtained for the parent-offspring regression, as far
 379 as data from at least three ramets is involved. Therefore, in agreement with Steffen-
 380 rem et al (2016), also we conclude that parent-offspring regression results in higher
 381 values of heritability. We observed that increasing progeny size increases preci-
 382 sion of the heritability estimates (i.e., lower standard errors). Moreover, increas-
 383 ing progeny size has its major impact in the transition from two to four progenies,
 384 whereas further increases do not result in a clear increase in the heritability values.

385 Conclusion

386 Our study resulted in the following conclusions:

- 387 • The correlations between the phenotypic values of the mother trees and the
 388 breeding values estimated on their half-sib progenies are low to moderate.
 389 Reasons for this may be management practices and lack of experimental de-
 390 sign in archives, contributing to the parent and progeny correlation.
- 391 • Offspring progeny heritability estimates based on SilviScan measurements
 392 were higher than parent-offspring regression using a single ramet from the
 393 archive. Both these approaches resulted in higher heritabilities than when
 394 traits had been determined with more efficient indirect measurements using
 395 Pilodyn and acoustic Hitman on the standing trees.
- 396 • When three ramets per plus tree were measured using Pilodyn and Hitman,
 397 the parent-offspring regression heritability estimates were higher than those
 398 based solely on progeny data.

399 • The influence of progeny size used was studied for the latter approach. The
400 standard error of the heritability estimates decreased with increasing progeny
401 size, and stabilised at four progenies for the heritabilities of all traits investi-
402 gated. Parent-offspring regression could thus be used to estimate heritabilities
403 using clonal archive parent for the investigated solid wood properties. Three
404 ramets and four progenies of each parent were sufficient for reaching the same
405 heritability levels as with more extensive analyses of progeny trials.

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573 Tables and Figures

Table 1: Heritability and repeatability estimates based on measurements of wood density, MFA and MOE with SilviScan from increment cores: area-weighted averages representing the cross-section of the stem at different cambial ages (ring numbers), density, MFA, MOE), and based on indirect measurements on standing trees of their proxies with Pilodyn and Hitman (velocity), from which also MOE(ind) was estimated. For comparison, all these heritability estimates were based only on the 162 families for which data on three ramets from the archive is available.

Methods	SilviScan			Indirect methods		
	Density	MFA	MOE	Pilodyn	Velocity	MOE _{ind}
Parent-offspring regression_1 ramet	0.35 (±0.16)	0.15(±0.16)	0.28(±0.16)	0.27 (±0.15)	0.13 (±0.15)	0.13 (±0.15)
Parent-offspring regression_3ramets	N/A	N/A	N/A	0.41 (±0.15)	0.29 (±0.15)	0.30 (±0.15)
Half-sib correlation (offspring only)	0.43 (±0.09)	0.29 (±0.08)	0.38 (±0.08)	0.31 (±0.08)	0.20 (±0.08)	0.28 (±0.08)
Repeatability	N/A	N/A	N/A	0.52 (±0.06)	0.30 (±0.04)	0.45 (±0.05)

Figure 1: Mean values for all rings of same cambial age (ring number) across all progeny trees of all families, and across all mother trees in the archive, respectively, measured with SilviScan and plotted versus ring number for ring width, density, MFA, and MOE.

Figure 2: Correlations between BVs and phenotypic values of archive mother trees for area-weighted averages calculated from SilviScan data to represent the stem cross-sections at each cambial age (ring number), using three types of data: 1) unadjusted, 2) after competition adjustment and 3) with outliers removed, for density (A), MFA (B) and MOE (C).

Figure 3: Heritability estimates using parents-offspring regression of area-weight data for area-weighted averages calculated from SilviScan data to represent the stem cross-sections at each cambial age (ring number), and using three types of data: 1) un-adjusted, 2) after competition adjustment and 3) with outliers removed for density (A), MFA (B) and MOE (C).

Figure 4: Heritability estimation based on different number of progenies for each mother and estimated by parent-offspring regression for Pilodyn, Velocity and MOE(ind). The number of ramets per mother clone varied among plus trees from one to three.