Modelling growth of genetically improved Norway spruce

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Master Thesis no. 283
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Abstract

In Latvia, Norway spruce *Picea abies* (L.) Karst. is a common forest tree species. It is often regenerated with planting, mostly using genetically improved stock. Since the middle of the 20th century breeding measures are active aiming for higher productivity and stem quality. However, there is a lack of studies related to possible changes in growth dynamics when using genetically improved material in Latvia. In addition, growth modelling of particularly young stands has gained attention only in recent years.

The aim of the study was to test a Swedish model for individual tree height growth for young Norway spruce stands in Latvian conditions. Data from four young genetic trials in Latvia were used to investigate whether the model based on data from unimproved material could be used to predict the height increment. Stand level projections for full rotation length were done based on the height growth model's results.

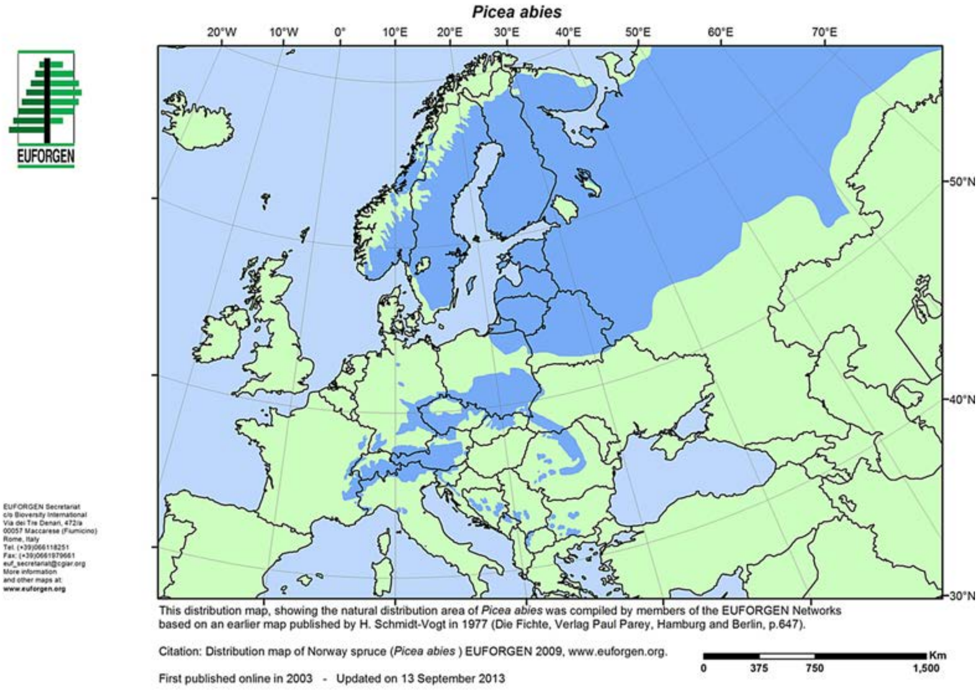
The height growth model intended for non-improved material predicted the height increment for genetically improved Norway spruce in Latvia with sufficient accuracy. No trends over estimated height increment and over improvement level were observed. Mean predicted genetic effect for the highest genetic entries was 0.17. For projected full rotation length, best genetic entries had on average by 11 % higher mean annual increment (MAI) and by 15 % higher net present value. Final felling age was decreased by 9 % comparing to group of the worst performing genetic entries. Rotation length for projected sites varied from 45 to 53 years. Final felling age according to economic maturity was estimated to be reached 5 -14 years earlier than culmination of MAI. First commercial thinning could be applied, when stand was on average 23 years old.

Key words: growth function, genetic gain, height increment, DSS, plantation, young forest stand.

Contents

1. Introduction

Latvia is located in the centre of Norway spruce's native range and close to optimum growing conditions (Fig.1) (Zālītis, 2006). On fertile sites in good climatic conditions, mean annual increment can reach 15 $m^3ha^{-1}year^{-1}$ (Zviedris, 1964). According to National Forest Inventory (NFI), Norway spruce is the third most common trees species in Latvia's forest after Scots pine and birch, being the main species in 18.3 % of all forest (Fig.2a). The species is common in pure as well as mixed stands, which frequently are formed together with Scots pine, birch, aspen and less often with ash and black alder (Zviedris, 1964). As in many European regions, planted stands of pure spruce are common (Szymański, 2007). The species has also important share in forest regeneration (Fig.2b). In 2015, 18 % of the clearcuts in Latvia were regenerated with Norway spruce, which is equal to the share of Scots pine and aspen (State Forest Service, 2016). Around 80 % of the spruce stands are regenerated using planting (Jansons et al., 2012), which highlights the practical importance of Norway spruce breeding. The species is rather easy to cultivate. High pulp yield, low frequency of damage in young stands and shorter rotation compared to Scots pine are reasons why Norway spruce has increasing importance during recent decades (Jansons et al., 2015), having a share of 23 % in total volume in forests younger than 40 years (79 % of yield in respective coniferous forests) (NFI, 2014). The mean annual planting area is more than 6000 ha (State Forest Service, 2016).



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This distribution map, showing the natural distribution area of *Picea abies* was compiled by members of the EUFORGEN Networks based on an earlier map published by H. Schmidt-Vogt in 1977 (Die Fichte, Verlag Paul Parey, Hamburg and Berlin, p.647).

Citation: Distribution map of Norway spruce (*Picea abies*) EUFORGEN 2009, www.euforgen.org.

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Figure 1. Natural distribution of Norway spruce (Euforgen, 2009)

Norway spruce has straight timber suitable for structural applications, panelling and furniture, and it is a well raw material for the pulp and paper industry due to fine branching and long, lean and straight fibres (Szymański, 2007; Mullin et al., 2011). Young trees are also used as Christmas trees.

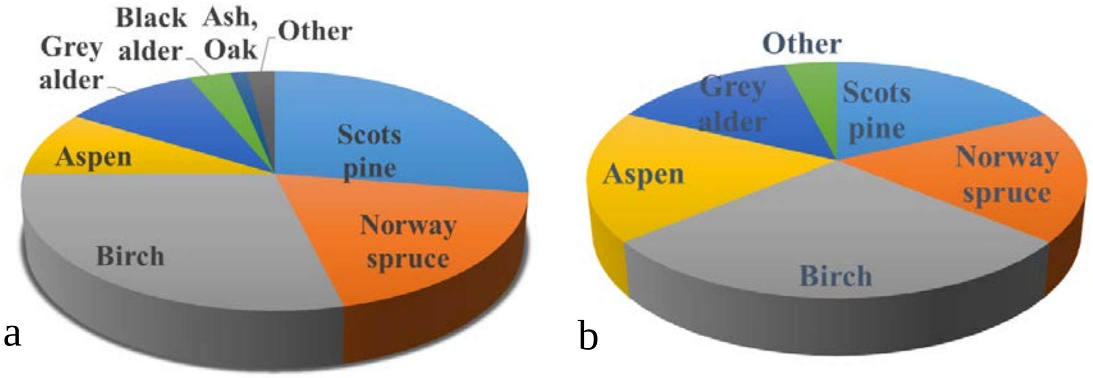


Figure 2. a) Share (ha) of main tree species in forest stands (NFI, 2014) and b) share (ha) of different tree species in forest regeneration (State Forest Service, 2016).

1.1. The growth potential of Norway spruce

The growth of young spruce stands can be described with several stages. Until the height of around 2 m, spruce has slow growth rate with an annual height increment of about 10 – 20 cm. After this initial stage, a period of rapid growth follows, when current annual increment can reach 20 m^3 ha^{-1} $year^{-1}$. Volume accumulates the most, when mean height of the stand is between 12-17 m (Lībiete, 2008). On fertile sites total yield at the age of 40 years may reach 350 m^3 ha^{-1}. According to Lībiete (2008), mean annual increment (MAI) is 9.5 $m^3ha^{-1}year^{-1}$ for 61-80 years old spruce stands and 7.5 $m^3ha^{-1}year^{-1}$ for 81-100 years old stands. In comparison, average MAI of Norway spruce in Europe during last decades was around 7.3 m^3 ha^{-1} (von Teuffel et al., 2004).

Studies in Latvia show that initial stand density plays an important role in stand growth. Lībiete (2008) concludes that growth of all stand parameters is more rapid in the stands thinned to 2000 trees ha^{-1} before mean height has exceeded 5 m compared to stands that were thinned when the mean height was 10 m.

Differentiation is observed when pure stands reach 30 – 40 years of age. In part of the stands, wood accumulation continues and at cutting age total yield may reach 500 m^3 ha^{-1}. In contrast, in other stands productivity drops and even a breakdown of stands occurs. Breakdown of stands is believed to be a result of root rot (Zālītis and Lībiete, 2005). Decline of the growth potential often has been observed in over-stocked stands (Lībiete, 2008). The lowest growth potential in Latvia is for stands on drained peat soils, but the highest – on drained mineral soils (Lībiete, 2008).

1.2. Management of Norway spruce stands

First pure Norway spruce stands in Latvia were established more than 100 years ago (Zālītis, 2006). During Soviet time silvicultural measures were strictly regulated, determining initial plant spacing, thinnings and final fellings. Traditionally, in coniferous stands infrequent thinnings until the age of 50 – 70 years were carried, and then commercial thinnings were interrupted for 25 – 40 years to accumulate maximum volume at final felling age (Brukas and Weber, 2009). Rough typical management cycle for Norway spruce stands in Latvia would be fallowing: 1) stand establishment with initial spacing of 2 m (2500 trees ha^{-1}); 2) two cleanings until the age of 4 years; 3) pre-commercial thinning at age of 10 years; 4) two commercial thinnings at the age of 35 and 52 years and 5) final felling at the age of 81 years, which is minimum allowable rotation in commercial forests dominated by Norway spruce (Brukas and Weber, 2009; Law on Forests, 2016).

Looking from different perspective, a mix of climate change, legislation and breeding achievements may work as driving factors for intensified Norway spruce management in Latvia. With increasing temperatures and vegetation period, yield of Norway spruce in the country is predicted to increase by 21 % until the end of the century (Jansons, 2015a). Selection of genotypes adapted to potential climate may reinforce the effect. Intensively managed highly productive spruce plantations on former agricultural land can be grown focusing purely on wood production, meanwhile diversifying ecosystem services in other stands. Such option coincides with Rural Development Programme (RDP). In Latvia, around 302000 ha of the agricultural land is not used effectively. The programme anticipates afforestation of less fertile land. This also corresponds to the objective to more effectively use forest potential for CO_2 sequestration via transforming partly overgrown unused agricultural land into productive plantations using genetically improved reproductive material (Ministry of Agriculture of Latvia, 2014).

Management itself can be also adjusted to improved material. More specifically, shortened rotation length and optimal thinning regimes may increase revenues from improved material (Jansons et al., 2015). To make a free decision about final felling time depending on market situation, new stand can be registered as plantation forest, for which minimum final felling age or target diameter does not apply (Regulations regarding forest regeneration, afforestation and plantation forests, 2012).

1.3. Norway spruce breeding in Latvia

1.3.1. History of tree breeding in Latvia

Forest tree breeding in Latvia was initiated in 1957 (Baumanis, Jansons and Neimane, 2014). The process started with identifying productive and qualitative forest stands (Gailis, 1964). The priority was given to conifers – Norway spruce and Scots pine - in order to ensure forest regeneration with fine reproductive material. For this purpose, it was allowed to use only local Norway spruce and Scots pine seeds and was forbidden to import foreign provenances due to their low germination capacity and doubtful tree quality (Vasiļevskis, 2007). In each of Latvia’s regions, firstly stands were selected, which had high yield, straight stems, fine natural pruning, thin branches and narrow crowns (Jansons, 2012). To increase the genetic gain, plus-trees were selected within these stands by phenotypic characteristics. In 1959, establishment of seed orchards started. In 1977, the total area of Norway spruce seed orchards had reached 171 ha (Mangalis, 2004). Also grafting methods and technology for grafted nursery stock was developed. Further activities were characterized by studies about inherent traits and geographic differences in provenance testing and genetic trials with open-pollinated progenies (Baumanis, Jansons and Neimane, 2014). In 1972/74, the most extensive provenience trials were established in Latvia, using also material from 16 IUFRO collections (Rone, 1984). Latvian spruce from 8 provenances is also represented in the IUFRO 1964/68 experiments (Gailis, 1993).

The experimentally detected differences among provenances from different parts of Latvia have been summarized into provenance regions for the main forest tree species including Norway spruce (Fig.3) (Rone, 1993).

1.3.2. Current Norway spruce breeding activities

The first breeding cycle of plus tree selection and progeny testing is completed in Latvia (Jansons et al., 2015). A new long-term forest breeding strategy for 30 years, which is focused mainly on Scots pine, Norway spruce, silver birch and hybrid aspen has been developed based on results of previous progeny testing. The aim of the program is a systematic realisation of forest breeding, developing seed production and raising the financial value of forests (Jansons et al., 2009).

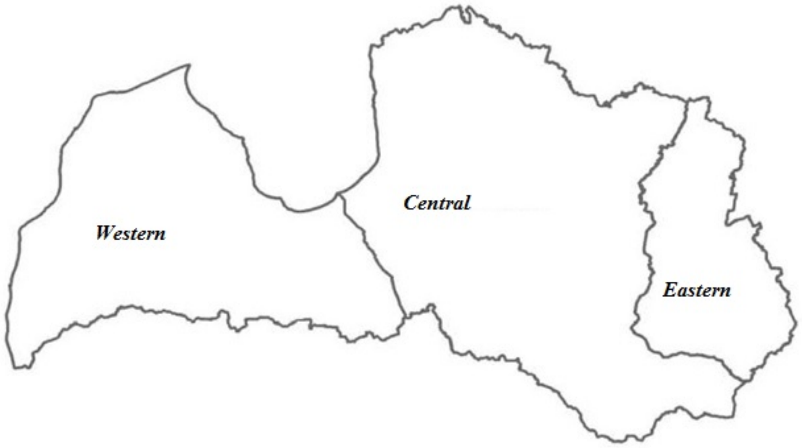


Figure 3. Norway spruce provenance regions in Latvia.

According to the strategy, a repeated selection scheme based on recombination of genetic material (control crosses) is used for Norway spruce. Thereby, genetic gain for important traits tested are increased in each cycle (Fig. 4) (Jansson et al., 2009; Gailis, 2014). Selections are done in accordance with results of progeny testing (Jansons, 2008).

At present, the primary material for spruce breeding is 1700 plus-trees and half-sib families from trees growing in qualitative stands and new progeny testing experiments are established. After testing, 200 out of 1700 plus-trees are going to be selected to establish three breeding populations (Jansons et al., 2015). As supplement material, 200 clones from seed orchards with and without progeny testing as well as 360 clones in new seed orchards without progeny testing experiments will be included (Gailis, 2014). Currently used seed orchards are based on around 400 plus-trees (Jansons, 2012).

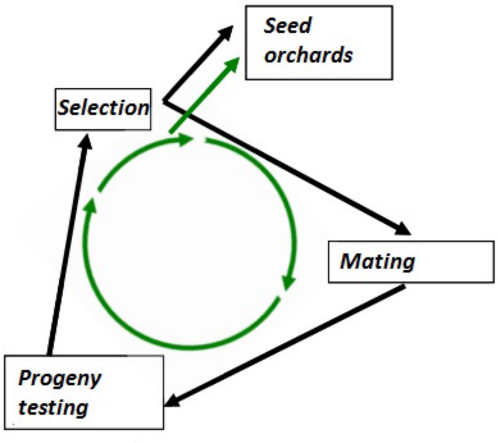


Figure 4. Breeding scheme for Norway spruce (black arrows – first breeding cycle; green arrows – future actions according to scheme) (Jansons, 2008).

A recent achievement is the list of clone candidates for Latvia's Western and Central provenance regions with a purpose to establish new seed orchards.

Currently, the total area of Norway spruce seed orchards in Latvia is around 120 ha (State Forest Service, 2015), but it does not sufficiently provide nurseries with seeds. According to the latest report (State Forest Service, 2016), in 2015 around 52 % of all Norway spruce nursery stock in Latvia was grown from genetically improved material (Fig.5). The situation is similar to Sweden, where the supply of improved reproductive material also is limited. The situation will be improved when the new seed orchards start to produce seeds. Consequently, the industry still needs to utilize older seed orchards with lower genetic gain (Haapanen et al, 2015).

Currently, there are a lack of experimental data about the increase in yield through using improved material (Jansons, 2008), but it is estimated to be similar to Sweden, where, according to latest forecasts, the gain is estimated to be 10 % (Rosvall et al., 2002, Mullin et al., 2011) or 7 – 8 %, when taking into account a shortage of improved material (Haapanen et al., 2015). According to Gailis (2005), 30 years old progeny of seed orchards in Western Latvia had on average 20 % higher yield than local provenances.

1.4. Breeding as a tool to adapt to changing climate

Maintaining the genetic adaptive capacity of the species is important to facilitate natural adaptation to climate change (Lindner et al., 2010). Tree breeding may provide an opportunity to significantly improve adaptive traits without compromising other traits; it combines survival and hardiness with desirable quality traits in a wide range of environmental conditions (Aarrestad et al., 2014). Therefore, possible strategies are, firstly, selection of forest reproductive material of high genetic diversity (beneficial diversity of provenances and seed orchard material) and, secondly, promotion of adapted material for potential climatic conditions (Lindner et al., 2008; Aarrestad et al., 2014).

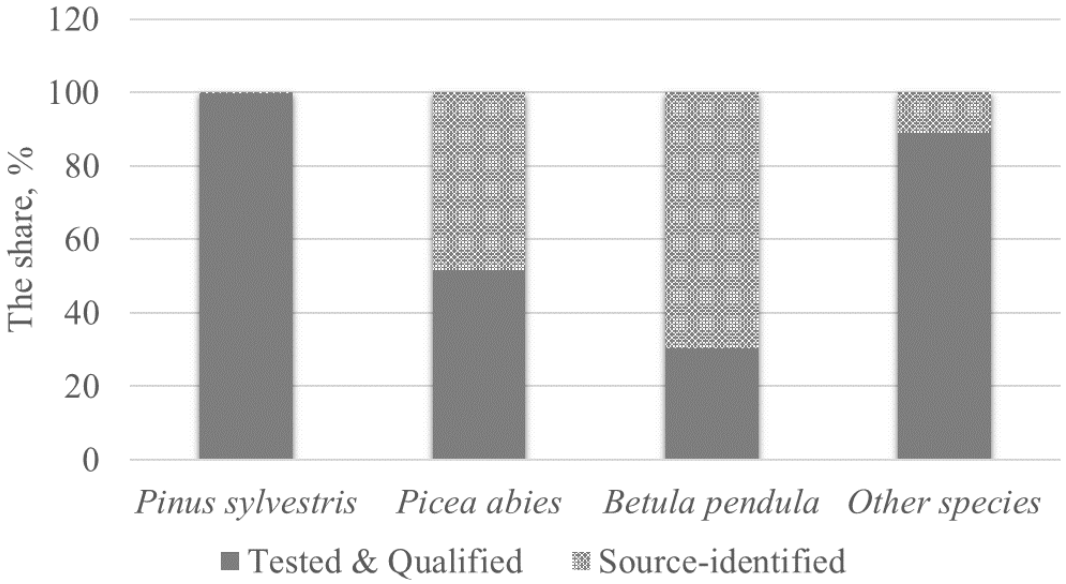


Figure 5. Nursery stock produced in Latvia in 2015 (State Forest Service, 2016).

Climate change with longer vegetation period and milder winters is observed and predicted also in the future in Latvia (Avotniece et al., 2010). This will have direct influences on tree phenology and damage by abiotic factors, as well as indirect effects on forest stands (Jansons, 2012). Onset of growth can be advanced with increasing temperatures, since budburst is primarily regulated by accumulation of heat in the spring (Schleip et al., 2008). In Latvia, vegetation period length is predicted to increase by 35 – 80 days until the end of the century (190 -200 days currently), total amount of precipitation will slightly increase, but the frequency of prolonged dry periods will also increase. Longer precipitation-free periods in the summer have already been observed (Avotniece et al., 2010). The frequency of storms is also predicted to increase (Jansons, 2015b).

Modelling of Norway spruce growth under predicted climate change impact forecast on average 21 % bigger height, 30% larger DBH and 21 % bigger yield (Jansons, 2015a). However, above mentioned forecasts for increased productivity are not taking into account increase in biotic and abiotic damage. Therefore, it is an important goal that via breeding minimize potential damage risks and ensure adaptation to climate changes and longer vegetation period (Neimane et al., 2016). In northern Europe, the focus in Norway spruce breeding in the context of climate change is its effect on frost hardiness, growth potential and wood quality traits. Important genetic traits are variation in bud flush, duration of the annual growth period in spring, cessation of growth and development of frost-hardiness in autumn (Mullin et al., 2011, Aarrestad et al., 2014). Late spring frosts are predicted to occur earlier, which might result in reduced risk of frost damage whereas first frosts in autumn are predicted to be 25 – 50 days later in the whole of Latvia (Jansons, 2010). For instance, recent studies in

Latvia already indicate that higher frequency of lamma growth results in a 15 – 20 % increase in height at young age but has no significant negative effect on wood quality, therefore, it may be possible to gain extra yield when using this trait in spruce breeding (Neimane et al., 2014; Neimane et al., 2015; Neimane et al., 2016).

1.5. Incorporation of genetics into tree growth modelling

Anticipated increase in growth for genetically improved material as well as possible altered growth dynamics with climate change draws attention to possible necessary changes in growth models used to predict growth of forests. Faster height growth of genetically improved trees results in a change in the height growth trajectory, therefore information about growth differences between genetically improved and unimproved material are necessary in order to incorporate genetic effect in the growth and yield models developed for unimproved stands (Rehfeldt et al., 1991; Sabatia, 2011). Growth models are usually based on extensive measurements of unimproved stands (Gould et al., 2008). Incorporation of genetic components into growth models are still not a common practice. There have been attempts to evaluate effects of genetic differences in height, taper or diameter on the individual tree level (Adams et al., 2006). Studies have been carried out mostly for fast growing conifer species in such countries as USA (Buford and Burkhart, 1987; Rehfeldt, 1991; Hamilton and Rehfeldt, 1994; Adams et al., 2006a; Adams et al., 2006b; Gould et al., 2008; Gould and Marshall, 2010; Sabatia, 2011, Smith et al., 2014) and New Zealand (Carson et al., 1999; Carson, 2004; Kimberley et al., 2015). Recent study by Egbäck (2016) analysed early height growth of genetically improved Norway spruce and Scots pine in Southern Sweden.

The most accurate approach would be to develop new functions for genetically improved stock. However, there is a lack of long-term data on improved stands and it would need extensive experiments with measurements throughout the rotation period on a range of site conditions (Gould and Marshall, 2010). By the time information is available for such long term experiments, improved genetic entries would have been replaced by better entries from next breeding cycle (Hamilton and Rehfeldt, 1994). Therefore, two approaches are commonly used to incorporate genetic gain information into existing growth and yield models; a) site index (SI) adjustment approach, and b) genetic gain multiplier approach (Sabatia, 2011). Knowe (2004) mentions also adjustment of the age as an option to incorporate genetic effects. With SI adjustment it is assumed that only SI is increasing and no changes in stand dynamics with genetic improvement are present (Sabatia, 2011). For loblolly pine, SI adjustment approach had been applied for seed sources and families (Nance and Wells, 1981; Buford and Burkhart, 1987). However, this approach works when the pattern of increased growth of selected genotypes is similar to that one of standard genotypes on more fertile sites (Kimberley et al., 2015).

Genetic multipliers adjust the height or DBH increment to reflect by how many times growth is faster than the growth of unimproved trees. Genetic multipliers modify existing growth models and thereby provide account for genetic gain (Rehfeldt et al., 1991, Hamilton and Rehfeldt 1994, Carson et al. 1999, Gould et al., 2008), but no other changes than modification of height increment in model function are applied (Gould and Marshall, 2010).

1.6. Tree and stand growth modelling in Latvia

Forest growth and yield tables have been used as a common practice to predict growth. Situation is similar to Estonia, for which Kiviste and Kiviste (2009) describe that forests are quite variable and growth tables could not describe the variability with sufficient accuracy. Several methods for calculation of current volume increment estimation have been developed earlier. In general, calculations are based on data from one-time surveyed radial increment cores and sample plots, of which the majority were established in the 1960-ies and 1970-ies (Donis, 2015). The sample plots had been established in forest stands with different age, site index, and stand density (Matuzānis, 1985). However, forest growth in Europe has changed in recent decades (Spiecker, 1999, Boisvenue and Running, 2006), namely, accelerated growth has been observed (Bontemps et al., 2009).

Important prerequisite for developing forest growth models is data from periodically re-measured permanent sample plots during long time periods (Bisenieks et al., 2010). National Forest Inventory (NFI) in Latvia was started in 2004, and during the first cycle several thousands of sample plots were established. A portion of the plots will be re-measured after every fifth years. NFI data now gives source of information for developing new models, which predict growth in a certain time period, for example, 5-year height increment (Donis, 2011).

In Latvia, forest owners are required by regulations to provide forest inventory, when they take possession of the property and afterwards at least once in every 20 years. During this period between inventories, data in State Forest Register (SFR) each year are updated using certain growth models. However, they are not suitable for forecasting increment of dendrometric parameters in young stands (up to 30-years old Scots pine, Norway spruce and birch stands) and mature/overgrown stands (Donis, 2014). Therefore, models appropriate for young stands would be needed. For instance, the model intended for updating data of periods no longer than 10 years predicts negative annual height increment in different age – height combinations. Another drawback is minimal stand age, until which the model intends illogical linear growth (for spruce even until 30 years of age) (Donis, 2014).

In recent studies by Donis (2011; 2014; 2015) about improvement of stand yield and growth forecast models in Latvia it was suggested for height increment to use equations based on generalized algebraic difference approach (*GADA*), which allows to forecast height increment only from stand height and age, without information about site index (SI) (Cieszewski and Bailey, 2000). Developed model for height increment of tree with quadratic mean diameter, using *Hossfeld IV* equation (Krumland and Eng, 2005). Using *Hossfeld IV* equation for individual trees the prediction error between observed height increment and predicted height increment in more than 90 % of occasions was less than 10 % (± 0.2 m for pine and spruce) (Donis, 2015).

Donis (2016) has recently studied possibilities to adapt stand and individual growth models from Baltic Sea region for Latvian conditions. He concludes that for all countries at issue (Estonia, Lithuania, Sweden, Finland) most of variables necessary for modelling are obtainable in NFI database directly or after calculations. However, some data might be missing, for example, information about fertilisation or characteristics of management activities before 10 years. Swedish and Finnish models use variables such as latitude and altitude, which are important factors affecting stand growth in those countries, but in Latvia, the amplitude of these parameters is small and subsequently not affecting growth significantly.

On the other hand, Swedish and Finnish individual tree growth models are potentially better than models designed in Latvia previously, so it would be useful to develop individual tree growth models for this country on the basis of models used in Sweden and Finland. The main advantage of an individual tree growth model is more adequate prediction of the impact of competition between trees on growth and mortality of different species; model is flexible, thereby permits modelling combinations of species mixtures, stand structures, management regimes or regeneration methods (Burkhart and Tomé, 2012, Donis, 2016). However, individual tree growth models are complicated, taking more time for data collection, input, processing and modelling (Weiskittel et al., 2011; Donis, 2016)

1.7. Objectives

The main objective of the study was to evaluate a Swedish individual tree height growth model for young Norway spruce trees using data of genetically improved Norway spruce planted on fertile sites in Latvia. The main questions were:

1. How accurate are model predictions over estimated height?
2. How does the model accuracy changes over predicted genetic effect and does the model need a genetic modifier in order to capture increased growth by genetic improvement?
3. Do stand level projections, with modelled height for different sets of genotypes as starting values, reflect initial differences in growth at the end of rotation?

2. Material and methods

2.1. Climate in Latvia

Climatic conditions are mild, determined by the dominant western winds bringing cool and moist air masses from the Atlantic and the Baltic Sea. Continentality is increasing eastwards Mean annual temperature is + 5.9 °C, ranging from + 6.1 to + 5.4 °C in the western and eastern regions, respectively (Harris et al., 2014). The warmest month is July with average temperature + 17.0 °C and average maximum temperature + 21.5 °C. The coldest month is January with average temperature from – 3.3 °C in western to – 6.2 °C in eastern regions. Mean annual precipitation in Latvia is 667 mm. The most precipitation falls during July and August with average rainfall 78 mm in each month. The least precipitation is in February and March (~33 mm each) (Latvian Environment, Geology and Meteorology Centre, 2017).

2.2. Study area

The model was evaluated for genetically improved material using four genetic trials established in Latvia by Latvian State Forest Research Institute "Silava" with variation from offspring from plus-trees, open-pollinated families to clonal material (Table 1). The initial spacing varied between 1.5 x 3 m and 2.5 x 2.5 m and families and clones were planted in randomized plots within blocks. All trials were established with 3-year old bare-root seedlings. Material used consisted of approximately 600 genetic entries and more than 20 000 trees. For validating the young-tree growth model, data from two measurements of heights at the age of 3-18 years with 4- to 5-year growth increments were used.

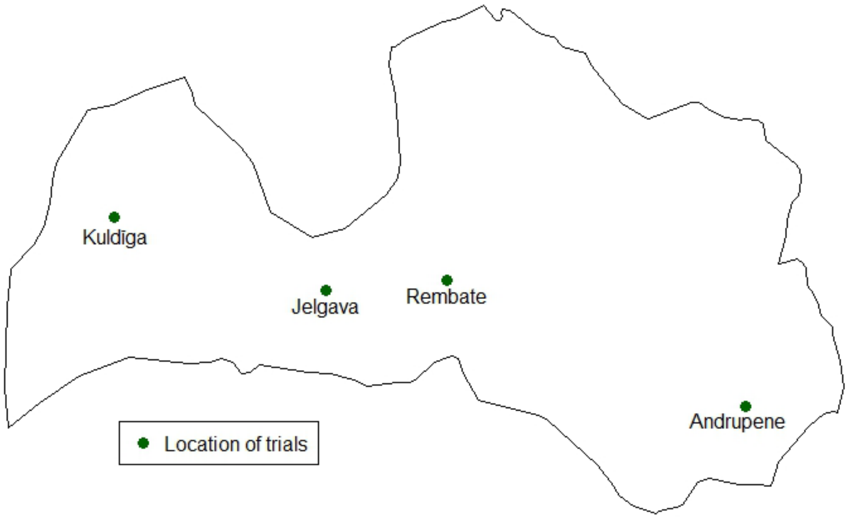


Figure 6. Location of the trials in Latvia.

The trial Jelgava is located in the central part of Latvia (56°43'N, 23°46') (Fig.6), based on set of 59 open-pollinated families from 7 Latvian provenances planted in four blocks. Rembate is located in central Latvia (56°46´N, 24°48´E) including 112 open-pollinated families of plus-trees selected from different regions of the country. The trial consists of four blocks, which were established as separated fields. Data were available for three of them: Rembate 1, Rembate 3 and Rembate 4. Progeny trial Andrupene is located in southeast Latvia (56°10'N, 27°21'E), including 115 open-pollinated families of plus-trees. The trial consists of four blocks arranged in 3 fields (blocks III and IV form one field): Andrupene 1, Andrupene 2 and Andrupene 3_4. Trial Kuldiga is located in western Latvia (57°03'N, 21°57'E) including 181 clones and 118 open-pollinated families of plus-trees. The trial is arranged in four fields: one field with clones and three fields with families and each field consisted of four blocks.

Except Jelgava, all the trials were established on fertile abandoned agricultural land. In Jelgava, blocks I and II correspond to drained *Myrtillosa mel*. type according to Latvian forest typology. Blocks III and IV correspond to *Hylocomiosa* forest type. Both are on mesic soils.

2.3. Height growth model

In the present study, a model for individual tree height growth in Norway spruce in young stands developed by Egbäck (2016) was used. The model is based on data from the HUGIN young stand survey, using individual tree data from Norway spruce dominated plots without overstory and with more than 500 trees per hectare (Fahlvik and Nyström, 2006).

The prediction variable used was the 5-year height increment (ih_5). It is assumed that the variables interact multiplicatively with the height increment with an additive independent random component (ε). The predictors were initial height, mean height, total age, distance independent competition index and site index (SI) (Fahlvik and Nyström, 2006; Egbäck, 2016).

Following general exponential model developed by Fahlvik and Nyström (2006) was used:

$$ih_5 = \exp(\beta_o + \sum \beta_i \times X_i) + \varepsilon \qquad (1)$$

where β_0 is a constant, β_i form a vector of coefficients for the independent variables (X_i) and ε is a random error component.

2.4. Evaluation of the height growth model on genetically improved material

The competition index was calculated as semi-spatially explicit index for each tree, summing the heights of all the taller surrounding trees closer than 5.6 m to the subject tree (Egbäck, 2016). Accordingly, trees closer than 5.6 m from the edge of the field were not evaluated.

Prediction of height increment ($\hat{ih}_{ijm}$) was compared with measured height increment (ih_{ijm}):

$$P_{ijm} = ih_{ijm} - i\hat{h}_{ijm} \tag{2}$$

where ih_{ijm} is the observed height increment of trees *m* belonging to trial *i* and genetic entry *j*; $\hat{ih}_{ijm}$ is the predicted height increment of particular tree and P_{ijm} is the prediction error. The accuracy of the model was evaluated by residual analysis using mean prediction error (MPE) and root mean square error (RMSE):

$$MPE = \frac{1}{n}\sum(P) \tag{3}$$

$$RMSE = \sqrt{\frac{1}{n}\sum(P^2)} \tag{4}$$

where *n* is number of observations.

To check any trend over improvement level predicted genetic effect (PGE) was estimated using methodology described by Egbäck (2016). PGE was calculated for each genetic entry j within each trial based on the tree heights from the first measurement:

$$Y_{ijkm} = \mu + g_{ij} + b_{ik} + \varepsilon_{ijkm} \tag{5}$$

where Y_{ijkm} is the height of tree m belonging to genetic entry j in block k and trial i, μ is the overall mean height, g_{ij} is the random effect of genetic entry j within trial i, b_{ik} is the fixed effect of block k within trial i, and ε_{ijkm} is the residual error.

The genetic entries had 0.10 added to estimated PGE to reflect 10 % increase in height comparing to unimproved material, which is assumed to be similar to Sweden (Jansons, 2008; Rosvall et al., 2001; Egbäck, 2016).

Residuals were plotted over model input variables to identify any residual trends that indicate the model is inadequate (Adams et al., 2006a).

2.5. Simulations of management regime

To estimate possible differences in growth of different genetic material during the whole rotation, simulations outside height growth model limits, i.e. after the tree height has reached 9 – 11 m (period 0 in simulations), were conducted with The Heureka Forestry Decision Support System using stand-level management simulator StandWise (Wikström et al., 2011). One field from each trial was chosen and full rotation was simulated for 10 genetic entries with lowest (group 1), average (group 2) and highest (group 3) mean height, respectively. Standard thinning regime in all simulations was applied: first thinning with 35 % intensity when basal area (BA) has reached 25 m^3ha^{-1} and second thinning with 30 % intensity when BA has reached 27 m^3ha^{-1} (Fig.7). Mean annual increment (MAI) at economic maturity age and net present value (NPV) was calculated using 2.5 % interest rate. For comparison, maximum MAI and corresponding age was estimated in a following way: firstly, with the simulator estimated MAI for a long rotation – several periods beyond MAI_{max}, and, secondly, estimated a second degree polynomial function for MAI against age, which was then tabulated to see at which age and at which level MAI maximizes.

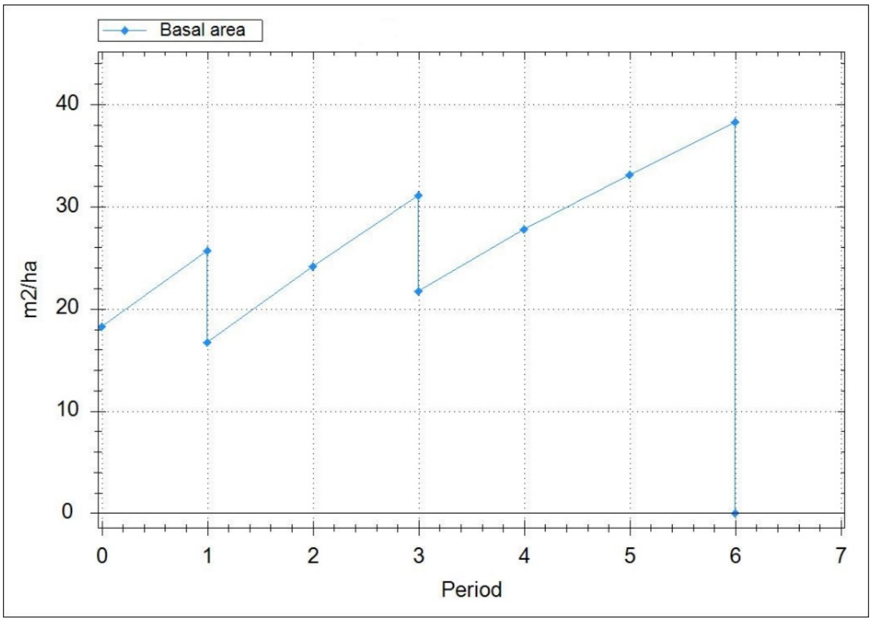


Figure 7. An example of simulated management regimes.

Table 1. Key features of the trials

Trial	Entry type	Spacing, m	No. of genetic entries	Established	Age at measurement, years	Range in entry specific mean height, m*	PGE	Latitude, °	Longitude, °	Altitude, m
Andrupene	Half-sib	2.5 x 2.5	115	1998	13, 17	3.86 - 6.66, 6.60 - 10.20	-0.01 – 0.21	56° 10'	27° 21'	180
Jelgava	Half-sib	2 x 3	61	2006	4, 9	0.84 - 1.37, 3.18 - 5.08	-0.07 – 0.22	56° 43'	23° 46'	20
Kuldīga	Clones	2 x 2	181	1985	8, 11	1.10 - 4.61, 1.85 - 6.78	-0.004 – 0.21	57° 03'	21° 57'	40
	Half-sib	1.5 x 3	118			0.90 - 4.00, 1.72 - 5.72	-0.035 – 0.34			
Rembate	Half-sib	2.5 x 2.5	112	2005	3, 8	0.81 - 3.39, 1.97 - 6.10	-0.05 – 0.25	56° 46'	24° 48'	50

* First row shows range in mean height for the first measurement; second row shows the mean height range during the second measurement

3. Results

3.1. Predictions of height growth model

In general, the height growth models intended for non-improved material predicted the height increment for Norway spruce progeny trials with sufficient accuracy. In all trials mean prediction error (MPE) did not exceed ± 0.4 m, in most trials being around ± 0.2 m. No overall obvious trend over estimated height increment was observed (Fig.8 and 9). However, some trends could be noticed for individual trials. For instance, in Kuldiga 1 and Rembate 1 height was underestimated for the smallest trees and overestimated for the largest ones. In contrast, in Andrupene 3_4 height was overestimated for the smallest trees and underestimated for the largest trees (Fig.9). In general, MPE was smallest around the middle of estimated height amplitude.

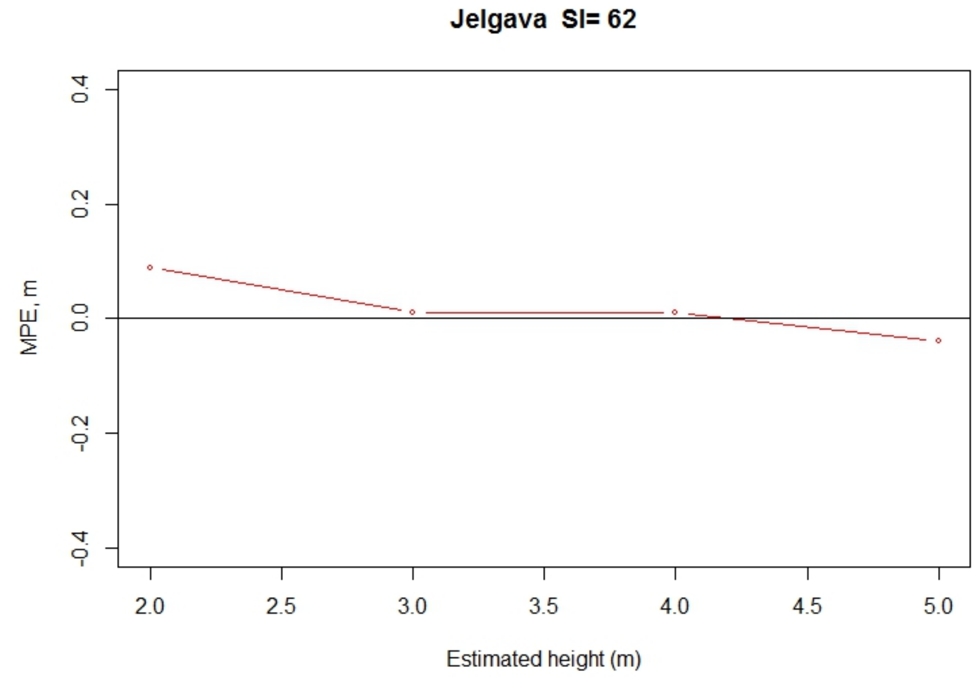
Predicted genetic effect (PGE) for families and clones in the trials varied from -0.072 to 0.340 indicating different improvement levels. Thus it was possible to investigate trends associated with improvement (Fig.10).

No overall trend over improvement level (PGE) was observed (Fig.11). The range of MPE was around -0.4 ... 0.3 m. The only exception was Rembate where there was an observed tendency for overestimation of the height for high PGE-classes and an underestimation when PGE was negative or small.

3.2. Simulations of management regime

Initial age at period 0 (when mean height was around 9-10 m) varied from 17 to 25 years depending on site and genetic group. Estimated SI from initial tree height and age was highest for Rembate 3, followed by Jelgava, Andrupene 1, Kuldiga 2 and Kuldiga’s clones (Table 2). Similar trend was observed for MAI_{max} as well as for NPV, which were notably lower in Kuldiga (for both – families and clones) than in other sites. An inverse tendency was found for final felling age at economic maturity and for age when MAI has reached maximum point which both were lowest for Rembate 3 and Jelgava followed by Andrupene 1, Kuldiga clones and Kuldiga 2.

MAI at final felling age, NPV and SI increased with more productive genetic material, but estimated final felling age was reduced (Table 2, Fig.12). Compared to group 1, MAI, NPV and SI of group 3 was increased by 11 %, 15 % and 8 %, respectively, but final felling age was decreased by 9 %.



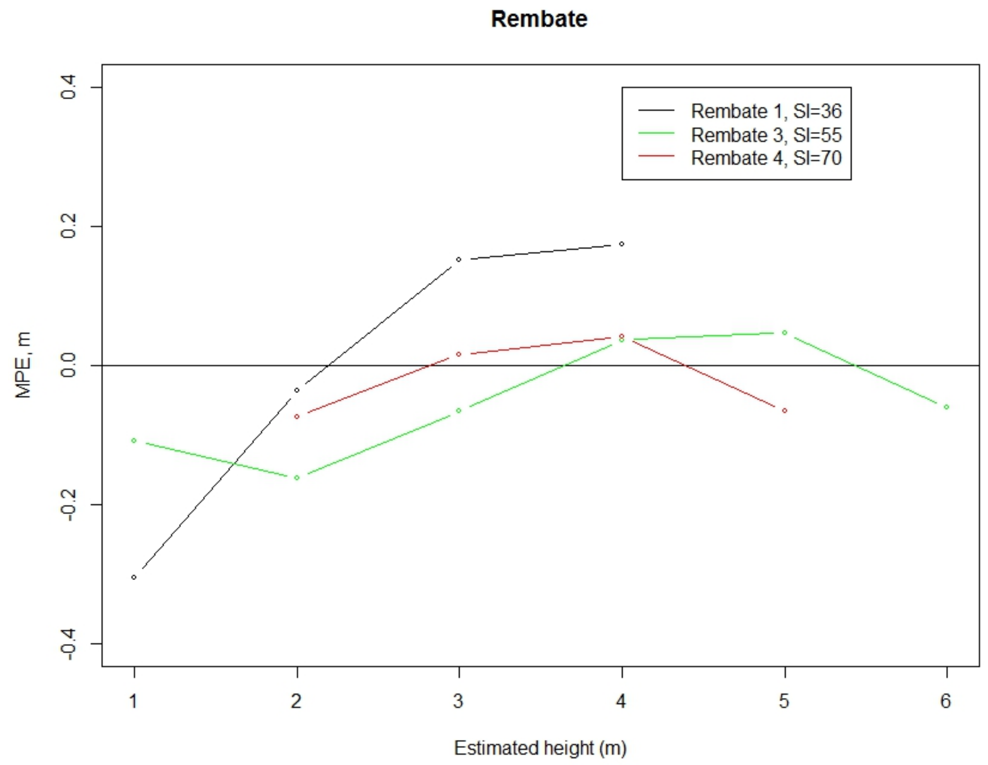
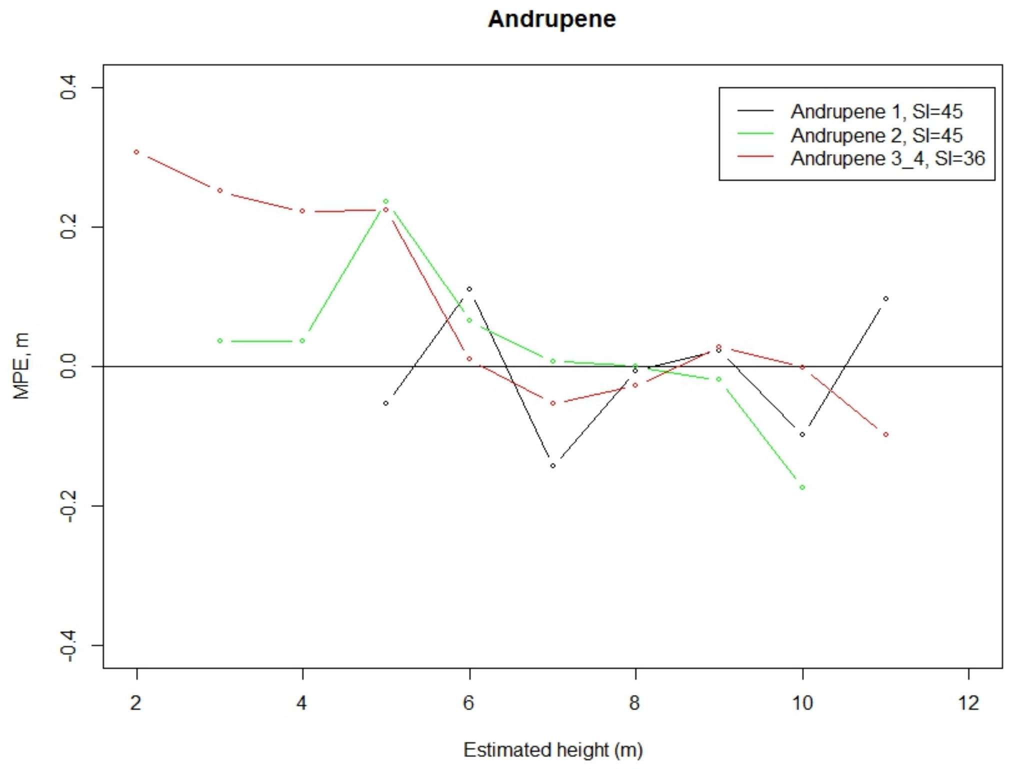


Figure 8. Mean prediction error (MPE) of height increment (m) over estimated height increment (m) in Jelgava's and Rembate's trials.



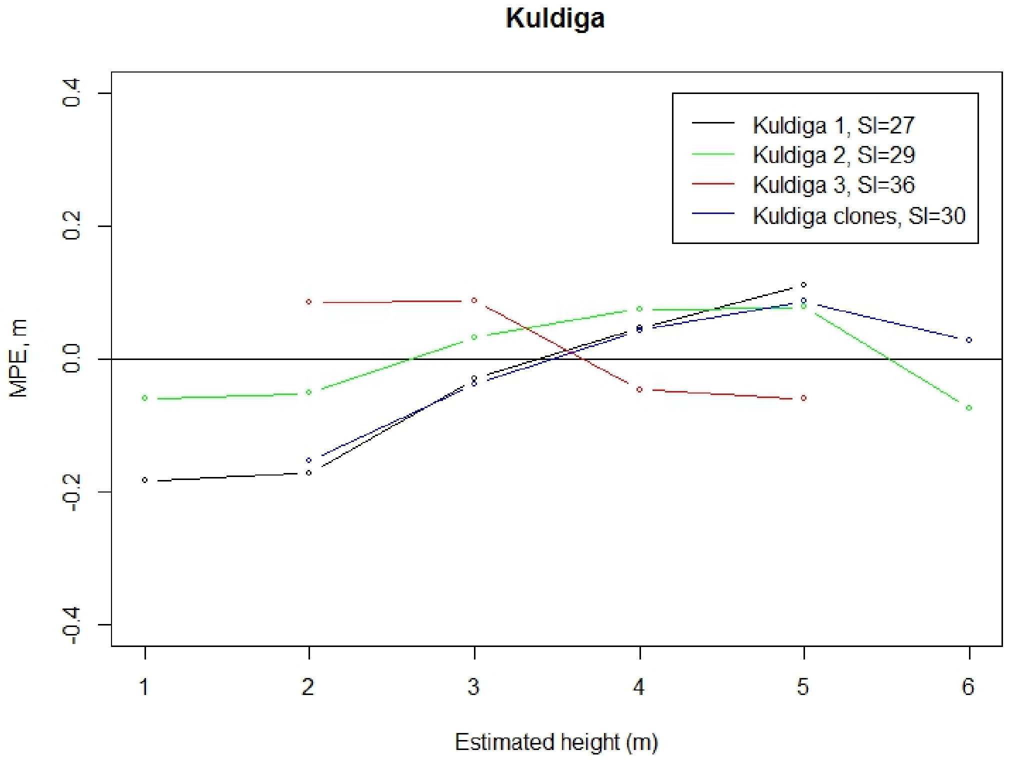


Figure 9. Mean prediction error (MPE) of height increment (m) over estimated height increment (m) in Andrupene's and Kuldiga's trials.

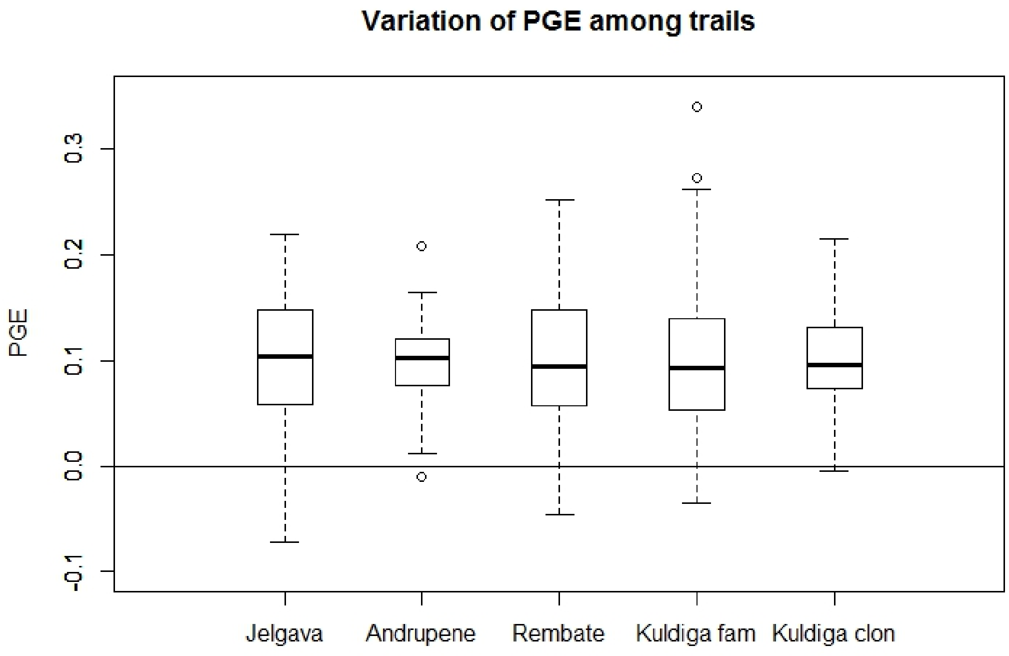


Figure 10. Variation of predicted genetic effect (PGE) for families and clones in the trials.

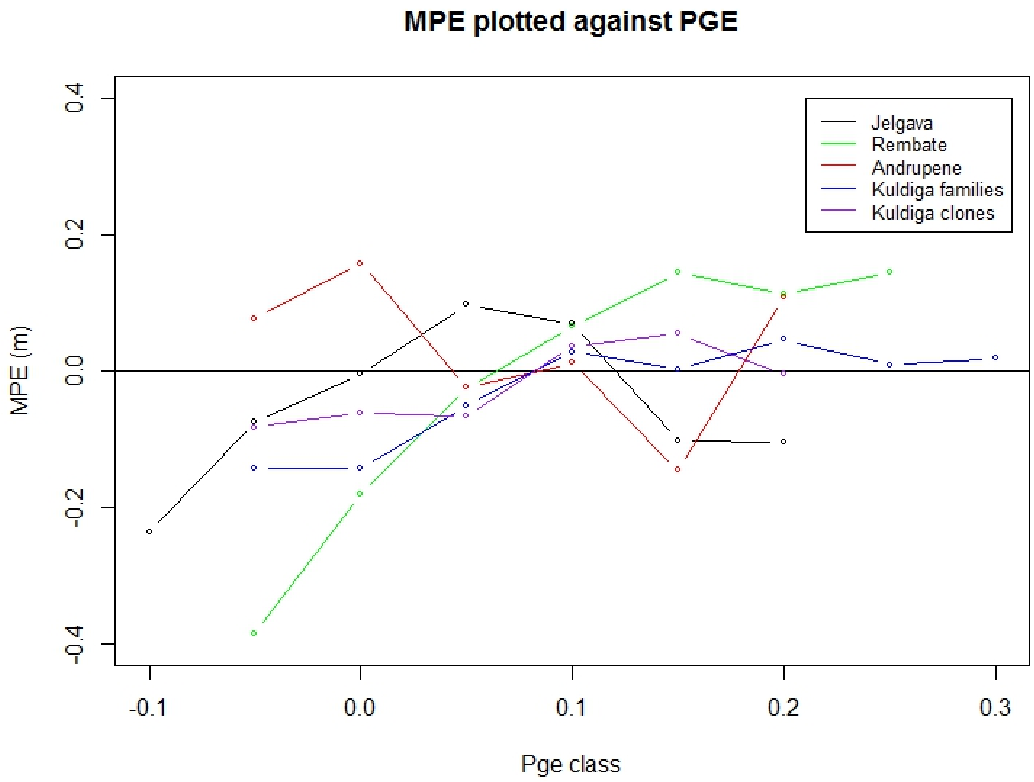


Figure 11. Mean prediction error (MPE) plotted against predicted genetic effect.

Table 2. Summary of estimated variables for sites used in simulations.
Group 1 - 10 families with lowest mean height, Group 2 - 10 families with average and Group 3 - 10 families with highest mean height

Site	Group	Site index	Final felling age (years)	MAI at final felling age (m^3 $ha^{-1}year^{-1}$)	NPV (Euro)	MAI_{max} ($m^3ha^{-1}year^{-1}$)	Age_{MAImax} (years)
Andrupene 1	1	33.2	54	14.8	6496	15.3	64
	2	34.7	51	16.2	7086	16.5	59
	3	35.7	49	17.1	7563	17.4	56
Jelgava	1	35.6	49	15.4	6425	15.9	59
	2	36.1	48	15.8	6661	16.3	58
	3	36.2	47	16.5	7036	16.7	55
Kuldiga 2	1	31.9	58	9.6	3270	10.0	72
	2	33.2	57	9.9	3448	10.3	71
	3	34.5	53	10.6	3885	10.9	63
Kuldiga clones	1	30	59	10.2	3664	10.5	69
	2	32.3	54	10.6	3770	11.0	68
	3	34.8	51	11.6	4297	11.9	60
Rembate 3	1	36.1	50	15.5	6639	15.9	60
	2	37.2	48	16.8	7325	17.1	55
	3	38	45	17.1	7350	17.5	50

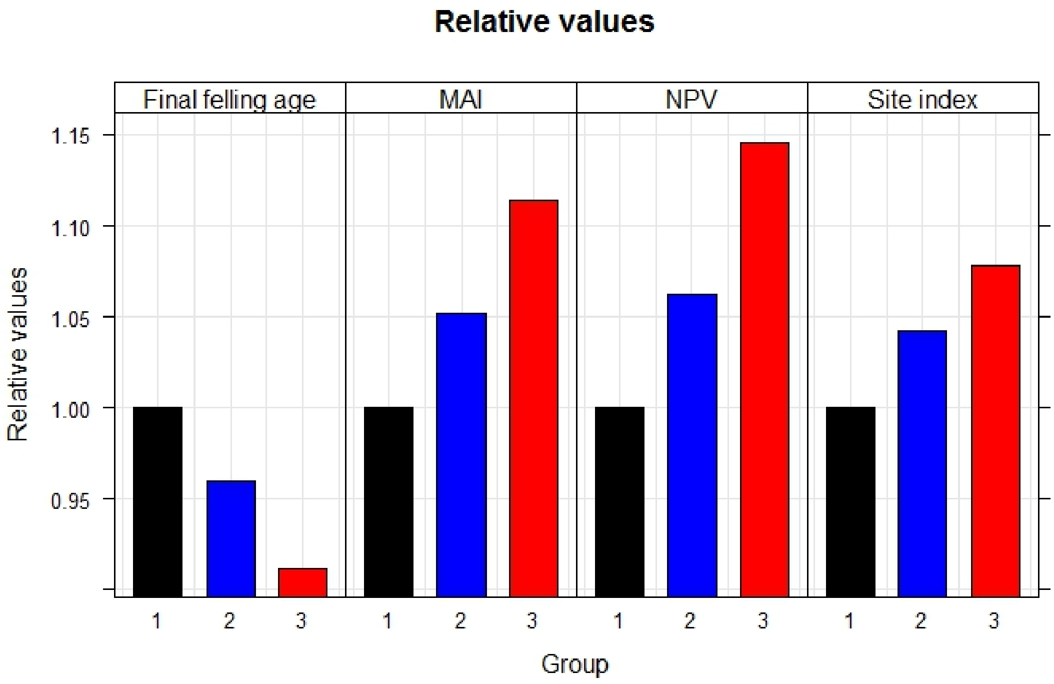


Figure 12. Comparison of relative values for final felling age, MAI, NPV and SI estimated for different groups of genetic material. See Table 2 for explanation of groups

Table 3. Differences in PGE among different groups of genetic entries used in simulations. See Table 2 for explanation of groups.

Group	Site	h_0 (m)	h_1 (m)	Mean PGE	Range of PGE
1	Andrupene 1	3.86	6.29	0.0623	0.0377 - 0.0851
	Jelgava	0.97	3.57	0.0048	- 0.0463 - 0.0656
	Kuldiga 2	1.59	2.62	0.0205	-0.0352 - 0.0775
	Kuldiga clones	1.44	2.36	0.0387	0.0167 - 0.0793
	Rembate 3	1.51	2.80	0.0094	-0.0459 - 0.0664
	Mean	-	-	0.0272	-
2	Andrupene 1	5.73	9.22	0.1027	0.0568 - 0.1340
	Jelgava	1.17	4.24	0.1075	0.0453 - 0.1835
	Kuldiga 2	2.29	3.85	0.0972	0.0725 - 0.1296
	Kuldiga clones	2.41	4.01	0.0976	0.0744 - 0.1207
	Rembate 3	2.21	4.42	0.1008	0.0616 - 0.1446
	Mean	-	-	0.1011	-
3	Andrupene 1	6.78	10.91	0.1305	0.0987 - 0.1552
	Jelgava	1.27	4.74	0.1573	0.1118 - 0.2090
	Kuldiga 2	3.45	5.37	0.2198	0.1388 - 0.3398
	Kuldiga clones	4.01	5.89	0.1845	0.1522 - 0.2143
	Rembate 3	3.01	5.73	0.1969	0.1571 - 0.2517
	Mean	-	-	0.1778	-

On average, group 1 had mean PGE slightly above baseline (PGE=0.0273), although some families in Jelgava, Kuldiga 2 and Rembate 3 have negative PGE values (Table 3). For the best families mean PGE was 0.178. Thus, predicted gain in height was on average 15 % higher for the group 3 than for group 1. However, the magnitude of the increse varied among sites.

Maximum MAI and corresponding age (volume production maturity) was estimated and compared to rotation length based on economic maturity. Diference in MAI_{max} between group 1 and group 3 reached 10 %. In general, at economic maturity age, MAI had not reached its maximum value yet, being 0.3 – 0.5 $m^3ha^{-1}year^{-1}$ lower (Table 2). Growth culmination was reached 5 – 14 years later than economic mautrity (Fig.8). As mentioned above, MAI_{max} much depends on site and its properties, but there is a clear trend within all sites: MAI_{max} increases and age of MAI_{max} decreases with better genetics (from group 1 to group 3). The earliest indicated final cutting age was 45 years for stand based on growth of the best 10 families in Rembate 3. For instance, growth culmination for this group is reached at the age of 50 years, and it is the smallest difference (5 years) between economic and volume production maturity age.

4. Discussion

4.1. The height growth model

The height growth models intended for non-improved material predicted the height increment for Norway spruce progeny trials in most cases with mean prediction error (MPE) less than 0.2 m. In addition, no obvious trend over estimated height increment was recognized. The results show that the same height growth model predicts 5-year height increment more precise for genetically improved material in Latvia than in Sweden, where model originally was developed. Egbäck (2016) report the model to underestimate development for Norway spruce. In their study MPE over estimated height increment in most trials reached 0.5 – 0.8 m, while in the present study MPE did not exceed 0.4 m.

When plotted against predicted genetic effect (PGE), MPE did not exceed 0.4 m, while reaching 0.6 m in Swedish study. However, in both cases no trend over estimated height increment was found.

There might be several reasons for more precise estimations for progeny trials in Latvia. Firstly, it was already taken as a prerequisite that the model shows tendency for the prediction errors above initial height of 9 m, therefore trials with available measurements within height limits were chosen. Initial height might be better predictor of future development with the same model's parameters in the present study than in Swedish conditions.

Another factor that might have improved model accuracy is the use of block plot trials in this study compared to of single-tree plot trials in Egbäck's study. Egbäck (2016) stresses that single-tree plots can create biased estimates of height due to effect of competition, when genetic entries with fast growth are favoured. The best genotypes in single-tree plots may not use site resources in the most efficient way (Smith et al., 2014). In row-plot or single-tree-plot trials trees are surrounded with trees of different genetic quality representing different tree-to-tree competition, opposite to stands where only the offspring of best performers are planted (Carson et al., 1999; Vergara et al., 2004). Single-family blocks reduce competitive advantage over neighbours (Smith et al., 2014), thus progeny trials with block parcels might have reduced bias caused by competition from faster growing genetic entries, although trees in outer rows of block-plots were still affected by trees from other families or clones. According to Kimberley et al. (2015), large plot-trials is a simple way to eliminate competition effect and make genetic gain estimates more accurate. However, single tree plots are more cost-effective and therefore often used (Vergara et al., 2004).

Accurate average level of growth was achieved adjusting site index, thus ensuring that in no case height increment was over- or underestimated for the whole trial. SI was not estimated from site properties. It is reflected in adjusted site indices for, e.g. Jelgava or Rembate 4, where SI ensuring the smallest bias was 62 and 70, respectively. Such unrealistic numbers cannot be used to characterize the site, therefore input "SI" should be redefined as a scale-factor, which is used to adjust residuals so average MPE is the closest to "0". However, extremely high SI values obtained might indicate superb growth of genetically improved material on fertile (in most cases former agricultural land) site at juvenile age.

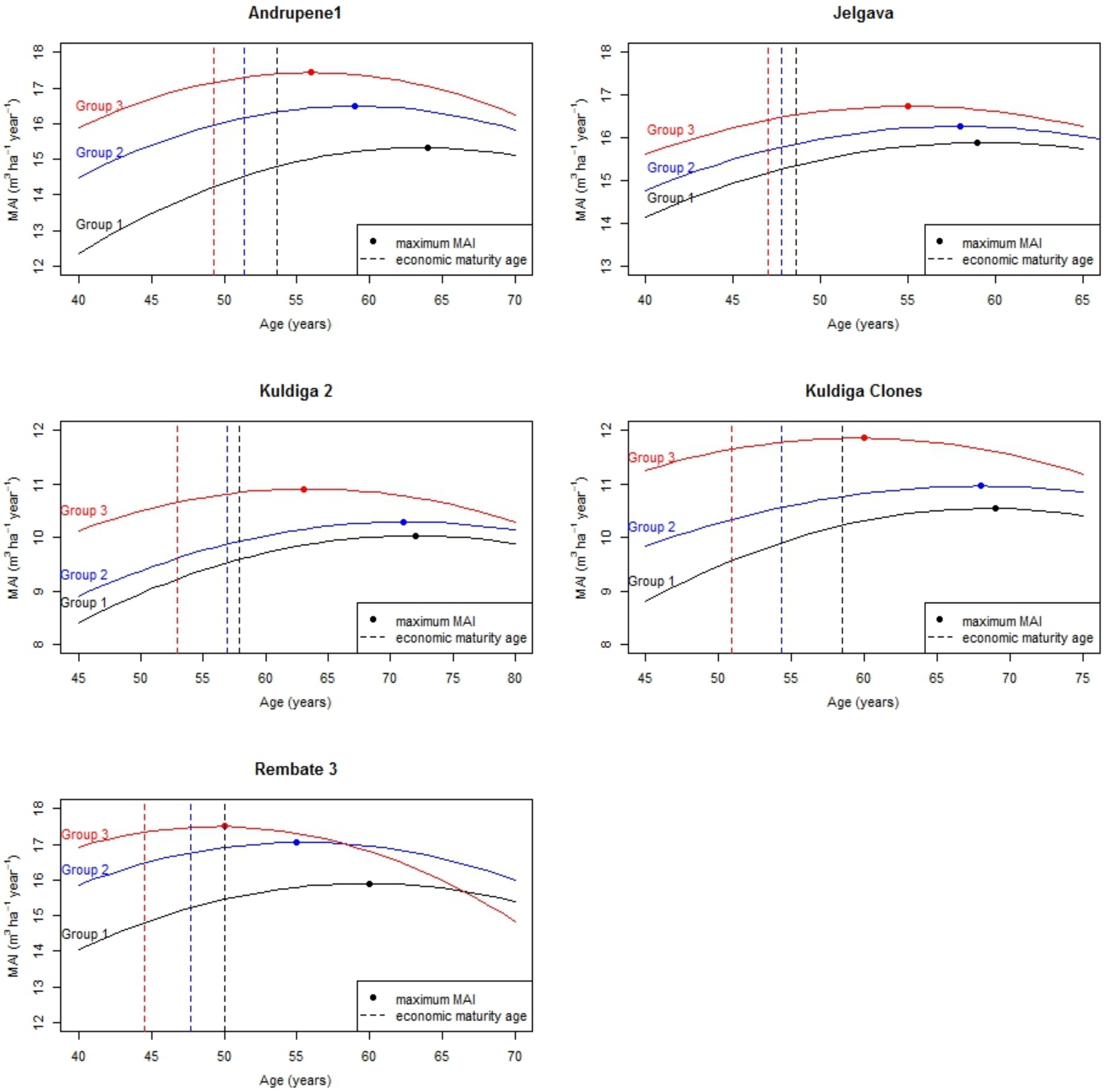


Figure 13. Estimated maximum MAI, corresponding age and economic maturity age. See Table 2 for explanation of groups

Commonly used approaches to incorporate genetic gain into existing growth and yield models are genetic gain multiplier approach or site index adjustment approach (Sabatia, 2011). There were no indications to consider incorporation of genetic component (genetic multiplier) into the model, since no overall trend over estimated height or PGE was observed using the model derived from unimproved genetic material. These results correspond to the conclusion that the seed source or family does not affect the shape of the height-age curve but dictates the level of the curve (Buford & Burkhart, 1987; Buford, 2004). Changes in development dynamics with genetic improvement might be explained by observed SI change (Hamilton and Rehfeld, 1994;

Sabatia, 2011). This approach fits, when the pattern of increased growth using superior genotypes is similar to that achieved by growing unimproved stock on more fertile sites (Kimberley et al., 2015). In the present study, estimated SI in each site for different groups of different genetic gain tend to confirm it, because SI is increasing with more productive genetic material (Table 2).

Accuracy achieved and no evidence of need to change the shape of the height-age curve leads to suggestion that the best option for use of the model in Latvian conditions would be to develop adjustments to site index used by the model, which would make modelling genetic improvement possible over a range of site types (Kimberley et al., 2015). Further, stand-level gains might be estimated by determining changes in SI (Hamilton and Rehfeldt, 1994).

4.2. Stand-level gains using genetically improved stock

Projecting the growth of improved stands could be worthwhile because genetic gains can result in greater final harvest volumes and changes in management regimes, e.g. earlier thinnings or different rotation lengths (Gould et al., 2008). Results of the present study show that groups of best genetic entries initially have almost two times higher trees than groups of 10 genetic entries with the lowest height at early age. The last ones may represent unimproved stands, since mean PGE for group 1 in most cases is only slightly above "0" (Table 3). When using genetically improved planting stock, anticipated increase in height growth for individual trees requires estimates of stand productivity at potential harvest time (Hamilton and Rehfeldt, 1994). Stand-level projections for whole rotations using Heureka reveal considerable differences among groups (Fig.12). However, the gain in productivity for the best genetic entries are reduced at estimated economic as well quantitative maturity age (at those ages relative difference in MAI among group 1 and group 3 is 12% and 10 %, respectively), being lower than estimated PGE for height at early age (mean PGE for group 3 is 0.17). The relative differences in MAI at the start of simulation are similar to differences in last measured height, which signals that the height increment model tested maintains differences after a number of 5-year periods. Though, relative differences in MAI_{max} among groups are reduced to only 10 % after simulation to economic maturity (Table 4). There are a number of reasons that may explain this result. Firstly, results could be affected by the simulator itself, because functions in it might do not take into account improvement levels. Besides, Heureka consists of a large set of sub-models (Fahlvik et al., 2014), so the triggering factors remain undetected. Accuracy of estimates may decrease as the errors of independent variables cumulate in each subsequent forecast period (Kangas, 1997). However, in earlier study relative prediction error for growth models in Heureka did not increase with increasing length of simulation period (Fahlvik et al., 2014). Obvious drawback of the simulations was ability to simulate only 5-year periods. For the best groups on fertile sites BA increment was so fast that thinnings could not be simulated at the predefined basal areas. Therefore, the reduced differences in productivity gain can be the standardized thinning program used in all simulations. Although time of thinning varied depending on time when critical BA was reached, individual application for each group in terms of intensity and number of interventions could results in better maintained PGE over the whole rotation. It has been marked in earlier studies that the amount of increase in yield depended on such parameters as stand density and rotation length (Rehfeldt et al., 1991). Also for slash pine (*Pinus elliotti* var. *Elliottii*) Vergara et al. (2004) reported realized gains to be lower than expected gains based on the breeding value. It was explained with competition differences. Adams et al. (2006a) highlight the need to evaluate effect of genetic differences in height and competitive ability on stand level in models. Not fully appropriate management regime with unadjusted thinning regime could hide the potential impact of genetically improved stock on the development of the stand in the present simulations.

Table 4. Differences among groups in last measured height and projected MAI. See Table 2 for explanation of groups.

Site	Group	Last measured height (m)	MAI at the start of simulation ($m^3ha^{-1}year^{-1}$)	MAI_{max} ($m^3ha^{-1}year^{-1}$)
Andrupene 1	1	6.45	4.9	15.3
	2	9.22	8.7	16.5
	3	10.92	10.1	17.4
Jelgava	1	3.57	4.1	15.9
	2	4.24	4.8	16.3
	3	4.73	5.2	16.7
Kuldiga 2	1	2.85	3.5	10.0
	2	3.83	4.2	10.3
	3	5.37	6.4	10.9
Kuldiga clones	1	2.31	3.3	10.5
	2	4.01	5.1	11.0
	3	6.01	7.7	11.9
Rembate 3	1	2.97	4.7	15.9
	2	4.42	6.6	17.1
	3	5.73	9.0	17.5

Nevertheless, obvious differences among the groups on all sites were observed. The overall estimated gain in MAI at estimated final felling for group 3 comparing to group 1 was 11 % (Fig.12). On average, material from group 3 (MAI_{mean}=14.6 $m^3ha^{-1}year^{-1}$) would produce an additional yield of 10 m^3ha^{-1} above yield of group 1 (MAI_{mean}=13.1 $m^3ha^{-1}year^{-1}$) at estimated final felling age - years 49 and 54, respectively. The gain in yield is small. However, it must be taken into account that average rotation length is reduced by 9% when selecting best genetic entries with highest PGE for height. With interest rate of 2.5 %, gained 11% in MAI and reduction in rotation length by 9 % resulted in a gain of 15 % in NPV. This indicates that reduced rotation may be at least as important as higher yield.

MAI_{max} followed the same trend as MAI at estimated final felling age and increased with higher PGE on all sites. On average, difference in MAI_{max} between group 1 and group 3 was 10 %. At economic maturity age MAI had not reached its maximum and growth culmination sets in 5 – 14 years later than economic maturity (Fig.13). It could be explained with projected net revenue dynamics with changing rotation length. At one moment the value of standing wood is so high that it need high growth in order to sustain the interest rate. In addition, once a critical number of stems reach certain DBH, increase in net revenue with longer rotation becomes slower, because for Norway spruce price of sawn timber sortiments is not vastly increasing with further increase in DBH and can even decrease for class 1 with DBH > 32 cm (Sveaskog, 2016). Subsequently, increase in NPV for next period drops lower than 2.5 %, therefore it is not beneficial to keep the stand growing.

4.3. Proposals for Norway spruce stands established with improved planting stock in Latvia

According to Latvia's Law on Forests, Norway spruce stand can be cut when final felling age has reached 81 years or alternatively final felling diameter (the smallest average DBH of the dominant tree species) is 30 cm. Another option is to register a new stand as plantation forest - forest stand established through afforestation, intended for specific purposes and registered in the State Forest Register (Law on Forests, 2016). Plantation forest does not have minimum felling age or diameter.

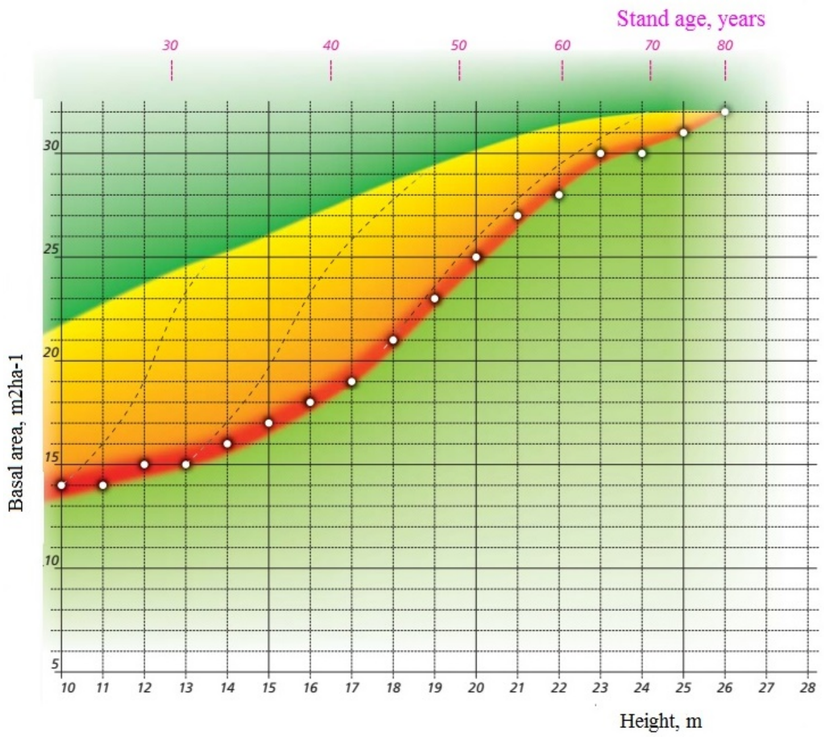


Figure 14. Thinning model for Norway spruce stands on fertile forest types (LVM, 2008). Yellow area – optimal zone of thinning. Red area – critical BA to thin until.

Results from the present simulations indicate that on any site both quantitative and economic maturity are reached long before 81 years (Fig.13). For instance, in Jelgava's trial, which is established on fertile forest land, estimated final felling age is reached 34 years earlier than legal final felling age, while MAI_{max} is reached 25 years earlier for group 3 (Table 2). Despite such age difference, basal area weighted mean diameter D_{gv} for particular simulated stand is 30.9 cm, therefore stand cutting anyway could be permitted according to final felling diameter. Results from this study indicate that a specified final felling age might not be applicable for growth rates of genetically improved material and present market demands.

The present study also reveals some trends related to thinning regime. For group 3 in the simulations mean age at first thinning was 23 years with mean H_{gv}= 13.7 m for BA exceeding 25 m^2ha^{-1}. Comparing results to commercial thinning guidelines developed by Joint Stock Company "Latvia's State Forests" (LVM) for Norway spruce stands on fertile sites (Fig.9) it can be seen that parameters in projections are achieved around 10 years earlier than presented in guidelines. It might signal for a need of further studies and revised thinning models in Norway spruce stands.

To summarize, results indicate that reduced rotation length and earlier thinnings compared to conventional practice may be the outcome of planting genetically improved Norway spruce on fertile soils.

5. Conclusions

The examined height growth model intended for non-improved material predicted the height increment for genetically improved Norway spruce in Latvia with sufficient accuracy and without obvious trends over estimated height increment and over improvement level. There are no indications to consider incorporation of genetic multiplier into the model. However, the accuracy was achieved adjusting site index to unrealistic numbers, which indicates that this input in Latvian conditions should be defined as a scale-factor to adjust residuals not to reflect site properties.

For projected full rotation length, best genetic entries had on average by 11 % higher MAI and by 15 % higher NPV, meanwhile having by 9 % decreased final felling age comparing to group of the worst performing genetic entries, indicating that reduced rotation may be at least as important as higher yield. According to economic maturity age, rotation length for the groups of top performing genetic entries was estimated to be 45 – 53 years.

Stand-level projections indicate that first thinning in plantations can be applied around a decade earlier for the top performing genetically improved Norway spruce which might signal for a need of further studies and revised thinning models in Norway spruce stands.

In general, reduced rotation length and earlier thinnings compared to conventional practice may be the outcome of planting genetically improved Norway spruce on fertile soils.

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