

1 **Genetic control of transition from juvenile to mature wood with respect to**
2 **microfibril angle (MFA) in Norway spruce (*Picea abies*) and lodgepole pine**
3 **(*Pinus contorta*)**

4 Haleh Hayatgheibi¹, Nils Forsberg¹, Sven-Olof Lundqvist², Tommy Mörling³, Ewa J.
5 Mellerowicz¹, Bo Karlsson⁴, Harry Wu¹, M Rosario García Gil¹

6 ¹ Department of Forest Genetics and Plant Physiology, SLU, Umeå, Sweden

7 ^{2a} IIC, Stockholm, Sweden

8 ^{2b} Innventia, now RISE Bioeconomy, Stockholm, Sweden

9 ³ Department of Forest Ecology and Management, SLU, Umeå, Sweden

10 4 Ekebo 268 90 Svalöv

11

12

13 Corresponding author: M Rosario García Gil, m.rosario.garcia@slu.se

14

15 **Abstract**

16 Genetic control of microfibril angle (MFA) transition from juvenile to mature was evaluated
17 in Norway spruce and lodgepole pine. Increment cores were collected at breast height from
18 5,618 trees in two 21-year-old Norway spruce progeny trials in southern Sweden, and from
19 823 trees in two 34-35 – year-old lodgepole pine progeny trials in northern Sweden. Radial
20 variations in MFA from pith to bark were measured for each core using SilviScan. To estimate
21 MFA transition from juvenile to mature, a threshold level of MFA 20° was considered and six
22 different regression functions were fitted to the MFA profile of each tree after exclusion of
23 outliers, following three steps. The narrow-sense heritability estimates (h^2) obtained for MFA
24 transition were highest based on the slope function, ranging from 0.21 to 0.23 for Norway
25 spruce and from 0.34 to 0.53 for lodgepole pine, while h^2 were mostly non-significant based
26 on the logistic function, under all exclusion methods. Results of this study indicate that it is
27 possible to select for an earlier MFA transition from juvenile to mature in Norway spruce and
28 lodgepole pine selective breeding programs, as the genetic gains (Δ_G) obtained in direct
29 selection of this trait were very high in both species.

30

31 **Introduction**

32 Wood properties have become an important focus in advanced tree breeding programs, along
33 with growth, vitality and form traits (Bouffier et al. 2009; Isik et al. 2008). The variability in
34 wood properties within a tree is very large (Larson 1967), owing to the within-ring
35 differences, the changes along a radius from pith to bark, and the differences associated with
36 different heights in the tree (Zobel and Van Buijtenen 1989).

37 Differences between juvenile and mature wood are the major sources of variation in wood
38 quality, both among and within trees (Zobel and Sprague, 1998). Such differences occur in
39 various wood characteristics, including specific gravity, mechanical properties (Bendtsen and
40 Senft, 1984), cell length (Shiokura, 1982, Yang et al., 1986), and pulp yields (Zobel and
41 Sprague, 1998).

42 The usual pattern for conifers is that wood density and MOE increase and MFA decreases as
43 trees become older (Dungey et al. 2006). As such, juvenile wood is mostly undesirable due to
44 its low density, low strength, high content of compression wood, high cellulose microfibril
45 angle (MFA, the angle between the prevailing cellulose orientation and the long cell axis),
46 low crystallinity and general high variability, as compared to mature wood (Barnett and
47 Jeronimidis 2009; Mellerowicz et al., 2001; Zobel and van Buijtenen 1989).

48 MFA, is one of the key determinants of solid-wood quality due to its strong influence on the
49 stiffness, strength, shrinkage properties and dimensional stability of structural lumber
50 (Bendtsen and Senft 2007; Cave and Walker 1994). Several studies in conifers have shown
51 that very large angles of MFA (about 45°) are common in the first 5 to 10 growth rings near
52 the pith and MFA values decline gradually until they stabilize towards the bark (Zobel and
53 Jett 1995). Furthermore, it has been shown that in conifers, the average MFA of the S2 layer
54 lies between 5°- 20° in mature wood (BOWYER and SHMULSKY 2007; Donaldson 2008).

55 The radial pith-to-bark variation of MFA is also altered by other environmental factors,
56 whereby MFA values increase in compression wood, decrease in tension wood, and mostly
57 increase following fertilization and thinning (Donaldson 2008).

58 In recent decades, most forest industries moved their attention towards usage of fast-growing
59 tree plantations (Gräns et al. 2009), which implies that trees are harvested at younger ages
60 than before and subsequently have greater proportion of juvenile wood (Larson 2001; Zobel
61 and Van Buijtenen 1989). However, the negative impact of using fast-growing plantations can
62 be reduced by changing the proportion of juvenile wood through breeding (Abdel-Gadir and
63 Krahmer 1993; Gapare et al. 2006; Zobel and Jett 1995). In addition to selecting for trees with
64 improved juvenile wood, it is also possible to select for an earlier transition from juvenile to
65 mature wood in breeding programs (Gapare et al. 2006).

66 Transition from juvenile to mature wood usually occurs over two to five growth rings,
67 depending on the wood property (Alteyrac et al. 2006; Mutz et al. 2004). The point at which
68 this transition occurs is of great importance for forest managers and tree breeders as it
69 determines the quality and value of end-use products. However, it is difficult to estimate this
70 boundary with adequate reliability as there is usually no clear demarcation line between
71 juvenile wood and mature wood in a tree stem (Mutz et al. 2004; Zobel and Sprague 1998).

72 The distinction between juvenile wood and mature wood has mostly been determined by
73 analyzing trends of radial variation (from pith to bark) for different wood properties such as
74 density (Alteyrac et al. 2006; Mansfield et al. 2007), MOE (Wang and Stewart 2013), fiber
75 length, and MFA (Bhat et al. 2001; Mansfield et al. 2009; Wang and Stewart 2012). This
76 method is so-called threshold or graphic method whereby plots of each wood property are
77 visually evaluated to locate a ring number or cambial age when the property reaches the
78 threshold value for mature wood (Clark et al. 2007). An alternative approach is to use
79 mathematical methods such as segmented regression (Abdel-Gadir and Krahmer 1993;

80 Gapare et al. 2006; Szymanski and Tauer 1991) and segmented non-linear models (Alteyrac
81 et al. 2006; Koubaa et al. 2007; Mutz et al. 2004).

82 It is well recognized that the proportion of juvenile wood and timing of transition in a tree is
83 influenced by both genetic and environmental factors (Abdel-Gadir and Krahmer 1993;
84 Mansfield et al. 2007). For instance, high heritabilities have been reported for age of transition
85 and juvenile-wood proportion in loblolly pine (*Pinus taeda* L.) specific gravity and tracheid
86 length (Loo et al. 1985; Stonecypher and Zobel 1966). Similarly, genetic control of time of
87 transition has been reported to be high in slash pine (*Pinus elliottii* Engelm.) (Hodge and
88 Purnell 1993).

89 The genetic control of MFA as a function of cambial age in two progeny trials of Norway
90 spruce (*Picea abies* L.) (Chen et al. 2014) and two progeny trials of lodgepole pine (*Pinus*
91 *contorta* Dougl.) (Hayatgheibi et al. 2017) have been recently investigated in Sweden.
92 Estimated heritabilities fluctuated near the pith and then stabilized after the cambial age of 10
93 years in both species (Chen et al. 2014; Hayatgheibi et al. 2017). However, genetic control of
94 MFA transition from juvenile to mature was not considered in those studies. The main
95 objective of this study was therefore to quantify genetic variation of transition between
96 juvenile and mature MFA based on application of different regression functions in these
97 species, using similar progeny trials to those used by Chen et al. (2014) and Hayatgheibi et al.
98 (2017).

99

100 **Material and Methods**

101 **Study materials and trial design**

102 This study utilized data from two large open-pollinated progeny trials of Norway spruce,
103 located in southern Sweden, and two genetically unrelated open-pollinated progeny trials of
104 lodgepole pine, located in northern Sweden (Table 1). Trials of Norway spruce, S21F9021146

105 aka F1146 (trial 1) and S21F9021147 aka F1147 (trial 2), comprised of 1,373 and 1,375 half-
106 sib families, respectively, were established in 1990. Both trials were planted as randomized
107 incomplete blocks with single-tree plots at spacing of 1.4×1.4 m. A set of 524 families
108 within 112 sampling provenances were selected for this study. More detailed information
109 about trial characteristics can be found in (Chen et al. 2014).

110 Furthermore, two trials of lodgepole pine, Övra (Skogforsk S23F8060373) with 178 families,
111 and Lagfors with 214 families (Skogforsk S23F7960), were established in 1980 and 1979,
112 respectively. These families at both trials were planted in a randomized complete block (RCB)
113 design. Each family was represented by 10 trees planted in a row with five replicates (blocks),
114 resulting in 50 planted trees per family. Tree spacing was 2 m between rows and 1.5 m within
115 rows. More details about trials characteristics have been further described in (Hayatgheibi et
116 al. 2017).

117 **Sampling and SilviScan measurement**

118 Increment cores (12-mm in diameter) were collected at breast height (1.3 m) from a total of
119 5618 Norway spruce, aged 21 years, and 823 lodgepole pine trees, aged 34-35 years, and
120 assessed by a SilviScan instrument (Innventia, now part of RISE, Stockholm, Sweden).
121 Before the SilviScan measurement, each increment core was sawn into a 7 mm high \times 2 mm
122 thick radial strip from the pith to the bark. The SilviScan system combines image analysis
123 with X-ray absorption and X-ray diffraction to determine high-resolution pith-to-bark radial
124 variations for several important wood properties, including wood density, MFA and MOE
125 (Evans 2006; Evans and Ilic 2001). The variations in MFA from pith to bark of each core was
126 measured as averages across consecutive 2 mm wide intervals. The annual rings were
127 identified from the corresponding variations in wood density, and the average MFA for all
128 rings were calculated. The number of annual rings ranged from 6 to 19 for Norway spruce and
129 from 20 to 32 for lodgepole pine.

130 **Model fitting and determination of MFA transition**

131 **Data exclusion**

132 The radial patterns for MFA of all 5618 Norway spruce and 823 lodgepole pine individual
133 trees were plotted against the cambial age. However, there were some individuals for which
134 the general MFA decreasing trend from pith to the bark had been changed, due to some
135 disturbances such as compression wood. Therefore, such outliers were identified and excluded
136 prior to data analysis. Following removal of such outliers, the remaining Norway spruce and
137 lodgepole pine individuals having fewer than 12 and 20 annual rings, respectively, were also
138 excluded from data analysis. The three applied exclusion methods are as follows:

139 1) Exclusion_1 or basic method: exclusion of those individuals for which MFA values
140 increased with cambial age (abnormal curves). This was the baseline of data treatment and
141 thus the first step of exclusion methods 2 and 3. This first exclusion step resulted in exclusion
142 of about 2.8 % and 5.1 % of Norway spruce (Höreda and Erikstorp, respectively) and 0.2 %
143 and 1.7 % of lodgepole pine individuals (Lagfors and Övra, respectively)

144 2) Exclusion_2 or shape-based method: following the baseline method, annual rings of the
145 individuals for which average MFA values were greater than their three previous rings
146 average MFA, were removed. Based on this method, about 480 and 959 annual rings in
147 Norway spruce (Höreda and Erikstorp, respectively) and about 613 and 398 annual rings in
148 lodgepole pine (Lagfors and Övra, respectively) were removed. This resulted in removal of
149 about 4.0 % and 7.5 % of Norway spruce (Höreda and Erikstorp, respectively) and 0.9 % and
150 7.3 % of lodgepole pine individuals (Lagfors and Övra, respectively).

151 3) Exclusion_3 or family-based method: the data after exclusion with the baseline method
152 were exposed to another method of data exclusion. Annual rings, which had average MFA
153 values deviating from their corresponding family-mean MFA values by more than $1.96 \times SD$,
154 were excluded from data analysis. Based on this method, about 838 and 665 annual rings in

155 Norway spruce (Höreda and Erikstorp, respectively) and about 177 and 159 annual rings in
156 lodgepole pine (Lagfors and Övra, respectively) were removed. This method resulted in the
157 removal of about 3.4 % and 5.2 % of Norway spruce (Höreda and Erikstorp, respectively) and
158 0.2 % and 1.5 % of lodgepole pine individuals (Lagfors and Övra, respectively).

159 **Regression functions and MFA transition**

160 After removal of outliers, six different regression functions were fitted to the pith-to-bark
161 MFA profiles of the individual trees. A threshold value of 20° was considered for MFA and
162 when the parameter of the fitted functions fell below the threshold, the estimated parameter
163 was defined as MFA transition.

164 All data analysis was carried out using the R statistical programming environment (R
165 Development Core).

166 The fitted models were as follow:

167 1. *Slope function*

$$Y_i = \beta_0 + \beta_1 CA + \varepsilon_i$$

168 where β_0 is the intercept and β_1 is the slope. In all equations, Y_i is the MFA value of the tree i
169 , CA is the cambial age, and ε_i is the random error.

170 2. *Logistic function*

$$171 Y_i = \beta_0 + \frac{\beta_1 - \beta_0}{1 + e^{\beta_3(\beta_2 - CA)}} + \varepsilon_i$$

172 where β_0 is the upper asymptote MFA, β_1 is the lower asymptote MFA, β_2 is the inflection
173 point, and β_3 is the sharpness.

174 3. *Central peak*

$$Y_i = \frac{\beta_0}{1 + \beta_1 \times CA^2} + \beta_2 + \varepsilon_i$$

175 where $\beta_0 + \beta_2$ is the upper asymptote MFA, $\sqrt{\frac{1}{\beta_1}}$ is the inflection point, and β_2 is the lower
176 asymptote MFA.

177 4. *Polynomial*

178 The radial profile of MFA from each tree was plotted with respect to cambial age and fitted
179 with a third-order polynomial regression as below:

$$Y_i = \beta_0 + \beta_1 CA + \beta_2 CA^2 + \beta_3 CA^3 + \varepsilon_i$$

180 5. *Arctangent*

$$Y_i = \frac{\beta_0 + \beta_1}{2} + \frac{(\beta_0 - \beta_1) \times \arctan((\beta_2 - CA) \times \beta_3)}{\pi} + \varepsilon_i$$

181 where β_0 is the upper asymptote MFA, β_1 is the lower asymptote MFA, β_2 is the inflection
182 point, and β_3 is the slope.

183 6. *Negative exponential*

$$Y_i = (\beta_0 - \beta_1) \times e^{(-\beta_2 \times CA)} + \beta_1 + \varepsilon_i$$

184 where β_0 is the MFA at cambial age zero, β_1 is the lower asymptote MFA, and β_2 is the slope
185 at cambial age zero.

186 **Genetic analysis**

187 Variance components for genetic analysis were estimated using ASReml 3.0 (Gilmour et al.
188 2009) based on linear mixed-effects model using joint-site analysis for Norway spruce and
189 single-site analysis for lodgepole pine as follows:

190 Norway spruce $y_{ijklm} = \mu + S_i + B_{j(i)} + P_k + F_{l(k)} + SF_{il(k)} + e_{ijklm}$

191 where y_{ijklm} is the observation on the m th tree from the l th family within the k th provenance
192 in the j th block within the i th site. μ is the overall mean; S_i is the fixed effect of the i th
193 site; $B_{j(i)}$ is the fixed effect of the j th block within the i th site; P_k is the fixed effect of the k th
194 provenance; $F_{l(k)}$ is the random effect of the l th family within the k th provenance; $SF_{il(k)}$ is
195 the random interaction effect of the i th site and the l th family within the k th provenance; and
196 e_{ijklm} is the random residual effect.

197 Lodgepole pine $y_{jklm} = \mu + P_k + B_j + F_{l(k)} + BF_{jl(k)} + e_{jklm}$

198 where y_{jklm} is the vector of observation on the m th tree from the l th family within the k th
199 provenance in the j th block. μ is the overall mean; P_k and B_j are the fixed effects of the k th
200 provenance and the j th block, respectively; $F_{l(k)}$ is the random effect of the l th family within
201 the k th provenance; $BF_{jl(k)}$ is the random interactive effect of the j th block and the l th family
202 within the k th provenance and e_{jklm} is the random residual effect.

203 Estimates of heritability were obtained using variance components from the univariate joint-
204 site (for Norway spruce) and single-site (for lodgepole pine) analysis. Approximate standard
205 errors were estimated using the Taylor series expansion method (Gilmour et al. 2009).
206 Individual-tree narrow-sense heritability (h_i^2) for MFA of each mathematical model was
207 calculated using the following equations assuming these open-pollinated family are half-sib
208 families (Falconer and Mackay 1996):

209 Norway spruce $h_i^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{sf}^2 + \hat{\sigma}_e^2}$

210 Lodgepole pine $h_i^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{bf}^2 + \hat{\sigma}_e^2}$

211 where $\hat{\sigma}_A^2$ is the additive genetic variance; $\hat{\sigma}_f^2$ is among family variance; $\hat{\sigma}_{sf}^2$ is the site by
212 family variance; $\hat{\sigma}_{bf}^2$ is the family by block variance; and $\hat{\sigma}_e^2$ is the residual variance.

213 Pooled-site analysis genetic gain (ΔG_t), expressed as percentage in direct selection of MFA
214 transition-age was estimated as:

215
$$\Delta G_t = i \times h_t^2 \times CV_t$$

216 where i is the selection intensity of 1% ($i=2.67$), h_t^2 is the narrow-sense heritability of MFA
217 transition and CV is the coefficient of variation of the phenotypic effect (calculated as the
218 phenotypic standard deviation divided by the mean of the trait).

219 **Results**

220 **MFA transition and model fitting in Norway spruce and lodgepole pine**

221 **MFA radial variation**

222 For both species, the MFA average profiles decreased from high values close to the pith
223 towards stable levels close to the bark (Fig. 1). In Norway spruce, mean MFA profile
224 decreased from about 30° at the pith and then stabilized after reaching a cambial age of 10
225 years at about 10° in Höreda and about 12° in Erikstorp. The mean MFA profile for lodgepole
226 pine started at 40° followed by a rapid decrease to about 30° after 3 years, after which the
227 shape of the development was similar to that for Norway spruce but slower, stabilizing after
228 cambial age of 15 years at about 12° in Övra and about 10° in Lagfors.

229 **Model fitting and MFA transition**

230 For each fitted regression function, different threshold values were tested to define the best
231 model fit for individual trees transition from juvenile to mature MFA. Although the threshold
232 value of 20° gave the best model fit, there were still some individuals for which the MFA
233 profile never passed the threshold, thus, they remained constantly above or below the
234 threshold. Figures 2 to 5 show the proportion of Norway spruce and lodgepole pine
235 individuals for which the MFA transition was estimated based on the applied six different
236 regression functions, under the threshold of 20°.

237 **Heritability estimates**

238 Narrow-sense heritability estimates were obtained for combined-site Norway spruce and
239 single-site lodgepole pine MFA transition.

240 **Norway spruce**

241 Estimated heritabilities were mostly stable following data exclusions. However, heritabilities
242 were slightly higher after shape-based exclusion (exclusion_2), while they were slightly lower
243 after the family-based exclusion (exclusion_3), particularly for arctangent, polynomial and
244 negative-exponential functions (Table 1). In general, h^2 ranged from 0.08 to 0.23 with the
245 highest estimate obtained based on the slope function and the lowest estimate obtained based
246 on the logistic function, under all exclusion methods.

247 **Lodgepole pine**

248 In general, h^2 estimates observed for lodgepole pine were higher than those for Norway
249 spruce (Table 1). Heritabilities in Övra increased significantly after exclusion_2 and
250 exclusion_3, particularly after exclusion_2, while they slightly decreased after exclusion_3 in
251 Lagfors. As similarly observed for Norway spruce, heritability estimates were lowest based
252 on the logistic function, while they were highest based on the slope function. In general,
253 heritabilities ranged from 0.15 to 0.53 in Övra and from 0.22 to 0.43 in Lagfors (logistic
254 function was excluded). In addition to the slope function, high heritabilities obtained based on
255 the central peak (ranging from 0.33 to 0.38) and negative exponential functions (ranging from
256 0.26 to 0.34) in Övra, and based on the arctangent (ranging from 0.41 to 0.43) and polynomial
257 (ranging from 0.36 to 0.38) in Lagfors.

258 **Genetic gain**

259 As was observed for heritability estimates, genetic gains obtained based on the slope function
260 were highest, while those obtained based on the logistic function were lowest, regardless of
261 which exclusion method was applied (Table 2). High genetic gains were also obtained based
262 on the negative-exponential function for both species when using exclusion-1. Similarly,
263 application of exclusion-2 and exclusion-3 led to high genetic gains when MFA was modelled

264 by negative-exponential and central peak functions in Norway spruce and by arctangent and
265 negative-exponential functions in lodgepole pine (Table 2).

266 **Discussion and conclusion**

267 Several investigations in various conifers have determined the age for MFA transition from
268 juvenile to mature, using different linear and non-linear models (Clark et al. 2007; Mansfield
269 et al. 2009; Wang and Stewart 2012). However, no study to date has examined genetic
270 variation of MFA transition and its possible genetic gain based on employing different
271 regression functions. Few studies have investigated the genetic control of transition age in fast
272 growing pines (Gapare et al. 2006). As such, a family heritability estimate of 0.36 and
273 moderate genetic gains in selection of early age of transition for specific gravity in loblolly
274 pine has been reported (Loo et al. 1985). Similarly, moderate genetic gains were reported for
275 latewood density transition age in radiata pine (*Pinus radiata* D. Don) (Gapare et al. 2006).

276 One of the central goals in forest tree breeding is to reduce costs and time of breeding cycles
277 by making genetic gains as early as possible. Additionally, due to the increased demand in
278 fast-grown plantations, which contain more juvenile wood, it is of vital importance to breed
279 for more uniform wood, or a wood with lower proportion of juvenile wood.

280 Therefore, the main focus of this study was to evaluate the degree of genetic control in MFA
281 transition from juvenile to mature in Norway spruce and lodgepole pine to ensure that future
282 end-use products obtained from these species have desirable wood characteristics.

283 Although the MFA average profiles started to stabilize at about 15° in both species (Fig. 1),
284 the chosen threshold value of 20° resulted in the best model fit for estimation of individual
285 trees MFA transition from juvenile to mature. Furthermore, as the wood of conifers having
286 MFA of 20° is considered as mature (Bowyer and Shmulsky 2007; Donaldson 2008), such a
287 high transition degree for MFA will enables incorporation of wood quality traits into selective
288 breeding programs of Norway spruce and lodgepole pine as early as possible.

289 Most of the narrow-sense heritability estimates obtained in this study were statistically
290 significant, except for those obtained based on the logistic function under all exclusion
291 models. This might be driven by the inability of this function to estimate MFA transition
292 under the selected threshold, particularly in lodgepole pine.

293 Overall, heritability estimates obtained for lodgepole pine were generally greater than those
294 obtained for Norway spruce. This is in line with results of the studies by Chen et al. (2014)
295 and Hayatgheibi et al. (2017), as h^2 obtained for area-weighted MFA in two progeny trials of
296 lodgepole pine were greater than that obtained for Norway spruce. Similarly, heritability
297 estimates obtained based on the slope function were highest in both species across all
298 exclusion methods. However, h^2 obtained for Norway spruce based on negative exponential
299 and central peak, were also high. Similarly, high h^2 were observed based on the negative
300 exponential and central peak functions in Övra, and based on the arctangent and polynomial
301 functions in Lagfors.

302 Results of this study, which made use of large genetic data sets of two important coniferous
303 species, revealed that there is a possibility to breed for earlier MFA transition from juvenile to
304 mature as genetic gains achieved for this trait were very high.

305 In general, genetic gains obtained for MFA transition, except for those obtained based on the
306 logistic function, were higher in lodgepole pine due to the higher narrow-sense heritability
307 estimates obtained for this trait in lodgepole pine. Further, in addition to the slope function,
308 highest genetic gains were achieved based on the negative exponential and central peak
309 functions in Norway spruce when data trimming by exclusion-2 was applied, and based on the
310 negative exponential and arctangent functions in lodgepole pine after applying exclusion-3.
311 Findings of this study indicate that there is a possibility to select for a reduction in MFA
312 transition age, and therefore, a decrease in proportion of the log containing juvenile wood in
313 Norway spruce and lodgepole pine selective breeding programs.

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References

- Abdel-Gadir, A.Y., and Krahmer, R.L. 1993. Genetic variation in the age of demarcation between juvenile and mature wood in Douglas-fir. *Wood Fiber Sci.* **25**(4): 384-394.
- Alteyrac, J., Cloutier, A., and Zhang, S. 2006. Characterization of juvenile wood to mature wood transition age in black spruce (*Picea mariana* (Mill.) BSP) at different stand densities and sampling heights. *Wood Sci. Technol.* **40**: 124– 138. doi:10.1007/s00226-005-0047-4.
- Bendtsen, B.A., and Senft, J. 1986. Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. *Wood Fiber Sci.* **18**(1): 23–38
- Bhat, K.M., Priya, P.B., and Rugmini, P. 2001. Characterisation of juvenile wood in teak. *Wood Sci. Technol.* **34**(6): 517–532. doi:10.1007/s002260000067
- Booker, R., and Sell, J. 1998. The nanostructure of the cell wall of softwoods and its functions in a living tree. *Holz als Roh-und Werkstoff* **56**(1): 1.
- Bouffier, L., Raffin, A., Rozenberg, P., Meredieu, C., and Kremer, A. 2009. What are the consequences of growth selection on wood density in the French maritime pine breeding programme? *Tree Genet. Genomes*, **5**(1): 11-25. doi: 10.1007/s11295-008-0165-x.
- Cave, I. 1968. The anisotropic elasticity of the plant cell wall. *Wood Sci. Technol.* **2**(4): 268-278.
- Cave, I.D., and Walker, J.C.F. 1994. Stiffness of wood in fast-grown plantation softwoods: the influence of microfibril angle. *For. Prod. J.* **44**(5): 43–48.
- Chen, Z.-Q., Gil, M.R.G., Karlsson, B., Lundqvist, S.-O., Olsson, L., and Wu, H.X. 2014. Inheritance of growth and solid wood quality traits in a large Norway spruce population tested at two locations in southern Sweden. *Tree Genet. Genomes*, **10**(5): 1291–1303. doi:10.1007/s11295-014-0761-x.
- Clark, A., Daniels, R.F., and Jordan, L. 2006. Juvenile/mature wood transition in loblolly pine as defined by annual ring specific gravity, proportion of latewood, and microfibril angle. *Wood Fiber Sci.* **38**(2): 292-299.
- Cown, D. 1992. Corewood (juvenile wood) in *Pinus radiata*—should we be concerned. *N. Z. J. For. Sci.* **22**(1): 87-95.
- Donaldson, L. 2008. Microfibril angle: measurement, variation and relationships—a review. *IAWA J.* **29**(4): 345–386. doi:10.1163/22941932-90000192.
- Dungey, H.S., Matheson, A.C., Kain, D., and Evans, R. 2006. Genetics of wood stiffness and its component traits in *Pinus radiata*. *Canadian Journal of Forest Research* **36**(5): 1165-1178.
- Evans, R. 2006. Wood stiffness by x-ray diffractometry. In *Characterisation of the cellulosic cell wall. In Proceedings of the Workshop, Grand Lake, Colo., 25–27 August 2003. Southern Research Station, University of Iowa, and the Society of Wood Science and Technology. Edited by D. Stokke and L. Groom. Blackwell Publishing, Ames, Iowa. Chapter 11, pp. 1–8.*
- Evans, R., and Ilic, J. 2001. Rapid prediction of wood stiffness from microfibril angle and density. *Forest products journal* **51**(3): 53.

- Fromm, J. 2013. Cellular aspects of wood formation. *Plant Cell Monographs* **20**.
- Gapare, W.J., Wu, H.X., and Abarquez, A. 2006. Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D. Don. *Annals of Forest Science* **63**(8): 871-878.
- Gilmour, A.R., Gogel, B., Cullis, B., Thompson, R., and Butler, D. 2009. ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK.
- Giroud, G., Defo, M., Bégin, J., and Ung, C.-H. 2015. Application of near-infrared spectroscopy to determine the juvenile–mature wood transition in black spruce. *Forest products journal* **65**(3): 129-138.
- Gräns, D., Hannrup, B., Isik, F., Lundqvist, S.-O., and McKeand, S. 2009. Genetic variation and relationships to growth traits for microfibril angle, wood density and modulus of elasticity in a *Picea abies* clonal trial in southern Sweden. *Scandinavian Journal of Forest Research* **24**(6): 494-503.
- Harris, J.M., and Meylan, B. 1965. The influence of microfibril angle on longitudinal and tangential shrinkage in *Pinus radiata*. *Holzforschung-International Journal of the Biology, Chemistry, Physics and Technology of Wood* **19**(5): 144-153.
- Hayatgheibi, H., Fries, A., Kroon, J., and Wu, H. 2017. Genetic analysis of lodgepole pine (*Pinus contorta*) solid wood quality traits. *Canadian Journal of Forest Research*(ja).
- Hodge, G., and Purnell, R. 1993. Genetic parameter estimates for wood density, transition age, and radial growth in slash pine. *Canadian Journal of Forest Research* **23**(9): 1881-1891.
- Hong, Z., Fries, A., and Wu, H.X. 2015. Age trend of heritability, genetic correlation, and efficiency of early selection for wood quality traits in Scots pine. *Canadian Journal of Forest Research* **45**(7): 817-825.
- Isik, F., Gumpertz, M., Li, B., Goldfarb, B., and Sun, X. 2008. Analysis of cellulose microfibril angle using a linear mixed model in *Pinus taeda* clones. *Canadian Journal of Forest Research* **38**(6): 1676-1689.
- Kininmonth, J.A., and Whitehouse, L. (eds)1991. Properties and uses of New Zealand radiata pine. I. Wood properties. Forest Research Institute: Rotorua. 216 pp
- Koubaa, A., Isabel, N., Zhang, S.Y., Beaulieu, J., and Bousquet, J. 2007. Transition from juvenile to mature wood in black spruce (*Picea mariana* (Mill.) BSP). *Wood and Fiber Science* **37**(3): 445-455.
- Larson, P.R. 1967. SILVICULTURAL CONTROL OF CHARACTERISTICS OF WOOD USED FOR FURNISH. *In* Tappi. TAPPI PRESS TECH ASSN PULP & PAPER IND 1 DUNWOODY PARK, ATLANTA, GA 30338. pp. A117-&.
- Larson, S.P. 2001. Formation and properties of juvenile wood in southern pines.
- Lenz, P., MacKay, J., Rainville, A., Cloutier, A., and Beaulieu, J. 2011. The influence of cambial age on breeding for wood properties in *Picea glauca*. *Tree Genetics & Genomes* **7**(3): 641-653.
- Lichtenegger, H., Reiterer, A., Stanzl-Tschegg, S., and Fratzl, P. 1999. Variation of cellulose microfibril angles in softwoods and hardwoods—a possible strategy of mechanical optimization. *Journal of Structural Biology* **128**(3): 257-269.

Loo, J.A., Tauer, C.G., and McNew, R.W. 1985. GENETIC-VARIATION IN THE TIME OF TRANSITION FROM JUVENILE TO MATURE WOOD IN LOBLOLLY-PINE (PINUS-TAEDA L). *Silvae Genetica* **34**(1): 14-19.

Lundgren, C. 2004. Microfibril angle and density patterns of fertilized and irrigated Norway spruce. *Silva Fennica* **38**(1): 107–117.

Mansfield, S.D., Parish, R., Di Lucca, C.M., Goudie, J., Kang, K.Y., and Ott, P. 2009. Revisiting the transition between juvenile and mature wood: a comparison of fibre length, microfibril angle and relative wood density in lodgepole pine. *Holzforschung* **63**(4): 449-456. doi: 10.1515/hf.2009.069.

Mansfield, S.D., Parish, R., Goudie, J.W., Kang, K.Y., and Ott, P. 2007. The effects of crown ratio on the transition from juvenile to mature wood production in lodgepole pine in western Canada. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **37**(8): 1450-1459. doi: 10.1139/xo6-299.

Mellerowicz EJ, Baucher M, Sundberg B & Bojeran W. 2001. Unraveling cell wall formation in the woody dicot stem. *Plant Mol Biol*, **47**: 239-274

Moore, J.R., Cown, D.J., and McKinley, R.B. 2014. Modelling microfibril angle variation in New Zealand-grown radiata pine. *New Zealand Journal of Forestry Science* **44**(1): 25.

Mutz, R., Guilley, E., Sauter, U.H., and Nepveu, G. 2004. Modelling juvenile-mature wood transition in Scots pine (*Pinus sylvestris* L.) using nonlinear mixed-effects models. *Annals of Forest Science* **61**(8): 831-841.

Schwarz, G. 1978. Estimating the dimension of a model. *The annals of statistics* **6**(2): 461-464.

Senft, J.F., Bendtsen, B.A., and Galligan, W.L. 1985. Weak wood: fast-grown trees make problem lumber. *Review Process: Non-Refereed (Other)*.

Stonecypher, R.W., and Zobel, B.J. 1966. INHERITANCE OF SPECIFIC GRAVITY IN 5-YEAR-OLD SEEDLINGS OF LOBLOLLY PINE. *Tappi* **49**(7): 303-+.

Szymanski, M.B., and Tauer, C. 1991. Loblolly pine provenance variation in age of transition from juvenile to mature wood specific gravity. *Forest science* **37**(1): 160-174.

Thamarus, K., Groom, K., Bradley, A., Raymond, C.A., Schimleck, L.R., Williams, E.R., and Moran, G.F. 2004. Identification of quantitative trait loci for wood and fibre properties in two full-sib pedigrees of *Eucalyptus globulus*. *Theoretical and Applied Genetics* **109**(4): 856-864. doi: 10.1007/s00122-004-1699-4.

Walker, J., and Butterfield, B. 1996. The importance of microfibril angle for the processing industries. *New Zealand Forestry* **40**: 34-40.

Wang, M.L., and Stewart, J.D. 2012. Determining the transition from juvenile to mature wood microfibril angle in lodgepole pine: a comparison of six different two-segment models. *Annals of Forest Science* **69**(8): 927-937. doi: 10.1007/s13595-012-0226-z.

Wang, M.L., and Stewart, J.D. 2013. Modeling the Transition from Juvenile to Mature Wood Using Modulus of Elasticity in Lodgepole Pine. *Western Journal of Applied Forestry* **28**(4): 135-142. doi: 10.5849/wjaf.12-026.

Zobel, B., and Van Buijtenen, J. 1989. Wood variation-its causes and control. Springer Verlag: Berlin, etc **363**: 439-440.

Zobel, B.J., and Jett, J.B. 1995. Genetics of wood production. Springer Verlag, 357pp.

Zobel, B.J., and Sprague, J.R. 1998. Juvenile wood in forest trees. Springer Science & Business Media.

Falconer, D., and Mackay, T. 1996. Introduction to quantitative genetics. 4th ed. Longman, New York.

Table 1. Narrow-sense heritability estimates of Norway spruce (combined-trial) and lodgepole pine (Övra and Lagfors) MFA transition from juvenile to mature wood obtained from six different regression functions applying three different exclusion methods. Standard errors of the heritabilities are in parenthesis.

Modelling method	Narrow-sense heritability estimates		
	Norway spruce	Lodgepole pine	
		Övra	Lagfors
	Exclusion_1		
1) slope	0.21 (0.05)	0.34 (0.21)	0.42 (0.19)
2) log	0.09 (0.03)	0	0.13 (0.19)
3) peak	0.18 (0.05)	0.33 (0.21)	0.28 (0.19)
4) atan	0.19 (0.04)	0.15 (0.21)	0.43 (0.19)
5) poly	0.19 (0.05)	0.19 (0.20)	0.36 (0.18)
6) nexp	0.19 (0.04)	0.26 (0.21)	0.29 (0.18)
	Exclusion_2		
1) slope	0.23 (0.05)	0.53 (0.23)	0.41 (0.19)
2) log	0.09 (0.04)	0	0
3) peak	0.21 (0.05)	0.35 (0.21)	0.22 (0.19)
4) atan	0.17 (0.05)	0.31 (0.22)	0.43 (0.19)
5) poly	0.19 (0.05)	0.19 (0.20)	0.36 (0.18)
6) nexp	0.20 (0.05)	0.34 (0.21)	0.32 (0.18)
	Exclusion_3		
1) slope	0.21 (0.05)	0.46 (0.20)	0.39 (0.19)
2) log	0.08 (0.04)	0	0
3) peak	0.20 (0.05)	0.38 (0.22)	0.27 (0.18)
4) atan	0.15 (0.04)	0.31 (0.22)	0.41 (0.19)
5) poly	0.17 (0.05)	0.28 (0.21)	0.38 (0.18)
6) nexp	0.18 (0.05)	0.34 (0.21)	0.29 (0.18)

Note: log= logistic, peak= central peak, poly=polynomial, atan= arctangent, n.exp= negative exponential

Table 2. Genetic gains (ΔG_t %) obtained for transition age in combined-site Norway spruce and combined-site lodgepole pine using the selection intensity of 1%

Norway spruce			
Model	ΔG_t (%)		
	exclusion-1	exclusion-2	exclusion-3
Slope	27.4	29.4	27.1
Log	13.3	13.0	11.1
Peak	20.9	24.1	23.2
Atan	23.2	20.2	17.1
Poly	23.3	23.0	21.6
N. ex	25.0	25.7	20.1
lodgepole pine			
Model	ΔG_t (%)		
	exclusion-1	exclusion-2	exclusion-3
Slope	40.2	48.4	45
Log	0	3.7	11
Peak	32.8	30.2	35.7
Atan	29.4	39.5	39.9
Poly	29.6	29.7	35.6
N. ex	33.4	38.2	38.9

Note: Log= logistic, Peak= Central peak, Poly=polynomial, Atan= arctangent, N.exp= negative exponential

Fig. 1. Radial trends for MFA of *Picea abies* at two trials (Höreda and Erikstorp) from cambial age 1 to 20 and for *Pinus contorta* at two trials (Övra and Lagfors) from cambial age

1 to 30. The black lines represent the actual observations from all individual trees and the red line is the mean radial variation of MFA against the cambial age.

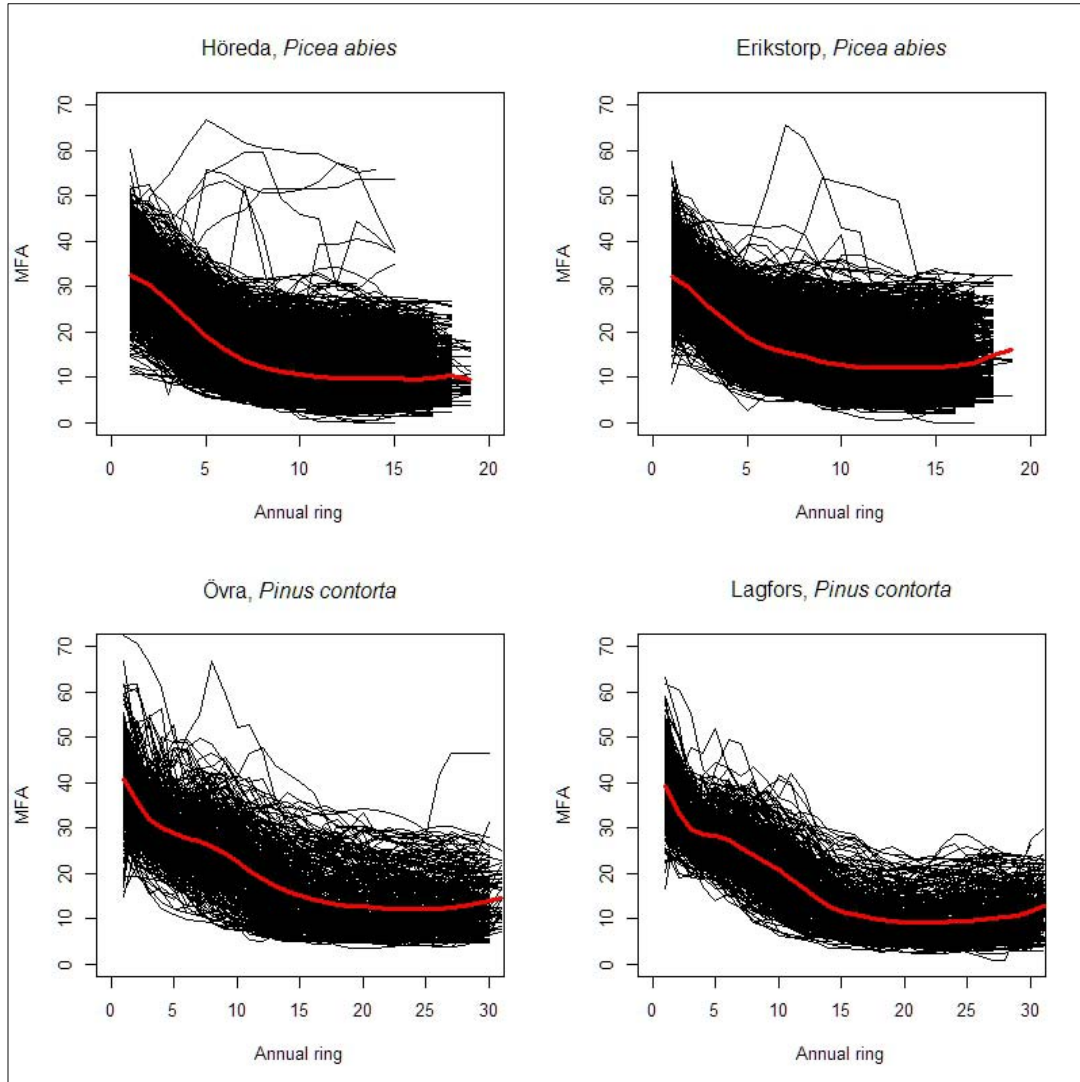


Fig. 2. Proportion of Norway spruce (Höreda) transition age under the mean (raw data) and six different regression functions using the threshold level of 20 degrees for MFA.

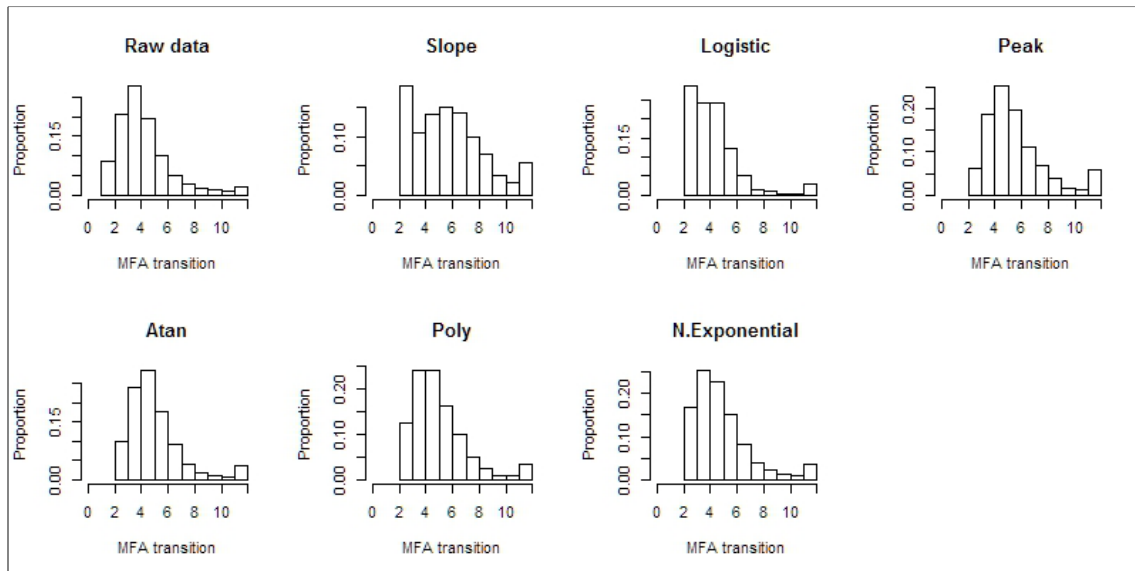


Fig. 3. Proportion of Norway spruce (Erikstorp) transition age under the mean (raw data) and six different regression functions using the threshold level of 20 degrees for MFA

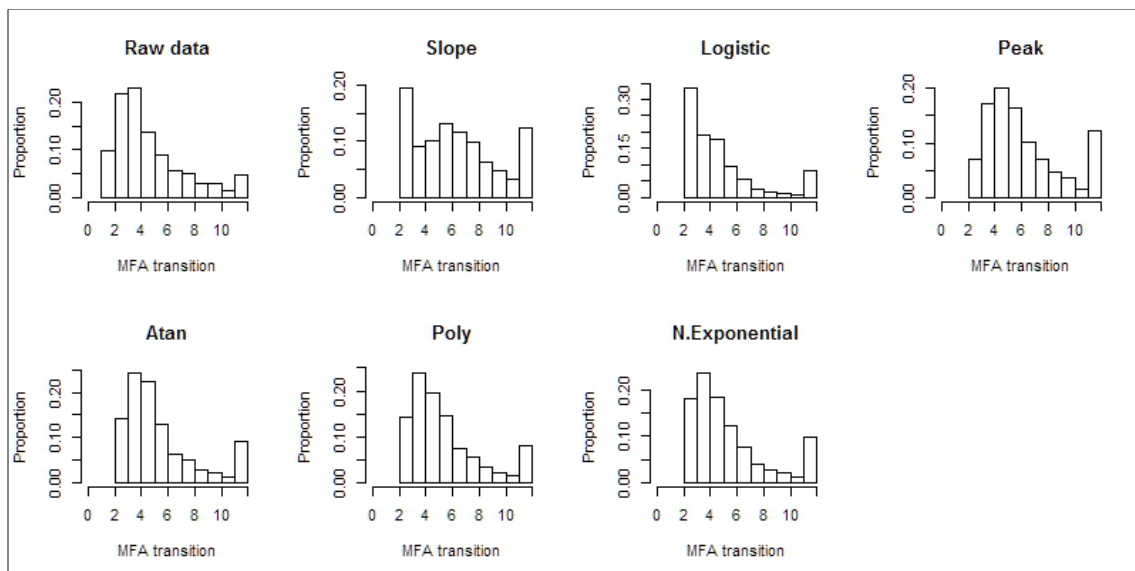


Fig. 4. Proportion of lodgepole pine (Övra) transition age under the mean (raw data) and six different regression functions using the threshold level of 20 degrees for MFA

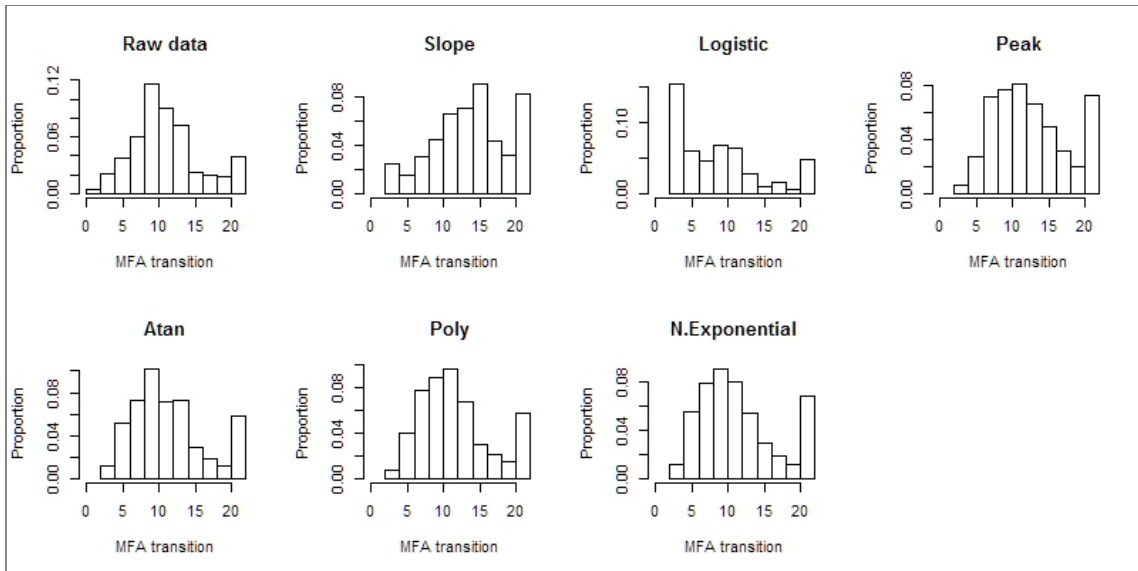


Fig. 5. Proportion of lodgepole pine (Lagfors) transition age under the mean (raw data) and six different regression functions using the threshold level of 20 degrees for MFA

