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**Parental and individual variation of  
growth traits and wood density in a  
progeny trial after a complete diallel  
crossing of 9 Silver birch (*Betula  
pendula*) trees in south-eastern Norway**

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## Abstract

In a progeny trial after a complete diallel crossing of nine Silver birch (*Betula pendula* Roth.) trees, both quality and growth traits were studied after 40 years. Quality and growth traits were dependant on competition and genetics, and significant differences in breast height diameter were found between the most contrasting parents. Diameter and height growth correlated positively with each other both on parental- and individual tree level, while branch-traits were mostly dependant on competition. Wood density increased from pith to bark, and decreased from stump to 60% of the total height. Variation in wood density were most notable at the inner section of the core, and in the stump. Since juvenile wood in birch has lower wood density than the mature wood, the proportion of juvenile wood was important for mean densities. Mean wood density at 12 % moisture content was measured to be  $680.4 \text{ kg/m}^{-3}$ , which was higher than many other studies on Silver birch. Models were made for prediction of both growth traits and grain angle, as well as six models for prediction of wood density. The density models explained around 50 % of the variation from breast height to 60 % of the total height of the tree. The parental effect was strong for wood density, and there were significant interactions both with radial and vertical positions. Parent 6 was slightly better than the others for most traits, which implies potential of combined gain in growth and quality with use of breeding programs for Norwegian birch industry. More research on this matter is therefore needed to develop a genetic material to base round wood production of birch.



## Sammendrag

I et avkomforsøk etter en komplett diallel krysning med ni eksemplarer av hengebjørk (*Betula pendula* Roth.) ble både kvalitet og vekstegenskaper undersøkt etter 40 år. Kvalitet- og vekstegenskaper viste seg å være avhengige av både konkurranse og genetisk opphav, og signifikante forskjeller i brysthøydiameter ble funnet mellom de mest forskjellige foreldrene. Diameter- og høydevekst korrelerte positivt med hverandre både på familie og individuelt nivå, mens greinegenskaper var mest avhengig av konkurranse. Densiteten økte fra kjernen mot barken og sank fra stubben til 60 % av totalhøyden. Variasjonen i densitet var mest tydelig i de indre seksjonene av kjernen og i stubben. Siden ungdomsveden i bjørk har lavere densitet enn eldre ved, har andelen ungdomsved mye å si for gjennomsnittsdensiteten. Gjennomsnittsdensiteten for hele feltet ble målt til  $680.4 \text{ kg/m}^{-3}$ , som er høyere enn i flere andre studier på hengebjørk. Modeller ble utredet for å predikere både vekst- og fiberhelningsmodeller og seks modeller ble utredet for prediksjon av densitet. Densitetsmodellene forklarte omkring 50 % av variasjonen fra brysthøyde til 60 % av totalhøyden, og foreldreeffekten viste seg å være sterk. Foreldreeffekten var signifikant både kombinert med radielle og vertikale variasjoner i treet. Avkommet til forelder nummer 6 var litt bedre enn alle de andre for de fleste egenskapene. Dette tilsier at det finnes et potensiale for kombinert gevinst mellom både hos vekst og kvalitet i avlsprogrammer i norsk bjørkeindustri. Mer forskning på dette feltet er derfor nødvendig for å utvikle et genetisk materiale som kan forbedre sagtømmerproduksjonen i bjørk.





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# 1. Introduction

The birch family is the most common broad-leaved trees in the northern parts of the world, and consists of way above 100 species. The birch is strongly represented in Scandinavia, and is the third most harvested species group in Norwegian forest industry, however its listed as broad-leaved species in the national register (Landbruksdirektoratet, s.a.). It is widely spread across the entire country, and three species and sub-species are commonly known. Silver birch (*Betula pendula* Roth.), downy birch (*B. pubescens* Ehrh.), also known as its sub-species mountain birch (*B. pubescens ssp. tortuosa*), and the smallest species called dwarf birch (*B. nana*). The continuous of silver birch in Norway extends from the southernmost tip of Agder county (58°N) to Levanger in Trøndelag county (64°N) except in the mountains. More sporadic findings are found as far north as Fauske in Nordland county (67°2N)(Artsdatabanken, s.a.). The trees, especially the silver and downy birch are known for their white bark and are relatively short-lived pioneers (Fischer et al., 2002). They produce seeds every year which is spread over long distances by wind. They are also fast growers, which makes them competitive pioneer species. Because of this, they are present in many parts of the Eurasian temperate and boreal zones. Birch are important for both biodiversity and industry. Several common and more vulnerable species of mammals, birds, insects and fungi are therefore dependent of birch presence and abundance to live and expand (Perala & Alm, 1990). In Norway the birch represented 16% of the total standing volume in 2010 (Hynynen et al., 2010), but broad-leaved trees were only 1,3% of the registered felling the same year (Landbruksdirektoratet, s.a.). The registered felling volume in 2017 was nearly twice as much, but still far from the potential.

Historically, fire wood has been the main application for birch in Norway, and the round wood production has been low compared to other species. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are more common industrial species. No saw mills of international size which are specialized on round wood from broad leaved trees are present in Norway (von Troil et al., 2014). However, neighbouring countries like Finland and Latvia have a functioning industry, and birch is considered a valuable raw material (Hynynen et al., 2010; Luostarinen & Verkasalo, 2000). It is applied both as construction material, plywood, and pulp wood for paper production. Birch however, are often seen as a weed in Norway. Former studies imply that this may correlate with little or no presence of well-tended pure

birch stands (Cameron, 1996). Birch is often removed during silviculture, or eaten by herbivores when abundant on high site index areas without high levels of resins (Jia et al., 1997). Pure stands are rare, and are only used in special areas or as a substitute for Norway spruce in cases with high rot percentage. Most high-quality birch is found in stands mixed with Norway spruce or Scots pine as a part of broad leaves required from certification standards like PEFC (PEFC, 2016). Production of the very expensive variate of silver birch called curly birch, also occur in rare stands (Hynynen et al., 2010).

Provenance and progeny tests of pure birch stands in Norway have been done by e.g. Skrøppa and Kohmann (2018). They showed that trees from breeding programs in Sweden and Finland grew better in Norway than trees from natural stands, which implies that there is an increased growth potential from breeding. Breeding programs can shorten both the rotation time, produce better quality timber, and are critical for economic sustainability in forest industry (Jansson et al., 2017). Breeding programs are often based on cloning or progeny tests from local pre-selected plus-trees (Koski & Rousi, 2005). Plus-trees show desirable traits, which are essential for complying to industrial purposes. Though, these desires might change during a rotation (Jansson et al., 2017). Traits considered in these programs are not only growth traits, like height and diameter. Quality traits are also important to meet broad industrial purposes. They are important to achieve the end products suited for a wide set of applications, and thereby expand the industry (Dunham et al., 1999; Herajarvi, 2001). Examples of quality traits are wood density, strength, variation in grain angle, grain length, stem straightness, defect on the stem and branch development among others. These develop different in several species, and some are more dependent on silviculture, while others depend more on genetics (Repola, 2006). Both growth and quality traits are known to correlate both positively and negatively. Density for example, seems to be positively correlated with hardness and strength (Dunham et al., 1999; Herajarvi, 2004; Kuchera, 1984), and negatively with diameter growth speed (Dunham et al., 1999; Liepins & Rieksts-Riekstins, 2013; Stener & Hedenberg, 2003). Some studies however, imply the opposite in downy birch (Luostarinen et al., 2009). Density is also known to change by age, as juvenile wood is presumed less dense (Kuchera, 1980). This means older more slow growing trees often have higher mean wood density (Dunham et al., 1999) than younger trees (Liepins & Rieksts-Riekstins, 2013). The density is therefore believed to increase as the proportion of juvenile wood decreases.

Branch traits are known to change both with silviculture and genetical variation. Crones and branch angles for example are dependant of stand density (Mäkinen, 2002; Niemisto, 1995a). Diameters and yield however, are explained by both silviculture and stand density (Niemisto, 1995b) as well as genetics (Malcolm & Worrell, 2001). Height growth is considered dependant on both the environment, growing conditions and genetics, but is less correlated with other quality traits than diameter grain length (Stener & Hedenberg, 2003). Luostarinen et al. (2009) claims few or no difference in downy birch wood density compared to silver birch. Longer fibre length with faster youth growth both considering height and diameter is also observed in this study. The wood density in silver birch is believed to decrease with height, and increase radially from pith towards the bark (Kuchera, 1980). Kuchera (1980) did not find any significant correlations between fibre length or growth ring width and density, because of great provenience variation.

Genetic studies on birch have revealed considerable variation in growth and quality traits between families (Stener & Jansson, 2005; Zeltins et al., 2018). Both studies concluded with a substantial genetic gain on both quality and growth traits with use of breeding. Programs often improve growth and yield, and the need for more research to reach the potential are discussed in (Koski & Rousi, 2005). However, the effect of silviculture is also proven important for good quality round wood in birch and other common species (Cameron, 1996; Hynynen et al., 2010). The genetic gain in quality trait improvement will therefore be of little use, if not combined with proper management. Knowledge about the trait development by genetics, might also inflict silviculture conduction (Kuchera, 1980). Tests from the same report imply that measurements at 20% of the tree height, give the best estimate for mean density in a single tree. Further, traits like wood density, spiral grain-angle and especially branch traits have appeared different in open areas than in dense stands (Mäkinen, 2002). Density is also known to be affected by vertical height in several species. Norway spruce density increases with height, while both Scots pine and Silver birch decreases (Repola, 2006). The birch however, decrease less than Scots pine. The aim of this master`s thesis was to study the genetic variation and correlations patterns between growth- and quality traits in silver birch. This was done using a 40-year old progeny trial from a 9 x 9 diallel crossing made at the former Norwegian Forest Research Institute, now Norwegian Institute of Bio-economy Research (NIBIO) in 1976. Both growth and wood quality traits were investigated on individual tree-, and family level. Models describing the variation in growth traits and wood density was developed based on correlations between traits and the family factor.

## 2. Material and methods

### 2.1 Background and study area

The material originates from a pure silver birch (*Betula pendula*) stand on old cultivated grounds at Hoxmark Experimental Farm in Ås (59°'67 N, 10°'71 E, 100 m a.s.l.). It was planted in August 1977, and consisted of material collected from Søndre Land, Oppland county (60°'33N) a year earlier. Nine trees were crossed in all possible combinations in a complete diallel, including reciprocal crosses and self-pollinations. They were selected from solitary trees standing more than 50 meters apart, and were between 30 and 40 years old. The total tree heights were 13-19 meters, and there were no visible phenotypical differences. For a more detailed background see (Skrøppa & Solvin, 2018).

### 2.2 Genetic origin and planting

All trees had male catkins in the spring of 1976. Branches were cut from the nine parents, and kept in a separate room to avoid pollen contamination. The female catkins were isolated with pollination bags until they were receptive. To make sure which tree the pollen came from, no male catkins were left in the pollination bags. Controlled pollinations were made using a 2mm pollination syringe, and all nine pollen donors were used three times. The bags were collected in July 1976, and the seed lots were stored until germination in a greenhouse in May 1977. Viable seedlings of all families were obtained. The planting site consisted of 12 blocks, herby referred to as replicates, and 6 of these were used in this study. Each block consisted of randomized family plots, containing 4 trees with one meter spacing. These 4 trees at each plot were reduced to 1 after six growing seasons when mean height were 2.8 meters. They were thinned again after 19 seasons. After the second thinning the tree density spacing were 1350 trees per hectare, and the mean height were 14.1 meters. The second thinning was based on height and stem quality, and some families turned out more abundant than others (Skrøppa & Solvin, 2018). Each tree had an observation number (Obs), consisting of the replicate number (1-6), and a two-digit number representing the parent combination. The observation number was also used as a tree number. Further measurements and details are presented in (Skrøppa & Solvin, 2018).

## 2.3 Selection of trees

To represent the remaining families and trees, a selection based on spacing and diameter was used. Because of severe buffer zone difficulties, no border trees of the replicates were selected. Figure 1 shows the distribution of replicates and the grey area describes the selection zone inside the buffer zone. All trees in this zone were stratified into three groups based on diameter in breast height (DBH). Sample trees were randomly selected based on half-siblings from these strata, leaving 81 trees of a total of 285 representing the 9 parents. Full-siblings were not included in the same strata. The parental distribution of the 81 selected trees is shown in table below.

Table 1. Distribution of parents 1-9. All trees are represented twice. Once with each parent.

<b>Parent</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>	<b>9</b>
<b>Trees (n)</b>	<b>16</b>	<b>24</b>	<b>20</b>	<b>18</b>	<b>16</b>	<b>22</b>	<b>13</b>	<b>18</b>	<b>15</b>

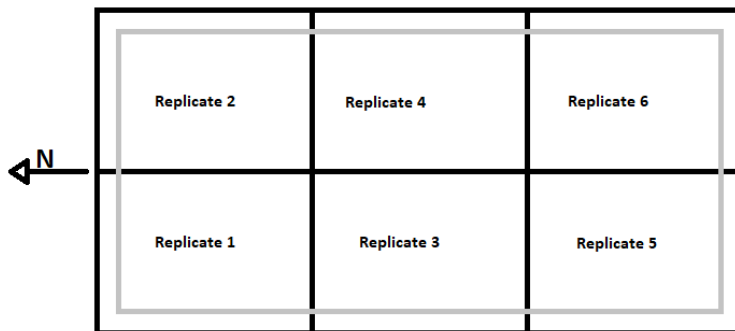


Figure 1. Organizing of the 6 replicates in the birch stand. The arrow points north, and the grey square resemble the remaining stand after removing the buffer zone.

## 2.4 Data collection

### 2.4.1 Spiral grain-angle

The angle measurements were done pre-felling in late autumn 2017, before the trees froze. A device developed by Chalmers institute in Sweden was used, and the method is described by Hannrup et al. (2003). The device measures the angle of the 2-3 outermost growth rings, and give angle measurements in form of positive and negative degrees from zero. Four measurements were done on each tree. Two at the north, and two at the south side, and the mean of these were used in the study. All trees were measured at breast height when the bark

was even. In cases of uneven bark, the closest possible alternative above breast height was used. Negative values indicate left oriented grain angle.

#### 2.4.2 Felling and measures

The felling was done in random direction to avoid errors caused by intraspecific competition, and ground differences. All trees were marked where measurements were supposed to be made in case of twisting in the cutting process. By doing this the measurements were consequently done in a predetermined, but random side on the tree. If the predetermined direction of cutting was impracticable, the tree was felled 180° degrees the other direction. After cutting, the total height (H) was measured, and the trees were marked at the stump, breast height (DBH) and at 20% (H20%), 40% (H40%) and 60% (H60%) of the total height. The height to a split or forking was also measured if present, as well as height to first green branch (HGB). The diameters were measured at all marks, as well the diameter for the first green branch (DGB) and most competitive branch (DCB). The most competitive branch was the largest branch within close range of the first green branch. All diameters were measured from the same predetermined random direction.

## 2.5 Disturbances

After the cutting, a cultivator destroyed eight of the tree tops prior to the measurements. This caused missing values in the data set. Some trees were more destroyed than others, and are not present in all calculations because of the lack of data. For two of the affected trees, estimates were good enough to be used. Two other trees were so strongly damaged, that total height estimates were impossible. The branch traits were most inflicted, as well as some of the higher diameter measurements and core samples. On the trees where total height was missing, core samples and other measurements were done on four and eight meters from the stump.

## 2.6 Density

Core samples were obtained with a 4.5mm increment borer. Each tree was drilled at the marks, and the core from pith to bark was preserved in plastic cassettes with room for several cores. (5mm × 5mm × 20cm). The bark was then removed, and they were dried for three weeks. They were later climatized to the preferred 12% moisture content according to (Steffenrem et al., 2009; Steffenrem et al., 2014). Mounting were then done in a styrofoam cube with coordinates, and the x-ray scans were done in a Siemens multi-slice CT-scanner at



Anicura Veterinary, Jeløya. The two best pictures of each core were selected manually, and the data string for each increment core were automatically extracted from the image using a SAS macro (SAS Institute Inc, 2003) written by Harald Kvaalen and Arne Steffenrem at NIBIO. After cleaning the data from error readings, the density for each pixel (approximately 0.31 mm<sup>3</sup>), were obtained from the DICOM-values as explained by Steffenrem et al. (2009). To achieve the actual mean density of the cores, each pixel-density had to be weighted with their actual area in the tree. The density closest to the bark will then count for more of the total density than the pith because of ring area.

$$\frac{\sum_{i=1}^n \left( \frac{\pi \left( \left( \frac{L}{N} n_i \right)^2 - \left( \frac{L}{N} (n_{i-1}) \right)^2 \right)}{10^6} \right) * D_i}{\pi L^2}$$

In the formula above N is the total number of radial pixels in the core sample, and L is the length of the core sample in millimetres. n<sub>i</sub> is the current radial pixel of investigation, and D<sub>i</sub> is the measured wood density in pixel n<sub>i</sub>. The standard formula  $A = \pi r^2$  is used to calculate area of a circle. This area is divided by a million to be able to present the wood density in kg/m<sup>-3</sup>. Since each pixel, only explains a single radial position, a sum of all pixel densities in a core sample is needed to present the actual weighted mean density. It is finally divided by the total area of the core. Mean density was measured for each vertical section (S, BH, H20%, H40% and H60%), each tree, (Tree no.) each family (Parent 1-9) and in total. Each core sample were cleaned for deviant data in both ends of the core. These removed pixels were marked, and are not present in the statistics, and consisted of three pixels at the beginning and at the end of each core. Pixels which did not fit the rest of the core pattern and at the same time had densities larger than 950 kg/m<sup>-3</sup> or less than 450 kg/m<sup>-3</sup> were also excluded as noise.

Table 2. Trait overview with descriptions.

Trait	Abbreviation	Description
Height	H, S1L, S2L, S3L, Split and H%	Total height and section heights measured in meters (m), while H% is the percentage of the total tree height.
Branch height and diameters	HGB, DGB, DCB	Height to first green branch (m), its diameter (cm) and diameter of most competitive branch (cm).
Diameter	SD, DBH, S1D, S2D, S3D	Diameters of stump, breast height and sections 1, 2 and 3. (cm)
Taper	Taper	Measurement of slenderness. Diameter divided by height in all sections measured.
Spiral grain-angle	GA	Average of four measurements done at breast height in north and south direction. (Chalmers index)
Rot	Ja/nei (Yes/no)	Observed rot or other damage on core cylinders
Wood density	Density (D)	Weight of one cubic meter timber weighted by area differences (kg/m <sup>-3</sup> )
Radial positions	Radpos and Radpos20	Radial individual pixel position, and the mean radial position of twenty positions

## 2.7 Statistical methods

For the statistical analysis JMP<sup>®</sup>, Pro 13. SAS Institute Inc., Cary, NC, 1989-2007 were used. The data was sorted in different data sets. All trees were represented two times in each set, one for each parent. To adjust for this in the parental calculations a frequency of 0.5 was added to weigh down the number of replicates. Whether it was maternal or paternal influence was not found to have importance for genetic influence by Skrøppa and Solvin (2018), and therefore not taken into account in this study. Growth traits, spiral grain and wood density was compared using the multivariate testing feature in JMP, and a Pearson's test was used to determine correlations. The correlations were also determined with significance in prediction models. The means calculated in JMP were also used in Microsoft Excel 2016 to produce graphs presenting vertical and radial differences as well as diameter distribution. One-way Anova analysis was used to obtain means and summary of fit for the traits. Each trait where analysed with Tukey Kramer's HSD to find significant differences between families. Hypotheses were rejected if the probability of type I error was smaller than 0.05. Correlations calculated between parent-means was considered estimates of the genetic correlation. However, these correlations might overestimate the true genetic correlation as the latter one is normally estimated from variances and co-variances of random effects that are truncated more for the experimental error.

Linear models that describe the total variation of the traits are shown beneath. Model 1 were used or analysis height, diameter and grain angle, while model 2 were used for analysis of wood density and includes radial and vertical measurements. Stump and inner core densities (30 pixels) were excluded from density modelling because of very high levels of variance, and little relevance for industry.

$$[1] \quad Y = \alpha + a_i + f(A, B, \dots) + e_i$$

Where  $f(A, B, \dots)$  represents the different fixed effects to be tested, and  $a_i$  ( $i = 1, \dots, 6$ ) represents the random replicate effect and  $e_i$  represents the residuals.

$$[2] \quad Y = \alpha + a_i + \beta(H\%) + \gamma(Radpos) + \delta(H\% * Radpos) + e_i$$

In the basic model above  $Y$  represents the trait modelled.  $Radpos$  represents the radial position from where the wood density was measured, and  $f(A, B, \dots)$  represents the different fixed effects to be tested. The random effect of the tree numbers is represented by  $a_i$ , and  $e_i$  represents the residuals. The radial positions in this model was represented by intervals of 20

pixels (6mm). The random elements  $a$  and  $e$  in [*Model 2*] were assumed to be normally distributed. Their variance components were  $\sigma_a^2$  and  $\sigma_e^2$ . Further, additional fixed effects were added to explain the random variance between the trees. The linear mixed models were calculated using the REML (restricted maximum likelihood) method in the model platform in JMP, version 13.00 pro software (SAS Institute Inc. 2016). Coefficient of determination ( $R^2$ ) and root mean square error values (RMSE) from the JMP modelling outputs include the effort of both fixed and random effects. Therefore,  $R^2$  and RMSE-values were calculated from a linear regression between density values and the measured density values.

### 3. Results

#### 3.1 Growth traits

The total height ranged from 17.8-24.3 m, with an average of 21.1 m, and only small parental differences were detected. None were shown to be significant. 37 of the 81 trees had a split or forking in their trunk. However, no parents had significantly more forking than others. ( $p < 0.05$ ). For the trees with split, the height differed, but no significant difference between parents were found. The means of height of first green branch (HGB), diameter of first branch (DGB) and diameter of most competitive branch (DCB) as well as other growth traits are presented in Table 3. Parental differences, standard deviations and significant differences on parental scale is also presented. Few or none significant differences were observed on height-dependant traits like total height, split or HGB. Diameter traits measured showed more variation than height traits, both considering single tree differences, and difference between parents. The average DBH for all trees was 17.8 cm. The lowest diameter measured at breast height was 11.5 cm, and the highest was 24.1 cm. Progenies from parent number 6 had an average DBH of 20.2 cm, while those from parent number 4 had an average of 14.7 cm. This difference was significant ( $p < 0.05$ ). The distribution of diameters by parents, and total tree height is plotted in Figure 2. The difference in diameter between parents were greatest at breast height, but visible at all five vertical positions sampled. Progenies from parent 4 had the least stem taper, but also the lowest diameter growth. Progenies from parent 6 had both the largest diameter growth, and the highest mean wood density. This family had more desirable mean values in most traits, both considering its fast growth and density compared to the rest. Only a slightly higher taper value compared to the mean was noted as un-desirable.

### *Rot or damaged cores*

21 of the 81 trees had registered damage in their core samples. This was either rot or other sorts of deformities. Most of them were found in the stump or breast height sections. It was more abundant for some replicates than others. Parent 1 had no damage at all, while parent 8 had notifications on 50 % of its progenies. However, no significance was found.

*Table 3. Table 3. Total and parental means and standard deviations (in parenthesis) of all investigated traits (for explanation see Table 2). Parents with statistical significant differences according to Tukey Kramer's HSD are shown with connecting letters.*

Parents	Height	DBH	HGB	DGB	DCB	GA	Density	Taper
<b>Mean</b>	21.14 (1.62)	17.81 (3.15)	9.65 (4.13)	2.98 (0.99)	3.15 (1.55)	-1.49 (1.44)	685.23 (29.52)	0.74 (0.17)
<b>1</b>	21.79 (1.55)	18.04 (2.53)	11.37 (4.32)	3.30 (0.89)	4.44 (1.79)	-1.47 (1.11)	679.60 (31.13)	0.72 (0.18)
<b>2</b>	21.43 (1.32)	18.07 (3.00)	9.04 (3.77)	2.80 (0.87)	3.67 (1.79)	-1.01 (1.55)	690.16 (28.19)	0.73 (0.14)
<b>3</b>	20.82 (1.59)	18.56 (3.10)	8.33 (3.42)	3.13 (0.81)	3.24 (0.85)	-2.10 (1.33)	680.68 (29.42)	0.79 (0.16)
<b>4</b>	20.46 (1.50)	14.74 (1.78) b	11.68 (3.81)	2.48 (0.92)	2.52 (0.70)	-1.61 (1.23)	688.13 (30.13)	0.63 (0.12)
<b>5</b>	20.22 (1.32)	17.71 (2.86)	7.30 (3.64)	3.05 (0.96)	3.49 (1.74)	-1.73 (1.88)	661.33 (23.03)	0.82 (0.21)
<b>6</b>	21.86 (1.64)	20.15 (2.89) a	9.59 (4.40)	3.36 (0.95)	3.89 (1.30)	-1.39 (1.38)	698.94 (34.45)	0.79 (0.19)
<b>7</b>	20.52 (1.48)	15.65 (2.92)	8.45 (3.51)	2.63 (1.50)	3.08 (1.27)	-2.10 (1.99)	693.20 (21.21)	0.66 (0.13)
<b>8</b>	21.07 (1.57)	17.77 (3.14)	9.85 (4.72)	2.61 (0.77)	3.08 (1.04)	-0.95 (1.11)	677.25 (25.77)	0.74 (0.17)
<b>9</b>	21.81 (1.99)	18.37 (2.90)	11.83 (3.84)	3.39 (1.05)	4.19 (2.35)	-1.37 (1.00)	694.02 (22.66)	0.70 (0.12)

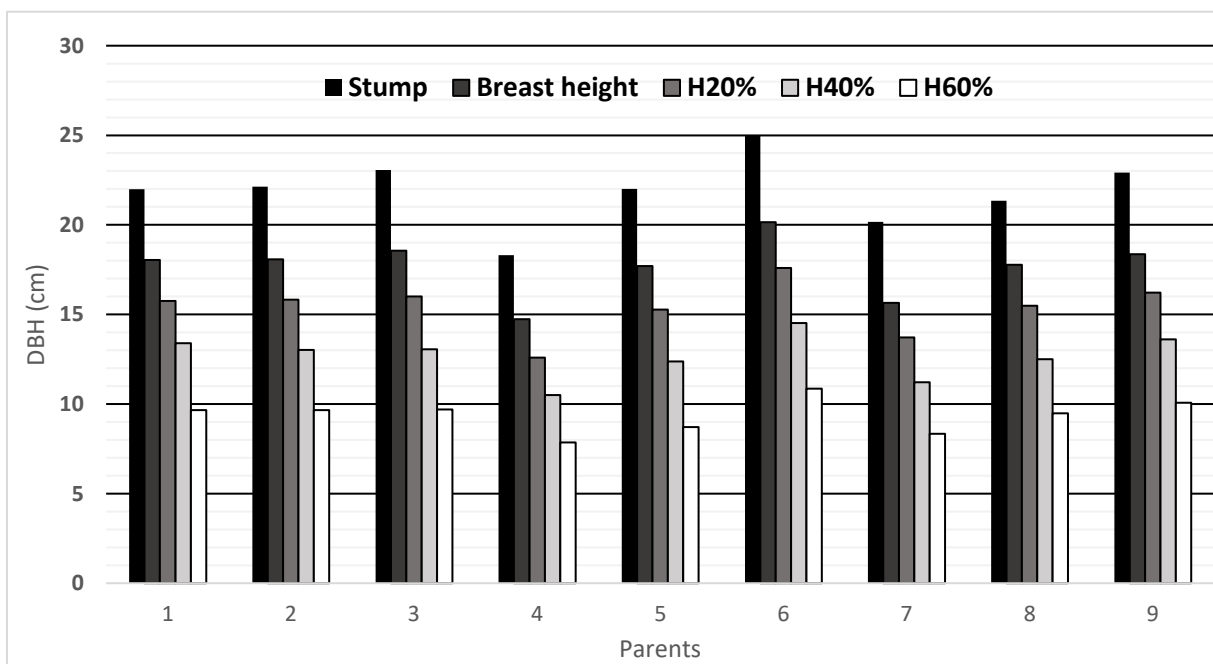
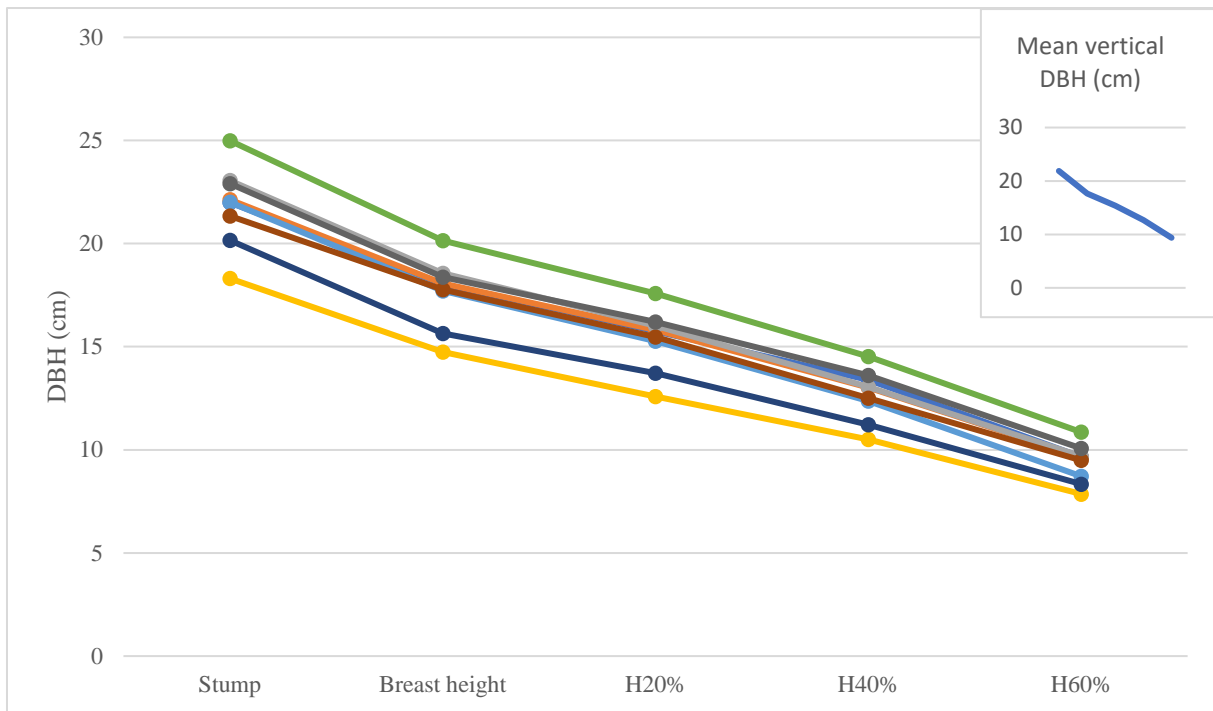


Figure 2. Distribution of breast height diameter (DBH) between parents (1-9) on a vertical scale (stump to 60% of the total height).

## 3.2 Density

Average wood density (at 12% relative moisture content) was  $680.4 \text{ kg/m}^3$ . The density decreased with increasing height in the tree. See Figure 3. Wood density at stump height was significantly higher than density at breast height. However, no significant difference in density was found between breast height, and the two next sections. From H40% to H60% the difference was significant again. The difference between parents was largest at breast height and smallest at stump height and H60%. All parents followed the same decreasing trend in density with height in the tree. The variation among parents for the vertical and radial positions are shown in Figure 3 and 7, respectively. At all vertical positions, except stump progenies of parent 6 (dark green) and of parent 5 (light blue) showed the most contrasting values. The difference was significant at breast height, H20% and H40%. Parent number 5 had lower wood density for all height sections compared to the other parents, except at stump height.

The radial variation in wood density is presented in Figures 6 (vertical positions) and 7 (parents), and the general pattern was that wood density increase towards the bark. The density observed closest to the pith varied a lot, but the highest observed mean density occurred here for the stump section. The same variance pattern among parents as seen vertically can also be seen in radial direction. For the higher parts of the trunk it was less variation, around the radial density profile (Figure 4). Figures 4 and 5 show examples of the radial density profile at stump (5) and at H60% (4). For the H60% core the growing seasons can be seen (Figure 4).

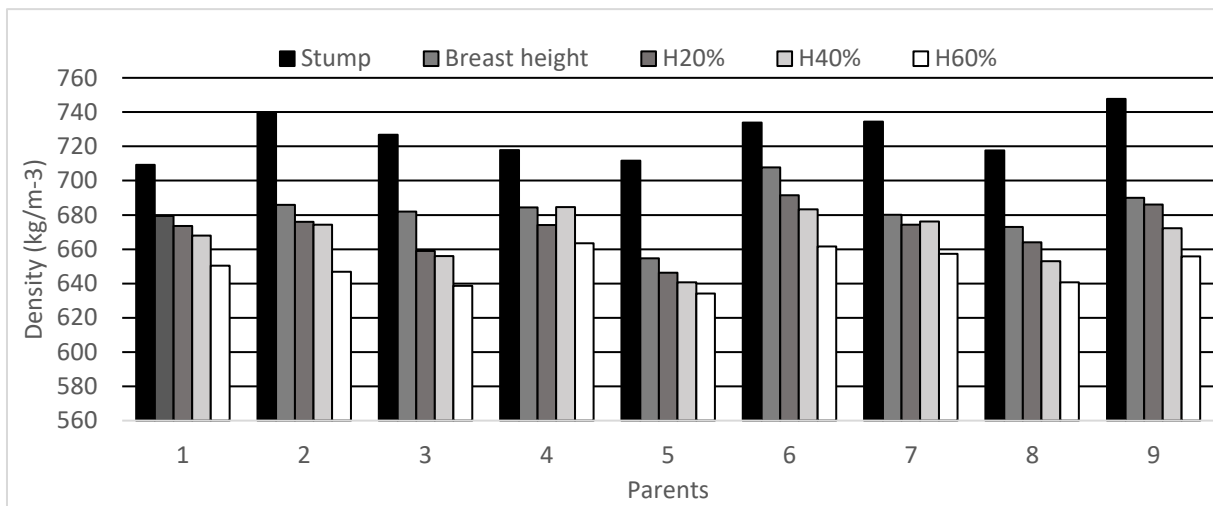
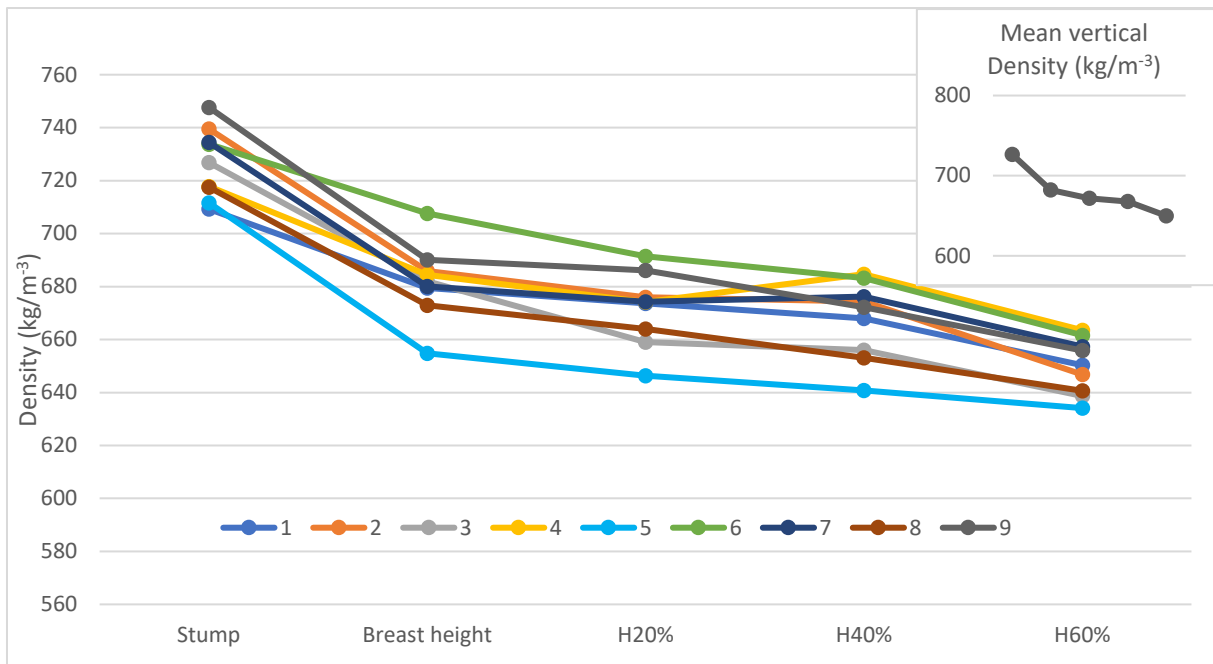


Figure 3. Distribution of wood density by parents (1-9) on a vertical scale from stump to 60% of total tree height

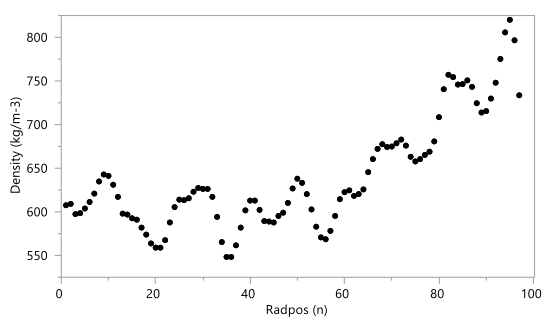


Figure 4. (to the left) Radial density distribution for tree no. 434 at H60%.

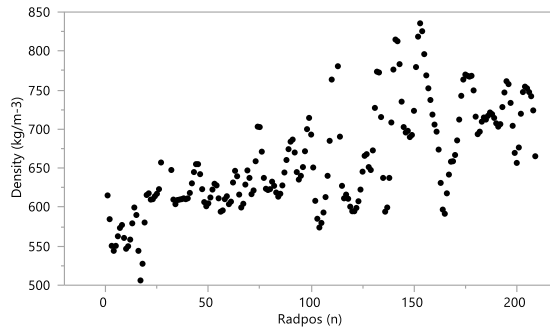


Figure 5. (to the right) Radial wood density for tree no 434 at the stump.



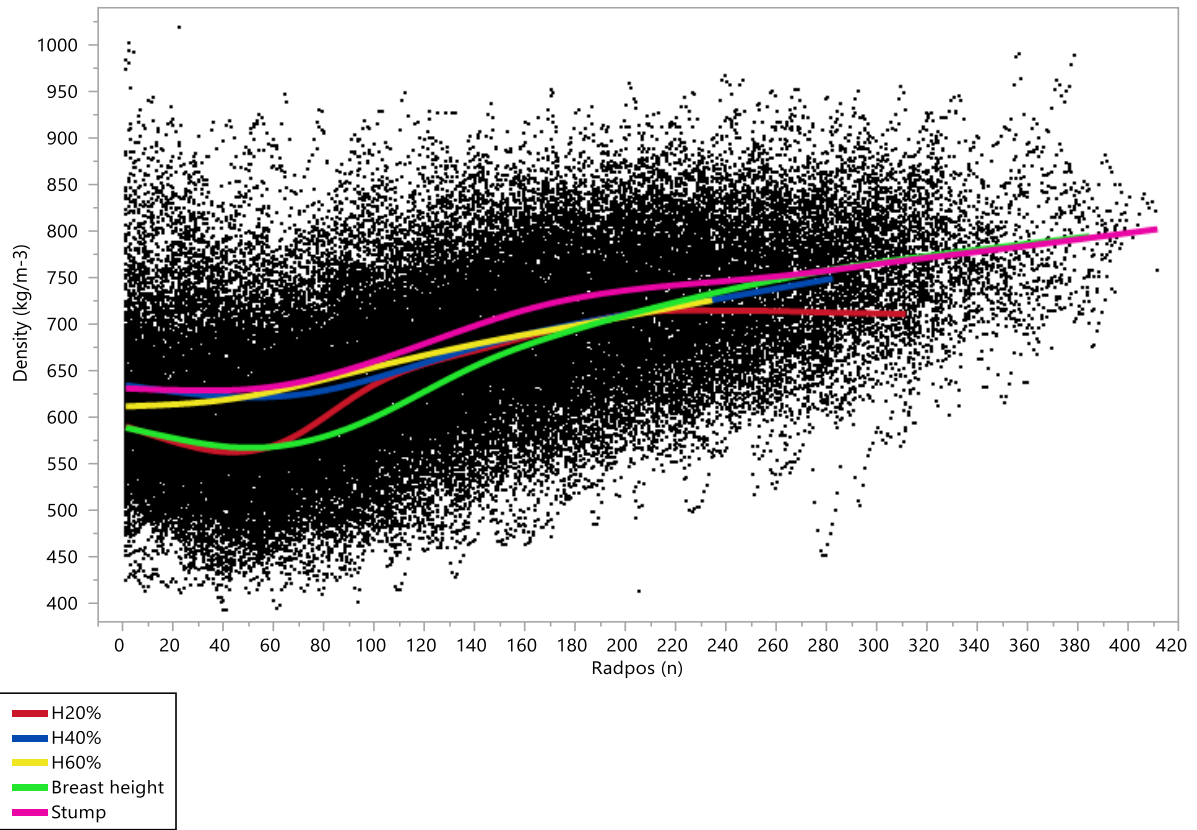


Figure 6. Radial density by vertical positions

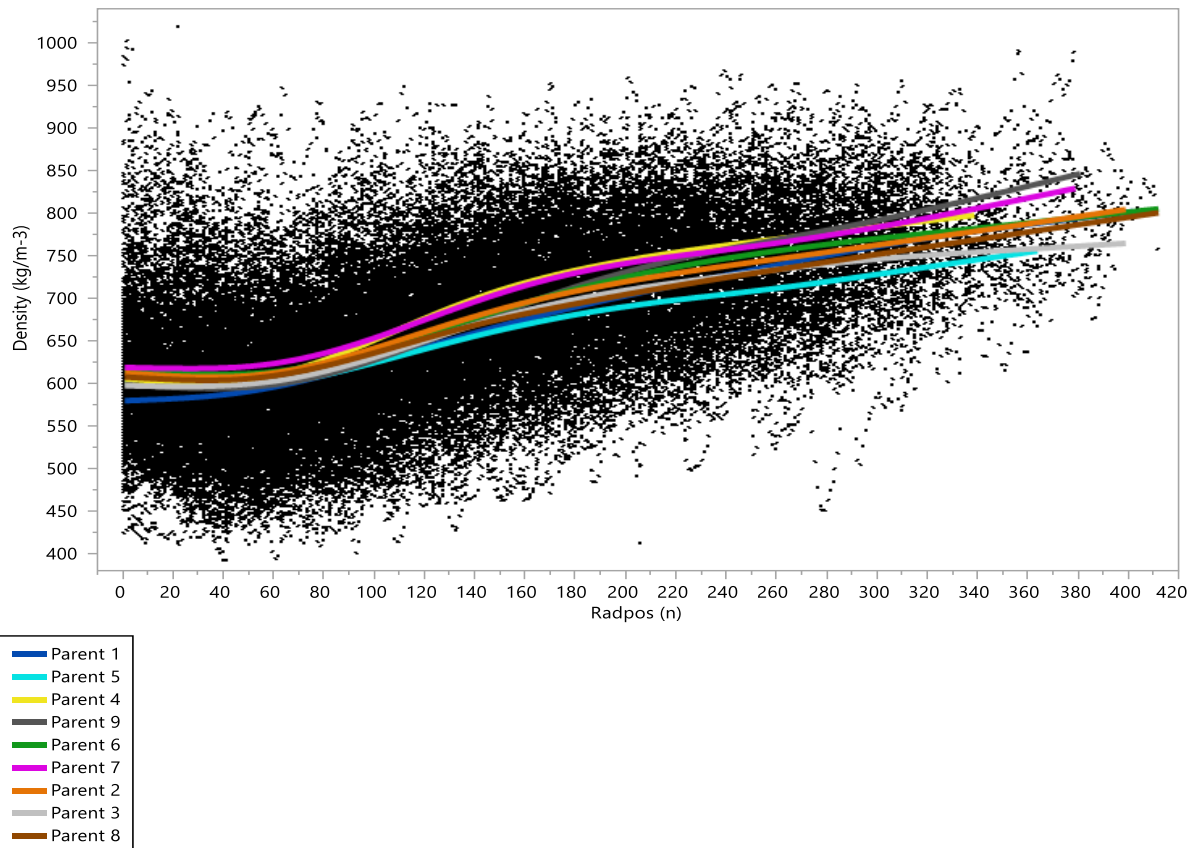


Figure 7. Radial density by parents

### 3.3 Correlations

Both parental-mean (A) and phenotypic (B) correlations between the traits are shown in Table 4. On phenotypic level, total height (H) was correlated with all other growth traits, except diameter of the first green branch (DGB). All significant correlations are positive, except for those related to taper. DBH was positively correlated with all growth traits except height to the first green branch, which was negative. None of the growth traits correlated well with quality traits, wood density and grain angle (GA). Based on parents, the total height was positively correlated with all diameter measured traits, except taper. Taper correlated positively, with diameter traits, and negatively with height traits. No significant correlations with quality traits was found, however positive trends between quality and height traits (H, HGB) occurred. The phenotypic correlations are more significant than the parental-mean correlations despite their lower correlation coefficients. This is due to the statistical test of significance that are heavily depending on the number of observations (81 vs. 9). Density showed no significant correlations with any other traits, but positive correlations with growth might indicate a trend.

Table 4. Pearson's correlation coefficients between pairs of traits. Table A.) Phenotypic correlation between all the 81 trees, and table B.) Genetic correlation estimated from means of the 9 parents.

A.)	H	HGB	DGB	DCB	DBH	GA	Taper
HGB	0.41**						
DGB	0.13	-0.18					
DCB	0.30**	0.03	0.38**				
DBH	0.43**	-0.28*	0.43**	0.42**			
GA	0.07	<-0.00	0.14	0.14	0.17		
Taper	-0.23*	-0.57**	0.31**	0.34**	0.48**	0,05	
Density	0.10	<-0.00	<-0.00	0.12	0.07	0.08	0.08
B.)							
HGB	0.28						
DGB	0.75*	0.11					
DCB	0.78*	0.23	0.86**				
DBH	0.80*	-0.15	0.79*	0.69*			
GA	0.38	0.38	-0.02	0.28	0.31		
Taper	0.30	-0.62	0.66	0.40	0.75*	-0.23	
Density	0.56	0.42	0.08	0.10	0.07	0.10	-0.34
*Correlation significant at the 0,05 level							
** Correlation significant at the 0,01 level							

### 3.4 Trait models

The six models (1.1-1.6) which are based on “Model 1” in the method are shown in Table 4. The 6 replicates were used as a random effect in all models, but was never significant ( $p>0.05$ ). Models 1.1<sub>H</sub> and 1.2<sub>H</sub> predict the total height. Model 1.1<sub>H</sub> is only based on DBH, which has a positive effect on height and is significant. In Model 1.2<sub>H</sub> the Parent and DCB were added as fixed effects, but none of these variables reduced the variance significantly. For the DBH Model 3<sub>DBH</sub>, total height was used as a fixed effect, while in Model 1.4<sub>DBH</sub> parent and DCB were added.  $R^2$  was 0.39 for Model 4<sub>DBH</sub>, and all 3 fixed effects were significant. RMSE was 2.66 cm. The variance of the intercept ( $\sigma^2_a$ ) increased from Model 1.1<sub>H</sub> to Model 1.2<sub>H</sub>, but decreased when going from Model 1.3<sub>DBH</sub> to Model 4<sub>DBH</sub>. In Model 4<sub>DBH</sub> this was negative (-0.17 cm). Grain angle was estimated poorly (Model 1.5<sub>GA</sub>). The best  $R^2$  was obtained when using DBH and stump diameter (SD) as explanatory variables, however SD was not significant when they were used as the only explanatory variable. None of the effects were significant. The most competitive branch (CBD) model, Model 1.6<sub>CBD</sub> included DBH, H and Parent as fixed effects. However, DBH was the only variable reducing the variance significantly. The  $R^2$ -value was 0.18. Equations for the models are presented at the bottom of the table.

Table 5. Table 5. Statistics for prediction models for height, (1.1H,1.2H), Diameter (1.3D,1.4D), grain angle (1.5GA) and diameter of the most competitive branch (1.6DCB).

Summary of statistics	Height		162 rows Diameter		Random = Replicate	
	Model 1.1 <sub>H</sub>	Model 1.2 <sub>H</sub>	Model 1.3 <sub>DBH</sub>	Model 1.4 <sub>DBH</sub>	Grain angle Model 1.5 <sub>GA</sub>	Branch (DCB) Model 1.6 <sub>DCB</sub>
<b>Variance components from model step</b>						
$\sigma^2_a$	0.10	0.21	0.59	-0.17	0.04	-0.08
$\sigma^2_e$	2.03	1.97	7.49	7.06	1.96	2.21
<b>Summary of statistics both fixed and random effects</b>						
$R^2$	0.26	0.38	0.29	0.39	0.12	0.18
RMSE	1.43	1.40	2.74	2.66	1.40	1.48
<b>Summary of statistics, only including fixed effects</b>						
$R^2$	0.22	0.29	0.22	0.42	0.10	0.24
RMSE	1.44	1.36	2.81	2.44	1.38	1.36
<b>p-values of the fixed effects in the 6 models</b>						
Parent		0.734		0.121		0.8274
H			<0.0001*	0.0081*		0.5904
DBH	<0.0001*	0.0023*			0.0430	0.0135*
DCB		0.238		0.0183*		
SD					0.1104	
Model no.	Equation					
1.1 <sub>H</sub>	H = 16.7 + 0.2485DBH					
1.2 <sub>H</sub>	H = 17.1 + 0.2041DBH + 0.1450DCB + Parent X					
1.3 <sub>DBH</sub>	DBH = -2.0 + 0.9399H					
1.4 <sub>DBH</sub>	DBH = 2.7 + 0.6197H + 0.5512DCB + Parent X					
1.5 <sub>GA</sub>	GA = -2.3 - 0.1791SD + 0.2699DBH					
1.6 <sub>GD2</sub>	CBD = -1.1 + 0.0703H + 0.1754DBH + Parent X					

### 3.5 Density models

Because of severe variance close to the stump and pith, the stump height densities and the 30 pixels (9 mm) closest to the pith for all other heights were excluded when modelling radial and vertical variation. Average density of every 20 pixels was used, and the random effect in these models was tree number (Tree no.). The radial variation in density by parents is presented in Figure 8. The figure is based on data from all vertical heights.

Radial position (Radpos20) and percentage of total height (H%) and their interactions, were very strong fixed effects reducing the variation in density. Without these variables included, the predictive force of the models was very low.  $R^2$  increased from 0.65 to 0.69, while the RMSE decreased from 45.0 kg/m<sup>3</sup> to 41.9 kg/m<sup>3</sup> with increasing number of factors in the model (Table 6). The intercept variance ( $\sigma^2_a$ ) was lowest in Model 2.1<sub>D</sub>, but the total variance was lowest for Model 2.3<sub>D</sub>. In Model 2.4<sub>D</sub> the parent was added to model 2.1<sub>D</sub>. However, parent did not reduce the variance significantly. Models 2.5<sub>D</sub> and 2.6<sub>D</sub> are more advanced models with crossings of traits and parent among the fixed effects. Here parent is significant in interaction with Radpos and %H. This improves  $R^2$  to 0.71, and decrease the RMSE to 40.7 kg. Parent is still not significant as a single fixed effect on 5 % level. The p-values for these models were 0.08 and 0.06. Model 2.6<sub>D</sub> also includes H, and H in interaction with H% as fixed effects. Both were significant, and the variance of the intercept ( $\sigma^2_a$ ) was as low as 914.7. The residual variance ( $\sigma^2_e$ ) was highest in Model 2.1<sub>D</sub> (2024.2) and 2.4<sub>D</sub>, (1955.0), medium, in 2.2<sub>D</sub> (1779.2) and 2.3<sub>D</sub> (1758.5), and lowest in 2.5<sub>D</sub> (1662.3) and 2.6<sub>D</sub> (1655.8). All model equations are shown in the bottom of the tables.

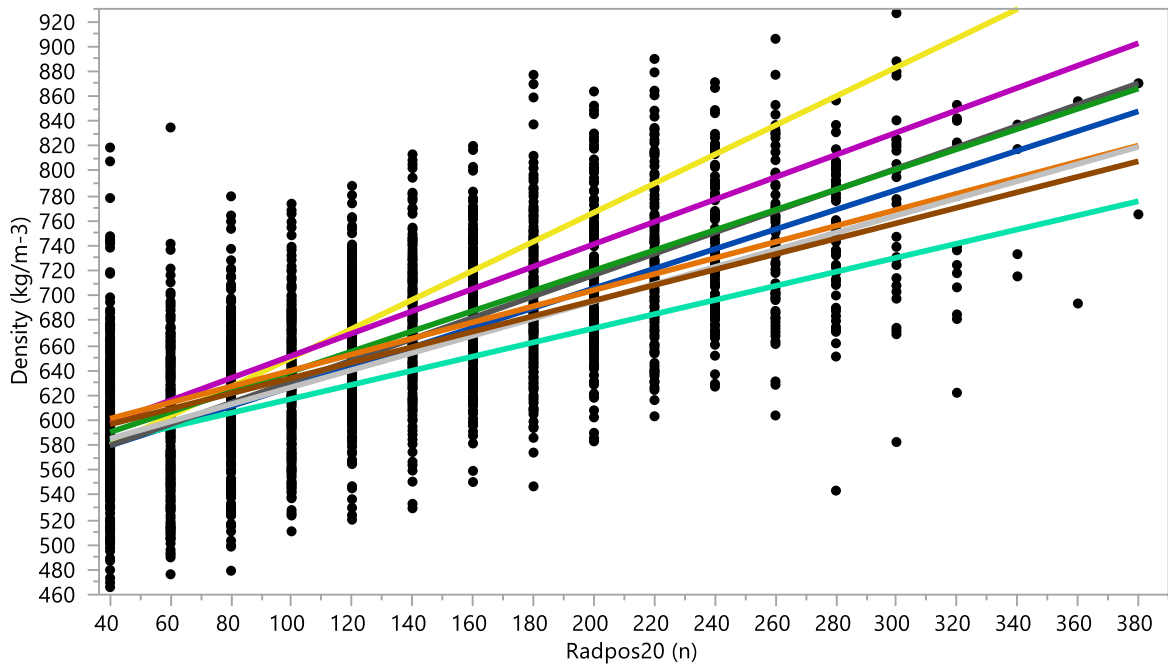


Figure 8. Radial means of each parent for all vertical positions except stump and the 30 pixels (9mm) closest to the pith.

Table 6. Statistics for the prediction models (2.1D-2.6D)

Summary of statistics	5966 rows				No stump	Rad 20
	Model 2.1 <sub>D</sub>	Model 2.2 <sub>D</sub>	Model 2.3 <sub>D</sub>	Model 2.4 <sub>D</sub>	Model 2.5 <sub>D</sub>	Model 2.6 <sub>D</sub>
<b>Variance components from model step</b>						
$\sigma^2_a$	975.1	1015.1	1006.6	940.4	976.6	914.7
$\sigma^2_e$	2024.2	1779.2	1758.5	1955.0	1662.3	1655.8
<b>Summary statistics including both fixed and random effects</b>						
R <sup>2</sup>	0.65	0.69	0.69	0.66	0.71	0.71
RMSE (Mpa)	44.99	42.18	41.93	44.21	40.77	40.69
<b>Summary statistics, only including fixed effects</b>						
R <sup>2</sup>	0.46	0.50	0.51	0.48	0.53	0.54
RMSE (Mpa)	54.61	52.67	52.40	53.53	51.01	50.36
<b>p-values of the fixed effects in the 6 models</b>						
Radpos	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
H%		<0.0001*	<0.0001*		<0.0001*	<0.0001*
Radpos * H%			<0.0001*		<0.0001*	<0.0001*
Parent				0.315	0.077	0.061
Radpos * Parent				<0.0001*	<0.0001*	<0.0001*
H% * Parent					<0.0001*	<0.0001*
H						0.0356*
Radpos * H						0.0003*
Model no.	Equation					
2.1 <sub>D</sub>	Dens = 556.3 + 0.7891Radpos					
2.2 <sub>D</sub>	Dens = 523.8 + 0.8681Radpos + 0.8543H%					
2.3 <sub>D</sub>	Dens = 528.0 + 0.8393Radpos + 0.7720H% - 0.004((Radpos-133.519) * (H%-26.1536))					
2.4 <sub>D</sub>	Dens = 553.4 + 0.8185Radpos + ((Radpos-133.519) * (Parent y)) + Parent X					
2.5 <sub>D</sub>	Dens = 522.2 + 0.8823Radpos + 0.8325H% - 0.004((Radpos-133.519) * (H%-26.1536)) + ((Radpos-133.519) * (Parent y)) + ((H%-26.1536) * (Parent z)) + Parent X					
2.6 <sub>D</sub>	Dens = 598.0 + 0.8792Radpos + 0.8305H% - 0.004((Radpos-133.519) * (H%-26.1536)) + ((Radpos-133.519) * (Parent y)) + ((H%-26.1536) * (Parent z)) + Parent X - 3.6128H + 0.024((Radpos-133.519) * (H-21.1663))					

## 4. Discussion

### 4.1 Generalization of the results

The trees in this study were strongly affected by competition and buffer zone differences. This was especially important for the branch traits, and promoted high variation. Just as expected from Mäkinen (2002). Branch traits are related to the crown, which again is related to total growth and yield. Therefore, a high degree of competition might disguise and subdue trait differences. Many of the branches in the lower parts of the crown were presumed dead, and was not measured, and sometimes there were long distance from the first green branch to the next. When using first green branch and total height, the mean crown percentage in the stand were estimated to be 55 %, but this was not a good reflection on how the crowns appeared. The trees with lowest breast height diameters and shortest crowns were barely alive, which may have affected both the growth and quality traits the last years. Slow growth and narrow rings, may also have increased the wood density (Liepins & Rieksts-Riekstins, 2013).

Because of few trees in some of the families, just a minimum of replicated could be sampled. See Table 1. This might be some of the reason for why several correlations and p-values were relatively poor. This was also implied in the not yet published article by Skrøppa and Solvin (2018). The last thinning focused on growth traits, and many of the smallest trees were cut. Some of the families were therefore less abundant than others, and the family means were shifted. If this thinning had been done solitary on spacing, some parental means could have been lower, and differences between them more significant. In the parent tree selection in 1977, the trees had relatively similar crown and other phenotypical traits. The underlying parental differences however, was uncertain. They have been proven significant for growth, which is a proof that solitary trees may appear differently when they are exposed to competition in stands. The variation in this study was probably caused by a combination of local site index, genetics, silviculture as well as geographical position. This is supported by (Cameron, 1996). The rot and damage discovered in the core samples were not significantly related to families. However, the number of damaged cores gave indication of self-thinning and poorer quality closest to the pith for low vertical positions. Especially the stump.

### 4.2 Growth traits

Skrøppa and Solvin (2018) also did measurements in the same stand three years prior to this study. These data correlate well, and only a small increase in mean growth traits was

discovered. Since the competition rate was high, and self-thinning had begun, a substantial growth was not expected. The crowns of the trees were small and therefore not optimal, and could not fulfil the demands discussed by Hynynen et al. (2010) to optimize production. Mäkinen (2002) show how diameter traits mainly depend on spacing, and stand density. This means that diameter traits would have developed different under a “better” silviculture regime than was the case for this research plot. However, genetic variation is also proven an important factor (Stener & Hedenberg, 2003). DBH was the most varied traits between the parents in this study, but how these differences could have been with optimal silviculture is uncertain. Most likely the strong competition only occurred the last 10-20 years, since the earlier management was more intensive. Parent 6 significantly larger diameters than parent 4 in all height sections measured. However, there were no significant differences between parents for any other traits. Considering branch diameter traits (DGB and DCB), parents 9 and 6 seemed to be weakly better than the rest, while the means of parent 4 were lowest in all diameter traits. Parent 4 also the lowest total height and splits when found, as well as the shortest crowns. Parent 6 had best survival (Skrøppa & Solvin, 2018), and was as mentioned among the best in most traits investigated. Only small differences were found between the height traits (H and HGB), and no significance was found in parental or individual tree means. This is supported by Zeltins et al. (2018). Considerable phenological variation between growth traits found in clones by Rousi and Pusenius (2005). This can explain the differences between the families in this study, since the length of growth periods might vary between parents. The fact that the original trees were gathered north of the planting site might have decreased the growth, and subdued differences (Vihera-Aarnio & Velling, 2008). In quality traits however, no latitude variation was expected (Vihera-Aarnio & Velling, 2017). This implies no effect on grain angle and wood density, all though these are shown to correlate with growth traits.

### 4.3 Density

The mean wood density of  $680.4 \text{ kg/m}^{-3}$  with 12 % moisture is higher than what is found studies on younger trees (Luostarinen et al., 2009). However it is closer related to older birch trees with medium to slow growth in (Dunham et al., 1999). This indicated that there might be a change in mean wood density after a certain point in the rotation. Kuchera (1980) concluded that mean dry wood density at 20 % tree height represents the average density of the tree well. In this study however, using cores from breast height was better. Density showed a non-linear



development from pith to bark. It was found a small drop in density for the inner part of the core, followed by a steady linear increase towards the bark. 30 pixels (9 mm) were therefore excluded from the data. This could be done since this area only represents a very small part of the total area. Variation in density close to the pith was large particularly for the stump, which might be related to mineral contaminations and rot. This is supported by other studies on birch (Kuchera, 1980; Liepins & Rieksts-Riekstins, 2013). The Latvian study implied that wood density in birch would continue to increase as diameter and age promotes. This is because the proportion of juvenile wood, which has lower density, will decrease with aging. The shown radial wood density also revealed seasonal changes, which was visible particularly in the upper parts of the tree. The seasonal changes in birch density were also discovered and discussed by Mottonen and Luostarinen (2006). This implies that wood density also changes with seasons, and may therefore be affected by climate change. Wood density was not significantly correlated with any traits. This is not surprising, all though correlation with DBH occurred in a study by (Stener & Hedenberg, 2003). In conifer trees like Norway spruce, wood density is negatively correlated with diameter growth (Steffenrem et al., 2016). No indications of this were observed in this study. Like (Kuchera, 1980) density decreased with increasing height in the tree. The difference from breast height, to 60 % of the total height was however less than the difference from stump to breast height. This implies that the parts used in industry have approximately the same wood density. The radial variation also decreased with increasing height in the tree.

#### 4.4 Grain angle

No correlations for grain angle with height, diameter or wood density was found. This is consistent with studies in Norway spruce with the same device (Hannrup et al., 2003; Hannrup et al., 2004; Steffenrem et al., 2009; Steffenrem et al., 2016). No significant results between individual trees or in total were found either. In Norway spruce, a strong family variation has been found. This was also absent in birch according to this study. The cause of this is probably the substantial variation both within each tree, and between trees, replicates and parents. It was also concluded difficult to do grain angle measurements on older birch because of its bark morphology. This might have affected the results, and further measurements should be done earlier in the lifespan or higher in the trees to avoid the effect of the rougher bark at the lower parts of the tree.

## 4.5 Parents

Parental or family differences were as mentioned most visible in growth traits. These differences match those found in the not yet published study by Skrøppa and Solvin (2018). The trunk diameters were the only ones found significant, but only between the two most contrasting parents. Parent 6 which had the highest mean DBH was also close to be significantly better than parent 7 ( $p$ -value = 0.06). The significance and trends between parents were consistent in all vertical positions. Parental correlations were based on the means of the 9 parents, and the standard deviations were great compared to the means. Parental correlation values of 0.56 for total height and 0.42 for DBH with wood density imply that there might be a positive trend between wood density with growth traits. This would be positive for plus tree selection in breeding, but more research is needed to confirm these assumptions. From the trends seen in this study, parent number 6 and 9 was better than the others. They were among the best both considering growth and quality traits, and showed good survival (Skrøppa & Solvin, 2018). Parent 4 which has the poorest growth and parent 5 which has the lowest mean wood density and is below average in growth, would be considered worst.

## 4.6 Growth trait and grain angle models

The strong positive correlation between height and diameter growth in the models is consistent with former studies (Liepins & Rieksts-Riekstins, 2013). This is probably because trees which have a well-developed height growth, also produce a bigger and better crone. With a more developed crown more photosynthesis products are made, and it improves diameter growth, both in the trunk and the branches (Mäkinen, 2002). The effect was not significant when modelling height traits, which is natural since the variation between parents was relatively small. For diameter however, a parental effect was expected to be significant, due to the large differences in mean diameter between parents, however, it was not. The  $p$ -value for parent as a fixed in Model 1.4<sub>DBH</sub> was 0.12. Diameter of the most competitive branch was also used to represent competition and branch traits. This was significant in Model 1.4<sub>DBH</sub>, was as expected, since DBH and branch thickness correlate positively (Stener & Hedenberg, 2003). DCB was not significant in height models, but increased the  $R^2$  when in interaction with parents. Models made to predict grain angle (GA) and most competitive branch (DCB) estimated poorly, and few or no significant effects were found. These traits had

a very strong variation, and the random effect explained most or all variation. Model 1.5<sub>GA</sub> was explained 100 % by the replicates, and is not suited for further use.

#### 4.7 Density models

Wood density in this study was most dependent on tree positions. Especially radial, but also vertical. These effects alone explained 50 % of the variance in wood density, and Models 2.1<sub>D</sub>, 2.2<sub>D</sub> and 2.3<sub>D</sub> were made using only these fixed effects. The random effect used was tree number. This was always significant, and explained between 32 % and 37 % of the models. The Wald-test was used to determine significance and percentage of the random effect which is disputed. However, the variance on individual tree level indicated that tree number was important. The mean parental was never significant as a single fixed effect, however, parent 4 was significant in all models. The other parents were significant only in interaction with vertical (H%) and radial positions (Radpos). In interaction with radial positions (Models 2.4<sub>D</sub>, 2.5<sub>D</sub>, and 2.6<sub>D</sub>) all parents except number 6 were significant. This implies substantial parental variation in the change of radial density. Parent 4 for example, has a steeper slope than the rest, and increase more as radial position increases. This can be explained by few trees in high diameter classes because of slow diameter growth. This fit the theory of density being highest in the latest growth rings when competition is strong (Dunham et al., 1999). Parent 5 which has the lowest mean wood density also has the lowest slope considering radial positions. The vertical positions were second most important to wood density, and it lowered the residual variance from 2024 to 1870 kg/m<sup>-3</sup> in Model 2.2<sub>D</sub>. It was significant as a fixed effect with a p-value <0.0001 in all models present (2.2<sub>D</sub>, 2.3<sub>D</sub>, 2.5<sub>D</sub> and 2.6<sub>D</sub>). Parents 2, 4 and 7 had significant interactions with H% in Models 2.5<sub>D</sub> and 2.6<sub>D</sub>. Total height (H) was important for wood density both as a single effect (p = 0.04) and in interaction with radial positions (p = 0.003) in Model 2.6<sub>D</sub>, but showed no effect in interaction with parents. This was expected because of small parental differences in height.

Models 2.1<sub>D</sub> and 2.2<sub>D</sub> were simple models for predicting density, and can be used for practical applications. They explain around 50 % of the variance without the random effect. For industrial round wood production, the most important parts on the trunk is from stump to 60 % of the total height which was the parts predicted by the models. To avoid complex models, and focus on predictions relevant for industry the models presented in this study were kept linear and does not contain all pixel data which was measured.

## 5. Conclusions

Growth and quality traits in silver birch are considered dependant on many factors. In this study, more correlations were found between growth traits than quality traits. All significant correlations were positive, except those between diameters and height to first green branch (HGB) as well as diameter traits and taper. Neither wood density or grain angle correlated with any other traits on individual or parental mean level, and the individual tree correlations were more and stronger than the parental ones. Only diameter at breast height (DBH) was found significantly different between parent 6 (20.15 cm) and parent 4 (14.74 cm). Other parental correlations and traits showed strong trends, but were not found significant because of variance in the data. In modelling height (H) and diameter (DBH), these were positively correlated to each other, and explained 22 % of the variation. The effects of parents and diameter of most competitive branch (DCB) was more important for prediction of DBH than H, and the DCB was even found significant. Parent as a fixed effect was never in any model, however the most contrasting parents often appeared significant on their own. The grain angle data found in this study had strong variation, and was never significant in any correlations or models. Wood density was mostly dependant on positions in the tree. Both radial and/or vertical positions was significant with p-values of  $<0.0001$  in all models. The best models obtained was for wood density, and explained more than 50 % of the variance. A wider study with more data and more trees per parent is needed to conclude with the data presented. This is needed to build functioning breeding program for birch in Norway.

## 6. References

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## 7. Appendix

### Gathered data

Tree no.	H	HGB	DGB	DCB	Split	D20%	D40%	D60%	SD	DBH	Mom	Dad	GA	Taper	Rot	Density
102	22,8	15,5	4,4	3,2	17,3	14,9	12,7	9,9	18,1	16,7	En	To	-0,3	0,55	Nei	695,3
114	20,8	3,9	3,1	3,2		15,9	12,7	9,1	22,3	18,8	To	Fem	-2,5	0,87	Nei	649,0
115	23,8	13,2	3	2,6	16,9	19,9	16,9	13,8	29,5	22,3	To	Seks	-0,5	0,65	Nei	706,9
117	20,9	5,3	2,3	2,9		16,8	13,9		23,6	19,6	To	Åtte	-0,3	0,80	Nei	718,6
119	21,3	6,4	3,7	3,4	11	17,9	13,3	8,1	20,9	18,9	Tre	En	-1,3	0,94	Nei	672,2
125	20,4	5,1	2,2	4	11,5	12,8	10,1	7,4	19,2	14,9	Tre	Sju	-0,8	0,69	Nei	702,0
126	22,2	11,6	3,5	3,2		19,4	15,9	12,6	25,5	21,8	Tre	Åtte	-1	0,77	Nei	659,7
128	19,6	14				11	9,4	7,3	15,7	13	Fire	En	-1	0,54	Nei	651,8
138	19,2	5,7							21,3	18,5	Fem	To	2,3		Nei	659,8
146	24,3	12,8	4,6	5,3	15	15,3	13,1	10,8	21,6	17,2	Seks	En	-2,3	0,48	Nei	720,4
152	22	6,3	4,1	3,2		16,4	13,8	10,5	24,1	18,9	Seks	Sju	-4,8	0,71	Nei	708,3
164	21,3	12,4	2,5	2,6		15,1	12,8	9,8	20,6	17,7	Åtte	En	0,8	0,69	Nei	690,9
166	21,1	4,2	3,7	4,2		18,7	15,1	11,9	27	22,7	Åtte	Tre	-1,3	0,92	Ja	667,9
178	21,7	4,2	3,7	4,2		18,7	15,1	11,9	27	22,7	Ni	Seks	-0,8	0,92	Ja	685,8
204	11,2					12,5	10,7	7,8	20,4	16	En	Fire	-2,3	0,85	Nei	709,8
213	19,3	3,7	3	2,7	10,7	13,7	11,7	8,2	18,9	16,8	To	Fire	0,8	0,83	Nei	693,3
218	21,7	8,9	2,1	2,6		16	13,5	10,3	24,7	18,9	To	Ni	-1,8	0,74	Nei	710,5
224	21	4,1	2,8	4,7	9,6	18,3	15,6	9,7	27	20,4	Tre	Seks	-1	0,99	Nei	763,6
229	20,9	12,7	2,3	4,1		13,6	12,2	9,1	19,9	16,8	Fire	To	0,3	0,69	Nei	746,4
243	19,7	5,2	2,7	2,9	16,3	11,8	9,6	7,4	19,6	14,2	Fem	Sju	-4,5	0,65	Nei	687,8
248	22,5	13,4	2,9	4,4		17,4	13,5	11	23,8	20,3	Seks	Tre	-3	0,76	Nei	720,3
249	22,2	13,9	3,1	3,3		14,5	12,4	9	21,3	16,2	Seks	Fire	-2	0,60	Nei	736,6
250	20,6	11,6	2,7	4,2		14,4	11,9	9	17,1	16	Seks	Fem	0,5	0,58	Nei	605,8
260	19,5	8,4	5,8	3,9	8,4	15,2	12,8	10,5	22,5	17,3	Sju	Seks	0,5	0,65	Nei	700,3
279	23,3	12	5,1	2,5	12	15,1	13,9	9,8	19,7	17	Ni	Sju	-2,8	0,55	Nei	709,2
304	20,1	6,2				14,5	13,5		17,9	16,4	En	Fire	-1,3	0,71	Nei	711,3
309	23,7	14,9	4,3	5,2	18,7	17,9	14,8	12,4	25,2	20	En	Ni	-0,8	0,59	Nei	636,4
322	20	6,3	2,8	2,3		14,5	11		17,9	16,2	Tre	Fire	-2,3	0,78	Ja	685,1
340	20,6	10,1	2,3	2,2		12,7	9,9	7,6	18,4	14,4	Fem	Fire	-0,8	0,61	Nei	675,0
345	22,7	11,6	3,8	3,1	16,4	15,4	13,8	9,3	20,5	16,8	Fem	Ni	-1,8	0,61	Nei	693,1
347	22,9	12,5	2,9	3,1		20,4	16,8	12,8	24,5	22,9	Seks	To	-0,5	0,81	Nei	700,7
349	22	17,7	1,9	2,7	12,4	11,7	10,2	7	17,7	13,3	Seks	Fire	-2,5	0,53	Ja	675,6
367	23,8	17,1	1,4	2,3		13	10,2	7,9	15,7	14,3	Åtte	Fire	-2	0,49	Ja	642,7
372	20	12,9	2,1	2,7		17,7	14,1	11,2	19,9	18,7	Åtte	Ni	-2,5	0,70	Nei	658,2
376	19,9	14,8	4,3	2,9	14,8	11,7	9,9	7,6	18,2	13,5	Ni	Fire	-1	0,56	Nei	702,0
403	20					16,9	15		20,9	19,2	En	Tre	-4,3	0,74	Nei	689,0
409	24	17,2	1,9	5,2	17,5	16,2	13,3	10,3	23,8	18,1	En	Ni	-1	0,60	Nei	709,1
415	23,3	5,7	2,3	3,5	15,5	18,7	15,4	11,6	24,6	20,7	To	Seks	-1,3	0,72	Nei	726,6
416	21,7	10,8	1,7	1,4		11,3	9,3	7	17,2	12,7	To	Sju	-3,3	0,49	Nei	653,0



425	19	9,7	1,4	3,4	12,1	13,1	11	7,2	19,9	14,9	Tre	Sju	-4,8	0,76	Nei	689,7
430	19,4	10,5	3,2	2,1		10,5	8,7	9,5	17,5	13,2	Fire	Tre	-3,3	0,36	Nei	645,2
434	19,6	9,3	0,8	1,5		10,6	8,3	6,1	17,9	12,4	Fire	Sju	-3,3	0,60	Nei	672,3
435	21,8	14,2	1,8	2	14,4	12,4	10,5	7,9	15,1	15	Fire	Åtte	0,3	0,60	Ja	659,0
439	21,1	3,4	2	3,6	15,3	17,1	12,7	8,7	23	21	Fem	Tre	-5	1,08	Nei	669,4
453	23,7	13,7	2,7	3	19,8	19,1	15,6	13,2	25,7	20,6	Seks	Åtte	-2,5	0,57	Nei	701,1
456	20,4	6,3	1,6	2,6		12,5	9,9	7,4	16,8	13,4	Sju	To	-0,5	0,55	Nei	698,8
458	17,8	13,7	1,4	1,9	11,6	10,4	8,2	6,4	14,1	11,5	Sju	Fire	-2,8	0,54	Nei	689,4
459	21	3	2,8	3	15,2	15,5	12,7	8,7	23,2	19,2	Sju	Fem	-1,3	0,93	Nei	668,9
460	22,1	5,9	2,2	3,4		18,3	14,4	10,9	25,9	21,1	Sju	Seks	0,3	0,85	Ja	738,5
465	20,7	7	1,5	2,2	14,2	13,3	11	8,4	15,8	15,6	Åtte	To	1	0,65	Ja	728,4
478	24,2	13,9	4	8,6	14,3	19,7	17,1	11,2	28,3	23,5	Ni	Seks	-0,5	0,93	Nei	711,7
505	21,1	10,6	3,4	9,2	11,3	15,9	15,1	7,7	22,4	17,7	En	Fem	-1,3	0,88	Nei	690,8
518	21,4	9,5	3,8	3,2		15,9	13,1	9,9	22,6	18,3	To	Ni	-0,3	0,73	Ja	712,5
529	20,3	12,1	2,6	3,2	14,1	12,7	10,3	7,7	20,2	14,9	Fire	To	-3	0,66	Ja	721,0
530	18,6	10,1	2,7	1,6	14,7	11,1	8,9	6,3	18	13,6	Fire	Tre	-2,3	0,74	Nei	712,4
542	18,8	4,1	4,8	3,7	13,8	19,2	15,2	10,6	26,5	21	Fem	Seks	-1	1,04	Nei	659,2
548	21,1	9,6	3,3	3,7	16,5	20,1	17	12,6	29,8	22,9	Seks	Tre	-1,5	0,90	Nei	663,8
550	21,9	11	3,5	3,1	16,9	20,6	16,1	12,4	28,4	23,4	Seks	Fem	0,3	0,93	Ja	653,4
565	14,9	7,2	2,7	3,3	11	13,4	9,5	7,8	19	14,5	Åtte	To	-2,5	0,88	Nei	650,3
566	20,9	7,9	3	2,5	16,7	14,3	11,6	8,9	23,8	17,3	Åtte	Tre	-1,3	0,75	Ja	704,7
574	22,1	11,9	3,7	6,7	15,4	18,2	15,3	11,6	25,8	19,3	Ni	To	-0,3	0,64	Nei	684,0
575	17,9	3,9	4,2	2,2		14,6	11,3	10	21,7	17,1	Ni	Tre	-1,3	0,76	Nei	686,2
603	23,3	13,1	2,6	3,4		17,8	15,1	11,4	26,3	20,3	En	Tre	-1	0,70	Nei	639,4
608	22,7	16	2,4	3,3		14,4	11,7	9,2	20,2	15,9	En	Åtte	-1,8	0,54	Nei	658,4
612	22,1	12,2	2,9	3	15,3	15,8	12,3	8,7	22,6	18,3	To	Tre	-2	0,80	Nei	667,8
617	20,7	3,5	2,9	3,4		17,2	13,4	9,7	23	20,2	To	Åtte	-1	0,95	Ja	651,7
618	22,8	12	3,7	9,3	12,4	17,2	15,3	8,2	24,3	18,8	To	Ni	-3,3	0,85	Ja	686,6
620	23,8	9,6	4,2	3,6	15,3	20,3	17,8	13,6	29,6	23,7	Tre	To	-2,8	0,78	Ja	664,1
622	21,9	12,2	3,6	3	16	15,6	13,3	10,4	24,8	17,9	Tre	Fire	-0,8	0,64	Ja	657,5
623	18,7	5	4,7		5	14	11,7	6,5	21,9	16,6	Tre	Fem	-1,5	1,02	Ja	653,6
637	20,4	3,4	2,8	3,3	12,1	17,2	13,9	9,8	26	20,7	Fem	En	-2,8	1,00	Nei	621,9
638	20,5	10,8	1,4	2,2	15,4	12,4	10,2	8,2	19,8	14,2	Fem	To	-3,5	0,55	Nei	662,1
642	18,6	4,8	3,7	3		14,8	9,8	6,9	22,3	17	Fem	Seks	-3,5	1,02	Nei	673,0
644	17,8	12,6	2	2,2		12,2	10,2	8,9	19,5	13,9	Fem	Åtte	-1,5	0,53	Ja	658,5
646	21,1	6	4	5,3	14,5	19,4	17,4	11,8	29,9	24,1	Seks	En	-1,8	1,08	Nei	713,3
653	20,3	3,3	3,6	3,9		17,1	14,3	9,5	26,5	21,1	Seks	Åtte	-0,3	1,06	Nei	690,4
654	23,4	14,9	2,3	2,8		17,7	15,2	12,2	25,8	20,4	Seks	Ni	-2,5	0,63	Ja	721,5
656	20,3	14,1	2,4	6,3	14,1	15,3	11,9	9,2	22	16	Sju	To	0,5	0,62	Nei	693,5
664	21,2	10,7	3	3,9	14,2	15,1	12,4	8,9	21,9	16,7	Åtte	En	-1,5	0,68	Nei	663,5
665	20,7	2,9	4	6,2	11,5	18,4	14,4	10,4	25,2	21,7	Åtte	To	0,3	1,02	Ja	682,9
680	18,3	14,8	1,8	1,7	15,1	11,1	8,5	5,2	16,1	12,5	Ni	Åtte	-0,3	0,75	Ja	703,4





**Norges miljø- og biovitenskapelige universitet**  
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