

# Growth and timber quality evaluation of 33 European beech (*Fagus sylvatica* L.) provenances from a site in Southern Sweden

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## Abstract

This study aims to shed more light on the differences in growth and timber quality characteristics between European beech provenances at its northern distribution margin. Data was collected from a provenance trial established in 1998 in southern Sweden to determine the growth and development of 33 provenances of European beech (*Fagus sylvatica* L.) originating from within Europe. A generalized linear mixed model with a post-hoc Tukeys' test was used to analyze survival, growth and tree structural traits that define timber quality in plantation forestry. Several provenances performed well with respect to height increment, stem crookedness, mortality, and the tendency to produce double stems and lateral branches in the lower or upper part of the stem.

Results showed higher survival rates for 'Brumov-Sidonie' and 'Val di Sella' from Czech Republic and Italy respectively. No difference was found between provenances in basal area increment (or diameter), but a good performance for native provenance 'Torup' from Sweden in height increment was found. The Austrian provenance 'Hinterstoder' showed the lowest stem crookedness. 'Perche' provenance from France and 'Alsted F.413' from Denmark had the lowest tendency to develop double stems below 4,5 m. Provenances 'Farchau (SH)' and 'Urach (BW)' both showed the lowest tendency to develop double stems above 4,5 m on the stem. Tree tendency to develop lateral branches below 4,5 m was lowest for 'Farchau (SH)' provenance from Germany. No significant differences were found between provenances for the frequency of lateral branch divisions above 4,5 m on the stem.

The results show that even though beech can be considered a plastic species with a good adaptive response to varying environmental conditions, the genetic background has an important role in shaping stand development. Establishment of specific beech provenances can lead to better quality development in Southern Sweden and should be considered.

**Keywords:** trial, climate change, adaptation, growth, survival, Sweden



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## Abbreviations

|      |                                                   |
|------|---------------------------------------------------|
| AIC  | Akaikes' Information Criterion                    |
| BAI  | Basal area increment                              |
| GLMM | Generalized Linear Mixed Model                    |
| NPP  | Net primary production                            |
| SMHI | Swedish Hydrological and Meteorological Institute |

# 1 Introduction

## 1.1 European beech in a changing climate

Tree growth and species distributions are expected to be impacted by anthropogenic climate change. Projected climate change scenarios include an increase in annual temperatures of 2-6 °C, and a decrease in precipitation of up to 40 % (Christensen et al 2007). Increasing risks of drought and heat-induced tree mortality emerge as potential associated risks for forests (Bosela et al 2018). The balance of the forest ecosystem depends on the environmental conditions, and as these conditions change, the equilibrium of the forest will be affected as well (Thuiller et al 2008; Robson et al 2018). Climate change will thus have significant implications for both natural forests and plantation forests globally (Kirilenko et al 2007).

The projected climate change scenarios presents challenges for Scandinavia with associated impacts on biodiversity and on the functioning of ecosystems (Felton et al 2010; Dury et al 2011; Kirilenko et al 2007). The effect of increasing carbon dioxide concentrations coupled with increasing temperatures could also have positive effects on plantation forestry with an associated increase in Net primary production (NPP) (Kirilenko et al 2007; Dury et al 2011). Accordingly, current indications are that Swedish forests are experiencing a growth increase due to longer growing seasons and warmer climate conditions (SCCV 2007; Kirilenko et al 2007; Michelot et al 2012). The estimated effect could result in a growth increase of 20-40 % for Norway spruce, Scots pine, and birch by the end of this century (SCCV 2007).

However, the increase in carbon allocation depends on the water and nutrient availability which might be limited under future climate change scenarios as well (Eilmann 2014; Bravo et al 2017).

The direct evolutionary pressure that climate change presents on European forests occurs within a timeframe that can be considered very short when put in relation to natural selective pressure (Bravo et al 2017). The natural adaptation ability of a tree

species to grow and develop depends on the genetic composition within the individual (Kramer 2007; Paffetti et al 2012; Bravo et al 2017).

The frequency and severity of extreme events and wind storms are expected to increase (IPCC 2013). Understanding of its implications and identification of the most severe risks posed for tree growth and survival becomes important (Felton et al 2010). The long-term response and resilience of tree species to extreme weather events are not fully understood (Malcolm et al 2002) as the ecosystems form complex interactions with the climate (Bravo et al 2017). In Sweden, since 1988, warm years with higher temperatures and precipitation rates of lower than normal have been increasingly common throughout the country. The summer of 2018 saw frequently occurring drought and several forest fires also in the northern parts of the country (SMHI (Swedish Meteorological and Hydrological Institute), 2019).

Broadleaves have recently received increasing attention in Sweden because of several traits considered advantageous as the forestry sector faces climate change related challenges. Establishing broadleaves has been promoted a possible option for decreasing climate change related risks that may affect the ecological values of the forest (Felton et al 2016). Beech has so far shown good ability to cope with wind-storm damage when established in a mixed forest with Norway spruce in Southern Sweden (Bolte et al 2010).

Anthropogenic climate change has implications also for changes in migration and colonization rates of forest tree species, which are projected to occur within this century (Malcolm et al 2002; Hamrick 2004; Bosela et al 2018). European beech (*Fagus sylvatica* L.) is likely to migrate further northward as the climate warms, the length of the growing season rises and late frost becomes less of limiting factor for recruitment (Bolte et al 2010; Bosela et al 2018). Beech may at the same time lose habitat at the southern edge of its distribution (Kramer et al 2010). Although European beech in particular is considered to have good adaptational response to abiotic and biotic stress, the expected changes in local temperature (Stömme et al 2018) and water regimes (Frank et al 2017) is still considered major threats to the species (Bravo et al 2017).

Understanding of the degree of influence of genetic predisposition as opposed to the environmental factors becomes increasingly important. Especially as sufficient information about development at the northern distribution limit is scarce (Stener, 2008). Thus, gathering knowledge of the adaptational ability of beech at its northern distribution margin could lead to further understanding of the future development and suitability of beech in a changing climate in Sweden.

## 1.2 Past and future of European beech in Sweden

European beech stands have in the past been considered to be of recent origin in southern Sweden. Historical evaluations from the 17th and 19th centuries show that beech dominated forest stands which covered large areas of southern Sweden during the Middle Ages (Brunet 1995). Beech could have started to form forest communities in southern Sweden as early as 1,500 years BC (Brunet & Fritz 2011). Socio-economic changes during the 19th century initiated a change in the Swedish forest landscape that transformed wood pastures into managed dense forests for timber production. This change led to an increment of the total amount of forested areas and standing timber stock, but also led to a decrease in relative shares of broadleaved trees. This altered the habitat conditions for many sensitive species associated with temperate broadleaved trees (Brunet et al 2012).

The current beech distribution in Sweden is characterized by stand structures in decline of old beech trees, with lower habitat availability for many specialised epiphytic and saproxylic species as a result (Brunet et al 2012). Several protected nature areas have been created which has helped to preserve old growth beech stands and their high biodiversity values. One example is the Söderåsen National Park, which was formed in 2001 and covers 1,625 hectares of broadleaved deciduous forest, consisting mainly of old beech trees (Sveriges Nationalparker, 2019).

The broadleaf component of Swedish forests has between 1985 and 2010 increased with 32 % (Nilsson & Cory 2018). The contribution of European beech to Swedish forests is modest with 2,5 % of all standing stock, including natural forest cover (Nilsson & Cory 2018). The beech forest stands are all located in southern Sweden. This region is characterized by lowland areas of average annual temperatures of 8 °C, with yearly mean precipitation rates of 700-800 mm (SMHI 2018).

The Swedish forest sector is preparing for continued exposure to extreme weather events and wind storms from forecasted climate change (SCCV, 2007). Consequently, Sweden has changed part of its forest policy and developed a strategy to increase the proportion of broadleaves in the landscape (Lodin et al 2017). By introducing a grant to forest owners the aim has been to increase the attractiveness of reforestation with deciduous species by lowering the cost of planting and of seedling protection. However, interest in broadleaf establishment from forest owners has so far been low (Lodin et al 2017). Possibly, alternative establishment of broadleaves could present a risk adverse choice in regions prone to the hazards of wildfires as well (Terrier et al 2013) and may act as important barriers to limit the fire spread (Girardin et al 2015).

Increasing the share of beech in mixed species stands in plantation forestry could also provide a possible risk reduction strategy as weather conditions become more extreme (Bolte et al 2010). The possible introduction of more southern provenances

of beech in Swedish forestry also constitute a possible risk adverse adaptation strategy (Löf et al 2012). This study aims to contribute with additional information on European beech provenances growth and development in Sweden.

### 1.3 The European beech provenance trials in southern Sweden

The regeneration material of many broadleaved species (including beech) from Swedish indigenous forestry is scarce, which is compensated by importing material mainly from Poland and Germany (Stener 2008). At the same time, the knowledge about northern transfer effects on survival, vitality and growth is limited. Gaining knowledge of these effects might be crucial since the northern limit of natural distribution for European beech is found in southern Sweden. To increase the knowledge of the transferring effects of beech material within Europe two series of international beech provenance trials (1993/95 and 1996/98) were established throughout Europe. One trial in each of the series was established in southern Sweden (*Figure 1.*).

The genetic origin of beech can be traced to several regions in Europe of differing climate conditions. In these areas, the species has adapted in response to the local selective pressure and the limits imposed by environmental conditions (Weigel et al 2018). Currently, the entire beech distribution in Europe is represented in 217 provenances (Robson et al 2018). 33 of these European provenances have been established at a trial in Trolleholm, southern Sweden (coordinates: 55°56'01.0"N 13°19'31.0"E, altitude 100 m a.s.l.). This trial is the basis for the data used in this thesis to determine the development and growth of beech at its northern distribution margin. The provenance trial was established in 1998 as part of a European collaborative research project to gain further understanding of beech development under changing climate conditions, and supply northern Europe with suitable regeneration material in the future (Stener 2008, Robson et al 2018).

The scientific base for the above mentioned approach is however, not fully developed, and although much research has been conducted so far (two inventories have been carried out in 2001 and 2007), the understanding of the response of various beech provenances to climatic conditions in southern Sweden is still limited.

## 2 Objectives of the thesis

The main objective of this work is to study the degree of influence of genetic predisposition on growth and development of European beech at the northern distribution margin of the studied species, situated in Southern Sweden. The 33 beech provenances included in this study originate from vastly different latitudes and altitudes, together making up a genetically diverse establishment. As the climate in the future will change it is of interest to find new plant material that originates from outside of Sweden that is well adapted to future growth conditions, and may continue to produce high quality timber. Results from the present study aim to improve and add to the understanding of the adaptability of European beech to Swedish growth conditions.

The results from the last inventory performed in 2007 by Skogforsk at this trial site concluded that additional growth and development was needed for further conclusions to be drawn about the studied variables. In this thesis, data was collected eleven years later (twenty years from establishment). The main survival and growth differences between provenances established in southern Sweden is assessed, with comparisons between inventories 2018/19 and 2007.

The specific objectives are:

- (1) To identify differences among European beech provenances on survival rate.
- (2) To evaluate the differences in growth (basal area, diameter and height) among European beech provenances from the last inventory in 2007.
- (3) To identify general trends and correlations in the timber quality characteristics from the tree shape of beech provenances along a Europe-wide geographical gradient of climate and elevation.

The following hypotheses were tested:

- (1) The mortality rate of south-eastern European beech provenances could be lower since they have adapted to harsher climate conditions and environments in the early stages of growth.
- (2) Swedish beech provenances could have better growth since they are naturally adapted to exploit resources at these latitudes.
- (3) Traits of the tree structure that included increased crookedness and development of double stems may lead to a decrease in growth.

The hope is to supply northern Europe with further information on the suitability of regeneration material in the future, with emphasis on the probable climate change scenarios and the projected northwards movement of beech populations.



## 3 Material & Methods

### 3.1 Beech – the studied species

Beech constitutes one of the most widespread tree species in Europe (*Figure 1.*), with a natural distribution range from Spain in the west to the Black Sea in the east. The southern limit of its distribution can be found in Sicily, stretching up to southern Sweden and southern Norway (Houston Durrant et al 2016). It is considered a plastic species with high genetic variability, a beneficial trait for adaptation to environmental disturbances (Paffetti et al 2012).

As a large deciduous tree species, beech normally reaches heights of up to 35-40 m. Contrary to many other broadleaves, it has the ability to grow well even towards the later stages of its life cycle. Beech dominates the temperate forest zone, where moisture availability is not a limiting factor for growth. In the south, dry conditions limit forest expansion. In Spain, beech is only found growing at altitudes of 1000 m or more (Houston Durrant et al 2016).

Compared to broadleaf species in lowland areas, beech can be considered a late flusher in areas of warm climate, where elevation is below 500 m. The bud burst date varies to some extent with temporal and spatial patterns, but not as much as for oak or larch (Vitasse & Basler 2013). On higher altitudes of over 1500 m, budbreak has shown to commence earlier than for example oak, sycamore and ash (Vitasse & Basler 2013). On high altitudes the bud burst date has shown to be regulated to a greater extent by temperature than by photoperiodism (Strömme et al 2019).

Beech is the most shade-tolerant tree species in the temperate zone and may regenerate well in full shade. For this reason, silvicultural systems with continuous crown coverage can be used with beech that relies on natural regeneration for the establishment of the new crop (Matthews 1989). The shelterwood system is commonly used in Germany, Sweden and Denmark. The shelterwood system is beneficial as it limits frost exposure (Agestam et al 2003), drought, and exposure to cold winds for

the regeneration. It also lowers the risk of growth of weeds that can compete with the trees for resources (Matthews 1989).

European beech is not demanding of soil conditions and can be found on both acidic and alkaline soils, with a pH ranging from 3,5 to 8,5. However, as a late successional species, beech dominates areas of moderately fertile soils. Its growth is optimal on humid, nutrient-rich soft soil. It does not grow however, in areas where flooding is common during parts of the year, or where soils are very compact and the root system is unable to penetrate into the ground properly (Houston Durrant et al 2016).

The root system of beech is quite shallow in comparison to that of other broadleaves, making it susceptible to drought at lower latitudes of its distribution (Bosela et al 2018). Beech is considered quite sensitive to late frost when the first leaves have flushed (Principe et al 2017). Late frost currently constitutes a limiting factor for

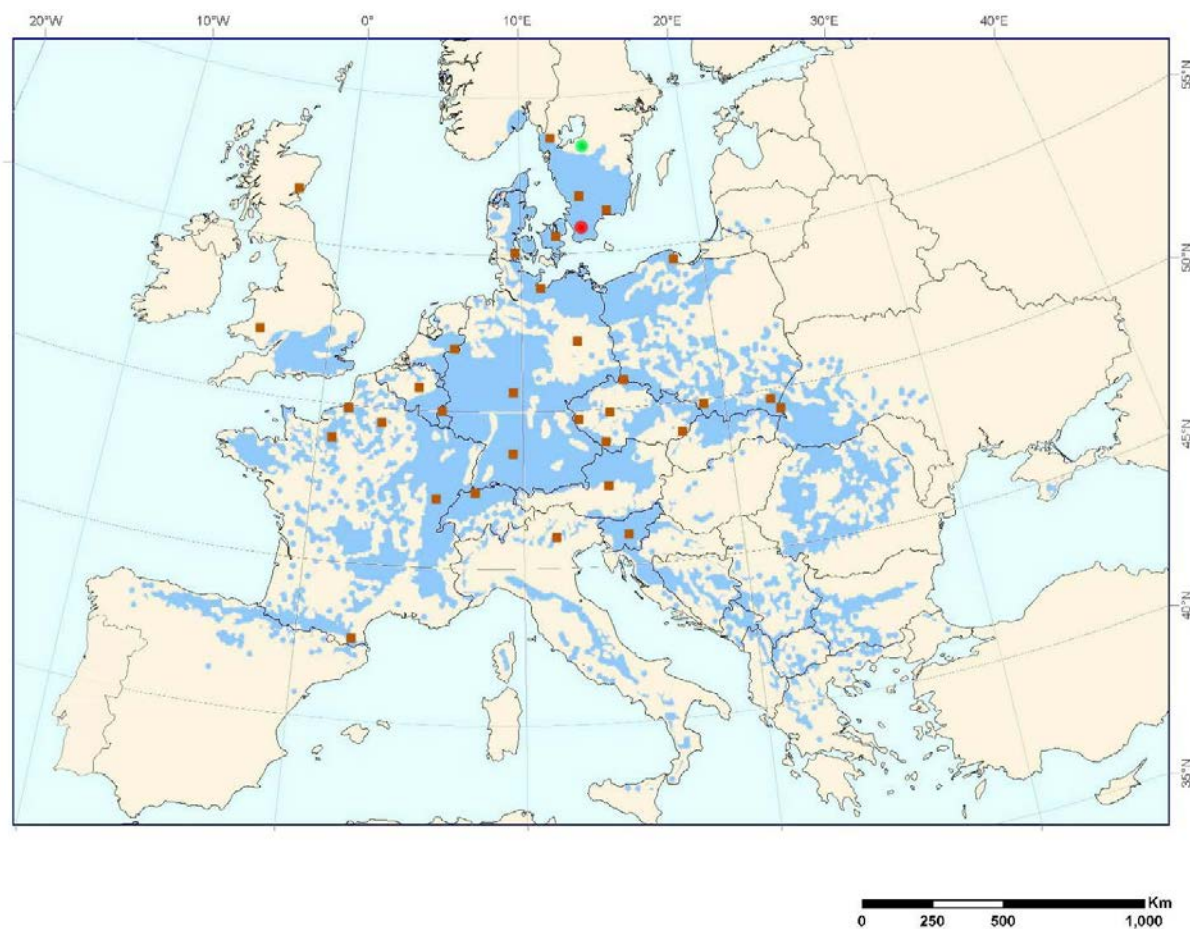


Figure 1. The current European beech distribution in Europe. The red circle indicates position of the Trolleholm trial site. The green circle indicates the position of Rånna trial site. The brown squares represent the locations of origin for the 33 provenances of European beech included in the study. Adapted after map provided by EUFORGEN, CC BY-SA2.0.

natural northward expansion in southern Scandinavia (Hofmann et al 2015). It is often found growing on slopes or in hilly terrain where cold air does not linger.

In the area of Götaland, Southern Sweden, beech constitutes 2,5 % of all standing stock (Nilsson & Cory 2018). Old-growth beech forest contributes as habitat for several species of lichens and bryophytes (Fritz et al 2009) and has important conservation value for several red-listed species.

Beech is commonly grown in forests in Germany, Belgium and Denmark and is important for the timber production in Europe. In Sweden, it can be found in plantation forestry to a very small extent. The wood after harvesting is fine-grained and hard, with few knots present. It has many different usages including furniture, boat-building, construction of musical instruments, flooring, stairs and for plywood (Houston Durrant et al 2016).

### 3.2 The site

The data was collected during autumn/winter 2018/2019 in a beech provenance trial situated at Trolleholm, Skåne (coordinates 55°56'01.0"N 13°19'31.0"E, altitude 100 m a.s.l.). The field trial was created as part of an international collaboration studying beech provenance trials throughout Europe (Robson et al 2018). In the trial 33 beech provenances were planted and they likely correspond to variations in gene expression towards growth and phenological expression. They also originate from areas of different environmental conditions (*Table 1.*). The experiment in Trolleholm is one out of two created in Sweden (see *Figure 1.*). The second trial is situated in Rånna, 58° 27'N, 13° 50'E, altitude 85 m.

The provenance trial at Trolleholm was established in spring 1998 on former agricultural land through planting of two year-old bare-root seedlings in a randomized block design with three blocks and 33 plots in each block. In total 99 plots were planted over 1 ha of even terrain, where each provenance was represented in 3 randomly distributed plots over the area (see *Figure 2.*) Each plot contains 7 rows with 7 trees in each row, giving a total of 49 trees per block. Initial tree planting distance was 1,25 m between each tree and between rows. In total, 4 851 seedlings were established as part of the trial. The seedlings were brought up at the Institute for Forest Genetics and Forest Tree Breeding in Grosshansdorf, Germany (see *Table 1.* for detailed description of provenances).

The soil at the site consists of deep, fertile glacial till containing particles of 0,2 to 0,02 mm. The soil had at establishment been ditched, presenting mesic water holding conditions. Average annual precipitation for the local area during years 1998-2018 were 755 mm. Rainfall during the period of growth (May-Sept) was 335 mm (44% of annual amount), indicating that drought has been infrequent in these parts.

## Trolleholm provenance trial

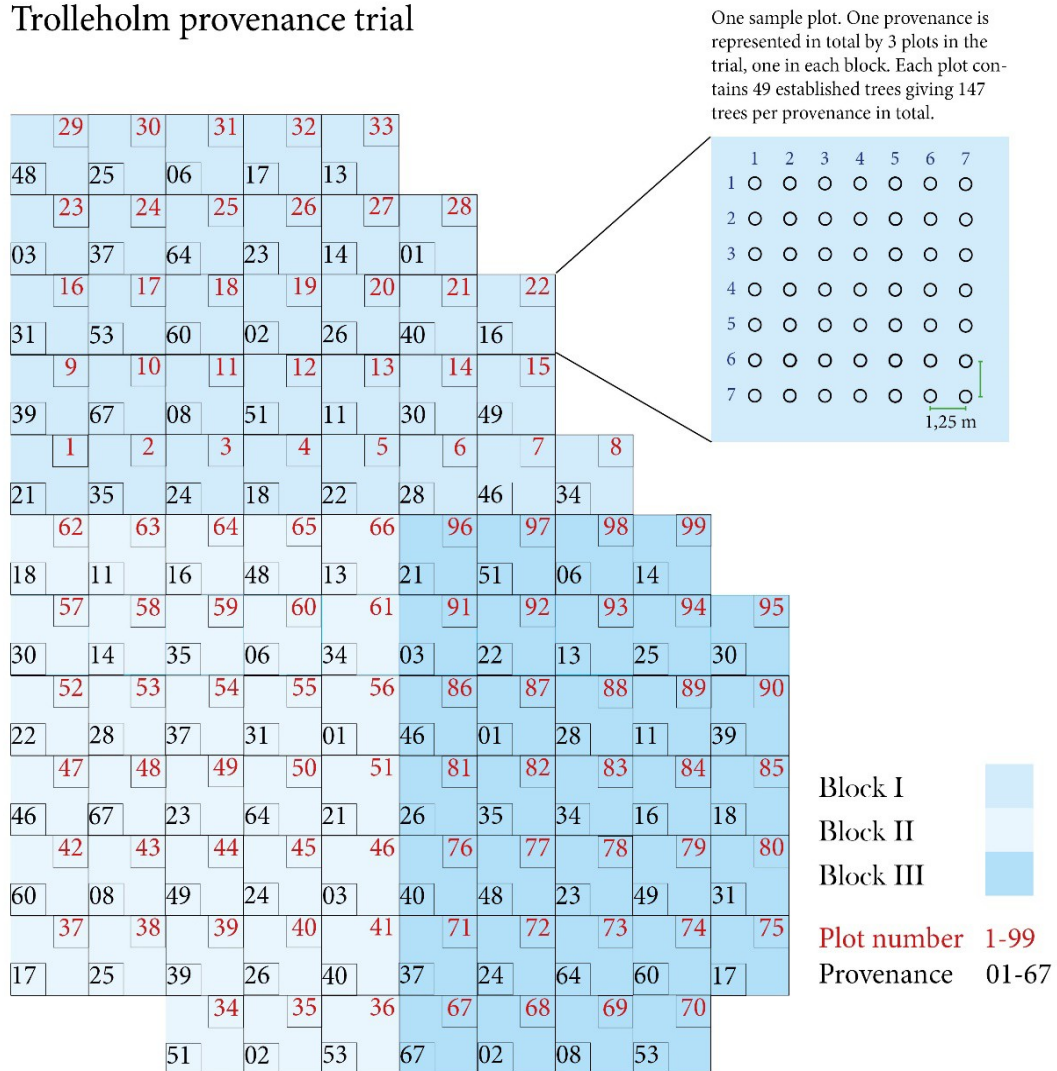


Figure 2. An overview of the trial site area.

Average annual temperature for 1998-2018 was 8,2 °C, with monthly max of 17,4 °C (July) and monthly minimum of 0 °C (January) (SMHI, 2018b). The trial site is surrounded by two rows of beech trees to prevent edge effects. The surrounding forest stands consist of mixed species of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Red oak (*Quercus rubra*) presenting moderate shelter against exposure to strong winds.

Initial evaluations of stand development were made in 2001-2002 by the Swedish forest research organization Skogforsk (Stener 2002). In 2007, a follow-up study

was performed with additional measurements of diameter, height, mortality rate, lateral branch division, stem crookedness and phenological expression (Stener 2008).

### 3.3 Data collection

Since 2007, stand development has been unrecorded until autumn/winter 2018/2019, when the data for this thesis was collected. The following variables were measured in the trial: survival, stem diameter, height, stem crookedness, amount of double stems above and below 4,5 m, and amount of lateral branch divisions above and below 4,5 m.

- a) **Survival** (Surv) Scored as 1 if alive and 0 if dead for all trees ( $n=4851$ )
- b) **Stem diameter** (dia18) was recorded for all living trees ( $n=2844$ ) on a continuous scale (in mm) with a *Haglöf DP II* measuring caliper connected to an *Allegro 2 Field Computer*.
- c) **Tree height** (H18) describes the total height, and was recorded for 101 randomly sampled trees (in dm) with a *Haglöf Vertex IV* with a T3 transponder, also on a continuous scale. Height increment was then calculated from the last data recorded in 2007 by Skogforsk.
- d) **Stem crookedness** ( $C_{rk}$ ) of the trees was determined subjectively on a scale from 0, 1, 2 through visual inspection from two perpendicular viewpoints for all living trees ( $n=2844$ ). A zero indicates a stem form that is straight from two onlooking angles, 1 indicates crookedness from one of the two onlooking angles, and 2 indicates poor stem quality where crookedness is found from both points of view.
- e) **Double stem** ( $D_{stmU}$  and  $D_{stmL}$ ). The frequency of double stems was measured for all living trees ( $n=2844$ ). Here, a double stem is defined as a branch larger in diameter than 1/3rd of the main stem it is branching off from. Double stems found in the lower portion of the trunk ( $D_{stmL}$ , below 4,5 m height) were recorded separately from double stems present on the trunk above 4,5 m ( $D_{stmU}$ ). For both of these two variables, the amount of double stems was recorded ranging in value from 0 to 4.
- f) **Lateral branch division** ( $F_{rkL}$  and  $F_{rkU}$ ) was measured on a discrete scale counting number of lateral branch divisions for all living trees ( $n=2844$ ). Branches forking off from the lower part of the stem ( $F_{rkL}$ , below 4,5 m) were recorded separately from the branches growing from the upper part of the stem ( $F_{rkU}$ , above 4,5 m). If the tree had several stems, lateral branches on the stem of largest diameter were only included.

Table 1. Established provenances at Trolleholm trial site

| Prov no | Name             | Country (region)          | Number of trees sampled | Long  | Lat.  | Alt (m) |
|---------|------------------|---------------------------|-------------------------|-------|-------|---------|
| 1       | Perche           | France                    | 98                      | 0,55  | 48,42 | 205     |
| 2       | Bordure Man      | France                    | 73                      | 0,77  | 49,53 | 80      |
| 3       | Picardie         | France                    | 72                      | 3,1   | 49,25 | 140     |
| 6       | Plateaux du      | France                    | 69                      | 5,83  | 46,8  | 600     |
| 8       | Pyreness Or      | France                    | 93                      | 2,32  | 42,92 | 670     |
| 11      | Heinerscheid     | Luxembourg                | 60                      | 6,12  | 50,08 | 423     |
| 13      | Soignes          | Belgium                   | 70                      | 4,42  | 50,83 | 110     |
| 14      | Aarnink          | Netherlands               | 102                     | 6,73  | 51,93 | 45      |
| 16      | Gotze Delchev    | Bulgaria                  | 86                      | 23,73 | 41,57 | 1450    |
| 17      | Westfield (2002) | Great Britain             | 93                      | 3,42  | 57,67 | 10      |
| 18      | BE 95 (4003)     | Great Britain             | 113                     | 2     | 51,72 | 140     |
| 21      | Grasten, F413    | Denmark                   | 58                      | 9,58  | 54,92 | 50      |
| 22      | Alsted, F.603    | Denmark                   | 82                      | 11,65 | 55,4  | 50      |
| 23      | Torup            | Sweden                    | 71                      | 13,2  | 55,57 | 40      |
| 24      | Trolle Ljungby   | Sweden                    | 87                      | 14,5  | 56,12 | 40      |
| 25      | Gullmarsberg     | Sweden                    | 91                      | 11,65 | 58,37 | 25      |
| 26      | Farchau (SH)     | Germany (Schlesw.-Holst.) | 108                     | 10,67 | 53,65 | 55      |
| 28      | Schulechtern     | Germany (Hesse)           | 94                      | 9,68  | 50,35 | 535     |
| 30      | Belzig (ST)      | Germany (Brandenburg)     | 99                      | 12,42 | 52,05 | 140     |
| 31      | Urach (BW)       | Germany (Baden-Wrtenb.)   | 62                      | 9,45  | 48,47 | 760     |
| 34      | Oberwil          | Switzerland               | 105                     | 7,45  | 47,17 | 570     |
| 35      | Hinterstoder     | Austria                   | 94                      | 14,1  | 47,72 | 1250    |
| 37      | Val di Sella     | Italy                     | 115                     | 13,5  | 46,02 | 1150    |
| 39      | Jaworze          | Poland                    | 102                     | 19,17 | 49,83 | 450     |
| 40      | Tarnawa 7        | Poland                    | 61                      | 22,33 | 49,47 | 540     |
| 46      | Domazlice-Vyhl.  | Czech Rep.                | 72                      | 12,77 | 49,4  | 760     |
| 48      | Jablonec N.N.    | Czech Rep.                | 98                      | 15,23 | 50,8  | 760     |
| 49      | Brumov-Sidonie   | Czech Rep.                | 116                     | 18,05 | 49,05 | 390     |
| 51      | Horni Plana-Ce.  | Czech Rep.                | 95                      | 14    | 48,85 | 990     |
| 53      | Postojna Masun.  | Slovenia                  | 84                      | 14,38 | 45,63 | 1000    |
| 60      | Sekowiec, 160b   | Poland                    | 61                      | 22,82 | 49,25 | 320     |
| 64      | Nizbor           | Czech Rep.                | 86                      | 14    | 50    | 480     |
| 67      | Bilowo 115, 116  | Poland                    | 74                      | 18,17 | 54,33 | 250     |

### 3.4 Statistical analysis

A Generalized Linear Mixed Model (GLMM) was used to analyze the effect of ‘*Provenance*’ on each of the studied variables in *section 3.3*. A random effects structure was included in the model to consider spatial dependence of measurements. Block, plot (nested in block) and tree (nested in plot), and block random effects were added to the model, affecting the intercept of regression. This made it possible to consider within stand variation that could not be explained only by the included independent variables (Winter 2013).

To determine the best random structure, different random structures were fitted by maximizing the restricted log-likelihood in a beyond optimal model (Zuur et al 2009). The random structures were then compared with each other, and the random structure with the lowest value of the Akaike information criterion (AIC) was then selected as the most parsimonious one.

In addition to ‘*Provenance*’, other fixed effects such as the traits of the tree structure as double stem, stem crookedness and lateral branch division were also included as independent variables to evaluate their effect on response variables. This allowed estimation of the main objective of the thesis: to estimate differences among beech provenances in survival, growth and the traits of the tree structure which define timber quality (*Table 2*). The model is summarized as follows:

$$y_{ijk} = \alpha_0 + \alpha_1 * f(traits) + \alpha_2 * Provenance + w_k + u_{jk} + v_{ijk} + \varepsilon_{ijk} \quad [1]$$

where  $y_{ijk}$  is the studied variable for tree  $i$  in plot  $j$  and block  $k$ ;  $\alpha_i$  represent the parameter regression covariate coefficients;  $f(traits)$  is linear function of traits of the tree structure variables. *Provenance* represents the dummy variable for beech provenances;  $w_k \sim N(0, \sigma_k)$  is the block random effect;  $u_{jk} \sim N(0, \sigma_{jk})$  is the plot random effect,  $v_{ijk} \sim N(0, \sigma_{ijk})$  is the tree random effect and  $\varepsilon_{ijk} \sim N(0, \sigma_e)$  is the error term.

A *post-hoc* analysis was then performed with multiple comparisons of means using Tukey’s contrasts to determine differences between beech provenances. In order to preserve model accuracy a visual inspection of residuals was also performed to determine the degree of heteroscedasticity of residuals. This was detected when the residual variance was not homogeneous. This was solved by fitting a variance function with weights to control the variance of residuals, when necessary (see ‘*Appendix 2 - Tables*’ for details) (Pinheiro & Bates 2000). Different error distributions were used to fit the final models depending on the possible values of the response variable (*Table 2*).

The packages ‘*nlme*’ (Pinheiro et al 2015) and ‘*multcomp*’ (Hothorn et al 2008) were used for the statistical analysis. All analyses were performed in the software *Rstudio version 1.2.1335* (R Core Team 2015)

### Survival

The data describing the ‘Survival’ variable was binary, where a 0 indicated a dead sample and a 1 indicated a living sample. The GLMM used a binomial error distribution to represent this in the model.

Table 2. The eight variables studied in this thesis, their abbreviations and the error distributions.

| Dependent variable ( $y_{ijk}$ )            | Description                                 | Abbreviation      | Error distribution | Variable type |
|---------------------------------------------|---------------------------------------------|-------------------|--------------------|---------------|
| Survival                                    | 1 = alive, 0 = dead                         | Surv              | Binomial           | Binary        |
| Basal area increment & final diameter size  | cm <sup>2</sup> /year & mm (2018)           | BAI               | Normal             | Continuous    |
| Height increment & Total height             | cm/year & m                                 | H18               | Normal             | Continuous    |
| Stem crookedness                            | Sum of crooked on-looking angles, 0, 1 or 2 | C <sub>rk</sub>   | Poisson            | Count         |
| Double stems lower part of stem             | Amount of double stems (< 4,5 m)            | D <sub>stmL</sub> | Poisson            | Count         |
| Double stems upper part of stem             | Amount of double stems (> 4,5 m)            | D <sub>stmU</sub> | Poisson            | Count         |
| Lateral branch division lower part of stem  | Amount of branch divisions (< 4,5 m)        | F <sub>rkL</sub>  | Poisson            | Count         |
| Lateral branch division, upper part of stem | Amount of branch divisions (> 4,5 m)        | F <sub>rkU</sub>  | Poisson            | Count         |

### Basal area increment & final diameter size

Following the recommendations of Garcia (2018), the stem diameter measurements were not included in the mixed linear regression as an independent variable. According to the author, when the aim is to model new growth development under changing environmental conditions, stem diameter and basal area should be omitted from the fixed effects. This is because these variables simplify a complex natural growth pattern. For this reason, the current size of the trees should not be included as an independent variable as there is no causal relationship between existing tree size and increased growth (Garcia 2018). Rather, the relationship is such that increased growth leads to greater tree size.

The diameter values recorded in 2018 were used to calculate basal area increment for each tree. Mean BAI was calculated based on a cylindrical tree shape in cm<sup>2</sup>/year. The six recorded variables D<sub>stmL</sub>, D<sub>stmU</sub>, F<sub>rkU</sub>, F<sub>rkL</sub>, C<sub>rk</sub> and ‘Provenance’ were then included in the fixed effects of the generalized linear mixed model to describe any potential effects on the basal area increment BAI. The random structure included plot nested in block and tree nested in plot and block.



### Height increment and total height

Only a subsample of trees and provenances were recorded for practical reasons in 2018/19. In order to predict the height accurately for the remainder of the trees, nine models describing the height-diameter relationship were made based on suggestions from previous literature (Table 3.). The height increment (HI) was then calculated for the period 2007-2018. Included in the random structure was tree nested in plot and block, and plot nested in block, as well as only block.

Table 3. Models suggested by previous literature describing the relationship between height and diameter fitted to a linear regression.

| Model | Formula                                                   | Author                                           |
|-------|-----------------------------------------------------------|--------------------------------------------------|
| 1     | $H18 \sim \mu + dbh18$                                    | Lei et al (2009)                                 |
| 2     | $\log^{H18} \sim \mu + dbh18$                             | Zucchini et al (2001)                            |
| 3     | $\log^{H18} \sim \mu + \log^{dbh18}$                      | Curtis R.O. (1967)                               |
| 4     | $H18 \sim \mu + a + b * dbh18 + c * (dbh18)^2$            | Henricksen H.A. (1950) & Curtis R.O. (1967)      |
| 5     | $H18 \sim a * (dbh18)^b$                                  | Stoffels & van Soest J (1953); Stage A.R. (1975) |
| 6     | $\log^{H18} \sim a + b / (dbh18+1)$                       | Schreuder HT, Hafley WL, Bennett FA (1979)       |
| 7     | $\log^{H18} \sim dbh18 / (a + b * dbh18 + c * (dbh18)^2)$ | Curtis RO (1967)                                 |
| 8     | $H18 \sim \log^{dbh18}$                                   | Aldea, J. pers. comm. (2019)                     |
| 9     | $H18 \sim dbh18^2 / (a + b * dbh18)^2$                    | Aldea, J. pers. comm. (2019)                     |

### Stem crookedness

Stem crookedness was evaluated on a scale from 0,1,2 as the sum of onlooking angles where crookedness was found. A generalized linear mixed model with Poisson error distribution was used to describe differences among beech provenances and the effect of traits that describes the tree structure as independent variables. The random structure included only block.

### Double stem

The tendency of beech to develop double stems was also analysed among provenances. Here, the data was fitted to a generalized linear mixed model with poisson distribution. For double stems on the upper part of the tree, five independent variables 'dia18', 'D<sub>stm</sub>L', 'F<sub>rk</sub>L', 'C<sub>rk</sub>' and 'Provenance' were included in the fixed effects. Block was included in the nested random effects.

### Lateral branch division

The tendency of the tree to develop several branches in the lower (< 4,5 m) and in the upper (> 4,5 m) portion of the stem can give an indication of timber quality for specific provenances. Two generalized linear mixed models were used to fit the relationship between amount of forks and several independent variables. For the

model describing forks at the lower part of the stem, block and plot were considered whereas only block was used in the final random effect structure.

## 4 Results

### 4.1 Survival

Overall stand mean survival was 58,7 % in 2018 which was lower in comparison to measurements taken in 2007 when mean survival was 77%. A Tukey's pairwise comparison revealed also a high performance for provenances '*Farchau (SH)*.' from Germany, and '*Val. Di Sella*' from Italy. Highest survival was found for the Czech provenance '*Brumov-Sidonie*' where survival was 78,9 % (*Figure 3*).

The Danish provenance '*Grasten F413*' had the highest mortality with stand survival of 39,5 %. Provenances '*Heinersheid*' from Luxembourg, '*Sekowiec 160b.*' and '*Tamawa*' from Poland had also high within-stand mortality. Swedish provenances showed modest results: '*Torup*', '*Trolle-Ljungby*', and '*Gullmarsberg*' had together 56,5 % as a mean value for survival. See *Appendix 2 – Supplementary Table 1* for further details.

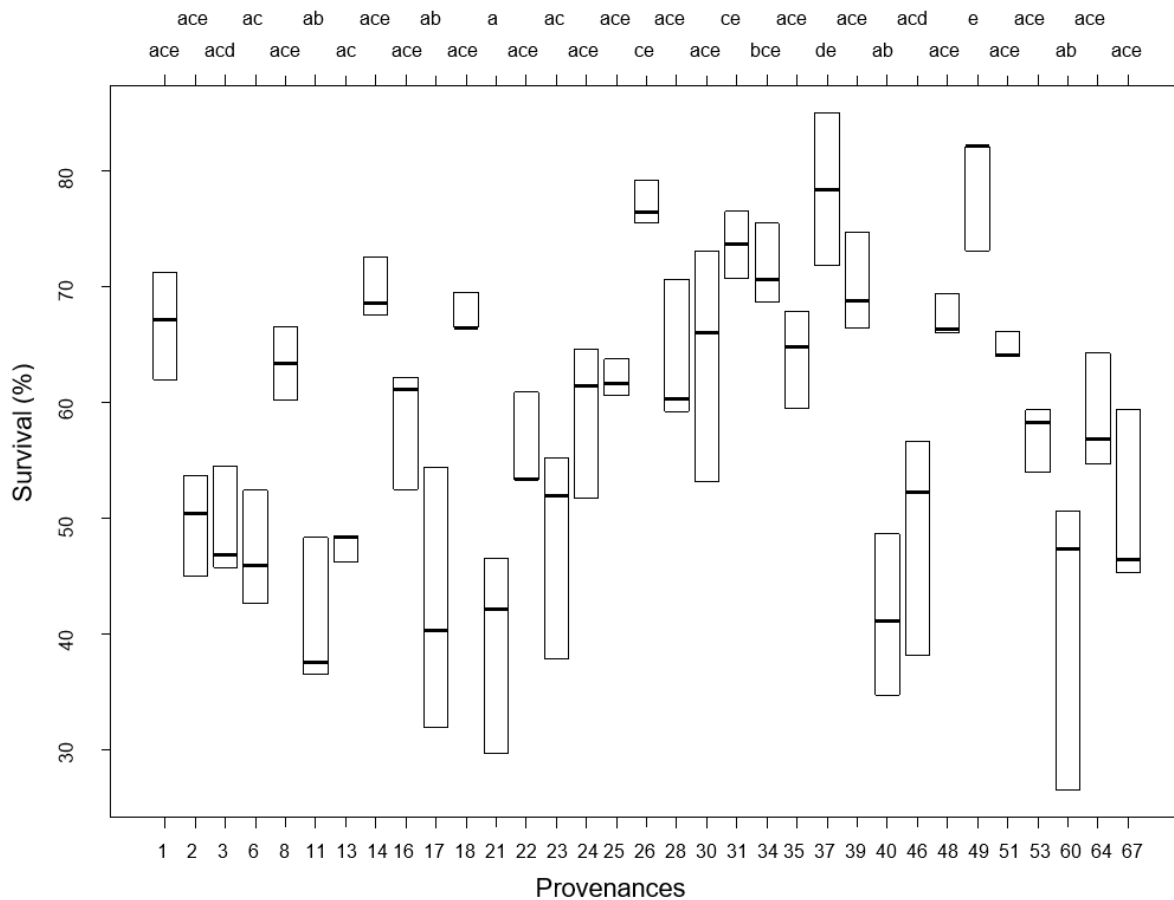


Figure 3. Survival provenance differences at 2018. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

## 4.2 Basal area increment & final diameter size

A pairwise comparison revealed that no significant differences between provenances could be found for BAI or diameter size at 2018/19 (*Figure 4 & Supplementary figure 2*). The general tree growth was quite even despite the varying genetic backgrounds of the plant material.

The six recorded variables  $D_{\text{stmL}}$ ,  $D_{\text{stmU}}$ ,  $F_{\text{rkL}}$ ,  $F_{\text{rkU}}$ ,  $C_{\text{rk}}$  and ‘Provenance’ showed to be significant independent variables in the mixed linear regression model that described the basal area increment BAI (*Appendix 2 - Supplementary Table 2*). BAI was negatively correlated with increased crookedness, indicating that straight tree stems had higher diameter growth. BAI increased double stems above & below 4,5 m, as well as lateral branch division above and below 4,5 m.

The average stem diameter for the whole stand was 8,1 cm at 2018, compared to 2007 when the diameter was 7,1 cm. The mean diameter for specific provenances at 2007 and 2018 are presented in Figure 5.

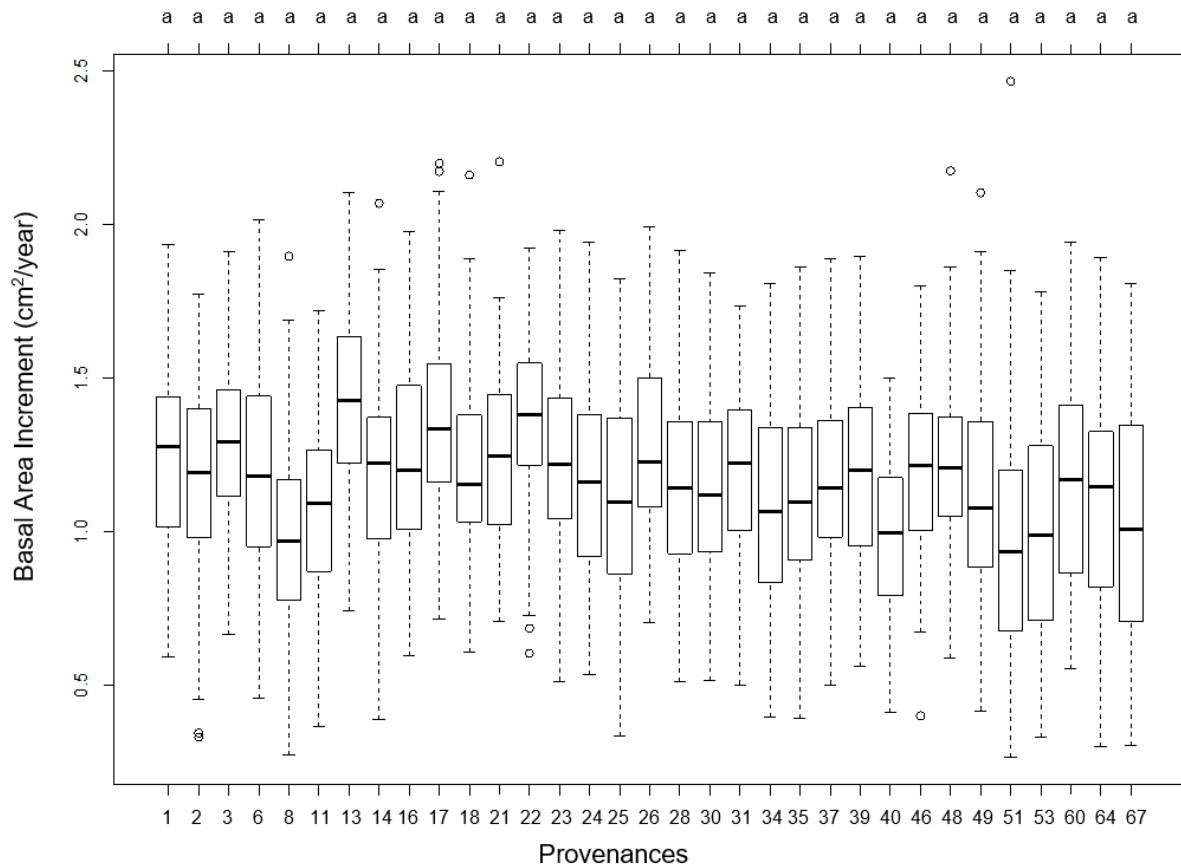


Figure 4. Differences in basal area increment for provenances in 2018. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

### 4.3 Height increment & total height

Mean stand height for 2018 was 9,60 m ( $n=101$ ). In comparison, the mean height of 2007 was 4,01 m ( $n=3744$ ). Pairwise comparisons revealed the provenances 'Westfield' from Great Britain, 'Torup' from Sweden, 'Sekowiec, 160b' from Poland and 'Nizbor' from Czech Republic as superior in height performance. The German provenance 'Urach (BW)' and the Swiss provenance 'Oberwil.' had lower height increment (Figure 6.).

The frequency of double stems in the lower and upper part of the stem ( $D_{\text{stmL}}$ ,  $D_{\text{stmU}}$ ) and the amount of lateral branch divisions in the lower and upper part of the stem ( $F_{\text{rkL}}$ ,  $F_{\text{rkU}}$ ) showed to be positively correlated with height. Height was affected negatively by increased stem crookedness (*Appendix 2 - Supplementary Table 3*).

The height-diameter curve for model 6 is presented in *Appendix 1 – Supplementary Figure 1*. Akaike's Information Criterion was used to evaluate the 9 height-diameter models (see *Table 3*). AIC selected number 6 as the most parsimonious. This model was used for predicting height values for 2018 and finally to calculate height increment from 2007.

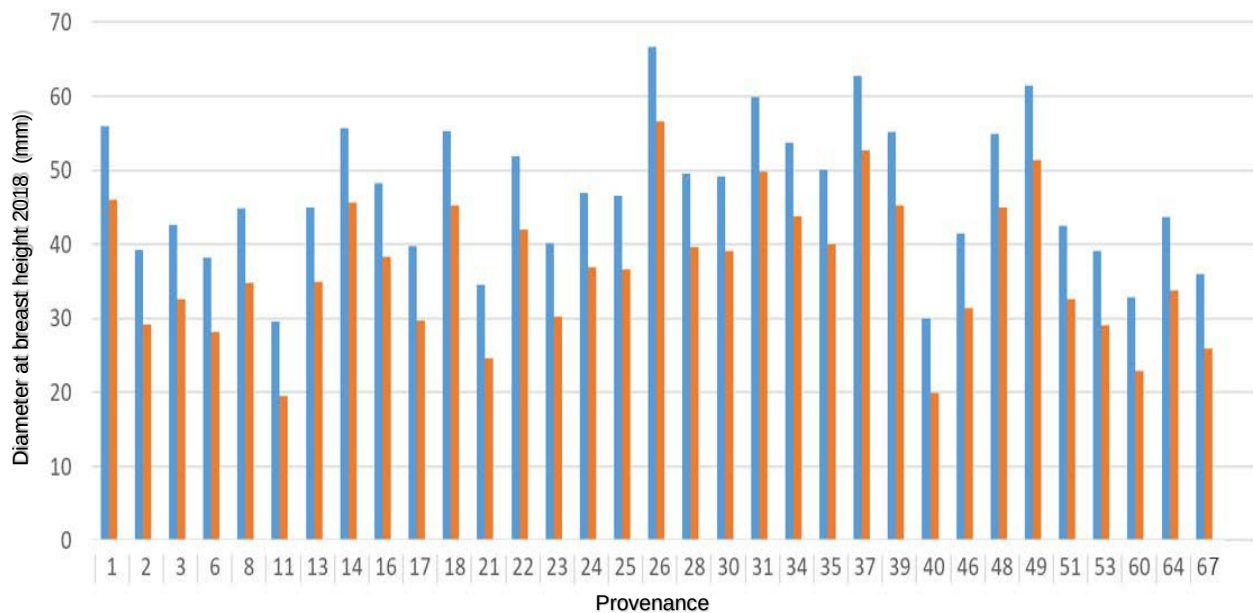


Figure 5. The mean stem diameter for each provenance at breast height in 2007 (orange) and 2018 (blue).

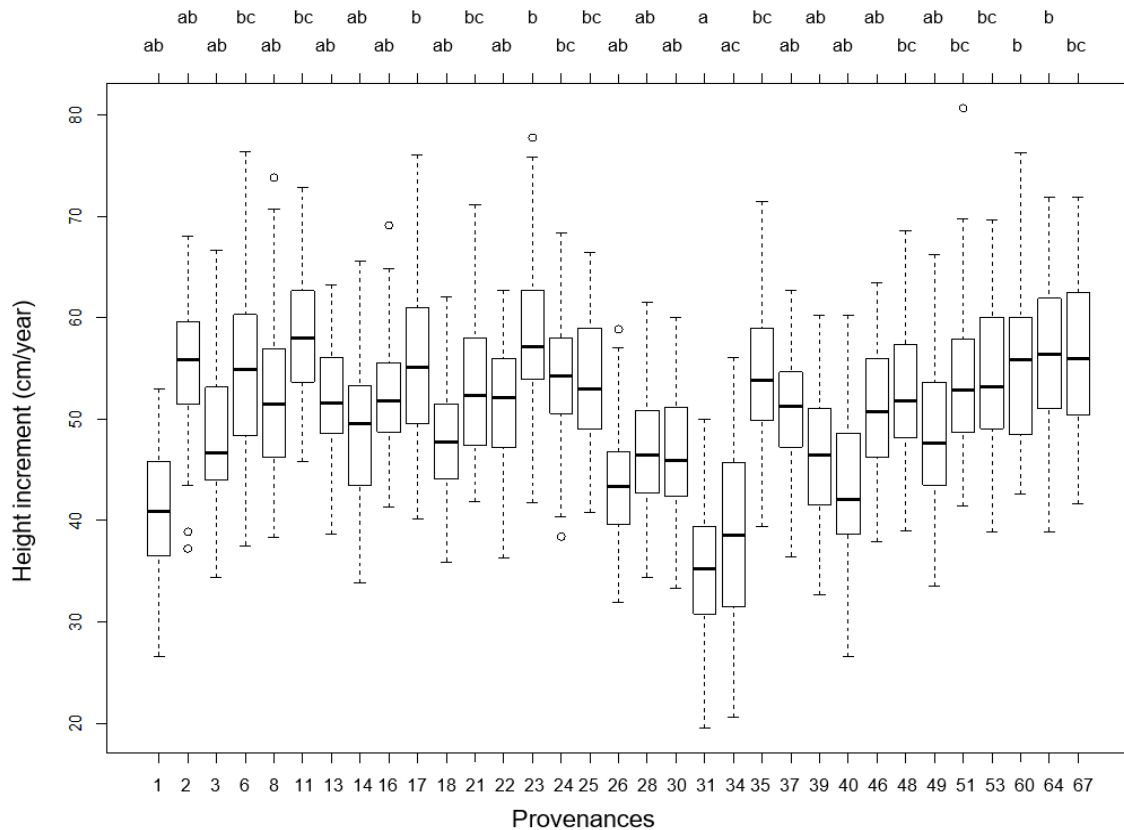


Figure 6. Differences in height increment for provenances in 2018. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

#### 4.4 Stem crookedness

The level of stem crookedness is an indicator for quality in wood production of beech. The provenance ‘*Hinterstoder*’ (Austria) had the lowest stem crookedness (Figure 7.). The German provenance ‘*Urach B.W.*’ and the Swiss provenance ‘*Oberwil.*’ showed the most crooked stems. Higher frequency of double stems in the lower part of the stem (< 4,5 m) increased stem crookedness (Supplementary Table 4, Appendix 2) an indication of poor quality for wood production.

#### 4.5 Double stem (< 4,5 m)

Provenances ‘*Perche*’ from France and ‘*Alsted F.413*’ from Denmark showed superior performance following post-hoc comparisons with a statistically significant low value, indicating higher quality for future wood production (Figure 8.). Provenances ‘*Heinerscheid*’ from Luxembourg, ‘*Aarnink*’ from the Netherlands, ‘*Urach (BW).*’ from Germany, and ‘*Bilowo 115,116*’ from Poland had a high tendency to develop double stems.

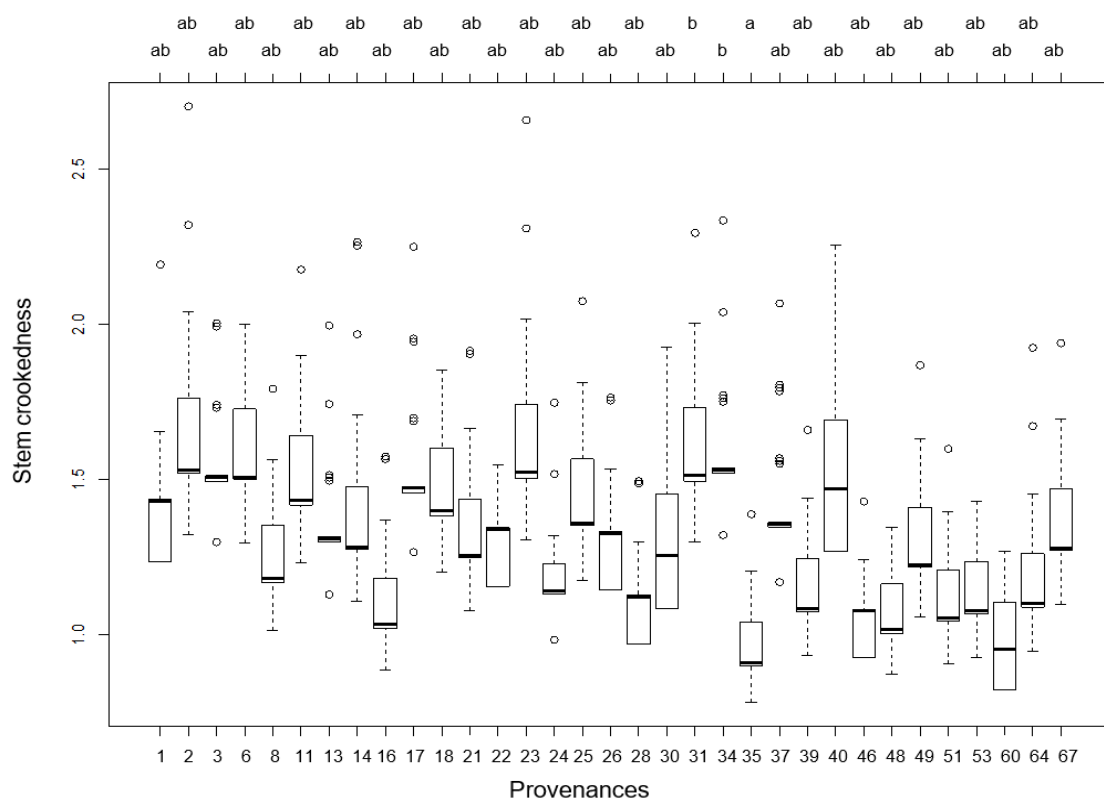


Figure 7. Differences in stem crookedness for provenances in 2018. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

#### 4.6 Double stem (> 4,5 m)

‘Farchau (SH)’ and ‘Urach (BW)’, both from Germany, presented lower tendency of developing double stems. The French provenance ‘Plateaux du.’ showed higher number of double stems on the upper part of the stem (Figure 9.). The tree tendency to develop double stems above 4,5 m height was increased with increased diameter and crookedness (Appendix 2 - Supplementary Table 6).



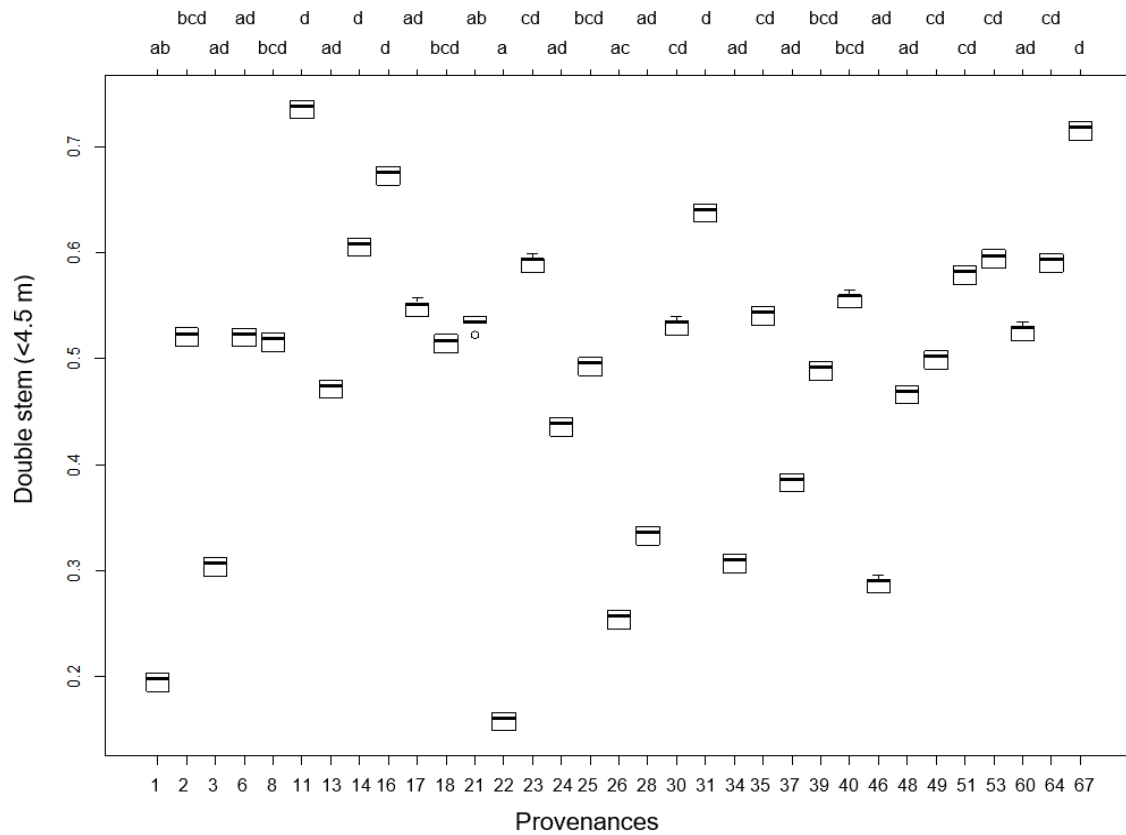


Figure 8. Differences between provenances for the tendency to develop double stems below 4,5 m on the stem in 2018. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

#### 4.7 Lateral branch division < 4,5 m

The amount of branches on the stem can give an indication of the amount of knots present in the wood. Large number of branches may increase the knot formation which can lead to decreased wood quality. ‘Farchau (SH)’ (Germany) had low tendency to develop large branches. Provenance ‘Postojna Masun.’ (Slovenia) developed significantly more branches (Figure 10).

The frequency of forks present below 4,5 m height on the tree increased with tree diameter and increased crookedness but decreased with the frequency of double stems below 4,5 m indicating that trees with fewer double stems have more low branches (Appendix 2 - Supplementary Table 7).

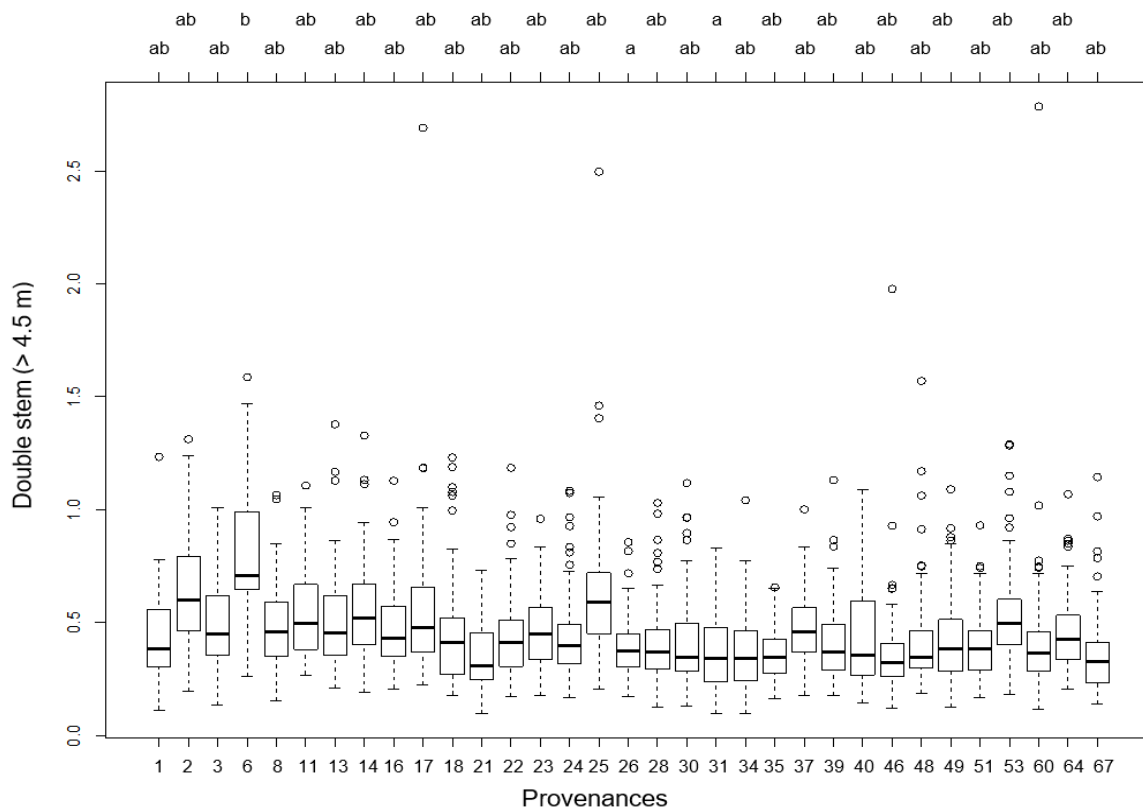


Figure 9. Differences between provenances for the tendency to develop double stems above 4,5 m on the stem in 2018. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

#### 4.8 Lateral branch division > 4,5 m

There were no differences between provenances for the tendency to develop lateral branches above 4,5 m (Figure 11.). Diameter at breast height increased number of lateral branches, but double stems and forks at lower part of the stem was negatively correlated with frequency of forks at upper parts (Appendix 2 - Supplementary table 8).

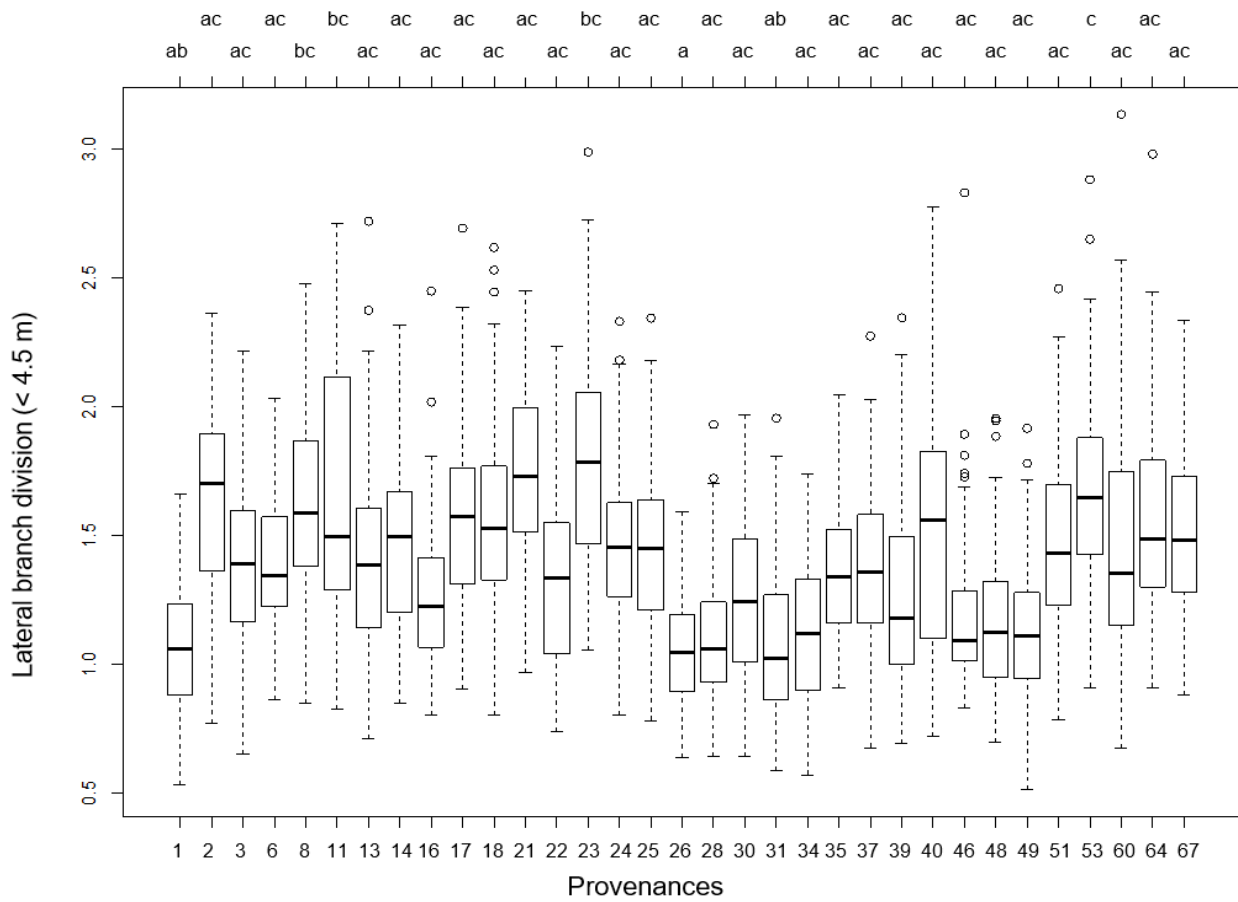


Figure 10. Differences between beech provenances for the mean number of lateral branches at lower part of the stem (< 4.5 m). Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

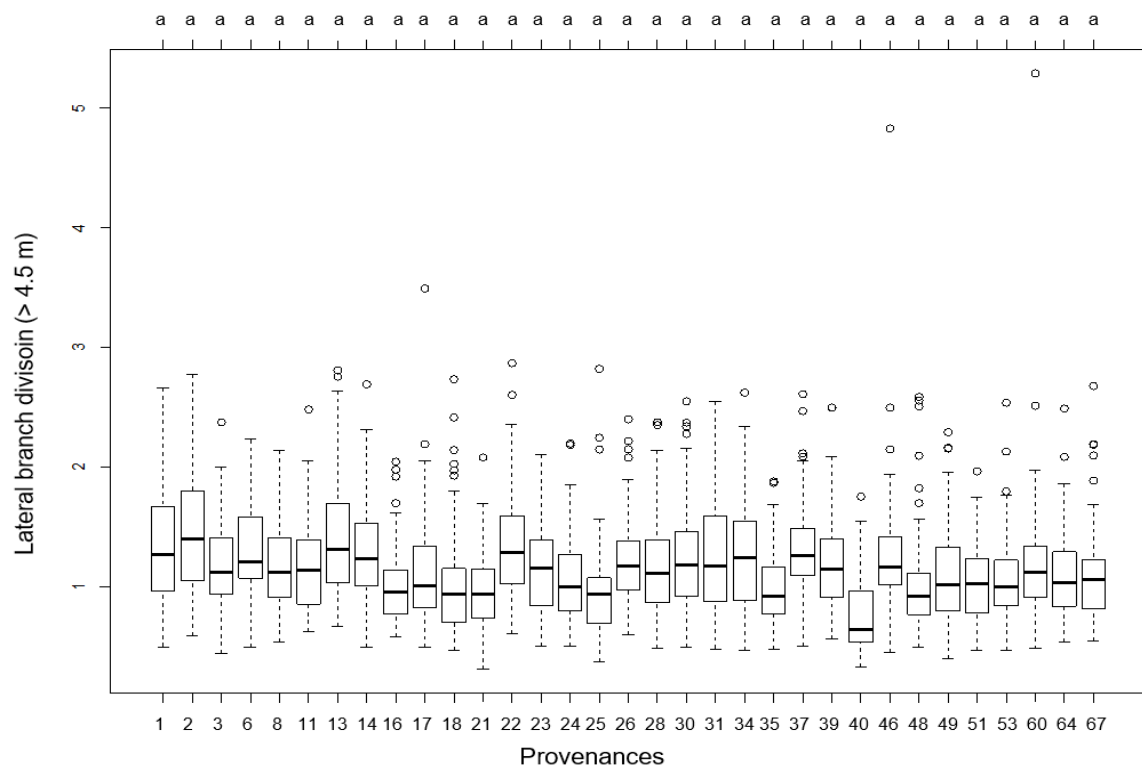


Figure 11. Differences between beech provenances for the mean number of lateral branches at the upper part of the stem (> 4.5 m). Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance.

## 5 Discussion

### 5.1 Survival, growth and timber quality traits of European beech at the trial site

The first specific objective of this thesis was to identify differences among European beech provenances on survival rate. Results show that provenances with low survival varied distinctly in latitude and altitude, revealing no clear pattern that could explain the higher mortality rates or support for the first hypothesis. The Swedish provenances generally showed lower survival in comparison to more southern provenances. The analysis of survival also showed similar results in 2008, with the Italian provenance ‘*Val di Sella*’ and German provenance ‘*Farchau (SH)*’ as having low stand mortality during this first assessment as well.

The Swedish provenance ‘*Torup*’ had a very good growth performance with respect to height increment, indicating that the Swedish genetic material is well adapted to growth conditions at these latitudes. This partially supported the second hypothesis of this thesis. No differences could be found between provenances for stem diameter or basal area increment. In order to make as accurate recommendations as possible it is essential to get more information about traits associated with the establishment for growth.

The third objective of the thesis was to identify general trends and correlations in the traits of the tree structure and growth of beech provenances along a Europe-wide geographical gradient of climate and elevation. A general trend in the tree structural traits could be identified as the results show a negative effect of stem crookedness and frequency of double stems on tree growth (*Appendix 2 - Supplementary Table 3.*). The results from this thesis correlate well with results from 2008 concerning stem crookedness. The Austrian provenance ‘*Hinterstoder*’ showed low values for stem crookedness at the time as well.

## 5.2 The consequences of differences among European beech provenances

Future climate change will have implications for the management of plantation forests (Felton et al 2016; Strömme et al 2019). The current regeneration of European beech in Sweden will at the end of its rotation experience significantly different growing conditions than at establishment (Kirilenko et al 2007). Having climatically well adapted regeneration material becomes increasingly important to reduce potential economic loss (Stener et al 2008). Climatic adaptation is therefore of importance for a successful establishment and to maintain a high quality production in beech plantation forestry.

The degree of plasticity and the adaptive response of European beech to environmental change will have an important role in shaping future forest development (Thuiller et al 2008). Seedling growth, phenological development, drought tolerance and frost sensitivity will all play vital roles in the future northern distribution of the species (Eilmann et al 2014; Vitasse & Basler, 2013; Strömme et al 2019).

Due to anthropogenic climate change, the environmental changes with associated fluctuations in local temperature, water and nutrient availability in Sweden will lead to a need for assessment of the suitability of the regeneration material.

Trees in particular have a high inherent genetic diversity within individuals (Bravo et al 2017). Studies show that beech forest cover is projected to decrease in the southern range of its distribution and increase its northward spread with current climate change model projections (Sykes and Prentice 1996; Kramer et al 2010.). The results of studied height increment for the Swedish provenance '*Torup*' indicate that this native genetic material performs well.

Leaf photosynthesis is the main factor determining radial growth increase in beech (Michelot et al 2012). Contrary to growth in other deciduous species such as oak, radial growth starts at the time of budburst in beech (Michelot et al 2012) and reaches maximum when leaves have developed to their full extent (Principe et al 2017). As the timing of spring flushing varies between provenances (Eilmann et al 2014; Vitasse & Basler 2013; Stener 2008), there is differing potential for carbon assimilation between provenances during one season of growth established at one single site. Provenances from maritime regions have a tendency to flush later in comparison to provenances from continental regions, resulting in a shorter period for potential stem diameter increment (Stener, 2008).

Low water availability and associated physiological stress could become a limiting factor for growth in the future. Southern beech provenances have previously shown better performance under water stress conditions (Eilmann et al 2014). However, no significant influence on basal area increment could be determined in this study that would support specific establishment of a more southern provenance. However, the

results from this study show that the frequency of tree branches above 4,5 m increased basal area increment. This might be because more high-positioned branches allow increased exposure of high leaves to sunlight. Reliable recommendations require additional studies of growth and development in the coming decades to determine the influence of provenance on traits related to growth.

The environmental controls of bud break are still not fully understood for beech (Vitasse & Basler, 2013; Strömme et al 2019), but susceptibility to frost damage has shown to vary between provenances as it is related to the timing of budburst (Hofmann et al 2015). Additional studies of the phenological development of European beech at the northern distribution limit may also prove vital to supply further information on the effect of late frost on stand development.

## 6 Conclusions

The results show that even though beech can be considered a plastic species with a good adaptive response to varying environmental conditions, the genetic background has an important role in shaping stand development for several timber quality characteristics. The native provenances performed well or better in some cases compared to Mediterranean and Central European provenances with respect to height increment, as seen in the Swedish provenance '*Torup*'. However, South and Central European beech provenances established at this northern location showed high plasticity and ability to adapt to Swedish growth conditions. This resulted in high survival ratios, and better timber quality features.

The interaction between the environmental controls of growth and the genetic predisposition is complex. Therefore, preserving as many populations of beech provenances as possible may prove an important means to keep future desirable traits to cope with climate change.

Comparison of growth between provenances at different sites can hopefully lead to better understanding of the effect of climate change in the future.



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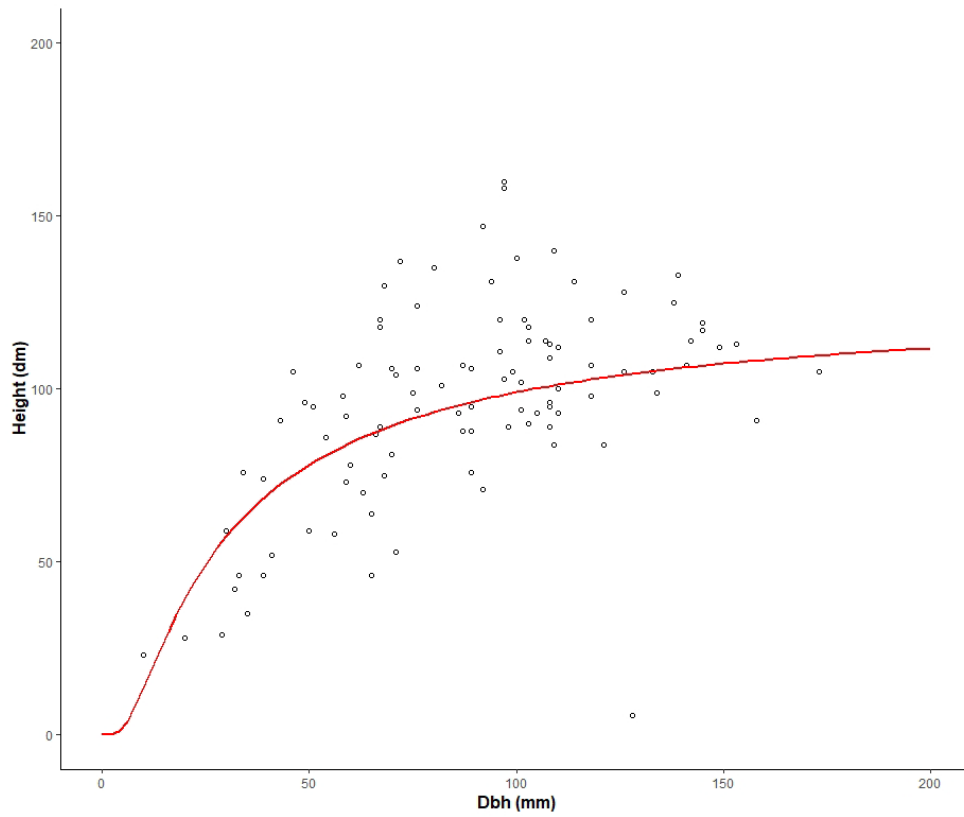
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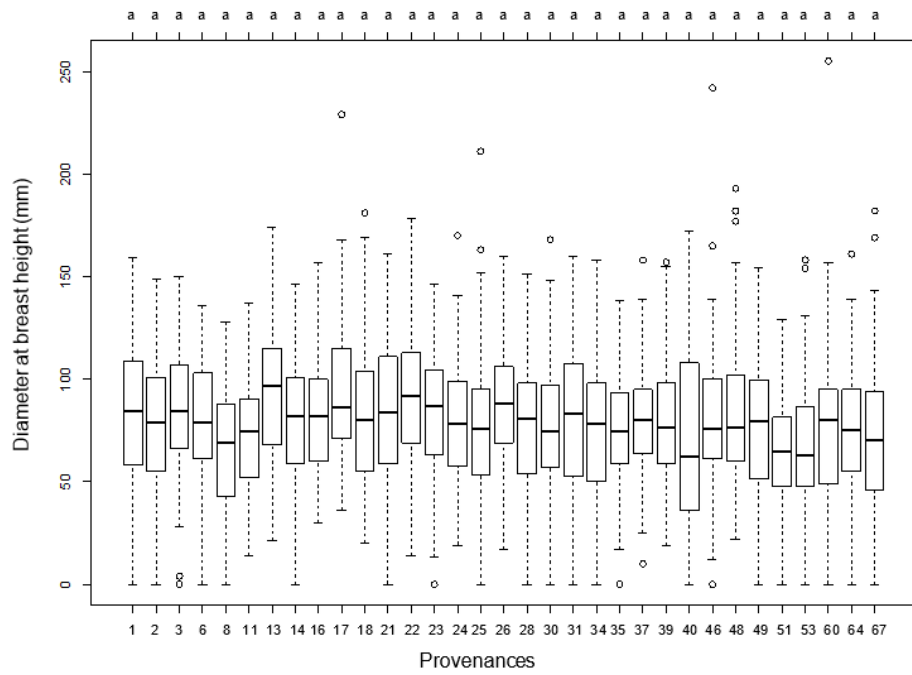
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## Appendix 1 – Supplementary figures



*Supplementary Figure S1. The height-diameter relationship fitted model (Table 3).*

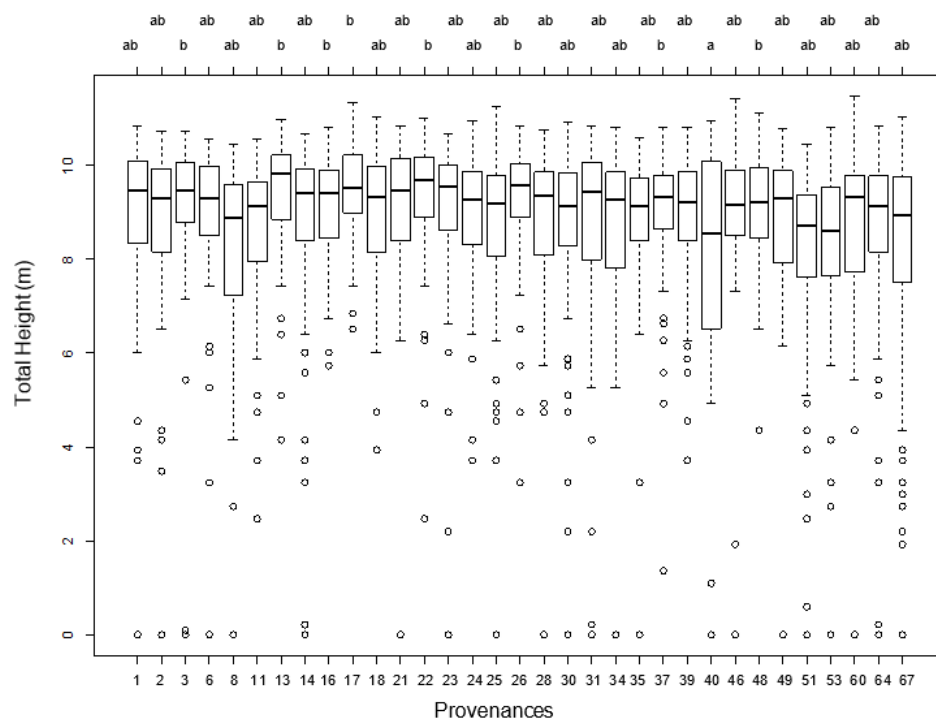
# DIAMETER AT 2018



Supplementary Figure S2. Differences between provenances in diameter at breast height (mm) at 2018. Different letters denote significant differences at the 0.05 significance level



# HEIGHT 2018



Supplementary Figure S3. Provenance differences in height (m) at 2018. Different letters denote significant differences at the 0.05 significance level.

## Appendix 2 – Supplementary tables

*Supplementary Table 1. Model-fitted coefficients for survival. n.s.: not significant.*

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | 0.706       | 0.047   |
| $\alpha_2$ (Provenance 2)  | -0.720      | 0.039   |
| $\alpha_2$ (Provenance 3)  | -0.747      | 0.032   |
| $\alpha_2$ (Provenance 6)  | -0.830      | 0.017   |
| $\alpha_2$ (Provenance 8)  | -0.154      | n.s.    |
| $\alpha_2$ (Provenance 11) | -1.085      | 0.002   |
| $\alpha_2$ (Provenance 13) | -0.802      | 0.021   |
| $\alpha_2$ (Provenance 14) | 0.124       | n.s.    |
| $\alpha_2$ (Provenance 16) | -0.356      | n.s.    |
| $\alpha_2$ (Provenance 17) | -1.035      | 0.003   |
| $\alpha_2$ (Provenance 18) | 0.027       | n.s.    |
| $\alpha_2$ (Provenance 21) | -1.150      | 0.001   |
| $\alpha_2$ (Provenance 22) | -0.469      | n.s.    |
| $\alpha_2$ (Provenance 23) | -0.776      | 0.026   |
| $\alpha_2$ (Provenance 24) | -0.326      | n.s.    |
| $\alpha_2$ (Provenance 25) | -0.215      | n.s.    |
| $\alpha_2$ (Provenance 26) | 0.511       | n.s.    |
| $\alpha_2$ (Provenance 28) | -0.149      | n.s.    |
| $\alpha_2$ (Provenance 30) | -0.109      | n.s.    |
| $\alpha_2$ (Provenance 31) | 0.328       | n.s.    |
| $\alpha_2$ (Provenance 34) | 0.226       | n.s.    |
| $\alpha_2$ (Provenance 35) | -0.123      | n.s.    |
| $\alpha_2$ (Provenance 37) | 0.618       | n.s.    |

|                             |        |       |
|-----------------------------|--------|-------|
| $\alpha_2$ (Provenance 39)  | 0.149  | n.s.  |
| $\alpha_2$ (Provenance 40)  | -1.058 | 0.003 |
| $\alpha_2$ (Provenance 46)  | -0.749 | 0.032 |
| $\alpha_2$ (Provenance 48)  | 0.0166 | n.s.  |
| $\alpha_2$ (Provenance 49)  | 0.647  | n.s.  |
| $\alpha_2$ (Provenance 51)  | -0.096 | n.s.  |
| $\alpha_2$ (Provenance 53)  | -0.414 | n.s.  |
| $\alpha_2$ (Provenance 60)  | -1.076 | 0.002 |
| $\alpha_2$ (Provenance 64)  | -0.356 | n.s.  |
| $\alpha_2$ (Provenance 67)  | -0.691 | 0.047 |
| $\sigma_{jk}$ (Plot)        | 0.305  |       |
| $\varepsilon_{ijk}$ (error) | 0.599  |       |

Supplementary Table 2. Model-fitted coefficients for basal area increment. n.s.: not significant.

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | 0.707       | <0.001  |
| $\alpha_1$ (Dstm_L)        | 0.095       | <0.001  |
| $\alpha_1$ (Dstm_U)        | 0.221       | <0.001  |
| $\alpha_1$ (Frk_L)         | 0.121       | <0.001  |
| $\alpha_1$ (Frk_U)         | 0.301       | <0.001  |
| $\alpha_1$ (Crk)           | -0.081      | <0.001  |
| $\alpha_2$ (Provenance 2)  | -0.251      | n.s.    |
| $\alpha_2$ (Provenance 3)  | 0.037       | n.s.    |
| $\alpha_2$ (Provenance 6)  | -0.177      | n.s.    |
| $\alpha_2$ (Provenance 8)  | -0.321      | n.s.    |
| $\alpha_2$ (Provenance 11) | -0.294      | n.s.    |
| $\alpha_2$ (Provenance 13) | 0.046       | n.s.    |
| $\alpha_2$ (Provenance 14) | -0.167      | n.s.    |
| $\alpha_2$ (Provenance 16) | -0.0158     | n.s.    |
| $\alpha_2$ (Provenance 17) | 0.1145      | n.s.    |
| $\alpha_2$ (Provenance 18) | -0.0241     | n.s.    |
| $\alpha_2$ (Provenance 21) | 0.0497      | n.s.    |
| $\alpha_2$ (Provenance 22) | 0.0916      | n.s.    |
| $\alpha_2$ (Provenance 23) | -0.0905     | n.s.    |
| $\alpha_2$ (Provenance 24) | -0.0917     | n.s.    |
| $\alpha_2$ (Provenance 25) | -0.137      | n.s.    |

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_2$ (Provenance 26) | 0.0864      | n.s.    |
| $\alpha_2$ (Provenance 28) | -0.073      | n.s.    |
| $\alpha_2$ (Provenance 30) | -0.138      | n.s.    |
| $\alpha_2$ (Provenance 31) | -0.0398     | n.s.    |
| $\alpha_2$ (Provenance 34) | -0.110      | n.s.    |
| $\alpha_2$ (Provenance 35) | -0.0778     | n.s.    |
| $\alpha_2$ (Provenance 37) | -0.116      | n.s.    |
| $\alpha_2$ (Provenance 39) | -0.0831     | n.s.    |
| $\alpha_2$ (Provenance 40) | -0.1895     | n.s.    |
| $\alpha_2$ (Provenance 46) | -0.0484     | n.s.    |
| $\alpha_2$ (Provenance 48) | 0.0134      | n.s.    |
| $\alpha_2$ (Provenance 49) | -0.0457     | n.s.    |
| $\alpha_2$ (Provenance 51) | -0.291      | n.s.    |
| $\alpha_2$ (Provenance 53) | -0.326      | n.s.    |
| $\alpha_2$ (Provenance 60) | -0.0578     | n.s.    |
| $\alpha_2$ (Provenance 64) | -0.1826     | n.s.    |
| $\alpha_2$ (Provenance 67) | -0.212      | n.s.    |
| $\sigma_k$ (Block)         | <0.001      |         |
| $\sigma_{jk}$ (Plot)       | 0.134       |         |
| $\sigma_{ijk}$ (Tree)      | <0.001      |         |
| $\sigma_e$ (error)         | 0.350       |         |
| $\delta_1^*$               | 0.100       |         |

\*Variance function parameter used to model variance residual structure to correct heteroscedasticity as an exponential value of the variance covariate covariate ( $g_{ijk}$ ):  $Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{(2\delta_1 g_{ijk})}$

Supplementary Table 3. Model-fitted coefficients for Height increment. n.s.: not significant.

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | 30.439      | <0.001  |
| $\alpha_1$ (Dstm_L)        | 1.949       | <0.001  |
| $\alpha_1$ (Dstm_U)        | 3.373       | <0.001  |
| $\alpha_1$ (Frk_L)         | 3.312       | <0.001  |
| $\alpha_1$ (Frk_U)         | 5.459       | <0.001  |
| $\alpha_1$ (Crk)           | -1.657      | <0.001  |
| $\alpha_2$ (Provenance 2)  | 10.952      | 0.014   |
| $\alpha_2$ (Provenance 3)  | 7.889       | n.s.    |
| $\alpha_2$ (Provenance 6)  | 11.662      | 0.009   |
| $\alpha_2$ (Provenance 8)  | 9.733       | 0.027   |
| $\alpha_2$ (Provenance 11) | 14.977      | 0.001   |
| $\alpha_2$ (Provenance 13) | 8.210       | n.s.    |
| $\alpha_2$ (Provenance 14) | 5.308       | n.s.    |
| $\alpha_2$ (Provenance 16) | 10.988      | 0.013   |
| $\alpha_2$ (Provenance 17) | 15.498      | 0.001   |
| $\alpha_2$ (Provenance 18) | 6.151       | n.s.    |
| $\alpha_2$ (Provenance 21) | 12.030      | 0.008   |
| $\alpha_2$ (Provenance 22) | 10.018      | 0.024   |
| $\alpha_2$ (Provenance 23) | 16.123      | 0.001   |
| $\alpha_2$ (Provenance 24) | 12.772      | 0.004   |
| $\alpha_2$ (Provenance 25) | 12.729      | 0.004   |
| $\alpha_2$ (Provenance 26) | 3.661       | n.s.    |
| $\alpha_2$ (Provenance 28) | 6.212       | n.s.    |
| $\alpha_2$ (Provenance 30) | 5.349       | n.s.    |
| $\alpha_2$ (Provenance 31) | -5.961      | n.s.    |
| $\alpha_2$ (Provenance 34) | -1.501      | n.s.    |
| $\alpha_2$ (Provenance 35) | 13.84       | 0.002   |
| $\alpha_2$ (Provenance 37) | 9.003       | 0.039   |
| $\alpha_2$ (Provenance 39) | 4.854       | n.s.    |
| $\alpha_2$ (Provenance 40) | 4.0244      | n.s.    |
| $\alpha_2$ (Provenance 46) | 10.273      | 0.022   |
| $\alpha_2$ (Provenance 48) | 12.194      | 0.006   |
| $\alpha_2$ (Provenance 49) | 7.776       | n.s.    |
| $\alpha_2$ (Provenance 51) | 11.863      | 0.007   |
| $\alpha_2$ (Provenance 53) | 11.267      | 0.011   |
| $\alpha_2$ (Provenance 60) | 16.444      | 0.001   |
| $\alpha_2$ (Provenance 64) | 14.965      | 0.001   |
| $\alpha_2$ (Provenance 67) | 14.650      | 0.001   |
| $\sigma_k$ (Block)         | 0.593       |         |

| Parameter             | Coefficient | p-value |
|-----------------------|-------------|---------|
| $\sigma_{jk}$ (Plot)  | 4.44        |         |
| $\sigma_{ijk}$ (Tree) | 0.008       |         |
| $\sigma_e$ (error)    | 7864        |         |
| $\delta_1^*$          | -1.622      |         |

\*Variance function parameter used to model variance residual structure to correct heteroscedasticity as an power value of the variance covariate ( $g_{ijk}$ ):  $Var(\epsilon_{ijk}) = \sigma_e^2 \cdot |g_{ijk}|^{2\delta_1}$

Supplementary Table 4. Model-fitted coefficients for crookedness. n.s.: not significant

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | 0.311       | 0.001   |
| $\alpha_1$ (Dstm_L)        | 0.141       | <0.001  |
| $\alpha_2$ (Provenance 2)  | 0.0683      | n.s.    |
| $\alpha_2$ (Provenance 3)  | 0.051       | n.s.    |
| $\alpha_2$ (Provenance 6)  | 0.048       | n.s.    |
| $\alpha_2$ (Provenance 8)  | -0.196      | n.s.    |
| $\alpha_2$ (Provenance 11) | -0.002      | n.s.    |
| $\alpha_2$ (Provenance 13) | -0.086      | n.s.    |
| $\alpha_2$ (Provenance 14) | -0.108      | n.s.    |
| $\alpha_2$ (Provenance 16) | -0.331      | 0.014   |
| $\alpha_2$ (Provenance 17) | 0.026       | n.s.    |
| $\alpha_2$ (Provenance 18) | -0.027      | n.s.    |
| $\alpha_2$ (Provenance 21) | -0.136      | n.s.    |
| $\alpha_2$ (Provenance 22) | -0.066      | n.s.    |
| $\alpha_2$ (Provenance 23) | 0.057       | n.s.    |
| $\alpha_2$ (Provenance 24) | -0.227      | n.s.    |
| $\alpha_2$ (Provenance 25) | -0.050      | n.s.    |
| $\alpha_2$ (Provenance 26) | -0.077      | n.s.    |
| $\alpha_2$ (Provenance 28) | -0.242      | n.s.    |
| $\alpha_2$ (Provenance 30) | -0.129      | n.s.    |
| $\alpha_2$ (Provenance 31) | 0.051       | n.s.    |
| $\alpha_2$ (Provenance 34) | 0.068       | n.s.    |
| $\alpha_2$ (Provenance 35) | -0.457      | <0.001  |
| $\alpha_2$ (Provenance 37) | -0.053      | n.s.    |
| $\alpha_2$ (Provenance 39) | -0.278      | 0.028   |
| $\alpha_2$ (Provenance 40) | 0.0277      | n.s.    |
| $\alpha_2$ (Provenance 46) | -0.287      | 0.044   |
| $\alpha_2$ (Provenance 48) | -0.347      | 0.008   |
| $\alpha_2$ (Provenance 49) | -0.155      | n.s.    |

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_2$ (Provenance 51) | -0.310      | 0.017   |
| $\alpha_2$ (Provenance 53) | -0.287      | 0.033   |
| $\alpha_2$ (Provenance 60) | -0.405      | 0.009   |
| $\alpha_2$ (Provenance 64) | -0.266      | 0.044   |
| $\alpha_2$ (Provenance 67) | -0.117      | n.s.    |
| $\sigma_k$ (Block)         | 0.075       |         |

*Supplementary Table 5. Model-fitted coefficients for Double stem below 4,5 m. n.s.: not significant*

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | 0.196       | <0.001  |
| $\alpha_2$ (Provenance 2)  | 0.325       | <0.001  |
| $\alpha_2$ (Provenance 3)  | 0.109       | n.s.    |
| $\alpha_2$ (Provenance 6)  | 0.325       | <0.001  |
| $\alpha_2$ (Provenance 8)  | 0.321       | <0.001  |
| $\alpha_2$ (Provenance 11) | 0.540       | <0.001  |
| $\alpha_2$ (Provenance 13) | 0.276       | 0.003   |
| $\alpha_2$ (Provenance 14) | 0.410       | <0.001  |
| $\alpha_2$ (Provenance 16) | 0.477       | <0.001  |
| $\alpha_2$ (Provenance 17) | 0.353       | <0.001  |
| $\alpha_2$ (Provenance 18) | 0.319       | <0.001  |
| $\alpha_2$ (Provenance 21) | 0.336       | 0.002   |
| $\alpha_2$ (Provenance 22) | -0.0371     | n.s.    |
| $\alpha_2$ (Provenance 23) | 0.395       | <0.001  |
| $\alpha_2$ (Provenance 24) | 0.241       | 0.004   |
| $\alpha_2$ (Provenance 25) | 0.298       | <0.001  |
| $\alpha_2$ (Provenance 26) | 0.059       | n.s.    |
| $\alpha_2$ (Provenance 28) | 0.138       | n.s.    |
| $\alpha_2$ (Provenance 30) | 0.336       | <0.001  |
| $\alpha_2$ (Provenance 31) | 0.442       | <0.001  |
| $\alpha_2$ (Provenance 34) | 0.112       | n.s.    |
| $\alpha_2$ (Provenance 35) | 0.345       | <0.001  |
| $\alpha_2$ (Provenance 37) | 0.188       | 0.010   |
| $\alpha_2$ (Provenance 39) | 0.294       | <0.001  |
| $\alpha_2$ (Provenance 40) | 0.361       | <0.001  |
| $\alpha_2$ (Provenance 46) | 0.093       | n.s.    |
| $\alpha_2$ (Provenance 48) | 0.271       | 0.001   |
| $\alpha_2$ (Provenance 49) | 0.304       | <0.001  |

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_2$ (Provenance 51) | 0.384       | <0.001  |
| $\alpha_2$ (Provenance 53) | 0.399       | <0.001  |
| $\alpha_2$ (Provenance 60) | 0.331       | 0.001   |
| $\alpha_2$ (Provenance 64) | 0.395       | <0.001  |
| $\alpha_2$ (Provenance 67) | 0.520       | <0.001  |
| $\sigma_k$ (Block)         | 0.0134      |         |

Supplementary Table 6. Model-fitted coefficients for Double stem above 4,5 m. n.s.: not significant

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | -2.044      | <0.001  |
| $\alpha_1$ (dbh18)         | 0.0123      | <0.001  |
| $\alpha_1$ (Dstm_L)        | -0.100      | <0.001  |
| $\alpha_1$ (Frk_L)         | -0.0963     | <0.001  |
| $\alpha_1$ (Crk)           | 0.145       | <0.001  |
| $\alpha_2$ (Provenance 2)  | 0.538       | n.s.    |
| $\alpha_2$ (Provenance 3)  | 0.124       | n.s.    |
| $\alpha_2$ (Provenance 6)  | 0.727       | n.s.    |
| $\alpha_2$ (Provenance 8)  | 0.447       | n.s.    |
| $\alpha_2$ (Provenance 11) | 0.491       | n.s.    |
| $\alpha_2$ (Provenance 13) | 0.119       | n.s.    |
| $\alpha_2$ (Provenance 14) | 0.412       | n.s.    |
| $\alpha_2$ (Provenance 16) | 0.257       | n.s.    |
| $\alpha_2$ (Provenance 17) | 0.211       | n.s.    |
| $\alpha_2$ (Provenance 18) | 0.110       | n.s.    |
| $\alpha_2$ (Provenance 21) | -0.119      | n.s.    |
| $\alpha_2$ (Provenance 22) | -0.044      | n.s.    |
| $\alpha_2$ (Provenance 23) | 0.243       | n.s.    |
| $\alpha_2$ (Provenance 24) | 0.169       | n.s.    |
| $\alpha_2$ (Provenance 25) | 0.545       | n.s.    |
| $\alpha_2$ (Provenance 26) | -0.087      | n.s.    |
| $\alpha_2$ (Provenance 28) | 0.0633      | n.s.    |
| $\alpha_2$ (Provenance 30) | 0.133       | n.s.    |
| $\alpha_2$ (Provenance 31) | -0.112      | n.s.    |
| $\alpha_2$ (Provenance 34) | -0.060      | n.s.    |
| $\alpha_2$ (Provenance 35) | 0.073       | n.s.    |
| $\alpha_2$ (Provenance 37) | 0.233       | n.s.    |
| $\alpha_2$ (Provenance 39) | 0.096       | n.s.    |
| $\alpha_2$ (Provenance 40) | 0.280       | n.s.    |



| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_2$ (Provenance 46) | -0.020      | n.s.    |
| $\alpha_2$ (Provenance 48) | 0.054       | n.s.    |
| $\alpha_2$ (Provenance 49) | 0.092       | n.s.    |
| $\alpha_2$ (Provenance 51) | 0.296       | n.s.    |
| $\alpha_2$ (Provenance 53) | 0.578       | n.s.    |
| $\alpha_2$ (Provenance 60) | 0.167       | n.s.    |
| $\alpha_2$ (Provenance 64) | 0.299       | n.s.    |
| $\alpha_2$ (Provenance 67) | 0.080       | n.s.    |
| $\sigma_k$ (Block)         | 0.090       |         |

*Supplementary Table 7. Model-fitted coefficients for lateral branch division below 4,5 m. n.s.: not significant*

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | -0.505      | <0.001  |
| $\alpha_1$ (dbh18)         | 0.005       | <0.001  |
| $\alpha_1$ (Dstm_L)        | -0.151      | <0.001  |
| $\alpha_1$ (Crk)           | 0.099       | <0.001  |
| $\alpha_2$ (Provenance 2)  | 0.495       | 0.001   |
| $\alpha_2$ (Provenance 3)  | 0.251       | n.s.    |
| $\alpha_2$ (Provenance 6)  | 0.320       | 0.044   |
| $\alpha_2$ (Provenance 8)  | 0.548       | <0.001  |
| $\alpha_2$ (Provenance 11) | 0.586       | <0.001  |
| $\alpha_2$ (Provenance 13) | 0.263       | n.s.    |
| $\alpha_2$ (Provenance 14) | 0.406       | 0.006   |
| $\alpha_2$ (Provenance 16) | 0.288       | n.s.    |
| $\alpha_2$ (Provenance 17) | 0.355       | 0.027   |
| $\alpha_2$ (Provenance 18) | 0.435       | 0.003   |
| $\alpha_2$ (Provenance 21) | 0.520       | 0.001   |
| $\alpha_2$ (Provenance 22) | 0.165       | n.s.    |
| $\alpha_2$ (Provenance 23) | 0.570       | <0.001  |
| $\alpha_2$ (Provenance 24) | 0.425       | 0.005   |
| $\alpha_2$ (Provenance 25) | 0.382       | 0.010   |
| $\alpha_2$ (Provenance 26) | -0.012      | n.s.    |
| $\alpha_2$ (Provenance 28) | 0.138       | n.s.    |
| $\alpha_2$ (Provenance 30) | 0.281       | n.s.    |
| $\alpha_2$ (Provenance 31) | 0.064       | n.s.    |

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_2$ (Provenance 34) | 0.099       | n.s.    |
| $\alpha_2$ (Provenance 35) | 0.379       | 0.012   |
| $\alpha_2$ (Provenance 37) | 0.316       | 0.030   |
| $\alpha_2$ (Provenance 39) | 0.230       | n.s.    |
| $\alpha_2$ (Provenance 40) | 0.485       | 0.003   |
| $\alpha_2$ (Provenance 46) | 0.193       | n.s.    |
| $\alpha_2$ (Provenance 48) | 0.153       | n.s.    |
| $\alpha_2$ (Provenance 49) | 0.148       | n.s.    |
| $\alpha_2$ (Provenance 51) | 0.497       | <0.001  |
| $\alpha_2$ (Provenance 53) | 0.636       | <0.001  |
| $\alpha_2$ (Provenance 60) | 0.457       | 0.005   |
| $\alpha_2$ (Provenance 64) | 0.505       | <0.001  |
| $\alpha_2$ (Provenance 67) | 0.474       | 0.002   |
| $\sigma_k$ (Block)         | 0.124       |         |
| $\sigma_{jk}$ (Plot)       | 0.089       |         |

Supplementary Table 8. Model-fitted coefficients for lateral branch division above 4,5 m. n.s.: not significant

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_0$ (Provenance 1)  | -0.550      | <0.001  |
| $\alpha_1$ (dbh18)         | 0.010       | <0.001  |
| $\alpha_1$ (Dstm_L)        | -0.134      | <0.001  |
| $\alpha_1$ (Frk_L)         | -0.068      | <0.001  |
| $\alpha_2$ (Provenance 2)  | 0.242       | n.s.    |
| $\alpha_2$ (Provenance 3)  | -0.102      | n.s.    |
| $\alpha_2$ (Provenance 6)  | 0.109       | n.s.    |
| $\alpha_2$ (Provenance 8)  | 0.141       | n.s.    |
| $\alpha_2$ (Provenance 11) | 0.125       | n.s.    |
| $\alpha_2$ (Provenance 13) | 0.016       | n.s.    |
| $\alpha_2$ (Provenance 14) | 0.111       | n.s.    |
| $\alpha_2$ (Provenance 16) | -0.157      | n.s.    |
| $\alpha_2$ (Provenance 17) | -0.182      | n.s.    |
| $\alpha_2$ (Provenance 18) | -0.199      | n.s.    |

| Parameter                  | Coefficient | p-value |
|----------------------------|-------------|---------|
| $\alpha_2$ (Provenance 21) | -0.232      | n.s.    |
| $\alpha_2$ (Provenance 22) | -0.051      | n.s.    |
| $\alpha_2$ (Provenance 23) | -0.005      | n.s.    |
| $\alpha_2$ (Provenance 24) | -0.107      | n.s.    |
| $\alpha_2$ (Provenance 25) | -0.176      | n.s.    |
| $\alpha_2$ (Provenance 26) | -0.088      | n.s.    |
| $\alpha_2$ (Provenance 28) | -0.042      | n.s.    |
| $\alpha_2$ (Provenance 30) | 0.066       | n.s.    |
| $\alpha_2$ (Provenance 31) | 0.033       | n.s.    |
| $\alpha_2$ (Provenance 34) | 0.063       | n.s.    |
| $\alpha_2$ (Provenance 35) | -0.153      | n.s.    |
| $\alpha_2$ (Provenance 37) | 0.093       | n.s.    |
| $\alpha_2$ (Provenance 39) | -0.007      | n.s.    |
| $\alpha_2$ (Provenance 40) | -0.333      | n.s.    |
| $\alpha_2$ (Provenance 46) | 0.010       | n.s.    |
| $\alpha_2$ (Provenance 48) | -0.211      | n.s.    |
| $\alpha_2$ (Provenance 49) | -0.103      | n.s.    |
| $\alpha_2$ (Provenance 51) | 0.042       | n.s.    |
| $\alpha_2$ (Provenance 53) | 0.067       | n.s.    |
| $\alpha_2$ (Provenance 60) | 0.033       | n.s.    |
| $\alpha_2$ (Provenance 64) | -0.002      | n.s.    |
| $\alpha_2$ (Provenance 67) | 0.039       | n.s.    |
| $\sigma_k$ (Block)         | 0.023       |         |